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 M₁ and M₂, single paracone in the upper molars and premolars and, particularly, by the lack of mesostyle in most M¹ and M², a trait not observed in any other species of *Microchoerus*. Some specimens from Eclépens B (late Eocene, Switzerland), determined previously to be *Microcherus* aff. *erinaceus*, are also ascribed to *M. hookeri*. *Microchoerus 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 *Microchoerus 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A detailed revision of the age of the localities containing remains of *Microchoerus* and the description of the still unpublished material from some European localities, are necessary to clarify the phylogenetic relationships among the members of this microchoerine group.

Keywords: Microchoerinae; Paleogene; Headonian; Iberian Peninsula, Spain.

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 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 the 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, 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 *Microchoerus 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 omomyforms (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 affected continental vertebrate fauna at the Eocene–Oligocene boundary, known as the "Grande Coupure".

Moreover, the analysis of the abundant sample from Sossís, intermediate in size and morphological features between *N. antiquus* and *M. erinaceus*, allows us to observe the changes that took place in this microchoerine lineage through the late Eocene and to examine other divergences from the genus *Necrolemur* that could have occurred earlier. As a result, it is then possible to consider whether the genus *Microchoerus* as currently described is a monophyletic group or if several independent lineages sharing some convergent features can be distinguished. This study therefore has the potential to expand our knowledge about the phylogenetic relationships among microchoerines considerably.

The Sossís fossil site: geological context and paleontological background

The fossil site of Sossís is situated close to the small town of Sossís (Conca de Dalt, Lleida Province), in the Southern Pyrenean Basins. Geologically, this fossil site belongs to the Collegats Formation, a 1000 m thick conglomeratic unit with clayey intercalations. The fossil bearing 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 (López-Martínez, 1998). The site was discovered in the 1940s during work in a lignite mine (see Casanovas-Cladellas, 1998 for further details). More

than thirty mammalian taxa have been recovered from this locality, including marsupials, insectivores, rodents, carnivores, creodonts, perissodactyls, artiodactyls and primates (Table 1). While most of the material has been studied in several unpublished dissertations, published descriptions only exist for the rodents (Crusafont-Pairó et al., 1963), insectivores (Sigé, 1997) and artiodactyls (Cuesta Ruiz-Colmenares et al., 2006). The lizards from Sossís were described by Bolet and Evans (2013) and Bolet and Augé (2014), who recognized a diverse assemblage that includes a new genus. The study of the entire fauna suggests the assemblage dates to MP17 (Headonian, late Eocene).

Four different primate taxa have been identified from Sossís. Crusafont-Pairó (1967) documented the existence of three species, all of them represented by a few specimens. The published material consists of descriptions of two isolated teeth of the large adapine *Adapis* cf. *parisiensis*; a mandible with C_1-M_3 and three fragments of maxillae with P^3-M^3 , M^1-M^3 and M^1-M^2 ascribed to "*Necrolemur erinaceus*" (which in fact correspond to *Microchoerus*) and a mandible with P_4-M_3 assigned to *Pseudoloris parvulus*. Later field campaigns carried out by the Institut Català de Paleontologia (ICP) led to the recovery of a large number of mammal remains from this fossil site, including additional specimens of these three primates. The rich collection of dental remains of *P. parvulus*, representing the most abundant sample of *Pseudoloris* from the Iberian Peninsula, has been recently described by Minwer-Barakat et al. (2015a). Moreover, this new material has allowed the identification of a fourth taxon, an anchomyin described as *Nievesia sossisensis* by Marigó et al. (2013).

The primate material from Sossís also includes a large number of remains of *Microchoerus*: five fragments of mandibles, two lower dental series and four fragments of maxillae bearing several teeth and more than 100 isolated teeth, representing nearly every dental elements. This material is housed in the ICP and represents by far the most complete sample of the genus from Spain. This collection was preliminarily studied by Minwer-Barakat et al. (2012b), who

noticed clear biometric and morphologic differences with the type population of *M. erinaceus* from Hordle Cliff, such as the smaller size, the absence of mesostyle in most upper molars, and the less accentuated enamel wrinkling in the lower molars from Sossís. This suggests that the previous assignment of this material to *M. erinaceus*, first made by Crusafont-Pairó (1965) and followed in later works (Crusafont-Pairó, 1967; Antunes et al., 1997; Casanovas-Cladellas, 1998; Marigó et al., 2014), is incorrect. Additional specimens of *Microchoerus* from Sossís have been recently found in the collections of the Naturhistorisches Museum Basel (NMB) in Switzerland, including a fragment of mandible with M₂ and M₃, an M¹⁻² (it is difficult distinguishing first and second upper molars when they are isolated, due to the strong similarity in size and morphology of these two dental elements), two M³ and a dental series with M¹ to M³ (Minwer-Barakat et al., 2014). 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, as is the case for other primate remains from Spanish localities in the NMB collections (Minwer-Barakat et al., 2013b, 2015a).

In this paper we describe, for the first time, all the *Microchoerus* material from Sossís, which shows clear differences from all the previously described forms of the genus, thus allowing the designation of a new species: *Microchoerus hookeri*. A detailed comparison with all the described species of *Microchoerus* and *Necrolemur* is carried out, as well as with some populations of the former genus without a definitive specific ascription. As we explain in the following sections, some specimens from Eclépens B in Switzerland can also be ascribed to the new species *M. hookeri*, indicating that this taxon was not restricted to the Iberian Peninsula.

Material and methods

Most of the described specimens from Sossís (catalogue numbers preceded by the acronym IPS) are housed in the collections of the Institut Català de Paleontologia Miquel Crusafont (Sabadell, Barcelona, Spain). Some specimens (catalogue numbers preceded by the acronym NMB) are curated at the Naturhistorisches Museum Basel (Basel, Switzerland). We compared the material from Sossís with all the described species of the genera *Microchoerus* and *Necrolemur*, and also with several samples of *Microchoerus* which still lack a definitive determination at the specific level, such as those from Euzet, Perrière, Grisolles and Ehrenstein. We studied original material stored at the Muséum National d'Histoire Naturelle (Paris), the Université of Montpellier, the Naturhistorisches Museum Basel, the Natural History Museum (London), as well as several high-quality casts stored in the same institutions. Details about the described sample and the comparative sample are summarized in Table 2.

The nomenclature used in the descriptions follows Minwer-Barakat et al. (2015a). The criteria employed for measuring the teeth are described in Godinot (2003). Measurements of the studied specimens from Sossís were taken using an optic caliper "Nikon measuroscope 10" connected to a monitor "Nikon SC112" at the ICP. Using the same equipment, measurements of *N. antiquus* var. *major* from Quercy were taken directly on two specimens curated at the NMB (Q.H.441 and Q.H.442), on loan to the ICP, and those of *M. edwardsi* and *M. ornatus* were taken on high-quality casts of the holotypes. The remaining data used for comparisons and statistical analyses were taken from the literature: data for *N. antiquus* from La Bouffie after Godinot (1983); data for *M. hookeri* from Eclépens B after Hooker and Weidmann (2000); data for *M. erinaceus* after Cray (1973); data for *M. wardorum* and *M. creechbarrowensis* after Hooker (1986). In all these cases, the criteria employed for measuring the teeth were similar to those used in this work. Micrographs were taken using the Environmental Scanning Electron Microscope (ESEM) at Universitat de Barcelona.

All statistical analyses were undertaken with Past3 (Hammer et al., 2001). Principal Component Analysis (PCA; using the variance-covariance matrix) was used to explore sample variability. This kind of analysis makes sense for more than three variables; as we usually considered only two variables for each tooth (length and width), we only included specimens that preserved several teeth, specifically mandibles preserving M_1 and M_2 , for which the sample was considerably larger than for specimens preserving the three lower molars.

Cluster analyses were used to explore grouping of the specimens (Quinn and Keough, 2002). For each case we developed three different analyses based on three different algorithms: UPGMA, Single Linkage and Ward's method. The Ward's method is based on the underlying principle that at each stage of clustering the variance within the cluster is minimized in relation to the variance between clusters (Ludwing and Reynolds, 1988 and references therein). All three analyses employed Euclidean distances. We carried out 9999 bootstrap replicates, and they were represented on the cluster as the percentage of replicates where each node is still supported. As in the case of the PCA, we used the sample comprising mandibles that preserved M_1 and M_2 , because of its larger sample size.

Statistical differences between species were tested by means of non parametric MANOVA or PERMANOVA (Anderson, 2001; McArdle and Anderson, 2001). Traditional MANOVA (Multivariate Analysis of Variance) assumes that the variables are normally distributed and that the covariances and correlations do not differ between groups, but PERMANOVA lacks the formal assumptions of other methods (Anderson 2001). Moreover, PERMANOVA allows the use of different dissimilarity measurements (Quinn and Keough, 2002) and is more robust to heterogeneity in dispersions than ANOSIM (Analysis of similarities) or the Mantel test (Anderson and Walsh, 2013). We carried out a PERMANOVA analysis on the M^{1-2} , choosing this tooth because it is the best-represented element for all the considered species. A sample

of more than three specimens of each group is recommended for this test; therefore, we considered all the valid species of *Microchoerus* and *Necrolemur* with three or more M¹⁻², thus excluding *M. ornatus*, *M. edwardsi* and *M. creechbarrowensis*. For this analysis we used Euclidean distance, as all the measurements were in the same units. The *p*-value of the pairwise comparisons was corrected by sequential Bonferroni. The sequential Bonferroni option does not provide corrected *p* values, its significance is assessed by first evaluating the smallest *p* value, with Bonferroni correction for *Np* pairs. If significant ($pNp < 0.05$) the next smallest *p* value is significant if $p(Np-1) < 0.05$, etc. (Holm, 1979).

Systematic Paleontology

Order Primates Linnaeus, 1758

Suborder Haplorhini Pocock, 1918

Infraorder Omomyiformes Schmid, 1982

Family Omomyidae Trouessart, 1879

Subfamily Microchoerinae Lydekker, 1887

Genus *Microchoerus* Wood, 1844

Microchoerus hookeri nov. sp.

(Figs. 2–8)

Etymology

This species is dedicated to Jeremy J. Hooker (Natural History Museum, London), in recognition of his excellent work on Paleogene mammals and, particularly, his contributions to the knowledge of the evolution of the genus *Microchoerus*.

Holotype

A fragment of right maxilla with M¹ and M² (IPS62073) from the late Eocene (Headonian , MP17) site of Sossís (Lleida, Spain), stored in the collections of the Institut Català de Paleontologia Miquel Crusafont.

Hypodigm

Four left I₁ (IPS61962–61965); five right I₁ (IPS61966–61969 and 89573); three left C₁ (IPS61970–61971 and 62001); three right C₁ (IPS61972–61974); one left P₃ (IPS61975); four right P₃ (IPS61976–61979); six left P₄ (IPS4296 and 4299–4303); five right P₄ (IPS61980–61984); five left M₁ (IPS61985–61989); three right M₁ (IPS4298, 61990 and 61991); three left M₂ (IPS4297, 61992 and 61993); three right M₂ (IPS61994–61996); one fragment of a left M₁ or M₂ (IPS62072); one fragment of a right M₁ or M₂ (IPS61997); one left M₃ (IPS61998); two right M₃ (IPS61999 and 62000); one left dental series with C₁–M₃ (IPS61957); one right dental series with P₃–M₃ (IPS61958); one left mandible fragment with C₁–M₃ (IPS61955); one left mandible fragment with P₃–M₁ (IPS61956); one right mandible fragment with P₃–M₁ and M₃ (IPS62074); two left mandible fragments with M₁–M₃ (IPS4330 and 61959); one left mandible fragment with M₂–M₃ (NMB Sos.1); three left C¹ (IPS62003, 62018 and 62019); six right C¹ (IPS62002, 62004 and 62020–62023); three left P² (IPS62005, 62024 and 62025); four right P² (IPS62006 and 62026–62028); four left P³ (IPS62007 and

62029–62031); six right P^3 (IPS62008 and 62032–62036); seven left P^4 (IPS62009 and 62038–62043); two right P^4 (IPS62037 and 62044); 12 left M^{1-2} (IPS62010, 62045–62054 and NMB Sos.2); 12 right M^{1-2} (IPS61961, 62011 and 62055–62064); four left M^3 (IPS62065–62067 and NMB Sos.12); six right M^3 (IPS62012, 62068–62071 and NMB Sos.13); one right dental series with M^1 – M^3 (NMB Sos.11); one maxillary fragment with right C^1 – P^3 , left P^3 and fragments of left P^4 and M^1 (IPS61960); one maxillary fragment with right P^4 – M^2 (IPS2538); one maxillary fragment with left M^1 – M^3 (IPS2545).

Diagnosis

Medium sized form of *Microchoerus* with wrinkled enamel in lower and upper cheek teeth. P_4 without paraconid, generally with a distinct metaconid. Mesoconid generally absent, occasionally single and small, in the lower molars. Hypoconulid small and generally single in the M_1 and M_2 . M_3 with moderately-developed hypoconulid lobe, better differentiated from the talonid buccally than lingually. P^3 and P^4 with single paracone and without hypocone. M^1 and M^2 with single paracone, well-developed tubercular paraconule and metaconules, small parastyle and metastyle, large hypocone connected to the protocone, no hypostyle, and mesostyle generally absent, occasionally present but very weak and crest-shaped. M^3 without hypocone and with moderately expanded distolingual region.

