Journal of Iberian Geology **40 (1) 2014:** 179-211
http://dx.doi.org/10.5209/rev_JIGE.2014.v40.n1.44094

www.ucm.es/info/estratig/journal.htm
ISSN (print): 1698-6180. ISSN (online): 1886-7995

Journal of Iberian Geology
AN INTERNATIONAL PUBLICATION OF EARTH SCIENCES

The primate fossil record in the Iberian Peninsula

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Received: 26 July 2013 / Accepted: 5 December 2013 / Available online: 25 February 2014

Abstract

During the last decade, new discoveries in several Iberian basins, together with the description of previously unpublished finds, have significantly increased the recorded paleodiversity of fossil Primates (Mammalia: Euarchonta) in the Iberian Peninsula. Here we provide an updated compendium of the primate fossil record in Iberia during the Cenozoic and further summarize the changes in primate paleodiversity through time, which are then analyzed in the light of changing climatic conditions. Thanks to favorable climatic conditions, the highest diversity of Iberian primates was reached during the Eocene, thus reflecting the radiation of both adapoids and omomyoids; only a single plesiadapiform genus is in contrast 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 omomyoids survived the Grande Coupure. From the Middle Miocene onwards, catarrhine primates are recorded in the Iberian Peninsula. During the Middle and Late Miocene, they are represented by pliopithecoids and hominoids, restricted to NE Iberia. The Miocene hominoids from Iberia are of utmost significance for understanding the Eurasian hominoid radiation and its role in the origins of the great-ape-and-human clade. Following the local extinction of these taxa during the early Late Miocene, due to progressively increased seasonality and concomitant changes in plant communities, cercopithecoids are also recorded in the Iberian Peninsula from the latest Miocene through the Plio-Pleistocene, although they finally became locally extinct, whereas hominoids are again represented by fossil humans during the Pleistocene.

Keywords: Primates, Paleogene, Neogene, Quaternary, Taxonomy, Spain

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Resumen

Durante la última década, nuevos descubrimientos en varias cuencas ibéricas, junto con la descripción de hallazgos previos inéditos, han incrementado significativamente la paleodiversidad de Primates fósiles (Mammalia: Euarchonta) registrada en la Península Ibérica. Proporcionamos aquí un compendio actualizado del registro fósil de los primates en Iberia durante el Cenozoico, y resumimos además los cambios en paleodiversidad de los primates a lo largo del tiempo a la luz de las condiciones climáticas cambiantes. Gracias a condiciones climáticas favorables, la diversidad más alta de primates ibéricos se produjo durante el Eoceno, reflejando así la radiación tanto de los adapoideos como de los omomioideos; en cambio, sólo un único género de plesiadapiformes se registra en la Península Ibérica. Hacia el límite Eoceno-Oligoceno, los cambios paleoclimáticos condujeron a una crisis de diversidad de los primates y otros cambios faunísticos, aunque dos omomioideos ibéricos sobrevivieron a la Grande Coupure. Del Mioceno Medio en adelante, los primates catarrinos se registran en la Península Ibérica. Durante el Mioceno Medio y Superior, están representados por pliopitecoideos y hominoideos, restringidos al NE de Iberia. Los hominoideos del Mioceno de Iberia son de gran importancia para comprender la radiación de los hominoideos eurasiáticos y su papel en los orígenes del clado de los grandes antropomorfos y los humanos. A continuación de la extinción local de estos taxones durante el Mioceno Superior inicial, debido al incremento progresivo de la estacionalidad así como a cambios en las comunidades vegetales, los cercopitecoideos también se registran en la Península Ibérica a partir del Mioceno más terminal en adelante. Los cercopitecoideos se registran en la Península Ibérica durante todo el Plio-Pleistoceno, aunque finalmente también se extinguieron localmente, mientras que los hominoideos vuelven a estar representados otra vez por los humanos fósiles durante el Pleistoceno.

Palabras clave: Primates, Paleógeno, Neógeno, Cuaternario, Taxonomía, España

1. Introduction

1.1. Primates

Primates (Mammalia: Euarchonta) are a eutherian order of moderate diversity, with about 300 extant species. They were traditionally divided into two major groups: prosimians and simians (or anthropoids) (e.g., Fleagle, 1999). Most authors, however, currently favor a distinction between strepsirrhines and haplorrhines. Unfortunately, many of the features that enable such division are related to soft anatomy, so that the classification of fossil 'prosimians' as either strepsirrhines or haplorrhines, albeit favored here, is not always straightforward. Crown primates (euprimates, or primates of modern aspect) constitute a monophyletic group including extant strepsirrhines and haplorrhines, together with the extinct taxa more closely related to either of them (see Fleagle, 1999, and Hartwig, 2002, for the most recent complete accounts on fossil primates). Morphologically, euprimates are characterized by the possession of a petrosal bulla (the auditory bulla is formed by an extension of the petrosal instead of by a separate entotympanic bone), which is a unique synapomorphy among mammals (Rasmussen, 2002). Other derived diagnostic traits of euprimates, uncommon in other mammals, are the following (e.g., Martin, 1990; Rasmussen, 2002): postorbital bar; orbital convergence, yielding stereoscopic binocular vision; grasping hands and feet, usually with opposable hallux and pollex; flat nails instead of claws on most digits; brains larger than expected on the basis of body size (high encephalization); and a slow life-history profile. The primate total group includes crown primates plus the primate stem lineage, the latter being those taxa preceding the haplorrhine-strepsirrhine divergence, but being more closely related to them than to other euarchontans, i.e. scandentians (tree shrews) and dermopterans (flying lemurs). It is generally thought that primates diverged from other mammals sometime during the Late Cretaceous. Undisputed fossil euprimates are not found until the earliest Eocene, ca. 56 Ma (Rasmussen, 2002), and although molecular estimates suggested in the past an ancient divergence data for crown subclades, recent studies suggest that haplorrhines and strepsirrhines diverged close to the Mesozoic/Cenozoic boundary (Steiper and Seiffert, 2012). The origin of euprimates has been related to plesiadapiforms, which show general dental similarities with primates but at the same time lack several euprimate derived features, such as the postorbital bone and the petrosal bulla. The phylogenetic relationships of plesiadapiforms with euprimates remain unresolved, but it seems currently likely that most of them constitute a paraphyletic assemblage of stem primates.

- Order **Primates** Linnaeus, 1758
  - Semiorder **Plesiadapiformes**† Simons and Tattersall, 1972
    - Superfamily **Paromomyoidea**† Simpson, 1940
    - Superfamily Plesiadapoidea† Trouessart, 1897
  - Semiorder **Euprimates** Hoffstetter, 1977
    - Suborder **Strepsirrhini** É. Geoffroy Saint-Hilaire, 1812
      - Infraorder **Adapiformes**† Hoffstetter, 1977
        - Superfamily **Adapoidea**† Trouessart, 1879
      - Infraorder Lemuriformes Gregory, 1915
        - Superfamily Lemuroidea Gray, 1821
        - Superfamily Cheirogaleoidea Gray, 1872
        - Superfamily Indrioidea Burnett, 1828
        - Superfamily Daubentonioidea Gray, 1863
      - Infraorder Lorisiformes Gregory, 1915
        - Superfamily Lorisoidea Gray, 1821
    - Suborder **Haplorrhini** Pocock, 1918
      - Infraorder **Tarsiiformes** Gregory, 1915
        - Superfamily **Omomyoidea**† Trouessart, 1879
        - Superfamily Tarsioidea Gray, 1825
      - Infraorder **Simiiformes** Hoffstetter, 1974 (=**Anthropoidea** Mivart, 1864)
        - Parvorder Platyrrhini É. Geoffroy Saint-Hilaire, 1812
          - Superfamily Ceboidea Bonaparte, 1831
        - Parvorder **Catarrhini** É. Geoffroy Saint-Hilaire, 1812
          - Superfamily Propliopithecoidea† Straus, 1961
          - Superfamily **Pliopithecoidea**† Zapfe, 1960
          - Superfamily **Cercopithecoidea** Gray, 1821
          - Superfamily **Hominoidea** Gray, 1825

Table 1. Primate systematics down to the superfamily rank. Taxa represented in Iberia are shown in bold type. A dagger (†) denotes extinct taxa.

1.2. Aims of this study

Most primates are linked to tropical or subtropical forested environments, and currently, modern humans are the only primates naturally inhabiting the Iberian Peninsula. This, however, has not always been the case: during the Paleogene and Neogene, several major primate groups occupied the Iberian Peninsula. In Table 1, we have summarized the systematic scheme employed for primates in this paper down to the superfamily rank, indicating with bold bype those taxa recorded in the Iberian Peninsula. For many years, the study of fossil Iberian primates was led by Miquel Crusafont-Pairó, founder of the Institut Català de Paleontologia Miquel Crusafont (ICP), which currently bears his name. Beginning in the early 1940s, Crusafont and co-workers such as Josep F. de Villalta and Juana M. Golpe-Posse reported new material and described new taxa of "prosimians" and anthropoids alike. It is not surprising, therefore, that Crusafont-Pairó and Golpe-Posse (1974) finally published a synthetic review on the fossil primates from Spain. Since then, some summary syntheses devoted to particular primate groups at the Iberian level have been published (e.g., Moyà Solà *et al.*, 1990; Marigó *et al.*, 2011c), but no detailed and comprehensive synthesis of all Iberian primates has been undertaken since 1974. In the meantime, many new fossil discoveries, together with the restudy of previously available material, have led to a significant increase in the knowledge of their paleodiversity, chronology and paleobiology. Here, we provide an updated synthesis of the fossil primates from the Iberian Peninsula (Spain and Portugal) during the Cenozoic (Paleogene, Neogene and Quaternary), enumerating all the recorded taxa at the species level (when possible), and also providing details on their systematics, chronologic and geographic distribution, paleobiology, and phylogenetic relationships. We further discuss the Iberian primate record in the framework of the evolutionary history of this group as a whole, with particular emphasis on its relationship to paleogeographic and climatic changes through time.

2. Systematic paleontology

Order Primates Linnaeus, 1758
Semiorder Plesiadapiformes Simons and Tattersall, 1972
Superfamily Paromomyoidea Simpson, 1940
Family Paromomyidae Simpson, 1940
Genus *Arcius* Godinot, 1984
(Fig. 1A-B)
Arcius sp.

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

Remarks: The genus *Arcius* is mainly known from several Early Eocene (Neustrian, MP7–MP8+9) French sites (Godinot, 1984; Smith *et al.*, 2011), and its Iberian record is comparatively scarce, including only *A. zbyszewskii* from Silveirinha (Portugal), and *Arcius* sp. from Masia de l'Hereuet (Spain). The scarce material (only four isolated molars) from the latter locality enable an attribution to the genus *Arcius*, to which all European paromomyids are currently attributed. This material is intermediate in size between *A. fuscus* and *A. lapparenti*, and shows several morphological differences compared to all the described species of this genus, but the scarcity of the material precludes erecting a new species.

Main references: Marigó *et al.* (2012a).

Arcius zbyszewskii Estravís, 2000

Geographic distribution: Exclusively known from the type locality.

Chronological range: 56–55.5 Ma (MP7, Neustrian, lowermost Eocene).

Iberian localities: Silveirinha [type locality] (Baixo Mondego).

Remarks: Previously attributed to *Phenacolemur* sp. by Antunes (1981) and *Phenacolemur* cf. *fuscus* by Antunes and Russell (1981), *A. zbyszewskii* is closely related to *Arcius rougieri* from Palette (France). The Portuguese species is however smaller and displays many other morphologic differences. The phylogenetic relationships between them are unclear.

Main references: Antunes *et al.* (1997); Estravís (2000).

Semiorder Euprimates Hoffstetter, 1977
Suborder Strepsirrhini É. Geoffroy Saint-Hilaire, 1812
Infraorder Adapiformes Hoffstetter, 1977
Superfamily Adapoidea Trouessart, 1879
Family Notharctidae Trouessart, 1879
Notharctidae indet.

Iberian localities: Silveirinha (Baixo Mondego).

Remarks: Besides *Dounrussellia lusitanica*, Estravís (2000) reported from Silveirinha some isolated teeth of another notharctid. Due to the scarce material available, this material has been left unassigned at the genus level, even though it resembles the Early Eocene genera *Cantius* and *Donrussellia*.

Main references: Antunes *et al.* (1997); Estravís (2000).

Subfamily Cercamoniinae Gingerich, 1975
Genus *Donrussellia* Szalay, 1976
Donrussellia lusitanica Estravís, 2000

Geographic distribution: Exclusively known from the type locality.

Chronological range: 56–55.5 Ma (MP7, Neustrian, lowermost Eocene).

Iberian localities: Silveirinha [type locality] (Baixo Mondego).

Remarks: *Donrussellia* is the most primitive known adapiform genus, and *D. lusitanica* is a very primitive species within this genus. It is much smaller than *D. magna*, somewhat larger than *D. gallica*, and of similar size or slightly larger than *D. provincialis*. The lower molars of *D. lusitanica* differ from those of the other species of the genus in the smaller paraconid and a shorter trigonid when compared to the talonid. The M^1 of *D. lusitanica* differ from those of *D. provincialis* and *D. gallica* in being larger and in having a more subquadrate outline among other features. Moreover, the nannopithex-fold present in the M^1 and M^2 of *D. lusitanica* is not present in those attributed to *D. gallica*, and the absence of a postparaconule crista in the upper molars of *D. lusitanica* makes them different from those of *D. provincialis.*

Main references: Estravís (2000).

Genus *Agerinia* Crusafont Pairó, 1973
Agerinia sp.

Iberian localities: La Coma (=La Morera del Monsant 2) (Tarragona); Casa Ramón (Huesca).

Remarks: This genus has been identified in several Spanish and French localities, ranging from the Neustrian (MP8+9) to the Geiseltalian (MP12). The scarce material from Casa Ramón (MP11 or MP12), which consists only of six isolated teeth, precludes erecting a new species, although it is smaller and displays some morphological differences compared to *A. roselli*. The material from La Coma (MP10), also very scarce, is still under study. Since these two localities are of different age, it is very plausible that two different species are represented.

Main references: Peláez-Campomanes (1995); Antunes *et al.* (1997); Marigó *et al.* (2011c).

Agerinia roselli (Crusafont-Pairó, 1967)

Geographic distribution: Spain and France.

Chronological range: 51–48.5 Ma (MP10, Grauvian, Early–Middle Eocene).

Iberian localities: Les Saleres [type locality] and Escarlà (Lleida); Can Picantón, Castigaleu, Les Badies and Güell I (Huesca).

Remarks: First attributed to the Necrolemuridae, it displays a very primitive upper dentition and a derived lower dentition without paraconid and with a very reduced trigonid (Crusafont-Pairó, 1967).

Main references: Crusafont-Pairó (1967, 1973); Szalay (1971); Crusafont-Pairó and Golpe-Posse (1968, 1973b, 1974, 1975); Antunes *et al.* (1997); Marigó *et al.* (2011c).

Genus *Cantius* Simons, 1962
Cantius sp.

Iberian localities: La Coma (=La Morera del Montsant 2) (Tarragona); Güell III (Huesca).

Remarks: The genus *Cantius* has a wide geographic distribution, including Europe (Spain and France) and North America. It has been identified in Neustrian (MP8+9) and Grauvian (MP10) sites. The material from the two Iberian localities is very scarce, so that an attribution to the species level is not possible until more material is recovered.

Main references: Antunes *et al.* (1997); Marigó *et al.* (2011c).

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

Iberian localities: Montblanc, Coll de l'Illa and Ulldemolins I (Tarragona).

Remarks: The attribution of material from Montblanc and Coll de l'Illa to Anchomomyini indet. by Antunes *et al.* (1997) cannot be confirmed based on the material currently housed at the Institut Català de Paleontologia Miquel Crusafont. Several isolated teeth from Ulldemolins I are also tentatively assigned to the tribe Anchomomyini, until a detailed study enables a more precise determination.

Main references: Antunes *et al.* (1997); Marigó *et al.* (2011c).

Anchomomyini nov.

Iberian localities: Sossís (Lleida).

Remarks: This taxon was previously thought to represent a new *Anchomomys* species (Marigó *et al.*, 2011c), but further study of the available material has revealed that it displays several features distinguishing it from other anchomomyin genera (very buccolingually compressed P^4, extremely reduced metacone in the M^3, and the complete premetacristid closing the trigonid basin from the lingual side on the lower molars).

Main references: Marigó *et al.* (2011b,c).

Genus *Anchomomys* Stehlin, 1916
Anchomomys sp.

Iberian localities: Sant Jaume de Frontanyà 1 (Barcelona); Caenes (Salamanca).

Remarks: The genus *Anchomomys* is well known from several European sites (Switzerland, France, Spain), ranging in age from the Geiseltalian to the Headonian (MP13–17a, Middle–Late Eocene, 44–37 Ma). The material from Caenes, curently under study, consists of two complete and one fragmentary right upper molars, and two left mandible fragments, one showing a complete P_4 and the other presenting an almost complete P_4, a partial M_1 and a complete M_2, and both with the rest of the alveoli from the lower C to the M_3. In addition, a few isolated teeth from Sant Jaume de Frontanyà 1 can be assigned to the genus *Anchomomys*, although the scarcity of material precludes a determination to the species level.

