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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 **Mammalia. Eocene. Endemism. Dispersal. Iberian Peninsula.**

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).

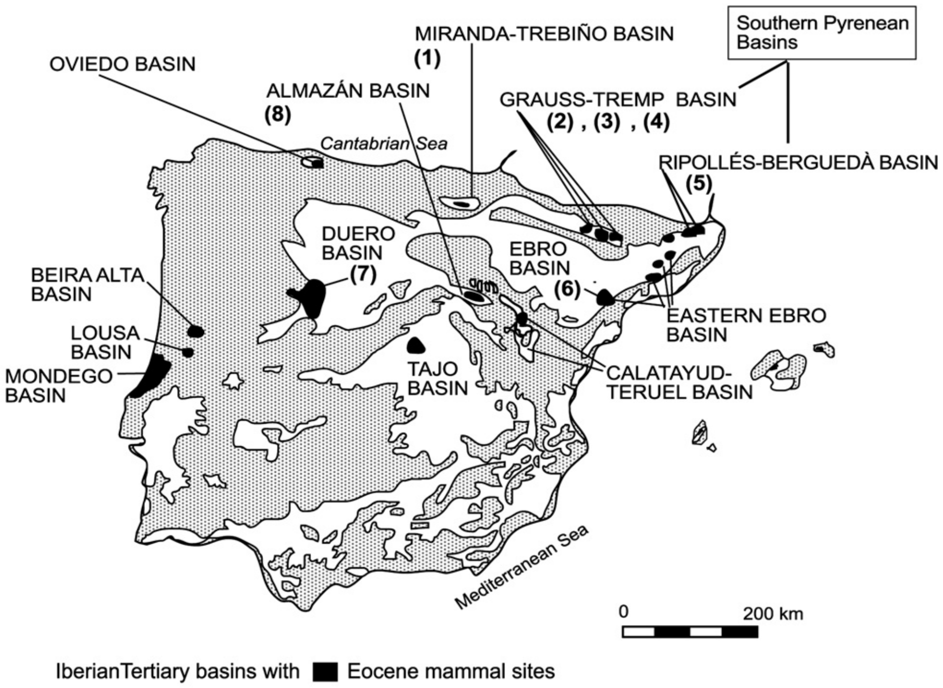
The Middle and Late Eocene on the Central European Island was also a period of important change in faunal and floral composition as a result of global climate change, plate tectonics and several immigration waves. Two intra-Eocene mammalian faunal turnovers involving immigration took place: one in the 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 paleoclimatic 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 paleoecological 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 Masia 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-



Eocene sites with new mammal finds:

