

A new mammalian fauna from the earliest Eocene (Ilerdian) of the Corbières (Southern France): palaeobiogeographical implications

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Received: 27 April 2012 / Accepted: 19 September 2012 / Published online: 4 November 2012
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Abstract A new mammal fauna from the earliest Eocene of Le Clot (Corbières, Southern France) is described. Some taxa identified there, such as *Corbarimys hottingeri* and *Paschatherium plaziati*, allow a correlation with the previously described Corbières fauna of Fordones. Moreover, the presence at Le Clot of *Lessnessina praecipuus*, which is defined in Palette (Provence, Southern France) allows correlating both localities. All three of these localities are referred to the MP7 reference level, even if a direct correlation with the type locality of MP7 (Dormaal, Belgium) is not ascertained. A Southern Europe biochronological sequence is proposed for the beginning of the Eocene: Silveirinha, Fordones/Palette/Le Clot, Rians/Fournes. The diagnosis of a new species of a neoplagiaulacid multituberculate (*?Ectypodus riansensis* nov. sp.) is proposed. From a compilation of data concerning the earliest Eocene faunas from both Northern Europe and Southern Europe, we conclude that two faunas corresponding to two distinct palaeobiogeographical provinces existed in Western Europe. This faunal disparity, probably related to climatic differences, makes correlations particularly difficult between the two provinces.

Keywords Ypresian · Europe · Mammals · Multituberculates · Palaeoclimate · Palaeobiogeography

1 Introduction

The beginning of the Eocene is characterized by two major phenomena: the warming event known as the Paleocene Eocene thermal maximum (PETM) (Stott et al. 1996), which likely triggered the second one: the mammalian dispersal event (MDE) (Beard and Dawson 1999; Hooker 2000). This MDE is a critical event in the history of mammals as it corresponds to both the origin and dispersal of several modern mammalian orders (Perissodactyla, Artiodactyla, Euprimates, Chiroptera) in Laurasia. This faunal change is particularly well documented in North America, especially in the Bighorn and Clarks Fork Basins, Wyoming (Gingerich 2003; Gingerich and Smith 2006) and to a lesser extent in China (Bowen et al. 2002) and Europe (Smith et al. 2006; Domingo et al. 2009). If the MDE has been known for long (Depéret 1908; Teilhard de Chardin 1922), the PETM and the associated carbon isotope excursion (CIE) have been more recently highlighted (Kennett and Stott 1991). New geochemical approaches have greatly stimulated interest for Early Eocene vertebrate faunas, particularly the earliest ones on each continent in order to determine the centers of origin and the dispersal routes of the newcomers (e.g., Smith et al. 2006; Beard 2008). In this context, Western Europe seems to have played a pivotal role (regarding the palaeobiogeographical event), which remains to be clarified. In contrast to the Paris/London/Belgian Basins, which have yielded the greater part of the earliest Eocene mammals of Western Europe, mammalian localities of this period are rather rare in Southern Europe. Four sites are located in Southern

Editorial handling: Daniel Marty.