Main references: Moyà-Solà and Köhler (1992); Antunes *et al.* (1997); Moyà-Solà *et al.* (2012); Marigó *et al.* (2011c, 2012b).

Anchomomys frontanyensis Marigó, Minwer-Barakat and Moyà-Solà, 2011a
(Fig. 1E-F).

Geographic distribution: Exclusively known from the type locality.

Chronological range: 43–42 Ma (MP14, Robiacian, Middle Eocene).

Iberian localities: Sant Jaume de Frontanyà 3 [type locality] (Barcelona).

Remarks: The material from this locality represents the largest collection of *Anchomomys* material ever described, including all the permanent teeth except for the incisors. *A. frontanyensis* resembles *A. pygmaeus* from Egerkingen (Ef 372) although it has a more reduced hypocone and paraconule, its hypocone is less projected lingually, and its upper molars have a less developed anterocingulum extending further lingually. Despite sharing features with other anchomomyins, *A. frontanyensis* also shares certain characters with extinct asiadapines and extant lemurs and lorises. Moreover, the presence of *A. frontanyensis* in the Iberian Peninsula reveals a different lineage from that present at the same time in the rest of Europe. Phylogenetic analyses suggest that anchomomyins might be related to either asiadapines or crown strepsirrhines.

Main references: Moyà-Solà and Köhler (1993b); Antunes *et al.* (1997); Marigó *et al.* (2011a, b, c); Minwer-Barakat et al. (2011a); Roig and Moyà-Solà (2011); Moyà-Solà *et al.* (2012).

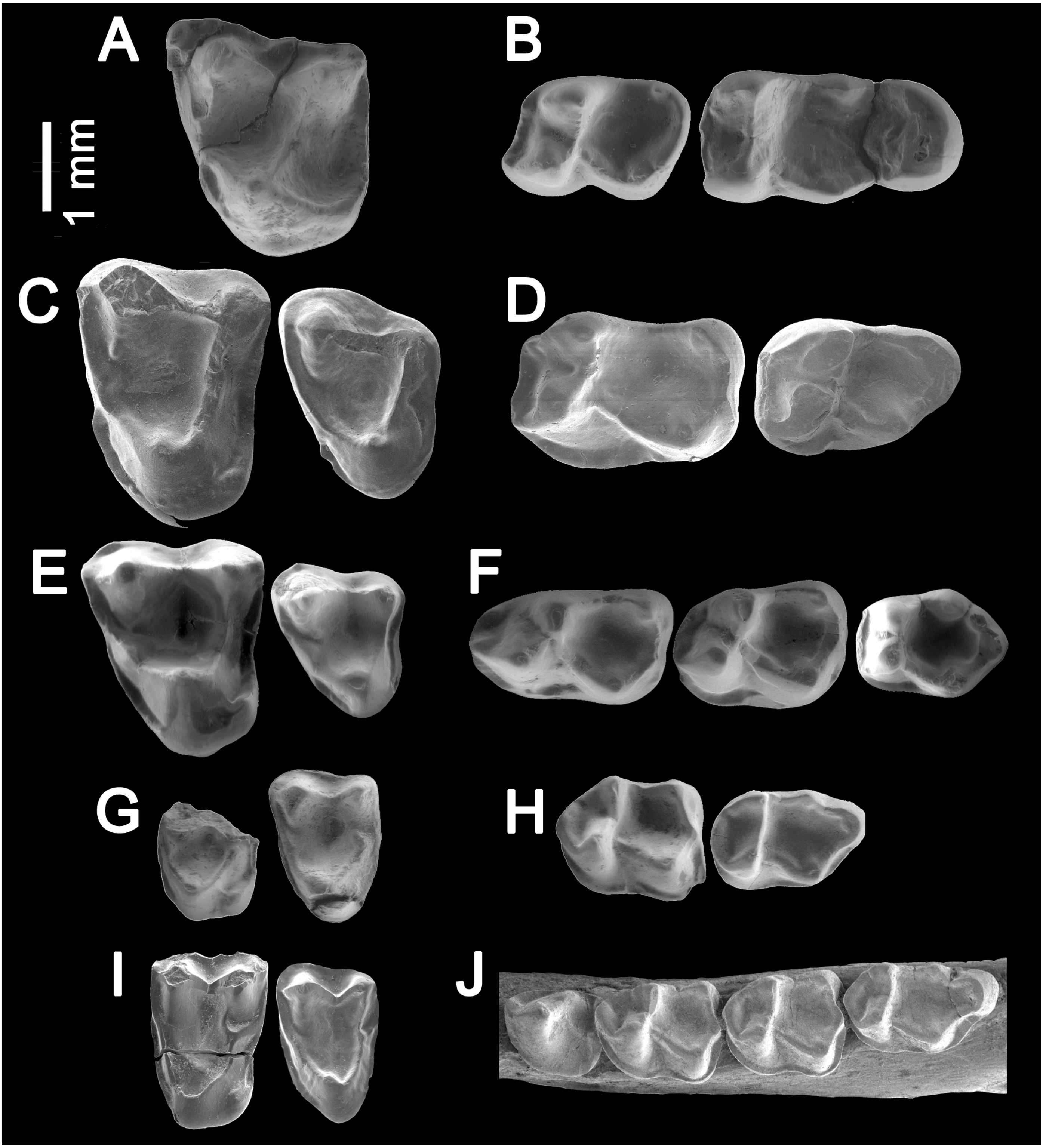

Fig. 1.- Selected dentognathic remains of fossil primates from the Iberian Paleogene. **A**, Left M^{1-2} (IPS57508) of *Arcius* sp. from Masia de l'Hereuet; **B**, Right M_{1-2} (IPS57510, reversed) and right M_3 (IPS57511, reversed) of *Arcius* sp. from Masia de l'Hereuet; **C**, Right M^{1-2} (IPS46263, reversed) and right M^3 (IPS46266, reversed) of *Mazateronodon endemicus* from Mazaterón; **D**, Left M_2 (IPS46232) and left M_3 (IPS46234) of *Mazateronodon endemicus* from Mazaterón; **E**, Right M^{1-2} (IPS8429, holotype, reversed) and right M^3 (IPS8423, reversed) of *Anchomomys frontanyensis* from Sant Jaume de Frontanyà 3; **F**, Left M_1 (IPS8543), left M_2 (IPS8487) and right M_3 (IPS8447, reversed) of *Anchomomys frontanyensis* from Sant Jaume de Frontanyà 3; **G**, Right M^{1-2} (IPS46205, reversed) and right M^3 (IPS46206, reversed) of *Pseudoloris cuestai* from Mazaterón; **H**, Right M_2 (IPS46195, reversed) and left M_3 (IPS46196, holotype) of *Pseudoloris cuestai* from Mazaterón; **I**, Left M^{1-2} (IPS46335) and right M^3 (IPS46342, reversed) of *Pseudoloris pyrenaicus* from Sant Jaume de Frontanyà 3; **J**, Fragment of a right mandible with P_4-M_3 (IPS46297, holotype, reversed) of *Pseudoloris pyrenaicus* from Sant Jaume de Frontanyà 3.

Anchomomys cf. *pygmaeus* (Gingerich, 1977)

Geographic distribution: Switzerland and Spain.

Chronological range: 44–42 Ma (MP13–14, Geiseltalian-Robiacian, Middle Eocene).

Iberian localities: Santa Clara (Zamora).

Remarks: The only available material is an M_2 that resembles that of *A.* cf. *pygmaeus* En-1 specimen from Egerkingen, first attributed to *A. stehlini* by Gingerich (1977), but later assigned to *A.* cf. *pygmaeus* by Godinot (1988).

Main references: Gingerich (1977); Godinot (1988); Peláez-Campomanes *et al.* (1989); Antunes *et al.* (1997); Marigó *et al.* (2011c).

Genus *Mazateronodon* Marigó, Minwer-Barakat and Moyà-Solà, 2010
(Fig. 1C-D).
Mazateronodon endemicus Marigó, Minwer-Barakat and Moyà-Solà, 2010

Geographic distribution: Exclusively known from the type locality.

Chronological range: 42–37 Ma, MP15–16, Robiacian, Middle Eocene.

Iberian localities: Mazaterón [type locality] (Soria).

Remarks: This taxon allowed the description, for the first time, of almost all the dental elements and the anterior dentition for a member of the Anchomomyini. The material attributed to *Mazateronodon endemicus* is the richest Eocene primate assemblage from the Western Iberian Bioprovince. *Mazateronodon* differs morphologically and biometrically from all the other anchomomyins, and it is characterized by its extremely buccolingually compressed P_3 and P_4, with the P_3 larger than the P_4, its highly imbricated premolars, with overlapping crowns and buccal and lingual cingulids. Some similarities with the material assigned to *Anchomomys* from Caenes (Duero Basin) and *Anchomomys frontanyensis* (Pyrenean Basin) strongly suggest an Iberian origin of this taxon. The unique features of *Mazateronodon* support the idea of endemism in the Eocene faunas of the Duero Basin, and the existente of a Western Iberian Bioprovince, isolated form the rest of Europe during the Eocene due to a marine transgression that connected the Cantabric and the Mediterranean seas.

Main references: Antunes *et al.* (1997); Marigó *et al.* (2009, 2010, 2011b, c).

Family Adapidae Trouessart, 1879
Subfamily Adapinae Trouessart, 1879
Genus *Leptadapis* Gervais, 1876
Leptadapis priscus (Stehlin, 1916)

Geographic distribution: Switzerland and Spain.

Chronological range: 44–42 Ma (MP13–14, Geiseltalian-Robiacian, Middle Eocene).

Iberian localities: Capella (Huesca).

Remarks: The material from Capella was the first adapiform recovered from Spain. It consists of a single mandible fragment with I_2-M_3, which was attributed to *Adapis priscus* by Crusafont-Pairó (1965b). Later on, *Adapis priscus* was transfered to *Leptadapis* by Szalay and Delson (1979).

Main references: Crusafont-Pairó (1958a, 1965b, 1967); Crusafont-Pairó and Golpe-Posse (1974, 1975); Antunes *et al.* (1997); Marigó *et al.* (2011c).

Leptadapis capellae (Crusafont-Pairó, 1967)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 43–42 Ma (MP14, Robiacian, Middle Eocene).

Iberian localities: Capella [type locality] (Huesca).

Remarks: This species, known exclusively from the holotype (a single M^3), was defined as *Arisella capellae* by Crusafont-Pairó (1965b), and then transfered to *Leptadapis* by Szalay (1971).

Main references: Crusafont-Pairó (1965b; 1967); Szalay (1971); Crusafont-Pairó and Golpe-Posse (1968, 1974); Antunes *et al.* (1997); Marigó *et al.* (2011c).

Leptadapis magnus (Filhol, 1874)

Geographic distribution: France, UK and Spain.

Chronological range: 40.5–34 Ma (MP16–MP18-19, Robiacian-Headonian, Middle–Late Eocene).

Iberian localities: Roc de Santa (Barcelona).

Remarks: Originally described within the genus *Adapis* by Filhol (1874), it was subsequently attributed to *Leptadapis* by Gervais (1876), which after more accurate studies was recently confirmed by Godinot and Couette (2008). The scarce material from Roc de Santa, a right maxilla with P^3-M^3 and a left mandible with a broken P_3 and the P_4-M_2 series, was assigned to *Adapis* cf. *magnus* by Crusafont-Pairó and Golpe-Posse (1974), given its somewhat smaller size compared to the type material. Nevertheless, subsequent studies have confirmed the ascription of the material from Roc de Santa to this species (Casanovas-Cladellas, 1975; Casanovas, 1998; Antunes *et al.*, 1997).

Main references: Crusafont-Pairó and Golpe-Posse (1974, 1975); Antunes *et al.* (1997); Marigó *et al.* (2011c).

Genus *Adapis* Cuvier, 1821
Adapis cf. *parisiensis* Cuvier, 1821

Geographic distribution: France, UK and Spain.

Chronological range: 40.5–34 Ma (MP16–19, Robiacian–Headonian, Middle–Late Eocene).

Iberian localities: Sossís (Lleida).

Remarks: The published material from Sossís consists of an upper molar (probably an M^1) and an upper premolar

(Crusafont-Pairó and Golpe-Posse, 1974). They were attributed to *Adapis* cf. *parisiensis*, although Antunes *et al.* (1997) cited them as *Leptadapis* cf. *ruetimeyeri*. Later studies, however, attributed the material again to *A.* cf. *parisiensis* (Casanovas, 1998), so we think that the attribution by Antunes *et al.* (1997) to *L.* cf. *ruetimeyeri* was merely a mistake. The detailed study of additional material from this locality, recovered from subsequent field campaigns and still unpublished, may increase the number of specimens ascribed to this taxon.

Main references: Crusafont-Pairó (1967); Crusafont-Pairó and Golpe-Posse (1974; 1975); Antunes *et al.* (1997); Casanovas (1998); Marigó *et al*. (2011c).

Adapis sp.

Iberian localities: Sant Jaume de Frontanyà 3 (Barcelona).

Remarks: The genus *Adapis* has an exclusively European geographic distribution, including France, Switzerland, UK and Spain. It is known from the Robiacian (MP14, Middle Eocene) to the Headonian (MP19, Late Eocene). The material from Sant Jaume de Frontanyà 3 consists of several isolated teeth, currently under study, that may allow a specific determination.

Main references: Moyà-Solà and Köhler (1993b); Antunes *et al.* (1997); Marigó *et al*. (2011c); Miwer-Barakat *et al*. (2011a).

cf. *Adapis* sp.

Iberian localities: Mazaterón (Soria).

Remarks: A mandibular fragment with the complete molar series from this locality is currently under study. It has been tentatively assigned to *Adapis*, although the material may be too scarce to be determined to the species level.

Main references: Antunes *et al.* (1997); Marigó *et al.* (2009, 2010, 2011c); Minwer-Barakat *et al.* (2012)

Genus *Microadapis* Szalay, 1974
Microadapis sp.

Iberian localities: Caenes (Salamanca).

Remarks: The genus *Microadapis* is known from several Swiss and Spanish Middle Eocene localities ranging in age from the MP13 (Geiseltalian) to the MP16 (Robiacian). The material from Caenes consists only of a single upper molar. Until more material is recovered, it is not possible to reach a species determination.

Main references: Moyà-Solà and Köhler (1992); Antunes *et al.* (1997); Marigó *et al.* (2011c).

Suborder Haplorrhini Pocock, 1918
Infraorder Tarsiiformes Gregory, 1915
Superfamily Omomyoidea Trouessart, 1879
Family Omomyidae Trouessart, 1879
Omomyidae indet.

Iberian localities: Pontils 38 (Barcelona).

Remarks: The material consists of two isolated molars of a very small omomyid. The detailed study of these remains, as well as further fieldwork for obtaining more material, may allow the description of a new taxon.

Main references: Antunes *et al.* (1997); Marigó *et al.* (2011c).

Subfamily Microchoerinae Lydekker, 1887
Microchoerinae indet.

Iberian localities: Zambrana (Álava).

Remarks: The material from Zambrana consists of two well-preserved right mandibular fragments with relatively complete dental series, including P_3-M_3 and P_4-M_3. The overall dental morphology and the presence of enamel wrinkling are similar to those observed in the genera *Necrolemur* and *Microchoerus*. The detailed study of this material, now under way, will lead to a more precise determination. This discovery, together with that of *Pseudoloris cuestai* from Mazaterón (Minwer-Barakat *et al.*, 2012), constitutes the first record of microchoerines in the Western Iberian Bioprovince.

Main references: Minwer-Barakat *et al.* (2011b).

Genus *Microchoerus* Wood, 1844
Microchoerus erinaceus Wood, 1844

Geographic distribution: UK, France, Switzerland and Spain.

Chronological range: 40.5–35 Ma (MP16–18, Robiacian–Headonian, Middle–Late Eocene).

Iberian localities: Sossís (Lleida).

Remarks: This large-sized microchoerine from Sossís was first reported by Crusafont-Pairó (1965b), and subsequently Crusafont-Pairó (1967) briefly described a quite complete sample of this species, including isolated teeth, some dental series and several fragments of mandibles and maxillae. This author further figured a lower dental series including P_3-M_3, and an upper dental series with M^1 and M^2. Crusafont-Pairó (1967) and Crusafont-Pairó and Golpe-Posse (1974) referred these remains to *Necrolemur erinaceus*, but later works (Antunes *et al.*, 1997; Casanovas, 1998) employed the correct denomination, i.e. *Microchoerus erinaceus*. Subsequent field work led to the recovery of more abundant material, which is still unpublished. A preliminary observation of this material reveals some biometric and morphologic differences relative to the material from the type locality (Hordle Cliff Crocodile Bed, Hampshire, UK). However, until a detailed study of the population from Sossís is carried out, we prefer mantaining the attribution to *M. erinaceus*.