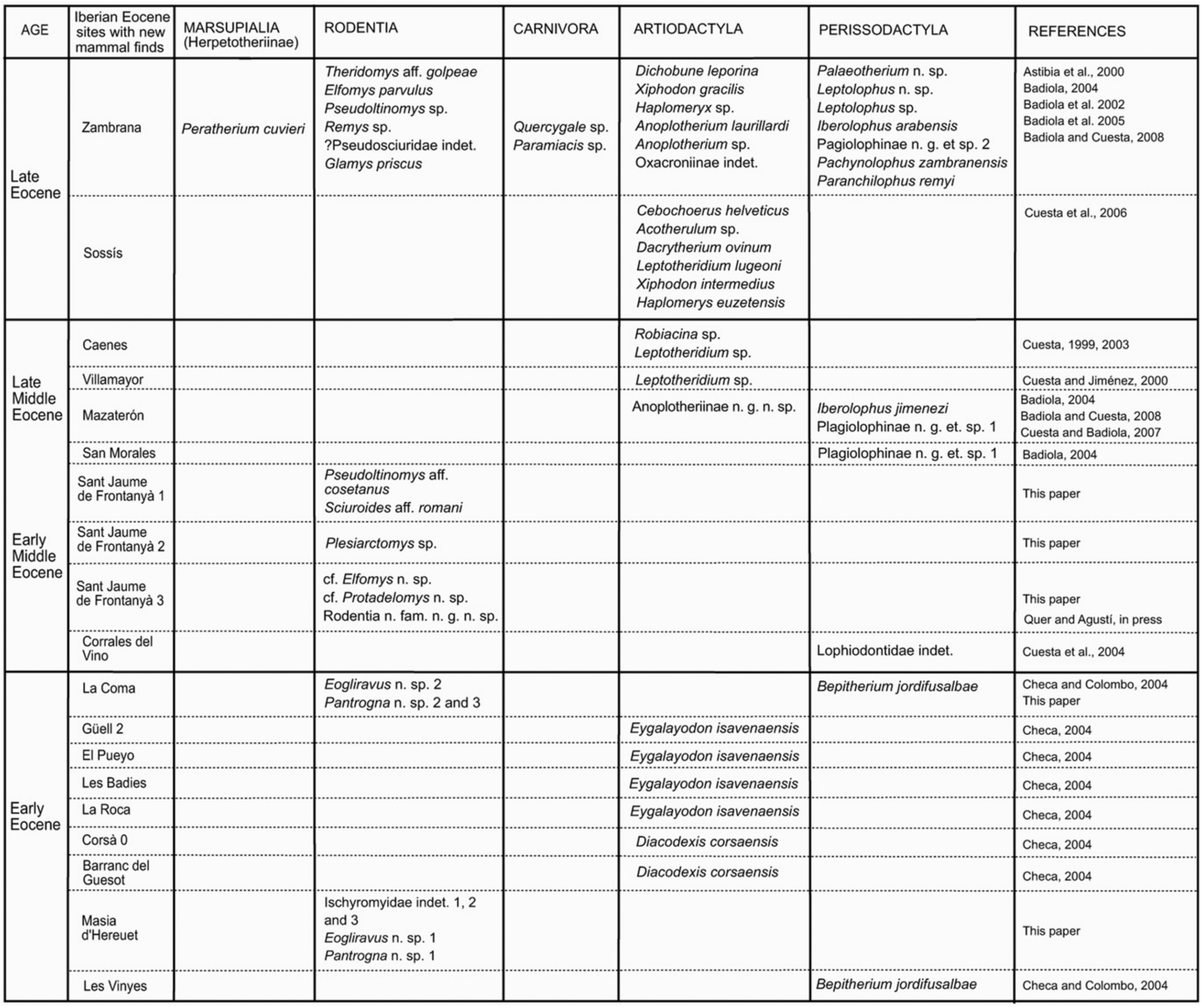
Miranda-Trebiño Basin	**(1)** Zambrana
Graus-Tremp Basin	**(2)** Ager sub-basin: Masia de l'Hereuet, Corsà 0, 2 & 3, Barranc del Guesot **(3)** Isávena Area: Güell 2, El Pueyo, Les Badies, La Roca, Montderoda **(4)** Pobla de Segur sub-basin: Sossís
Ripollés-Berguedà Basin	**(5)** Sant Jaume de Frontanyà (SJF) 1, SJF 2, SJF 3
Eastern Ebro Basin	**(6)** La Coma, Les Vinyes
Duero Basin	**(7)** Caenes, Corrales del Vino, Villamayor, and San Morales
Almazán Basin	**(8)** Mazaterón

FIGURE 1 **The main Tertiary continental basins of the Iberian Peninsula with Eocene mammal sites (modified from Antunes et al., 1997). Sites with new mammal finds are indicated in the table below the map. See Fig. 3 for their biochronological context.**

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 and Mazaterón (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