Differential diagnosis

Microchoerus hookeri differs from *N. antiquus* in the larger size, thicker cristid obliqua, occasional presence of a mesoconid, and more developed hypoconulid in the M_1 and M_2 , more expanded hypoconulid lobe in the M_3 , more developed paraconule and metaconules in

the upper molars, much larger hypocone in the M^1 and M^2 , and proportionally longer M^3 . It differs from all the known species of *Microchoerus* in the absence of a mesostyle in most M^1 and M^2 (with the exception of *M. edwardsi*, only known from lower molars). It further differs from *M. erinaceus* in the smaller size, the less accentuated enamel wrinkling in all the cheek teeth, the smaller metaconid in the P_4 , the much more reduced or absent mesoconid and hypoconulid in the M_1 and M_2 , the shorter and less differentiated from the talonid hypoconulid lobe of the M_3 , the lack of hypocone in the P^3 and P^4 , the lack of hypostyle in the upper premolars and molars, the smaller paraconule, metaconules, parastyle and metastyle in the upper molars, and the shorter M^3 , with a less expanded talon basin. It differs from *M. edwardsi* in the smaller size, the weaker enamel wrinkling, the less molarized P_4 without distinct paraconid and premetacristid, the absent or small mesoconid in the lower molars and the smaller and generally single hypoconulid in the M_1 and M_2 , and the shorter hypoconulid lobe in the M_3 . It differs from *M. ornatus* in less accentuated enamel crenulation, in the single paracone in the P^3 , P^4 and upper molars, in the lack of hypocone in the P^3 , P^4 and M^3 , in the absent hypostyle and the smaller lingual metaconule in the upper molars, and in the proportionally shorter M^3 . It differs from *M. wardorum* in the larger size, the less-developed mesoconid and hypoconulid in the M_1 and M_2 and the relatively shorter hypoconulid lobe in the M_3 ; moreover, *M. wardorum* presents a hypostyle in the M^1 , double paracone in the M^2 and M^3 and hypocone in the M^3 , elements that are absent in *M. hookeri*. It differs from *M. creechbarrowensis* in the less mesiolingually compressed P_4 , in the smaller hypoconulid in the lower molars, in the absence of hypostyle in the P^4 , and the lack of pericone and hypostyle in the M^1 .

Description of the material from Sossís

I₁ (Fig. 2A–H). Long incisor, with a buccolingually compressed crown curved apically. The buccal face is convex, the lingual side is concave. These two faces are separated by a sharp posterior crest. There is a flat, broad, triangular-shaped mesial surface separated from the lingual face by a strong cingulid, which borders the lingual base of the crown, and reaches the posterior crest. In some specimens, the mesial surface shows striations (Fig. 2G), which have been also observed in other species of the genus and been attributed to fur grooming by some authors (Rose et al., 1981; Schmid, 1983). There is a weak cingulum on the buccal base of the crown. The root is compressed laterally.

C₁ (Fig. 2I–L). The crown is asymmetrical, with a convex buccal face and a concave lingual side. The base of the crown rises markedly on the mesial part of the tooth, and descends further in the lingual part than in the buccal one. The anterocristid is shorter and thicker than the posterocristid; both cristids reach the base of the crown. The lingual cingulid is strong. The buccal cingulid is much weaker and restricted to the distobuccal part of the tooth.

P₃ (Figs. 2M–P, 3E). This premolar is wider distally than mesially. Three cristids descend from the top of the protoconid. The first reaches the mesial end of the tooth. The other two cristids, directed distolingually and distobuccally, do not reach the base of the crown. In one specimen (IPS61976, Fig. 2M) only one distal cristid descends from the protoconid, which is divided into two branches in a more distal position. In some specimens, several enamel ridges can be observed on the distal slope of the protoconid. There is neither paraconid, nor metaconid. The cingulid is strong on the lingual and distal borders of the tooth, and weaker or absent on the buccal border. In four out of nine specimens preserving this region, there is an enamel bulge at the distolingual part of the cingulid.

P₄ (Figs. 2Q–T, 3E). The tooth is notably wider distally than mesially. A sharp paracristid runs mesially from the protoconid; at the mesial end of the tooth it curves lingually and

continues in a strong lingual cingulid that occupies the mesial half of the lingual face. There is no paraconid. A short protocristid is directed distolingually from the protoconid; in 10 out of 12 specimens with good preservation of this region, this protocristid ends in a distinct metaconid. From the metaconid (or from the distolingual end of the protocristid, if no metaconid exists), a cristid descends distally, reaches the distolingual corner of the tooth and continues in a strong distal cingulid. Another cristid descends distobuccally from the protoconid; it generally ends at the middle of the crown height, while in two of 12 specimens it reaches the base of the crown. Besides these main cristids, the distal slope of the trigonid is crossed by a variable number (1–5) of ridges; in most specimens there is a central ridge that is especially long and well-marked, crossing the entire trigonid slope and reaching the distal face. The distal face is flat and inclined distally. A narrow basin is delimited between this distal face and the slope of the trigonid. In four out of 10 specimens the distal face extends along the entire distal border of the tooth, being higher at its central part; in the other six, it occupies only the distolingual part of the premolar, whereas in the distobuccal corner there is a distinct, rounded tubercle. Another well-marked cingulid occupies the buccal border.

M₁ (Figs. 3A, B, E, 4A–F). The trigonid is notably narrower than the talonid. The paraconid is always distinct, but much lower than the protoconid and metaconid. It is connected to the protoconid by a curved, continuous paracristid, which in four out of 11 specimens preserving this part is seen one or more enamel bulges. The protoconid is smaller than the metaconid; both cuspids are connected by a protocristid, which is either continuous (in three specimens), interrupted or constricted by a weak notch (in six specimens), or clearly broken, with the lingual part more distal than the labial one (in three specimens). The metaconid is separated from the paraconid by a very deep, generally narrow notch, so the trigonid basin opens lingually, with the exceptions of specimens IPS62074, IPS61986 and IPS61989, which present a weak, low premetacristid. Several ridges are observed in the trigonid, starting at the

main three cuspids and running towards the centre of the basin. One or two ridges run buccally from the metaconid, and another one or two run lingually from the protoconid; the ridge running distobuccally from the paraconid is usually thicker and less differentiated. The cristid obliqua is straight, continuous, and weakly connected to the posterior wall of the trigonid at the level of the protoconid-metaconid joint; usually this cristid is somewhat thickened near its mesial end, but only one out of 12 specimens presents a distinct mesoconid. The hypoconid and entoconid are lower and less voluminous than the trigonid cuspids; they are connected by a continuous, slightly convex postcristid that bears a very small hypoconulid. Only one specimen (IPS61988) shows two tiny hypoconulids. Preentocristid and postmetacristid are not connected, and the talonid basin is open lingually by a marked notch. The enamel wrinkling in the talonid basin is more complex than in the trigonid, with several ridges running down from the main cuspids (hypoconid, entoconid, hypoconulid) and cristids (protocristid, cristid obliqua, postcristid) to the centre of the basin; the most marked ridges are those starting at the entoconid. A well-marked and continuous cingulid surrounds the entire mesial, buccal and distal borders of the tooth. In five out of 14 specimens preserving this part there is also a weak and short lingual cingulid, limited to the mesial part of the lingual border, or just below the notch separating paraconid and metaconid.

M₂ (Figs. 3A–D, 4G–L). The trigonid is notably wider and shorter than in the M₁. The paracristid is continuous, connecting protoconid and metaconid. There is no paraconid. The protocristid is continuous in seven out of nine specimens preserving this part and interrupted by a notch in two teeth; no specimen shows the displacement between the lingual and labial parts of the protocristid observed in some M₁. The trigonid is crossed by a continuous cristid connecting protoconid and metaconid in two specimens, and by two cristids running from the protoconid and metaconid towards the centre of the basin in seven teeth. In four specimens there is also another short, more mesial cristid starting at the metaconid. The cristid obliqua is

straight; in three out of nine specimens it bears a small mesoconid. The entoconid is smaller and lower than the hypoconid. The postcristid is convex and has a small hypoconulid, which in some specimens is hardly observable. Both the postmetacristid and the preentocristid are curved buccally and not connected to each other, and the talonid basin opens lingually through a narrow and deep valley. As in the case of the M_1 , enamel wrinkling in the talonid is more complex than in the trigonid, with several cristids directed to the centre of the basin, often sinuous and/or bifurcated. The buccal cingulid is long; it is weak or absent on the mesial face, very strong on the buccal border, and somewhat thinner on the distal side. Three out of 11 specimens also display a weak lingual cingulid.

M_3 (Figs. 3A–E, 4M–P). The talonid is much longer than the trigonid, but similar in width. As in the M_2 , the paracristid is continuous and there is no paraconid. The protocristid is continuous and sinuous. There is a short cristid running buccally from the metaconid, directed to the centre of the trigonid. One specimen also shows a cristid running lingually from the protoconid. There is no mesoconid. The entoconid is less voluminous than the hypoconid. There is a small accessory cuspid placed distally to the entoconid. The postmetacristid and the preentocristid are not connected, so the talonid basin opens lingually through a notch. The hypoconulid lobe is broad and long, with three or four differentiated small cuspids in the postcristid. The distolingual border is slightly convex, but in the buccal outline there is a marked concavity separating the hypoconid from the hypoconulid lobe, so this lobe is better differentiated buccally than lingually; only two specimens also display a concavity between the entoconid and the hypoconulid lobe. The enamel wrinkling is more developed than in the M_1 and the M_2 , with numerous wrinkles starting at the main cuspids and cristids, which become bifurcated or connect with other wrinkles near the centre of the talonid basin, forming a complex pattern. The buccal cingulid, extending from the mesiolingual corner of the tooth

to the buccal base of the hypoconulid lobe, is weaker than in the other lower molars. There is no lingual cingulid.

C¹ (Fig. 5A–F). High-crowned teeth, longer than wide, with a convex buccal side and a concave lingual face. The outline is asymmetrical, with a marked expansion in the distolingual part. The apex is placed mesially. A long posterocrista reaches the base of the crown. Two other cristae run mesially and mesiolingually from the apex, forming an acute angle and delimiting a small, triangular mesiolingual basin. There is a strong cingulum occupying the entire lingual border; a weaker buccal cingulum is present in two out of eight specimens with well-preserved enamel.

P² (Fig. 5A, B, G–J). Very similar in morphology to the upper canine, but markedly lower-crowned. The outline is oval, more symmetrical than in the C¹, without a distolingual expansion. The disposition of the cristae is as in the canine. In addition to the strong lingual cingulum, a buccal cingulum is present in all the available specimens, although it is weaker than the lingual one and generally restricted to the distobuccal part of the tooth.

P³ (Fig. 5A, B, K–N). The outline is subtriangular, with a round buccal border, nearly straight mesial and distal borders, and a short lingual side. The paracone is high and voluminous. The lingual lobe is narrow. A small but distinct protocone is placed in the mesiolingual position. The posterocrista curves distobuccally at the middle of the crown height and reaches the base of the crown, connecting to a minuscule metastyle; in some specimens, at the point where this crista turns, there is a very short and weak branch directed distally. Similarly to the C¹ and P², two cristae run mesially and mesiolingually from the apex, which enclose a triangular basin in mesiolingual position. There is no parastyle. Some specimens show enamel wrinkling on the lingual slope of the paracone. A cingulum surrounds the border of the tooth, being thicker on the lingual side and weak on the buccal base.

P⁴ (Figs. 5O–T, 6I–J). This premolar is proportionally wider than the P³ and has a more quadrate outline. The buccal border is curved, whereas the mesial, distal and lingual borders are nearly straight, with the lingual border being somewhat shorter than the buccal. The paracone is high, the lingual lobe is broad and the protocone is relatively large and more developed than in the P³. There is no hypocone. The anterocrista is straight and reaches the base of the crown. In three out of six specimens with good enamel preservation there is a very small parastyle. The posterocrista descends distally from the paracone and curves buccally to reach the distobuccal corner of the tooth, connecting to a small metastyle. The enamel is crenulated on the lingual slope of the paracone and on the lingual lobe. The cingulum is very thick in the lingual part, also strong in the mesial and distal borders, and weak or absent on the buccal face.

