NEW ENDEMIC EOCENE EQUOIDS FROM THE IBERIAN PENINSULA (WESTERN EUROPE)

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ABSTRACT—A new plagiolophine equoid from the Eocene of the Iberian Peninsula, *Iberolophus* gen. nov., is herein reported. This new genus includes two species: *I. arabensis* sp. nov. (type species) from the Late Eocene (Headonian) of Zambrana (Araba, Basque Country) and *I. jimenezi* sp. nov. from the late Middle Eocene (Robiacian) of Mazaterón (Soria, Castilla y León). *Iberolophus* exhibits an unusual dental pattern that has not yet been reported in any other perissodactyl or ungulate to date. A complete (with P1/p1) and very long non-lophoid premolar series, in which premolars exhibit one (in the earlier members) or two (in the later members) high and pointed cusp(s) anteriorly and a low and long backward extended talon/talonid posteriorly, with a bumpy surface texture, is combined with a typical plagiolophine type lophodont and heterodont molar series. The new taxa are ranked as members of the endemic fauna of the Western Iberian Bioprovince. The latter includes the Eocene sites of the central and western Iberian basins (Duero, Almazán, Oviedo, and Miranda-Trebiño Basins), which have yielded Middle and Late Eocene mammal fossil assemblages (mainly perissodactyls, rodents and primates) which differ from those of the Southern Pyrenean Basins and the rest of Europe. The endemism of the perissodactyl faunas persisted during the Late Eocene in the central and western Iberian basins, on the basis that the perissodactyl fossils from the middle Headonian beds at Zambrana (Miranda-Trebiño Basin) are related to endemic taxa from the late Robiacian beds of the Duero, Almazán, and Oviedo Basins.

INTRODUCTION

From the late Early Eocene to the earliest Oligocene, Europe was an archipelago inhabited by an endemic mammalian fauna, which was clearly different from the contemporary fauna in North America and Asia. Perissodactyls were one of the most abundant Eocene mammalian fauna and consisted of a mainly tapir-like group known as lophiodonts and a horse-like group known as equoids. Many of these European endemic mammals became extinct in the earliest Oligocene synchronously with the appearance of Asian immigrants, in an event named by Stehlin (1909) the "Grande Coupure" (e.g., Brunet, 1977; Prothero, 1985; Hooker, 1992; Blondel, 2001; Hooker et al., 2004).
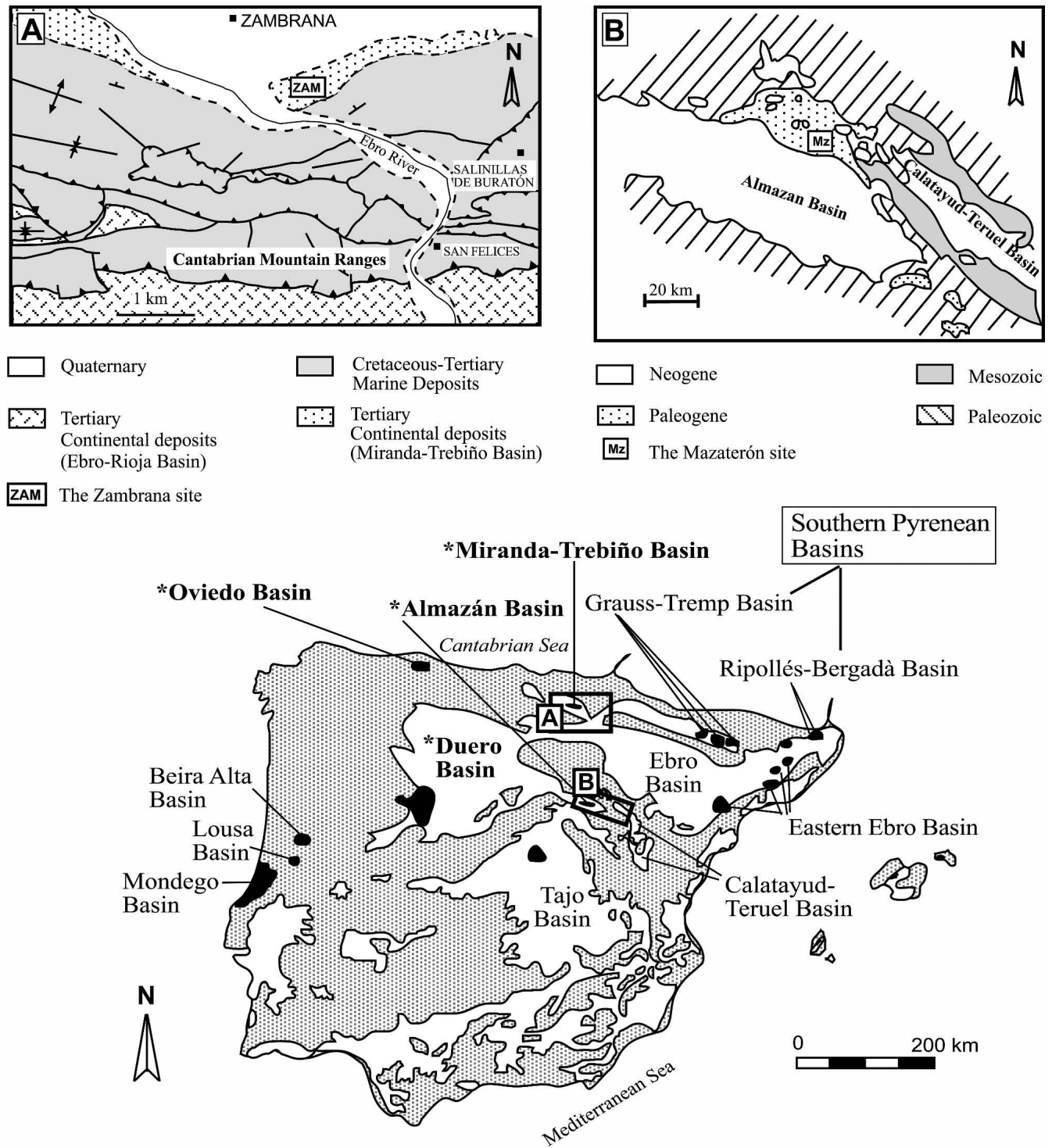
In the Iberian Peninsula, there was a wide diversity of perissodactyls during the Eocene. A faunal list was included in the last synthesis on Eocene mammal faunas presented at the Paleogene biochronological congress which took place in Montpellier (France) in 1997 (see Antunes et al., 1997). This was subsequently updated by Checa (1997), Cuesta (1999, 2003), and Badiola (2004). The recorded biodiversity of the Iberian Eocene perissodactyls is increasing. Eight new equoid taxa, of which three are new genera, have recently been reported by Badiola et al. (in press). Details of two of these have already been published; one refers to a new genus as *Bepitherium jordifusalbae* Checa and Colombo, 2004 and the other refers to a new species as *Pachynolophus zambranensis* Badiola, Pereda and Cuesta, 2005. The other new taxa consist of the unpublished species of *Leptolophus* Remy, 1965 and *Palaeotherium* Cuvier, 1804 and two new plagiolophine genera (Badiola, 2004). In this paper, one of the two new equoid genera mentioned previously is described, being represented by two species. The type species comes from the Late Eocene beds at Zambrana (Miranda-Trebiño Basin,

Araba) and an older species comes from the late Middle Eocene beds at Mazaterón (Almazán Basin, Soria). They exhibit an unusual dental pattern that has not yet been reported in any other perissodactyl or ungulate to date. On the basis of the molar series features, they have been assigned to the Plagiolophinae subfamily Cuesta, 1994a. The new taxa are ranked as members of the endemic fauna of the Western Iberian Bioprovince (see last section).