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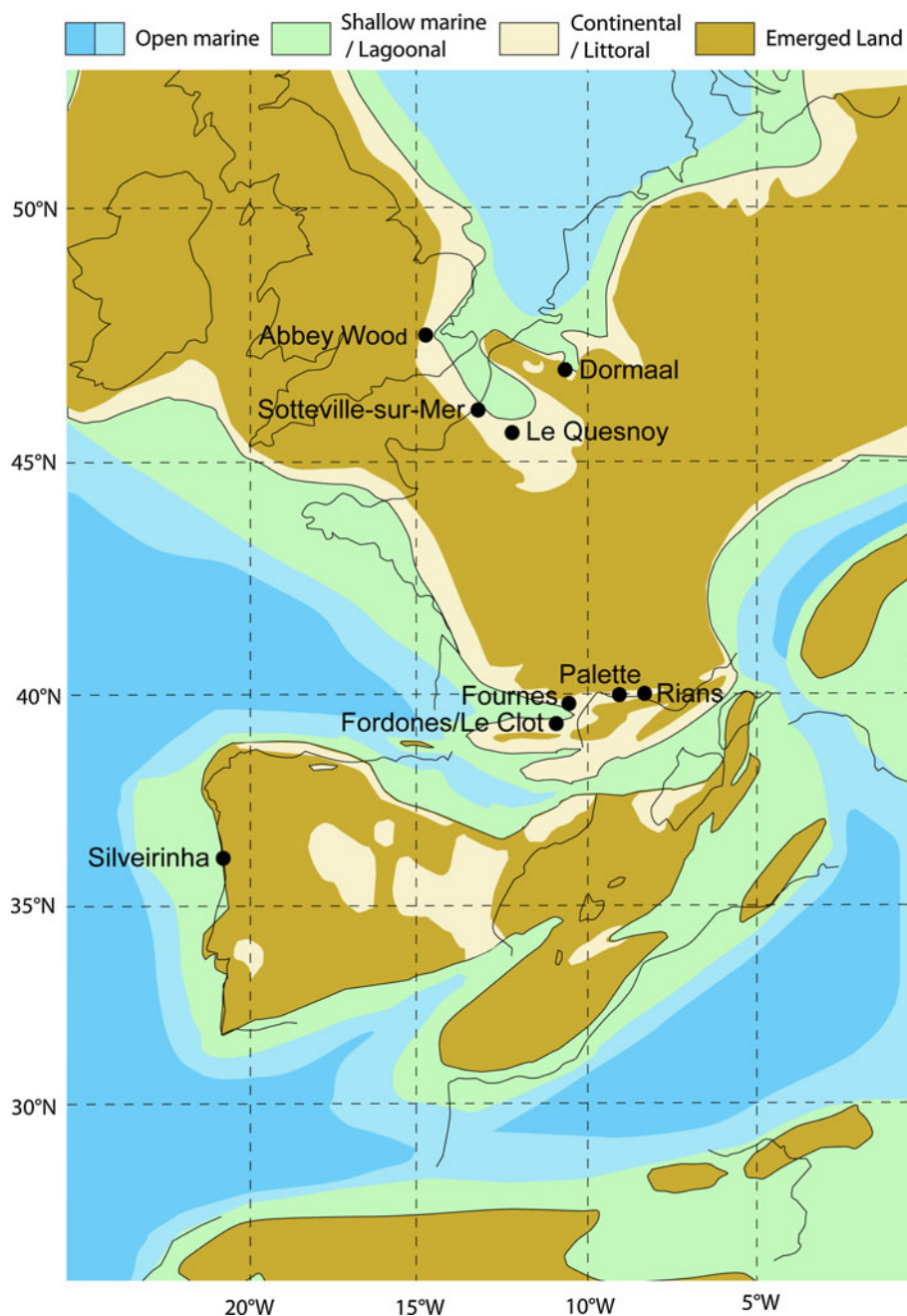
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France and one in Portugal (Silveirinha) (Fig. 1). The fauna of the Portuguese locality has been extensively published (Estravis 1994, 2000; Estravis and Russell 1989, 1992) but some additional new taxa have been recently described (Tabuce et al. 2009, 2011).

Until the 1980s, the only localities reported from the earliest Eocene in Southern France were Palette (Depéret 1910; Savage et al. 1965; Godinot et al. 1987) and Rians (Godinot 1978, 1981) in the Provence area. An early Ypresian age (“Sparnacian”) had been formerly proposed for the latter on the basis of the co-occurrence of the genera *Hyracotherium*, *Diacodexis*, *Pelycodus* (= *Cantius*) and

Paschatherium (Godinot 1978). But, a less advanced evolutionary stage than that from Mutigny and Avenay (MP8+9) in several specific lineages led Godinot (1981) to propose for Rians an age close to that of Dormaal (i.e. near the first Eocene European Reference Level: MP7). The study of the perissodactyls from Palette, also from the Provence area, had led Savage et al. (1965) to propose an Early Ypresian age (Sparnacian) or eventually late Early Ypresian (basal “Cuisian”) age. Later on, the Early Ypresian age (Sparnacian) has been confirmed by the presence of a paromyid primate, *Arcius rougeri*, which is considered as a more primitive species than *Arcius*

Fig. 1 Palaeogeography of Western Europe during the earliest Eocene and location of some selected faunas (modified from Andeweg 2002; Steurbaut et al. 2003; Smith et al. 2011)



fuscus from Mutigny and even than *A. cf. fuscus* from Rians (Godinot 1984). The rodent *Pseudoparamys cezannei* from Palette has been proposed as possibly more primitive than the *Pseudoparamys* sp. from Dormaal (Hartenberger in Godinot et al. 1987). Consequently, an age close to that of Dormaal (MP7) and even possibly older was proposed for Palette (Godinot et al. 1987; Godinot 1996).