M¹⁻² (Figs. 6A, B, E–L, 7A–L). These two dental elements have been described together due to their strong similarity in size and morphology, which makes distinguishing isolated specimens very difficult. The outline is subquadrate, somewhat wider than long. Paracone and metacone are similar in size and connected by a centrocrista. Most specimens lack any sign of a mesostyle; only four out of 19 specimens preserving the buccal part have a weak crest starting at the middle point of the centrocrista, and this crest reaches the ectocingulum in only two of them. Parastyle and metastyle are small but always present. All the available specimens have a single paraconule and double metaconule; these three cuspules are voluminous and tubercular in shape. The paraconule is separated from the paracone by a valley and can be either isolated from the protocone or connected to it by a preprotocrista. The paraconule is variable in size, being larger than the lingual metaconule in 12 out of 15 teeth preserving all the conules, and larger than the buccal metaconule in only five specimens. The buccal metaconule is always larger than the lingual metaconule and usually connected to the metacone by a premetaconule crista. The hypocone is a perfectly individualized tubercular

cuspid, smaller and lower than the protocone and connected to it by a postprotocingulum, which in some specimens is very weak. There is no pericone. The posthypocrista continues in a postcingulum that reaches the metastyle. In few specimens (e.g., IPS62073, Fig. 6A) the posthypocrista is thickened behind the hypocone, but it does not develop a distinct hypostyle. The precingulum occupies the entire mesial border, from the mesiolingual corner of the tooth to the parastyle. The ectocingulum, running from the parastyle to the metastyle, is slightly stronger than the other cingula. Enamel crenulation is well developed in the trigon basin, with several ridges descending from the paracone, metacone, protocone and buccal metaconule, which do not reach the centre of the basin. Some specimens also show several weak ridges in the talon basin, between the hypocone and the metaconules.

M³ (Figs. 6C, D, K, L, 7M–V). The mesial border is straight, the buccal and distal borders are markedly convex, and the lingual border varies from straight to slightly convex. The mesial part is notably wider than the distal part. The metacone is much smaller than the paracone and placed distolingually with respect to it. The centrocrista is markedly asymmetrical, with the postparacrista longer than the premetacrista. The protocone is high. There is no hypocone. Conules are much less developed than in the M¹⁻². The paraconule is weak, appearing to be a swelling of the preprotocrista in two out of five unworn specimens, and distinct in the other three. The metaconule is variable: all the available specimens have a large tubercle in a rather lingual position (lingual metaconule), closer to the protocone than to the metacone. This metaconule bears a postmetaconule crista directed to the metacone, which in some specimens (IPS62066, IPS62068, IPS62069, NMB Sos.12) thickens, forming a buccal metaconule. Only one specimen (IPS62067, Fig. 7O) lacks the postmetaconule crista, but it shows a complex net of ridges in its place. Finally, specimen IPS62071 (Fig. 7Q) displays a tubercle distobuccal to the metaconule and attached to the postcingulum. The postprotocingulum continues in a thick postcingulum that occupies the distal border, reaching

the metacone. The precingulum, bordering the entire mesial face, is low and thin. The ectocingulum is stronger on the base of the paracone and weaker or even interrupted below the metacone. The enamel wrinkling is well marked in the trigon basin and, especially, in the talon basin, where several short ridges perpendicular to the distal border are observed.

Comparative anatomy

Material from Eclépens B, Switzerland

The material from Eclépens B previously ascribed by Hooker and Weidmann (2000) to *M. aff. erinaceus* shows a strong resemblance to *M. hookeri* from Sossís. We directly compared the material from Sossís with the specimens from Eclépens B housed in the NMB, some of which are illustrated in Figure 8. The P² from Eclépens is virtually identical to the specimens from Sossís. The P³ from Eclépens B is similar to those from Sossís in having the lingual side shorter than the buccal one, two cristae running mesially from the paracone, a very small protocone and no hypocone; the P³ of specimen Mt.1211 slightly differs from the premolars from Sossís in being proportionally wider. The P⁴ of the specimen Mt.1211 from Eclépens differs from those of *M. hookeri* in having a very small hypocone. The M¹ and M² from Eclépens (Fig. 8, C–H) show a wide range of size and development of conules (as is the case of the sample from Sossís) and they are very similar to those of *M. hookeri* in the main morphological traits: they are relatively long, with a quadrate outline, and lack a mesostyle, like most specimens of *M. hookeri* from Sossís. The M³, without mesostyle and with a moderately expanded distolingual region, is also very similar in the samples from Eclépens B and Sossís. Lower teeth, scarce in Eclépens B, also resemble those of *M. hookeri* from Sossís. The single P₄ is identical to most specimens from Sossís, lacking a paraconid and showing a well-developed metaconid, flat and inclined distal face and a marked central cristid on the

distal slope of the trigonid. The two incomplete M_1 and the single M_2 from Eclépens B are also very similar in overall morphology to the lower molars from Sossís. One of the two M_1 from Eclépens has a small mesoconid, which is present in one specimen from Sossís. The development of the hypoconulid (very small in Sossís and Eclépens B) and of the enamel wrinkling is very similar in both samples. Therefore, taking into account the similarity of the material from these two localities, particularly regarding the lack of mesostyle in all the M^1 and M^2 from Eclépens B and in most specimens from Sossís, and the size (i.e., distinctly larger than that of *N. antiquus* and smaller than that of *M. erinaceus*), we consider that the specimens from Eclépens B previously assigned to *M. aff. erinaceus* can be ascribed to the new species *M. hookeri*. Moreover, this assignation is supported by the statistical analysis of the M^{1-2} (see Results).

Material from other species

Microchoerus erinaceus We compared the material of *M. hookeri* with the holotype of *M. erinaceus*, a palatal fragment with almost complete upper dentition (only lacking the left upper canine and right I^2) and an associated left mandibular ramus with P_4 - M_3 from Hordle Cliff (Mammal/Crocodile Bed), curated at the Natural History Museum, London. We also studied the abundant additional material from the type locality, described in part by Cray (1973) and Hooker (1986), and consisting of about 100 specimens including mandibular and maxillary fragments and isolated teeth.

The first and most obvious difference between *M. erinaceus* and *M. hookeri* from Sossís is that *M. erinaceus* is much larger (see Fig. 9). The lower incisors, apart from the difference in size, are morphologically very similar in both species. The P_4 of *M. erinaceus* have a notably

larger metaconid, more marked ridges on the distal slope of the trigonid and stronger cingulids than those of *M. hookeri*. Moreover, the paracristid is more inflated in the P₄ from Hordle Cliff, developing in some specimens an incipient paraconid that is absent in *M. hookeri*. The lower molars of *M. erinaceus* show very strong differences with those of *M. hookeri* from Sossís. The enamel wrinkling is more complex and the buccal cingulids are higher in the three lower molars of *M. erinaceus*. The M₁ and M₂ differ in several traits. The mesoconid is absent in Sossís with the exception of four specimens with a small tubercule; on the contrary, it is well developed in Hordle Cliff, with some specimens (e.g., M12563) even having two mesoconids. Similarly, the hypoconulid is very small and single-cusped in *M. hookeri* (with the exception of one molar with two minuscule cuspids), while all the specimens of *M. erinaceus* display a very large or even double (e.g., in 30346b, M34712, M34713) hypoconulid. There is, however, some morphological variability in the sample of *M. erinaceus* from Hordle Cliff, with some specimens bearing a relatively small hypoconulid (e.g., the M₁ 30338). Moreover, in *M. erinaceus* the M₁ and M₂ have a distinctly broken protocristid, with the lingual part more distal than the buccal one (this morphology is observed in only a few M₁ from Sossís). The hypoconulid lobe of the M₃ is longer in *M. erinaceus* from Hordle Cliff, but narrower and better differentiated from the talonid, with more marked concavities separating this lobe from the hypoconid and entoconid.

Apart from the obvious difference in size, the upper canines and P² of *M. erinaceus* and *M. hookeri* are morphologically very similar. On the contrary, the P³ of *M. erinaceus* distinctly differ from those of *M. hookeri* in having a more quadrate outline with a longer lingual border, a higher and larger protocone, a distinct hypocone, a more developed metastyle and a small but distinct parastyle that is absent in the specimens from Sossís. The P⁴ of *M. erinaceus* are proportionally wider and shorter than those of *M. hookeri*, and display a large hypocone and, with a few exceptions (e.g., 30338), a small but distinct hypostyle that are

absent in *M. hookeri*. Moreover, the parastyle and metastyle are also more developed in the P⁴ of *M. erinaceus*.

Morphological differences in the upper molars are even more accentuated. The M¹ and M² of *M. erinaceus* from Hordle Cliff have a large mesostyle (tubercular in most specimens, being crest-shaped only in some molars, e.g., M35038) that is absent in most upper molars of *M. hookeri*, and present as only a very weak crest in a few specimens from Sossís. Conules are, in general, much more voluminous in *M. erinaceus*, especially the paraconule and the buccal metaconule. However, the development of the conules is variable in both samples, and the relative size of the paraconule and metaconules of some specimens from Hordle Cliff (e.g., M35038) is similar to that of some upper molars from Sossís (e.g., IPS62073). Both parastyle and metastyle are better developed in *M. erinaceus* than in *M. hookeri*. In addition, the specimens from Hordle Cliff display a tubercular hypostyle that is absent in all the upper molars from Sossís. The M³ of *M. erinaceus* from Hordle Cliff are more enlarged distolingually, with a more expanded talon basin, and show stronger enamel wrinkling than the specimens from Sossís. Moreover, the holotype of *M. erinaceus* and most M³ from Hordle Cliff (except for M34700 and M34815) have a small crestiform mesostyle that is absent in *M. hookeri*.

Microchoerus edwardsi We directly compared the material from Sossís with the holotype of *M. edwardsi*, a fragment of a left mandible (Qu.10946) from Quercy, stored at the Muséum National d'Histoire Naturelle, Paris. Besides the smaller size (Fig. 9), the specimens of *M. hookeri* from Sossís show even more marked morphological differences from *M. edwardsi* than from *M. erinaceus*. The P₄ of *M. edwardsi* is more molarized than the specimens of *M. hookeri*, having a perfectly distinct paraconid connected to the metaconid by a premetacristid

and, therefore, a well-defined and closed trigonid basin. Moreover, the P₄ of the holotype of *M. edwardsi* displays better-developed cingulids and stronger ridges on the posterior slope of the trigonid. The lower molars of *M. edwardsi* show more accentuated enamel wrinkling. The most notable difference is the development of mesoconid(s) and hypoconulid(s): both the M₁ and the M₂ of *M. edwardsi* have two large mesoconids, contrary to the situation in *M. hookeri* from Sossís where a small mesoconid is present in only a few specimens. Similarly, the molars of *M. edwardsi* display two large, perfectly distinct hypoconulids, instead of the tiny and generally single-cusped hypoconulid of *M. hookeri*. The M₃ of *M. edwardsi* has a longer and broader hypoconulid lobe and more complex enamel crenulation.

"*Microchoerus edwardsi*" from La Débruge, France A single specimen from La Débruge comprising a fragment of maxilla with P⁴, broken M¹, M² and M³ is assigned to *M. edwardsi* (Schmidt-Kittler, 1971; Hooker, 1986). The holotype is a fragment of jaw from an unknown level of the Quercy phosphorites with no associated upper dental elements, so it is not possible to know if the specimen from La Débruge can be ascribed to the same species as the material from Quercy. As a result, the specific assignation must be taken with caution. In any case, we compared *M. hookeri* with the La Débruge specimen, stored at the Natural History Museum, London. Differences with *M. hookeri* are obvious. The P⁴ of "*M. edwardsi*" from La Débruge differs distinctly from those of *M. hookeri* in the higher protocone, the stronger metastyle and parastyle, and the presence of a well-developed and high hypocone and a distinct tubercular hypostyle. The preservation of the M¹ does not allow comparisons, but the M² from La Débruge is very different from the M¹⁻² from Sossís: the molar of "*M. edwardsi*" is proportionally shorter and wider and has a large, rounded mesostyle. Moreover, it has stronger parastyle, paraconule and metaconules than the specimens of *M. hookeri*, and bears a large, tubercular hypostyle. The hypocone is separated better from the protocone in the

specimen from La Débruge. Finally, the M^3 of "*M. edwardsi*" from La Débruge differs from those of *M. hookeri* in the presence of a small but distinct mesostyle and a well-developed hypocone, in the stronger conules and in the somewhat more expanded talon basin.

"*Microchoerus edwardsi*" from Ehrenstein, Germany We compared the *M. hookeri* material with casts of several isolated teeth from Ehrenstein 1A (Schmidt-Kittler, 1971) and with a mandible with M_1 – M_3 from Ehrenstein 3 (Schmidt-Kittler, 1977) attributed to *M. edwardsi*. The lower teeth from Ehrenstein are similar in size to the specimens of *M. hookeri* from Sossís (with the exception of the M_3 , which is distinctly longer in the Ehrenstein material), and differ in the much more complex enamel wrinkling. The P_4 from Ehrenstein have an incipient paraconid, and the ridges crossing the distal slope of the protoconid are much more marked than in the specimens of *M. hookeri*. The M_1 and M_2 from the German site have one large or even two mesoconids, and two hypoconulids much better developed than the specimens from Sossís. The element showing the strongest difference is the M_3 , which in "*M. edwardsi*" from Ehrenstein is extremely elongated, with a very long and broad hypoconulid lobe, and the enamel much more crenulated than in *M. hookeri* from Sossís.