The Zambrana site is situated near the village of Zambrana (Araba, Basque Country), about 70 km south of Bilbao. Geologically, the fossiliferous beds, which consist of palustrine-lacustrine coal bearing marls and marlstones, are located in one of the oldest lacustrine systems from the Miranda-Trebiño Basin (Basque-Cantabrian Region) (Astibia et al., 2000; Fig. 1A). The depositional setting was a shallow and low-gradient freshwater lake margin with a peripheral swamp (Iriarte et al., 2003). To date, 25 vertebrate taxa have been recovered. They consist of anurans, squamates, chelonians, crocodilians, and mammals, including herpetotheriid marsupials, rodents, carnivores, artiodactyls, and perissodactyls (Astibia et al., 2000; Badiola, 2004; Badiola and Cuesta, 2007a; Badiola et al., 2002, 2005). A primate mandible was recently found during the most recent field work. Perissodactyls consist of seven equoids, of which five (two genera and three species) are new taxa as mentioned above. Zambrana is currently the first Paleogene locality in the Iberian Peninsula to have yielded a fossil mammal assemblage belonging to the MP 18 reference level.

The Mazaterón site is situated near the village of Mazaterón (Soria, Castilla y León) about 40 km southeast of Soria. Geologically, the grey marls that contain the vertebrate fossils are included within the Mazaterón Formation, which consists of lacustrine-palustrine limestones and marls. It is located in the Almazán Basin, which is situated in the eastern sector of the Duero Basin (Fig. 1B). The depositional setting is a shallow lacustrine system, which was subjected to constant flooding and

Iberian Tertiary continental basins with ■ Eocene mammal sites

FIGURE 1. The main Tertiary continental basins of the Iberian Peninsula with Eocene mammal sites indicated in black. Basins which are included in the Western Iberian Bioprovince are indicated with an asterisk. A list of the Iberian Eocene sites can be consulted in Antunes et al. (1997), Checa (1997) and Badiola et al. (in press: fig. 1). **A** and **B**, geological context of Zambrana and Mazaterón sites, respectively (modified from Astibia et al., 2000; and Armenteros, 1994).

drying processes. For more geological details of the Duero Basin, see Alonso-Gavilán et al. (2004) and for details of the Almazán Basin and its depositional setting, see Huerta and Armenteros (2006) and references therein. To date, 27 Eocene vertebrate taxa, consisting of chelonians, crocodilians and mammals, have been recovered. The mammal fossil assemblage includes rodents, primates, carnivores, artiodactyls and perissodactyls. It is Robiacian (MP 15–16) in age (Cuesta, 1991, 1999; Antunes et al., 1997). The perissodactyl assemblage contains a large lophiodontid and eight equoids (Cuesta, 1991, 1993, 1994a, 1994b, 1994c, 1996). For the summary of other vertebrates from the Duero Basin, see Jiménez (1992) and Cuesta and Jiménez (1994).

Institutional Abbreviations—**EHU/UPV**, Euskal Herriko Unibertsitatea/Universidad del País Vasco; **ANZM/MCNA**, Arabako Natur Zientzien Museoa/Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz; **NHM**, Natural History Museum, London; **FPO**, Laboratory of Vertebrate Paleontology and Human Paleontology, Université de Poitiers, Poitiers; **US**, Universidad de Salamanca, Salamanca.

Eocene Locality Abbreviations—From the Iberian Peninsula: In Asturias, **LLAM**, Llamaquique. In The Basque Country, **ZAM**, Zambrana. In Castilla y León; **CAE**, Caenes; **CASC**, Casaseca de Campeam; **CV**, Corrales del Vino; **DEZ**, Deza; **FUE**, Fuentesaúco; **JB**, Jambrina; **MAZ**, Mazaterón; **MLP**, Molino del Pico; **SC**, Santa Clara de Avedillo; **SM**, San Morales; and **VS**, El Viso-Sanzoles. In Castilla-La Mancha, **HU**, Huérmeces del Cerro; **VJ**, Viana de Jadraque. In Catalonia, **AG**, Ager XII; **BA**, Les Badies; **BFO**, Barranc de Forals, **BG**, Barranc del Guesot; **BO**, La Boixedat; **CA**, Capella; **CB**, Costa de Baró; **CC**, Can Camperol; **CE**, Central ENHER; **CG**, Castigaleu; **CH**, Chirivieta; **CM**, La Coma; **CMO**, Castellnou de Montsec; **CO**, Corsá; **COR**, Corral de l'Andreu Nord I& Sud IV; **CP**, Can Picatón; **EM**, Empordá de Terrades; **ES**, Escarlà; **FT**, Fet IV; **GR**, Grauss; **GÜ**, Güell; **Km 86 & 87** in the Benabarre main road; **LI**, Litera; **LO**, Los Olivares; **LS**, Les Saleres; **LV**, Les Vinyes; **MH**, Masia de l'Hereuet; **MOL**, Molí del Pont; **MT**, Montderola; **MTL**, Montllobar; **M-2**, Camí de la Masia de l'Hereuet; **MY**, Pont de Montanyana; **PM**, Sant Pere Martir; **PS**, Partida de Solà; **PU**, El Pueyo; **RB**, La Ribera; **RC**, La Roca; **ROC**, Roc de Santa; **SB**, Sobrenoguera; **SJF**, Sant Jaume de Frontanyà; **SMQ**, Sant Miquel; **SOS**, Sossís; **TM**, Torre del Moro; **TR**, Torrelabad; and **ULL**, Ulldemolins. In Portugal, **CÔJ**, Cojâ; **FE**, Feligueira Grande; **NA**, Naia; **SI**, Silveirinha; and **VF**, Vale Furado. From Western Europe: In the Quercy Area, **RAY**, Raynal (Phosphorites du Quercy); **PQ**, undetermined locality from Phosphorites du Quercy. In Aquitaine, **RU**, Ruch; **SCE**, St. Capraise d'Eymet; **SO**, Soumailles; and **VIL**, Villebramar. In Auvergne, **RO**, Ronzon. In Languedoc, **EUZ**, Euzet-les-Bains; **FA**, Faveirol, **FN**, Fons (without F4); and **ROB**, Robiac. In Provence, **LDB**, La Débruge; and **MR**, Murs. In Tarn-et-Garonne, **CAS**, Castrais. In The Isle of Wight, England, **HC**, Hordle Cliff. In the Solothurn Canton, Switzerland, **EG**, Egerkingen. In Baden-Württemberg, Germany, **FH**, Frohnstetten.

Remarks

The biochronological scale used in this paper is that of the MP Mammal Paleogene reference levels (Schmidt-Kittler, 1987, updated by Aguilar et al., 1997). These levels are calibrated with respect 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). Many and indeed often contradictory systematic propositions for Equoidea Gray, 1821 have been reported (e.g. MacFadden, 1976; Remy, 1976; Franzen, 1989; Hooker 1994; Froehlich, 1999). Here, we do not follow any particular systematic proposition of Equoidea, until a new extensive phylogenetic study can be performed. The new genus herein described is as-

signed to the family Palaeotheriidae Bonaparte, 1850, because all authors to date include the genera *Plagiolophus* Pomel, 1847a and *Palaeotherium* and their relatives within this family. However, Cuesta (1994a) classifies only the palaeotheres sensu stricto within Palaeotheriidae, whereas the genera *Plagiolophus* and *Pachynolophus* Pomel, 1847b and their relatives are included within the family Pachynolophidae Cuesta (1994a). Remy (2004: 168) has challenged the hypothesis of Cuesta (1994a). *Plagiolophus* and relatives have been assigned to the Plagiolophinae subfamily Cuesta (1994a) or to the Plagiolophini tribe Remy (1976). We include the new genus within the same group of *Plagiolophus* and relatives, considering it as a plagiolophine equoid.

