

DUEROTHERIUM SUDREI GEN. ET SP. NOV., A NEW ANOPLOTHERIINE ARTIODACTYL FROM THE MIDDLE EOCENE OF THE IBERIAN PENINSULA

MIGUEL-ÁNGEL CUESTA¹ and AINARA BADIOLA^{*2}; ¹Departamento de Geología, Facultad de Ciencias, Universidad de Salamanca, Plaza de los Caídos s/n, 37008 Salamanca, Spain, macuesrc@telefonica.net; ²Departamento de Ciencias de la Tierra, Área de Paleontología, Facultad de Ciencias, Universidad de Zaragoza, Pedro Cerbuna, 12, 50009 Zaragoza, Spain, abadiola@unizar.es

Anoplotheriines were endemic artiodactyl faunas in Europe during the Eocene. Europe was made up of several large and small islands from the late Early Eocene to the earliest Oligocene (e.g., Meulenkamp et al., 2000), and was inhabited by an endemic mammalian fauna that was clearly different from contemporary faunas in North America and Asia. Anoplotheriines were medium- to large-sized ungulates with brachydont and bunoseledont dentition and likely used terrestrial locomotion (Sudre, 1988). Hooker (2007) recognized a bipedal browsing adaptation for the large *Anoplotherium* species, which would have been able to browse 2–3 m above the ground with no competition from other contemporaneous European terrestrial mammals. Anoplotheriines are regarded as members of the immigrant taxa that appeared on the Central European Island around the Middle-Late Eocene transition. They seem to have originated within Europe, but their area of origin and the dispersal directions that they took through the different areas of the Eocene European archipelago are still poorly characterized.

Here we describe a new anoplotheriine that is assigned to a new genus on the basis of a left maxilla fragment with the P3-M3 series (see preliminary account in Cuesta and Badiola, 2007). This fossil material comes from the late Middle Eocene bed located near the village of Mazaterón, about 40 km southeast of Soria (Castilla y León, central Spain). The new anoplotheriine fossil at Mazaterón site is an important finding because representatives of the first anoplotheriines are still scarce. This discovery is crucial for comparing the composition of the Middle Eocene artiodactyl faunas of western and northeastern Iberia (see next section) and for studying the origin and dispersal of anoplotheriines. The material we described here is deposited at the “Sala de las Tortugas” of the University of Salamanca (STUS), in Salamanca city (Castilla y León, Spain).

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). 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). We follow recent phylogenetic analyses of artiodactyls in placing anoplotheres more closely to Tylopoda (Gentry and Hooker, 1988, Hooker and Weidmann, 2000, Theodor et al., 2005) than to Suiformes (Simpson, 1945, McKenna and Bell, 1997). We use the systematic classification of Gentry and Hooker (1988) and Hooker and Thomas (2001), recognizing Anoplotherioidea which includes Anoplotheriidae (with Anoplotheriinae and Dacrytheriinae) and Xiphodontidae. For details about the dental nomenclature of artiodactyl cheek teeth, see Hooker (1986:377).

GEOLOGICAL AND PALEONTOLOGICAL BACKGROUND

The fossiliferous beds that contain the vertebrate fossils of the Mazaterón site are included within the Mazaterón Formation, which outcrops in the northern part of the Almazán Basin and belongs to the first depositional sequence of the Paleogene succession of this basin (Huerta and Armenteros, 2004). The Almazán Basin is connected with the eastern sector of the larger Duero Basin by the Neogene deposits (Fig. 1A, B). The filling of the Almazán Basin started in the Middle Eocene as the Iberian chain was being uplifted during the Alpine compression (Huerta, 2007). The Mazaterón Formation is composed mainly by limestones, dolostones and marls and it represents the installation of a low-gradient lake system, with the central areas permanently inundated (Fig. 1C). The seasonal lake-level oscillations allowed the deposition of a fringe of palustrine facies, which were connected with an external calcrete fringe that separated the lake system from the alluvial deposits. The grey marls that contain the vertebrate fossils correspond to lacustrine sediments formed in the central anoxic bottom. These marls pass laterally and upwards to palustrine limestones, which record the seasonally exposed areas (Fig. 1C). Further details about the geology and the stratigraphy are available in Alonso-Gavilán et al. (2004) for the Duero Basin, and in Armenteros (1994), Huerta (2007), and Huerta and Armenteros (2004, 2006) for the Almazán Basin and the Mazaterón Formation.