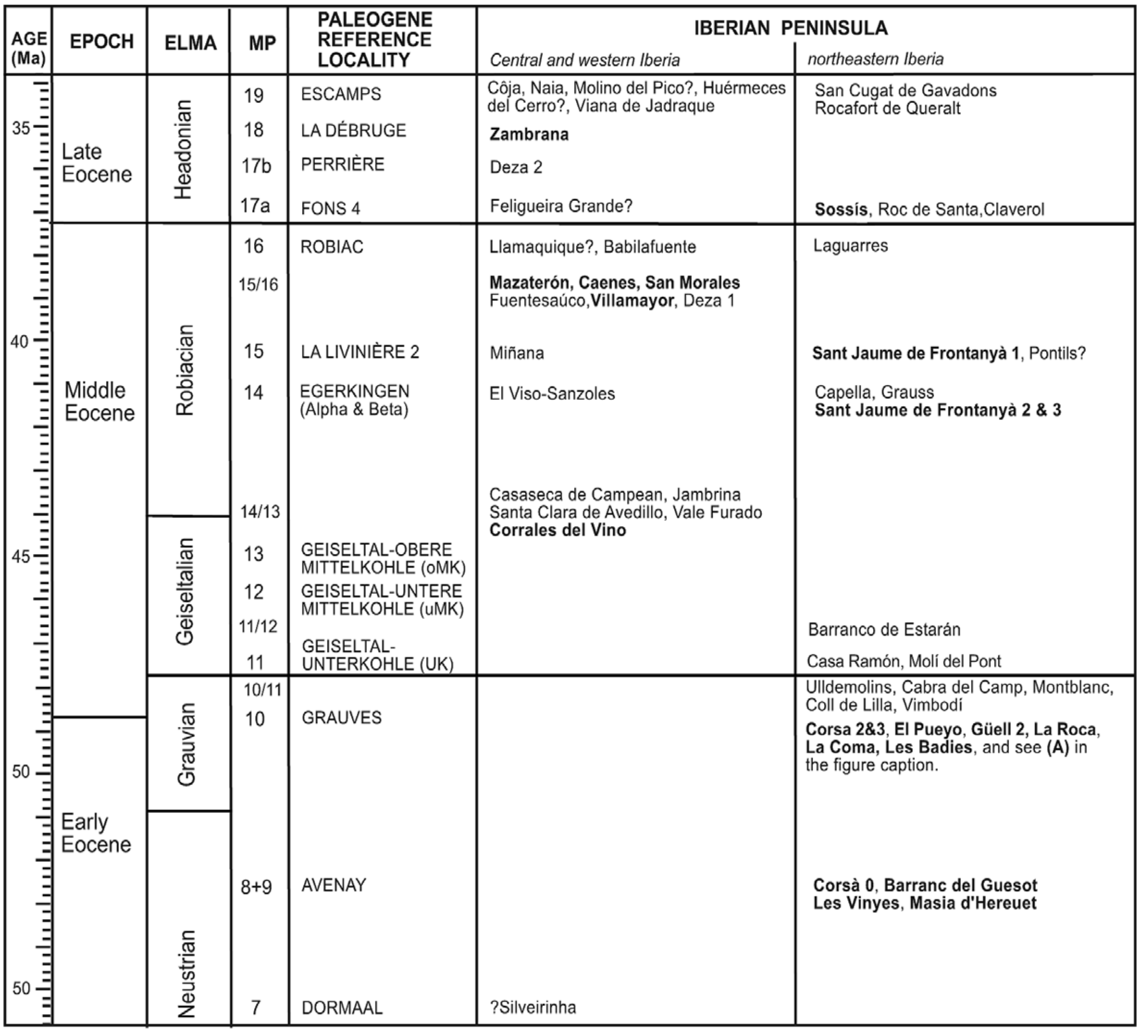
AGE	Iberian Eocene sites with new mammal finds	MARSUPIALIA (Herpetotheriinae)	RODENTIA	CARNIVORA	ARTIODACTYLA	PERISSODACTYLA	REFERENCES
Late Eocene	Zambrana	*Peratherium cuvieri*	*Theridomys* aff. *golpeae* *Elfomys parvulus* *Pseudoltinomys* sp. *Remys* sp. ?Pseudosciuridae indet. *Glamys priscus*	*Quercygale* sp. *Paramiacis* sp.	*Dichobune leporina* *Xiphodon gracilis* *Haplomeryx* sp. *Anoplotherium laurillardi* *Anoplotherium* sp. Oxacroniinae indet.	*Palaeotherium* n. sp. *Leptolophus* n. sp. *Leptolophus* sp. *Iberolophus arabensis* Pagiolophinae n. g. et sp. 2 *Pachynolophus zambranensis* *Paranchilophus remyi*	Astibia et al., 2000 Badiola, 2004 Badiola et al. 2002 Badiola et al. 2005 Badiola and Cuesta, 2008
	Sossís				*Cebochoerus helveticus* *Acotherulum* sp. *Dacrytherium ovinum* *Leptotheridium lugeoni* *Xiphodon intermedius* *Haplomerys euzetensis*		Cuesta et al., 2006
Late Middle Eocene	Caenes				*Robiacina* sp. *Leptotheridium* sp.		Cuesta, 1999, 2003
	Villamayor				*Leptotheridium* sp.		Cuesta and Jiménez, 2000
	Mazaterón				Anoplotheriinae n. g. n. sp.	*Iberolophus jimenezi* Plagiolophinae n. g. et. sp. 1	Badiola, 2004 Badiola and Cuesta, 2008 Cuesta and Badiola, 2007
	San Morales					Plagiolophinae n. g. et. sp. 1	Badiola, 2004
Early Middle Eocene	Sant Jaume de Frontanyà 1		*Pseudoltinomys* aff. *cosetanus* *Sciuroides* aff. *romani*				This paper
	Sant Jaume de Frontanyà 2		*Plesiarctomys* sp.				This paper
	Sant Jaume de Frontanyà 3		cf. *Elfomys* n. sp. cf. *Protadelomys* n. sp. Rodentia n. fam. n. g. n. sp.				This paper Quer and Agustí, in press
	Corrales del Vino					Lophiodontidae indet.	Cuesta et al., 2004
Early Eocene	La Coma		*Eogliravus* n. sp. 2 *Pantrogna* n. sp. 2 and 3			*Bepitherium jordifusalbae*	Checa and Colombo, 2004 This paper
	Güell 2				*Eygalayodon isavenaensis*		Checa, 2004
	El Pueyo				*Eygalayodon isavenaensis*		Checa, 2004
	Les Badies				*Eygalayodon isavenaensis*		Checa, 2004
	La Roca				*Eygalayodon isavenaensis*		Checa, 2004
	Corsà 0				*Diacodexis corsaensis*		Checa, 2004
	Barranc del Guesot				*Diacodexis corsaensis*		Checa, 2004
	Masia d'Hereuet		Ischyromyidae indet. 1, 2 and 3 *Eogliravus* n. sp. 1 *Pantrogna* n. sp. 1				This paper
	Les Vinyes					*Bepitherium jordifusalbae*	Checa and Colombo, 2004

