The role of new Iberian finds in understanding European Eocene mammalian paleobiogeography
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The role of new Iberian finds in understanding European Eocene mammalian paleobiogeography

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ABSTRACT

This paper summarizes the new Eocene mammalian discoveries in western and northeastern Iberia and analyses the paleobiological data they provide towards an understanding of the evolutionary and paleobiogeographic history of the Eocene mammalian faunas across Europe. Fifty-one mammalian taxa, of which nineteen are new, have been identified since the last synthesis on Eocene mammal faunas presented at the Paleogene biochronological congress that took place in Montpellier in 1997. The new taxa consist of eight rodents, three artiodactyls and eight perissodactyls. A period of isolation from the Central European Island, albeit with intermittent faunal exchange with the rest of Europe and with other continents (probably Asia and Africa), most likely caused the endemism of the Eocene mammal faunas of the Iberian Peninsula. Middle and Late Eocene mammalian faunas (mainly primates, rodents and perissodactyls) of the western and central Iberian basins (Duero, Almazán, Oviedo and Miranda-Trebiño Basins) were clearly different from those of the Southern Pyrenean Basins and the rest of Europe. The special paleoecological conditions of western Iberia seem to have been one of the main causes of this faunal differentiation. The Iberian Peninsula could have played an important role as one of the dispersal routes for some Eocene mammal faunas that appeared in the Central European Island during the Middle and Late Eocene through two intra-Eocene faunal turnovers involving immigrations.

KEYWORDS
INTRODUCTION

It is well known that the history of Paleogene mammal faunas at the Paleocene-Eocene and Eocene-Oligocene transitions is marked by different phases of extinction and origination related to paleoenvironmental changes (e.g., Hooker, 2000; Gingerich, 2004, 2006). A profound faunal reorganization occurred near the Paleocene-Eocene boundary, when most modern groups of mammals appeared in the Northern Hemisphere continents (e.g., Hooker, 1998; Gingerich, 2000, 2001, 2003; Bowen et al., 2002). Europe was an archipelago from the late Early Eocene to earliest Oligocene, inhabited by an endemic mammalian fauna, which was clearly different from its contemporaries in North America and Asia. Many of these European endemic mammals became extinct in the earliest Oligocene synchronous with the appearance of Asian immigrants, in an event known as the “Grande Coupure” (e.g., Brunet, 1977; Prothero, 1985; Hooker, 1992; Blondel, 2001; Hooker et al., 2004).

The Middle and Late Eocene on the Central European Island was also a period of important change in faunal and floral composition as a result of global climate change, plate tectonics and several immigration waves. Two intra-Eocene mammalian faunal turnovers involving immigration took place: one in the Middle Eocene and the other around the Middle-Late Eocene transition (Hooker, 1992; Franzen, 2003). The incoming taxa seem not to have originated outside Europe, but their origin and dispersal directions are still unresolved. In addition to the intermittent presence of land bridges between the different areas of Europe, the palaeoclimatic conditions also seem to have played a role in these immigrations. From this perspective, the relative diversity of different mammal groups and the modifications of their tooth morphology, which reflect dietary changes, resulting from vegetation modification, have been widely analysed from the Middle Eocene to Early Oligocene in several regions of Western Europe. The palaeoecological analyses of the mammal assemblages from France, England and Germany suggest a change from a forest habitat to a more open environment in the Late Eocene, influencing faunal composition (Legendre, 1986, 1987, 1989; Legendre et al., 1991; Vianey-Liaud, 1991; Hooker, 1992; Sudre and Legendre, 1992). The vegetation modification is supported by floral data (e.g., Hochuli, 1984; Ollivier-Pierre et al., 1987; Schuler, 1990; Collinson and Hooker, 2003). Blondel (2001) has demonstrated that important adaptive changes occurred in the ungulate dental pattern (selenodonty in artiodactyls, semihypsodonty in perissodactyls), which coincided with the paleoenvironmental changes that occurred from the Middle Eocene to Early Oligocene. Competitive exclusion by the newcomers also could have been an important factor in the faunal turnovers (Hooker, 2000).