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Superfamily EQUOIDEA Gray, 1821
Family PALAEOTHERIIDAE Bonaparte, 1850
IBEROLOPHUS, gen. nov.

Etymology—Plagiolophine equoid from the Iberian Peninsula.
Type Species—*Iberolophus arabensis* sp. nov.
Diagnosis—Medium-sized plagiolophine, characterized by having a complete (with P1/p1) and very long unusual non-lophoid premolar series, combined with a very lophodont and heterodont molar series. Premolars with one (in the earlier members) or two (in the later members) high and pointed cusp(s) anteriorly and with a low and backward extended talon/talonid posteriorly, with a bumpy enamel surface texture. Anterior premolars longer than posterior ones. Upper molars without discrete paraconule and metaconule and with the protoloph and metaloph obliquely oriented to the ectoloph. Thick ribs on the labial side of the parastyle, mesostyle and metastyle. No twinned metaconid in the lower molars and a small hypoconulid is visible in the unworn m1–m2. Large size, hypsodonty and crown outline gradient in the molar series. Thick and sharp cingulum in all premolars, but not continuous in the molars. No cement in the crown of the teeth.

Differential Diagnosis—In addition to the obvious differences with other plagiolophines apparent in the premolar series, *Iberolophus* gen. nov. can be distinguished from *Paraplagiolophus* Depéret (1917) in terms of having (1) a more hypsodont, lophodont and heterodont molar series; (2) without discrete paraconule and metaconule and thinner protoloph and metaloph; and (3) a more accentuated size and outline crown gradient in the molar series. From *Plagiolophus* in having (1) a more lophodont and heterodont molar series; (2) without discrete paraconule in the upper molars; and (3) a more accentuated size and crown outline gradient in the molar series. From *Leptolophus* in having (1) more brachyodont molars, without a trapezoidal outline in all of them; (2) a thicker protoloph and metaloph; (3) a less flatter ectoloph in the occlusal view; (4) more prominent cingulum; and (5) the absence of cement in the crown of the teeth. From *Metaplagiolophus* Checa, 1993 in having (1) narrower, more trapezoidal and hypsodont upper molars, with the protoloph and metaloph longer; and (2) a more heterodont molar series, with M3/m3 considerably larger than M2/m2.
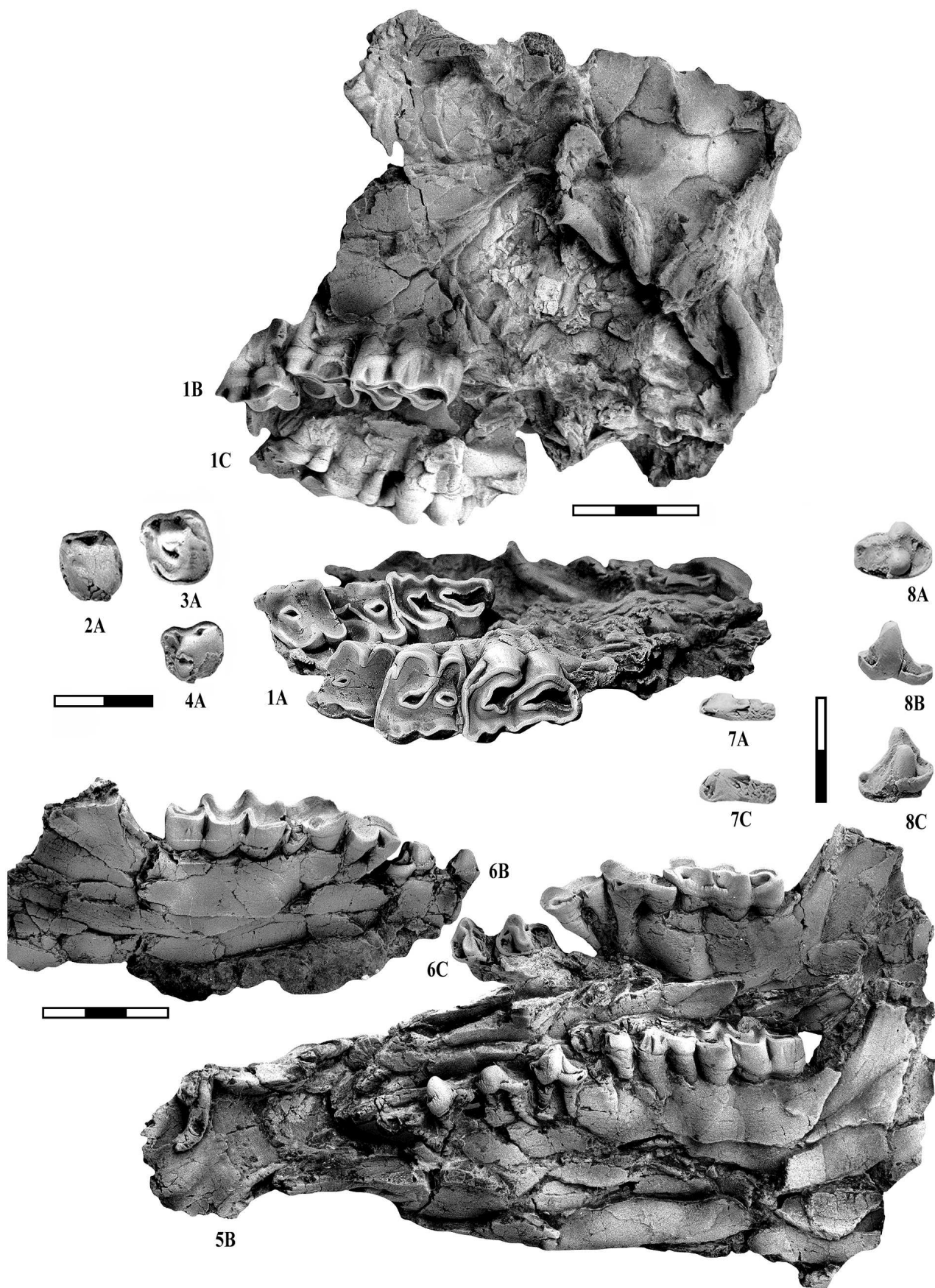
Included Species—*Iberolophus arabensis* sp. nov. and *Iberolophus jimenezi* sp. nov.

Distribution—Late Middle Eocene (late Robiacian) to Late Eocene (middle Headonian), Almazán and Miranda-Trebiño Basins, Iberian Peninsula.

IBEROLOPHUS ARABENSIS, sp. nov.
(Figs. 2, 3)

Holotype—MCNA 11953, mandible, showing the incisor and canine alveoli, a fragment of the right canine root, and the left C-m3 (p1 and m1 incomplete) and right p3-m3 series.

1B

1C

2A

3A

4A

1A

8A

8B

7A

8C

7C

6B

6C

5B

Etymology—After "Araba" / "Álava" (Basque/Spanish bilingual names, respectively), a province of the Basque Country, where the Zambrana site is located.