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 ?Pseudosciuridae indet. should be assigned to the genus *Remys* 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: *Pachynolophus zambranensis* BADIOLA, PEREDA and CUESTA, 2005, and the unpublished species of *Leptolophus* REMY, 1965 and *Palaeotherium* CUVIER, 1804, and two new plagiolophine 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 equoid (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



EPOCH	ELMA	MP	PALEOGENE REFERENCE LOCALITY	IBERIAN PENINSULA	
				Central and western Iberia	*northeastern Iberia*
Late Eocene	Headonian	19	ESCAMPS	Côja, Naia, Molino del Pico?, Huérmeces del Cerro?, Viana de Jadraque	San Cugat de Gavadons Rocafort de Queralt
		18	LA DÉBRUGE	**Zambrana**	
		17b	PERRIÈRE	Deza 2	
		17a	FONS 4	Feligueira Grande?	**Sossís**, Roc de Santa,Claverol
Middle Eocene	Robiacian	16	ROBIAC	Llamaquique?, Babilafuente	Laguarres
		15/16		**Mazaterón, Caenes, San Morales** Fuentesaúco,**Villamayor**, Deza 1	
		15	LA LIVINIÈRE 2	Miñana	**Sant Jaume de Frontanyà 1**, Pontils?
		14	EGERKINGEN (Alpha & Beta)	El Viso-Sanzoles	Capella, Grauss **Sant Jaume de Frontanyà 2 & 3**
		14/13		Casaseca de Campean, Jambrina Santa Clara de Avedillo, Vale Furado **Corrales del Vino**	
	Geiseltalian	13	GEISELTAL-OBERE MITTELKOHLE (oMK)		
		12	GEISELTAL-UNTERE MITTELKOHLE (uMK)		
		11/12			Barranco de Estarán
		11	GEISELTAL-UNTERKOHLE (UK)		Casa Ramón, Molí del Pont
	Grauvian	10/11			Ulldemolins, Cabra del Camp, Montblanc, Coll de Lilla, Vimbodí
		10	GRAUVES		**Corsa 2&3**, **El Pueyo**, **Güell 2, La Roca**, **La Coma, Les Badies**, and see **(A)** in the figure caption.
Early Eocene	Neustrian	8+9	AVENAY		**Corsà 0**, **Barranc del Guesot** **Les Vinyes**, **Masia d'Hereuet**
		7	DORMAAL	?Silveirinha	

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, Chirivieta, El Mas de Montanyana, Empordà de Terrades, Escarlà, Fet 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 Camí de la Masia de l'Hereuet, Montllobar, Partida de Solà, Poble Vell de l'Ametlla, Pont de Montanyana, Repeu del Güaita, Sant Pere Màrtir, Sant Miquel, Santes Creus East and North, Sobrenoguera, Torre del Moro, Torrelabad.**

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; Hooker and Dashzeveg, 2003; Smith et al., 2006).

