



The earliest primates from the Iberian Peninsula: 60 years of research

Judit Marigó^{1,2} · Oriol Monclús-Gonzalo² · Joan Femenias-Gual^{2,3,4} · Raef Minwer-Barakat^{2,5}

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Abstract

New findings of Paleogene primates in Spain have occurred during the last decade, including the discovery of new fossil-bearing levels as well as the description and erection of new taxa. This research line has a long tradition in Spain thanks to paleontologists like Crusafont and, more especially, Moyà-Solà, who have led research on these primates as well as other mammals for decades. A warm climate and the presence of tropical forests at high latitudes during the Eocene have provided us with the highest diversity of Iberian primates during the Eocene, thus reflecting the radiation of both adapiforms and omomyiforms. In contrast, only a single plesiadapiform genus has been recorded in the Iberian Peninsula. Near the Eocene–Oligocene boundary, paleoclimatic changes led to a primate diversity crisis and other faunal changes, although two Iberian omomyiforms survived the Grande Coupure. The paleodiversity of Paleogene fossil primates keeps increasing thanks to the field campaigns organized annually by our team, devoted to the recovery of new levels and study of new taxa. Moreover, already known taxa are further studied thanks to the recovery and identification of not only dental but also postcranial remains that have provided insights into the locomotor repertoire of these taxa. In addition, traditional locomotor studies have been refined thanks to the use of 3D geometric morphometric techniques combined with evolutionary modelling. This has provided new insights into the evolutionary history of the group and the evolution of their locomotor repertoires at the dawn of the primate family tree.

Keywords Adapiforms · Diversity · Locomotion · Omomyiforms · Plesiadapiforms · 3D geometric morphometrics

Introduction

At the beginning of the Cenozoic, after the catastrophic event that led to the extinction of non-avian dinosaurs at the Cretaceous–Paleogene (K/Pg) boundary at 66 Ma, an adaptive radiation gave rise to modern orders of mammals. Among them, the first primates appear in the fossil record during the Paleocene. These primates are represented by the extinct group Plesiadapiformes or primates *sensu lato*, generally characterized by a prominent snout, small brain, no postorbital bar, claws in all digits, large incisors, and a diastema (Fleagle 2013).

The beginning of the Eocene was marked by the Paleocene–Eocene Thermal Maximum (PETM), which allowed the proliferation of tropical forests in high latitudes. These ecological changes favored the diversification of the Euprimates or primates of modern aspect, which share several synapomorphies such as a petrosal bulla, stereoscopic vision, a postorbital bar, opposable thumbs and big toes, and nails on most digits, among other traits (Cartmill 2018). Since the very beginning, euprimates experienced an

✉ Judit Marigó
Judit.marigo@uab.cat

¹ Departament de Geologia, Universitat Autònoma de Barcelona, Cerdanyola del Vallès (Barcelona), Spain

² Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n, 08193 Cerdanyola del Vallès (Barcelona), Spain

³ PostDoc (Margalida Comas), Departament de Biodiversitat Animal i Microbiana, Institut Mediterrani d'Estudis Avançats (UIB-CSIC), Maria de Maeztu Center of Excellence, Miquel Marqués 21, 07190 Esporles, Mallorca, Spain

⁴ Grup de Recerca de Ciències de la Terra, Departament de Biologia, Universitat de les Illes Balears, 07122 Palma, Mallorca, Spain

⁵ Departamento de Estratigrafía y Paleontología, Universidad de Granada, Avda. Fuente Nueva S/N, 18071 Granada, Spain

important radiation and split into two well-defined suborders, the strepsirrhines, represented initially by adapiforms, and the haplorrhines, represented by omomyiforms and early anthropoids (the latter scarce and restricted to Asia and Africa). Adapiforms are usually larger than omomyiforms, with a longer snout and smaller eyes. Adapiforms generally have small incisors and large canines, whereas omomyiforms generally have large incisors and small canines (Fleagle 2013; Silcox et al. 2017; Silcox and López-Torres 2023).

The Eocene–Oligocene boundary was marked by a global cooling event and a subsequent faunal renewal known as the "Grande Coupure" that led to the extinction of a large number of Eocene mammals (Prothero 1994; Hooker et al. 2004). Primates nearly disappeared from Europe after this event, with the exception of two records of omomyiforms in the Iberian Peninsula (Köhler and Moyà-Solà 1999; Peláez-Campomanes 2000).

The study of these groups of Paleogene primates from the Iberian Peninsula has a long tradition, with three well-differentiated stages: the first during the 1960s, the second in the 1990s, and the third from 2010 onwards. The first stage, which started in the 1960s, includes the studies led by members of the "Institut de Paleontologia de Sabadell" (former "Institut Català de Paleontologia Miquel Crusafont", ICP). At that time, Miquel Crusafont described the first Paleogene primates from the locality of Sossís (Crusafont-Pairó 1965) and helped to characterize the continental fossil bearing levels of Àger (Crusafont-Pairó and Rosell Sanuy 1966). At the same time, different localities with fossil primate remains were discovered (Crusafont-Pairó 1965, 1967, 1973; Crusafont Pairó and Golpe Posse 1968, 1974). These first studies developed by Crusafont and collaborators involved the definition of several genera and species including *Agerina roselli*, *Arisella capellae*, *Pivetonia isabena* and *Pseudoloris reguanti*, although some of these taxa were later transferred to other genera (see Marigó et al. 2014 for details). Shortly after, in the PhD dissertation of Lourdes Casanovas-Cladellas, some remains attributed to primates such as *Adapis magnus* and *Necrolemur antiquus* were also described from the late Eocene locality of Roc de Santa (Casanovas-Cladellas 1975). Little progress was achieved during the 1980s, except for the discovery of the fossiliferous levels from the locality of Pontils, which yielded foraminifera and rodents (Anadón et al. 1983), plant remains including charophytes (Anadón and Feist 1981) and pollen (Cavagnetto and Anadón 1995, 1996). These works mentioned other vertebrate remains, including primates and eulipotyphlans, which were not described in detail.