Main references: Crusafont-Pairó (1965b, 1967); Crusafont-Pairó and Golpe-Posse (1974); Antunes *et al.* (1997); Casanovas (1998); Marigó *et al*. (2011c).

Microchoerus ornatus Stehlin, 1916

Geographic distribution: Switzerland and Spain.

Chronological range: 35–34 Ma (MP19, Headonian, Late Eocene).

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

Remarks: Only known from upper teeth, *Microchoerus ornatus* has been considered doubtfully distinct from *M. edwardsi* (Hooker, 1986; Gunnell and Rose, 2002). In the Iberian Peninsula, the only material assigned to this species is a fragment of maxilla with P^4-M^1 from Sant Cugat de Gavadons, which according to Crusafont-Pairó (1967) and Crusafont-Pairó and Golpe-Posse (1974), shares strong similarities with the material from the type locality of *M. ornatus* (Mormont-Entreroches, Switzerland).

Main references: Crusafont-Pairó (1967); Crusafont-Pairó and Golpe-Posse (1974); Golpe-Posse (1982c); Marigó *et al*. (2011c).

Microchoerus sp.

Iberian localities: Aguatón (Teruel).

Remarks: The genus *Microchoerus* is well represented in Central and Western Europe (Spain, France, UK, Switzerland and Germany), in localities that range in age from the Robiacian (MP16, Middle Eocene) to the Suevian (MP21, Early Oligocene). In the Iberian Peninsula, besides the above-mentioned remains ascribed to *M. erinaceus* and *M. ornatus*, a single M_1 from the site of Aguatón was described by Peláez-Campomanes (2000). This tooth, similar in size to those of *M. erinaceus*, shows morphological and/or metrical differences with all the previously described species of *Microchoerus* (except for *M. ornatus*, only known from upper teeth). However, due to the scarcity of material, the author preferred not to describe a new species until more material is available.

Main references: Peláez-Campomanes (2000).

Genus *Pseudoloris* Stehlin, 1916

Pseudoloris isabenae (Crusafont-Pairó, 1967)

Geographic distribution: Spain and France.

Chronological range: 44–43 Ma (MP13–14, Geiseltalian-Robiacian, Middle Eocene).

Iberian localities: Capella [type locality] (Huesca).

Remarks: This species was originally ascribed to the genus *Pivetonia* by Crusafont-Pairó (1967); however, most authors have considered *Pivetonia* to be a junior subjective synonym of *Pseudoloris* (Szalay, 1971; Godinot, 1983; Gunnell and Rose, 2002; Minwer-Barakat *et al.*, 2010, 2012). The only available material from Capella is a mandible fragment with P_3-M_2. It differs from other species of *Pseudoloris* found in the Iberian Peninsula in the smaller size and the presence of a well-individualized tubercular paraconid in the lower molars.

Main references: Crusafont-Pairó (1965b, 1967); Szalay (1971); Crusafont-Pairó and Golpe-Posse (1968, 1974); Antunes *et al.* (1997); Minwer-Barakat *et al.* (2010, 2012); Marigó *et al*. (2011c).

Pseudoloris pyrenaicus Minwer-Barakat, Marigó and Moyà-Solà, 2010

(Fig. 1I-J)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 43–42 Ma (MP14, Robiacian, Middle Eocene).

Iberian localities: Sant Jaume de Frontanyà 3 [type locality] (Barcelona).

Remarks: The material of this species represents the most complete sample of the genus *Pseudoloris* published from the Iberian Peninsula, having enabled the description of almost all the dental elements, including upper and lower incisors, undescribed for most species of this genus. *P. pyrenaicus* can be distinguished from the other *Pseudoloris* species by its medium size and by several morphological features, such as the absence of a distinct paraconid and the thickened paracristid in the lower molars, the large hypoconulid in the M_3, the small hypocone and paraconule in the M^1 and M^2, and the absence of these two cusps in the M^3. This species, an intermediate form between *P. isabenae* and *P. parvulus*, forms part of an anagenetic lineage that evolved in Europe during the Middle–Late Eocene.

Main references: Moyà-Solà and Köhler (1993b); Antunes *et al.* (1997); Minwer-Barakat *et al.* (2010, 2011a); Marigó *et al.* (2011b, c).

Pseudoloris cuestai Minwer-Barakat, Marigó and Moyà-Solà, 2012

(Fig. 1G-H).

Geographic distribution: Exclusively known from the type locality.

Chronological range: 42–37 Ma (MP15–16, Robiacian, Middle Eocene).

Iberian localities: Mazaterón [type locality] (Soria).

Remarks: *P. cuestai* represents, together with the undetermined Microchoerinae from Zambrana, the only record of this subfamily in the Western Iberian Bioprovince. It can be distinguished from the other *Pseudoloris* species by its medium size, high and thick paracristid and absence of a distinct paraconid in the lower molars, large hypoconulid in the M_3, well-developed protocone in the P^3 and P^4, small hypocone in the upper molars, and especially for its particular lower incisors, with a large, buccolingually enlarged crown and a thick root. It shows several similarities with *P. pyrenaicus* and *P. parvulus*, the closest species in age and geographic situation. Nevertheless, there are also clear differences with those species, especially in the anterior dentition. The peculiar morphology of the I_1, together with the short roots of the lower canine and P_3, suggests an anterior dentition that differs from that of *P. pyrenaicus* and *P. parvulus*, perhaps in relation to dietary differences.

Main references: Antunes *et al.* (1997); Marigó *et al.* (2009, 2011b, c); Minwer-Barakat *et al.* (2010, 2012).

Pseudoloris parvulus (Filhol, 1890)

Geographic distribution: France and Spain.

Chronological range: 40.5–36.5 Ma (MP16–17, Robiacian-Headonian, Middle-Late Eocene).

Iberian localities: Sossís (Lleida).

Remarks: The material described by Crusafont-Pairó (1965b, 1967) and Crusafont-Pairó and Golpe-Posse (1974) consists of a single mandibular fragment with P_4-M_3. However, there is additional, still unpublished material of *P. parvulus* from Sossís housed at the Institut Català de Paleontologia Miquel Crusafont. Among other features, *P. parvulus* from Sossís shows a low and sharp paracristid in the lower molars, a compressed hypoconulid in the M_3, and the hypocone of the upper molars more developed than *P. pyrenaicus* and *P. cuestai*. This species has been identified in several Robiacian and Headonian French sites, but the only mention in the Iberian Peninsula corresponds to Sossís.

Main references: Crusafont-Pairó (1965b, 1967); Crusafont-Pairó and Golpe-Posse (1974); Antunes *et al.* (1997); Minwer-Barakat *et al.* (2010); Marigó *et al.* (2011c).

Pseudoloris reguanti Crusafont-Pairó, 1967
(nomen dubium)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 35–34 Ma (MP19, Headonian, Late Eocene).

Iberian localities: Sant Cugat de Gavadons (=Collsuspina) [type locality] (Barcelona).

Remarks: This species was described by Crusafont-Pairó (1967) on the basis of a single isolated lower molar from Sant Cugat de Gavadons, larger than those of *P. parvulus,* and with a paracristid instead of a tubercular paraconid. Schmidt-Kittler (1977) considered this species as a *nomen nudum* because of the lack of illustrations of the holotype; however, according to the International Code of Zoological Nomenclature, this reason does not invalidate the species name from a nomenclatural viewpoint. Unfortunately, as pointed out by Köhler and Moyà-Solà (1999), this specimen was lost in the 1970s. Therefore, until more material is available, the taxonomic validity of this nominal taxon cannot be further evaluated, so we consider it a *nomen dubium*.

Main references: Crusafont-Pairó (1967); Crusafont-Pairó and Golpe-Posse (1974); Schmidt-Kittler (1977); Golpe-Posse (1982c); Köhler and Moyà-Solà (1999); Minwer-Barakat *et al.* (2010, 2012); Marigó *et al.* (2011c).

Pseudoloris godinoti Köhler and Moyà-Solà, 1999

Geographic distribution: Exclusively known from Spain.

Chronological range: 34–31 Ma (MP21–22, Suevian, Early Oligocene).

Iberian localities: Fonollosa 13 [type locality] and Santpedor 2 (Barcelona).

Remarks: *P. godinoti* is known only by six complete teeth (including an upper series of P^2-M^1 designated as the holotype) and two fragments, recovered from the Oligocene localities of Santpedor-2 and Fonollosa-13. The M^1 has a reduced trigon basin, a large and well-individualized hypocone and a prominent metastyle, and the M_1 shows a distinct paraconid. This is the only record of the genus *Pseudoloris* after the Eocene-Oligocene boundary.

Main references: Köhler and Moyà-Solà (1999); Minwer-Barakat *et al.* (2010, 2012); Marigó *et al.* (2011c).

Pseudoloris sp.

Iberian localities: Casa Ramón (Huesca).

Remarks: The genus *Pseudoloris* is known from several sites in France, UK, Germany and Spain, ranging in age from the Geiseltalian (Middle Eocene, MP11–12) to the Suevian (Early Oligocene, MP22). The Geiseltalian Spanish site of Casa Ramón (Peláez-Campomanes, 1995) has yielded two fragments of M^1 and M^3 and a complete M^2 ascribed to *Pseudoloris* sp., being similar in size but morphologically different compared to those of *P. parvulus*. The M^2 from Casa Ramón shows poorly-developed metaconule crests, and small paraconule and metaconule. The scarce material from this Spanish site, assigned to the MP11 or MP12, represents the earliest record of the genus *Pseudoloris*.

Main references: Peláez-Campomanes (1995); Antunes *et al.* (1997); Minwer-Barakat *et al.* (2010, 2012); Marigó *et al.* (2011c).

Genus *Necrolemur* Filhol, 1873
Necrolemur antiquus Filhol, 1873

Geographic distribution: France and Spain.

Chronological range: 37–36.5 Ma (MP17–20, Headonian, Late Eocene).

Iberian localities: Roc de Santa (Barcelona).

Remarks: Known from several Late Eocene sites from France, *N. antiquus* has only been mentioned in the Iberian Peninsula from the locality of Roc de Santa. The material consists of a single, heavily worn M_3 described by Casanovas-Cladellas (1975). The scarcity and poor preservation of the material makes such specific assignation doubtful, but until a more detailed study is carried out, we prefer maintaining the above-mentioned determination.

Main references: Casanovas-Cladellas (1975); Antunes *et al.* (1997); Casanovas (1998); Marigó *et al.* (2011c).

Necrolemur sp.

Iberian localities: Sant Jaume de Frontanyà 1 and 2, and Sant Cugat de Gavadons (=Collsuspina) (Barcelona).

Remarks: The genus *Necrolemur* is known from several French, Swiss and Spanish sites ranging in age from the Geiseltalian (MP13, Middle Eocene) to the Headonian (MP20, Late Eocene). There are two citations of the genus *Necrolemur* without specific determination in the Iberian Peninsula. On the one hand, Crusafont-Pairó (1967) and Crusafont-Pairó and Golpe-Posse (1974) assigned to this genus a single, large and very worn M^2 from Sant Cugat de Gavadons. There is no available illustration of this specimen, whose attribution cannot be confirmed based on the material from the Institut Català de Paleontologia Miquel Crusafont. The generic ascription of this tooth is therefore doubtful, since another large-sized microchoerine, ascribed by the same authors to *Microchoerus ornatus*, was identified in this locality; it seems probable that these remains belong to the same taxon. On the other hand, *Necrolemur* sp. has also been cited from the Robiacian levels of Sant Jaume de Frontanyà 1 and 2 (Busquets *et al.*, 1992; Antunes *et al.*, 1997). The material consists of several isolated teeth and a mandible with P_4-M_3 of a small microchoerine. A detailed study, currently under way, will allow a more precise determination of this material.

Main references: Crusafont-Pairó (1967); Crusafont-Pairó and Golpe-Posse (1974); Golpe-Posse (1982c); Busquets *et al.* (1992); Antunes *et al.* (1997); Marigó *et al.* (2011c).

Infraorder Simiiformes Hoffstetter, 1974
(=Anthropoidea Mivart, 1864)

Remarks: Hoffstetter (1974) proposed Simiiformes as a replacement name for Anthropoidea, apparently on the basis of insufficient grounds (Delson, 1977), although it has several advantages such as avoiding the standard superfamily ending in –oidea for a taxon above the family-group level (see Delson, 1977, and Hoffstetter, 1982, for further details). Both Simiiformes and Anthropoidea have been recently used by several authors with the same meaning (e.g., Groves, 2001 and Fleagle, 1999, respectively; but see Rosenberger, 2006, for a different option), and hence are considered synonyms here. The International Code of Zoological Nomenclature does not regulate these taxonomic ranks, and hence the use of one or the other remains arbitrary.

Parvorder Catarrhini É. Geoffroy Saint-Hilaire, 1812
Superfamily Pliopithecoidea Zapfe, 1960
Family Pliopithecidae Zapfe, 1960
Subfamily incertae sedis
Pliopithecidae indet.

Iberian localities: Abocador de Can Mata/C3-B2.

Remarks: The oldest record of Iberian pliopithecids corresponds to an isolated M^3 from ACM/C3-B2 (Alba *et al.*, 2012a), which has an estimated age of 12.0 Ma (MN7, late Aragonian, Middle Miocene). This tooth displays a very peculiar occlusal morphology, which enables it to be distinguished from all other pliopithecids for which this dental position is known (including *Barberapithecus*, see below, but not *Pliopithecus canmatensis*). It is also possible that this primate tooth does not belong to the Pliopithecidae but to some other group of stem catarrhines previously not recorded in Eurasia. However, on paleobiogeographic grounds, an attribution to the Pliopithecidae was favored by Alba *et al.* (2012a).

Main references: Alba *et al.* (2012a).

Subfamily Pliopithecinae Zapfe, 1960
Genus *Pliopithecus* Gervais, 1849
Pliopithecus canmatensis Alba *et al.*, 2010d
(Fig. 2A)

Geographic distribution: Restricted to the Vallès-Penedès Basin (Barcelona).

Chronological range: 11.8–11.7 Ma (MN8, late Aragonian, Middle Miocene).

Iberian localities: Abocador de Can Mata localities ACM/C5-C3, ACM/C4-Cb, ACM/C5-C2, ACM/C5-A8 and ACM/C4-A1.

Remarks: This species is known from several mandibles, dentognathic fragments and isolated teeth that overall record most of the permanent dentition as well as the dP_4. These remains correspond to at least 8 individuals from 5 different localities of the Abocador de Can Mata series; although an age range of 11.7–11.6 was originally reported for this species (Alba *et al.*, 2010d), subsequent analyses have redated it to 11.8–11.7 Ma (Alba *et al.*, 2012a). The pliopithecine morphology and the small size of the dental remains from these several localities from Abocador de Can Mata is most similar to that of *Pliopithecus antiquus* from the French localities of Sansan (MN6) and La Grive (MN7+8), but dental proportions as well as several occlusal details (less peripheral position of the protoconid and more median position of the hypoconulid, more mesial position of the buccal cuspids compared to the lingual ones, narrower but distinct mesial fovea, higher trigonid, and more extensive buccal cingulid) justify a taxonomic distinction at the species level for the ACM material (Alba *et al.*, 2010d).

Main references: Alba *et al.* (2010c, d, 2012a).

Pliopithecus sp.

Iberian localities: Sant Quirze (Barcelona).

Remarks: Pliopithecids are recorded in the late Aragonian (MN8, ca. 11.8–11.2 Ma) locality of Sant Quirze by an isolated M^2 described by Harrison *et al.* (2002). Both in size and morphology, this tooth is consistent with an attribution to *Pliopithecus platyodon*, otherwise unknown from the Iberian Peninsula. However, the scarcity of the available material precludes evaluating whether it might represent a different species. In any case, an attribution to *P. canmantensis* can be easily discarded on the larger size of the Sant Quirze molar.

Main references: Harrison *et al.* (2002).