Type Locality and Horizon—Zambrana (Araba), Iberian Peninsula; Basque-Cantabrian Region, Miranda-Trebiño Basin, middle Headonian (MP 18) Z4 and Z6 beds (Fig. 1A).

Paratype—MCNA 10183, skull fragment, showing the right and left M1–M3 molar series; MCNA 11888, left P3–4; MCNA 11906, left P1–2; MCNA 13372, left p4; and MCNA 13373, right p1.

Referred Specimens—MCNA 11904, right P3–4; MCNA 11887, 11893, left P3–4; MCNA 13375, fragment of the left P3–4; MCNA 11905, fragment of the left P3–4; MCNA 11950, right P1-2 (incomplete lingually); MCNA 13374, fragment of the right upper premolar; MCNA 11951, fragment of the upper premolar; MCNA 11952, fragment of the lower premolar.

Distribution—Only known in the type locality.

Diagnosis—Species of *Iberolophus* gen. nov., characterized by having in combination (1) four similar premolars, with two well-developed high and pointed cusps in all of them and without a significant talon/talonid length gradient between them; (2) a very lophodont and heterodont molar series, without discrete paraconule and metaconule, and with a large length increase from M2/m2 to M3/m3; and (3) a long postcanine diastema.

Differential Diagnosis—Bigger species than that of Mazaterón, differing from it in having (1) a shorter premolar series; (2) premolars with two well-developed high and pointed cusps anteriorly and similar talon/talonid length; and (3) a larger length increase from M2/m2 to M3/m3.

DESCRIPTION

The mandible and the skull fragments were found in close proximity to each other. Despite the absence of all upper premolars in the maxilla, the correspondence in size and the morphology and wear pattern of the preserved molars suggest that these fragments belong to the same taxon; they could even belong to the same individual. The upper isolated premolars exhibit a size and morphology which is similar to that of the lower premolars preserved in the mandible, so they are also included within the same taxon.

Mandible and Skull

The mandible is crushed (Figs. 2, 3: *5*, *6*). The right hemimandible was found broken anteriorly, but stuck to the rest of the mandible by a calcite crust (Fig. 2: *6*). The mandibular ramus is low, gradually increasing in height backwards. The mandibular symphysis appears to be quite narrow and long. There is a long postcanine diastema (Table 1). The ascending ramus is not preserved in any of the hemimandibles. The skull fragment is also crushed and broken (Figs. 2, 3: *1*). Its size seems small in relation to molar robustness, but it is difficult to provide any reliable measurements due to crushing. The incomplete occipital and parietal regions are the best preserved elements of the skull, which can be described as follows: the occipital crests and condyles are thick; the medial, left and big occipital crests, and the left condyle are visible. The eye socket is not preserved. The zygomatic arch is broken and crushed, but it seems to have been thin and extended backward. The temporal fossa may have been quite wide.

Dentition

The incisor alveoli and the right canine root fragment preserved in the mandible suggest that the incisors are small and the canines are not thick (Figs. 2, 3: *5*). There are four premolars, which have similar size and morphology. Although the first is incomplete, an isolated p1 is available for study (Figs. 1, 2: *7*). Premolars are considerably smaller than the molars and exhibit unusual non-lophoid morphology, which has not been reported in any other equoid. In contrast, the morphology of the molars is typical of the Paleogene equoids, showing well-developed crests (lophs and lophids) (Figs. 2, 3: *1*). The complete (with P1/p1) and very long premolar series is combined with a very lophodont and heterodont molar series, and a long postcanine diastema. The enamel of the teeth is quite thick.

It is not easy to differentiate the P1-P4 isolated teeth, although the slightly smaller and wider than longer teeth seem be anterior premolars (Table 1). They have a semicircular outline in the occlusal view and a sharp cingulum encircles all of them (Figs. 2, 3: *2–4*). It is difficult to describe the occlusal surface of the anterior premolars in detail, due to their substantial wear. However, all premolars seem to have two well-developed high and pointed cusps anteriorly, and a low and wide talon posteriorly, the latter being characterized by having a bumpy enamel surface texture. Two very short and narrow crests leave from the internal cusp toward the labial side; the posterior crest terminates in the external cusp, whereas the anterior crest descends towards the crown base on the labial side. The M1-M3 series is lophodont, without discrete paraconule and metaconule, and heterodont. M1 is smaller and less hypsodont than M2-M3. M1 and M2 are wider than longer, with a rectangular outline in the occlusal view, whereas M3 exhibits a narrower posterior lobe than the anterior one, showing a trapezoidal outline (Figs. 2, 3: *1*). Severe M1 wearing prevents a detailed description of its crests in the occlusal view. In the M2-M3 the protoloph and metaloph are obliquely oriented to the ectoloph. The metaloph is joined with the ectoloph at the level of the mesostyle. Although the styles (parastyle, mesostyle and metastyle) are thick, exhibiting prominent ribs on the labial side, they do not strongly protrude labially in the occlusal view, and do not show a strong "W"-shaped ectoloph. The lingual cingulum is thick, but it is only present on the base of the protocone. The labial cingulum is almost continuous.

The p1–p4 series is very long (Table 1). All premolars have high and pointed internal and external cusps, which are connected by a short and narrow transverse crest in the worn teeth, and a low and long backward extending talonid, with a bumpy enamel surface texture (Figs. 2, 3: *5–8*). Their cingulum is sharp and continuous. The talonid length decreases slightly from p1 to p4, with the anterior premolars appearing slightly longer than the posterior ones (Table 1). The molar series is lophodont and heterodont, with m3 appearing to be significantly larger than m2 (Table 1). There is no twinned metaconid in m1–m3. The m1 and m2 are too worn to evaluate the development of the hypoconulid. The hypoconulid size of m3 is similar to those of the anterior and posterior lobes (Figs. 2, 3: *5, 6*). The labial cingulum only appears on the labial grooves, between the protoconid and hy-