The outline of the P^3 and P^4 is similar in both species, quadrate in the P^4 and subtriangular in the P^3 , but the premolars from Ehrenstein have more accentuated enamel wrinkling in the lingual face of the paracone. Moreover, the P^4 from Ehrenstein display a small but distinct hypocone and a enamel bulge in the lingual side of the paracone that may constitute a distinct lingual paracone; these elements are absent in all the specimens from Sossís. Differences are stronger in the M^{1-2} . The specimens from Ehrenstein 1A have a very large, tubercular mesostyle. The paracone is double in the specimens of "*M. edwardsi*" from Ehrenstein 1A, meaning that there is a distinct cusp between paracone and paraconule, which is absent in *M.*

hookeri from Sossís. In addition, the enamel wrinkling in the trigon basin is much more marked in the molars from Ehrenstein 1A.

In our opinion, the specific determination of the material from Ehrenstein must be reconsidered. It resembles the holotype of *M. edwardsi* in the complexity of the enamel crenulation, but also shows several differences. The molars from Ehrenstein are narrower than those of the type specimen of *M. edwardsi*. Moreover, the P₄ of the type specimen of *M. edwardsi* has a large paraconid and a premetacristid that closes the trigonid basin, contrary to the specimens from Ehrenstein, in which the paraconid is incipient and the trigonid is open lingually. The M₃ is even more elongated in the specimens from Ehrenstein than in the holotype of *M. edwardsi*, and the enamel wrinkling is more complex. Indeed, Godinot (1983) noticed the similarity between the upper molars from Ehrenstein and those of the holotype of *M. ornatus* (see below), and referred to this form as *M. cf. ornatus*. For these reasons, a more detailed analysis is required to clarify if the material from these fissure fillings corresponds, in fact, to the same species as the mandible of *M. edwardsi* from Quercy or if it may be referred to another species.

Microchoerus ornatus This species, described by Stehlin (1916) on the basis of a fragment of maxilla with P²–M³ from Mormont Entreroches (Switzerland), was considered by some authors to be a synonym of *M. edwardsi* due to the complexity of its dental pattern (Insole, 1972; Hooker, 1986). In contrast, more recent work states that these species are probably distinct because of the difference in size (Hooker and Weidmann, 2000). In any case, the type material of *M. edwardsi* only consists of lower teeth and therefore cannot be directly compared to *M. ornatus*, so we consider them to be separate species.

In the holotype (Mt. 132), housed at the Naturhistorisches Museum Basel, P⁴ and M¹ are broken, lacking the buccal part, so comparisons mainly focus on the other teeth. The P² of *M. ornatus* is similar to that of *M. hookeri* in overall shape, but it shows a crista crossing the lingual face, which is absent in the specimens from Sossís. The P³ of *M. ornatus* is distinctly different from that of *M. hookeri*. It is smaller, with a more quadrate outline (the buccal and lingual borders are similar in length), and its pattern is much more complicated (see Minwer-Barakat et al., 2016). The paracone is double. From the buccal paracone, one mesial and two distal cristae descend. The lingual paracone (absent in all the specimens from Sossís) is distinct and also bears one mesial and one distal cristae. The protocone is distinctly higher than in *M. hookeri* and, at the distolingual extreme, there is a distinct hypocone that is not present in the specimens from Sossís. The P³ of *M. ornatus* also differs from the specimens from Sossís in having a broad distolingual basin between paracone, protocone and hypocone, with well-developed enamel wrinkling. The P⁴ and M¹ are partially broken in the holotype of *M. ornatus*, but some differences with the specimens from Sossís can still be noted: the P⁴ of *M. ornatus* displays a distinct lingual paracone and hypocone (as in the P³) that are absent in *M. hookeri*, and the M¹ shows a tubercular hypostyle that is not present in the specimens from Sossís. The M², well preserved in the holotype from Mormont Entreroches, shows clear differences with the specimens from Sossís, including the presence of a large, rounded mesostyle, the double paracone (there is a distinct, large cusp between the paracone and the paraconule), the large lingual metaconule (similar in size to the buccal metaconule) and the well-developed, tubercular hypostyle. The M³ of *M. ornatus* is also very different from those of *M. hookeri*: it is proportionally much longer, with a more expanded talon basin. The metacone is lower than in the M³ from Sossís, and separated from the paracone by an elevation of the centrocrista that constitutes a small mesostyle, which is absent in *M. hookeri*. The lingual metaconule is larger than in *M. hookeri*. Moreover, the M³ of *M. ornatus* has a

double paracone and a distinct hypocone distal to the protocone, followed by two other cusps attached to the postcingulum. Finally, the enamel crenulation is much more accentuated in *M. ornatus* than in *M. hookeri*.

Microchoerus wardorum This species from Creechbarrow (UK) was originally described by Hooker (1986) under the name *Microchoerus wardi* and later amended to *M. wardorum* (see Hooker and Weidmann, 2000). We have compared the material from Sossís with the original type material of *M. wardorum* stored at the Natural History Museum, London. *Microchoerus wardorum* is much smaller (Fig. 9) and clear morphological differences with *M. hookeri* are present. The upper canines are much more distolingually expanded in *M. hookeri*, thus having a more asymmetrical outline. The only available P³ of *M. wardorum* is more quadrate, with a proportionally longer lingual border than those of *M. hookeri*. One of the most obvious differences is the presence of a crest-shaped but strong mesostyle in the M¹ and M² of *M. wardorum*, which is absent in most specimens from Sossís and, when present, is very weak. A mesostyle is present even in the M³ of *M. wardorum*, contrary to the specimens of *M. hookeri*. The conules are, in general, smaller in *M. hookeri*, especially the paraconule. Other differences in the upper molars include the presence of a hypostyle in the M¹, the double paracone in the M² and M³, and the presence of a hypocone in the M³ of *M. wardorum*. Regarding the lower molars, the mesoconid is more frequent in the M₁ and M₂ of *M. wardorum* (distinct in the two complete M₁ and in one of the two available M₂ from Creechbarrow), and the hypoconulid is distinctly more developed in *M. wardorum* than in *M. hookeri*, especially in the M₂. On the contrary, the buccal cingulid is higher and more marked in the lower molars of *M. hookeri*. Finally, the hypoconulid lobe of the M₃ is relatively longer and better differentiated from the talonid in *M. wardorum* than in *M. hookeri* from Sossís, especially in specimen M35751 from Creechbarrow.

Microchoerus creechbarrowensis We directly compared the sample from Sossís with the type material of the species *M. creechbarrowensis*, also described from Creechbarrow, which shows clear differences with *M. hookeri*. The canines and premolars are slightly smaller in *M. creechbarrowensis* than in *M. hookeri*, whereas the molars are similar in size in both species (Fig. 9). The upper canines are relatively shorter and wider in *M. creechbarrowensis*. The P⁴ of *M. hookeri* have a more convex buccal border, and lack the small hypostyle that is present in the single specimen of *M. creechbarrowensis*. The most evident morphological differences are found in the upper molars. The M¹ and M² of *M. creechbarrowensis* have a large, tubercular mesostyle, which in the M¹ is strongly displaced distally. In addition, the two M¹ of *M. creechbarrowensis* display a well-developed pericone at the mesiolingual corner and a distinct hypostyle, cusps that are not observed in any upper molar from Sossís. The two complete M³ of *M. creechbarrowensis* have very different outlines: one of them (M35734) is proportionally wider and shorter than most specimens from Sossís, whereas the other one (M37156) is distolingually expanded, showing a talon basin broader than in most molars of *M. hookeri*. Apart from the overall outline of the teeth, specimen M35734 has a small crest-shaped mesostyle that is absent in *M. hookeri*, and M37156 displays a cusp distally attached to the protocone that is not observed in any M³ of *M. hookeri*. The P₄ of *M. creechbarrowensis* are much shorter (mesiolingually compressed) than those of *M. hookeri*. In addition, two of the three available specimens from Creechbarrow show a distinct paraconid, which is not present in the P₄ of *M. hookeri*, and a proportionally broader trigonid basin. Lower molars of *M. creechbarrowensis* are particularly scarce. The only complete tooth is a M₂, which displays more marked enamel wrinkling, a thicker cristid obliqua and a more prominent hypoconulid than those of *M. hookeri*. The single M₃ of *M.*

creechbarrowensis lacks the distal part, so the morphology of the hypoconulid lobe cannot be observed.

Microchoerus aff. *creechbarrowensis* from Eclépens B, Switzerland We also directly compared the sample from Sossís with the material from Eclépens B ascribed to *M.* aff. *creechbarrowensis* by Hooker and Weidmann (2000) and housed at the NMB (specimens Mt.1217–Mt.1222). *Microchoerus* aff. *creechbarrowensis* is markedly smaller than *M. hookeri*. Morphologically, the upper molars of *M.* aff. *creechbarrowensis* differ from those of *M. hookeri* in the very large mesostyle and in the presence of a well-developed mesiolingual crest descending from the protocone. The conules and the parastyle are also proportionally larger in *M.* aff. *creechbarrowensis*. Furthermore, the P⁴ from Eclépens B has a hypocone that is absent in the specimens from Sossís. Regarding the lower dentition, in *M. hookeri* the P₄ is wider, more robust, and has a more convex buccal side. The M₁ and M₂ of *M.* aff. *creechbarrowensis* show a distinct mesoconid that is absent in most lower molars of *M. hookeri*. The M₃ is proportionally longer and narrower in *M.* aff. *creechbarrowensis*. In addition, the hypoconulid lobe is much narrower and better differentiated from the talonid in the M₃ from Eclépens B, with much deeper indentations separating it from the entoconid and hypoconid than in the specimens from Sossís.

Microchoerus cf. *erinaceus* from Euzet, France The microchoerine from this locality was assigned to *M. edwardsi* by Depéret (1917), later considered to belong to *M. erinaceus* by Hürzeler (1948), named after *Microchoerus* sp. A (within the "group *erinaceus*") by Godinot (1983) and finally ascribed to *M.* cf. *erinaceus* by Godinot (1985). We compared the Sossís material with casts of a mandible with C₁–M₃ (6488) and a maxilla with P⁴–M³ (6489),

described and figured by Depéret (1917), and also with the original material from this locality housed at the NMB, described and figured by Hürzeler (1948), including a fragment of mandible with P₄–M₂ (StH-1640), an isolated M₃ (StH-2511) and a M¹⁻² (StH-2076). Lengths and widths are, with a few exceptions, larger in the sample from Euzet than the mean values from Sossís (Fig. 10). The lower dentition of *M. hookeri* from Sossís resembles that of the population from Euzet more than that of *M. erinaceus* and *M. edwardsi*. However, some differences also exist. The lower molars from Euzet display some more advanced features than those of *M. hookeri* (although a certain degree of variability exists in the population from Sossís for all the considered characters). The enamel wrinkling is more complex (especially in the trigonids) and the protocristid is more curved in the teeth from Euzet. The cristid obliqua is thicker in the M₁ and M₂ from Euzet and bears a small mesoconid that is present in only a few teeth from Sossís. Moreover, the hypoconulid is more developed in the molars from Euzet, especially in the M₂, which displays a more convex postcristid with two small cuspids. Differences are more evident in the M₃, which in Euzet has a more elongated outline and a distinctly narrower and better-differentiated hypoconulid lobe. Regarding the upper molars, the specimens from Sossís are, in general, smaller than those from Euzet and with less developed paraconule and metaconules, although both the size and the development of the conules are variable in the population from Sossís. However, the most obvious difference is the presence of a well-developed, crest-shaped mesostyle connecting the centrocrista to the ectocingulum in the M² of specimen 6489 and in the isolated molar StH-2076 from Euzet; this mesostyle is absent in most upper molars of *M. hookeri* and, when present, it is weaker than in the specimens from Euzet. In the M³ of *M. cf. erinaceus* from Euzet the metacone is notably larger than in *M. hookeri* and placed in a more buccal position, making the outline of the molar more quadrate.

Microchoerus cf. erinaceus from Perrière, France We also studied the material from Perrière ascribed by Louis and Sudre (1975) to *M. erinaceus edwardsi* but later included in the lineage of "*Microchoerus* sp. A", within the "*erinaceus* group" by Godinot (1983). Following Godinot (1985), we refer to this material as *M. cf. erinaceus*. The material from Perrière, stored at the Université de Montpellier, consists of a well-preserved cranium with C¹–M³, a fragment of maxila with C¹–M³, two fragments of mandibles with P₃–M₃ and M₁–M₂, and several isolated teeth.

Lower teeth from Perrière are, in general terms, larger than those from Sossís (Fig. 10): the smallest specimens from Perrière are similar in size to the largest teeth from Sossís. However, the sample for Perrière shows a wide size range, as is the case of that from Sossís.

Morphologically, the only P₄ available from Perrière has a thicker paracristid and more marked ridges on the distal wall of the trigonid than the specimens from Sossís. The M₁ from Perrière have, in general terms, a more complicated dental pattern than those from Sossís: they have a relatively higher paraconid, an always discontinuous protocristid and a thicker cristid obliqua, and four out of six specimens preserving the buccal part show a distinct mesoconid. The M₂ have not been compared due to the poor preservation of the specimens from Perrière. The single well-preserved M₃ from Perrière is slightly more elongated and shows more complex enamel wrinkling than the molars from Sossís. The C¹ and P² from Perrière are somewhat larger than those from Sossís, but similar in morphology. The P³ from Perrière differ from those of *M. hookeri* in the more quadrate outline and in the larger protocone. The M¹⁻² from Perrière are proportionally wider than those from Sossís and have more developed paraconule and metaconules, but the most obvious difference is the presence in all the specimens from Perrière of a distinct mesostyle, ranging from an inflated crest to a voluminous tubercule.