The second stage, starting in the 1990s, was led by Salvador Moyà-Solà and collaborators, who discovered other relevant Paleogene sites with primate remains. Specifically,

they preliminarily described three primate taxa from the middle Eocene locality of Sant Jaume de Frontanyà in the southern Pyrenean basins (Moyà-Solà and Köhler 1993), and described *Pseudoloris godinoti* from the early Oligocene of Fonollosa and Santpedor in the Ebro Basin, one of the few findings of omomyiforms in Europe after the "Grande Coupure" (Köhler and Moyà-Solà 1999). At that time, more primate fossils were documented from the Duero Basin in localities like Santa Clara, Caenes, Mazaterón and Miñana (Moyà-Solà and Köhler 1992). During that same decade, a synthetic work that included all the localities with Paleogene mammal remains from the Iberian Peninsula was published, including faunal lists and ages of each of the fossil sites (Antunes et al. 1997). Other research groups also published about different levels in the Tremp area discovered during the 1990s and dated as Ilerdian (late Paleocene-early Eocene) yielding mammal and bird remains (López-Martínez et al. 1996, 2006; López-Martínez and Peláez-Campomanes 1998; Peláez-Campomanes et al. 2000), as well as foraminifera (López-Martínez and Peláez-Campomanes 1999). In addition, Peláez-Campomanes (2000) reported a single lower molar of *Microchoerus* sp. in the earliest Oligocene site of Aguatón (Sierra Palomera, Teruel province), which represents the other primate that survived the Eocene–Oligocene climatic deterioration, together with *P. godinoti*.

At the end of the 1990s, the primate remains from the early Eocene site of Silveirinha (Portugal, Mondego Basin) were described by Estravís (2000). This locality is the only one in Portugal that has yielded Paleogene primate remains, including the plesiadapiform *Arcius zbyzewskii*, the adapiform *Donrussellia lusitanica*, and another adapiform attributed to the family Notharctidae that was unassigned to genus.

From 2008 onwards, the third stage began, although publications were not available until 2010. At that time, new members of the ICP restarted the research line on Paleogene primates with the aim of studying the historical specimens already available in the collection as well as the sampling of new levels in Catalan basins that could potentially yield new primate remains. This stage has brought the knowledge of Eocene primates from Spain a significant step forward, including not only a high number of publications but also a huge amount of Paleogene levels sampled during annual fieldwork campaigns in the Ebro and Pyrenean basins, an enormous effort that has resulted in a large amount of fossils recovered, including primate and other vertebrate remains, many of them still awaiting for a detailed study.

The first published results of this last stage included the description of the new primate species, *Anchomomys frontanyensis* and *Pseudoloris pyrenaicus* from the Robiacian locality of Sant Jaume de Frontanyà (Marigó et al. 2011;

Minwer-Barakat et al. 2010). The study of the similarly-aged primate remains from Mazaterón in the Almazán Basin also resulted in the erection of two new species, *Mazateronodon endemicus* and *Pseudoloris cuestai* (Marigó et al. 2010; Minwer-Barakat et al. 2012).

In 2014 our team published a paper that updated all taxonomic attributions of Iberian primate remains up to that point (Marigó et al. 2014). This work was accepted in 2013 and therefore did not include some results achieved later in 2013. The discovery of new primate fossils and revisions of previously-described specimens since then has significantly improved the knowledge of Eocene primates from the Iberian Peninsula. The aim of this study is to provide updated information about new discoveries since late 2013 and new inferences about the locomotor repertoire of primates whose postcranial remains have been studied in recent years. The latter include functional morphology studies using 3D geometric morphometrics, with insights into the modifications on the tarsus that occurred at the dawn of euprimates (Monclús-Gonzalo et al. 2023, 2025a). In the next section, we summarize the main advances achieved in the study of Paleogene primates from Spain from late 2013 to 2025, including not only the description of newly recovered material, but also the revision of previously studied fossils, which sometimes has involved new taxonomic allocations. These results are presented following the classic format of a Systematic Paleontology work.

Abbreviations: ICP, Institut Català de Paleontologia Miquel Crusafont; **M/m**, Upper/lower molar; **MP**, Mammal Paleogene reference level; **NMB**, Naturhistorisches Museum Basel; **P/p**, Upper/lower premolar

Systematic paleontology

Order Primates Linnaeus, 1758

Semioorder Plesiadapiformes Simons and Tattersall in Simons, 1972

Superfamily Paromomyoidea Simpson, 1940

Family Paromomyidae Simpson, 1940

Genus *Arcius* Godinot, 1984

Arcius sp.

Geographic distribution: Spain.

Chronological range: Neustrian, early Eocene.

Iberian localities: Masia de l'Hereuet (Lleida).

Remarks: The material from this locality attributed to the genus *Arcius* presented morphological features different from other species of the genus. However, due to the scarcity of material, a new species was not erected when it was originally described (Marigó et al. 2012). A later study of the same material gave rise to the new species *A. ilerdensis*

(López-Torres and Silcox 2018). However, according to Beard and Métais (2023), the holotype of *A. ilerdensis*, a right m2, belongs to the apatemyid genus *Heterohyus*, so these authors proposed the new combination *Heterohyus ilerdensis*. The rest of specimens originally described by Marigó et al. (2012), namely an m3 and two M1-2, are still considered to belong to *Arcius*, and consequently referred to *Arcius* sp. (Beard and Métais 2023).

Main references: Marigó et al. (2012, 2014), López-Torres and Silcox (2018), Beard and Métais (2023).

Semioorder Euprimates Linnaeus, 1758

Suborder Strepsirrhini Geoffroy Saint-Hilaire, 1812

Infraorder Adapiformes Hoffstetter, 1977

Family Notharctidae Trouessart, 1879

Genus *Agerinia* Crusafont-Pairó, 1973

Agerinia roselli (Crusafont-Pairó, 1967)

Geographic distribution: Spain.

Chronological range: Neustrian, early Eocene.

Iberian localities: Les Saleres [type locality].

Remarks: Although this species was first attributed to the Necrolemuridae, it was later recognized as an adapiform with a derived lower dentition (Crusafont-Pairó 1967). Later analyses of more material allowed the redescription of the entire hypodigm as well as an emended diagnosis for the species (Femenias-Gual et al. 2016b). The more recent study identified the presence of a distinct hypoconid and entoconid in the p4, as well as the presence of a tiny paraconid in the m1. Moreover, a body mass estimation of this primate was calculated, ranging from 650 to 900 g (Femenias-Gual et al. 2016b).

Main references: Crusafont-Pairó (1967, 1973), Szalay (1971), Femenias-Gual et al. (2016b), Femenias-Gual (2020).

Agerinia smithorum Femenias-Gual, Minwer-Barakat, Marigó and Moyà-Solà, 2016b

Figure 1a

Geographic distribution: Spain.

Chronological range: Neustrian, early Eocene.