Until now, the paucity of the Eocene mammal fossil record in the Iberian Peninsula has inhibited study of the biodiversity and evolution of the Eocene mammalian faunas in relation to paleoenvironmental changes in this area. However, knowledge of Iberian Eocene mammals is growing, as a result of the discovery of new remains found in western and northeastern Iberia (Figs. 1 and 2). This work summarizes these new data from the Duero, Almazán (Cuesta, 1999, 2003), Ebro, Southern Pyrenean (Checa and Casanovas, 1989-1990; Checa, 1997, 2004; López-Martínez et al., 1998; Checa and Colombo, 2004; Cuesta et al., 2006) and Miranda-Trebiño (Astibia et al., 2000; Badiola, 2004, Badiola and Cuesta, 2008; Badiola et al. 2002, 2005) Basins and updates the last synthesis on Eocene mammal faunas of the Iberian Peninsula (Antunes et al., 1997). We also analyse the paleobiological data provided by these new finds to help in an understanding of the evolutionary and paleobiogeographic history of Eocene mammalian faunas across Europe.

The biochronologic scale used in this paper is that of the MP Mammal Paleogene reference levels (Schmidt-Kittler, 1987, updated by Aguilar et al., 1997). The levels are calibrated to the most recent International Stratigraphic Chart and the Eocene European Land Mammal Ages (ELMA: Neustrian, Grauvian, Geiseltalian, Robiacian and Headonian) (Gradstein et al., 2004; Fig. 3). A new chronostratigraphy of the MP 14 to MP 17 reference levels, with a time scale that substantially changes the traditionally accepted ages, has been proposed by Beamud et al. (2003). According to their new magnetostratigraphic results obtained in the continental sequence of the South-Central Pyrenees, MP 14 and MP 15 correspond to the Lutetian, whereas MP 16 and early MP 17 correlate with the early Bartonian. However, this does not accord with the association of Robiacian mammals with Bartonian calcareous nannoplankton zone NP 17 and the superposed sequence of Headonian faunas in the UK (Hooker, 1986). Here, we therefore use the traditionally accepted ages, but we are aware that the current chronostratigraphic age attributions based on MP reference levels in the Iberian Peninsula should be revised with the available regional litho-, bio- and magnetostratigraphic information.

NEW EOCENE MAMMALIAN FOSSILS FROM IBERIAN PENINSULA

New finds in the Early Eocene involve especially rodents, artiodactyls and perissodactyls (Figs. 1 and 2). The study of the rodent assemblages is ongoing and a preliminary classification is given by one of us (R. Q.). The new rodent fossils come from the Early Eocene beds at Masía de l’Hereuet and La Coma, which are located in the Southern Pyrenean (Ager sub-basin) and Ebro Basins, respectively, and from the early Middle Eocene (Robia-
cian) beds at Sant Jaume de Frontanyà 3, SJF 2 and SJF 1 of the Eastern Pyrenees (Ripollés-Berguedà Basin) (Figs. 1-3). Masia de l’Hereuet and Barranc del Guesot were reported as Early Eocene (Grauvian, MP 10) in the last synthesis on the Iberian Eocene mammal faunas (Antunes et al., 1997). The rodent and artiodactyl fossil assemblages suggest a Neustrian age, belonging to the MP 8+9 reference level (Fig. 3). The perissodactyl Propachynolophus (Lemoine, 1891) from these sites described as P. remyi Checa, 1997 should not be referred to that species. Its smaller size and more plesiomorphic dentition than those of the type specimen from Les Badies (South-Central Pyrenees, Isàvena Area; Grauvian, MP 10) suggest that it belongs to a more primitive form than P. remyi. The recently described Early Eocene artiodactyls (Checa, 2004) and perissodactyls (Checa and Colombo, 2004) are from the Southern Pyrenean and Ebro Basins, respectively (Figs. 1 and 2).

More remains of artiodactyls (Cuesta and Jiménez, 2000; Cuesta, 2003) and perissodactyls (Cuesta et al., 2004) come from the late Middle Eocene (Robiacian) beds at Villamayor, Caenes, Corrales del Vino, Villamayor, and San Morales (Duero and Almazán Basins, Figs. 1-3).

The Iberian Late Eocene mammal faunas are sparsely represented with perissodactyls being the best-known group. However, our knowledge of these faunas is increasing. Artiodactyls from the Late Eocene (early Headonian, MP 17) of Sossís (South-Central Pyrenees, Pobla de Segur sub-basin; Figs. 1 and 3) have been studied by Cuesta et al. (2006; Fig. 2). A new Late Eocene (middle Headonian, MP
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<td>Pachylophus primavum sp.</td>
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**FIGURE 2** Iberian Eocene sites with new mammal finds. See Figs. 1 and 3 for their geological and biochronological context.