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FIGURE 2. *Iberolophus arabensis* gen. et sp. nov. (Equoidea, Perissodactyla) from the Late Eocene of Zambrana (Araba, Basque Country). **1**, skull fragment (MCNA 10183, paratype), showing the right and left M1-M3 series; **2**, left P1-2 (MCNA 11906, paratype); **3–4**, left P3-4 (MCNA 11887; 11888, paratype); **5–6**, mandible (MCNA 11953, holotype), showing incisors and canine alveoli, a fragment of the right canine root, and the left C-m3 (p1 and m1 incomplete) and right p3-m3 series; **7**, right p1 (MCNA 13373, paratype); and **8**, left p4 (MCNA 13372, paratype). **A**, occlusal; **B**, labial; and **C**, lingual views. Scale bars equal 2 and 3 cm. Fossils are coated with ammonium chloride.
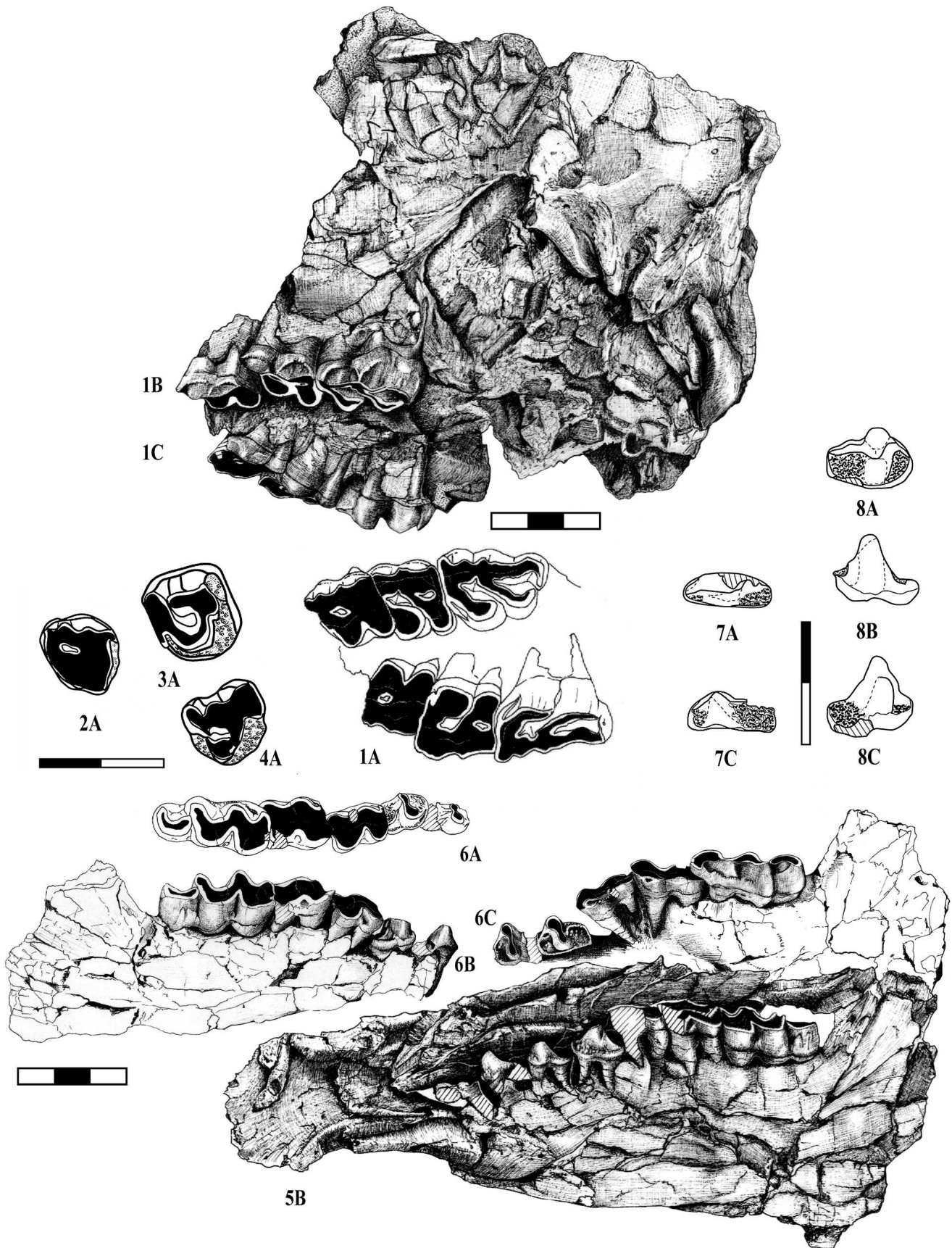
FIGURE 3.   Drawings of the cranial and dental elements of *Iberolophus arabensis* gen. et sp. nov. (Equoidea, Perissodactyla) from the Late Eocene of Zambrana (Araba, Basque Country). Scale bars equal 2 and 3 cm. See abbreviations in legend to Figure 2. Drawings 1, 5, and 6 by H. Astibia.

TABLE 1. Dental measurements (in mm) of *Iberolophus arabensis* gen. et sp. nov. (Equoidea, Perissodactyla) from the Late Eocene (Headonian) of Zambrana (Araba, Basque Country).

	MCNA	L	W	L/W	D	d
P1–2	11906	12.1	14.2	0.85		
	11950	12.1	14.4	0.84		
P3–4	11904	12.1	13	0.93		
	11888	12	13.7	0.88		
	11893	12.7	13.6	0.93		
	11887	13.6	14	0.97		
	11905	ca. 14.8	—			
M1	10183(l)	ca. 16.2	—		21.5	17.1
	10183(r)	ca. 15.5	17.7	ca. 0.88	20.3	17.5
M2	10183(l)	ca. 18	—		ca. 22.4	ca. 18.4
	10183(r)	18.7	20	0.94	22.7	19.4
M3	10183(l)	27.9	—		23.9	20.1
	10183(r)	27.9	20.5	1.36	22.9	20.9

	MCNA	L	W	Wa	Wp	Wpp
p1	11953(l)	(14)	—			
	13373	14.7	5.4			
p2	11953(l)	(13.8)	—			
p3	11953(l)	(13.6)	—			
	11953(r)	14	8.8			
p4	11953(l)	(13.6)	—			
	11953(r)	14.1	9.2			
	13372	14.3	9.6			
m1	11953(l)	(15.6)	—			
	11953(r)	16		10.2	10	
m2	11953(l)	(16.4)	—			
	11953(r)	ca. 16.5		12.5	ca. 12.4	
m3	11953(l)	(28.3)	—			
	11953(r)	28.4		13.5	12.3	9.3

MCNA	LC-p1	ID′	Lp1–p4	Lm1–m3	Lp1–m3	PMI′
11953(l)	(23.5)	ca. 20.38	(55)	(60.3)	(115.3)	ca. 91.21

Abbreviations: **L**, length; **W**, width; **D**, maximum diagonal from the parastyle to the hypocone; **d**, perpendicular diagonal to D; **Wa**, width of the anterior lobe; **Wp**, width of the posterior lobe; **Wpp**, width of the hypoconulid; **ID′**, diastema index including the p1 (LC-p4/Lp1–m3 × 100); and **PMI′**, molarization index including the p1 (Lp1–p4/Lm1–m3 × 100).

poconid, whereas the lingual cingulum is more continuous, mainly in m3.

IBEROLOPHUS JIMENEZI, sp. nov.
(Fig. 4)

Holotype—US 11800, right hemimandible, exhibiting p1 and m1 alveoli, and the p2–p4 and m2–m3 series.

Etymology—After Dr. Emiliano Jiménez, professor of Geology of the University of Salamanca (Castilla y León), for his important contribution to the study of reptilian fossils of the Duero Basin, and for his untiring efforts to manage an impressive vertebrate fossil collection of the Duero Basin in the "Sala de las Tortugas" of the University of Salamanca.

Type Locality and Horizon—Mazaterón (Soria), Iberian Peninsula; Almazán Basin, Robiacian (MP 15–16) beds (Fig. 1B).

Distribution—Only known in the type locality.

Diagnosis—Species of *Iberolophus* gen. nov., characterized by having an extremely long premolar series, clearly longer than the molar series, together with premolars having only one well-developed high and pointed cusp and with longer talonids in the anterior teeth than in the posterior ones.

Differential Diagnosis—Smaller species than that of Zambrana, differing from it in having (1) a longer premolar series; (2) premolars with only one well-developed high and pointed cusp; (3) a larger talonid length gradient in p1–p4; and (4) with a smaller length increase from m2 to m3.

DESCRIPTION

Mandible

The right hemimandible found in Mazaterón is anteriorly broken, where the p1 and m1 alveoli and the p2–p4 and m2–m3 series are preserved (Fig. 4). The mandibular ramus is quite thin and the ascending ramus is quite short; it does not seem to extend backwards further than the level of the mandibular condyle. The latter is thick. The angular and coronoid processes are not completely preserved.