Iberian localities: Casa Retjo-1 [type locality], Casa Retjo-3 and Cabana del Llúcio-1 (Lleida).

Remarks: This new species was erected based on the most complete specimen attributed to this genus (a mandible preserving the alveoli of the canine and the p1, the roots of the p2 and all teeth from p3 to m3), which allowed Femenias-Gual et al. (2016a) to provide an emended diagnosis for the genus *Agerinia*. *Agerinia smithorum* differs from *A. roselli* in having a less molarized p4, a larger paraconid on the m1, and a tiny protoconid on the m2 (Femenias-Gual et al. 2016a). Its primitive traits as well as

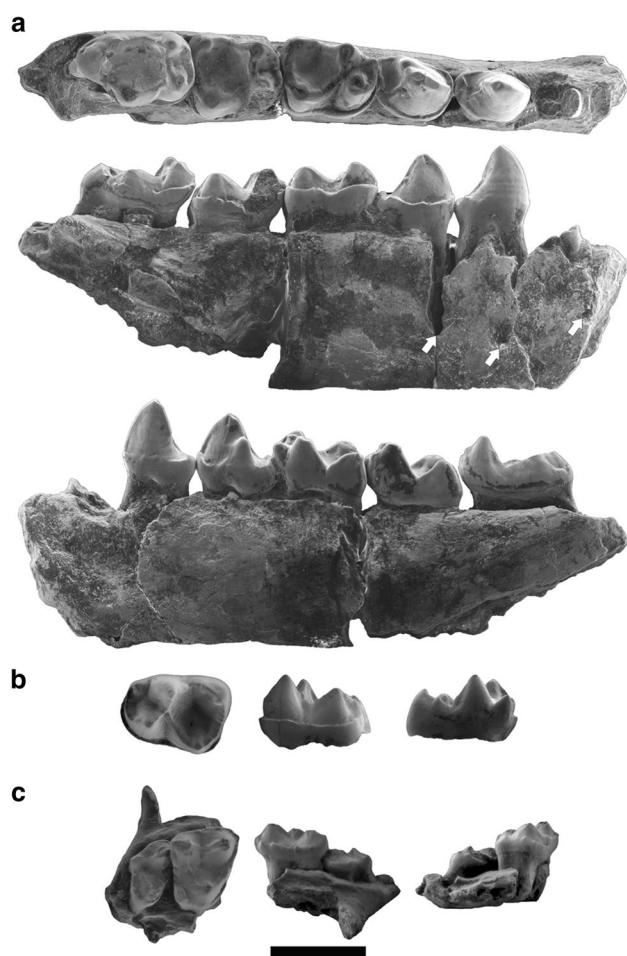


Fig. 1 Environmental scanning electron microscope images of the types of Paleogene primates described since the submission of Marigó et al. (2014). **a.** *Agerinia smithorum* from Casa Retjo-1 stored at ICP (IPS-84291, holotype), right mandible with alveoli of the canine and the p1, the roots of the p2, and all teeth from p3 to m3 in occlusal view (top), buccal view (middle; white arrows indicate the three mental foramina) and lingual view (bottom); **b.** *Agerinia marandati* from Masia de l'Hereuet stored at Institut Català de Paleontologia Miquel Crusafont, ICP (IPS-82801, holotype), a left m1 in occlusal (left), buccal (middle) and lingual (right) views; **c.** *Nievesia sossisensis* from Sossís stored at ICP (IPS-57271, holotype), a right maxillary fragment with M2 and M3 in occlusal (left), buccal (middle) and lingual (right) views. Scale bar equals 3 mm

phylogenetic analyses argue in favor of *A. smithorum* being the earliest diverging species of the genus (Femenias-Gual et al. 2016a, 2017b). New dental material and a calcaneus were later recovered from the type locality, allowing the first description of the upper dentition of the species to complement knowledge of its lower dentition (Femenias-Gual et al. 2017a). The study of the calcaneus provided the first glimpse into its locomotor behaviour, revealing that *A. smithorum* was a moderately active arboreal quadruped with less leaping proclivity than notharctines but more than asiadapids (Femenias-Gual et al. 2017a). Later discoveries

of new fossil sites, including some incisors (previously unknown for the genus), confirmed the presence of this species in the localities of Cabana del Llúcio-1 and Casa Retjo-3 (Femenias-Gual et al. 2020). Another calcaneus fragment of *A. smithorum* was recovered from the former locality, confirming previous interpretations of its locomotor repertoire (Femenias-Gual et al. 2020).

Main references: Femenias-Gual et al. (2016a, 2017a, 2020).

Agerinia marandati Femenias-Gual, Minwer-Barakat, Marigó, Poyatos-Moré and Moyà-Solà, 2017b
Figure 1b

Geographic distribution: Spain.

Chronological range: Neustrian, early Eocene.

Iberian localities: Masia de l'Hereuet (Lleida).

Remarks: The discovery of this species provided previously unknown details of the upper and lower dentition of the genus *Agerinia* as well as the presence of an unfused mandible (Femenias-Gual et al. 2017b). Representing the most complete sample of the genus at the moment of publication, *A. marandati* showed intermediate dental characters between *A. smithorum* and *A. roselli*. Moreover, phylogenetic analyses confirmed its intermediate position between the two latter species and, in some cases, that the *Agerinia* clade could be closely related to sivaladapids and asiadapines (Femenias-Gual et al. 2017b).

Main references: Femenias-Gual et al. (2017b).

Agerinia sp.

Geographic distribution: Spain and France.

Chronological range: Grauvian, early to middle Eocene.

Iberian localities: Font del Torricó-1 and 3 as well as Escarlà (Lleida); La Morera-2 (Tarragona); Casa Picantón, Castigaleu, Les Badies, Güell I and Casa Ramón (Huesca).

Remarks: The scarce primate remains found in the localities of Font del Torricó-1 (a right deciduous p4) and Font del Torricó-3 (a fragment of a left m2 or m3) did not allow their attribution to a certain species of *Agerinia*. However, they highlighted that this genus was present in more localities than previously thought (Femenias-Gual et al. 2020).

Main references: Crusafont-Pairó and Golpe-Posse (1973, 1974, 1975), Szalay (1971), Peláez-Campomanes (1995), Marigó et al. (2014), Femenias-Gual et al. (2020), Femenias-Gual (2020).

Tribe Anchomomyini Szalay and Delson, 1979 (sensu Godinot 1988)

Anchomomyini indet.