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

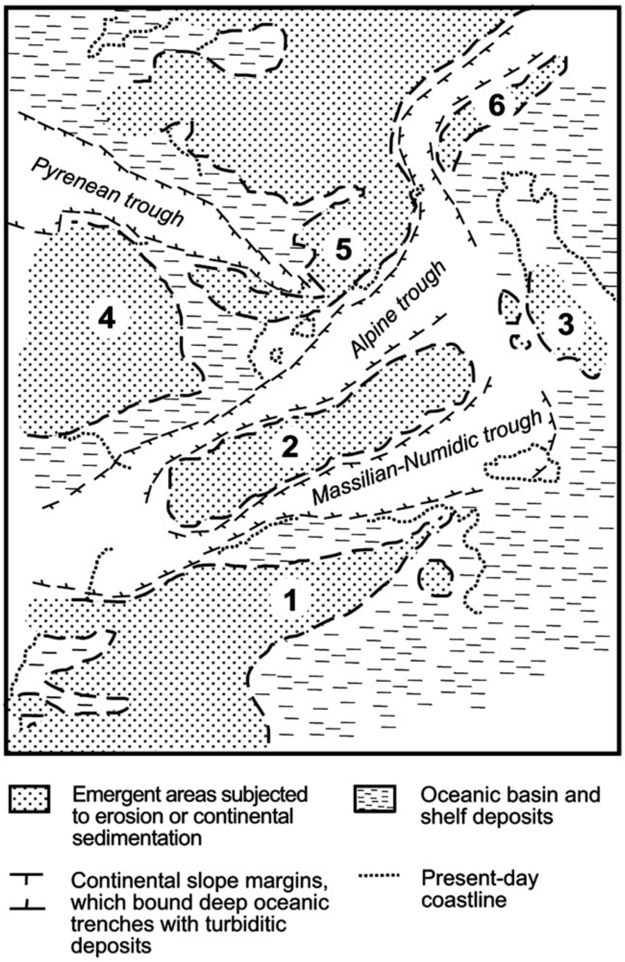


FIGURE 4 **Paleogeography of southwestern Europe during the Early Eocene. 1) Atlas Massif; 2) Betic-Rifean Massif; 3) Apulian Massif; 4) Iberian Massif; 5) Catalanid-Balearic-Tyrrhenian-Provence Massif; 6) Alpine Massif. Modified from López-Martínez, 1989.**

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 paleoebiogeographical distribution was due to vicariance or to Iberia being their centre of origin or a dispersal route towards the Central European Island.

The Early Eocene rodent *Eogliravus* n. sp. 1 from Masia de l'Hereuet (MP 8+9) is similar to "*Microparamys*" sp. 3 from Mutigny (MP 8+9), France, which is known by only one lower molar (Hartenberger, 1971). It differs from *Eogliravus wildi* HARTENBERGER, 1971 from Mas de Gimel (MP 10), France, by its smaller size and more plesiomorphic dentition (less lophodonty). This new species from Masia de l'Hereuet is the most primitive known member of the Gliridae. The microparamyine *Pantrogna* n. sp. 1 from the same locality differs from the European *Pantrogna marandati* ESCARGUEL, 1999 (Prémontré, France; MP 10) by its smaller size and from *Pantrogna russelli* MICHAUX, 1964 (Avenay, France; MP 8+9) by having a protocone well separated from the hypocone, and by having well developed paraconule and mesoconid. These new species of *Eogliravus* HARTENBERGER, 1971 and *Pantrogna* HARTENBERGER, 1971 are closely related to the earlier species from Silveirinha (?MP 7), Portugal, *Corbarimys paisi* ESTRAVIS, 1994 and *Microparamys* cf. *nanus*, respectively, sharing with them teeth with simply developed lophodonty. The earliest representatives of the Microparamyinae and Gliridae have been recorded in North America (Ivy, 1990) and in Europe, in Belgium, France and Portugal (Teilhard 1927; Hartenberger, 1971; Estravis, 1994). The Iberian new finds suggest that the ancestral stock of the microparamyines and glirids also existed in the Iberian Peninsula from this time. Phylogenetic relationships between the Early Eocene representatives of microparamyines are 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.