The Mazaterón site has yielded the richest Eocene continental vertebrate fossil assemblage of the Duero Basin. To date, twenty-seven vertebrate taxa have been identified, including chelonians, crocodylians, and mammals (e.g., Cuesta and Jiménez, 1994). The mammal fossil assemblage, which includes rodents, primates, creodonts, artiodactyls, and perissodactyls (Cuesta, 2003 and references therein, and Badiola and Cuesta, 2008), is late Robiacian in age, corresponding to the MP 15–16 paleogene reference level (Cuesta, 1991, 1999; Cuesta and Jiménez, 1994). The primate, rodent, and perissodactyl faunas of the Mazaterón site and other Middle and Late Eocene localities of central and western Iberian basins (Duero, Almazán, Oviedo, and Miranda-Trebiño Basins) were clearly different from those of the Southern Pyrenean Basins (see Fig. 1A) and the rest of Europe. On the basis of this faunal differentiation, the existence of a Western Iberian Bioprovince has been hypothesized (Cuesta, 1991, Badiola, 2004). 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-day southern France and Switzerland — where the typical western Iberian endemic taxa were absent (see Badiola et al., 2009 for a bibliography). However, relatively little is still known about the Middle Eocene artiodactyl fossil assemblages from the Western Iberian Bioprovince. The discovery of a new Middle Eocene artiodactyl fossil at Mazaterón is crucial for comparing the Middle Eocene artiodactyl faunal composition in both areas of Iberia.

*Corresponding author.

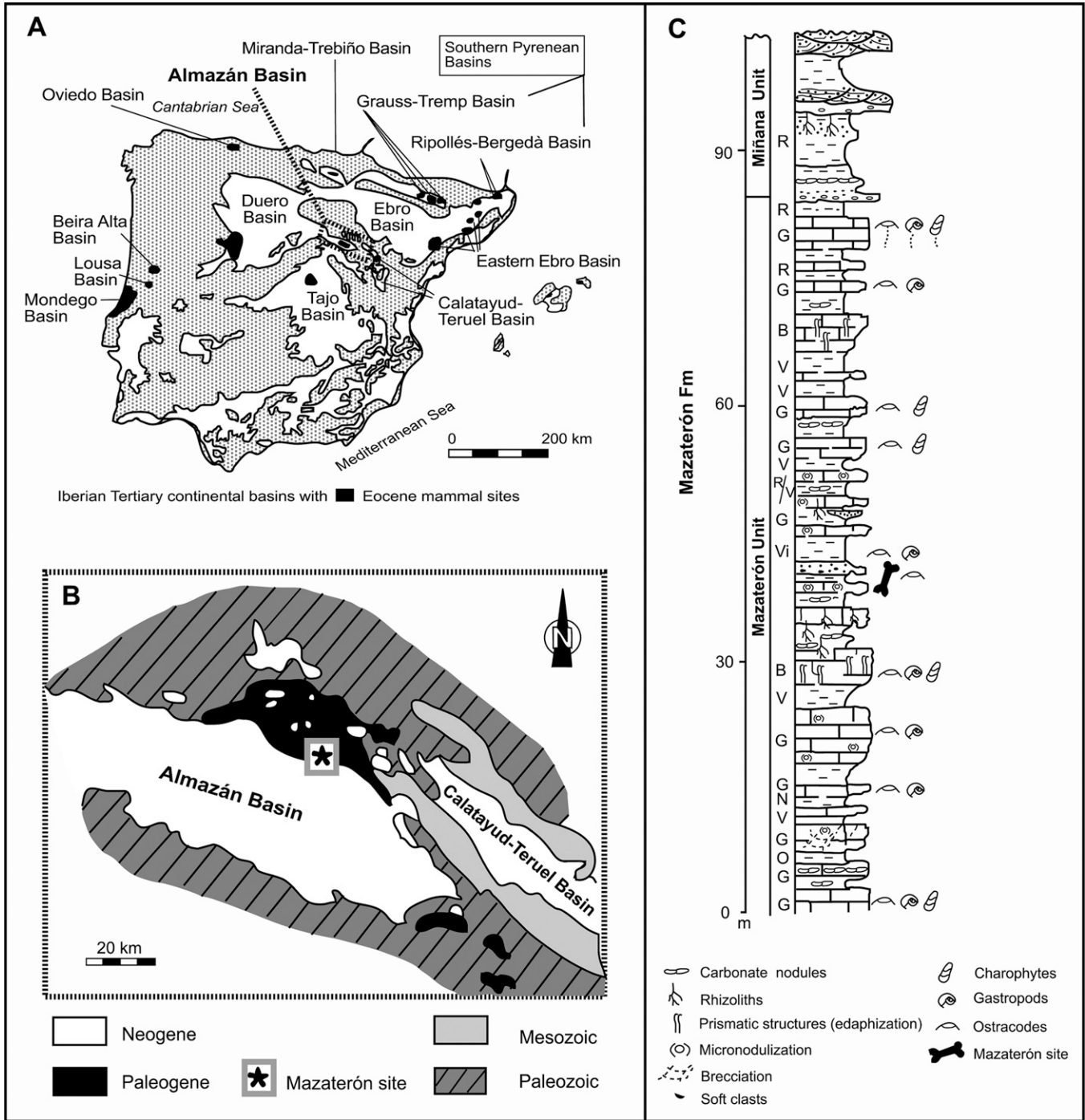


FIGURE 1. **A**, the main Tertiary continental basins of the Iberian Peninsula with Eocene mammal sites indicated in black. Iberian Eocene mammal sites can be consulted in Antunes et al. (1997), Checa (1997), and Badiola et al. (2009). **B**, geological context of the Almazán Basin, which is situated in the eastern sector of the Duero Basin. **C**, stratigraphic column of the Mazaterón Formation (modified from Armenteros, 1994).

SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Owen, 1848

Suborder TYLOPODA Illiger, 1811

Superfamily ANOPLOTHERIOIDEA Bonaparte, 1850 (sensu Gentry and Hooker, 1988)

Family ANOPLOTHERIIDAE Bonaparte, 1850

Subfamily ANOPLOTHERIINAE Bonaparte, 1850

DUEROTHERIUM, gen. nov.

Anoplotheriinae indet. Cuesta, 1993:84, pl.1, fig.4

Etymology—“Duero-”: after the Duero Basin, where this taxon is described; “-therium”: meaning beast or mammal.

Type and Only Included Species—*Duerotherium sudrei*, sp. nov. (Fig. 2, Table).

Diagnosis—Small-sized anoplotheriine, known only by its maxilla fragment, which is characterized by having an unusual P3, which is a mesio-distally elongated triangular tooth with a

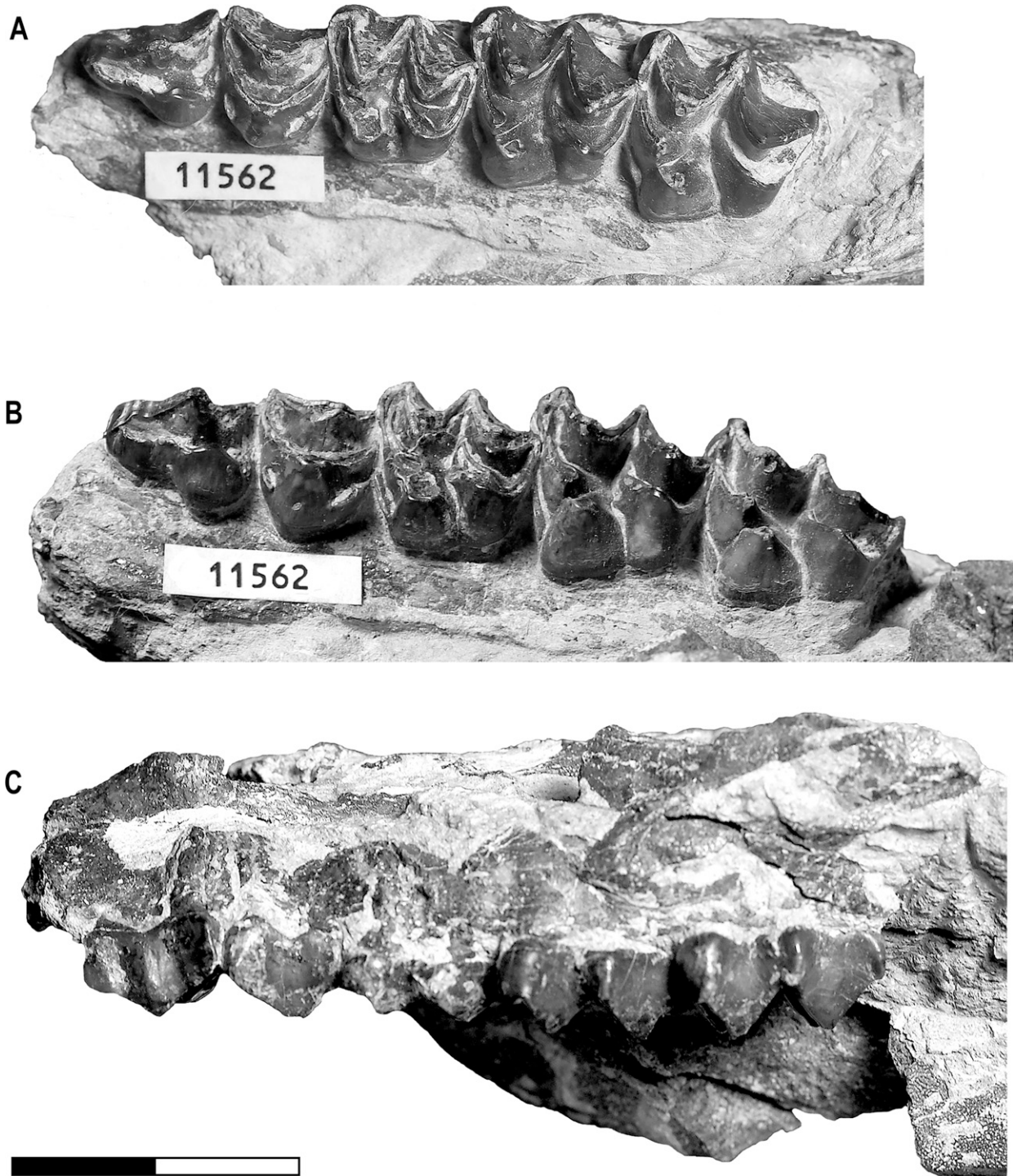


FIGURE 2. *Duerotherium sudrei* gen. et sp. nov. (Anoplotheriidae, Artiodactyla) from the late Middle Eocene of the Mazaterón site (Castilla y León, Soria). Left maxilla fragment, showing the P3-M3 series (STUS 11562, holotype) in occlusal (A), semi-lingual (B), and labial (C) views. Scale bar equals 2 cm.