Geographic distribution: Spain.

Chronological range: Robiacian, middle Eocene.

Iberian localities: Pontils-38 (Tarragona).

Remarks: A medium-sized anchomomyin is known from a single m3 from the Pontils-38 level of the Pontils section. This primate is larger than *Anchomomys* and *Nievesia* and smaller than *Buxella* and *Periconodon* (similar in size to *Mazateronodon*), but a specific determination is not possible until more material is recovered (Minwer-Barakat et al. 2023).

Main references: Minwer-Barakat et al. (2023).

Anchomomys frontanyensis Marigó et al., 2011

Geographic distribution: Spain.

Iberian localities: Sant Jaume de Frontanya [type locality] (Barcelona).

Chronological range: Robiacian, middle Eocene.

Remarks: This species, described by Marigó et al. (2011) and correctly classified in Marigó et al. (2014), is included herein because during the last decade our team has described several postcranial remains attributed to it, including the astragalus, calcaneus and navicular.

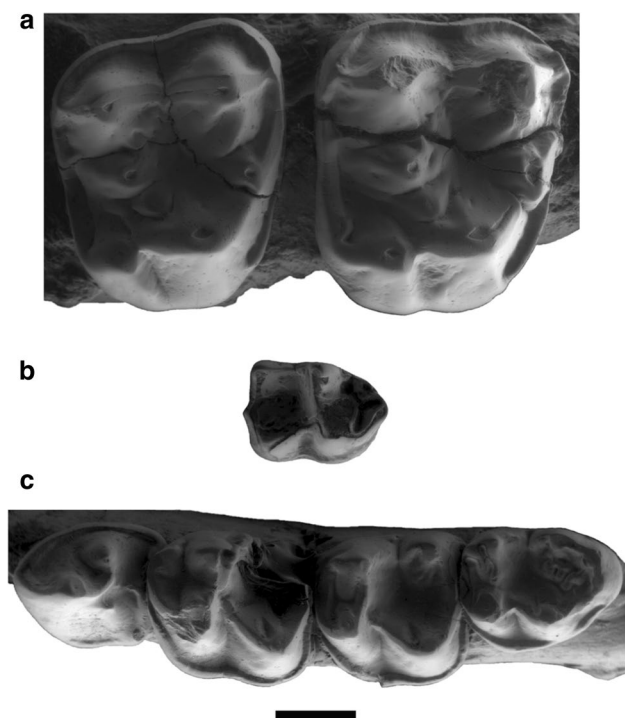


Fig. 2 a. *Microchoerus hookeri* from Sossis stored at ICP (IPS-62073, holotype), occlusal view of fragment of a right maxilla with M1 and M2; b. *Pseudoloris reguanti* from Sant Cugat de Gavaldons (Collsuspina) stored at the Naturhistorisches Museum Basel (Switzerland) (NMB Css.1, neotype), right m1 in occlusal view; c. *Necrolemur anadoni* from Sant Jaume de Frontanya-1 stored at ICP (IPS-4431, holotype), occlusal view of left mandible with p4-m3. Scale bar equals 1 mm

Main references: Marigó et al. (2016, 2020), Monclús-Gonzalo et al. (2023, 2025a).

Nievesia sossisensis Marigó et al., 2013

Figure 1c

Geographic distribution: Spain.

Iberian localities: Sossis [type locality] (Lleida).

Chronological range: Headonian, late Eocene.

Remarks: This taxon was previously thought to correspond to a new *Anchomomys* species, but further studies revealed that it displayed several features distinguishing it from other anchomomyin genera such as a very buccolingually compressed P4, an extremely reduced metacone in the M3, and the presence of a complete premetacristid closing the trigonid basin from the lingual side on the lower molars. This species was attributed to *Anchomomyini* nov. in Marigó et al. (2014) because this paper was accepted prior to publication of Marigó et al. (2013), which formally attributed this material to the new genus and species *Nievesia sossisensis*, dedicated to the paleontologist Nieves López Martínez.

Main references: Marigó (2013), Marigó et al. (2013, 2014).

Suborder Haplorrhini Pocock, 1918

Infraorder Tarsiiformes Gregory, 1915

Superfamily Omomyoidea Trouessart, 1879

Family Omomyidae Trouessart, 1879

Subfamily Microchoerinae Lydekker, 1887

Microchoerinae indet.

Geographic distribution: Spain.

Chronological range: Robiacian, middle Eocene.

Iberian localities: Pontils-22, 25, 33, 38, 38 TOP and 39 (Tarragona).

Remarks: Initially, two isolated molars attributed to a very small omomyid were identified from level 38 of the Pontils section (Antunes et al. 1997; Marigó et al. 2014). Subsequent fieldwork in this locality provided a larger sample including upper and lower dentitions from the levels Pontils-22, 25, 33, 38, 38 TOP and 39. This material allowed the attribution of these remains to a microchoerine smaller than *Pseudoloris* that may represent a new taxon (Minwer-Barakat et al. 2023).

Main references: Antunes et al. (1997), Minwer-Barakat et al. (2023).

Genus *Microchoerus* Wood, 1844

Microchoerus hookeri Minwer-Barakat et al., 2017

Figure 2a

Geographic distribution: Spain and Switzerland.

Chronological range: Headonian, late Eocene.

Iberian localities: Sossís [type locality] and Roc de Santa (Lleida).

Remarks: The material now attributed to this species was previously assigned to other taxa. On the one hand, the rich sample of more than 120 specimens from the locality of Sossís referred by Crusafont-Pairó (1965, 1967) to *Microchoerus erinaceus* formed the basis for the description of the species *Microchoerus hookeri* (Minwer-Barakat et al. 2017). This species can be distinguished from other species of *Microchoerus*, including *M. erinaceus*, by several morphological traits, such as the moderate enamel wrinkling, generally absent mesoconid and small hypoconulid in the m1 and m2, single paracone in the upper molars and premolars and, particularly, the lack of mesostyle in most upper molars. Minwer-Barakat et al. (2017) also assigned to this new species some specimens from the Swiss site Eclépens B, previously attributed to *Microchoerus* aff. *erinaceus* by Hooker and Weidmann (2000). On the other hand, the material from Roc de Santa assigned by Casanovas-Cladellas (1975, 1998) to *Adapis magnus*, a maxillary fragment with P3-M3 (now missing the M3), and later transferred to *Lepidadapis* (Godinot and Couette 2008), as well as an isolated m3 attributed to *Necrolemur antiquus*, were later ascribed to *M. hookeri* by Minwer-Barakat et al. (2018). In addition, Minwer-Barakat et al. (2018) assigned an upper incisor from Roc de Santa to *M. hookeri* and provided the first detailed study of the material from this site.