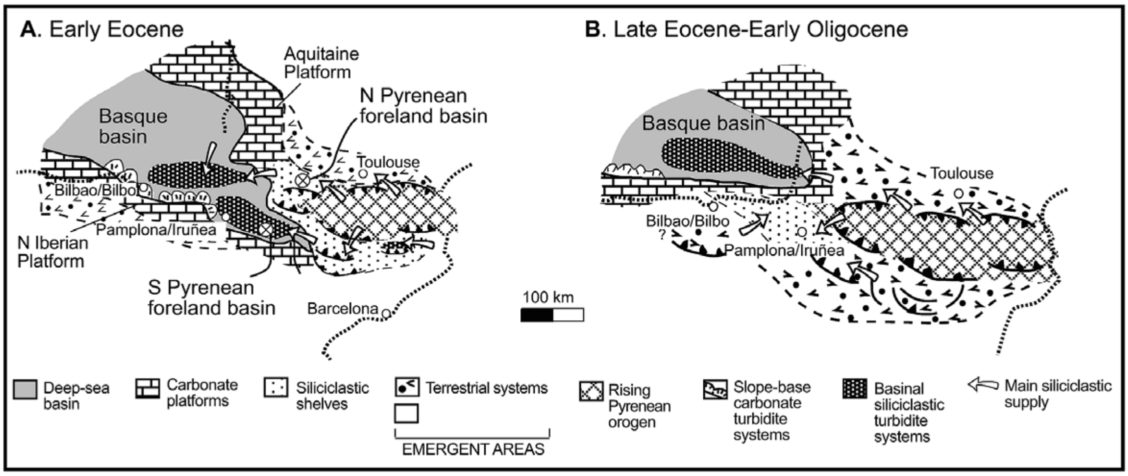


FIGURE 5 **Paleogeography of the Pyrenean and Basque-Cantabrian region during the Early Eocene (A) and Late Eocene-Early Oligocene (B). Modified from Alonso-Zarza et al., 2002 after Plaziat, 1981.**

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 equoid 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 equoid 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 euzetensis* (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 us 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 compari-