disto-lingually placed protocone and a prominent postero-lingual talon, in combination with a typical P4 and molar series of anoplotheriines. P4 has only one external cusp. Molars have anteriorly placed protocone, almost in front of the paracone, a slightly asymmetric metaconule with a moderate postmetaconule crista, and quite divergent parastyle and metastyle, showing a moderately open “W”-shaped ectoloph. Heterodont molar

series: large increase in molar size from M1 to M3, and a pronounced gradient of the style development and the crown outline in the molar series, with M1 quadrate and more trapezoidal M2 and M3 in the occlusal view as a result of the large decrease in the disto-lingual lobe width from M1 to M3, and with more protruding styles in the M2 and M3 than in M1. In addition to the obvious differences with other anoplotheriines apparent in

TABLE. Dental measurements (in mm) of the maxilla fragment (STUS 11562, holotype) of the *Duerotherium sudrei* gen. et sp. nov. (Anoplotheriidae, Artiodactyla) described in the late Middle Eocene (late Robiacian) site of Mazaterón (Castilla y León, Spain).

Measurements in mm	STUS		11562		
	P3	P4	M1	M2	M3
Length	10.3	8	11	12.5	14
Width	8.9	10	10.8	12.4	13.6
Length of the P3-M3 series	53.4				
Length of the M1-M3 series	36				

The length measurement corresponds to the maximum mesio-distal dimension of the tooth, whereas the maximum labial-lingual dimension corresponds to the width measurement.

the structure of P3, *Duerotherium* gen. nov. can be distinguished from *Robiatherium* and *Anoplotherium* in terms of having molars with (1) a wider posterior lobe; (2) less asymmetric metaconule and a larger postmetaconule crista; (3) more anteriorly placed protocone; and (4) less divergent parastyle and metastyle, showing a shorter ectoloph. Moreover, molars of *Robiatherium* are more bunodont and brachyodont than those of *Duerotherium*, with thicker and labially more protruding styles, and *Anoplotherium* exhibits a less heterodont molar series (see details above). *Duerotherium* differs from *Diplobune* in having (1) mesio-distally longer molars, with a trapezoidal crown outline in the occlusal view, instead of rectangular; (2) a more centrally placed protocone; (3) a smaller metaconule crista, which is more labially placed; (4) mesio-distally longer ectoloph, with more divergent parastyle and metastyle and thinner and less protruding styles; and (5) a more heterodont molar series. *Duerotherium* differs from *Ephelcomenus* in having: (1) mesio-distally longer molars, with a trapezoidal crown outline in the occlusal view, instead of triangular; (2) a protocone more anteriorly placed, (3) a larger metaconule, and (4) a mesio-distally longer ectoloph, with much thinner and less protruding styles.

DUEROTHERIUM SUDREI, SP. NOV.

Etymology—Dedicated to Dr. Jean Sudre (University of Montpellier II or USTL) in honour of his contribution to the study of the European Eocene artiodactyl faunas.

Holotype—STUS 11562, a fragment of the left maxilla, showing the P3-M3 series.

Type Locality and Horizon—Mazaterón (Castilla y León, Soria), Spain. Almazán Basin, Mazaterón Formation, late Robiacian (MP 15-16) bed (Fig. 1).

Diagnosis—Same as for the genus.

Distribution—Only known in the type locality.

Description—P3 is a mesio-distally elongated triangular tooth, wider distally than mesially due to the disto-lingual position of the protocone and the presence of a large postero-lingual talon. In the labial view, the paracone has a central position. The metacone is small and labially slightly prominent, and it is situated near the paracone. The protocone is lower than the paracone and it is mesiodistally elongated. A long crest extends from the protocone toward the parastyle, and a posterior crest, which is shorter than the anterior one, connects to the small metastyle. The parastyle is large, showing a rounded outline. The preparaconule is long, whereas the postmetaconule is quite short. There is no cingulum. P4 is a subquadrangular tooth, with a labial side longer than the lingual side. There is only one external cusp, from which two crests extend toward the parastyle and metastyle. The parastyle is smaller than that of P3, and the metastyle is weak. The protocone has a central position and is joined to the paraconule and metaconule by the preprotocrista and postprotocrista, respectively. The preparaconule and