18) vertebrate site, called Zambrana (Miranda-Trebiño Basin, Astibia et al., 2000; Fig. 1), was discovered after the last synthesis on Iberian Eocene mammal faunas. Up to now, twenty-one mammal taxa have been recovered, which have been described in Badiola (2004; Fig. 2); some of the rodent specimens previously described as ?Pseudosorciidae indet. should be assigned to the genus Remy sp. Thaler, 1966 (Quer, pers. obs.). A primate mandible has been recently found. Zambrana is the first Paleogene locality in the Iberian Peninsula to have yielded a fossil mammal assemblage belonging to the MP 18 reference level (Fig. 3). Seven perissodactyl taxa are identified, of which five (two genera and three species) are new: Pachylophus zambranensis Badiola, Pereda and Cuesta, 2005, and the unpublished species of Leptolophus remy, 1965 and Palaeotherium cuvier, 1804, and two new plagioline genera (Badiola et al., 2002; Badiola, 2004). Representatives of these new genera have also been found in the late Middle Eocene of Mazaterón and San Morales (Almazán and Duero Basins, respectively) (Badiola, 2004; Figs. 1-3). One of these genera exhibits an unusual dental pattern that has never been described in any other European Eocene equid (Badiola and Cuesta, 2008).

**NEW PALEOBIOGEOGRAPHIC DATA**

The new Iberian Eocene mammalian fossils mentioned above provide important paleobiological data for understanding European Eocene mammalian paleobiogeography. Although we are aware of the limitations of our data, some tentative hypotheses can be proposed in relation to the following issues: 1) the possible area or areas of origin and a paleobiogeographic scenario for some mammals, which
appeared at the beginning of the Eocene in the northern Hemisphere continents; 2) the existence of a Western Iberian Bioprovince in the Iberian Peninsula; and 3) the dispersal directions of the intra-Eocene incoming taxa related to the mammal faunal turnovers that occurred on the Central European Island during the Middle Eocene and around the Middle-Late Eocene transition. These aspects are discussed below and illustrated in Figs. 4 to 6.

### Paleobiogeographic scenario and provenance of the Early Eocene mammal dispersal

Most modern groups of mammals appeared suddenly in the Northern Hemisphere continents at the beginning of the Eocene, but their area or areas of origin are still controversial. This early Eocene Mammalian Dispersal Event (MDE; e.g., Hooker, 2000) coincided with brief but intense warming at the P/E boundary (55.8 Ma, Gradstein et al., 2004) and the newcomers are inferred to have moved northwards to the northern continents. Their origin has been hypothesized at different times to be Africa, Central America, India and other parts of Asia (Gingerich, 1976, 1989; Gheerbrant, 1987; Franzen, 1987, 1989; Krause and Maas, 1990; Hooker, 1998; Bowen et al., 2002; Godinot and Lapparent de Broin, 2003; Smith et al., 2006).

Systematic study of the new Early Eocene mammal finds of the Iberian Peninsula, which are summarized in

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**Figure 3**

Biochronological context of the Iberian Eocene mammal sites (see Introduction section for explanation of the biostratigraphic scale used in this figure). The Iberian Eocene sites with new mammal finds are indicated in bold type. Abbreviations: (A) the rest of MP 10 sites: Ager XII, Barranc del Forals, Can Picantón, Can Camperol, Capella, Castellnou de Montsec, Castigaleu, Central ENHER, Corral de l’Andreu Sud 4 and Nord 1, Costa de Baró, Chiriviet, El Mas de Montanyana, Empordà de Terrades, Escaríà, Fét IV, Güell 1 and 3, Km.86, Km. 87, La Boixedat, La Morera, La Ribereta, Les Saleres, Les Oliveres, Litera, Localidad 4, Mas de Minguet, Mas de Faro, M-2 Cami de la Masia de l’Hereuet, Montllorbar, Partida de Solà, Poble Veil de l’Anetilla, Pont de Montanyana, Repeu del Güaita, Sant Pere Mártir, Sant Miquel, Santes Creus East and North, Sobrenoguera, Torre del Moro, Torrelabad.
the following paragraphs, suggests that the first Early Eocene representatives of rodents, artiodactyls and perissodactyls not only existed in the Central European Island, but they were also present in the Iberian Peninsula. The latter could have played an important role as one of the areas of origin and/or a dispersal route for some of these Early Eocene mammals, which appeared at the beginning of the Eocene on Northern Hemisphere continents (at the MDE). However, cladistic analysis of these European mammals is required in order to discover whether their present paleobiogeographical distribution was due to vicariance or to any paleogeographic area being their centre of origin. In addition to these undescribed species from Masia de l’Hereuet, some Middle Eocene fossils identified as Rodentia n. g. n. sp. have also been found in the Eastern Pyrenees, at Sant Jaume de Frontanyà (SJF) 3, which could explain the presence of the rodents Remys and Pairomys Thaler, 1966 in the Iberian Peninsula. A close phylogenetic relationship is found between Remys and the more primitive new form from SJF3. The latter seems to belong to a new rodent family (Quer and Agustí, in press). This new family as well as the Gliridae and the Theridomyidae could be descended from European Eocene microparamyine rodents.

