

First record of the genus *Leptolophus* Remy, 1965 (Mammalia, Perissodactyla) in the late Eocene (Priabonian) of Europe

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ABSTRACT

We describe *Leptolophus* sp. (Equoidea) teeth from the late Eocene at Zambrana (Alava, Basque Country). The features of the M2 are comparable to those of *Leptolophus* sp. from the upper part of the middle Eocene (MP 15-16) of Mazaterón (Soria, Spain). However, there are a number of differences, including the large size and more accentuated hypsodonty. This discovery extends the stratigraphical distribution of *Leptolophus* Remy, 1965 to the Ludian (Priabonian, MP 18).

KEY WORDS

Mammalia,
Perissodactyla,
Leptolophus,
late Eocene,
Zambrana,
Basque Country.

RÉSUMÉ

Première mention du genre Leptolophus Remy, 1965 (Mammalia, Perissodactyla) dans l'Éocène supérieur (Priabonien) d'Europe.

Des restes dentaires de *Leptolophus* sp. (Equoidea) provenant de l'Éocène supérieur de Zambrana (Alava, Pays basque) sont décrits. La M2 montre des ressemblances avec celle de *Leptolophus* sp. de la partie supérieur de l'Éocène moyen (MP 15-16) de Mazaterón (Soria, Espagne). Il existe néanmoins quelques différences, notamment une plus grande taille et une plus forte hypsodontie chez la forme de Zambrana. Cette découverte permet d'étendre la distribution stratigraphique de *Leptolophus* Remy, 1965 jusqu'au Ludien (Priabonien, MP 18).

MOTS CLÉS

Mammalia,
Perissodactyla,
Leptolophus,
Éocène supérieur,
Zambrana,
Pays basque.

INTRODUCTION

The locality of Zambrana (Alava, Basque Country) has yielded a vertebrate fauna which consists of turtles, crocodylians and several species of mammals, especially perissodactyls (Badiola *et al.* 1999; Astibia *et al.* 2000). The outcrop is situated near the village of Zambrana, about 30 km southeast of Vitoria-Gasteiz and about 70 km south of Bilbao. Geologically, the Zambrana site is located in the southern part of the Basque-Cantabrian region and consists of continental deposits of the Miranda-Treviño Basin. The fossiliferous beds are lacustrine coal-bearing marls and limestones (Astibia *et al.* 2000). The Zambrana fossil association is indicative of a late Eocene (Ludian = Priabonian) age, corresponding to the mammal unit MP 18 (*sensu* Schmidt-Kittler 1987). In this paper, tooth remains of *Leptolophus* Remy, 1965 are described for the first time. The fossils are kept at the Museo de Ciencias Naturales de Alava/Arabako Natur Zientzien Museoa (MCNA) in Vitoria-Gasteiz (Basque Country).

SYSTEMATICS

Order PERISSODACTYLA Owen, 1848
 Superfamily EQUOIDEA Gray, 1821
 Family PACHYNOLOPHIDAE Pavlow, 1888
 Subfamily PLAGIOLOPHINAE Remy, 1976
 (Cuesta, 1994)

Genus *Leptolophus* Remy, 1965

TYPE SPECIES. — *Leptolophus stehlini* Remy, 1965, by original designation.

Leptolophus sp.
 (Figs 1-3)

MATERIAL EXAMINED. — Right M1 (MCNA 9947); right M2 (MCNA 9948); right upper (P4?) tooth (MCNA 9963); fragment of upper tooth (MCNA 9964); left mandible with the m1-2 molar series (MCNA 9002).

LOCALITY AND AGE. — Zambrana, Alava; late Eocene (Priabonian, MP 18) (see Astibia *et al.* 2000).

REMARKS

The classical systematic nomenclature considers *Plagiolophus* Pomel, 1847 and *Palaeotherium* Cuvier, 1804 as members of either the Equidae or the Palaeotheridae (Savage *et al.* 1965; Franzen 1968; Remy 1976). Here we follow the systematic proposition of Cuesta (1993, 1994) who classified *Plagiolophus* and closer relatives as Pachynolophidae.

DESCRIPTION

The upper tooth remains which we described were found at the same level and in close proximity to each other. They probably belong to the same species and even to the same individual.

The molar series exhibits a strong height gradient (Fig. 1). The size of the M1 is much smaller than that of the M2. The crown of M1 is very worn and less high (17.5 mm) than that of the M2 (31 mm). The M1 is very molariform and it has a trapezoidal outline, with the lingual wall being shorter than the labial one (Fig. 1A-C). Morphologically, the M1 is similar to the M2, but its cingula are more developed. The labial cingulum is W-shaped, quite thick and prominent. The anterolingual cingulum is also well developed and it ascends up to the occlusal surface. Moreover, the development of the parastyle and metastyle is decreasing in the molar series. These styles are less developed in M1 than in the M2.