postmetaconule cristae run toward the anterior and posterior edges of the crown, closing the central part of the tooth. There is an incipient cingulum at the base of the protocone. Molars are bunoselenodont, with selenodont paracone, metacone and metaconule, and semi-selenodont paraconule. They are slightly longer than wide, with the anterior lobe wider than the posterior one, mainly in M2 and M3. In the three molars, the protocone is a conical and large cusp, and is quite anteriorly placed, situated almost in front of the paracone, and clearly separated from the paraconule by a groove. The preprotocrista is present, but the postprotocrista is absent. The preparaconule crista extends from the paraconule toward the parastyle. There is no well-developed postparaconule crista. The metaconule is slightly asymmetric, with a moderate postmetaconule crista. The ectoloph is oblique, mainly in the M3. The styles (parastyle, mesostyle, and metastyle) are thick at the base of the crown, but much thinner on the top, which are slightly protruding labially. The parastyle and metastyle are quite divergent, showing a moderately open “W”-shaped ectoloph. The cingulum is only mesially present. The molar series is heterodont: there is a large increase in molar size from M1 to M3, and a pronounced gradient of the style development and the crown outline in the molar series, with M1 quadrate and more trapezoidal M2 and M3 in the occlusal view as a result of the large decrease in the disto-lingual lobe width from M1 to M3, and with more protruding styles in the M2 and M3 than in M1.

Discussion—The specimen we describe here (STUS 11562) has the upper dentition characters described by Viret (1961), Depéret (1917), and Stehlin (1910) for anoplotheriids: molars with a mesio-labially oriented preparaconule, with an enlarged paraconule, and without postprotocrista. The latter is an apomorphic character of anoplotheriids according to the cladistic analysis of Gentry and Hooker (1988: fig. 9.8). Other upper dentition characters described by Viret (1961) for anoplotheriines are also present in the studied specimen, which can be distinguished from dacrytheriine anoplotheriids by having a mesio-distally shorter P3, and narrower and more selenodont molars with (1) a trapezoidal crown outline; (2) an oblique and more marked “W”-shaped ectoloph, with thicker styles at the base, but thinner and more protruding on the top; (3) flat paracone and metacone in the labial view, without tubercles; and (4) a protocone less anteriorly placed and more separated from the paraconule. Within the anoplotheriines, the studied specimen differs from the rest of the genera by having a special combination of characters: an unusual structure of P3, which is a mesio-distally elongated triangular tooth with a disto-lingually placed protocone and a prominent postero-lingual talon, combined with typical P4 and molar series of anoplotheriines. The morphology of P3 is close to that of *Dacrytherium* (*Dacrytheriinae*), with the same distribution of cusps, though the P3 of *Dacrytherium* is a more mesio-distally elongated tooth. The STUS 11562 specimen has been herein assigned to a new anoplotheriine taxon, *Duerotherium sudrei* gen. et sp. nov. The latter is slightly larger in size than *Robiatherium*, but smaller than *Ephelcomenus*, and clearly smaller than *Anoplotherium* and *Diplobune*, except *D. minor*, which is similar in size to *D. sudrei*. The differences found between *Duerotherium* and the rest of the anoplotheriines (see diagnosis of the new genus) suggest that the molar structure of *D. sudrei* with respect to the crown outline in the occlusal view, the development of the metaconule, metaconule crista, and styles, the length of the ectoloph, and the position of the protocone can be situated morphologically between *Robiatherium*-*Anoplotherium* and *Diplobune*.

DISTRIBUTION AND PALEOBIOGEOGRAPHY

Anoplotheriine artiodactyls are regarded as members of the immigrant taxa, which appeared on the Central European Island, the largest islands of the Eocene European archipelago,

around the Middle-Late Eocene transition related to the second intra-Eocene faunal turnover involving immigration. Two intra-Eocene mammalian faunal turnovers involving immigration took place in the Central European Island, one in the Middle Eocene and the other around the Middle-Late Eocene transition. In addition to the intermittent presence of land bridges between the different areas of Europe, the paleoclimatic conditions also played a role in these immigrations (see Franzen, 2003 for a bibliography). Anoplotheriines seem not to have originated outside Europe, but their area of origin and dispersal directions through the different areas of the Eocene European Archipelago are still unresolved. The first immigrant, *Robiatherium*, appeared in the southern part of the Central European Island, now southern France, in the late Middle Eocene. Fossil specimens come from the late Robiacian beds (MP 16) at the Le Bretou and Robiac sites (Sudre, 1988). In this paper, another late Middle Eocene anoplotheriine, *Duerotherium* gen. nov., is described in a slightly older site at Mazaterón (late Robiacian, MP 15-16), Almazán Basin, in the Iberian Peninsula (Fig. 1). There are no anoplotheriines known in the early Late Eocene, in the early Headonian (MP 17a and 17b), even though artiodactyl faunas at this time are well known in the Central European Island (e.g. Sudre, 1978; Hooker, 1986; Hooker and Weidmann, 2000) and in the Iberian Peninsula (Cuesta et al., 2006). The next immigrants, the anoplotheriines *Anoplotherium* and *Diplobune*, arrived in the mid Headonian (MP 18) and were abundant and represented by several species during the mid and late Headonian (Aguilar et al., 1997 and references therein, Hooker and Weidmann, 2000). In the West European Island, now Britain, they are recorded from the late Headonian (MP 19) to earliest Oligocene (Hooker, 2007; Hooker et al., 1995), whereas in the Iberian Peninsula, they are recorded in the mid Headonian (MP 18), late Headonian (MP 19), and earliest Oligocene. However, except for the mid-Headonian anoplotheriine fossils at Zambrana (Miranda-Trebiño Basin, see Fig. 1; MP 18), which comprise a large amount of cranial and dental elements (Badiola, 2004), the rest of Late Eocene anoplotheriine fossils of the Iberian Peninsula are represented by scarce dental and postcranial elements (see Antunes et al., 1997 for a bibliography). A third anoplotheriine immigration wave is known with the presence of *Ephelcomenus* in the Middle Oligocene of Mouillac (Phosphorites du Quercy, Southern France; Hürzeler, 1938). According to Erfurt et al. (2007: fig.1), however, the stratigraphic range of *Ephelcomenus* remains uncertain, and *Diplobune* is known since the Robiacian instead of Headonian.