The Early Eocene artiodactyl Eygalayodon isavenaensis Checa, 2004 (Dichobunidae, Eurodexeinae) is considered the most plesiomorphic form of the subfamily Eurodexeinae and closely related to the more plesiomorphic Diacodexis corsaensis Checa, 2004 (Figs. 2 and 3). The latter exhibits some similarities with Diacodexis antunesi Estravis and Russell, 1989 from Silveirinha (Checa, 2004), which is reported as the oldest (Smith et al., 1996) or one of the oldest species (Erfurt and Sudre, 1996) of the genus. This is the first time that a representative of the Eurodexeinae has been found in the Iberian Peninsula. The two new Iberian species Eygalayodon isavenaensis and Diacodexis corsaensis are important for understanding the evolution and paleogeographic distribution of some of the oldest European artiodactyls.
Using cladistic analysis and paleogeographic reconstructions, three cases of land mammal dispersal across the Turgai Straits from Asia to Europe near the P/E boundary, including the order Perissodactyla, have been recognized by Hooker and Dashzeveg (2003). These authors suggested that the differentiation of equoids must have taken place within Europe, as was hypothesized earlier by Hooker (1998). Up to now, perissodactyls, including equoids, have been recorded in northwest Europe (Cymbalophus Hooker, 1984) at the beginning of the Eocene. More Early Eocene equoids have been found in the Iberian Peninsula. It is critical to establish the phylogenetic relationships of the perissodactyl Bepitherium jordifusalbae Checa and Colombo, 2004, recently discovered in the Ebro Basin, to other basal members of the order.

Casanovas and Santafé (1991a) proposed that the palaeotheriids could have entered Europe from Africa, using two different dispersal routes: one through the Iberian Peninsula and the other through the nearest emergent islands of the Apulian Plate. According to paleogeographic reconstructions the Iberian Peninsula was close to Africa at this time, making faunal exchange between the two areas feasible (Figs. 4 and 5A). Unfortunately, there is no pre-Miocene equid fossil record in Africa to test this hypothesis. On the other hand, for Casanovas and Santafé (1991a) the presence of a wide diversity of equoids, mainly palaeotheriids, in the Iberian Peninsula is other evidence that indicates their possible route from the South (Iberian Peninsula) to the North (Central Europe). The recorded biodiversity of the Iberian Eocene perissodactyls is increasing. Eight new equid taxa, of which three are new genera (Fig. 2), have been described since the last synthesis on Iberian Eocene mammal faunas (Antunes et al., 1997). Some of these perissodactyls are ranked as members of the endemic fauna of the Iberian Peninsula (see next section). The wide diversity of palaeotheriids in the Iberian Peninsula and the presence of the oldest known representative of the palaeotheriid Leptolophus in Mazaterón, western Iberia, and others slightly younger in the southern part of the Central European Island—now southern France and Switzerland—support the hypothesis of the South to North mammal route proposed by Casanovas and Santafé (1991a) (see Figs. 6A, 7 and last section). The ancestral stocks could have evolved in the Iberian Peninsula and then spread towards Central Europe after the Iberian plate became connected to the Central European Island in the late Lutetian (see last section).