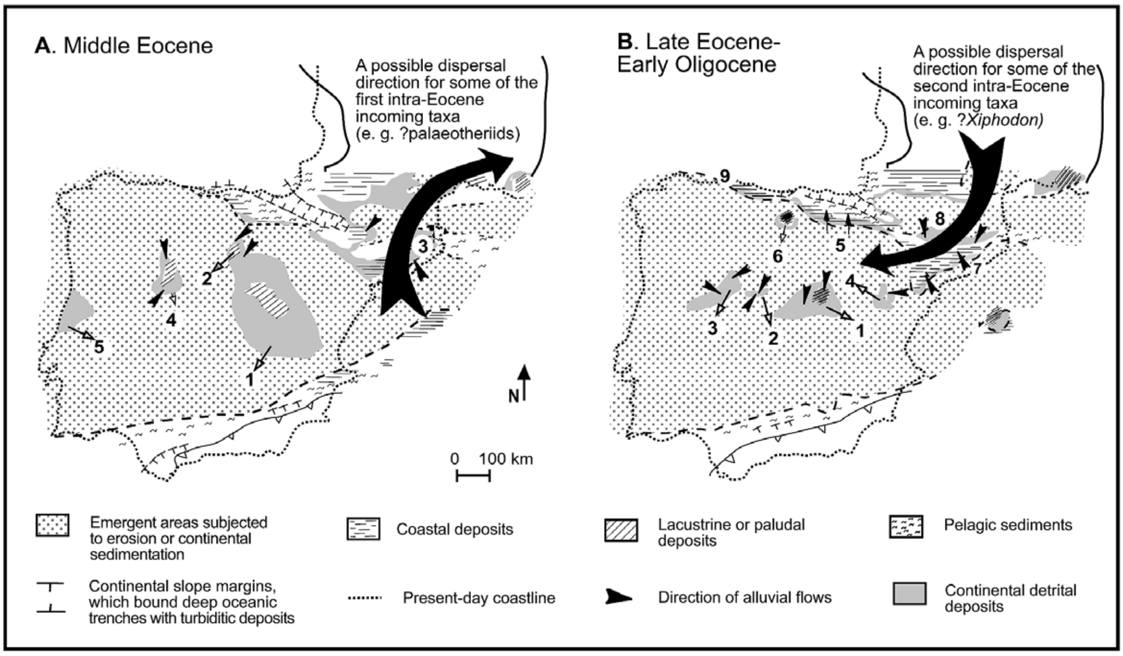


FIGURE 6 **Paleogeography of the Iberian Peninsula during the Middle Eocene (A) and Late Eocene-Early Oligocene (B). The arrows indicate a possible dispersal direction for some of the incoming taxa that appeared in the Central European Island through the first (A) and second (B) intra-Eocene faunal turnovers related to immigrations. A) In the Iberian Mountain Range only continental sediments were deposited: Lower Detrital Unit from Loranca (1) and Unit IV in the eastern part of the Duero Basin (2). In the Pyrenees and Catalan Coastal Ranges large fan deltas developed (Montaña, Montserrat, Terrades, etc.) (3). In the Iberian Massif, the Duero Basin (Corrales and Aldearrubia Formations) (4) and the Coimbra-Lousa Basin (5) were formed. B) The tectonic uplift of the Central Mountain Range caused the sedimentation of the Beleña de Sorbe molasse deposits (1) and formed the Amblés (2) and Ciudad Rodrigo (3) small basins. In the Ebro-Iberian Massif small basins were formed (Villarrosano and Montalbán) (4) and fine grained fluvial sediments were transported to the northern area: Bibán, Anzánigo (5). In the Miranda-Trebiño Basin lacustrine sediments were deposited (6). In the Pyrenees and Catalan Coastal Ranges thick alluvial sediments were deposited: Scala Dei, Montserrat (7), Berga, Sta. Orosia-Laguarta (8). In Cantabria the last marine turbiditic deposits were deposited during the Early Oligocene prior to the disappearance of the Pyrenean trough (9). Modified from López-Martínez, 1989.**

son to those of northeastern Iberia and the rest of Europe. Although a new Middle Eocene anoplotheriine artiodactyl has been found at one locality in the Western Iberian Bioprovince, Mazaterón (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 jordifusalbae* 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. lusitanicus* 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 Mazaterón 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 Bioprovince, influencing its faunal composition (Badiola, 2004). In addition to the results obtained from the cenograms and the ecological diversity spectra for the Mazaterón 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-Trebiño 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 paleogeographic 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-

AGE	ELMA	MP	Portugal (Beira Alta, Lousa and Mondego Basins)	Western Iberian Bioprovince (Duero, Almazán, Oviedo, and Miranda-Trebiño Basins)	Eastern Ebro Basin (Catalan Coastal Ranges, Ulldemollins Area)	Southern Pyrenean Basins (Grauss-Tremp Basin, Ripollés-Berguedà Basin)
		19	*Palaeotherium* cf. *crassum* *Palaeotherium magnum* cf. *Palaeotherium* sp.			
		18		*Paranchilophus remyi* *Pachynolophus zambranensis* *Palaeotherium* n. sp. *Leptolophus* n. sp. *Leptolophus* sp. *Iberolophus arabensis* Plagiolophinae n. g. et sp. 2		
Late Eocene	Headonian	17	*Paranchilophus lusitanicus*			*Palaeotherium magnum stehlini* *Palaeoherium medium euzetense* *Palaeotherium crassum sossisensis* *Palaeotherium curtum villerealense* *Palaeotherium crusafonti* *Palaeotherium* sp. *Plagiolophus annectens* *Lophiotherium cervulum* *Anchilophus dumasi* *Anchilophus gaudini*
		16/17		*Paranchilophus remyi* *Palaeotherium llamaquiquense* *Cantabrotherium truyolsi* *Franzenium tetradactyum*		
Middle Eocene	Robiacian	15/16		*Paranchilophus remyi* *Paranchilophus* sp. cf. *Anchilophus* sp. *Palaeotherium giganteum* *Cantabrotherium casanovasae* *Franzenium durense* Palaeotheriinae indet. *Plagiolophus mazateronensis* *Plagiolophus* sp. *Leptolophus* sp. *Iberolophus jimenezi* Plagiolophinae n. g. et. sp. 1 *Lophiodon* sp. *Lophiodon sanmoralense* ?Lophiodontidae indet.		
		15				*Plagiolophus* sp.
		14		*Plagiolophus* sp.		*Metaplagiolophus atoae* cf.*Anchilophus* sp. *Plagiolophus* sp. *Lophiodon rhinocerodes*
		14/13	*Paralophiodon* cf. *leptorhynchus*	*Pachynolophus* sp. Pachynolophinae indet. *Plagiolophus casasecaensis* *Plagiolophus* cf. *casasecaensis* *Plagiolophus* sp. Palaeotheriinae indet. *Lophiodon* cf. *tapirotherium* *Paralophiodon* aff. *isselense* Lophiodontidae indet.		
	Geiseltalian	12				
		11/10			*Propachynolophus* sp. 4 *Pachynolophus molipontiensis* *Lophiaspis* cf. *occitanicus*	
Early Eocene	Grauvian	10			*Bepitherium jordifusalbae* *Propachynolophus* sp. 2	*Pachynolophus boixedatensis* *Propachynolophus remyi* *Propachynolophus* sp. 1 *Propachynolophus* sp. 2 *Propachynolophus* sp. 3 *Lophiodon baroensis* *Lophiodon corsaensis* *Lophiodon* cf. *remensis* cf. *Lophiodon* sp. *Hyrachyus modestus* *Lophiaspis baicherei* *Lophiaspis maurettei* *Lophiaspis* cf. *occitanicus* cf. *Lophiaspis* sp. Perissodactyla indet.
	Neustrian	8+9			*Bepitherium jordifusalbae*	*Propachynolophus* sp. *Lophiodon corsaensis* *Lophiodon* sp.
		7	*Pachynolophus hookeri* cf. *Lophiaspis? maurettei*			