The M2 (Fig. 1D-F) is moderately worn. It is very hypsodont, with its internal wall being as high as the external one. The crown is trapezoidal, with the basal part being narrower than the occlusal surface. The ectoloph is anteroposteriorly flat, showing an external wall that is lingually inclined and slightly concave on both sides of the mesostyle. The latter is very sharp and prominent. The ribs of the paracone and metacone are absent. In contrast, the parastyle and metastyle are well developed. The parastyle protrudes notably on the labial side, while the metastyle extends more posteriorly. Protoloph

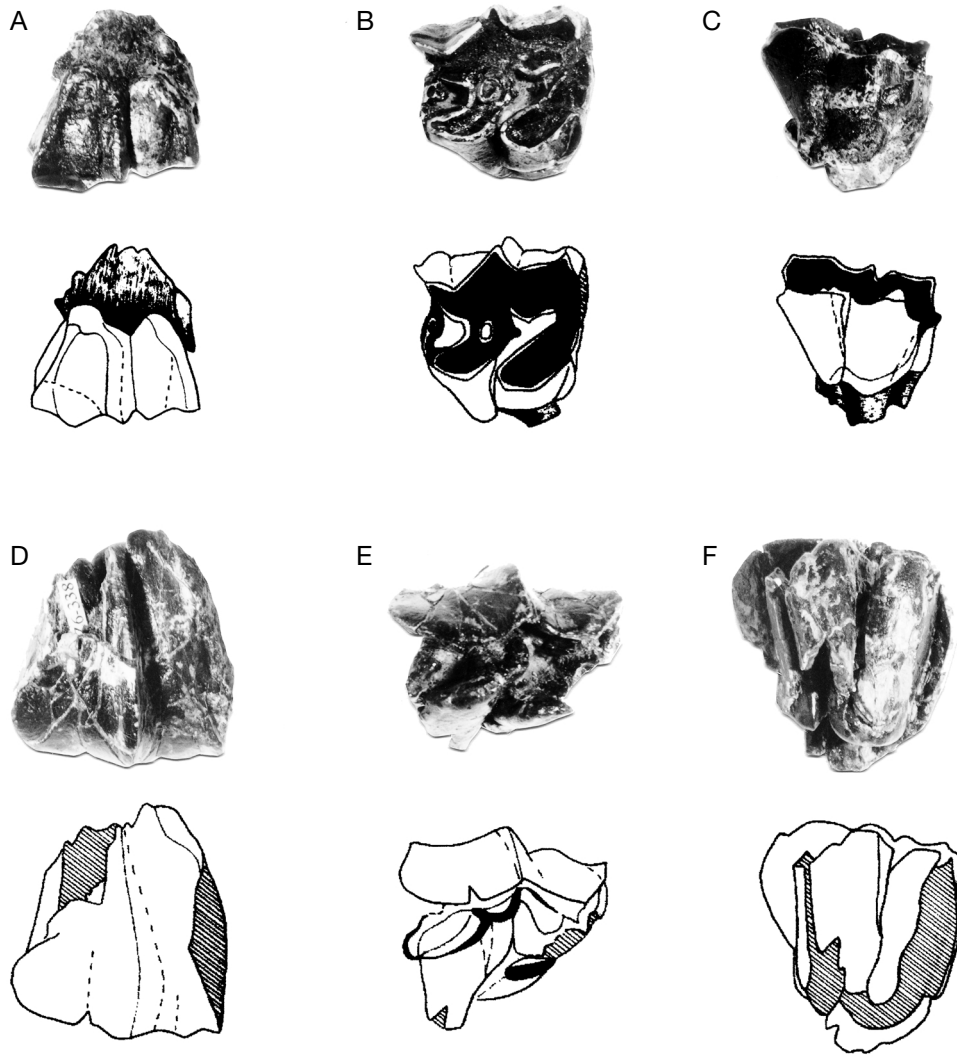


FIG. 1. — Upper series M1 and M2 of *Leptolophus* sp. from Zambrana (Alava, Basque Country); **A-C**, right M1 (MCNA 9947); **A**, labial view; **B**, occlusal view; **C**, lingual view; **D-F**, right M2 (MCNA 9948); **D**, labial view; **E**, occlusal view; **F**, lingual view. Scale bar: 5 cm.