The existence of a Western Iberian Bioprovince in the Iberian Peninsula

In Europe, several bioprovinces are recognized to have existed during the Late Eocene on the basis of regional differences between rodent, primate, artiodactyl and perissodactyl faunas (e.g., Franzen, 1968; Hartenberger, 1973; Schmidt-Kittler and Vianey-Liaud, 1975; Sudre, 1978; Vianey-Liaud, 1991; Hooker, 1992). However, this faunal differentiation is particularly pronounced between western Iberia and the rest of Europe. In the Iberian Peninsula, Middle Eocene mammalian faunas (mainly perissodactyls, rodents and primates) of the western and central Iberian basins (mainly Duero, Almazán and Oviedo Basins) were clearly different from those of the Southern Pyrenean Basins (e.g., Casanovas and Santafé, 1987, 1989, 1991b; Casanovas and Moyà-Solà, 1992; Cuesta, 1991, 1999, 2003; Peláez-Campomanes, 1993) (see Fig. 1). In contrast, in the Southern Pyrenean Basins, the Eocene mammalian faunas were similar to those of the southern part of the Central European Island.
where the typical western Iberian endemic taxa were absent (e.g., Casanovas, 1975; Checa, 1997; Casanovas et al., 1998; Cuesta et al., 2006). On the basis of this faunal differentiation, the existence of a Western Iberian Bioprovince has been hypothesized by Cuesta (1991). There is evidence that this bioprovince existed from the late Middle Eocene to Late Eocene, because the perissodactyls found in the Late Eocene beds at Zambrana (Miranda-Trebiño Basin; Headonian, MP 18; Figs. 1 and 3) are related to endemic forms from the late Middle Eocene of the Duero, Almazán and Oviedo Basins (Badiola, 2004).

With respect to perissodactyls, to date, five genera and sixteen species of equoids and five taxa of lophiodonts, which are unknown elsewhere in Europe, are identified in the Western Iberian Bioprovince (Fig. 7). This bioprovince includes at least the Duero, Almazán, Oviedo, and Miranda-Trebiño Basins (Fig. 1). In the context of Iberian biochronology, primate and rodent fossils are less well known than perissodactyls. However, various taxa have been described from the Middle and Late Eocene beds of the Duero and Miranda-Trebiño Basins, respectively (Peláez-Campomanes et al., 1989; Moyà and Köhler, 1992; Peláez-Campomanes, 1992, 1993, 1996; Badiola, 2004). The Middle Eocene rodent fossil assemblages contain several genera (Pairomys, Zamoramys PELÁEZ-CAMPOMANES and LÓPEZ-MARTÍNEZ, 1996), which are not present elsewhere in Europe. Some Middle and Late Eocene fossils belong to the same species as those of northeastern Iberia and the southern part of the Central European Island [e.g., Theridomys euxetensis (DEPÉRET, 1917), Glamys priscus (STEHLIN and SCHAUB, 1951)], but others, because of their more derived dental features (mainly larger size and more hypsodont dentitions), are not included within the same species (e.g., Theridomys aff. golpeae, Remys aff. minimus) (Peláez-Campomanes et al., 1989; Peláez-Campomanes, 1996; Badiola, 2004). The late Middle Eocene primate fossils found in several localities of the Duero and Almazán Basins, such as Caenes (Microadapis sp. and Anchomomys sp.), and Mazaterón and Miñana (Adapidae indet., Anchomomyini indet., and Pseudoloris sp.), respectively, seem to belong to different species from those elsewhere in Europe (Moyà and Köhler, 1992). The paucity of the artiodactyl fossil assemblages in the western and central Iberian basins mentioned above, however, prevents their compa-r...
son to those of northeastern Iberia and the rest of Europe. Although a new Middle Eocene anoplotherine artiodactyl has been found at one locality in the Western Iberian Bioprovince, Mazatérón (Almazán Basin; Robiacian, MP 15-16; Cuesta and Badiola, 2007), more Middle Eocene artiodactyl fossils are required to test the hypothesis of an artiodactyl faunal differentiation between the two areas at this time. The only well-known artiodactyl fossil assemblage in this bioprovince comes from the Late Eocene beds at Zambrana, where the typical central European artiodactyl taxa are identified (Fig. 2).

The presence of the endemic perissodactyl Bepitherium jordifusalbæ in the Ebro Basin, which according to Checa and Colombo (2004) seems to be closely related to the Iberian genus Paranchilophus CASANOVAS and SANTAFÉ, 1989, suggests that the Western Iberian Bioprovince could have existed since the Early Eocene. This was hypothesized earlier by Checa (1997) for the early Middle Eocene perissodactyl faunas of the eastern part of the Ebro Basin (Catalan Coastal Ranges, Ulldemolins area), where several new taxa were described (Fig. 7). However, in order to resolve this issue satisfactorily, we need to find Early Eocene fossils and more early Middle Eocene fossils in the central and western Iberian basins. An early Late Eocene species of Paranchilophus, i.e. P. Iusitanicus GINSBURG, 1965, is described in the Mondego Basin, in Portugal (ANTUNES, 1995; Figs. 1 and 7), and the new perissodactyl remains found in Huérmeces del Cerro and in the nearby new locality Viana de Jadraque (Tajo Basin, Figs. 1 and 7), in Guadalajara, Spain, seem belong to the Iberian equoid Cantabrotherium CASANOVAS and SANTAFÉ, 1987 (Iriarte et al., 2006). However, more fossils are needed to compare with those of the rest of the western Iberian regions. The mammal fossil assemblage of the Huérmeces del Cerro was suggested as Early Oligocene age, belonging to MP 20 reference level (Antunes et al., 1997), but a revision and the study of the new mammal fossils of these sites are required to characterize their biochronology.