Dentition

The premolar series is complete (with p1) and considerably longer than the molar series (Table 2). Regarding the premolars, the internal cusp is absent or it is not well-developed, and the low talonid, which exhibits a bumpy enamel surface texture, is clearly longer in the anterior premolars than in the posterior ones (Table 2). The molars are lophodont with narrow and closed "V"-shaped crests (Fig. 4B). There is no twinned metaconid in the m1–m3 series. A small hypoconulid is visible in m2, whereas in m3 it is as high as the anterior and posterior lobes (Fig. 4A, C). A sharp cingulum encircles all premolars, whereas it is not continuous in the molars. There is no cement in the teeth.

DISCUSSION

The unusual dental pattern that is exhibited by the new taxa from Zambrana and Mazaterón has not been reported to date in any other equoid. Non-lophoid premolars, which exhibit one (in the earlier members) or two (in the later members) well-developed high and pointed cusp(s) anteriorly, and a low and backward extending talon/talonid posteriorly, with a bumpy surface texture, are present together with typical Paleogene equoid molars in the same cheek tooth row. With respect to the molar series, the new equoid *Iberolophus* gen. nov., differs from *Palaeotherium* and relatives in lacking (1) lower molars with thinner enamel on the lingual side than on the labial side; (2) upper molars with a smaller hypocone than protocone; (3) higher external cusps (paracone and metacone) than the internal ones (hypocone and protocone); (4) a short and low protoloph and metaloph; and (5) a strong "W"-shaped ectoloph. The new taxa are bigger than those of Pachynolophinae Pavlow, 1888 and they differ from *Pachynolophus* and relatives in having a well-developed mesostyle in the upper molars, and in lacking a twinned metaconid in the lower molars. On the basis of the molar series features, the new specimens have been assigned to Plagiolophinae and they are here referred to as a new genus, i.e., *Iberolophus arabensis* sp. nov. (type species) and *Iberolophus jimenezi* sp. nov. Differences in the molar series are visible between *Iberolophus* gen. nov. and the rest of the plagiolophines (see differential diagnosis of the new genus).

Within plagiolophines, a number of teeth and skull features are shared in common between *Iberolophus* gen. nov., *Metaplagiolophus* and *Leptolophus*. In *Metaplagiolophus* and *Iberolophus* gen. nov., the upper molars are robust in comparison to the skull size, and thick occipital condyles and crests are visible in the occipital region. In the three genera, the upper molars are characterized by having a flat ectoloph, which is not strongly "W"-shaped in the occlusal view, in comparison to that of the other plagiolophines (mainly *Plagiolophus*), and the lower molars do not have a twinned metaconid. However, there are differences in the molar and premolar series between them. With respect to the length of the premolar series, it is much shorter in *Leptolophus* than in *Iberolophus* gen. nov. In the mandible and skull fragments assigned to *Metaplagiolophus,* only four incomplete premolar alveoli have been preserved (Checa, 1993:97, 100, figs. 2, 3). Consequently, the morphology of the premolar series is incompletely known, but the premolar series is shorter than in
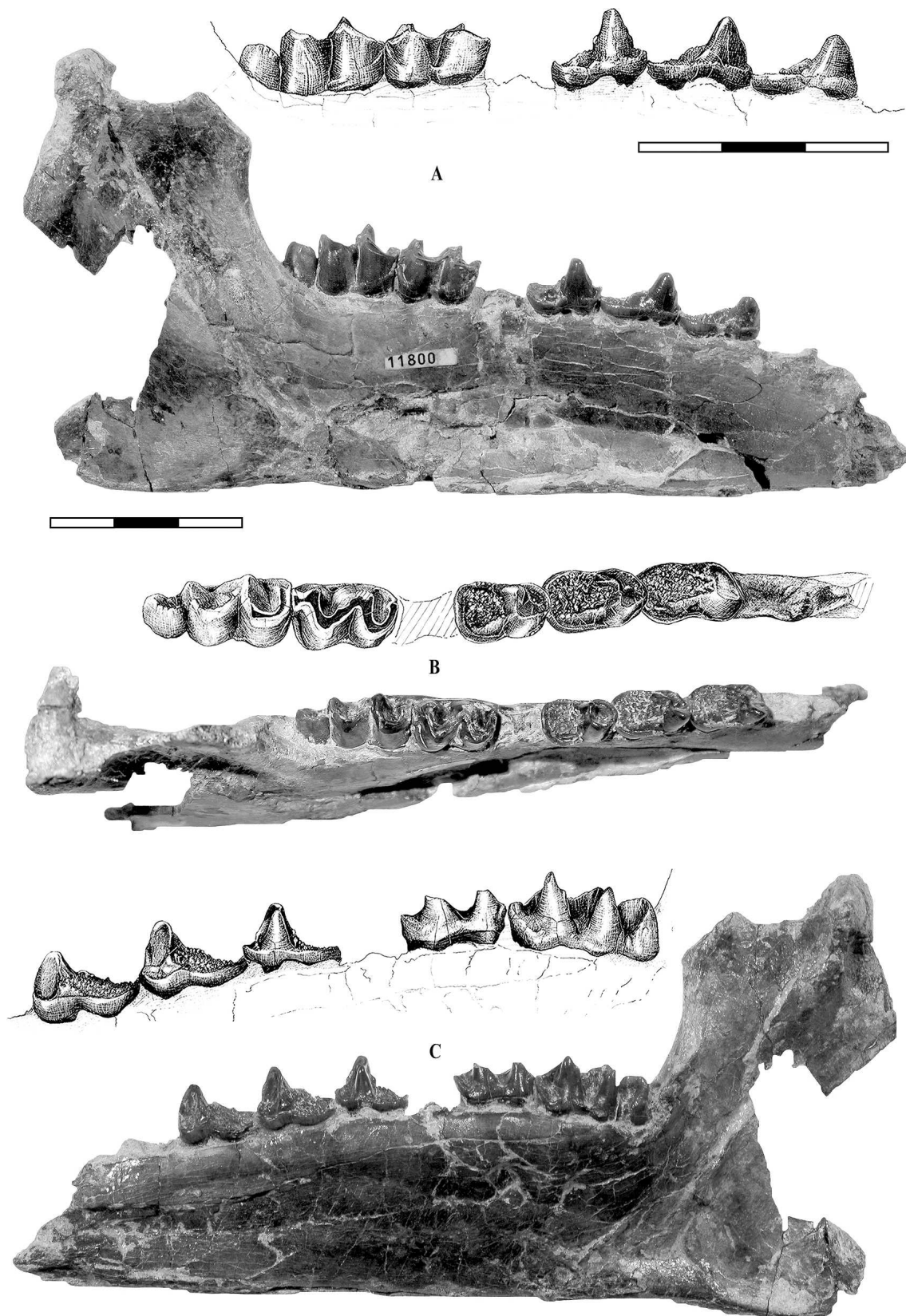
FIGURE 4. *Iberolophus jimenezi* gen. et sp. nov. (Equoidea, Perissodactyla) from the late Middle Eocene of Mazaterón (Soria, Castilla y León). Photos and drawings of the right hemimandible (US 11800, holotype) with the p1 and m1 alveoli, and the p2-p4 and m2-m3 series. **A**, labial; **B**, occlusal; and **C**, lingual views. Scale bar equals 3 cm. Drawings by H. Astibia.

TABLE 2. Dental measurements (in mm) of *Iberolophus jimenezi* gen. et sp. nov. (Equoidea, Perissodactyla) from the late Middle Eocene of Mazaterón (Soria, Castilla y León).