Microchoerus aff. *erinaceus* from Zambrana, Spain The material from Zambrana (MP18, Miranda-Trebiño Basin, Northern Spain), consisting of two mandibles bearing P₃–M₃ and P₄–M₃, was ascribed to *M. aff. erinaceus* by Minwer-Barakat et al. (2013a). The lower molars from Zambrana differ strongly from those of *M. hookeri* in the much larger size, the more accentuated enamel wrinkling, the stronger mesoconid, the presence of two well-developed hypoconulids in the M₁ and M₂, and the hypoconulid lobe of the M₃ which is better differentiated from the talonid than in *M. hookeri*.

Microchoerus sp. from Grisolles, France *Microchoerus* from Grisolles was first attributed to *M. aff. erinaceus* by Louis and Sudre (1975) and later cited as *Microchoerus* sp. by Hooker (1986). However, at this site two different forms of the genus can be distinguished primarily by their size, as was noted by Godinot (1983). This author used the names *Microchoerus* sp. B for the species of medium size, which is the most abundant, and *Microchoerus* sp. C. for the larger but less numerous specimens.

The medium-sized form from Grisolles, *Microchoerus* sp. B, is similar in size to *M. hookeri* from Sossís, but shows some morphological differences. In the P₄ of *Microchoerus* sp. B from Grisolles the metaconid is much higher than in *M. hookeri*, reaching almost the same height as the protoconid. The M₁ and M₂ are similar in overall morphology, although those of *Microchoerus* sp. B have more accentuated enamel wrinkling. In the M₃ of *Microchoerus* sp. B from Grisolles, the hypoconulid lobe is slightly better differentiated from the talonid than in *M. hookeri*, with more marked concavities in the buccal and lingual borders. C¹ and P² are similar in size and morphology in both species. The P³ and P⁴ of *Microchoerus* sp. B from Grisolles have a larger lingual lobe, so they are proportionally wider than those of *M. hookeri*. In addition, the buccal border is straighter, and the distolingual region is more extended in the

specimens from Grisolles, so the outline is more rectangular than in those from Sossís. The M^1 and M^2 of *Microchoerus* sp. B differ from those of *M. hookeri* in the less-developed lingual metaconule, which is very small or even absent in some specimens; moreover a small but perfectly distinct crest-shaped mesostyle is present in almost all the specimens from Grisolles.

Differences between *M. hookeri* and *Microchoerus* sp. C from Grisolles are more marked. First, the species from Grisolles is much larger in size. Moreover, the M_1 and M_2 of *Microchoerus* sp. C differ from those of *M. hookeri* in the better-developed mesoconids and hypoconulids, showing one or two distinct mesoconids, and one prominent or, most commonly, two well-differentiated hypoconulids. The M_1 displays a reduced paraconid, smaller than in *M. hookeri*. The P^2 of *Microchoerus* sp. C from Grisolles, besides its larger size, is more extended lingually than the specimens from Sossís. The P^3 and P^4 of *Microchoerus* sp. C from Grisolles are much wider than those of *M. hookeri*, with a buccolingually elongated outline. Moreover, in the premolars from Grisolles the protocone is higher, the parastyle and mesostyle more developed and the enamel wrinkling more accentuated than in those from Sossís. The M^1 and M^2 of *Microchoerus* sp. C, besides their notably larger size, are proportionally wider than those from Sossís, and have better developed parastyle, paraconule and buccal metaconule. In addition, the specimens from Grisolles differ from those of *M. hookeri* in having a distinct mesostyle. In the M^3 , the main difference is the dissimilarity in size between paracone and metacone, which is even more accentuated in *Microchoerus* sp. C from Grisolles than in *M. hookeri*.

Necrolemur antiquus We compared our material with high-quality casts of the holotype of *N. antiquus* from Quercy (a skull and a mandible conserving lower dentition from C_1 to M_3 and

upper dentition from P² to M³, Qu.11013), with the large collection of *N. antiquus* from La Bouffie, representing the richest sample of the species recovered until now, and with the material of the same species from Le Bretou and Lavergne, housed at the Université de Montpellier. The most evident difference is the size of the teeth, which are notably smaller in *N. antiquus* than in *M. hookeri* from Sossís (Figs. 9, 10). Morphologically, no differences are observed in the I₁, C₁, P₃, C¹ and P². In general terms, the metaconid of the P₄ is distinctly larger in *M. hookeri* than in *N. antiquus* from La Bouffie, and similar in size to that of Lavergne, although this character is variable in all these samples. The ridges on the distal slope of the trigonid are more marked in *M. hookeri* than in *N. antiquus*. P³ and P⁴ are very similar in overall morphology, only differing in the more marked cristae in *N. antiquus*. Lower and upper molars of *N. antiquus* have sharper crests, less voluminous cusps and, in general, a simpler dental pattern. The M₁ and M₂ of *N. antiquus* have a sharper cristid obliqua than those of *M. hookeri*, without any trace of mesoconid. The small hypoconulid that is present in most specimens of *M. hookeri* is absent in those from Le Bretou and in most specimens from La Bouffie; it is frequent in *N. antiquus* from Lavergne, but only represented by a small peak of the postcristid, less developed than in the molars from Sossís. The protocristid is continuous in the few lower molars from Le Bretou (one M₁ and two M₂), whereas it can be continuous or interrupted in Lavergne and La Bouffie, as is the case in the sample from Sossís; the discontinuous protocristid is always more frequent in the M₁ than in the M₂. The M₃ of *N. antiquus* are more reduced, with a shorter and narrower hypoconulid lobe than those of *M. hookeri*, while enamel crenulation is very variable in both species.

Regarding the upper molars, the paraconule and the metaconules are more developed in the M¹ and M² of *M. hookeri* than in *N. antiquus*. This difference is more obvious in the oldest sample of *N. antiquus* from Le Bretou, in which one of three observed M¹⁻² lacks a distinct paraconule. In the samples from Lavergne and La Bouffie the development of these cusps

is variable, and some specimens show conules as well-developed as those from Sossís, but in general terms paraconule and metaconules are larger in *M. hookeri*. The most evident difference in the M^{1-2} is the development of the hypocone, which is distinctly more voluminous in *M. hookeri* than in *N. antiquus*. The M^3 of *M. hookeri* are, in general terms, proportionally longer than those of *N. antiquus* from La Bouffie and Lavergne (no M^3 is available from Le Bretou), with a more expanded talon basin, and better developed conules, although these characters are variable in all the observed samples (especially in the rich population from La Bouffie).

Comparison with some specimens from Quercy, described by Stehlin (1916) under the name "*Necrolemur antiquus* var. *major*", deserves particular attention, since this form has been considered by Godinot (2003) as a valid species (i.e., *Necrolemur major*). Comparison was only possible with two of the specimens figured by Stehlin (mandibles Q.H.441 and Q.H.442), housed in the collections of the NMB. Mandibles without catalogue numbers figured in Fig. CCCXV, as well as the maxilla with I^2-M^3 from Larnagol, mistakenly called Q.H.470 (this catalogue number corresponds in fact to a specimen of "*Anchomomys quercyi*" also described and figured by Stehlin, 1916), are not available in the NMB. Lower incisors and P_3 of *M. hookeri* from Sossís are similar in size to those of specimen Q.H.442 and larger than those of Q.H.441 (lower canines are broken in both mandibles from Quercy). The P_4 from Sossís are notably larger than those from Quercy and, in general, have more developed metaconids, distal sides and cristids on the distal slope of the trigonid. Lower molars are, in general, larger in *M. hookeri* than in *N. antiquus* var. *major* from Quercy (Fig. 9). The morphology of these teeth can only be observed in specimen Q.H.442, because Q.H.441 is strongly worn. The overall morphology is similar, although the lower molars of *M. hookeri* from Sossís have more accentuated enamel wrinkling, and the M_1 and M_2 have a small but distinct hypoconulid that is absent in those of Q.H.442. Therefore, *M. hookeri* from Sossís

resembles, in general terms, the scarce material referred to *N. antiquus* var. *major*, although it also shows some differences. In any case, as we will explain with further details in the discussion, we do not consider this variety to represent a valid species.

Necrolemur zitteli Differences with the holotype and only known material of *N. zitteli*, a fragment of mandible with P₃–M₃ of uncertain provenance described by Schlosser (1888), are even more marked than with *N. antiquus*. *Necrolemur zitteli* is much smaller than *M. hookeri*, the enamel wrinkling is notably less accentuated and the hypoconulid lobe of the M₃ is distinctly shorter and narrower in *N. zitteli*.

Necrolemur anadoni The recently described species *N. anadoni* (Minwer-Barakat et al., 2015b) from Sant Jaume de Frontanyà-1 (Eastern Pyrenees), dated to the Middle Eocene (MP15, Bonilla-Salomón et al., 2016), is markedly different from *M. hookeri*. The main differences are the much smaller size, the less accentuated enamel wrinkling, the absence of hypoconulid in the M₁ and M₂, the presence of a very small paraconid in the M₂ and M₃, the narrower trigonid in the lower molars, the presence of a crest-shaped lingual metaconule (instead of a tubercular cusp) in the M¹ and M², and the shorter M³, without a distinct talon basin, in *N. anadoni*.

Results

Measurements of the teeth of *M. hookeri* from Sossís are shown in Table 3. Univariate statistics of the material from Sossís and the comparative sample are summarized in Table S1 (Supplementary Online Material). In the PCA of the M₁ and M₂ (Fig. 11, Table 4) the first

principal component (PC) explained 95.85 % of the variance, while the second PC explained 3.29 %. As the first PC explained more than 90 % of the variance and all its loadings had positive and high values, it can be interpreted as reflecting size (taking into account that all the considered variables were linear measurements). From negative to positive, the first component orders the species from smaller to larger. Considering the multivariate space defined by the first two PCs, all the analyzed groups (i.e., *N. antiquus*, *N. antiquus* var. *major*, *M. hookeri*, *M. cf. erinaceus* from Euzet and *M. erinaceus*) clustered separately from each other. The considered specimens of *M. hookeri* from Sossís formed a distinct group, intermediate in size between *N. antiquus* var. *major* from Quercy and *M. cf. erinaceus* from Euzet.

Regarding the cluster analyses, the three algorithms showed similar results (Fig. 12). It is worth noting that all specimens of *M. hookeri* clustered together in all cases. The analyses performed using UPGMA and Ward's method (Figs. 12A and 12B) showed three main groups: *N. antiquus*, *M. erinaceus*, and a third group integrated by *M. hookeri*, *M. cf. erinaceus* from Euzet and *N. antiquus* var. *major*. Within this last group, the most similar sample to *M. hookeri* is that represented by *M. cf. erinaceus* from Euzet, while *N. antiquus* var. *major* lies further away. In the analysis performed using the Single Linkage algorithm (Fig. 12C), the specimens of *M. erinaceus* from Hordle Cliff were split into two groups; however, this split does not affect the relationships of *M. hookeri* with the rest of the samples. The PERMANOVA analysis on the M^{1-2} length and width yielded significant results (Tables 5 and 6). Based on the pairwise comparisons after the sequential Bonferroni correction (Table 6), *M. hookeri* from Sossís was significantly different from all other samples with the exception of that from Eclépens B, which supports the assignation of this specimen to *M. hookeri*.

Discussion

Evolutionary trends in the Necrolemur antiquus–Microchoerus erinaceus lineage

The existence of a gradual lineage evolving from *N. antiquus* and finally leading to *M. erinaceus* has been proposed by previous authors, although intermediate stages between these two species have not been well established. Godinot (1983, 1985) described a continuous anagenetic lineage consisting of intermediate forms between *N. antiquus* and *M. erinaceus*, including, among others, those from Euzet, Perrière and also Sossís (based on the very small sample from this last locality that was known at the time). Nevertheless, this author referred to these forms first as "*Microchoerus* sp. A" (Godinot, 1983), and later as *M. cf. erinaceus* (Godinot, 1985), without providing a formal description of one or more new species corresponding to these intermediate stages of evolution.