The special mammalian faunal association in the Western Iberian Bioprovince could be related to the paleoecological and paleogeographic conditions in this region. Paleogeographic reconstructions indicate that the Iberian Peninsula was an island during the Early Eocene and that it did not become connected to the Central European Island until the late Lutetian (e.g., Meulenkamp et al., 2000). However, this did not prevent some selective faunal exchange between the two areas. The presence of the Middle Eocene perissodactyls Leptolophus and Mekodontherium REMY, 2000 in southern France and Switzerland, the latter according to Remy (2000) is closely related to the Iberian genus Franzenium CASANOVAS and SANTAFÉ, 1989, indicate sporadic faunal exchange between the two areas at this time. On the other hand, the occurrence of the rodent Zamoramys in the Middle Eocene beds (Robiacian, MP 14) at Santa Clara and Sanzoles (Duero Basin), which seems to be related to Asian taxa (Peláez-Campomanes and López-Martínez, 1996), and the presence at Santa Clara of an anagalid similar to those in China (cf. Anagalida, Peláez-Campomanes et al., 1989) suggests some faunal exchange between the Iberian Peninsula and Asia during this time. The occurrence of typical central European artiodactyl taxa in the Late Eocene beds at Zambrana suggests also a connexion between the Iberian Peninsula and the rest of Europe at this time (Badiola, 2004).

The paleoecological conditions of the Western Iberian Bioprovince seem to have played an important role in influencing this special faunal composition. Current paleoecological analysis of the Mazatérón and Zambrana mammal assemblages suggests that the change from a complex forest habitat to a more open environment observed in the Late Eocene in several regions of Europe could have started earlier in the Western Iberian Bioprovence, influencing its faunal composition (Badiola, 2004). In addition to the results obtained from the cenograms and the ecological diversity spectra for the Mazatérón and Zambrana mammal fossil assemblages (Badiola, 2004), there is more evidence of unusual paleoecological conditions for this bioprovince. The low species diversity of the rodent fauna observed in the Middle Eocene (Miñana and Mazaterón) and Late Eocene (Zambrana) localities of the Almazán and Miranda-Trebíño Basins, respectively (Fig. 1), with more species of theridomyids than pseudosciurids, glirids or ischyromyids (see Peláez-Campomanes, 1993, 1996; Badiola, 2004), suggest the existence of less densely forested areas. Moreover, some dental features (precocious development of cement on the external wall of premolars and molars, and the reduction of the premolar series combined with large and hypsodont molars) observed in perissodactyls and rodents could be interpreted as representing adaptations to chewing tough plants associated with the increasingly more arid conditions in this region (Badiola, 2004).

The paleoecological and paleoecological barriers could not have influenced the entire mammalian fauna equally, because perissodactyl fossils from the Late Eocene beds at Zambrana are clearly related to endemic forms from the late Middle Eocene of the Duero, Almazán and Oviedo Basins, whereas typical Central European artiodactyl taxa are present alongside them.

Dispersal directions during the Middle Eocene and around the Middle-Late Eocene transition

Two important intra-Eocene mammal faunal turnovers involving immigration took place on the Central Euro-
pean Island: one in the Middle Eocene, between MP 13 and 14, and the other around the Middle-Late Eocene transition, between MP 16 and 17 (Hooker, 1992; Franzen, 2003). The incoming taxa seem not to have originated outside Europe, but their origin is still enigmatic. The first immigration brought the first adapines that