Main references: Crusafont-Pairó (1965, 1967), Casanovas-Cladellas (1975, 1998), Antunes et al. (1997), Hooker and Weidmann (2000), Marigó et al. (2014), Minwer-Barakat et al. (2017, 2018).

Microchoerus aff. *erinaceus* Wood, 1844

Geographic distribution: Spain.

Chronological range: Headonian, late Eocene.

Iberian localities: Zambrana (Álava).

Remarks: First attributed to *Microchoerinae* indet. (Marigó et al. 2014), this material was later assigned to the genus *Microchoerus* (Minwer-Barakat et al. 2013a). The recovered material from Zambrana consists of two well-preserved right mandibular fragments bearing p3-m3 and p4-m3. The overall dental morphology and size is similar to that observed in *Microchoerus erinaceus*, although some traits are slightly different and prevent a definitive taxonomic attribution to this species (Minwer-Barakat et al. 2013a). These remains represent the first Paleogene primates recovered from the Miranda-Trebiño Basin and the westernmost record of *Microchoerus*. In addition, their similarities with

other European taxa support the existence of connections between European basins and western Iberia during the late Eocene (Minwer-Barakat et al. 2013a).

Main references: Minwer-Barakat et al. (2013a, b), Marigó et al. (2014).

Microchoerus sp.

Geographic distribution: Spain.

Chronological range: Headonian, late Eocene.

Iberian localities: Sant Cugat de Gavadons (=Collsupina) (Barcelona).

Remarks: Crusafont-Pairó (1967) and Crusafont-Pairó and Golpe-Posse (1974) described a fragment of a maxilla with P4-M1 from the locality of Sant Cugat de Gavadons and assigned it to the species *Microchoerus ornatus*, which was only known at the time from the upper dentition (Hooker 1986, Gunnell and Rose 2002). However, further studies confirmed that these two teeth correspond to P3 and P4 (Minwer-Barakat et al. 2016). This material differs from *Microchoerus ornatus* from Mormont-Entreroches by its larger size, the presence of a simple paracone, and the well-developed hypostyle in the P3. Moreover, it presents significant differences from the other known species of *Microchoerus* (*M. erinaceus*, *M. wardorum*, *M. creechbarrowensis*) and therefore it must be ascribed to *Microchoerus* sp., thus restricting the geographical distribution of *M. ornatus* to Central Europe (Minwer-Barakat et al. 2016).

Main references: Crusafont-Pairó (1967), Crusafont-Pairó and Golpe-Posse (1974), Golpe-Posse (1982), Marigó et al. (2014), Minwer-Barakat et al. (2016).

Genus *Pseudoloris* Stehlin, 1916

Pseudoloris reguanti Crusafont-Pairó, 1967

Figure 2b

Geographic distribution: Spain.

Chronological range: Headonian, late Eocene.

Iberian localities: Sant Cugat de Gavadons (=Collsupina) (Barcelona).

Remarks: This species was described by Crusafont-Pairó (1967) based on an isolated lower molar, larger than those of *P. parvulus* and without a tubercular paraconid. Unfortunately, the holotype and only known specimen was lost during the 1970s; therefore, this species has subsequently been considered a nomen nudum (Schmidt-Kittler 1977) or a nomen dubium (Marigó et al. 2014). Nevertheless, several isolated teeth of *Pseudoloris* from Sant Cugat de Gavadons were later found by our team in the collections of the ICP and the Naturhistorisches Museum Basel, Switzerland. This new material includes a lower canine, a p3, a trigonid of a

lower molar, and two complete lower molars. One of these latter specimens strongly resembles the holotype and was designated the neotype by Minwer-Barakat et al. (2013b), who also provided an emended diagnosis for the species.

Main references: Crusafont-Pairó (1967), Schmidt-Kittler (1977), Minwer-Barakat et al. (2013b).

Pseudoloris parvulus (Filhol, 1890)

Geographic distribution: Spain, France, Switzerland, England.

Chronological range: Robiacian-Headonian, middle-late Eocene.

Iberian localities: Sossís (Lleida).

Remarks: The material ascribed to *P. parvulus* by Crusafont-Pairó (1967) only included a mandibular fragment with p4-m3 from Sossís, which resembled the specimens of this species known from other European sites. Minwer-Barakat et al. (2015a) later described abundant material of this species from Sossís among remains housed at the ICP and in the collections of the Naturhistorisches Museum Basel, Switzerland. The entire sample comprises 11 mandible fragments with several teeth, three upper dental series, and nearly 80 isolated teeth, representing the most complete sample of the genus *Pseudoloris* from the Iberian Peninsula. These authors also provided an emended diagnosis of the species.

Main references: Crusafont-Pairó (1967), Marigó et al. (2014), Minwer-Barakat et al. (2015a).

Pseudoloris sp.

Geographic distribution: Spain.

Chronological range: Robiacian, middle Eocene.

Iberian localities: Pontils-22, 25, 33, 38, 38 TOP and 39 (Tarragona).

Remarks: The material attributed to *Pseudoloris* recovered from different levels of the section of Pontils shows upper and lower molars that match the dental morphology of this genus. The size of this material is similar to *Pseudoloris pyrenaicus* from Sant Jaume de Frontanyà-3C as well as *Pseudoloris parvulus* from Sossís, but further studies are needed to refer it to any of these species.

Main references: Minwer-Barakat et al. (2023).

Genus *Necrolemur* Filhol, 1873

Necrolemur sp.

Geographic distribution: Spain.

Chronological range: Robiacian, middle Eocene.

Iberian localities: Pontils-33 (Tarragona).

Remarks: A single trigonid fragment of a m2 or m3 attributed to the genus *Necrolemur* was recovered from

level Pontils-33 in the section of Pontils. It was attributed to *Necrolemur* sp. based on the presence of enamel wrinkling and large size, but more material is needed for a specific determination (Minwer-Barakat et al. 2023).

Main references: Minwer-Barakat et al. (2023).

Necrolemur anadoni Minwer-Barakat, Marigó and Moyà-Solà, 2015b

Figure 2c

Geographic distribution: Spain.

Chronological range: Robiacian, middle Eocene.

Iberian localities: Sant Jaume de Frontanyà 1 and 2.