Several morphological changes are observed in the lineage from *N. antiquus* to *M. erinaceus*, including an increase in the size of all the dental elements (Figs. 10, 11), progressive development of mesoconid and hypoconulid in the M_1 and M_2 , increasing length and differentiation of the hypoconulid lobe of the M_3 from the talonid, increase in size of hypocone, paraconule and metaconules in the M^1 and M^2 , occurrence and progressive enlargement of a mesostyle in these latter molars, as well as an expansion of the talon basin in the M^3 (see Table 7). Some of these changes are even observable (in their very earliest stages) in several populations of *N. antiquus*, such as the size of conules and hypocone in the upper molars, which are less developed in older (Le Bretou) than in younger samples (Lavergne, La Bouffie; see Minwer-Barakat et al., 2015b). This latter population, the richest one known of *Necrolemur*, shows a great range of morphological variability and includes some specimens similar in overall shape to those of *M. hookeri*. Despite this resemblance with some specimens of *Necrolemur*, the teeth of *M. hookeri* from Sossís are notably larger than those of *N.*

antiquus (Fig. 9) and show a distinctly more developed hypoconulid and an incipient mesoconid in the lower molars, a longer and wider hypoconulid lobe in the M_3 , larger conules and hypocone in the M^1 and M^2 and a longer M^3 (Table 7). The new species resembles *Necrolemur* in the absence of a mesostyle in most M^1 and M^2 , but the presence of this structure in some upper molars (Table 7) indicates that *M. hookeri* occupies an intermediate position in the lineage between *N. antiquus* and later populations with a more developed mesostyle, such as in those from Euzet and Perrière and, later, the species *M. erinaceus*. This sequence is also supported by the PCA results (Fig. 11).

The type sample of *M. erinaceus* from Hordle Cliff also shows a degree of variability (see Hooker, 1986), with some specimens showing less complex traits and thus resembling more primitive samples. For instance, the M_1 30338 displays a small hypoconulid and a cristid obliqua that is more inflated than in most specimens from Sossís, but without a distinct mesoconid; in any case, this specimen differs considerably from *M. hookeri* in the much larger size and the interrupted protocristid. This variability can also be seen in other tooth positions: the P^4 from Hordle Cliff with the same catalogue number (30338) is larger than those of *M. hookeri*, has a distinct hypocone, well-developed parastyle and metastyle (differing from the specimens from Sossís), but resembles the premolars of *M. hookeri* in the absence of hypostyle. In the same way, the M^1 of *M. erinaceus* M35038 notably differs from those of *M. hookeri* in the larger size and the presence of a strong mesostyle, but the latter is crest-shaped and less developed than in other specimens from Hordle Cliff. Moreover, the conules of this specimen from Hordle Cliff are notably stronger than in most upper molars of *M. hookeri*, but similar in size to those specimens with the largest paraconule and metaconules among the sample from Sossís. To sum up, the specimens with intermediate morphologies would support an anagenetic evolution from *M. hookeri* to *M. erinaceus*.

Taxonomic ascription of the samples of Microchoerus from Eclépens B and Euzet

The small sample from Eclépens B strongly resembles the population from Sossís in size (Figs. 9 and 10) and main morphological traits (shape of the premolars, size of the hypoconulid in the M_1 and M_2 , development of the conules in the M^1 and M^2 and, particularly, the lack of mesostyle in all the upper molars from this Swiss locality). In any case, there are some features that seem to indicate that the sample from Eclépens B is somewhat more advanced, occupying an intermediate position between those from Sossís and Hordle Cliff. More specifically, the molars of specimen Mt.1211 from Eclépens are wider than those from Sossís, the P^4 of this same specimen has a very small hypocone (this cusp is absent in all the specimens from Sossís, and well developed in *M. erinaceus*), and one out of two M_1 from Eclépens shows a small mesoconid (this cuspid is observed in a few specimens from Sossís, and is large or even doubled in *M. erinaceus*). Furthermore, the statistical analysis on the M^{1-2} measurements (Table 6) shows that there are not significant differences between the samples from Sossís and Eclépens B, supporting their ascription to the same species.

At this point, it is important to note that, for a long time, the presence of a mesostyle in the M^1 and M^2 was considered to be a diagnostic character of *Microchoerus*, useful for distinguishing this genus from *Necrolemur* (see Hooker, 1986, among others). Later, Hooker and Weidmann (2000) found some upper molars from Eclépens B with size and morphology corresponding to those of *Microchoerus*, but lacking a mesostyle; they ascribed these specimens to *M. aff. erinaceus* and we include them now in the new species *M. hookeri*. The material from Sossís, notably more abundant than the sample from Eclépens B, also includes large-sized upper molars, similar to those of *Microchoerus* in overall morphology, most of them lacking a mesostyle but, in some cases, showing a weak, crest-shaped mesostyle. This trait suggests a phylogenetic relationship of these samples with later populations, such as those from Euzet

and Perrière, with a more developed mesostyle. At the same time, it is clear that the presence or absence of a mesostyle is not a definitive criterion for distinguishing *Microchoerus* and *Necrolemur*, which are easily differentiated by a set of characters that also include overall size, the development of the hypoconulid and mesoconid in the lower molars, the shape of the hypoconulid lobe in the M₃, the size of the hypocone and conules in the upper molars, the distolingual expansion of the M³, and, in most but not all cases, the frequency of occurrence and size of the mesostyle (Table 7).

The sample from Euzet was considered by Godinot (1983) to correspond to the same evolutionary stage as represented at Sossís on the basis of the small sample from Sossís known at that time. However, we find some morphological differences between these two samples, such as the slightly more developed mesoconid and hypoconulid in the lower molars, the better individualized hypoconulid lobe in the M₃ and, particularly, the more frequent and more developed mesostyle in the upper molars from Euzet. These features indicate that the sample from Euzet occupies a somewhat more advanced position within this lineage than that from Sossís. The results of the PCA and cluster analyses (Figs. 11, 12) indicate that the sample from Euzet resembles *M. hookeri* from Sossís more than other species from the lineage, including *M. erinaceus*. However, these analyses only take into account linear measurements rather than qualitative morphological features. A definitive taxonomic ascription of the sample from Euzet must be done after the detailed study of this material, which remains mostly unpublished. Regarding the sample from Perrière, as already noted by Godinot (1983, 1985), it is larger (Fig. 10) and possesses more advanced features than those from Euzet and Sossís, resembling the morphology of *M. erinaceus*. Further analyses are needed to clarify the taxonomic determination of these and other French assemblages (Aubrelong 2, Salesmes, Fons 6): they are currently under study by M. Godinot.

Validity of the nomen "Necrolemur antiquus var. major"

Stehlin (1916) first proposed the variety *Necrolemur antiquus* var. *major* for some specimens of *N. antiquus* from the Quercy phosphorites that were somewhat larger than the rest.

Although this author did not give this group the status of species, Godinot (2003) claimed it as a valid species (i.e., *Necrolemur major*). We do not agree with this opinion. While it is generally accepted that a trend exists for larger size and morphological change from *N.*

antiquus to *M. erinaceus* (Fig. 10, Table 7), every population of *Necrolemur* and

Microchoerus contains some degree of intraspecific variability in size and morphology. The

material referred to *N. antiquus* var. *major* comes from undetermined levels of the Quercy phosphorites, a large area that includes many different fissures ranging in age from the early

Eocene to the early Miocene, although most of the well-dated levels fall between MP16 and MP26 (Legendre et al., 1997). In fact, Stehlin (1916) specifically stated that this material

came from different sites (Lamandine, Larnagol, Cajarc) of mostly unknown age and

stratigraphic position. Moreover, other specimens from some of these sites (e.g., Larnagol),

have been ascribed to *N. antiquus* and to *M. erinaceus*, thus suggesting a mixture of remains of different ages. It is therefore possible that the specimens grouped together by Stehlin under

the name *N. antiquus* var. *major* represent, in fact, the largest specimens of the samples of *N.*

antiquus from several levels, or, in other words, the largest extremes of the size spectrum of

various populations that lived at different times. If so, this taxon would have no biological

meaning. In fact, Godinot (2003) considered that the name *N. antiquus* var. *major*

corresponded to "the first part of a lineage showing an increase in size from the reference

level of Fons-6" (Godinot, 2003, p. 204). This statement would only be valid if it could be

demonstrated that the specimens ascribed to this variety come from the same level or from

sites equivalent in age, but this is not the case. Furthermore, some of the specimens of *N.*

antiquus var. *major* figured by Stehlin (1916) are not found in the collections of the NMB

(see comparisons section), including the single maxillary fragment, thus preventing any observation on the size and morphology of the upper dentition, which is essential for evaluating the state of some characters like the size of the conules and the presence/absence of a mesostyle. For all these reasons, we consider that the name *N. antiquus* var. *major*, originally used for the largest forms among the range of variability of *N. antiquus*, is not a valid nomen.

In any case, apart from several morphological differences (such as the less developed metaconid in the P₄, the less accentuated enamel wrinkling in the lower molars and the absence of hypoconulid in the M₁ and M₂ of *N. antiquus* var. *major*), the results of the PCA and cluster analyses (Figs. 11, 12) show that the specimens of *N. antiquus* var. *major* from Quercy do not cluster with those of *M. hookeri* from Sossís. These differences prevent the assignation of these few specimens from several localities of Quercy previously determined as *N. antiquus* var. *major* to the new species *M. hookeri*.

Other lineages: is Microchoerus monophyletic or paraphyletic?

In addition to the lineage leading from *N. antiquus* to *M. hookeri* and finally to *M. erinaceus* (with intermediate populations such as those from Euzet and Perrière), other lineages were present in Europe from, at least, MP16 (Fig. 13). The complex evolutionary scheme of this genus is documented not only by the relatively large number of species, but also by the presence of different forms coexisting in some levels, as is the case at Grisolles (Godinot, 1983), Creechbarrow (Hooker, 1986) and Eclépens B (Hooker and Weidmann, 2000). The existence of several lineages within this genus has already been proposed by Godinot (1983), who established the existence of two large groups (named "*erinaceus* group" and "*edwardsi* group"), each one including a number of lineages that suggested a complicated evolutionary

scenario, including, besides the already described species (*erinaceus*, *edwardsi*, *ornatus*), at least four unnamed forms (referred as "*Microchoerus* sp. A, B, C and D"). The relationships among these taxa and lineages are in most cases hypothetical and they remain unresolved.

Hooker (1986) established a much simpler evolutionary model with only two lineages, one of them including *M. wardorum* and its putative descendant *M. edwardsi* (with *M. ornatus* being considered a junior synonym of the latter) and the other one formed by *M. creechbarrowensis* and *M. erinaceus*. However, as stated by Hooker and Weidmann (2000) this model is, at least in part, refuted by the finding of two different forms of *Microchoerus* in Eclépens B (Fig. 13): one of them related to *M. creechbarrowensis*, small and showing a well-developed mesostyle, and the other one, ascribed by those authors to *M. aff. erinaceus*, which is virtually identical to the specimens from Sossís and therefore assigned to the new species *M. hookeri* (thus not supporting an ancestor-descendant relationship for *M. creechbarrowensis* and *M. erinaceus*).

In any case, it appears that an initial differentiation from *Necrolemur* appeared by at least the MP16 level, and that it involved the origin of relatively large forms with some derived characters, such as the well-developed mesostyle (Fig. 13). This first radiation would include, at least, the species from Creechbarrow (*M. wardorum* and *M. creechbarrowensis*) and the unnamed forms from Grisolles. The evaluation of the relations between these forms will be only possible after a detailed study of the still unpublished material from Grisolles and other French localities of similar age is completed. Nevertheless, a relationship between *M. wardorum* from Creechbarrow, *M. ornatus* from Mormont Entreroches (already proposed by Hooker, 1986), and *Microchoerus* from Ehrenstein seems very probable (Fig. 13), since all these forms share an unusual character, the double paracone in at least some upper molars, which may represent a synapomorphy.

The emergence of some forms larger than *Necrolemur* and with fully developed mesostyles in the Robiacian (MP16), and the later divergence of another line that independently acquired

the mesostyle during the Headonian (MP17), first represented by *M. hookeri* and finally leading to *M. erinaceus*, would mean that the genus *Microchoerus* is paraphyletic, an idea already expressed by Godinot (1983, 1985). This second, independent acquisition of the mesostyle is clear after the description of the material from Sossís, where most upper molars lack a mesostyle while some specimens display an incipient, crest-shaped one. As stated in previous works (Godinot, 1983, 1985), one or more new genera must be erected in order to preserve the monophyly of *Microchoerus*; those taxonomical descriptions must be made after the exhaustive study of the early forms derived from *Necrolemur* in the Robiacian, and are beyond the scope of the present work. In any case, as the type species of *Microchoerus* is *M. erinaceus*, the generic name must be preserved for the forms included in its lineage (including *M. hookeri*), and new names must be proposed for other genera if and when they are formally described. Moreover, the age of the fossil sites containing remains ascribed to *Microchoerus* must be revisited if we are to have an accurate chronostratigraphic framework in which all the records of this microchoerine can be situated precisely.

Our proposal is mainly in accordance with the opinion of former authors. On the one hand, the line deriving from *N. antiquus* and integrating *M. hookeri* from Sossís and Eclépens B, *M. cf. erinaceus* from Euzet and Perrière, and leading finally to *M. erinaceus* (Fig. 13) basically coincides with the "*Microchoerus* sp. A lineage" proposed by Godinot (1983). On the other hand, the proposed ancestor-descendant relationship between *M. creechbarrowensis* and *M. erinaceus* as originally suggested by Hooker (1986) was later reconsidered after a sample similar to *M. erinaceus* but still lacking the mesostyle (here ascribed to *M. hookeri*) was discovered at Eclépens B, alongside a different form, displaying a well-developed mesostyle and probably related to *M. creechbarrowensis* (Hooker and Weidmann, 2000).