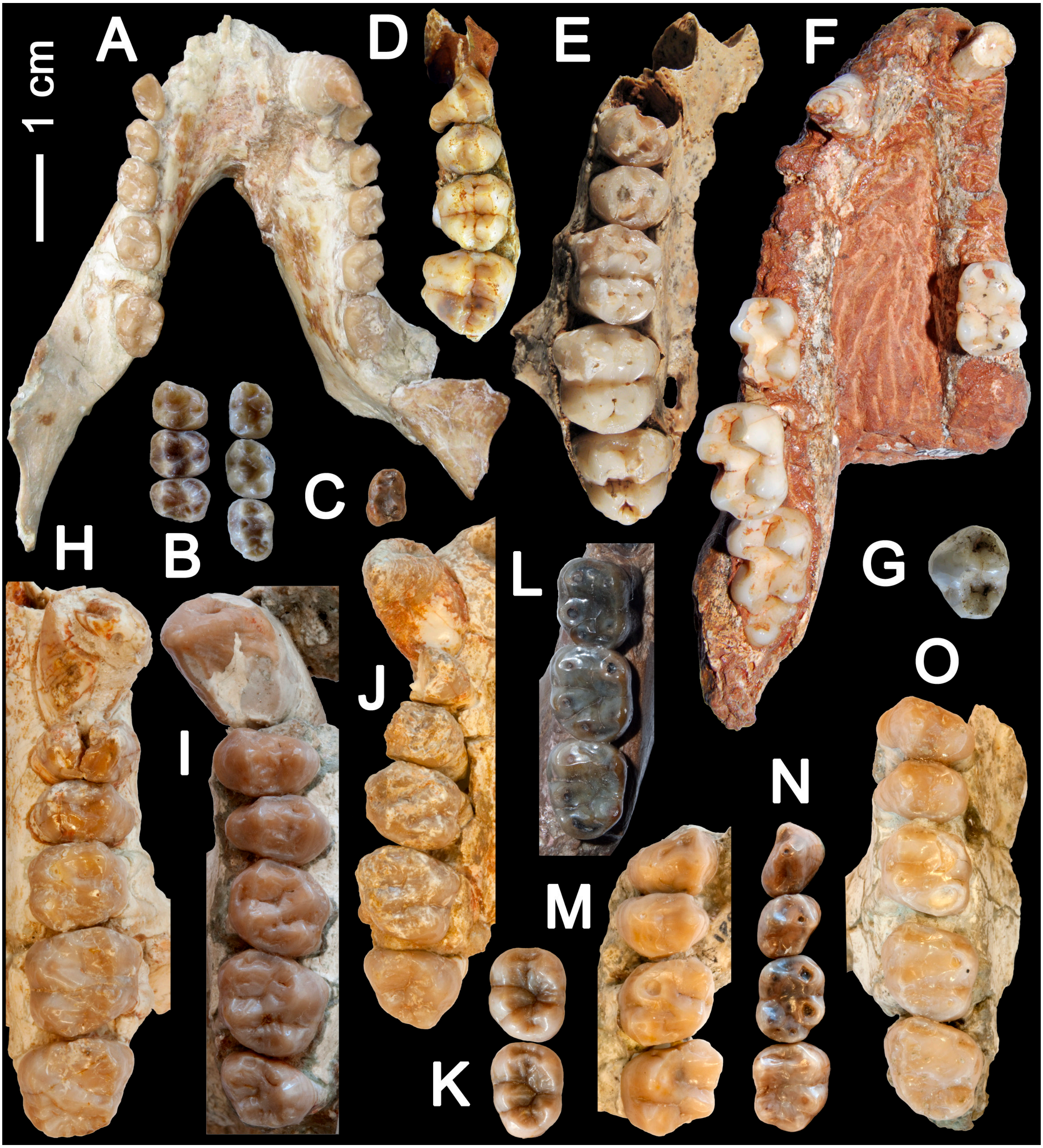

Fig. 2.- Selected dentognathic remains of fossil primates from the Iberian Neogene and Quaternary. **A**, Mandible with left P_3-M_3 and right C_1-M_3 (IPS35036, holotype) of *Pliopithecus canmatensis* from ACM/C4-A1; **B**, Right M^1-M^3 and left M_1-M_3 (IPS1724, holotype; M_2 reversed) of *Barberapithecus canmatensis* from Castell de Barberà; **C**, Right dP_4 (IPS35565) of cf. Anapithecini indet. from Can Sant Feliu; **D**, Right P^3-M^2 (EVT24036) of *Macaca sylvanus* cf. *florentina* from Vallparadís Estació; **E**, Right P^3-M^3 (Q05-Ec-88) of *Macaca sylvanus florentina* from Quibas; **F**, Mandible with right M_1-M_3 and left M_1 (Museu del Seminari) of *Paradolichopithecus* sp. from Cova Bonica; **G**, Left P_4 (no catalogue number) of *Theropithecus oswaldi* from Cueva Victoria; **H**, Left C^1-M^3 (IPS35026) of *Dryopithecus fontani* from ACM/C3-Ae; **I**, Right C^1-M^3 (IPS21350, holotype) of *Pierolapithecus catalaunicus* from ACM/BCV1; **J**, Right C^1-M^3 (IPS43000, holotype) of *Anoiapithecus brevirostris* from ACM/C3-Aj; **K**, Left M_2-M_3 (IPS1826+IPS1827, holotype) of *"Sivapithecus" occidentalis* (nomen dubium) from Can Vila; **L**, Mandible with left M_1-M_3 (Museu del Seminari) of *Hispanopithecus crusafonti* from Teuleria del Firal; **M**, Left P^3-M^2 (IPS1798, holotype) of *Hispanopithecus crusafonti* from Can Poncic 1; **N**, Right P_3-M_2 (IPS1803, holotype) of *Hispanopithecus laietanus* from La Tarumba 1; **O**, Right P^3-M^3 (IPS18000.5) of *Hispanopithecus laietanus* from Can Llobateres 2.

Subfamily Crouzeliinae Ginsburg and Mein, 1980
(Fig. 2B)
Tribe Anapithecini Alba and Moyà-Solà, 2012a
Genus *Barberapithecus* Alba and Moyà-Solà, 2012a
Barberapithecus huerzeleri Alba and Moyà-Solà, 2012a

Geographic distribution: Exclusively known from the type locality.

Chronological range: 11.2–10.5 Ma (MN8 or MN9, late Aragonian or early Vallesian, Middle or Late Miocene).

Iberian localities: Castell de Barberà [type locality] (Barcelona).

Remarks: This taxon is only known from isolated dental remains recovered at the locality of Castell de Barberà, initially attributed to the Aragonian, but currently attributable to the latest Aragonian or, most likely, the earliest Vallesian. The find was initially reported more than three decades ago (Crusafont-Pairó, 1978). Most of the remains, including upper and lower teeth, correspond to a single, female adult individual. They were partly described and initially attributed to *Pliopithecus* sp. by Crusafont-Pairó and Golpe-Posse (1981), who nevertheless noted dental similarities with *Plesiopliopithecus lockeri*, currently attributed to the Crouzeliini. These authors noted that this material was likely to represent a new pliopithecid taxon, but refrained from formally erecting it. Later, Ginsburg (1986) attributed the Castell de Barberà remains to Crouzeliinae nov., but subsequently the taxon was considered a pliopithecine similar or attributable to *Pliopithecus antiquus* by several authors (Moyà Solà *et al*., 1990; Andrews *et al*., 1996; Harrison *et al*., 2002). Both Begun (2002a) and Alba *et al*. (2010d) considered it to be a new pliopithecid taxon, and most recently Alba and Moyà-Solà (2012a) erected a new genus and species for it within the Crouzeliinae. Besides the holotype individual, an isolated P_3 and male C^1 from the type locality are also attributed to this taxon (Alba and Moyà-Solà *et al*., 2012a). The latter was formerly considered a female upper canine of the hominoid *Hispanopithecus laietanus* (Harrison, 1991; Golpe Posse, 1993), but on morphological grounds it is best attributable to the Pliopithecidae (Begun, 2002a; Alba *et al*., 2010d; Alba and Moyà-Solà, 2012a). Like crouzeliins, *Barberapithecus* is characterized by buccolingually-compressed cusps, well-developed and sharp crests, and large and well-defined occlusal foveae. Its dental morphology, however, might have evolved from a pliopithecine ancestor similar to *Pliopithecus canmatensis*, which leaves open the possibility that, as currently conceived, the crouzeliines are polyphyletic (Alba and Moyà-Solà, 2012a).

Main references: Crusafont-Pairó (1978); Crusafont-Pairó and Golpe-Posse (1981, 1982); Moyà Solà *et al*. (1990); Andrews *et al*. (1996); Begun (2002a); Alba and Moyà-Solà (2012a); Alba *et al*. (2012a).

Genus *Egarapithecus* Moyà-Solà, Köhler and Alba, 2001
Egarapithecus narcisoi Moyà-Solà, Köhler and Alba, 2001

Geographic distribution: Exclusively known from the type locality.

Chronological range: 9.0–8.9 Ma (MN10, Vallesian, Late Miocene).

Iberian localities: Torrent de Febulines [type locality] (Barcelona).

Remarks: This taxon is known on the basis of a fragmentary mandible with right P_3-M_3 and left P_3-M_2 (holotype), as well as an isolated P^3 probably from the same individual. This material was initially published by Golpe-Posse (1982b), who attributed it to *Pliopithecus* sp. in spite of noting several differential features that, according to her, might justify the erection of a new taxon. This was confirmed by Moyà Solà *et al*. (1990) and Andrews *et al*. (1996), although the new genus and species were not erected until Moyà-Solà *et al*. (2001) described it and attributed it to the Crouzeliinae. Subsequently, Begun (2002a) considered it to be a Pliopithecinae, but this has been subsequently dismissed by other authors (Harrison *et al*., 2002; Alba *et al*., 2010d; Alba and Moyà-Solà, 2012a).

Main references: Golpe Posse (1982b); Moyà-Solà *et al*. (1990, 2001); Andrews *et al*. (1996); Begun (2002a); Alba *et al*. (2010c).

cf. Anapithecini indet.
(Fig. 2C)

Iberian localities: Can Sant Feliu (=Can Feliu, Barcelona).

Remarks: Crouzeliine affinities were noted by several authors (Moyà Solà *et al*., 1990; Andrews *et al*., 1996) for the isolated dP_4 from the late Aragonian (MN8, ca. 11.8–11.2 Ma) locality of Can Sant Feliu, initially mistaken for an M_3 (Crusafont-Pairó and Golpe-Posse, 1981). Begun (2002a) suggested that it might correspond to a larger individual of the same taxon represented at Castell de Barberà (currently, *Barberapithecus huerzeleri*), but given the presence of other pliopithecids (*Pliopithecus canmatensis*) during the late Aragonian in the same basin, most recently Alba and Moyà-Solà (2012a) refrained from providing a formal taxonomic attribution.

Main references: Crusafont-Pairó and Golpe-Posse (1981, 1982); Moyà Solà *et al*. (1990); Begun (2002a); Harrison *et al*. (2002); Alba and Moyà-Solà (2012a).

Superfamily Cercopithecoidea Gray, 1821
Family Cercopithecidae Gray, 1821
Subfamily Cercopithecinae Gray, 1821
Tribe Papionini Burnett, 1828
Subtribe Macacina Owen, 1843
Genus *Macaca* Lacépède, 1799
Macaca sp.

Iberian localities: Almenara-Casablanca M (Castellon); Orrios 7 (Teruel); Sima del Elefante TE9 (Burgos); Ambrona (Soria).

Remarks: The genus *Macaca* is first recorded in Europe in the latest Miocene locality of Almenara-Casablanca M (Köhler *et al*., 2000), after which it is known across the continent throughout the Pliocene and Pleistocene. Although there is consensus that fossil European macaques belong to the *Macaca sylvanus* lineage (Szalay and Delson, 1979; Alba *et al*., 2011c), of African origin, the scarce material from Almenara-Casablanca M does not enable an attribution to the species level. All other Iberian citations of *Macaca* sp. are most likely attributable to *M. sylvanus*, since this is the only fossil European macaque species recognized besides the endemic *M. majori* from Sardinia.

Main references: Aguirre and Fuentes (1969); Delson (1974); Szalay and Delson (1979); Delson (1980); Ardito and Mottura (1987); Mein *et al*. (1990); Moyà Solà *et al*. (1990); Köhler *et al*. (2000); Carbonell *et al*. (2008).

Macaca sylvanus (Linnaeus, 1758)

Geographic distribution: W. Eurasia and N. Africa.

Chronological range: Pliocene and Pleistocene.

Remarks: This species, the Barbary macaque, currently presents a disjunct distribution in Algeria and Morocco, and is also represented by the Gibraltar population, which has an anthropocorous origin (Fooden, 2007). This species was also widely distributed throughout the Plio-Pleistocene in Western Eurasia, where three distinct subspecies are customarily recognized (Szalay and Delson, 1979; Delson, 1980): *M. s. prisca*, from the earlier Pliocene; *M. s. florentina*, from the late Pliocene to the early Pleistocene; and *M. s. pliocena,* from the Middle and perhaps Late Pleistocene.

Macaca sylvanus ssp.

Iberian localities: Cova Negra (Valencia); Cueva Negra del Estrecho del Quípar (Murcia); Solana del Zamborino (Granada); Galeria Pesada - Gruta da Aroeira (Ribatejo); Canal Negre I (Barcelona).

Remarks: With the exception of Solana del Zamborino (Martín Penela, 1983, 1988), the material from the abovementioned localities has not been described in detail, and the published citations did not include an attribution to the species level except for Guillén-Castejón (2010; see below). On chronological grounds, the macaque remains from the Middle Pleistocene localities of Cueva Negra, Solana del Zamborino and Gruta da Aroeira probably belong to *M. s. pliocena.* The remains from Canal Negre I, of uncertain age, have been attributed to both *M. s. florentina* and *Macaca* cf. *sylvanus prisca* by Guillén-Castejón (2010), mainly on the basis of size. However, size does not seem to be a reliable criterion for distinguishing among the several extinct subspecies of *M. sylvanus* (Rook *et al*., 2001), and given that no detailed description or measurements are provided by Guillén-Castejón (2010), the remains from Canal Negre are best left unassigned at the subspecies level.

Main references: Pérez Ripoll (1977); Martín Penela (1983, 1988); Ardito and Mottura (1987); Trinkaus *et al*. (2003); Walker *et al*. (2010).

Macaca sylvanus florentina (Cocchi, 1872)
(Fig. 2E)

Geographic distribution: Southern and Central Europe.

Chronological range: Late Pliocene to Early Pleistocene.

Iberian localities: Quibas (Murcia).

Remarks: The sample from the late Early Pleistocene site of Quibas (ca. 1.3–1.0 Ma) includes dentognathic remains, isolated teeth and some postcranial bone fragments (Alba *et al*., 2010c). Dental morphometric comparisons indicate that this sample is morphologically similar to *M. s. florentina* from the type locality (Upper Valdarno, Italy), further reinforcing the view that this subspecies is morphologically distinct from the extant nominotypical subspecies, by displaying on average absolutely longer upper molars, relatively wider upper molars, longer M^3 compared to the M^2, absolutely longer M_1 and M_3, and relatively narrower M_3 (Alba *et al*., 2011c).

Main references: Montoya *et al*. (1999, 2001); Alba *et al*. (2011c).

Macaca sylvanus cf. *florentina* (Cocchi, 1872)
(Fig. 2D)

Iberian localities: Cal Guardiola D7, Vallparadís Estació EVT7 and EVT10, and Canal Negre I (Barcelona), and maybe La Puebla de Valverde (Teruel).

Remarks: Although the macaque dentognathic remains from the Vallparadís Section (Cal Guardiola and Vallparadís Estació, ca. 1.0–0.78 Ma) differ metrically from the extant, nominotypical subspecies, its taxonomic attribution will remain tentative until the taxonomic distinction between *M. s. florentina* and the Middle Pleistocene *M. s. pliocena* is further clarified (Alba *et al*., 2008). The specimens from Canal Negre, previously attributed to *M. s. florentina* by Guillén-Castejón (2010), have an uncertain age, and a more detailed morphometric study would be required in order to more conclusively ascertain its taxonomic attribution to this subspecies. A dP_4 from the Early Pleistocene locality (Middle Villafranchian, MN17) of La Puebla de Valverde, initially attributed to *Macaca* sp. (Heintz *et al.*, 1971), might belong to this taxon, although subsequently Moyà Solà *et al*. (1990) attributed it to *Paradolichopithecus* sp.

Main references: Heintz *et al.* (1971); Alba *et al*. (2008, 2010c); Madurell-Malapeira *et al*. (2010); Guillén-Castejón (2010).

Macaca sylvanus cf. *pliocena* Owen, 1846

Geographic distribution: Europe, Caucasus and Israel.

Chronological range: Late Pleistocene.

Iberian localities: Lezetxiki II (Guipúzcoa).

Remarks: The mandible from Lezetxiki was tentatively attributed to *M. s. pliocena* by Castaños *et al*. (2011) merely on chronological grounds.

Main references: Castaños *et al*. (2011).

Genus *Paradolicopithecus* Necrasov, Samson and Radulesco, 1961
cf. *Paradolichopithecus* sp.

Iberian localities: Almenara-Casablanca 1 (Castellón).

Remarks: A fragmentary incisor from this Early Pleistocene locality (ca. 1.8 Ma) was tentatively assigned to the genus *Paradolichopithecus* by Moyà Solà *et al*. (1990). Additional dental material would be required to discount an alternative attribution to the genus *Macaca*.

Main references: Moyà Solà *et al*. (1990).

Paradolichopithecus sp.
(Fig. 2F)

Iberian localities: Moreda 1a (Granada) and Cova Bonica (Barcelona).

Remarks: The Late Pliocene remains from Moreda 1a (3.5–3.2 Ma) and Cova Bonica (3.2–2.6 Ma) represent de oldest records of this genus in the Iberian Peninsula. According to Moyà Solà *et al*. (1990), they may correspond to a different species than *P. arvernensis*. Additional studies, however, are required in order to clarify the taxonomic status of these remains. In the past, several authors also cited the presence of *Macaca* at Cova Bonica (e.g., Delson, 1971; Crusafont-Pairó and Golpe-Posse, 1974, 1984), whereas, according to Moyà Solà *et al*. (1990), only *Paradolichopithecus* is recorded there. The detailed study of the material from Moreda and Cova Bonica, currently in progress, will enable a decision as to whether *Macaca* is present in either of these localities and hopefully also provide a determination of the *Paradolichopithecus* remains to the species level.