<table>
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<tr>
<th>AGE</th>
<th>ELMA</th>
<th>MP</th>
<th>Portugal (Brah Rio Alto, Louro and Montes de Cabora Basin)</th>
<th>Western Iberian Bioprovence (Duero, Almaza, Ouido, and Miranda dels Tres Pasos Basins)</th>
<th>Eastern Ebro Basin (Catalan Coastal Ranges, Llut cemetery Area)</th>
<th>Southern Pyrenean Basins (Graus-Teberia Basin, Ripolles-Bergueda Basin)</th>
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<tr>
<td>19</td>
<td></td>
<td></td>
<td>Paleaeotherium crassum cf. Paleaeotherium magnus cf. Paleaeotherium sp.</td>
<td>Parachilophus rami</td>
<td>Paleaeotherium zampronensis</td>
<td>Paleaeotherium n. sp.</td>
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<td>18</td>
<td></td>
<td></td>
<td>Paleaeotherium magnus stehlini</td>
<td>Paleaeotherium intermedius</td>
<td>Paleaeotherium castaneum s. n.</td>
<td>Paleaeotherium curvum</td>
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<td>17</td>
<td></td>
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<td>Parachilophus lusitanicus</td>
<td>Paleaeotherium magnus stehlini</td>
<td>Paleaeotherium intermedius</td>
<td>Paleaeotherium castaneum s. n.</td>
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<td>16/17</td>
<td></td>
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<td>Parachilophus rami</td>
<td>Paleaeotherium farnesianum</td>
<td>Cantabrotherium trypaip asi</td>
<td>Franzenium tetradactylum</td>
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<td>15/16</td>
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<td>Archilophus sp.</td>
<td>Paleaeotherium giganteum</td>
<td>Cantabrotherium casanovae</td>
<td>Franzenium densum</td>
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<td>15</td>
<td></td>
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<td>Parachilophus rami</td>
<td>Paleaeotherium magnus stehlini</td>
<td>Paleaeotherium intermedius</td>
<td>Paleaeotherium castaneum s. n.</td>
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<td>14</td>
<td></td>
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<td>Plagiophiallaeinae n. g. et s. 1</td>
<td>Lophiodon sp.</td>
<td>Lophiodon sammarrense</td>
<td>?Lophiodontidae indet.</td>
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<td>13</td>
<td></td>
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<td>Plagiophiallaeinae n. g. et s. 2</td>
<td>Lophiodon sp.</td>
<td>Plagiophiallaeinae n. g. et s. 2</td>
<td>?Lophiodontidae indet.</td>
</tr>
</tbody>
</table>

replaced cercamoniine adapids, and the first semihypso- 
dodont palaearctotheres that replaced step by step the brachy- 
odont palaearctotheres. Most of the bunoselodont and 
selenodont artiodactyls also appeared at this time and 
they replaced the brachyodont and bunodont forms of the 
Early Eocene and the early Middle Eocene (early Lutet- 
ian) (see references in Franzen, 2003). The second intra- 
Eocene faunal turnover led to considerable replacement 
of taxa particularly among the palaearctotheres and artio-
dactyls around the Middle-Late Eocene transition. How-
ever, some immigrants like the first cainotheriids, 
Robiacina Sudre, 1969, and the palaearctotheres Palaeotheri-
dium duvali Romel, 1853 arrived earlier, in MP 16, whereas 
the large anoplotherines Diplobothium Rütimeyer, 1862 and 
Anoplotherium Cuvier, 1804 arrived later, beginning in 
MP 18 (see references in Franzen, 2003).

The existence of certain paleobiological adaptations 
in the immigrants (increasing hypsodonty and develop-
ment of cement in perissodactyls as well as bunose-
leno–and selenodonty in artiodactyls), which are inter-
preted as representing adaptations to chewing more 
abrasive food, indicates that, apart from the presence of 
land bridges, which appeared between Iberia and the 
Central European Island at the Ypresian-Lutetian bound-
ary and between the West and Central European Islands 
at the end of the Lutetian, paleoclimatic conditions 
could have played a role in these immigrations (Franzen, 
2003). Floral evidence shows that the forests at the 
beginning of the Middle Eocene were tropical and para-
tropical, but a floristic change towards cooling and dry-
ing conditions coincided with the first intra-Eocene fau-
nal turnovers (Collinson et al., 1981; Janis, 1993). At the 
beginning of the Late Eocene the vegetation was even 
less tropical than earlier, when subtropical forests were 
dominant (Collinson and Hooker, 1987, 2003; 