To sum up, the existence of a continuous lineage differentiated from *N. antiquus* and giving rise to *M. erinaceus*, with smaller-sized forms showing simpler (more primitive)

morphologies and larger-sized populations displaying more complex (more derived) features, is demonstrated by the gradual increase in size and the change in some morphological traits in the populations from Sossís, Eclépins B, Euzet, Perrière and Hordle Cliff. These changes include, particularly, the frequency and development of the mesostyle, but also the size and number of mesoconids and hypoconulids in the M_1 and M_2 , the development of paraconule, metaconules, parastyle, metastyle, hypocone and hypostyle in the upper molars, and the elongation of M_3 and M^3 . This lineage differentiated from *N. antiquus* in the late Eocene, with its oldest known representative being *M. hookeri* from Sossís, while *N. antiquus* continued into the late Eocene (Fig. 13), as proved by samples with small size and lacking a mesostyle attributed to *N. antiquus* that were contemporaries of *M. cf. erinaceus* from several fossil sites (Godinot, 1985; Hooker and Weidmann, 2000).

Conclusions

The *Microchoerus* material from Sossís (late Eocene) represents the most abundant sample of this genus from the Iberian Peninsula and is described for the first time. This material shows clear differences with *M. erinaceus* from Hordle Cliff, contrary to the opinion of several authors (Crusafont-Pairó, 1965, 1967; Antunes et al., 1997; Casanovas-Cladellas, 1998; Marigó et al., 2014). The sample from Sossís can also be clearly distinguished from all the other described species of the genera *Microchoerus* and *Necrolemur* (including *M. edwardsi*, *M. ornatus*, *M. wardorum*, *M. creechbarrowensis*, *N. antiquus*, *N. zitteli* and *N. anadoni*), therefore allowing the description of a new species, *M. hookeri*.

Microchoerus hookeri is characterized by its medium size, the absence of a mesoconid in almost all lower molars, the small and generally single hypoconulid in the M_1 and M_2 , the single paracone and the lack of hypocone in the P^3 and P^4 , and the well-developed hypocone,

paraconule and metaconules in the M¹ and M². One of the most distinctive features of the new species is the lack of a mesostyle in most M¹ and M² (or the presence of a very weak and crest-shaped mesostyle in few specimens), which distinguishes *M. hookeri* from all previously described species of *Microchoerus*.

The material from Eclépens B, formerly assigned to *M. aff. erinaceus* by Hooker and Weidmann (2000), shows a strong resemblance to the sample from Sossís. On the basis of this similarity and the support of the statistical analyses, we ascribe the material from that Swiss locality to the species *M. hookeri*, suggesting that the new species had a wide geographical range, that extended from the Iberian Peninsula to Central Europe.

The species *M. hookeri* was part of a lineage that diverged from *N. antiquus* and led to *M. erinaceus*, with some intermediate stages represented by samples such as those from Euzet and Perrière (referred to *M. cf. erinaceus* after Godinot, 1985), that were more derived than *M. hookeri* from Sossís, but did not reach the size and morphological complexity of *M. erinaceus*. In this lineage, the acquisition and progressive development of a mesostyle in the M¹⁻² is evidenced from *N. antiquus* (without any sign of mesostyle) to *M. hookeri* (mesostyle absent in most specimens and present but very weak in some molars), *M. cf. erinaceus* (frequent and generally large mesostyle) and *M. erinaceus* (mesostyle always present and very large).

The existence of several samples from older localities (such as Creechbarrow and Grisolles) with relatively large size and a well-developed mesostyle implies a different, earlier divergence from *Necrolemur* and the independent acquisition of the mesostyle. Therefore, the genus *Microchoerus*, as currently construed, would be paraphyletic. An exhaustive description of the still unpublished material from several French localities (including Grisolles, Perrière, Malpérié, Robiac, and Fons), which will probably lead to the erection of some new species, is

therefore necessary to clarify the phylogenetic relationships among this rather diverse microchoerine group.

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Figure captions

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 Entreroches); 9: Euzet; 10: Quercy phosphorites (including many Eocene important sites such as Le Bretou, Lavergne, La Bouffie, Perrière and Malpérié).

Figure 2. Environmental Scanning Electron Microscope images of the lower incisors, canines and premolars of *M. hookeri* nov. sp. from Sossís. A–C: left I₁ (IPS61962) in mesial (A), posterior (B), and apical (C) views; D–F: left I₁ (IPS61963) in mesial (D), posterior (E), and apical (F) views; G–H: right I₁ (IPS61967) in mesial view (G corresponds to an enlarged image of H, showing the marks attributed to fur grooming); I–J: left C₁ (IPS61970) in occlusal (I) and lingual (J) views; K–L: right C₁ (IPS61972) in occlusal (K) and lingual (L) views; M–N: right P₃ (IPS61976) in occlusal (M) and buccal (N) views; O–P: right P₃ (IPS61977) in occlusal (O) and buccal (P) views; Q–R: left P₄ (IPS4296) in occlusal (Q) and buccal (R) views; S–T: right P₄ (IPS61980) in occlusal (S) and buccal (T) views. Scale bar for G represents 500 µm. Scale bar for the rest of the images represents 3 mm.

Figure 3. Environmental Scanning Electron Microscope images of several mandibles of *M. hookeri* nov. sp. from Sossís. A–B: left mandible fragment with M₁–M₃ (IPS4330) in occlusal (A) and buccal (B) views; C–D: left mandible fragment with M₂–M₃ (NMB Sos.1) in occlusal (C) and buccal (D) views; E: right mandible fragment with P₃–M₁ and M₃ (IPS62074) in occlusal view. Scale bar represents 3 mm.

Figure 4. Environmental Scanning Electron Microscope images of the lower molars of *M. hookeri* nov. sp. from Sossís. A–B: left M₁ (IPS61985) in occlusal (A) and buccal (B) views;

C–D: left M_1 (IPS61986) in occlusal (C) and buccal (D) views; E–F: left M_1 (IPS61987) in occlusal (E) and buccal (F) views; G–H: left M_2 (IPS61992) in occlusal (G) and buccal (H) views; I–J: right M_2 (IPS61994) in occlusal (I) and buccal (J) views; K–L: right M_2 (IPS61995) in occlusal (K) and buccal (L) views; M–N: right M_3 (IPS61999) in occlusal (M) and buccal (N) views; O–P: right M_3 (IPS62000) in occlusal (O) and buccal (P) views. Scale bar represents 3 mm.

Figure 5. Environmental Scanning Electron Microscope images of the upper canines and premolars of *M. hookeri* nov. sp. from Sossís. A–B: maxillary fragment with right C^1 – P^3 (IPS61960) in occlusal (A) and buccal (B) views; C–D: left C^1 (IPS62018) in occlusal (C) and buccal (D) views; E–F: right C^1 (IPS62020) in occlusal (E) and buccal (F) views; G–H: left P^2 (IPS62024) in occlusal (G) and buccal (H) views; I–J: right P^2 (IPS62026) in occlusal (I) and buccal (J) views; K–L: left P^3 (IPS62029) in occlusal (K) and buccal (L) views; M–N: right P^3 (IPS62033) in occlusal (M) and buccal (N) views; O–P: left P^4 (IPS62038) in occlusal (O) and buccal (P) views; Q–R: left P^4 (IPS62039) in occlusal (Q) and buccal (R) views; S–T: left P^4 (IPS62040) in occlusal (S) and buccal (T) views. Scale bar represents 3 mm.

Figure 6. Environmental Scanning Electron Microscope images of the upper premolars and molars of *M. hookeri* nov. sp. from Sossís. A–B: right maxillary fragment with right M^1 and M^2 (IPS62073, holotype) in occlusal (A) and buccal (B) views; C–H: right dental series with M^1 – M^3 (NMB Sos.11); C–D: M^3 in occlusal (C) and buccal (D) views; E–F: M^2 in occlusal (E) and buccal (F) views; G–H: M^1 in occlusal (G) and buccal (H) views; I–J: right maxillary fragment with P^4 – M^2 (IPS2538) in occlusal (I) and buccal (J) views; K–L: left maxillary fragment with M^1 – M^3 (IPS2545) in occlusal (K) and buccal (L) views. Scale bar represents 3 mm.

Figure 7. Environmental Scanning Electron Microscope images of the upper molars of *M. hookeri* nov. sp. from Sossís. A–B: left M^{1-2} (IPS62045) in occlusal (A) and buccal (B) views; C–D: left M^{1-2} (IPS62048) in occlusal (C) and buccal (D) views; E–F: left M^{1-2} (NMB Sos.2) in occlusal (E) and buccal (F) views; G–H: right M^{1-2} (IPS62055) in occlusal (G) and buccal (H) views; I–J: right M^{1-2} (IPS62056) in occlusal (I) and buccal (J) views; K–L: right M^{1-2} (IPS62057) in occlusal (K) and buccal (L) views; M–N: left M^3 (IPS62065) in occlusal (M) and buccal (N) views; O–P: left M^3 (IPS62067) in occlusal (O) and buccal (P) views; Q–R: right M^3 (IPS62071) in occlusal (Q) and buccal (R) views; S–T: right M^3 (IPS62070) in occlusal (S) and buccal (T) views; U–V: right M^3 (IPS62068) in occlusal (U) and buccal (V) views. Scale bar represents 3 mm.

Figure 8. Environmental Scanning Electron Microscope images of the upper teeth of *M. hookeri* nov. sp. from Eclépens B. A–B: left P^3 (Mt.1215) in occlusal (A) and buccal (B) views; C–D: left M^{1-2} (Mt.1216) in occlusal (C) and buccal (D) views; E–F: right M^{1-2} (Mt.1213) in occlusal (E) and buccal (F) views; G–H: right maxillary fragment with M^1 – M^3 (Mt.1212) in occlusal (G) and buccal (H) views. Scale bar represents 3 mm.

Figure 9. Length $\times$ width (in mm) of the M_1 , M_2 , M_3 , P^4 , M^{1-2} and M^3 of *N. antiquus* and all the described species of *Microchoerus*. Measurements of *M. hookeri* from Sossís are those presented in this work. Measurements of *N. antiquus* var. *major* were taken directly from two specimens from Quercy curated at the Naturhistorisches Museum Basel (Q.H.441 and Q.H.442). Measurements of *M. edwardsi* and *M. ornatus* were taken directly from a high-quality cast of the holotypes. Data on *N. antiquus* from La Bouffie after Godinot (1983); data on *M. hookeri* from Eclépens B after Hooker and Weidmann (2000); data on *M. erinaceus* after Cray (1973); data on *M. wardorum* and *M. creechbarrowensis* after Hooker (1986).

Figure 10. Length and width ranges (in mm) of the upper and lower molars of several samples of *N. antiquus*, *M. hookeri*, *M. cf. erinaceus* and *M. erinaceus*. Mean values are indicated by vertical lines in each horizontal bar. Measurements of *M. hookeri* from Sossís are those presented in this work; data on *N. antiquus* from La Bouffie, *M. cf. erinaceus* from Euzet and Perrière after Godinot (1983); data on *M. hookeri* from Eclépens B after Hooker and Weidmann (2000); data on *M. erinaceus* after Cray (1973).

Figure 11. Space delimited by the two principal axis of the PCA; analysis includes the mandibles preserving M₁ and M₂ of *M. hookeri* from Sossís, *N. antiquus* from La Bouffie, *N. antiquus* var. *major* from Quercy, *M. erinaceus* from Hordle Cliff and *M. cf. erinaceus* from Euzet. Convex hulls show the smallest convex polygon containing all points.

Figure 12. Dendograms for the clusters developed using length and width of M₁ and M₂. Only those groups that have specimens preserving both teeth were included in the analyses. Numbers on the branches represent the percentage of replicates where each node is still supported. A: Cluster using UPGMA algorithm. B: Cluster using Ward's method. C: Cluster using Single Linkage.

Figure 13. Proposed phylogenetic relationships between the different species ascribed to the genera *Necrolemur* and *Microchoerus*. Fossil localities are referred to the corresponding Mammal Paleogene Units (MP) and European Land Mammal Ages (ELMAs). Dotted lines indicate tentative relationships. Circled numbers from 1 to 14 indicate the appearance of some significant morphological traits. Convergences (i.e., characters that appear independently in several lineages) are indicated by grey circles.

Table 1

Table 1. Mammal faunal list of Sossís, after Sigé (1997), Casanovas-Cladellas (1998), Cuesta Ruiz-Colmenares et al. (2006), Marigó et al. (2013) and this paper.