Main references: Delson (1971); Crusafont-Pairó and Golpe-Posse (1984); Moyà Solà *et al*. (1990); Alba *et al*. (2010c).

Paradolichopithecus cf. *arvernensis* Depéret, 1929

Geographic distribution: Europe and Central Asia.

Chronological range: Late Pliocene to Early Pleistocene (Middle Villafranchian, MN17).

Iberian localities: La Puebla de Valverde (Teruel); Canal Negre I (Barcelona).

Remarks: The *Paradolichopithecus* material from La Puebla de Valverde was attributed to *P.* cf. *arvernensis* by Aguirre and Soto (1978). We provisionally maintain such an attribution here, although noting that the species attribution might be further refined after the study of the *Paradolichopithecus* remains from Moreda 1a and Cova Bonica, currently under study (see comments above). Several isolated dental remains from Canal Negre, of uncertain age, have been also attributed to *P. arvernensis* by Guillén-Castejón (2010), but given the lack of a detailed description and uncertainties in the attribution of other Iberian *Paradolichopithecus* remains, the teeth from this locality are only tentatively attributed to that species here.

Main references: Heinz *et al*. (1971); Aguirre and Soto (1974, 1978); Ardito and Mottura (1987); Moyà Solà *et al*. (1990); Guillén-Castejón (2010).

Subtribe Papionina Burnett, 1828
Genus *Theropithecus* I. Geoffroy Saint-Hilaire, 1843
Subgenus *Theropithecus* I. Geoffroy Saint-Hilaire, 1843
Theropithecus (Theropithecus) oswaldi Andrews, 1916
(Fig. 2G)
Theropithecus (Theropithecus) oswaldi ssp. indet.

Geographic distribution: Africa, India, Spain and perhaps Israel.

Chronological range: Late Pliocene to Late Pleistocene.

Iberian localities: Cueva Victoria (Murcia).

Remarks: Here we follow the distinction in *T. oswaldi* of three distinct subspecies (Jablonski, 2002): late Early to Late Pleistocene remains of *T. oswaldi* are attributed to *T. oswaldi leakeyi*, whereas the remains from the late Early or Middle Pleistocene of India are attributed to *T. oswaldi delsoni*, morphologically more similar to the latter, and remains from the Late Pliocene to the Early Pleistocene of Africa are attributed to the nominotypical subspecies (Delson, 1993; Jablonski, 2002). The Iberian remains of *Theropithecus*, unambiguously recorded at Cueva Victoria by dental remains (Gibert *et al*., 1995), were attributed to *T. o. oswaldi*, although it is uncertain that it belongs to the same subspecies recorded in Africa (E. Delson, pers. com.). A phalanx from the same locality, originally attributed to humans (Gibert Clols and Pons Moyà, 1985; Gibert *et al*., 1985; Gibert and Pérez-Pérez, 1989), was later reassigned to *Theropithecus* (Martínez-Navarro *et al*., 2005); although no consensus has been reached in this regard (see discussion in Gibert *et al*., 2008; Martínez-Navarro *et al*., 2008), we tentatively favor the former interpretation.

Main references: Gibert *et al*. (1995); Martínez-Navarro *et al*. (2005).

Subfamily Colobinae Blyth, 1863
Tribe incertae sedis
Genus *Mesopithecus* Wagner, 1839
Mesopithecus sp.

Geographic distribution: Eurasia.

Chronological range: Late Miocene to Pliocene.

Iberian localities: Venta del Moro (Valencia); Canal Negre I (Barcelona).

Remarks: The presence of the genus *Mesopithecus* in the Iberian Peninsula was first reported by Montoya *et al*. (2006) as *Mesopithecus* sp., on the basis of the Turolian remains from Venta del Moro (5.8–5.5 Ma). An ongoing study of the available dental remains from this locality will hopefully determine whether these remains correspond to the type species *M. pentelicus* (undoubtedly known from MN11–MN13 of Europe, Iran and Afghanistan) or to *M. monspessulanus* (from MN14–MN17 and perhaps also MN13 of Europe) (Andrews *et al*., 1996; Koufos, 2009). The presence of *Mesopithecus* in the Iberian Peninsula is further confirmed by the remains of uncertain age from Canal Negre reported by Guillén-Castejón (2010). The latter author attributed these remains to both *M. pentelicus* and *Mesopithecus* sp., but given age uncertainties and the lack of detailed metrical comparisons, here these remains are provisionally left unassigned to the species level.

Main references: Montoya *et al.* (2006); Guillén-Castejón (2010); Alba *et al*. (2010c).

Genus *Dolichopithecus* Depéret, 1889
Dolichopithecus ruscinensis Depéret, 1889
Geographic distribution: Europe and Russia.

Chronological range: Pliocene (4.0–3.2 Ma).

Iberian localities: Layna (Soria); Canal Negre I (Barcelona).

Remarks: A juvenile mandible from the Late Pliocene locality of Layna (4.2–3.6 Ma; Minwer-Barakat *et al*., 2012, their Fig. 6), even though not described in detail, was attributed to this colobine species by Delson (1973, 1974; also Szalay and Delson, 1979; Pérez and Soria, 1990; Moyà Solà *et al*., 1990). A single molar from Canal Negre, of uncertain age, was also assigned to this taxon (albeit with some doubts) by Guillén-Castejón (2010).

Main references: Delson (1973, 1974); Moyà Solà *et al*. (1990); Guillén-Castejón (2010).

Superfamily Hominoidea Gray, 1825
Family Hominidae Gray, 1825
Subfamily incertae sedis
Hominidae indet.

Iberian localities: Abocador de Can Mata locality ACM/C1-E* (Barcelona).

Remarks: With an estimated age of 12.3–12.2 Ma (MN7, late Aragonian), the two partial upper postcanine series of a single individual from ACM/C1-E* constitute the oldest hominoid record from the Vallès-Penedès Basin (Casanovas-Vilar *et al*., 2011; Alba *et al*., 2012a). The description and study of these remains, currently under way, will hopefully enable to ascertain whether they correspond to any of the other dryopithecin taxa recorded at Abocador de Can Mata (*Pierolapithecus*, *Anoiapithecus*, *Dryopithecus*) or to another, otherwise unrecorded hominid taxon.

Main references: Casanovas-Vilar *et al*. (2011); Alba *et al*. (2012a).

Subfamily Dryopithecinae Gregory and Hellman, 1939
Tribe incertae sedis
Dryopithecinae indet.

Iberian localities: Hostalets de Pierola indeterminate, Can Mata 1, Sant Quirze, and Abocador de Can Mata localites ACM/C4-Cp and ACM/BCV4 (Barcelona).

Remarks: Several upper teeth of a single individual from ACM/C4-Cp and a mandibular fragment from ACM/BCV4, with similar estimated ages of 11.9 Ma (late Aragonian), are currently under study; attributed to Hominidae indet. by Casanovas-Vilar *et al*. (2011), their dental morphology indicates that they can be attributed to the Dryopithecinae, and most likely, any of the three dryopithecine genera recorded at Abocador de Can Mata (*Pierolapithecus*, *Anoiapithecus*, *Dryopithecus*). An isolated upper molar from Hostalets de Pierola indeterminate, initially mistaken for a suid, was attributed by van der Made and Ribot (1999) to *Dryopithecus*. Given the greater diversity of hominoids evidence in the area of Hostalets during the last decade, Casanovas-Vilar *et al*. (2011) merely attributed it to the Hominidae, although on the basis of its occlusal morphology, an attribution to the Dryopithecinae is warranted. A female lower canine from the same area, in particular from the locality of Can Mata 1 (ca. 11.2 Ma, MN8, late Aragonian), was tentatively attributed to *Hispanopithecus laietanus* by Crusafont-Pairó and Golpe-Posse (1973a), and subsequently Golpe Posse (1993) reafirmed such attribution. Again, given the unexpected diversity of dryopithecines in this area, and the lack of homologous material for the three above-mentioned genera, Casanovas-Vilar *et al.* (2011) attributed this canine to Hominidae indet., although an assignment to the Dryopithecinae is most likely. Finally, a fragment of molar crown attests the presence of dryopithecines in the locality of Sant Quirze (11.8–11.2 Ma, MN8, late Aragonian); attributed to *H. laietanus* in the past (Golpe Posse, 1993), and most recently to Hominidae indet. (Casanovas-Vilar *et al*., 2011), the preserved morphology precludes an attribution to the genus level.

Main references: Crusafont-Pairó and Hürzeler (1969); Crusafont-Pairó and Golpe-Posse (1973a, 1974); Moyà Solà *et al*. (1990); Golpe Posse (1993); van der Made and Ribot (1999); Casanovas-Vilar *et al*. (2011); Alba *et al*. (2012a).

"Sivapithecus" occidentalis Villalta Comella and Crusafont Pairó, 1944 (nomen dubium) (Fig. 2K)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 12.5–11.5 Ma.

Iberian localities: Can Vila [type locality] (Barcelona).

Remarks: This nominal taxon is based on two lower molars of a single individual (Villalta Comella and Crusafont Pairó, 1941, 1944; Pickford, 2012) from the locality of Can Vila, of uncertain stratigraphic provenance (Moyà-Solà *et al.*, 2004; Casanovas-Vilar *et al.*, 2011). Initially attributed to *Dryopithecus fontani* by Villalta Comella and Crusafont Pairó (1941), the same authors subsequently used them to erect a new taxon (Villalta Comella and Crusafont Pairó, 1944), which was subsequently synonymized with *Hispanopithecus* *laietanus*. According to the description of the site location provided by Villalta Comella and Crusafont Pairó (1941), the type locality must have been situated within or very near the area of Abocador de Can Mata, with an estimated age of 12.5–11.5 Ma (Casanovas-Vilar *et al*., 2011). However, according to the recollections of Jordi Martinell (pers. comm. to DMA), the classical locality of Can Vila would have been situated in the Barranc de Can Vila, in a lower stratigraphic position than BCV1 (the type locality of *Pierolapithecus catalaunicus*), in which case an estimated age of 12.1–11.9 Ma would be attributable to the former. Even though an attribution to the genus *Sivapithecus* can be readily dismissed, *"Sivapithecus" occidentalis* remains a nomenclaturally valid taxon, whose taxonomic affinities remain to be ascertained. This is complicated by the presence of several dryopithecine genera at Abocador de Can Mata around 11.9–11.8 Ma, and especially by the lack of lower teeth attributable to *Pierolapithecus catalaunicus*. At the species level, *"S." occidentalis* is potentially a senior synonym of *P. catalaunicus*, in which case, the former would take precedence. However, this potential synonymy cannot be resolved on the basis of currently available material, so we concur with other authors (Moyà-Solà *et al*., 2004; Casanovas-Vilar *et al*., 2011) that this nominal taxon is best considered a *nomen dubium*. Most recently, Pickford (2012) synonymized *"S." occidentalis* with *Neopithecus brancoi* (Schlosser, 1901); the latter, however, has been also considered a *nomen dubium* by Casanovas-Vilar *et al.* (2011). Additional material is required to solve this taxonomic and nomenclatural conundrum.

Main references: Villalta Comella and Crusafont Pairó (1941, 1944); Golpe Posse (1993); Moyà-Solà *et al*. (2004); Pickford (2012); Alba (2012).

Tribe Dryopithecini Gregory and Hellman, 1939
Genus *Dryopithecus* Lartet, 1856
Dryopithecus fontani Lartet, 1856
(Fig. 2H)

Geographic distribution: Spain, France and Austria.

Chronological range: MN7 and MN8, late Aragonian (Middle Miocene).

Iberian localities: Abocador de Can Mata localities ACM/C3-Ae and ACM/C4-Ap.

Remarks: A partial face of an adult male individual from ACM/C3-Ae (11.9 Ma, MN7 or MN8, late Aragonian) was attributed to *Dryopithecus fontani* by Moyà-Solà *et al.* (2009a) on the basis of several craniodental features that do not fit with other Vallès-Penedès hominoids. If this attribution is correct, this is the only specimen representing the facial morphology of the type species of *Dryopithecus*, otherwise known from several mandibles and a few isolated upper teeth. On the basis of the Abocador de Can Mata specimen, *D. fontani* displays a mosaic of derived great-ape features, coupled with several primitive hominoid retentions and several gorilla-like features of uncertain phylogenetic interpretation (Moyà-Solà *et al*., 2009a). An upper male canine from ACM/C4-Ap (11.9 Ma, MN7 or MN8, late Aragonian), figured but incorrectly attributed by Pickford (2012) to *Hispanopithecus laietanus*, is in fact attributable to *Dryopithecus fontani* (Alba and Moyà-Solà, 2012b).

Main references: Moyà-Solà *et al*. (2009a); Begun (2009); Alba *et al*. (2010b, c); Casanovas-Vilar *et al*. (2011); Pickford (2012); Begun *et al*. (2012); Alba and Moyà-Solà (2012b).

cf. *Dryopithecus fontani* Lartet, 1856

Iberian localities: Abocador de Can Mata locality ACM/C3-Az and Castell de Barberà (Barcelona).

Remarks: A partial (proximal) femur from ACM/C3-Az, with an estimated age of 11.9 Ma (MN7 or MN8, late Aragonian), and an estimated body mass around 44 kg, has been tentatively attributed to *D. fontani* mainly on the basis of its large size (Moyà-Solà *et al*., 2009a). This specimen displays several modern hominoid-like characteristics, coupled with pronograde-related features, suggesting a greater emphasis on quadrupedalism than in *Hispanopithecus laietanus* (Moyà-Solà *et al*., 2009a). With regard to Castell de Barberà (ca. 11.2–10.5 Ma), the presence of hominoids at this locality was originally reported on the basis of a purported female upper canine (e.g., Golpe Posse, 1993), which in fact belongs to a male specimen of *Barberapithecus* (Begun, 2002a; Alba and Moyà-Solà, 2012a). However, the undoubted presence of hominoids at Castell de Barberà is documented by two (proximal and distal) pollical phalanges as well as a partial humeral diaphysis (Moyà Solà *et al*., 1990; Alba *et al*., 2011a; Almécija *et al*., 2011, 2012). The humeral diaphysis displays several modern hominoid-like features, most closely resembling the more complete and slender (presumably female) humerus of *D. fontani* from Saint Gaudens in France (Alba *et al*., 2011a). The phalanges more closely resemble those of other Miocene apes than those of extant great apes, indicating a significant degree of thumb-assisted, powerful grasping during above-branch quadrupedalism and cautious climbing (Almécija *et al*., 2012).

Main references: Moyà-Solà *et al*. (1990, 2009a); Casanovas-Vilar *et al*. (2011); Alba *et al*. (2011a, 2012a); Almécija et *al*. (2011, 2012).

Genus *Pierolapithecus* Moyà-Solà *et al*., 2004
Pierolapithecus catalaunicus Moyà-Solà *et al*., 2004
(Fig. 2I)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 11.9 Ma (MN7, late Aragonian, Middle Miocene).

Iberian localities: Abocador de Can Mata – Barranc de Can Vila 1 (ACM/BCV1) [type locality] (Barcelona).

Remarks: The holotype and currently only known individual of this taxon includes a partial face and skeleton with more than 80 bones or bone fragments from an adult male individual (Moyà-Solà *et al.*, 2004), with an estimated body mass of 34 kg. Although an age of ca. 12.5–13.0 Ma was initially proposed (Moyà-Solà *et al*., 2004), based on magnetostratigraphic data, ACM/BCV1 has been subsequently dated to 11.9 Ma (Moyà-Solà *et al*., 2009a; Casanovas-Vilar *et al*., 2011; Alba *et al*., 2012a). *Pierolapithecus* displays a low face with a posteriorly-situated glabella and a prognathous profile, coupled with a modern, great-ape-like facial configuration (Moyà-Solà *et al*., 2004). In turn, the postcranial remains indicate that *Pierolapithecus* possessed a modern-hominoid-like, orthograde bodyplan (Moyà-Solà *et al*., 2004; Ward, 2007; Susanna *et al*., 2010), so that this taxon represents the oldest evidence of orthogrady combined with a cranial morphology more derived than that of hylobatids. On this basis, *Pierolapithecus* was originally interpreted as a stem hominid, i.e. as a basal member of the great-ape-and-human clade (Moyà-Solà *et al.*, 2004, 2009b), although the possession of several pongine-like cranial features (such as the lack of frontal sinus; Pérez de los Ríos *et al*., 2010, 2012) suggest that it might be alternatively interpreted, probably together with other dryopithecins, as a sister-taxon of the Asian Pongini (see discussion in Casanovas-Vilar *et al.*, 2011; Alba, 2012; Pérez de los Ríos *et al.*, 2012). Interestingly, despite its orthograde body plan, *Pierolapithecus* still retains manual adaptations for powerful-grasping and above-branch palmigrady (Moyà-Solà *et al*., 2004, 2005; Almécija et al., 2009) further suggesting that unlike *Hispanopithecus* (see below) this taxon lacked adaptations to below-branch suspensory behaviors (Moyà-Solà *et al*., 2005; Almécija *et al*., 2009; Alba *et al*., 2010a; for an alternative interpretation, see Begun and Ward, 2005; Deane and Begun, 2008, 2010). Some authors (Begun, 2009; Begun *et al*., 2012) remain skeptical on the taxonomic distinctiveness of *Pierolapithecus* from *Dryopithecus*, but this is contradicted by several differences in craniodental morphology (Moyà-Solà *et al.*, 2004, 2009a), including the possession of much thicker-enameled molars in *Pierolapithecus* (Alba *et al*., 2010b; contra Begun, 2009).