The discovery of the oldest known anoplotheriine in the Iberian Peninsula (*Duerotherium sudrei* gen. et sp. nov.) at the Mazaterón site (Almazán Basin, Fig. 1), along with the discovery of the slightly younger Middle Eocene anoplotheriine from the southern Central European Island (*Robiatherium cournoverse* [Sudre, 1969]) in what is now southern France (Sudre, 1988), suggests that the first anoplotheriine immigrants could have entered the Central European Island from the Iberian Peninsula after the Iberian plate became connected to the Central European Island in the late Lutetian (e.g., Meulekamp et al., 2000). The same dispersal route, from South (Iberian Peninsula) to North (Central European Island), has been hypothesized for the palaeotheriid perissodactyls that appeared in Central Europe in the Middle Eocene, related to the first intra-Eocene faunal turnover involving immigration (Badiola et al., 2009). The next anoplotheriine immigrants (*Anoplotherium* and *Diplobune*), however, may have entered the Iberian Peninsula from the Central European Island, from where they may have also later moved to the Western European Island. The recorded biodiversity and the biostratigraphic distribution range of *Diplobune*, however, are still poorly characterized for further evaluation of this hypothesis. Moreover, detailed study of the phylogenetic relationships between Iberian and European anoplotheriines is

crucial for studying the area of origin and the dispersal directions of these artiodactyls. Unfortunately, most of the anoplotheriine representatives are still scarcely represented by incomplete upper or lower cheek teeth, making it difficult to carry out an adequate cladistic analysis.

ACKNOWLEDGMENTS

We would like to thank B. Engesser (NMB, Basel), J. Sudre (USTL, Montpellier), Abel Prieur (FSL, Lyon), and L. Ginsburg (MNHN, Paris) for their help and access to specimens; and P. Huerta (University of Salamanca) for his revision of the geological section of this article. We are also grateful to the editors (Drs. M. Wilson, R. Asher, and R. Reisz) and the anonymous referees of this paper for helpful comments on an earlier version. Financial support was provided by The Ministerio de Educación y Ciencia (MEC research project CGL2004-02338/BTE), by the Universidad del País Vasco/Euskal Herriko Unibertsitatea (9/UPV 00121.310-15303/2003), and the autonomous community of Castilla y León (excavation campaigns of 1988–1990) of Spain. The research work of the second author (A. B.) was supported by the Programa Juan de la Cierva of the Ministerio de Educación y Ciencia.