FIGURE 7 | **Iberian Eocene perissodactyl taxa and chronology. Data source: This paper and a) Portugal (e.g., Antunes, 1986, 1992, 1995, Estravis, 2000, and Hooker, 1998: p. 433 for the reidentification of *Hyracotherium* cf. *vulpiceps* as *Pachynolophus hookeri*); b) Western Iberian Bioprovince (e.g., Casanovas and Santafé, 1987, 1989, 1991b; Cuesta, 1991, 1993, 1994a, b, c, 1996, 1999, 2003; Astibia et al., 2000; Badiola, 2004; Badiola and Cuesta, 2008; Badiola et al., 2002, 2005; and Cuesta et al., 2004); c) Eastern Ebro Basin (e.g., Checa, 1995, 1997; Checa and Colombo, 2004); and d) Southern Pyrenean Basins (e.g., Casanovas, 1975; Casanovas et al., 1992, 1993, 1998; Checa and Casanovas, 1989-1990; and Checa, 1993, 1995, 1997).**

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 replaced cercamoniine adapids, and the first semihypsodont palaeotheres that replaced step by step the brachyodont palaeotheres. Most of the bunoselenodont 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 Lutetian) (see references in Franzen, 2003). The second intra-Eocene faunal turnover led to considerable replacement of taxa particularly among the palaeotheres and artiodactyls around the Middle-Late Eocene transition. However, some immigrants like the first cainotheriids, *Robiacina* SUDRE, 1969, and the palaeotheres *Palaeotherium duvali* POMEL, 1853 arrived earlier, in MP 16, whereas the large anoplotheriines *Diplobune* 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 development of cement in perissodactyls as well as bunoseleno–and selenodonty in artiodactyls), which are interpreted 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 boundary 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 paratropical, but a floristic change towards cooling and drying conditions coincided with the first intra-Eocene faunal 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; Collinson, 1992).

For Franzen (2003) both turnovers were probably driven by climatic conditions shifting in a northward direction, but alternatively, decreasing paleotemperatures during 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 Middle Eocene (some of the equoids, e.g., palaeotheriids) could have entered the Central European Island from the Iberian Peninsula. This is suggested by the paleogeographic 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., *Treposciurus* 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 Robiacian (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 Gavadons; Figs. 1 and 2) of this artiodactyl, but not earlier, is tentative evidence of the southwards migration mentioned 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 faunas 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 mammal finds from the Iberian Peninsula are crucial for comparing with those of elsewhere in Europe with the aim of investigating the evolutionary and paleobiogeographic history 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 Africa), 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 Robiacian beds of the Duero, Almazán and Oviedo Basins. However, the occurrence at Zambrana of typical European artiodactyls suggests a connexion between the Iberian Peninsula and the other European regions during this time. Moreover, it indicates that the special paleoecological 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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