Remarks: Some of these remains were attributed to *Necrolemur* sp. in previous works. Later, a mandible fragment with p4-m3 and 15 isolated teeth were described from these sites and attributed to the new species *N. anadoni*. This species is characterized by being intermediate in size and morphological traits between *Nannopithecus filholi* and *Necrolemur antiquus*. A stratocladistic analysis recovered *N. anadoni* as a descendant of *N. filholi* and the ancestor of *N. antiquus*.

Main references: Antunes et al. (1997), Minwer-Barakat et al. (2015b).

Discussion

New discoveries since 2013

Several new findings have been published since the last update of Paleogene primates from the Iberian Peninsula by Marigó et al. (2014). Among these studies, several new taxa have been described and/or reassigned (*Agerinia smithorum*, *Agerinia marandati*, *Nievesia sossisensis*, *Necrolemur anadoni*, *Microchoerus hookeri*, *Microchoerus* sp. from Sant Cugat de Gavadons and *Microchoerus* aff. *erinaceus* from Zambrana).

The study of the early Eocene primates from the Àger Basin (southern Pyrenees) included the review of historical material of *Agerinia roselli* (Femenias-Gual et al. 2016b), but also the description of newly recovered material from recently discovered fossil sites such as Casa Retjo (Femenias-Gual et al. 2016a, 2017a) and Cabana del Llúcio (Femenias-Gual et al. 2020), which allowed the description of the new species *Agerinia smithorum*. In addition, other primates have been documented at new sites, such as *Agerinia* sp. from Font del Torricó-1 and 3. Also in that basin, the study of the remains from Masia de l'Hereuet led to the description of the species *Agerinia marandati* (Femenias-Gual et al. 2017b) and the documentation of the first evidence of Plesiadapiformes from Spain (Marigó et al. 2012).

Regarding middle Eocene primates, the erection of the new species *Necrolemur anadoni* from Sant Jaume de Frontayà has expanded knowledge of the evolution of this genus in the Iberian Peninsula (Minwer-Barakat et al. 2015b). But one of the most relevant advances in the study of Eocene primates from Spain has been the preliminary description of the assemblage from Pontils (Minwer-Barakat et al. 2023), which includes four species: *Pseudoloris* sp., *Necrolemur* sp., a new anchomomyin adapiform, and a new microchoerine omomyiform. Even though new material is still under study, the research done by our team during the last decade updates the geographical distribution of certain Paleogene primate taxa and increases the diversity of adapiforms and omomyiforms in Iberian sites.

Not less important has been our team's contribution to knowledge of the late Eocene Iberian primates, which in the last decade has involved the study of different sites. First, several species have been studied from the historical locality of Sossís (Pyrenean basins): the above-mentioned new taxa *Nievesia sossisensis* and *Microchoerus hookeri* as well as the vast collection of remains of the omomyiform *Pseudoloris parvulus* (Marigó et al. 2013; Minwer-Barakat et al. 2015a, 2017). Another late Eocene historical locality studied is Roc de Santa, also in the Pyrenees, where the thorough review of the remains previously assigned to *Adapis magnus* and *Necrolemur antiquus* by Casanovas-Cladellas (1975) resulted in the new taxonomic referral of these fossils to *M. hookeri* (Minwer-Barakat et al. 2018). The primate material from Sant Cugat de Gavadons in the Ebro Basin has also been reviewed, including the species *Pseudoloris reguanti* (Minwer-Barakat et al. 2013b) and *Microchoerus* sp. (Minwer-Barakat et al. 2016). Another late Eocene site from which the primates have been studied is Zambrana in the Miranda-Trebiño Basin (Minwer-Barakat et al. 2013a).

Investigation of the postcranial anatomy of Paleogene primates from Iberian basins has also been undertaken in recent years. On one hand, members of our team have carried out the description and traditional morphometric analyses and morpho-functional interpretations of historical as well as newly recovered remains attributed to *Anchomomys frontanyensis* (Moyà-Solà et al. 2011; Marigó et al. 2016, 2020) and *Agerinia* (Femenias-Gual et al. 2017a, 2020). The adapiform *Anchomomys frontanyensis* is especially interesting due to its small size, comparable to some omomyiforms. A considerable amount of postcranial material of this primate has been studied, including tarsal bones such as the astragalus, calcaneus and navicular. These studies have revealed that the tarsal morphology of *A. frontanyensis* closely resembles that of omomyiforms, suggesting convergent locomotor adaptations (Marigó et al. 2016, 2020). The calcaneus of *A. frontanyensis* is especially remarkable, as it exhibits greater relative calcaneal elongation than similarly

sized adapiforms like *Marcgodinotius*, approaching the condition observed in omomyiforms and ruling out small size as the sole explanation for calcaneal elongation (Marigó et al. 2016). This concurs with the view that leaping capabilities evolved independently in different primate lineages multiple times (Boyer et al. 2013). In addition, the morphology of the cuboid and cuneiform facets on the navicular is suggestive of a habitually inverted foot posture, a feature likely associated with enhanced grasping on narrow branches. This specialization suggests that *A. frontanyensis* exploited different parts of the canopy than sympatric omomyiform primates, resulting in niche partitioning and ecological differentiation (Marigó et al. 2020). The postcranial material attributed to the adapiform *Agerinia*, although scarce, has revealed that this genus was likely an arboreal quadruped with more proclivity for leaping than asiadapids but less than the smaller *Anchomomys frontanyensis* (Femenias-Gual et al. 2017b).

On the other hand, more in-depth studies of some of this material—implementing techniques such as 3D geometric morphometrics (3DGM)—have allowed us to investigate the relationship between form and function of the pedal anatomy of some of these Paleogene primates, particularly of the small adapiform *Anchomomys frontanyensis* (Monclús-Gonzalo et al. 2023, 2025a). In these studies, we developed a modified version of the two-block partial least-squares analysis (Rohlf and Corti 2000), which is more comparable to a partial least-squares regression (PLSR). Along with different types of ecological variables (in this case, locomotor percentages compiled from literature), this new method permits the reconstruction of the locomotor repertoire of fossil primates, yielding a good predictive performance (for more examples on the application of this method, see Monclús-Gonzalo et al. 2025b; Raventós-Izard et al. 2025). Additionally, these morpho-functional analyses have been complemented by a suite of phylogenetic comparative methods, including evolutionary modelling, phylogenetically-informed discriminant analyses and the estimation of evolutionary rates across the primate phylogenetic tree (Venditti et al. 2011; Clavel et al. 2019, Clavel and Morlon 2020), which have provided an informed understanding of the origin and early diversification of primates during the Paleogene based on pedal evidence (Fig. 3).