Main references: Moyà-Solà *et al*. (2004, 2005, 2009b); Begun and Ward (2005); Deane and Begun (2008, 2010); Almécija *et al*. (2009); Begun (2009); Alba *et al*. (2010a, b, c, 2011d); Pérez de los Ríos *et al*. (2010); Susanna *et al.* (2010); Begun *et al*. (2012); Alba (2012); Pérez de los Ríos *et al.* (2012).

Genus *Anoiapithecus* Moyà-Solà *et al*., 2009b
Anoiapithecus brevirostris Moyà-Solà *et al*., 2009b
(Fig. 2J)

Geographic distribution: Exclusively known from the type locality.

Chronological range: 11.9 Ma (MN7, late Aragonian, Middle Miocene).

Iberian localities: Abocador de Can Mata locality ACM/C3-Aj [type locality] (Barcelona).

Remarks: *A. brevirostris* has been described on the basis of a partial face and associated mandible from ACM/C3-Aj (Moyà-Solà *et al*., 2009b), although unpublished dental remains from a second individual have been recovered from the same locality. As for *Pierolapithecus*, doubts have been raised regarding the distinct taxonomic status of *Anoiapithecus* relative to *Dryopithecus* (Begun, 2009; Begun *et al*., 2012). In fact, however, *Anoiapithecus* can be distinguished from both *Pierolapithecus* and *Dryopithecus* by the strikingly orthognathous facial profile of the former (Moyà-Solà *et al*., 2009b), which cannot be merely discounted on the basis of purported distortion (contra Begun *et al*., 2012). Moreover, *Anoiapithecus* further differs from the other dryopithecins by several other craniodental features, most notably, in the case of *Pierolapithecus*, by the presence of a frontal sinus (Moyà-Solà *et al*., 2009b; Pérez de los Ríos *et al*., 2010, 2012). Nevertheless, the three dryopithecin genera display several hominid facial synapomorphies, suggesting that they are more closely related to crown hominids than to kenyapithecines from the earlier Middle Miocene (Moyà-Solà *et al*., 2009b; Casanovas-Vilar *et al*., 2011).

Main references: Moyà-Solà *et al*. (2009b); Begun (2009); Alba *et al*. (2010b, c, 2011d); Pérez de los Ríos *et al*. (2010); Begun *et al*. (2012); Alba (2012).

Tribe Hispanopithecini Cameron, 1997
Genus *Hispanopithecus* Villalta Comella and Crusafont Pairó, 1944
Subgenus *Hispanopithecus* Villalta Comella and Crusafont Pairó, 1944
Hispanopithecus (Hispanopithecus) laietanus Villalta Comella and Crusafont Pairó, 1944
(Fig. 2N-O).

Geographic distribution: Only known from several localities of the Vallès-Penedès Basin (NE Spain).

Chronological range: 10.0–9.5 Ma (MN9–MN10, early to late Vallesian, Late Miocene).

Iberian localities: La Tarumba 1 [type locality], Can Llobateres 1 and 2, Polinyà 2, Can Feu, EDAR6 and EDAR7 (Barcelona).

Remarks: *H. laietanus* (the type species of the genus *Hispanopithecus*) was originally defined on the basis of lower jaw and dental remains from La Tarumba 1 (Villalta Comella and Crusafont Pairó, 1944). Subsequently, *Hispanopithecus* was treated as a junior subjective synonym of *Dryopithecus* by many authors (Szalay and Delson, 1979; Moyà Solà *et al*., 1990; Begun *et al*., 1990; Harrison, 1991; Andrews *et al*., 1996; Begun, 1992, 2002b), albeit with some exceptions (Golpe Posse, 1993; Cameron, 1997, 1999). Recently, *Hispanopithecus* was resurrected (Moyà-Solà *et al*., 2009a), including not only the type species, but also *H. crusafonti* (see below)—a proposal that has been subsequently followed by most researchers (e.g., Begun, 2009; Alba *et al*., 2010a, 2011a, b, 2012b; Begun *et al*., 2012). Dental remains of *H. laietanus* are known from several localities, although the largest sample comes from the early Vallesian site of Can Llobateres 1 (Begun *et al*., 1990; Harrison, 1991; Golpe Posse 1993; Alba *et al*. 2012b), with an estimated age of 9.7 Ma. The intial hominoid dental finds from Can Llobateres 1 were attributed to *H. laietanus*, but subsequent finds resulted in the naming of two additional taxa (*Dryopithecus piveteaui* and *Rahonapithecus sabadellensis*), which are currently considered *nomina nuda* (e.g., Golpe Posse, 1993; but see Pickford, 2012). During the last decades, the dental sample from this locality has been generally attributed to a single species (e.g., Begun *et al*., 1990; Harrison, 1991; Alba *et al*., 2012c), with some authors setting apart an upper canine (Crusafont-Pairó and Golpe-Posse, 1973a; Golpe Posse, 1993) that nevertheless can be also attributed to the same taxon. With regard to the cranial anatomy of *H. laietanus*, it is known by a partial cranium from Can Llobateres 2 (Moyà-Solà and Köhler, 1993a, 1995; Köhler et al., 2001a, b), with an estimated age of 9.6 Ma. This taxon displays several cranial features indicative of hominid status, being in some regards more derived towards the modern great-ape condition than the Middle Miocene dryopithecins. Finally, besides some isolated bones from Can Llobateres 1 and the unpublished remains from EDAR (Checa Soler and Rius Font, 2003), the postcranial anatomy of *H. laietanus* is best known from the partial skeleton (comprising about 60 elements) from Can Llobateres 2 (Moyà-Solà and Köhler, 1996; Köhler *et al*., 2001a; Almécija *et al*., 2007) and the more incomplete partial skeleton from Can Feu (Alba *et al*., 2011b, 2012d). Several features of these skeletons indicate the possession of an orthograde body plan with suspensory adaptations (Moyà-Solà and Köhler, 1996; Köhler *et al*., 2002; Almécija *et al*., 2007; Alba *et al*., 2010a; Susanna *et al*., 2011; Pina *et al*., 2012a,b), although some manual features and other anatomical characteristics indicate the simultaneous retention of features functionally-related to above-branch quadrupedalism (Almécija *et al*., 2007; Alba *et al*., 2010a, 2012d).

Main references: Villalta Comella and Crusafont Pairó (1944); Crusafont Pairó (1958b, 1965a); Crusafont-Pairó and Hürzeler (1961, 1969); Crusafont-Pairó and Golpe-Posse (1973a); Golpe Posse (1982a, 1993); Moyà Solà *et al*. (1990); Begun *et al*. (1990); Harrison (1991); Moyà-Solà and Köhler (1993a, 1995, 1996); Andrews *et al*. (1996); Cameron (1997, 1999); Köhler *et al*. (1999, 2001a, b, 2002); Ribot *et al*. (1996); Begun (2002b, 2009); Checa Soler and Rius Font (2003); Almécija *et al*. (2007); Deane and Begun (2008); Alba *et al*. (2010a, c, 2011b, 2012b,c,d); Casanovas-Vilar *et al*. (2011); Susanna *et al*. (2011); Pickford (2012); Pina *et al*. (2012b); Alba (2012).

Hispanopithecus (Hispanopithecus) crusafonti (Begun, 1992) (Fig. 2L-M).

Geographic distribution: NE Spain.

Chronologic range: 10.4–10.0 (MN9, early Vallesian, Late Miocene).

Iberian localities: Can Poncic 1 [type locality] (Barcelona); Teuleria del Firal (Lleida).

Remarks: Most of the dentognathic remains attributed to *H. crusafonti* come from Can Poncic 1. Although initial finds were assigned to *Hispanopithecus laietanus*, after the recovery of more abundant material, *Dryopithecus crusafonti* was distinguished (Begun, 1992); it was recently transferred to the genus *Hispanopithecus* by Moyà-Solà *et al*. (2009a). After its description, this taxon has been accepted (Begun, 2002b; Casanovas-Vilar *et al*., 2011; Pickford, 2012), questioned (Andrews *et al*., 1996), or formally synonymized with *H. laietanus* (Ribot *et al*., 1996). On the basis of dental differences between the Can Poncic 1 sample and those of *H. laietanus* from later Vallesian localities (Begun, 1992), a distinct species status is favored here, following Alba *et al.* (2012c). At the same time, several shared-derived dental features suggest that they belong to a single genus, even though the lack of cranial material from Can Poncic makes the generic attribution to *Hispanopithecus* somewhat provisional, and some authors maintain its original assignment to *Dryopithecus* (Pickford, 2012). The partial mandible from Teuleria del Firal (Vidal, 1913a, b; Woodward, 1914), traditionally attributed to *Dryopithecus fontani* (Harrison, 1991; Andrews *et al*., 1996; Ribot *et al*., 1996), is also included here in the hypodigm of *H. crusafonti* (Begun, 1992; Casanovas-Vilar *et al*., 2011; Alba *et al*., 2012c), given some dental differences relative to *D. fontani* from France and several resemblances to the few lower teeth available from Can Poncic 1.

Main references: Vidal (1913a, b); Woodward (1914); Golpe Posse (1982a, 1993); Moyà Solà et al. (1990); Harrison (1991); Begun (1992, 2002b, 2009); Andrews *et al.* (1996); Ribot *et al*. (1996); Alba *et al.* (2010c); Casanovas-Vilar *et al.* (2011); Pickford (2012); Alba *et al.* (2012c); Alba (2012).

Subfamily Homininae Gray, 1825
Tribe Hominini Gray, 1825
Genus *Homo* Linnaeus, 1758
Homo sp.

Iberian localities: Sima del Elefante TE9 (Burgos).

Remarks: The partial mandible recovered from the Early Pleistocene site (ca. 1.2 Ma) of Sima del Elefante (Atapuerca) was initially assigned to *H. antecessor* by Carbonell *et al.* (2008), but most recently it has been argued that it might correspond to a different taxon (Bermúdez de Castro *et al.*, 2011). On this basis, we prefer to leave unassigned to the species level the remains from this locality, which represent the oldest osteological record of the genus *Homo* in the Iberian Pensinsula. Slightly older stone tool assemblages from Fuente Nueva-3 and Barranco León-5 in Orce (Guadix-Baza Basin) further record the early presence of humans in southern Iberia (Martínez-Navarro *et al.*, 1997; Oms *et al.*, 2000), although the even older (1.4 Ma; Duval *et al.*, 2011), purported human remains from Venta Micena (e.g., Gibert *et al.*, 2002), in the same region, are not currently accepted as such (Moyà-Solà & Köhler, 1997; Martínez-Navarro, 2002; Martínez-Navarro *et al*., 1997).

Main references: Carbonell *et al*. (2008), Bermúdez de Castro *et al*. (2011); Martinón-Torres *et al*. (2011).

Homo heidelbergensis Schoetensack, 1908 s.l.

Geographic distribution: Eurasia and Africa.

Chronological range: Latest Early Pleistocene to Middle Pleistocene.

Iberian localities: Gran Dolina TD6 and Sima de los Huesos in Atapuerca (Burgos); Cueva Negra del Estrecho del Quípar (Murcia); Galeria Pesada - Gruta da Aroeira (Ribatejo); Cova de Mollet I (Girona).

Remarks: The classification of latest Early and Middle Pleistocene humans is still one of the most hotly debated topics in paleoanthropology and remains largely unresolved (e.g., Rightmire, 2007; 2008; Hublin, 2009; Harvati *et al*., 2010). Traditionally, they were lumped, together with Neandertals, into a single informal category termed 'archaic' *H. sapiens*. In this way, the phylogenetic affinities of such taxa with later *Homo* and their mosaic morphology, showing a combination of plesiomorphic (*Homo erectus*-like) traits with some more derived features, were recognized. However, such grade classification failed to address the alpha taxonomy of these specimens (Harvati *et al*., 2010). Currently, there are two main views on the phylogeny and taxonomy of these forms (Rightmire, 2007; Hublin, 2009). One considers that there is a single species *H. heidelbergensis* s.l., which would be ancestral to both *Homo neanderthalensis* and modern *H. sapiens*, being distributed in Europe, Africa and probably Asia (e.g., Rightmire, 1998, 2007, 2008; Mounier *et al*., 2009). Alternatively, several authors (e.g., Arsuaga *et al*., 1997) have argued that European Middle Pleistocene humans display several Neandertal derived features, thereby indicating that these forms should be classified into *H. neanderthalensis*, or alternatively that *H. heidelbergensis* should be restricted to European forms (a chronospecies ancestral to Neandertals, i.e. *H. heidelbergensis* s.s.), their African counterparts being attributed to a different species, *H. rhodesiensis* (see also Stringer, 2012).

The hominin remains from Sima de los Huesos (0.53 Ma; but see Stringer, 2012, regarding dating uncertainties) were initially attributed to *Homo heidelbergensis* by Arsuaga *et al*. (1993), although most recently Martinón-Torres *et al*. (2012) argued that the dental remains from this locality display more derived Neandertal traits than the typical *H. heidelbergensis* from Mauer or Aragó. We however think that an attribution to *H. heidelbergensis* is still warranted, especially when it is taken into account that this taxon is here considered in a broad sense. Similarly, the older hominin remains from Gran Dolina TD6 (ca. 0.88–0.78 Ma) were also initially assigned to an archaic form of *H. heidelbergensis* by Carbonell *et al*. (1995), but later Bermúdez de Castro *et al*. (1997) erected a new species, *Homo antecessor*, arguing that it would be the common ancestor of both modern humans and Neandertals. Such a phylogenetic hypothesis is currently uncertain, although the validity of the species, definitely identified only from Atapuerca, is accepted by some researchers (Stringer, 2012). Its distinctive taxonomic status, either at the species or subspecies level, might ultimately be vindicated in the future by the find of additional remains. Currently, however, the available remains from TD6 are relatively scarce, fragmentary and/or subadult, and one of its purported most diagnostic features (the development of the canine fossa) is much more obvious in the juvenile than in the adult specimen, this feature further being variable in other populations attributed to *H. heidelbergensis* (Rightmire, 2008). Resolving the taxonomy of fossil European hominins is of course outside the scope of this paper. However, given recent taxonomic analyses favoring the distinction of a single, Afro-European species *H. heidelbergensis* s.l. (Mounier *et al*., 2009; see Stringer, 2012, for a recent review on this species), we provisionally prefer to attribute the Gran Dolina hominins to the latter taxon. The somewhat younger population from Sima de los Huesos, on the other hand, display a mosaic of morphologic features indicating that they are already derived towards Neandertals (Martinón-Torres *et al*., 2012), so that their removal from *H. heidelbergensis* and their inclusion into *H. neanderthalensis* might be justified (Stringer, 2012). Following the same criterion of *H. heidelbergensis* understood in a broad sense, the Middle Pleistocene remains from Cueva Negra del Estrecho de Quípar (Walker *et al*., 2010), Galeria Pesada (Trinkaus *et al*., 2003) and Cova de Mollet (Maroto *et al*., 1987) are here also attributed to *H. heidelbergensis* s.l.

Main references: Arsuaga *et al*. (1993, 1997, 1999); Carbonell *et al*. (1995, 2005); Bermúdez de Castro *et al*. (1997, 2008, 2012a); Carretero *et al*. (1999); Lorenzo *et al*. (1999); Trinkaus *et al*. (2003); Maroto *et al*. (1987); Walker *et al*. (2010); Martinón-Torres *et al*. (2012); Maroto *et al*. (2012).

Homo neanderthalensis King, 1864

Geographic distribution: Europe and Middle East.

Chronological range: Latest Middle to Late Pleistocene.

Iberian localities: Banyoles (Girona); Cova del Gegant (Barcelona); Cova del Tossal de la Font (Castellón); Cova Negra, Cova del Bolomor and Cova Foradà (Valencia); El Salt (Alicante); Sima de las Palomas del Cabezo Gordo (Murcia); Cueva de los Moros de Gabasa (Huesca); Pinilla del Valle (Madrid); Valdegoba (Burgos); Cueva del Castillo, Cueva del Esquilleu, Cueva de Covalejos and Cueva del Castillo (Cantabria); Cueva del Sidrón (Oviedo); Arrillor (Álava); Axlor (Vizcaya); Lezetxiki VII, IV (Guipúzcoa); Cueva de los Casares and Cueva de los Torrejones (Guadalajara); Cueva del Boquete de Zafarraya (Málaga); Cueva de La Carihuela (Granada); Forbe's Quarry (=Gibraltar I), Devil's Tower (=Gibraltar II) and Cueva Genista (Gibraltar, UK); Gruta da Figueira Brava (Setúbal); Gruta de Salemas (Lisboa); Gruta da Oliveira (Santarém); Gruta Nova da Columbeira (Leiria); Lapa da Rainha (Lisboa).