LITERATURE CITED

- Aguilar, J.-P., S. Legendre, and J. Michaux. 1997. Synthèses et tableaux de corrélations; pp. 769–805 in J.-P. Aguilar, S. Legendre, and J. Michaux (eds.), *BiochroM'97: Biochronologie mammalienne du Cénozoïque en Europe et domaines reliés*. Actes du Congrès BiochroM'97. Mémoires et Travaux de l'Institut de Montpellier (EPHE) 21, Montpellier, France.
- Alonso-Gavilán, G., I. Armenteros, J. Carballeira, A. Corrochano, P. Huerta, and J. M. Rodríguez. 2004. Cuenca del Duero; pp. 550–557 in J. A. Vera (ed.), *Geología de España*. Sociedad Geológica de España, Instituto Geológico y Minero de España, Madrid.
- Antunes, M. T., M. L. Casanovas, M. A. Cuesta, Ll. Checa, J. V. Santafé, and J. Agustí. 1997. Eocene mammals from Iberian Peninsula; pp. 337–352 in J. P. Aguilar, S. Legendre, and J. Michaux (eds.), *BiochroM'97: Biochronologie mammalienne du Cénozoïque en Europe et domaines reliés*. Actes du Congrès BiochroM'97. Mémoires et Travaux de l'Institut de Montpellier (EPHE) 21, Montpellier, France.
- Armenteros, I. 1994. Síntesis del Paleógeno del borde oriental de la Cuenca de Almazán (Soria): Geología del Yacimiento de Mazaterón. *Studia Geologica Salmanticensis* 29:145–156.
- Badiola, A. 2004. Estudio paleontológico del yacimiento del Eoceno superior de Zambrana (Álava, Región Vasco-Cantábrica). *Tafonomía, Paleobiología de Mamíferos e implicaciones Biocronológicas*. Ph.D. dissertation (unpublished) Euskal Herriko Unibertsitatea/Universidad del País Vasco, Bilbao, 417 pp.
- Badiola, A., and M. A. Cuesta. 2008. New endemic Eocene equids from the Iberian Peninsula (Western Europe). *Journal of Vertebrate Paleontology* 28:1149–1161.
- Badiola, A., Ll. Checa, M. A. Cuesta, R. Quer, J. I. Hooker, and H. Astibia. 2009. The role of new Iberian finds in understanding European Eocene mammalian palaeobiogeography. *Geologica Acta* 7:243–258.
- Bonaparte, C. L. 1850. 1. *Conspectus Systematis Mastozoologiae*. Editio Altera Reformata. In *Conspectus Systematum*, Leiden.
- Cuesta, M. A. 1991. *Perisodáctilos del Eoceno de la Cuenca del Duero*. Ph.D. dissertation (unpublished) Universidad de Salamanca, Salamanca, Castilla y León, Spain, 322 pp.
- Cuesta, M. A. 1993. Cuatro formas de Artiodactyla del yacimiento Eoceno de Mazaterón (Soria, Cuenca del Duero, España). *Treballs del Museu de Geologia de Barcelona* 3:81–90.
- Cuesta, M. A. 1999. Las faunas de mamíferos del Eoceno de la Cuenca del Duero (Castilla y León, España). *Síntesis Bioestratigráfica y Biogeográfica*. *Revista Española de Paleontología* 14:203–216.
- Cuesta, M. A. 2003. Mamíferos del Paleógeno de la Cuenca del Duero; pp. 197–236 in E. Jiménez Fuentes and J. Civis Llovera (eds.), *Los Vertebrados fósiles en la Historia de la vida: excavación,*