The recent studies by Monclús-Gonzalo et al. (2023, 2025a) build upon earlier research on the tarsal morphology of *A. frontanyensis* while significantly expanding the analytical scope of this research line into a broader phylogenetic context by including representatives of all major Paleogene primate groups. Overall, Monclús-Gonzalo et al. (2023, 2025a) provides a broad comparative overview of the locomotor behavior of Paleogene primates—like previous studies including Walker (1974), Gebo (1988), Rose (1994), and Boyer et al. (2013)—showing that early

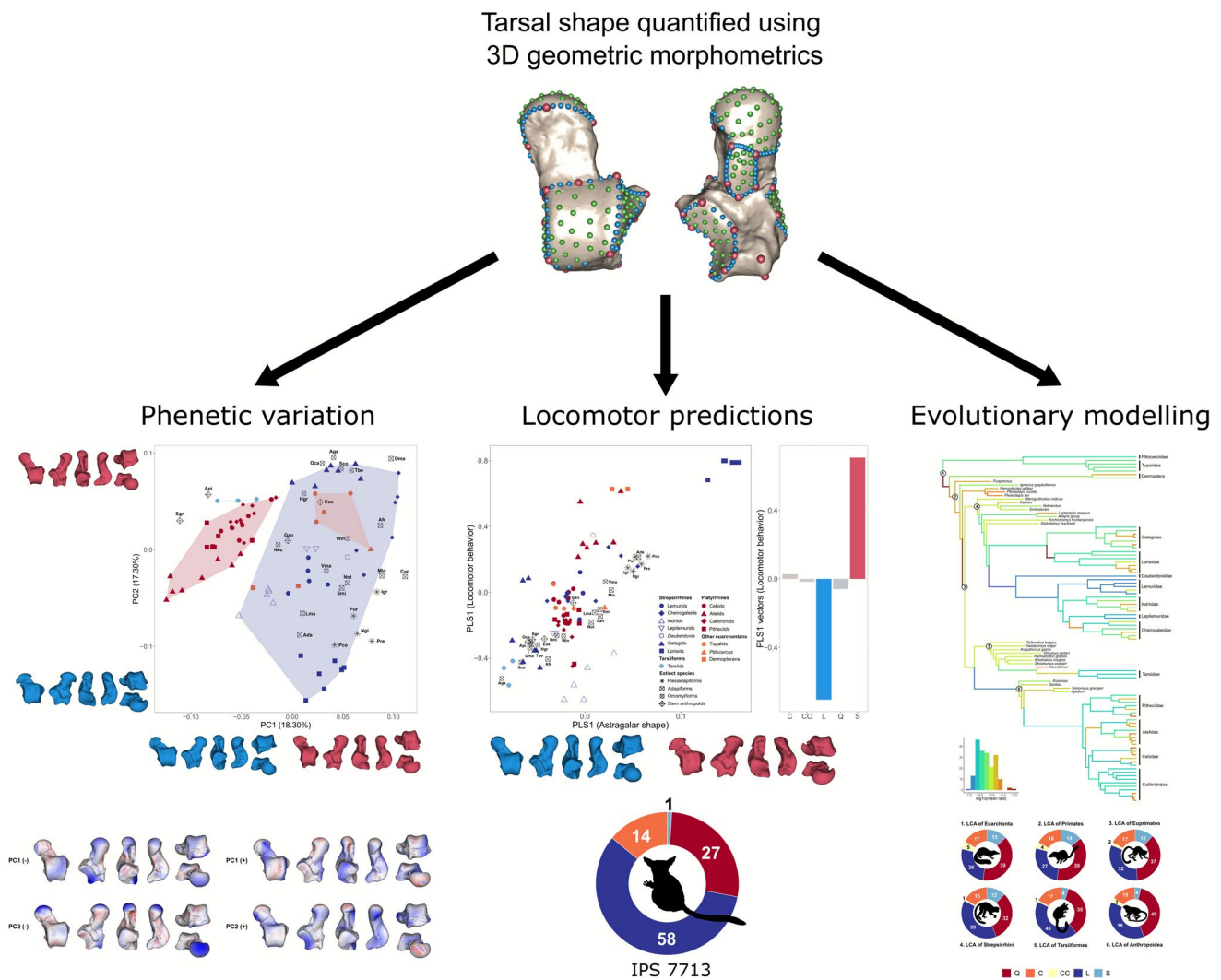


Fig. 3 Workflow applied in the morpho-functional studies by Monclús-Gonzalo et al. (2023, 2025a) illustrating the application of three-dimensional geometric morphometrics to quantify tarsal bone shape and their subsequent analyses

euprimates displayed a diverse array of locomotor repertoires comparable to extant species, with several cases of convergence between distantly related clades. Moreover, a comparison between plesiadapiforms—which, irrespective of their systematic position within Euarchonta, remain key to understanding primate origins—and euprimates provide additional evidence that the origin and early diversification of euprimates involved a major locomotor shift, which included a greater use of leaping by the latter (Dagosto 2007; Boyer et al. 2013). Additionally, Monclús-Gonzalo et al. (2023, 2025a) introduce novel analytical tools to address key paleobiological questions regarding early primate evolution, aligning with the general disciplinary shift towards the use of quantitative and phylogenetically-informed approaches as exemplified in recent studies by Boyer et al. (2013, 2015), Yapuncich et al. (2017, 2019), and Llera Martín et al. (2022), among others.

In addition to the research stated above, around 100 fossiliferous levels have been sampled thanks to annual field campaigns since 2010. Of these, around half have provided positive results, yielding fossils of not only primates but also artiodactyls, perissodactyls, rodents, eulipotyphlans, and marsupials, among other mammals, as well as amphibians, squamates, crocodiles, turtles, fish, invertebrates and plants. Although these remains usually are not the priority for members of our group who focus on early primate evolution, these discoveries have resulted in some publications in collaboration with researchers devoted to other groups of flora and fauna (see below). These studies include the recent paper about the flora and fauna of the fossiliferous levels of the Pontils section by Minwer-Barakat et al. (2023) concerning remains of rodents, metatherians, eulipotyphlans, apatotherians, chiropterans, artiodactyls, perissodactyls, crocodyliforms, squamates, amphibians, fish, foraminifera

and charophytes, among other undetermined mammals in addition to primates.