US11800	L	W	Wa	Wp	Wpp
p1	(15.8)				
p2	13.3	8			
p3	13.4	8.3			
p4	12	7.5			
m2	13		7.8	7.9	
m3	ca. 19.2		8.3	7.4	ca. 5.7

	Lp1–p4	Lm1–m3	Lp1–m3	PMI′
US11800	ca. 51.8	ca. 38.4	ca. 89.3	ca. 134.89

Abbreviations: **L**, length; **W**, width; **D**, maximum diagonal from the parastyle to the hypocone; **d**, perpendicular diagonal to D; **Wa**, width of the anterior lobe; **Wp**, width of the posterior lobe; **Wpp**, width of the hypoconulid; and **PMI′**, molarization index including the p1 (Lp1-p4/Lm1-m3 × 100).

Iberolophus (Table 3). For the differences in the molar series see the differential diagnosis of the new genus.

Iberolophus arabensis sp. nov. from Zambrana is bigger than *Iberolophus jimenezi* sp. nov. from Mazaterón and exhibits a shorter premolar series (Table 3), in which all premolars exhibit two well-developed high and pointed cusps anteriorly, instead of only one, and a smaller talonid length gradient is observed in the p1–p4 series. In the molar series, a larger length increase from m2 to m3 is present in *I. arabensis* sp. nov. (Table 3). The dentition features of *I. arabensis* sp. nov. can be considered more derived than those of *I. jimenezi* sp. nov. This interpretation is consistent with the younger age of Zambrana (Headonian, MP 18) relative to Mazaterón (Robiacian, MP 15–16). It is clear that both species are related to each other. *Iberolophus jimenezi* sp. nov. may be a possible ancestor of the species from Zambrana. The presence of four non-molariform premolars and a long premolar series are considered plesiomorphic features within Plagiolophinae, whereas the tendency to shorten the premolar series, the accentuation of lophodonty, and the presence of a very heterodont molar series and a long postcanine diastema are more derived features. Heterodonty in the molar series is associated with a shorter premolar series, whereas lophodonty is usually accompanied by the presence of cement in the crown (e.g., in *Leptolophus* and in the Late Eocene species of *Plagiolophus*). However, these combinations are not observed in the new taxa from Zambrana and Mazaterón. The long premolar series exhibited by *I. arabensis* sp. nov., is unusual for the Late Eocene plagiolophines. In contrast, other dentition features, such as lophodonty, hypsodonty and heterodonty of the molar series, and the length of the postcanine diastema, are similar to those of taxa from the late Middle Eocene and Late Eocene. The postcanine diastema index and the m3/m2 ratio length are similar to those of *Leptolophus* and to the Late Eocene and Oligocene species of *Plagiolophus*. In contrast, the molarization index (the ratio length of the premolar and molar series) is much higher (Table 3). The new plagiolophine *Iberolophus* gen. nov. is characterized by having a combination of plesiomorphic (complete, with P1/p1, and very long non-molariform premolar series) and specialized tooth features (lophodont and heterodont molar series and a long postcanine diastema) which is clearly distinct to that of its nearest European relatives.

TABLE 3. Comparison of the postcanine diastema index (**ID** = LC-p2/Lp2-m3 × 100), the molarization index (**PMI** = Lp2–p4/Lm1–m3 × 100) and the m3/m2 length (Lm3/Lm2) in several Eocene and Oligocene plagiolophines of Europe.

Taxa	Site and MP Level	Source of data	ID (%)	PMI (%)	Lm3/Lm2
Plagiolophus javali	RAY (MP25)	Brunet & Jehenne (1989) Remy (2004). Qu-16516	42.9	49	1.22
Plagiolophus huerzeleri	MR (MP 23)	Remy (2004)	52.5	50	—
Plagiolophus ministri	VIL (MP 22)	Remy (2004)	52.9	51.4	1.52
Plagiolophus ovinus	RO (MP 21)	Brunet & Jehenne (1989)	ca. 52.5	ca. 46.63	1.42
	RO (MP 21)	Remy (2004)	47.3	50.9	1.41
Plagiolophus ringeadei	RU (MP 21)	Remy (2004). FPO RU-3	48.9	49.3	1.64
Plagiolophus fraasi	FH (MP 20)	Remy (2004)	—	54.5	1.42*
Plagiolophus minor	SO (MP 21)	Brunet & Jehenne (1989)	44.27	56.16	—
	SCE (MP 20)	Brunet & Jehenne (1989)	45.52	47.98	—
	LDB (MP 18)	Remy (2004)	36	54.59	1.57
Plagiolophus major	SCE (MP 20)	Brunet & Jehenne (1989)	27.98	48.53	1.72
Plagiolophus oweni	FA (MP 18)	Remy (2004)	32.2	53.31	1.46
Plagiolophus annectens	LDB (MP 18)	NHM-M.28229(l)		ca. 53.1	—
		NHM-M.28229(r)		ca. 52.52	ca. 1.46
	HC (MP 17)	NHM-B.M.29730(l)	ca. 28.91	ca. 55.77	1.33
		NHM-B.M.29730(r)	ca. 33.8	ca. 54.52	1.39
	EUZ (MP 17)	NHM-M.9842(l)		ca. 55.47	1.57
		NHM-M9842(r)	29.61	51.74	ca. 1.47
		Remy (2004)	28.1	55.4	1.53
	FN (MP 17)	Remy (2004)	36.4	52.1	1.43
	ROC (MP 17)	Remy (2004)	32.5	50.9	1.49
	ROB (MP 16)	Remy (2004)	—	55.6	1.51
Iberolophus arabensis	ZAM (MP 18)	This paper	ca. 43.78 ca. 20.38*	ca. 68 ca. 91.21*	1.72
Iberolophus jimenezi	MAZ (MP 15–16)	This paper		ca. 93.57 ca. 134.89*	1.48
Leptolophus nouleti	CAS, ROB (MP 16)	Remy (1998)		53.68	1.56
Leptolophus stehlini	CAS, ROB (MP 16)	Remy (1998)			1.73
Plagiolophus mamertensis	ROB (MP 16)	Remy (2004)	—	46.7	—
Plagiolophus mazateronensis	MAZ (MP 15–16)	Cuesta (1994a)		56.36 54.87*	1.55
Metaplagiolophus atoae	SJF (MP 15)	Checa (1993)	23.3	49.65	1.53
Plagiolophus cartieri	EG (MP 14)	Remy (2004)	—	57.7	1.49
Plagiolophus casasecaensis	CASC (MP 13–14)	Cuesta (1994a)		66.16 81.17*	1.29

The average measurements are taken from Remy (2004).
*ID′ and IPM′ measurements that include p1.
Abbreviations: **ID**, diastema index (LC-p2/Lp2-m3 × 100); **L**, length; **PMI**, molarization index (Lp2/p4/Lm1-m3 × 100). See site abbreviations in the Introduction.