- estudio y Patrimonio. Universidad de Salamanca, Salamanca, Castilla y León.
- Cuesta, M. A., and A. Jiménez. 1994. Síntesis del Paleógeno del borde oriental de la Cuenca de Almazán (Soria): vertebrados de Maza-terón. *Studia Geologica Salmanticensia* 29:157–170.
- Cuesta, M. A., and A. Badiola. 2007. A new anoplotheriine artiodactyla from the Middle Eocene of the Iberian Peninsula. *Journal of Vertebrate Paleontology* 27(supplement to 3):63A.
- Cuesta, M. A., L. I. Checa, and M. L. Casanovas. 2006. Los artiodáctilos del yacimiento ludiense de Sossís (Cuenca Prepirenaica, Lleida, España). *Revista Española de Paleontología* 21:123–144.
- Depéret, C. 1917. Monographie de la faune de mammifères fossiles du Ludien inférieur d'Euzet-les-Bains (Gard). *Annales de l'Université de Lyon (Sciences, Médecine)* 40:1–274.
- Erfurt, J., G. Métais, and J. Sudre. 2007. Diversity of European Paleogene Artiodactyla (Mammalia), and their biostratigraphic significance for European Land Mammal Ages. 5th Meeting of the European Association of Vertebrate Palaeontologists/12th European Workshop of Vertebrate Palaeontology. Carcassonne-Espéras, France, May 15–19, 2007. Abstract volume 21–28.
- Franzen, J. L. 2003. Mammalian faunal turnover in the Eocene of central Europe. *Geological Society of America, Special Paper* 369:455–461.
- Gentry, A. W., and J. J. Hooker. 1988. The phylogeny of the Artiodactyla; pp. 235–272 in J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods. Vol. 2: Mammals. Systematics Association, Special 35B*. Clarendon Press, Oxford.
- Gradstein, F. M., J. G. Ogg, A. G. Smith, F. P. Agterberg, W. Bleeker, R. A. Cooper, V. Davydov, P. Gibbard, L. Hinnov, M. R. House, L. Lourens, H.-P. Luterbacher, J. McArthur, M. J. Melchin, L. J. Robb, J. Shergold, M. Villeneuve, B. R. Wardlaw, J. Ali, H. Brinkhuis, F. J. Hilgen, J. J. Hooker, R. J. Howarth, A. H. Knoll, J. Laskar, S. Monechi, J. Powell, K. A. Plumb, I. Raffi, U. Röhl, A. Sanfilippo, B. Schmitz, N. J. Shackleton, G. A. Shields, H. Strauss, J. Van Dam, J. Veizer, Tl. van Kolschoten, and D. Wilson. 2004. *A Geological Time Scale 2004*. Cambridge, UK: Cambridge University Press; 500 pp.
- Hooker, J. J. 1986. Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England. *Bulletin of the British Museum (Natural History), Geological series* 39:191–478.
- Hooker, J. J. 2007. Bipedal browsing adaptation of the unusual Late Eocene-earliest Oligocene tylopod *Anoplotherium* (Artiodactyla, Mammalia). *Zoological Journal of the Linnean Society* 151: 609–659.
- Hooker, J. J., and M. Weidmann. 2000. The Eocene mammal faunas of Mormont, Switzerland. *Schweizerische Paläontologische Abhandlungen* 120:1–143.
- Hooker, J. J., and K. M. Thomas. 2001. A new species of *Amphirhagatherium* (Choeropotamidae, Artiodactyla, Mammalia) from the Late Eocene Headonian Hill Formation of southern England and Phylogeny of endemic European “Anthracotherioids”. *Palaeontology* 44: 827–853.
- Hooker, J. J., M. E. Collinson, P. F. Van Bergen, R. L. Singer, J. W. De Leeuw, and T. P. Jones. 1995. Reconstruction of land and freshwater palaeoenvironments near the Eocene-Oligocene boundary, southern England. *Journal of the Geological Society, London* 152: 449–468.
- Huerta, P. 2007. El Paleógeno de la Cuenca de Almazán. Relleno de una cuenca *Piggyback*. Ph.D. dissertation (unpublished) Universidad de Salamanca, Salamanca.
- Huerta, P., and I. Armenteros. 2004. Asociaciones de carbonatos continentales en el Eoceno de la Cuenca de Almazán. *Geo-Temas* 6:75–78.
- Huerta, P., and I. Armenteros. 2006. Estratigrafía secuencial del Paleógeno de la cuenca de Almazán. *Geo-Temas* 9:121–124.
- Hürzeler, J. 1938. *Ephelcomenus* nov.gen. ein Anoplotheriidae aus dem mittleren Stampien. *Verh.schweiz.Naturf.Ges* 119–174.
- Illiger, C. 1811. *Prodromus systematis Mammalium et Avium terminis zoographicis utriusque classis, eorumque versione Germanica*. Berlin, 311.
- McKenna, M. C., and S. K. Bell. 1997. *Classification of Mammals Above the Special Level*. New York, NY: Columbia University Press; 631 pp.
- Meulenkamp, J. E., W. Sissingh, J. V. Calvo, R. Daams, L. Londeix, B. Cahuzac, M. Kovac, A. Nagyrosy, D. Badescu, A. Rusu, B. Studencka, V. N. Beniamovskii, I. G. Scherba, J. Roger, J.-P. Platel, F. Hirsch, A. Sadek, G. I. Abdel-Gawad, D. Zaghbib-Turki, K. Ben Ismail-Latrache, S. Bouaziz, N. Karoui-Yaakoub, and C. Yaich. 2000. Map 17: Early to Middle Ypresian (55–51 Ma), Map 18: Late Lutetian (44–41 Ma); in J. Decourt, M. Gaetani, B. Vrielynck, E. Barrier, B. Biju-Duval, M. Brunet, J. P. Cadet, S. Crasquin, and M. Sandukescu (eds.), 2000-Peri-Tethys: Paleogeographical maps. Paris: Commission de la carte Géologique du Monde (24 maps, scale = 1: 10.000.000).
- Owen, R. 1848. Description of teeth and portions of jaws of two extinct Anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyopotamus bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N. W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. *Quaternary Journal of the Geological Society of London* 4:103–141.
- Schmidt-Kittler, N. (ed.). 1987. *International Symposium on Mammalian Biostratigraphy and Paleoecology of the European Paleogene. Münchner Geowissenschaftliche Abhandlungen* 10:1–311.
- Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 85:1–350.
- Stehlin, H. G. 1910. Die Säugetiere des schweizerischen Eocaens, 6: *Catodonthium, Dacrytherium, Leptotheridium, Anoplotherium, Diplobune, Xiphodon, Pseudamphimeryx, Amphimeryx, Dichodon, Haplomeryx, Tapirulus, Gelocus*. Nachträge, Artiodactyla incertae sedis, Schlussbetrachtungen über die Artiodactylen, Nachträge zu den Perissodactylen. *Abhandlungen der Schweizerische Paläontologischen Gesellschaft* 38:839–1164.
- Sudre, J. 1969. Les gisements de Robiac (Eocène supérieur) et leurs faunes de Mammifères. *Palaeovertebrata* 2:95–156.
- Sudre, J. 1978. Les Artiodactyles de l'Eocène moyen et supérieur d'Europe Occidentale: systématique et évolution. *Mémoire et travaux de l'E.P.G.E., Montpellier* 7:1–229.
- Sudre, J. 1988. Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertébrés de Eocène supérieur. VII. Artiodactyles. *Palaeontographica A* 205(1–6):129–154.
- Theodor, J. M., K. D. Rose, and J. Erfurt. 2005. Artiodactyla. Chapter 14; pp. 215–233 in K. D. Rose and J. D. Archibald (eds.), *The rise of the placental mammals. Origins and relationships of the major extant clades*. Baltimore, Maryland: The Johns Hopkins University Press.
- Viret, J. 1961. Artiodactyla; pp. 887–1021 in Piveteau (ed.), *Traité de Paléontologie*. 6(1).

Submitted January 5, 2008; accepted July 13, 2008.