and metaloph are quite slender and oblique relative to the ectoloph. The latter is incomplete but it seems that the metaloph is connected to it, so that the two transversal valleys are separate. Owing to the oblique metaloph, a short and slender crista (hypoloph?) is present between the ectoloph and metaloph; it is slightly convex and closes the posterior fossa. The labial cingulum is quite incomplete, but it continues and ascends

up to the occlusal surface. The basal part of the internal surface is also incomplete, but it seems that the internal cingulum is not present. MCNA 9963 and 9964 look like the M1 and M2 described above, but they are much smaller and less hypsodont than these teeth (Fig. 2). The best preserved tooth (MCNA 9963) is quite molariform (Fig. 2A-C). The protoloph is slender, arches anteriorly and posteriorly; it is connected to the

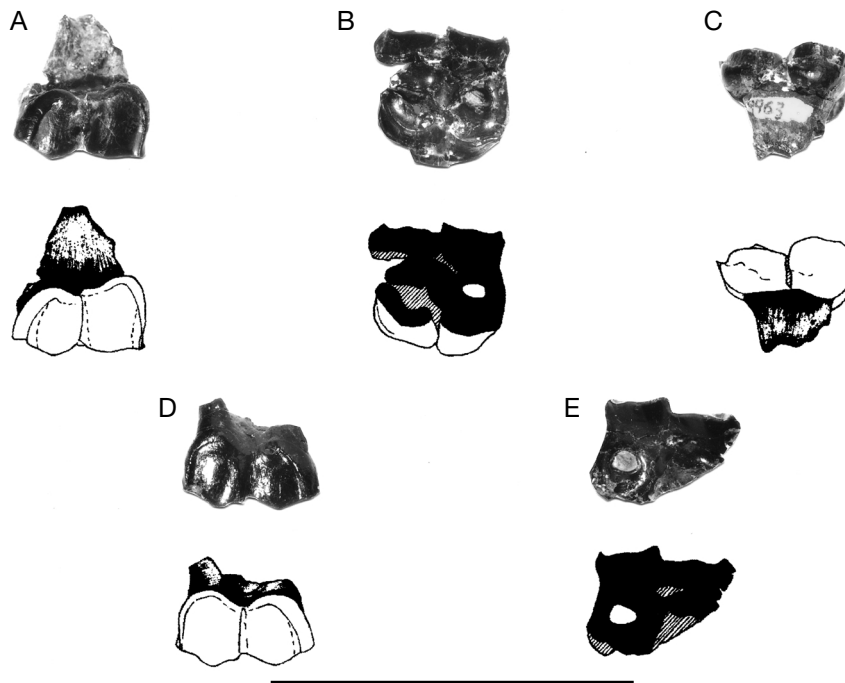


FIG. 2. — Upper teeth of *Leptolophus* sp. from Zambrana (Alava, Basque Country); **A-C**, right P4? (MCNA 9963); **A**, labial view; **B**, occlusal view; **C**, lingual view; **D, E**, left fragment of upper tooth (MCNA 9964); **D**, labial view; **E**, occlusal view. Scale bar: 5 cm.

ectoloph and exhibits a U shape. The development of the styles is very similar to that of the M1. The ribs of the paracone and metacone are absent. These teeth are reminiscent of the premolars (probably the P4) of *Leptolophus* (Remy 1998). The mandible MCNA 9002 preserves only the m1 and m2 (Fig. 3). These teeth are hypsodont, narrow and exhibit a strong height gradient: the size of the m2 is much larger and longer than the m1. The crowns are trapezoidal and the internal wall is as high as the external one. In lateral view, the lophids are rounded and have a U shape, with a concave aspect in the internal wall. The paralophid is well developed and it protrudes notably on the lingual side. The m2 has a small hypoconulid, but does not ascend up to the occlusal surface; in m1 it is absent.

COMPARISONS

The M1 and M2 of Zambrana are typical of the genus *Leptolophus* and differ from those of *Plagiolophus* by the following characteristics:

- 1) trapezoidal outline, with the basal part being more narrower than the occlusal surface;
- 2) proto- and metaloph much longer and more slender, very lophodont and oriented more obliquely to the ectoloph;
- 3) less developed intermediate conules;
- 4) much higher internal cusp, with the hypsodonty of the labial and lingual surfaces being almost equal;
- 5) ectoloph anteroposteriorly flat; and
- 6) absence of ribs of the paracone and metacone.