Remarks: There are more than 30 Iberian localities where osteological remains of *H. neanderthalensis* have been found, although no partial or complete skeletons have been unearthed up to date. Several of these localities, situated in southwestern Iberia, record the latest Neandertals from Europe (Hublin *et al*., 1995), with a chronology of 35 ka (Trinkaus, 2007).

Main references: Alférez *et al*. (1982, 1985); Dean *et al*. (1986); Arsuaga *et al*. (1984, 1989, 2007); Antunes and Santinho Cunha (1992); Hublin *et al*. (1995); Sanchez (1999); Quam *et al*. (2001); Barroso (2003); Daura *et al*. (2005); Grün *et al*. (2006); Rosas *et al*. (2006); Aguirre Enríquez (2007); Trinkaus *et al*. (2007); Walker *et al*. (2008, 2010, 2011); Arsuaga *et al.* (2012).

Homo sapiens Linnaeus, 1758

Chronological range: Latest Middle Pleistocene to Holocene.

Geographic distribution: Worldwide.

Oldest Iberian localities: Gruta do Caldeirão (Santarém); Lagar Velho (Leiria); Malladetes (Valencia).

Remarks: There are numerous Iberian localities with fossil remains of *H. sapiens*, so that only the oldest citations are provided above. On the basis of osteological remains, *H. sapiens* is first recorded at the Iberian Peninsula in Lagar Velho (Duarte *et al*., 1999) and Malladetes (Arsuaga *et al*., 2002), and slightly later at Gruta do Caldeirão (Trinkaus *et al*., 2001). These remains of modern humans postdate the last Iberian Neandertals, but this is not the case of the archeological remains associated to the former. Thus, although the attribution of archeological remains to a particular human species is questionable when not accompanied by osteological remains, the recent dating of Paleolithic cave art from Spain—presumably made by *H. sapiens*—to 40.8 ka suggests that modern humans arrived to the Iberian Peninsula ca. 41.5 ka, like in other areas of Western Europe (Pike et al., 2012). The find of an almost complete skeleton of a child in the Lagar Velho cave caused a lot of controversy, because Duarte *et al*. (1999) initially concluded that it displayed modern human and Neandertal traits simultaneously. Subsequently, however, other authors have pointed out that the Lagar Velho child is clearly *H. sapiens* and does not display Neandertal characters (Tattersall and Schwartz, 1999).

Main references: Duarte *et al*. (1999); Arsuaga *et al*. (2002); Trinkaus *et al*. (2001).

3. Results

An updated summary of Iberian primate taxa and localities from the Cenozoic is provided here, based on the revision of more than 200 bibliographic references. A total of 25 primate genera, corresponding to 7 families (one of plesiadapiforms, 2 of strepsirrhines and 4 of haplorrhines), from up to 116 different localities, are reported (27 from the Eocene, 3 from the Oligocene, 32 from the Miocene, 4 from the Pliocene, 51 from the Pleistocene and one with an undetermined age). This information is summarized in Figures 3 and 4, which show the ranges of the different Iberian primate taxa in relation to climatic evolution during the Cenozoic. In the following section, we discuss primate diversity dynamics in the Iberian Peninsula through time, further emphasizing its interplay with global and regional paleogeographic and climatic events.

4. Discussion

4.1. Iberian primate diversity in the Paleogene (Fig. 3)

In Europe, the earliest occurrence of plesiadapiforms is dated to the Late Paleocene, as documented by the record of *Berruvius* and some members of the Saxonellidae and Plesiadapidae in France and Germany (Silcox, 2001; Bloch *et al*., 2007). In contrast, the record of primates (including plesiadapiforms) in the Iberian Peninsula does not go back beyond the Early Eocene. This lack of evidence for Paleocene primates in Iberia may be due to the scarcity of Paleocene continental sites: mammal remains from this epoch have been only identified in the localities of Claret, Tendruy, Palau, Fontllonga and Campo (Gheerbrant *et al.*, 1997; López-Martínez and Peláez-Campomanes, 1999; Peláez-Campomanes *et al.*, 2000). Anyway, the Eocene record of plesiadapiforms in this area is sparse, being restricted to the paromomyoid *Arcius*, known from the locality of Silveirinha (Mondego Basin, Portugal; Estravís, 2000) and recently identified also in Masia de l'Hereuet (Àger sub-basin, Spain; Marigó *et al.*, 2012a). In the former locality, eight isolated teeth enabled description of the species *A. zbyszewskii*, whereas the four molars recovered from the latter site did not allow a specific determination.

The record of euprimates during the Iberian Eocene shows a much greater diversity, being represented by two distinct groups of Paleogene "prosimians": adapoids and omomyoids (8 and 3 genera, respectively, apart from several forms without generic ascription, which in some cases may lead to the description of new taxa after further studies). The record of adapoids begins, together with that of plesiadapiforms, in the Neustrian, with the presence of the genus *Donrussellia* in the Mondego Basin. In the Grauvian, the genera *Cantius* and *Agerinia* are well represented in several localities from the Pyrenean and Ebro basins, *Agerinia* persisting into the Geiseltalian. The Robiacian records a great diversity of adapoids, represented in the Pyrenean and Duero basins by the genera *Anchomomys, Mazateronodon, Microadapis, Adapis* and *Leptadapis,* the latter two being also identified in Headonian levels. With respect to omomyoids, the genus *Pseudoloris* has its oldest record in the Iberian locality of Casa Ramón (Geiseltalian). It is also well represented, together with *Necrolemur*, in the Robiacian and Headonian, while *Microchoerus* is recognized in several Headonian sites. Such

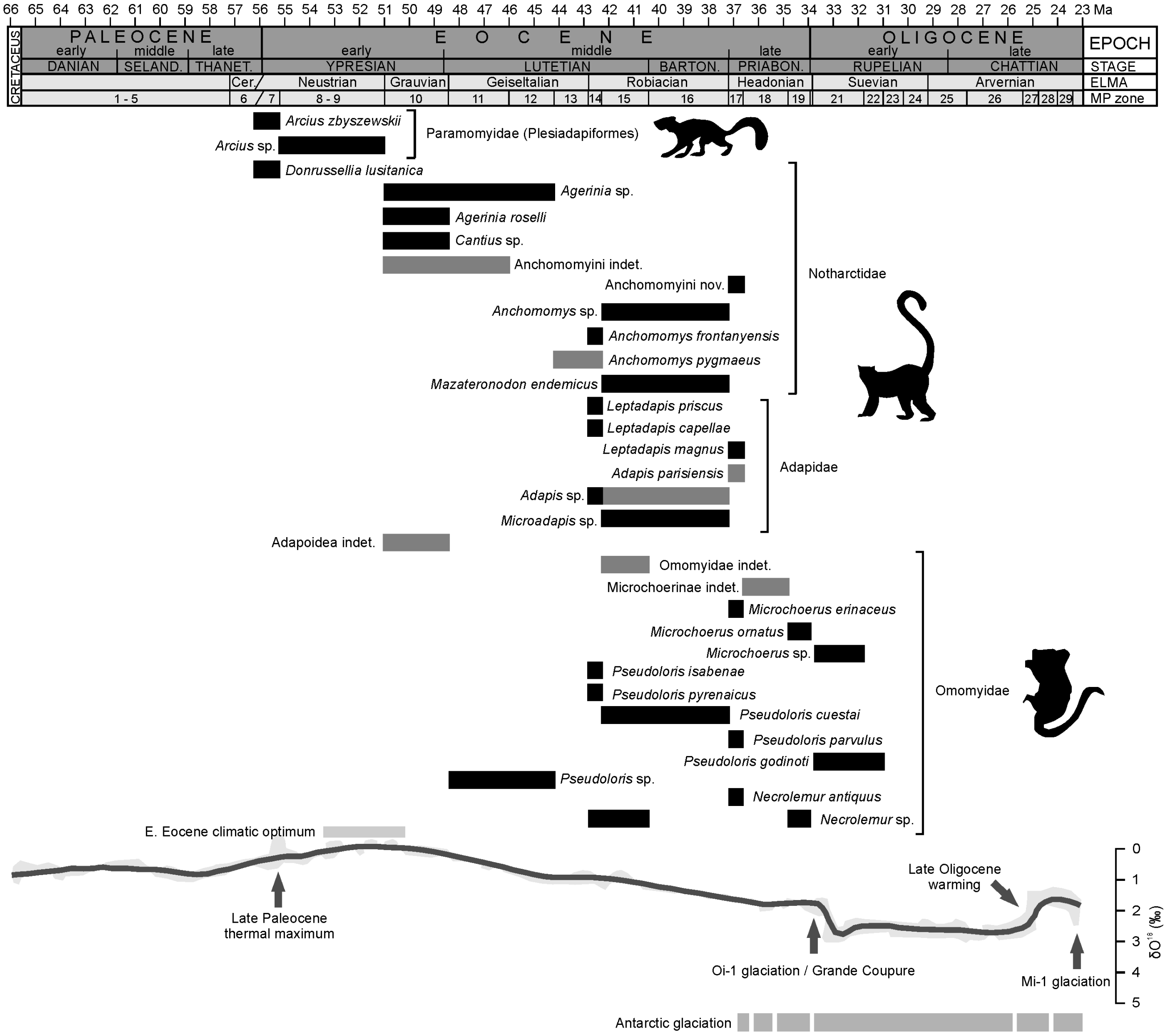

Fig. 3.- Range chart of Paleogene Iberian primate taxa. Uncertain attributions (cf., indet.) are shown in dark gray, whereas *nomina nuda* and *nomina dubia* are not considered. The global oxygen isotope record, together with the development of ice-sheets and major climatic/physiographic events, are also included. Age boundaries for epochs, stages, European Land Mammal Ages (ELMA) and Paleogene Mammal Zones (MP) are after Luterbacher *et al.* (2004). Climatic data are taken from Zachos *et al.* (2001).

abundance and diversity of both adapoids and omomyoids parallels the diversity peak that primates experienced during the Eocene in the Northern hemisphere (e.g., Fleagle, 1999). The Eocene represents the warmest epoch of the Tertiary, especially during the Paleocene/Eocene Thermal Maximum and the subsequent sustained period of global warmth known as the Early Eocene Climatic Optimum (Zachos *et al.*, 2001). Warm temperatures and not-marked seasonality favored the development of tropical forests with a predominance of evergreen thermophilic elements in latitudes as far north as 50º (Collison and Hooker, 2003). Although variable in different regions and time intervals, these dense forests would have provided suitable habitats for the radiation of these groups of prosimians.

During the Middle and Late Eocene, the mammal faunas from the western and central Iberian basins were clearly different from those of the Pyrenean basins, the latter being similar to those from Central Europe (France and Switzerland). This faunal differentiation, mainly observed in perissodactyls, artiodactyls and rodents, led to the definition of the Western Iberian Bioprovince (Cuesta, 1991), which included several western and central Iberian basins (Duero, Almazán and Oviedo Basins) characterized by Eocene mammal faunas different from those of the Pyrenees and the rest of Europe. Subsequent studies of these mammalian groups have further reinforced this contention (see Badiola *et al.*, 2009, and references therein). The recent description of the adapiform *Mazateronodon endemicus* and the microchoerine *Pseudoloris cuestai* (Marigó *et al.*, 2010; Minwer-Barakat *et al.*, 2012) from the site of Mazaterón demonstrates that primates from the Western Iberian Bioprovince were also clearly different from their counterparts in the Pyrenean basins, thus reinforcing the endemic nature of the mammal faunas from this bioprovince.

The Eocene–Oligocene boundary was marked by a major faunal turnover that dramatically affected the continental vertebrate faunas and involved the extinction of a large number of Eocene mammals. This global event, named the "*Grande Coupure*" by Stehlin (1910), was mainly related to the climatic deterioration that took place at the Eocene–Oligocene transition, which led to a marked loss of diversity in both the marine and continental realms (Prothero, 1994; Hooker *et al*., 2004). Primates were not an exception, and the number of species of both adapoids and omomyoids, which had been highly succesful during the Eocene, drastically decreased in the Early Oligocene. Adapiforms persisted until the Miocene, although their record is very scarce and geographically restricted to Southeastern Asia (Gebo, 2002), whereas in Europe there is no mention of this group after the Eocene–Oligocene boundary. Regarding omomyoids, there are some brief appearances in the Oligocene and the earliest Miocene of North America (MacDonald, 1963; Albright, 2005) and Egypt (Simons *et al*., 1986). In Europe, however, after the *Grande Coupure* the omomyoid record is restricted to two finds from the Early Oligocene of Spain. Thus, *Pseudoloris* was able to survive the Eocene–Oligocene faunal turnover, as evidenced by *Pseudoloris godinoti* from the Suevian sites of Fonollosa and Santpedor in the Ebro Basin (Köhler and Moyà-Solà, 1999). Also, a single lower molar from the Early Oligocene of Aguatón evidences the persistence of *Microchoerus* in the Calatayud-Teruel Basin (Peláez-Campomanes, 2000). Therefore, at least two (*Pseudoloris* and *Microchoerus*) of the three microchoerine genera that inhabited the Iberian Peninsula during the Eocene further persisted, although rarely at best, into the Early Oligocene, constituting the only record of this group in Europe—the German fissure fillings of Ehrenstein and Harrlingen, containing microchoerine remains and originally assigned to the Early Oligocene (Schmidt-Kittler, 1971, 1977), were later considered to be Late Eocene in age (BiochroM'97, 1997). This might be related to maintenance of warmer temperatures in the Iberian Peninsula, compared to more northern areas of Europe, which would have favored the persistence of tropical to subtropical forested areas allowing the survival of some omomyoids until the Early Oligocene.

In summary, the Paleogene primate record in the Iberian Peninsula shows a great diversity of both adapoids and omomyoids in the Eocene, followed by a marked drop in the number of species in the Oligocene, in agreement with other areas of the Northern hemisphere (e.g., Fleagle, 1999). However, it is remarkable that the diversity of Eocene primates from the Iberian Peninsula has notably increased in recent years. For instance, in the last three years four new primate taxa have been described from the Iberian Eocene: the adapoids *Mazateronodon endemicus* and *Anchomomys frontanyensis*, and the omomyoids *Pseudoloris pyrenaicus* and *P. cuestai* (Marigó *et al*., 2010, 2011a; Minwer-Barakat *et al*., 2010, 2012). Moreover, the first citation of plesiadapiforms in Spain has been reported (Marigó *et al*., 2012a), raising to two the mentions of this group in the Iberian Peninsula. Therefore, it seems highly probable that the diversity of Paleogene (especially Eocene) primates in the Iberian Peninsula recorded by currently available remains is even higher than recognized, and that the knowledge of this group of mammals will grow in the next few years as more detailed studies are carried out.

4.2. Primate Iberian diversity in the Miocene and Plio-Pleistocene (Fig. 4)

In the Iberian Peninsula, simians (anthropoids) are not recorded until well within the Miocene (late Aragonian), being represented by pliopithecoids (a Eurasian clade of stem catarrhines) as well as hominoids (apes and humans), whereas cercopithecoids (Old World monkeys) are recorded from the latest Miocene onwards.