For Franzen (2003) both turnovers were probably driven 
by climatic conditions shifting in a northward direc-
tion, but alternatively, decreasing paleotemperatures dur-
ing the Late Eocene resulted in a southern movement of 
climatic zones together with their faunas. Some of the 
first intra-Eocene incoming taxa that appeared in the Mid-
dle Eocene (some of the equoids, e.g., palaeotheriids) 
could have entered the Central European Island from the 
Iberian Peninsula. This is suggested by the paleogeog-
ographic evidence and the presence of a wide diversity of 
equoids, mainly palaeotheriids, in this area, together with 
the presence of the oldest known representative of the late 
Middle Eocene palaeotheriid Leptolophus in Mazaterón 
(Cuesta, 1994b), western Iberia, and other representatives 
of this genus slightly younger in southern France and 
Switzerland (Remy, 1998) (see Figs. 4 and 6A and first 
and second sections). Some of the second intra-Eocene 
incoming taxa, however, seem to have arrived from the 
West; some of the pseudosciurid rodents (e.g., Treposciu-
rus Schmidt-Kittler, 1970 and probably Tarnomys 
Hartenberger and Schmidt-Kittler, 1976), dispersed 
South from the Western European Island at the Middle-
Late Eocene boundary, which are recorded in late Robia-
cian (MP 16) beds of England (Hooker, 1986). Others, 
such as the artiodactyl Xiphodon Cuvier, 1822, appeared 
in the southern part of the Central European Island in the 
late Middle Eocene, with no clear centre of origin, and 
seem to have moved from there towards the South and 
West. The occurrence at Zambrana (Miranda-Trebiño 
Basin) and other Late Eocene localities of the Iberian 
Peninsula (Sossís, Roc de Santa, Sant Cugat de 
Gavaldons; Figs. 1 and 2) of this artiodactyl, but not earli-
er, is tentative evidence of the southwards migration men-
tioned above (Figs. 5B and 6B). The same artiodactyl has 
not been recorded in England before the late Headonian 
(MP 19) (Hooker, 1994; Hooker et al., 1995).

CONCLUSIONS

Knowledge of the diversity of the Eocene mammal fau-
as of the Iberian Peninsula is increasing. Fifty-one mammal 
taxa, of which nineteen are new, have been identified since 
the last synthesis on Eocene mammal faunas presented at the 
Paleogene biochronological congress that took place in 
Montpellier in 1997. The new taxa consist of eight rodents, 
three artiodactyls and eight perissodactyls, of which four 
have been already published. The new Early Eocene mam-
mal finds from the Iberian Peninsula are crucial for com-
paring with those of elsewhere in Europe with the aim of 
investigating the evolutionary and paleobiogeographic histo-
ry of the mammals that appeared at the beginning of the 
Eocene on Northern Hemisphere continents (MDE).

A period of isolation from the Central European Island, 
(albeit with intermittent faunal exchange with the rest of 
Europe and with other continents (probably Asia and Afrique), 
could have caused the endemism of the Eocene mammal faunas of the Iberian Peninsula. The special paleoecological 
conditions of western Iberia, with more open environments 
and probably more arid ecological conditions, which seem to 
have existed since the late Middle Eocene, could have been 
the main cause of the faunal differentiation (mainly of 
rodents, primates and perissodactyls) of the Western Iberian 
Bioprovince. The latter includes some central and western 
Iberian basins (at least the Duero, Almazán, Oviedo, and 
Miranda-Trebiño Basins).

The mammal fossil assemblage of Zambrana (Álava, 
Miranda-Trebiño Basin) has significant implications for 
Iberian and wider European mammalian paleoecology 
and paleobiogeography, and land-sea distribution in the
Late Eocene. The endemism of the perissodactyl faunas can be shown to persist during the Late Eocene in the central and western Iberian basins, because the perissodactyl fossils from the middle Headonian beds at Zambrana are related to endemic taxa from the late Rhibian beds of the Duero, Almazán and Oviedo Basins. However, the occurrence at Zambrana of typical European artiodactyls suggests a connection between the Iberian Peninsula and the other European regions during this time. Moreover, it indicates that the special palaeoecological conditions of western Iberia could not have influenced the entire mammalian fauna equally.

The Iberian Peninsula could have played an important role as dispersal route for some mammals that appeared in Europe during the Middle and Late Eocene through two intra-Eocene faunal turnovers involving immigrations. Some of the first intra-Eocene incoming taxa that appeared in Europe in the Middle Eocene could have entered Central Europe from the Iberian Peninsula (e.g., palaeotheriids), whereas some of the second intra-Eocene incoming taxa (e.g., Xiphodon) that appeared around the Middle-Late Eocene transition may have entered the Iberian Peninsula from the Central European Island, from where it may have also moved later to the Western European Island.

Detailed paleobiological study of the new Iberian Eocene mammal finds reported in this paper, including cladistic analysis, together with additional field work in the Eocene beds of the Iberian Peninsula, will be essential for testing the hypotheses proposed here.

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