MARSUPIALIA	ARTIODACTYLA
<i>Peratherium lavergnense</i>	<i>Cebochoerus helveticus</i>
<i>Peratherium perriense</i>	<i>Acotherulum</i> sp.
CIMOLESTA	<i>Dacrytherium ovinum</i>
<i>Heterohyus nanus</i>	<i>Leptotheridium lugeoni</i>
Apatemyidae indet.	<i>Haplomeryx euzetensis</i>
LIPOTYPHILA	<i>Xiphodon intermedium</i>
<i>Leptictis</i> sp.	RODENTIA
<i>Saturninia pirenaica</i>	<i>Treposciurus mutabilis</i>
<i>Euronyctia montana</i>	<i>Estellomys ibericus</i>
CARNIVORA	<i>Paradelomys crusafonti</i>
<i>Miacis exilis</i>	<i>Theridomys euzetensis</i>
CREODONTA	<i>Pseudoltinomys</i> cf. <i>phosphoricus</i>
<i>Hyaenodon minor</i>	<i>Elfomys parvulus</i>
PERISSODACTYLA	<i>Gliravus robiaciensis</i>
<i>Palaeotherium magnum stehlini</i>	PRIMATES

Palaeotherium medium euzetense

Adapis cf. parisiensis

Palaeotherium crassum sossisenses

Nievesia sossisensis

Plagiolophus annectens

Pseudoloris parvulus

Anchilophus dumasi

Microchoerus hookeri

Table 2. Detailed list of the studied material of *M. hookeri* from Sossís and Ecléps B and comparative sample, including all the described species of *Microchoerus* and *Necrolemur*, as well as some samples of *Microchoerus* without a definitive specific determination. Institutional abbreviations: ICP: Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain; NMB: Naturhistorisches Museum Basel, Switzerland; NHM: Natural History Museum, London, United Kingdom; MNHN: Muséum National d'Histoire Naturelle, Paris, France; BSPGM: Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; FSL: Faculté des Sciences de Lyon, France; ISEM: Institut des Sciences de l'Évolution-Université de Montpellier, France; MCNA: Museo de Ciencias Naturales de Álava, Spain.

Species	Locality	Specimens	Repository	Studied material	References
<i>Microchoerus hookeri</i>	Sossís	Maxilla with M ¹ –M ² ; maxilla with right C ¹ –P ³ and left P ³ –M ¹ ; maxilla with P ⁴ –M ² ; maxilla with M ¹ –M ³ ; dental series with M ¹ –M ³ ; mandible with C ₁ –M ₃ ; mandible with P ₃ –M ₁ ; mandible with P ₃ –M ₁ and M ₃ ; two mandibles with M ₁ –M ₃ ; mandible with M ₂ –M ₃ ; dental series with C ₁ –M ₃ ; dental series with P ₃ –M ₃ ; 119 isolated teeth including nine I ₁ , six C ₁ , five P ₃ , 11 P ₄ , eight M ₁ , six M ₂ , two fragments of M ₁ or M ₂ , three M ₃ , nine C ¹ , seven left P ² , 10 P ³ , nine P ⁴ , 24 M ¹⁻² and 10 M ³	ICP; NMB	Original material	This work
<i>Microchoerus hookeri</i>	Ecléps B	Maxilla with P ² –M ³ ; maxilla with M ¹ –M ³ ; nine isolated teeth	NMB	Original material	Hooker and Weidmann (2000); this work
<i>Microchoerus erinaceus</i>	Hordle Cliff	Palatal fragment with upper dentition (lacking the left C ¹ and right I ²); about	NHM	Original material	Cray (1973); Hooker (1986)

		100 specimens including mandibles, maxillae and isolated teeth			
<i>Microchoerus edwardsi</i>	Quercy phosphorites	Mandible with C ₁ –M ₃	MNHN	Original material	Filhol (1880)
" <i>Microchoerus edwardsi</i> "	La Débruge	Maxilla with P ⁴ –M ³	NHM	Original material	Hooker (1986)
" <i>Microchoerus edwardsi</i> "	Ehrenstein	Mandible with M ₁ –M ₃ ; 59 isolated teeth	BSPGM	Casts	Schmidt-Kittler (1971, 1977)
<i>Microchoerus ornatus</i>	Mormont Entreroches	Maxilla with P ² –M ³	NMB	Original material	Stehlin (1916)
<i>Microchoerus wardorum</i>	Creechbarrow	24 isolated teeth	NHM	Original material	Hooker (1986)
<i>Microchoerus creechbarrowensis</i>	Creechbarrow	17 isolated teeth	NHM	Original material	Hooker (1986)
<i>Microchoerus</i> aff. <i>creechbarrowensis</i>	Eclépens B	Maxillae with P ⁴ –M ² , P ⁴ –M ¹ , and M ² – M ³ ; mandibles with P ₃ –M ₃ , P ₄ –M ₃ , P ₃ – M ₁ ; two mandibles with M ₂ –M ₃ ; 6 isolated teeth	NMB	Original material	Hooker and Weidmann (2000)
<i>Microchoerus</i> cf. <i>erinaceus</i>	Euzet	Mandibles with C ₁ –M ₃ and P ₄ –M ₂ ; maxilla with P ⁴ –M ³ ; isolated M ₃ and M ¹⁻²	NMB; FSL	Original material and casts	Depéret (1917); Hürzeler (1948); Godinot (1985)
<i>Microchoerus</i> cf. <i>erinaceus</i>	Perrière	Cranium with C ¹ –M ³ ; maxilla with C ¹ – M ³ ; two mandibles with P ₃ –M ₃ and M ₁ –M ₂ ; 10 isolated teeth	ISEM	Original material	Godinot (1983, 1985)
<i>Microchoerus</i> aff. <i>erinaceus</i>	Zambrana	Two mandibles with P ₃ –M ₃ and P ₄ –M ₃	MCNA	Original material	Minwer-Barakat et al. (2013a)
<i>Microchoerus</i> sp. B	Grisolles	Five mandibles with several teeth; more than 90 isolated teeth	ISEM	Original material	Godinot (1983)
<i>Microchoerus</i> sp. C	Grisolles	38 isolated teeth	ISEM	Original material	Godinot (1983)
<i>Necrolemur antiquus</i>	Quercy	Skull with P ² –M ³ ; mandible with C ₁ –M ₃	MNHN	Casts	Filhol (1873)

<i>Necrolemur antiquus</i>	La Bouffie	21 mandibles and 10 maxillae bearing several teeth; more than 550 isolated teeth	ISEM	Original material	Godinot (2003)
<i>Necrolemur antiquus</i>	Le Bretou	11 isolated teeth	ISEM	Original material	Godinot (1983, 1985)
<i>Necrolemur antiquus</i>	Lavergne	Six mandibles bearing several teeth; 12 isolated teeth	ISEM	Original material	Godinot (1983, 1985)
<i>Necrolemur antiquus</i> var. <i>major</i>	Quercy phosphorites	Two mandibles with I ₁ –M ₃	NMB	Original material	Stehlin (1916)
<i>Necrolemur zitteli</i>	Uncertain provenance	Mandible with P ₃ –M ₃	BSPGM	Casts	Schlosser (1888)
<i>Necrolemur anadoni</i>	Sant Jaume de Frontanyà- 1 and 2	Mandible with P ₄ –M ₃ ; 15 isolated teeth	ICP	Original material	Minwer-Barakat et al. (2015b)

Table 3. Measurements (in mm) of the teeth of *M. hookeri* nov. sp. from Sossís. Abbreviations: L': length perpendicular to the root axis; H': height parallel to the root axis.

Table 4. Loadings for each variable in the Principal Component Analysis of the M₁ and M₂ length and width of *N. antiquus*, *N. antiquus* var. *major*, *M. hookeri*, *M. cf. erinaceus* from Euzet and *M. erinaceus*.

	PC1	PC2	PC3	PC4
M ₁ length	0.5192	-0.40697	0.737	0.14711
M ₁ width	0.45097	0.61238	0.14672	-0.63252
M ₂ length	0.5858	-0.46895	-0.63498	-0.18365
M ₂ width	0.42883	0.48933	-0.17919	0.73794

Table 5. PERMANOVA statistics of the analysis on the M¹⁻² of *N. antiquus*, *M. wardorum*, *M. hookeri* from Sossís, *M. hookeri* from Eclépens B and *M. erinaceus*.

Total sum of squares	60.12
Within-group sum of squares	5.699
F	267.4
<i>p</i> -value	0.0001
Total sum of squares	60.12

Table 6. Pairwise comparisons of the PERMANOVA analysis on the M¹⁻² of *N. antiquus*, *M. wardorum*, *M. hookeri* from Sossís, *M. hookeri* from Eclépens B and *M. erinaceus*.^a

	<i>Microchoerus</i> <i>erinaceus</i>	<i>Microchoerus</i> <i>hookeri</i> Sossís	<i>Microchoerus</i> <i>hookeri</i> Eclépens B	<i>Microchoerus</i> <i>wardorum</i>	<i>Necrolemur</i> <i>antiquus</i>
<i>Microchoerus erinaceus</i>		0.0001	0.0003	0.0009	0.0001
<i>Microchoerus hookeri</i> Sossís	0.0001		0.667	0.0015	0.0001
<i>Microchoerus hookeri</i> Eclépens B	0.0003	0.667		0.0168	0.0001
<i>Microchoerus wardorum</i>	0.0009	0.0015	0.0168		0.0003
<i>Necrolemur antiquus</i>	0.0001	0.0001	0.0001	0.0003	

^a Raw *p*-values are presented in the table. *p*-values in bold are not significant after sequential Bonferroni correction.

Table 7

Table 7. Character states of different morphological traits in the teeth of the microchoerine species *Nannopithecus filholi*, *N. anadoni*, *N. antiquus*, *M. hookeri* and *M. erinaceus*.

	<i>Nannopithecus filholi</i>	<i>Necrolemur andadoni</i>	<i>Necrolemur antiquus</i>	<i>Microchoerus hookeri</i>	<i>Microchoerus erinaceus</i>
M ₁ and M ₂ hypoconulid	Absent	Absent	Sometimes present, small	Small and single, rarely double (<5%)	Large, single or double
M ₁ and M ₂ mesoconid	Absent	Absent	Absent	Generally absent (<25%)	Present, single or double
M ₂ and M ₃ paraconid	Often well separated from the metaconid	Very small and attached to the metaconid	Generally absent	Absent	Absent
M ₂ and M ₃ trigonid	Very narrow	Narrower than the talonid	Relatively wide	Relatively wide	Relatively wide
P ³ and P ⁴ hypocone	Absent	Absent	Absent	Absent	Present
M ¹⁻² hypocone size	Small	Large	Large	Very large	Very large
M ¹⁻² protocone-hypocone connection	Absent	Weak	Usually strong	Strong	Strong
M ¹⁻² metaconule (single or double)	Single	Double	Double	Double	Double
Shape of the lingual metaconule in M ¹⁻²	-	Crest-shaped	Tubercular	Tubercular	Tubercular
M ¹⁻² mesostyle	Absent	Absent	Absent	Generally absent (<25%)	Always present
M ¹⁻² mesostyle (size and shape)	-	-	-	Weak, crest-shaped	Strong, generally tubercular
M ¹⁻² hypostyle	Absent	Absent	Absent	Absent	Present
M ³ shape	Very short, without	Short, without	Slightly enlarged	Enlarged	Very enlarged

	distinct talon basin	distinct talon basin	distolingually, with a distinct talon basin	distolingually, with a well-defined talon basin	distolingually, with a broad talon basin
Enamel wrinkling in molars and premolars	Very weak	Weak	Moderate to complex	Complex	Very complex

Figure 1

Figure 2

Figure 3

A

C

B

D

E

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9

Figure 10

Figure 11

Figure 12

- *Microchoerus hookeri*
- *Microchoerus erinaceus*
- *Necrolemur antiquus*
- *Necrolemur antiquus* var. *major*
- *Microchoerus* cf. *erinaceus* from Euzet

A

B

C

ELMA	Mammal Paleogene Unit	Locality	
Headonian	MP19	Mormont Entreroches	
	MP18	Ehrenstein	
	MP17	Hordle Cliff	
		Perrière	
		Euzet	
		Eclépens B	
		Sossis	
		La Bouffie	
	Robiacian	MP16	Creechbarrow
		MP15	Le Bretou
Sant Jaume de Frontanyà-1			
MP14		Lissieu	
Gelseltian	MP13	Egerkingen y	
		Bouxwiller	

Phylogenetic tree showing relationships between various species across different geological units and localities. The tree is rooted at the bottom with *Nannopithecus filholi* and branches upwards. Species names are in boxes. Characters are marked with numbers 1-14 on the branches. The tree shows a clear lineage from *Nannopithecus filholi* to *Necrolemur antiquus* and *Microchoerus* species. The *Microchoerus* lineage includes *Microchoerus hookeri*, *Microchoerus cf. erinaceus*, *Microchoerus erinaceus*, *Microchoerus cf. creechbarrowensis*, *Microchoerus creechbarrowensis*, *Microchoerus wardorum*, *Microchoerus edwardsi*, and *Microchoerus ornatus*.

① Hypocone-protocone connection	⑤ Single mesoconid in some lower molars.	⑨ Hypocone in the P ⁴
② Double metaconule	⑥ Weak mesostyle in some M ¹⁻² (< 25%)	⑩ Hypocone in the P ³
③ Loss of the paraconid in M ₁ and M ₂	⑦ Strong mesostyle in all M ¹⁻²	⑪ Double paracone in upper molars
④ Tubercular-shaped lingual metaconule	⑧ Double mesoconid in some lower molars	⑫ Double paracone in the P ⁴
		⑬ Double paracone in the P ³
		⑭ Pericone in the M ¹