Pliopithecoids from the Miocene of Eurasia are currently considered to be stem catarrhines on the basis of the possession of only two premolars (e.g. Andrews *et al*., 1996; Begun, 2002a), although it is uncertain whether they are more derived than African propliopithecoids and other stem catarrhines (Begun, 2002a). Once considered to be phylogenetically related to hylobatids, in fact they retain several primitive features indicating that they precede the cercopithecoid-hominoid split. In any case, they were the first anthropoids that dispersed into Eurasia, where they experienced an evolutionary radiation, in a continent previously devoid of other anthropoids, from the Early Miocene onwards (Begun, 2002a; Harrison, 2005). Pliopithecoids are first recorded by dionysopithecins from the Early Miocene of Asia (Harrison and Gu, 1999), whereas pliopithecines and crouzeliines are recorded in the Middle and Late Miocene of both Europe and Asia (Begun, 2002a; Harrison, 2005). In the Iberian Peninsula, pliopithecoids are exclusively known from the Vallès-Penedès Basin (NE Spain), where they are recorded by both pliopithecines (the genus *Pliopithecus*) and crouzeliines (the genera *Barberapithecus* and *Egarapithecus*). This restricted geographic distribution is probably attributable to the peculiar physiographic and paleoecological conditions of the Vallès-Penedès Basin, which by the Middle and early Late Miocene was more similar to France and other Central European countries than to the inner Iberian Basins (Agustí *et al*., 1984; Agustí, 1990; Casanovas-Vilar and Agustí, 2007; Casanovas-Vilar *et al*., 2008). Their oldest record in Iberia (ca. 12.0 Ma; Alba *et al*., 2012a), however, is quite late compared to France and Central Europe (where finds occur from MN5), perhaps due to the lack of adequate outcrops from the early Middle Miocene in the Vallès-Penedès Basin. The best known pliopithecine from Iberia is *Pliopithecus canmatensis*, from the late Middle Miocene of several localities from the Abocador

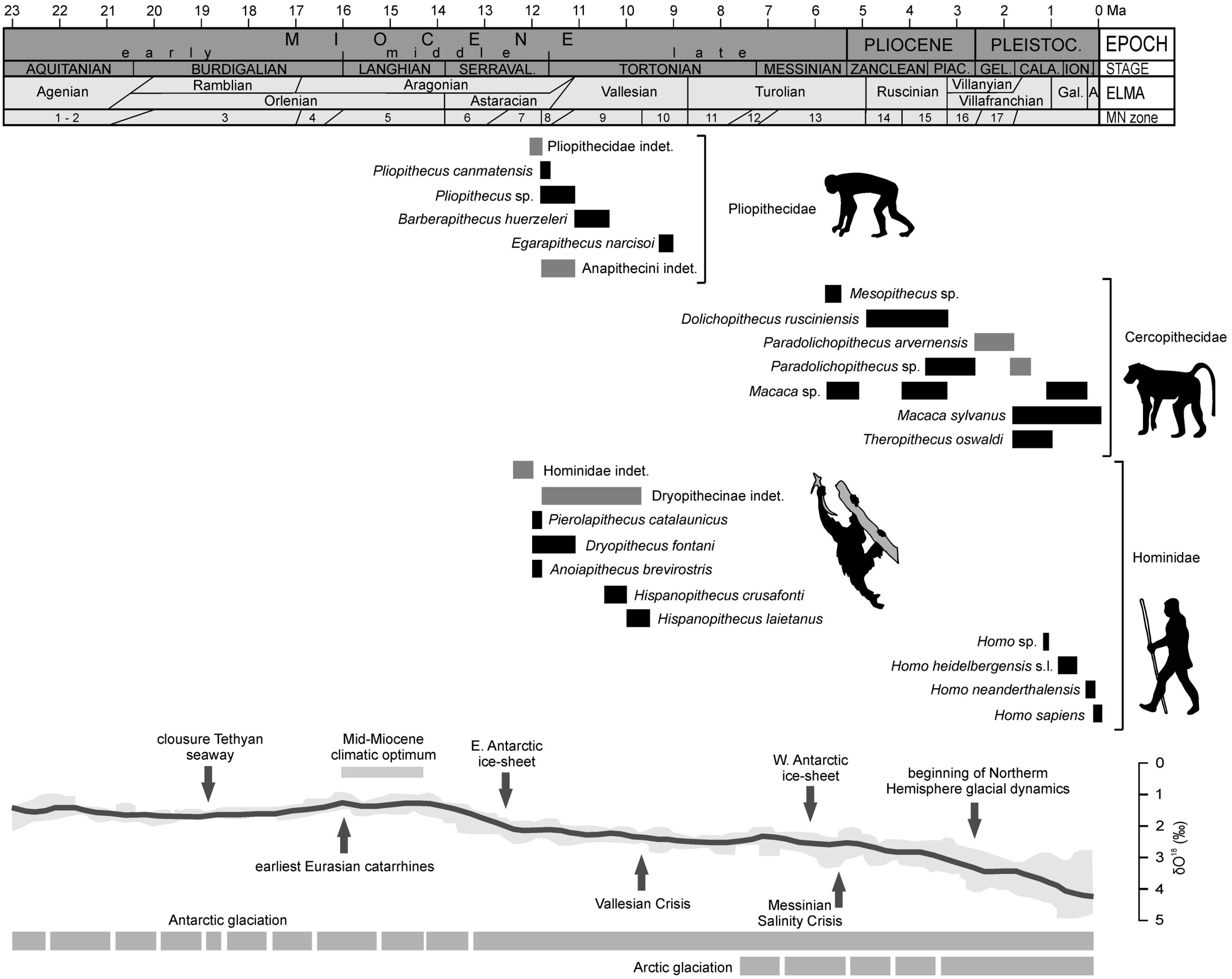

Fig. 4.- Range chart of Neogene and Quaternary Iberian primate taxa. Uncertain attributions (cf., indet.) are shown in dark gray, whereas *nomina nuda* and *nomina dubia* are not considered. The global oxygen isotope record, together with the development of ice-sheets and major climatic/physiographic events, are also included. Age boundaries for epochs and stages are after Lourens *et al.* (2004). European Land Mammal Ages (ELMA) and Neogene Mammal Zones (MN) after Steiniger (1999), Agustí *et al.* (2001), Rook and Martínez-Navarro (2010) and Van der Meulen *et al.* (2011). Climatic data are taken from Zachos *et al.* (2001).

de Can Mata series (Alba *et al.*, 2010d). Crouzeliines, in turn, are recorded by the anapithecins *Barberapithecus huerzeleri*, from the latest Middle or earliest Late Miocene of Castell de Barberà (Alba and Moyà-Solà, 2012), and *Egarapithecus narcisoi*, from the Late Miocene of Torrent de Febulines (Moyà-Solà *et al.*, 2001). With an estimated age of ca. 9 Ma, *Egarapithecus* represents the last record of a Miocene primate in Iberia before the occurrence of cercopithecoids.

With regard to hominoids, like pliopithecoids and probably due to the same paleoecological reasons, in the Iberian Neogene they are restricted to the late Middle and early Late Miocene, further displaying a similar geographic distribution, restricted to the Vallès-Penedès Basin and to the small, intra-Pyrenean Seu d'Urgell Basin (Casanovas-Vilar *et al.*, 2011). This group, including extant apes and humans, originated around the Oligocene/Miocene boundary in Africa, where they experienced a remarkable evolutionary radiation during the Early and Middle Miocene (Begun, 2007; Harrison, 2010). From the beginning of the Middle Miocene, hominoids are also recorded in Eurasia, where they diversified into a plethora of genera, most of which are considered members of the great-ape-and-human clade (Hominidae) (Begun, 2002b, 2007; Kelley, 2002; Casanovas-Vilar *et al.*, 2011). Some authors have favored a Eurasian origin of hominids and their early divergence during the middle Miocene into pongines and hominines, followed by a later hominine dispersal event back into Africa by the late Miocene (Begun, 2002b, 2007, 2009; Begun *et al.*, 2012). However, given the incomplete nature of the primate fossil record and the probable multidirectional nature of hominoid intercontinental dispersal and range extension events during the Middle Miocene, the place of origin of hominids cannot be currently resolved. The oldest record of Eurasian hominoids corresponds to the latest Early Miocene, just before the Langhian transgression (ca. 16.3

Ma), but undoubted kenyapithecines such as *Griphopithecus* (most likely being stem hominids) are not recorded until the early Middle Miocene (ca. 14 Ma) (Casanovas-Vilar *et al*., 2011; contra Andrews and Kelley, 2007, who favor an older dating). By this time, roughly coinciding with the following Mid-Miocene Climatic Optimum (Zachos *et al*., 2001), the kenyapithecines of African origin apparently expanded their range into eastern Europe and Turkey, and apparently gave rise to the Eurasian radiation of hominids (Moyà-Solà *et al*., 2009b; Casanovas-Vilar *et al*., 2011; Alba, 2012).

Whereas Miocene hominoids from Asia are generally regarded as pongines (i.e., members of the orangutan clade) (Kelley, 2002; Begun, 2007), the Miocene hominoids from Europe, here included into the Dryopithecinae, have been variously considered to be stem hominids (e.g., Casanovas-Vilar *et al*., 2011), pongines (e.g., Agustí *et al*., 1996) or hominines (e.g., Begun, 2009; Begun *et al*., 2012). Despite these phylogenetic disagreements, the discoveries of Miocene hominoids from Spain that have taken place during the last two decades have provided a wealth of new information that provides several insights into hominoid evolution. The fact that the pongine *Sivapithecus* is first recorded at ca. 13.0–12.5 Ma in Asia (Kunimatsu *et al*., 2004), whereas almost simultaneously (ca. 12.3–12.2) a hominid of uncertain affinities is recorded at the other end of Eurasia in the Vallès-Penedès Basin, suggests that the initial diversification of Eurasian hominoids took place somewhat earlier, probably between 14–13 Ma (Casanovas-Vilar *et al*., 2011). At the same time, the cranial and dentognathic characteristics of the later, Middle Miocene Spanish dryopithecins, suggest they descended from a thick-enameled kenyapithecine ancestor (Moyà-Solà *et al*., 2009b; Alba *et al*., 2010b; Casanovas-Vilar *et al*., 2011). The global climatic trend towards progressive cooling and increased seasonality initiated during the middle Miocene (Zachos *et al*., 2001; Kovar-Eder, 2003; Mosbrugger *et al*., 2005) apparently favored the adaptive radiation of Eurasian hominoids (Casanovas-Vilar *et al*., 2011), as reflected by their widened geographic range and increased taxonomic diversity, probably as a result of the new selection pressures posed by changing ecological conditions towards more heterogeneous biotopes with increased seasonality (Begun *et al*., 2012). Soon after the early/late Vallesian transition (ca. 9.6 Ma), however, hominoids became extinct in Western and Central Europe, with the exception of the insular endemic *Oreopithecus*, which survived until ca. 7 Ma in Italy (Casanovas-Vilar *et al*., 2011).

In the Iberian Peninsula, dryopithecines are last recorded by *Hispanopithecus* at ca. 9.5 Ma, slightly predating the last occurrence of pliopithecoids ca. 9.0 Ma. The extinction of European hominoids has been linked to the vegetation changes that took place during the late Vallesian (Fortelius and Hokkanen, 2001; Agustí *et al*., 2003), which further resulted in the extinction of many other mammalian taxa (i.e., the Vallesian Crisis; see Agustí and Moyà-Solà, 1990; Agustí *et al*., 1999; Casanovas-Vilar *et al*., 2010). The climatic trend towards cooling and increased seasonality initiated after the Mid-Miocene Climatic Optimum (Zachos *et al*., 2001) apparently led to the crossing of some paleoenvironmental threshold, to which hominoids and several other mammals did not adapt (Casanovas-Vilar *et al*., 2011). This is further supported by the paleoenvironmental reconstruction of Can Llobateres 1 (Marmi *et al*., 2012), which records one of the latest occurrences of the hispanopithecin *Hispanopithecus laietanus* (9.6 Ma) before its last apperance datum at ca. 9.5 Ma (Casanovas-Vilar *et al*., 2011). The vegetation from Can Llobateres 1 is consistent with a subtropical to warm-temperate climate, but evidence from other Vallès-Penedès sites indicates that such habitats would have been restricted to lowland humid areas, with warm-temperate mixed forests with a significant proportion of deciduous elements growing elsewhere (Marmi *et al*., 2012). Following global climatic changes (Zachos *et al*., 2001), the progressive disappearance of tropical and subtropical plants—providing a continuous supply of fruits all year long—, and the concomitant increasing dominance by deciduous trees, may have resulted in the lack of adequate trophic resources for both hominoids and pliopithecoids during the unfavorable season, ultimately leading to their extinction not only in Iberia but also in the rest of Europe and most of Asia.

The same global changes that, in most of Eurasia, drove the extinction of pliopithecoids and hominoids, probably favored the dispersal and diversification of monkeys. By the Early and Middle Miocene, cercopithecoids were already distinct but much less diverse than hominoids, but from the Late Miocene onwards, their disparity, geographic distribution and paleodiversity increased dramatically (Szalay and Delson, 1979; Jablonski, 2002; Eronen and Rook, 2004; Jablonski and Frost, 2010). This might be related to different dietary adaptations between both groups (Andrews, 1981) and/or to differences in life-history parameters between them (Jablonski and Kelley, 1997). Such factors likely conditioned differently the evolutionary responses of cercopithecoids and hominoids to the changing climatic conditions initiated by the Middle Miocene, but most strongly expressed during the latest Miocene and the Pliocene. Thus, both colobines and cercopithecines possess specific dietary adaptations for more efficient folivory and/or consumption of unripe fruits compared to hominoids (Andrews, 1981), thereby enabling the former to more easily thrive when the ripe fruits habitually consumed by most hominoids are scarce. Moreover, hominoids display a low life-history profile, suitable for the tropical to subtropical forested conditions with low seasonality of the African Early Miocene, providing an abundant provision of high-quality food resources; in contrast, the faster life history of cercopithecoids is more suitable for the highly seasonal environments that prevailed in Europe by the latest Miocene, thus enabling them to thrive in a wider range of habitats compared to hominoids (Jablonski and Kelley, 1997; Eronen and Rook, 2004). Hence, many latest Miocene and Pliocene cercopithecoid lineages occupied less heavily forested and more seasonal habitats than the preceding hominoids. Two distinct families of cercopithecoids are usually distinguished: crown cercopithecoids are classified into a single family, Cercopithecidae, with two distinct subfamilies (Colobinae and Cercopithecinae), distinguished at the family level by some authors (e.g., Jablonski, 2002); whereas stem cercopithecoids are classified into another, extinct family (the Victoriapithecidae). In the Iberian Peninsula, both cercopithecines and colobines are recorded. Colobines are represented by *Mesopithecus* in the latest Miocene, and by its presumed descendant, *Dolichopithecus*, during the Pliocene. Cercopithecines, in turn, are recorded by *Macaca*, from the latest Miocene onwards, as well as by *Paradolichopithecus* from the Late Pliocene and Early Pleistocene, and *Theropithecus* from the Early Pleistocene.

Until recently, the colobine *Mesopithecus* had not been recorded in the Iberian Peninsula, but recent finds (Montoya *et al*., 2006; Guillén Castejón, 2010) have shown that this was merely an artifact of the record. At Venta del Moro, *Mesopithecus* is recorded ca. 5.8–5.5 Ma (Montoya *et al*., 2002, 2006), thus conclusively indicating that *Mesopithecus* dispersed into westernmost Europe by at least the latest Turolian (MN13). Similarly, *Macaca* is recorded by ca. 6.1–5.3 Ma at Almenara-Casablanca M (Köhler *et al*., 2000). The dispersal of these semi-terrestrial and oportunistic genera into the Iberian Peninsula must be understood within the framework of the significant faunal turnovers that took place in Europe by this time (van der Made, 2006; Agustí *et al*., 2006), apparently before the first evaporitic cycle of the Messinian Salinity Crisis. This event implied the clousure of the Gibraltar strait, ultimately leading to the total (or almost complete) desiccation of the Mediterranean between 5.5–5.3 Ma (Hsü *et al*., 1973). At the same time, this created an African-European connection that allowed the dispersal of certain mammal taxa including hippopotamids, gerbils, crested rats and likely cercopithecines as well (Agustí *et al*., 2006).

Subsequent dispersal and range extension events took place into the Iberian Peninsula during the Pleistocene, as reflected by the record of the gelada *Theropithecus* at ca. 1.0 Ma in Cueva Victoria (Gibert *et al*., 1995), and that of early *Homo* from ca. 1.2 Ma (Carbonell *et al*., 2008; Bermúdez de Castro *et al*., 2011, 2012b) onwards. Throughout the remaining Pleistocene, humans and macaques were apparently the only primates that managed to survive in the Iberian Peninsula and the rest of Europe, being (for different biological reasons) well suited to survive under the changing paleoenvironmental conditions (with marked glacial cycles) of the Pleistocene (Eronen and Rook, 2004). In the case of European macaques, they apparently extended their geographical range much farther northwards during the interglacials, and retreated into their Mediterranean refugia during glacials, although they ultimately became locality extinct due to their inability to tolerate the most severe stage of the last glaciation (Fooden, 2007), being last recorded in Iberia by ca. 80 ka (Castaños *et al*., 2011). With regard to humans, there is the possibility that different dispersal events of early humans into the Iberian Peninsula and Western Eurasia in general took place during the Pleistocene (Bermúdez de Castro and Martinón-Torres, 2013), thus being still uncertain (see discussion in Madurell-Malapeira *et al*., 2012) whether humans continuously occupied the Iberian Peninsula between their early record at ca. 1.2 Ma and their subsequent record at ca. 0.88–0.78 Ma (Carbonell *et al*., 1995; Bermúdez de Castro, 1997).

Acknowledgments

This work has been funded by the Spanish Ministerio de Ciencia e Innovación (CGL2011-27343; CGL2011-28681; CGL2010-21672/BTE; JCI-2010-08241 to I.C.-V.; RYC-2009-04533 to D.M.A.); the Generalitat de Catalunya (2009 SGR 754, GRC, predoctoral fellowship 2010FIB176 to J.M., and travel grants 2010BE00758, 2011BE100009 and 2011CTP00011 to J.M.); and the SYNTHESYS Project (FR-TAF-80 and FR-TAF-1735 to J.M.; http://www.synthesys.info/), which is financed by the European Community Research Infrastructure Action under the FP6 ''Structuring the European Research Area'' Programme. We thank the reviewers Eric Delson and Peter Andrews, whose comments helped to improve a previous version of this paper.

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