The mandible MCNA 9002, previously referred to as *Plagiolophus* aff. *mazateronensis* Cuesta, 1994 by Astibia *et al.* (2000), differs from that of *Plagiolophus* by the following characters: 1) the height gradient of the m1-2 series is well developed; 2) the teeth have a trapezoidal outline; 3) the internal wall is as high as the external one; and 4) m1 without hypoconulid, m2 with a small one which does not ascend up to the occlusal surface.

The Zambrana upper teeth are larger and more hypsodont than those of the *Leptolophus* species from the late middle Eocene of southern France

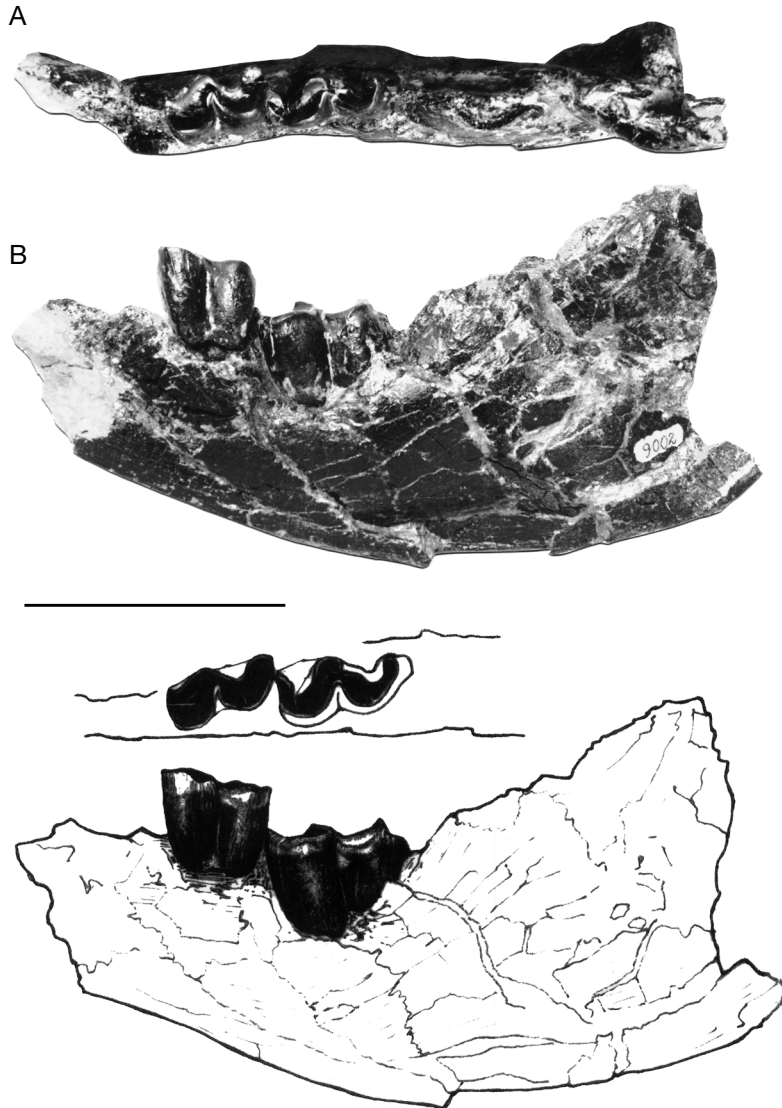


FIG. 3. — Left mandible (MCNA 9002) showing the m1-2 series of *Leptolophus* sp. from Zambrana (Alava, Basque Country); A, occlusal view; B, labial view (modified from Astibia *et al.* 2000). Scale bar: 5 cm.

and Switzerland (*L. stehlini* and *L. nouletii* Stehlin, 1904; see Remy 1998) (Fig. 4). Morphologically, the teeth are comparable to those of *Leptolophus* sp. from Mazaterón, but the Zambrana teeth are clearly larger and more hypsodont. The large size and the more accentuated hypsodonty are considered as derived characters compared to *Leptolophus* from Mazaterón. This

interpretation is coherent with the younger age of the Zambrana locality (MP 18) relatively to Mazaterón (MP 15-16) (see Antunes *et al.* 1997). On the basis of these differences, the Zambrana specimens may belong to a new species of *Leptolophus*. By pending a revision of all the material of *Leptolophus*, the Zambrana teeth are referred to *Leptolophus* sp.