AGE	ELMA	MP	Iberian Eocene sites with p.f.	Portugal (Beira Alta, Lousa and Mondego Basins)	Western Iberian Bioprovince (Duero, Almazán, Oviedo, and Miranda-Trebiño Basins)	Tajo Basin	Eastern Ebro Basin (Catalan Coastal Ranges, Ulldemolins Area)	Southern Pyrenean Basins (Grauss-Tremp Basin and Ripollés-Bergadà Basin)
Late Eocene	Headonian	19	CÔJ,?HU ?MLP, ?NA,?VJ	*Palaeotherium* cf. *crassum* *Palaeotherium magnum* cf. *Palaeotherium sp.*		*Plagiolophus* sp. *?Cantabrotherium* sp. *Palaeotherium crassum* *Palaeotherium magnum*		
		18	ZAM		**Paranchilophus remyi** **Pachynolophus zambranensis** **Palaeotherium n. sp.** **Leptolophus n. sp.** **Leptolophus sp.** **Iberolophus arabensis n. g. et sp.** **Plagiolophinae n. g. et sp. 2**			
		17	?FE,ROC SOS	*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	LLAM		**Paranchilophus remyi** **Palaeotherium llamaquiquense** **Cantabrotherium truyolsi** **Franzenium tetradactyum**			
Middle Eocene	Robiacian	15/16	CAE DEZ-1 FUE,MAZ SM		**Paranchilophus remyi** **Paranchilophus sp.** cf. *Anchilophus* sp. **Palaeotherium giganteum** **Cantabrotherium casanovasae** **Franzenium durense** Palaeotheriinae indet. **Plagiolophus mazateronensis** *Plagiolophus* sp. **Leptolophus sp.** **Iberolophus jimenezi n. g. et sp.** **Plagiolophinae n. g. 2 n. sp. 1** **Lophiodon sp.** **Lophiodon sanmoralense** ?Lophiodontidae indet.			
		15	SJF-1					*Plagiolophus* sp.
		14	CA,GR SJF-2&3 VS		*Plagiolophus* sp.			*Metaplagiolophus atoae* cf. *Anchilophus* sp. *Plagiolophus* sp. *Lophiodon rhinocerodes*
		14/13	CASC,CV JB,SC,VF	*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	MOL,ULL				*Propachynolophus* sp. 4 *Pachynolophus molipontiensis* *Lophiaspis* cf. *occitanicus*	
Early Eocene	Grauvian	10	AG,BA BFO,BO CB,CC CE,CG CH,CM CMO,CO CP,COR EM,ES,FT GÜ-3 Km86&87 M-2,MT MTL,MY Ll,LO,LS PM,PS PU,RB RC,SB SMQ TM,TR				*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	CO-0,BG LV,MH				*Bepitherium jordifusalbae*	*Propachynolophus* sp. *Lophiodon corsaensis* *Lophiodon* sp.
		7	SI	*Pachynolophus hookeri* cf. *Lophiaspis? maurettei*				

FIGURE 5. Iberian Eocene sites with perissodactyl fossils and chronology. Data source: 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 & Santafé, 1987, 1989, 1991; Cuesta, 1991, 1993, 1994a, 1994b, 1994c, 1996, 1999, 2003; Astibia et al., 2000; Badiola et al., 2002, 2005, in press., Badiola, 2004, and Cuesta et al. 2004); Tajo Basin (e.g., this paper, Crusafont et al., 1960, and Iriarte et al., 2006); d) Eastern Ebro Basin (e.g., Checa, 1995, 1997; Checa and Colombo, 2004); and e) Southern Pyrenean Basins (e.g., Casanovas, 1975; Casanovas et al., 1998; Checa and Casanovas, 1989-1990; and Checa, 1993, 1995, 1997). **Abbreviations**: **p.f.**, perissodactyl fossils, **ELMA**, Eocene European Land Mammal Ages; **MP**, mammal Paleogene reference level; see the rest of abbreviations in the Introduction section (modified from Badiola et al., in press).

ENDEMIC PERISSODACTYL FAUNA 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 and Late Eocene mammalian faunas (mainly perissodactyls, rodents and primates) of the western and central Iberian basins (Duero, Almazán, Oviedo and Miranda-Trebiño Basins) were clearly different to those of the Southern Pyrenean Basins (Fig. 1) and the rest of Europe (e.g., Casanovas and Santafé, 1987, 1989, 1991; Casanovas and Moyà-Solà, 1992; Cuesta, 1991, 1999, 2003; Peláez-Campomanes, 1993). On the basis of this faunal differentiation, the existence of a Western Iberian Bioprovince has been hypothesized (Cuesta, 1991; Badiola, 2004; Badiola et al. in press). In contrast, the Middle and Late Eocene mammalian faunas of the Southern Pyrenees were similar to those of the southern part of the Central European Island—present southern France and Switzerland—where the typical western Iberian endemic taxa were absent (e.g., Casanovas, 1975; Checa, 1997; Casanovas et al., 1998; Cuesta et al., 2006).

The best-known localities in the Western Iberian Bioprovince are the late Middle Eocene beds at Mazatarón (Almazán Basin) and the Late Eocene beds at Zambrana (Miranda-Trebiño Basin), which have yielded twenty and twenty-two mammalian taxa, of which nine and seven are perissodactyls, respectively (e.g., Cuesta, 1999, 2003; Astibia et al. 2000; Badiola, 2004; Badiola et al., 2002, 2005). The mammal fossil assemblages of these localities have increased the resolution of Iberian late Middle Eocene and Late Eocene mammalian biostratigraphy, and they have been essential for testing the hypothesis of faunal differentiation in this bioprovince. Moreover, the endemism of the perissodactyl faunas can be shown to exist at least from the late Middle Eocene to 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 late Robiacian beds of the Duero, Almazán and Oviedo Basins (Badiola, 2004). The paleobiological study of the mammal fossil assemblage from Zambrana has also provided significant data on the Iberian and wider European mammalian paleoecology and paleobiogeography in southwestern Europe at this time (Badiola et al., in press). With respect to perissodactyls, to date, five genera and sixteen species of equoids and five taxa of lophiodonts, which are unknown elsewhere in Europe, have been identified to date in the Western Iberian Bioprovince (taxa indicated in black in Fig. 5). 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 Almazán Basins and Miranda-Trebiño Basin, respectively, which are unknown elsewhere in Europe. Others are close to those of southwestern Europe, but because of their more derived dental features (mainly larger size and more hypsodont dentition), they are not included within the same species (see taxa in Badiola et al., in press).

A period of isolation of the Iberian Peninsula from the Central European island until the late Lutetian (Decourt et al. 1986; Meulekamp et al. 2000), albeit with intermittent faunal exchange with the rest of Europe and with the other continents (probably Asia and Africa), could have caused the endemism of the Eocene mammal faunas of the Iberian Peninsula. Moreover, the special paleoecological conditions of western Iberia, with more open environments and probably more arid ecological conditions, which seem to have existed at least since the late Middle Eocene (Badiola and Cuesta, 2007b), could have been the main causes of the faunal differentiation of the Western Iberian Bioprovince (Badiola et al., in press). The paleogeographic and paleoecological barriers, however, could not have been influenced in the same way for all mammalian fauna, 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: *Anoplotherium laurillardi* Pomel, 1851, *Anoplotherium* sp., Oxacroniinae indet., *Xiphodon gracilis* Cuvier, 1822, *Haplomeryx* sp., and *Dichobune leporina* Cuvier, 1822 (Badiola, 2004). A new Middle Eocene anoplotheriine artiodactyl has recently been found at the Mazatarón site in the Western Iberian Bioprovince (Cuesta and Badiola, 2007), but more Middle Eocene artiodactyl fossils are required to test the hypothesis of an artiodactyl faunal differentiation between the two areas during the late Middle Eocene.

Detailed paleobiological studied of the mammal fossil assemblages of the Western Iberian Bioprovince, including cladistic analysis, together with additional field work in the Eocene beds in the Iberian Peninsula, will be essential for further evaluation of faunal differentiation and endemism in the Western Iberian Bioprovince.

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