Apart from primates, the most studied vertebrate groups from the localities sampled by our team have traditionally been rodents and squamates. Regarding rodents, the remains from Sant Jaume de Frontanyà-1 were described in detail and allowed us to establish the age of this level as MP15 and to erect two new species (Bonilla-Salomón et al. 2016). Moreover, the description of the rodents from Santpedor-2 has supported an Oligocene age of this locality, which documents one of the few European primates crossing the Eocene–Oligocene boundary (Vianey-Liaud et al. 2019). Regarding squamates, it is worth mentioning an exhaustive study including lizard and amphisbaenian remains of several early Eocene Pyrenean sites, including both new and classical localities (Bolet 2017), and the description of the remains of lizards and amphisbaenians from Sossís (Bolet and Evans 2013; Bolet and Augé 2014) and Mazaterón (Bolet 2023).

Invertebrate remains apart from those recovered from Pontils have also been studied from the levels Roc de Santa-1, 3 and 5, including five species of aquatic gastropods and 15 terrestrial species. Thanks to the study of these remains, five new genera and nine new gastropod species have been erected (Harzhauser et al. 2020).

Primate evolution during the Paleogene in the Iberian Peninsula

The diversity of primates during the Paleogene in the Iberian Peninsula increases throughout the Eocene and abruptly declines at the Eocene–Oligocene boundary. Concerning plesiadapiforms (considered herein as primates *sensu lato*), they are restricted to the early Eocene, with scarce remains found in only two sites, Silveirinha (Mondego Basin, Portugal), and Masia de l'Hereuet (Central Southern Pyrenean basin, Lleida). All these findings have been attributed to the genus *Arcius* (Estravís 2000; Marigó et al. 2012; López-Torres and Silcox 2018; Beard and Métais 2023).

Regarding Paleogene euprimates (adapiforms and omomyiforms), the first findings occur during the Neustrian with the genus *Donrussellia* in the Mondego Basin (Portugal). During the Neustrian and Grauvian, the adapiform genera *Cantius* and *Agerinia* have been mentioned from different sites of the Pyrenean basins as well as the Ebro basin such as Masia de l'Hereuet, Les Saleres, Font del Torricó and Casa Retjo (Marigó 2013; Femenias-Gual et al. 2016a, 2016b, 2017a, 2017b, 2020; Femenias-Gual 2020). *Agerinia* ranges into the Geiseltalian in the Iberian Peninsula, appearing in later localities such as Casa Ramón (Peláez-Campomanes 1995; Marigó 2013). Omomyiforms do not come into play up until the Geiseltalian, represented by the remains

attributed to *Pseudoloris* sp. from the latter locality (Marigó 2013). Since then, adapiforms and omomyiforms coexist for some time in many Iberian sites. In the most studied or richest ones, such as Sant Jaume de Frontanyà, Sossís and Pontils, up to four different primate species cohabitate in the same environments, although it has been argued that they occupied different ecological niches (Marigó et al. 2020). The peak of primate diversity occurs in some of these sites during the Robiacian (middle Eocene), coinciding with the Middle Eocene Climatic Optimum (MECO) or Middle Eocene Thermal Maximum (METM), a period of warm climate recorded in both continental and marine ecosystems, although more exhaustively studied in the latter (Sharma et al. 2024). During that time, we find the highest diversity of adapiforms in the Iberian basins, represented by anchomomyin genera such as *Anchomomys*, *Mazateronodon*, *Nievesia* as well as adapine genera such as *Adapis*, *Leptadapis* and *Microadapis* (Marigó 2013; Marigó et al. 2014). Concerning omomyiforms, apart from the first appearance of *Pseudoloris* from Casa Ramón mentioned above, this genus is also well represented in Robiacian and Headonian sites such as Sant Jaume de Frontanyà, Pontils, Sossís and Sant Cugat de Gavadons. Other microchoerine genera such as *Microchoerus* and *Necrolemur* are also represented in Iberian basins during the middle and late Eocene, with some genera ranging into the Oligocene at some sites.

Conclusions

Knowledge of Paleogene primates from the Iberian Peninsula has increased notably in recent years, especially since 2008, thanks to the efforts of Salvador Moyà-Solà, who built a new research team dedicated to these mammals. Since 2010, publications devoted to remains of different Paleogene primate groups have provided new clues about their taxonomic attributions and diversity through time, revealing a very diverse group with different ecological roles, sometimes with up to four primate species coexisting in the same site.

Apart from the results achieved by the study of craniodental remains, the study of their postcranial skeleton has also provided new insights into their locomotor diversity and evolution. In addition to qualitative descriptions and the use of linear measurements, our team is currently applying methods that allow for a high-dimensional quantification of shape (such as 3DGM) to more accurately investigate the linkages between form and function. Notably, PLSR analyses have been employed for the first time to infer locomotor behavior in extinct primates. This approach departs from conventional classification-based methods, such as discriminant analysis, by using locomotor percentages rather than

categories, the latter of which do not fully capture the full locomotor spectrum of primates. The characterization of the locomotor behavior of multiple Paleogene species has demonstrated that early euprimates exhibited diverse locomotor repertoires, challenging the idea that complexity only arose later in primate evolution. Thanks to this macroevolutionary perspective, this research has also highlighted that the emergence of euprimates was characterized by increases in the rates of tarsal evolution, shedding light on the timing and drivers of functional diversification.

In order to fully comprehend Paleogene primate ecology, other remains of groups of accompanying fauna and flora must also be undertaken for different Iberian sites. Our team has also made a huge effort to consolidate fruitful collaborations with researchers devoted to other groups, although some recovered remains are still understudied. On the one hand, some groups like rodents could provide new insights into the dating of several new levels and clarify biostratigraphy for some sites in which there is still debate. On the other hand, studies of macromammals, which could provide valuable information on Paleogene ecosystems, are also lacking for many sites. Moreover, squamate faunas, although further analyzed than other groups, can also be useful in determining climatic changes throughout the Paleogene. Unstudied squamate remains from different localities sampled by our team range from the earliest to latest Eocene. All in all, it is expected that future studies of not only primates but also accompanying faunas will further contribute to understanding the ecological scenarios that these faunas inhabited and will raise awareness of Paleogene ecosystems as well as early primate evolution.

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Data availability All data generated and analyzed during this study are included in this published article.

Declarations The authors disclose financial or non-financial interests that are directly or indirectly related to the work submitted for publication.

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