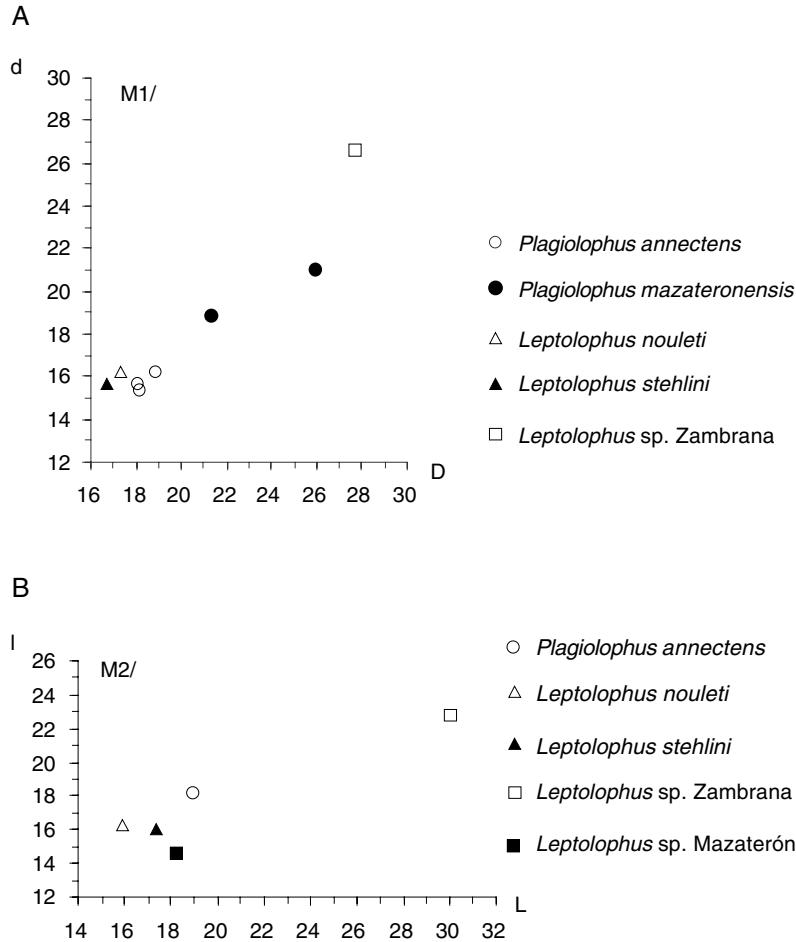


FIG. 4. — **A**, diagram d/D (in mm) of the M1 of several Pachynolphidae from the Eocene of Europe, D , largest diagonal (from the parastyle to the hypocone) of the upper teeth, d , diagonal perpendicular to D ; **B**, diagram I/L (in mm) of the M2 of several Pachynolphidae from the Eocene of Europe, I , maximum width, L , average length of the external wall of the ectoloph. Measurements from Casanovas 1975 and Casanovas *et al.* 1998 for *Plagiolophus annectens* (Owen, 1848); Cuesta 1994 for *Plagiolophus mazateronensis* Cuesta, 1994 and *Leptolophus sp.*; Remy 1998 for *Leptolophus stehlini* Remy, 1965 and *Leptolophus nouleti* Stehlin, 1904.

FINAL CONSIDERATIONS

Up to now, *Leptolophus* has been recorded from the middle Eocene (MP 16) of southern France and Switzerland, and from the Iberian Peninsula (MP 15-16; see Cuesta 1994). Remy (1998) distinguished three species of *Leptolophus*: *L. stehlini* from Robiac (Gard, France), Le Bretou (Tarn-et-Garonne, France) and Mormont-Eclépens (Switzerland); *L. nouleti* from Viviers-lès-Montagnes (Tarn, France) and

several localities of Le Castrais; and *L. magnus* Remy, 1998 from Robiac. In the Iberian Peninsula, the presence of *Leptolophus sp.* has been reported from the Mazaterón site of Soria (Almazan Basin). The Zambrana discovery extends the stratigraphic distribution of *Leptolophus* into the upper Eocene (middle Priabonian; MP 18).

Besides *Leptolophus*, the Zambrana perissodactyls comprise *Paranchilophus sp.* and *Palaeotherium sp.* (Astibia *et al.* 2000). Material

originally described as *Plagiolophus* aff. *mazonensis* is here assigned to *Leptolophus*. The perissodactyl association, which resembles those of western Iberian basins, was first described as containing Iberian endemic forms, in contrast to the Mediterranean and central European faunas (Astibia *et al.* 2000). Nevertheless, recent palaeontologic excavations at Zambrana have yielded other taxa such as *Anoplotherium* Cuvier, 1804 which are unknown in the mammalian faunas of the western Iberian basins (Badiola *et al.* 2002). As a result, Zambrana offers significant information related to the biogeographic distribution of some mammalian faunas during the late Eocene.

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