The Fordones locality was discovered in 1988 in lagoonal-marine levels of the earliest Eocene (Middle Ilerdian) of the Corbières (Languedoc area), 250 km to the west of Palette. The Fordones fauna was described by Marandat (1989, 1991), who demonstrated that this Corbières locality and Palette share a significant number of taxa at the species level. As such, Marandat (1991) proposed that Fordones and Palette were coeval. Eighteen taxa were formerly recorded at Fordones, but one additional specimen has recently been found there, which can be referred to the tapiromorph perissodactyl *Pachynolophus hookeri* (GODINOT 1987), originally described from Palette, thereby strengthening the correlation between these localities. The locality of Fournes is located on the northern side of the Carcassonne strait (Minervois). It was discovered in 1986 at the base of the Ventenac limestone, which overlies the marine Ilerdian Alveoline Limestone (Marandat 1991). Fourteen taxa, including the perissodactyl *Pachynolophus hookeri*, the primates *Donrussellia gallica* and the paromomyid *Arcius fuscus*, and the incertae sedis mammal *Ilerdoryctes sigei*, have been recorded at Fournes. The locality is slightly younger than Fordones (Marandat 1991).

More recently, new field work by one of us (A. Martinez) led to the discovery of the locality of Le Clot, which is located 7 km southeast of Fordones. About 600 kg of sediment from the fossiliferous layer were screen-washed and a hundred mammalian specimens have been collected. The Le Clot fauna includes mammalian taxa formerly described from Fordones as well as a few other forms showing affinities with taxa known from Palette and Rians. Although the description of these forms from Le Clot is the main purpose of this paper, we also discuss the relative biochronological position of the different earliest Eocene faunas from Southern France in light of these new data.

2 Geological setting

In the Corbières, the Early Eocene deposits were initially attributed to the Ilerdian, a regional stage defined in the Spanish Pyrenees (Hottinger and Schaub 1960; Molina et al. 1992; Pujalte et al. 2009). On the French side of the Pyrenees (Corbières), the Early to Middle Ilerdian deposits were generally divided into three members (Massieux 1973): a basal marine limestone, followed by the marine

lower and upper marls with turrillids and the sandstones with Nummulitidae, Cerithidae and Ostreidae. These marine levels are about 300–400 m thick (more than 500 m in the “Carcassonne Strait”). Contrary to the situation in Spain where the Late Ilerdian is still marine, in Southern France this time period is documented by continental deposits, which are commonly named “Molasse de Carcassonne”. The marine Ilerdian overlies a thick late Paleocene (Thanetian) sequence (145 m), which is composed of a succession of red and yellow marls interbedded with small layers of calcareous sandstones or fine sandstones, easily visible around the village of Albas. In the Spanish Pyrenees, such as in the Tresp area, the Paleocene deposits which underlie the Ilerdian ones have yielded some mammalian faunules (Lopez-Martinez and Pelaez-Campomanes 1999; López-Martinez et al. 2006).

The Le Clot site is situated in a thin continental level, which conformably overlies the very thick section of the marine Early Ilerdian (Fig. 2). This section can be best observed along the “Clot de Pécault” (NW of Albas) and consists in regular layers of lagoonal and/or marine deposits, gently dipping (20–30°) to the North West. The mammal bearing deposits of Le Clot are located 300 m above the first marine level of the Ilerdian, a pink limestone with Foraminifera (Tambareau et al. 1966; Massieux 1973). This limestone can be observed in a section outcropping 2 km eastwards (Massieux 1973) and also in the “Moulin d’Albas” cross section previously described in Tambareau et al. (1966). The Le Clot layer which bears terrestrial vertebrates consists of grey/white marls in which many specimens of continental gastropods, such as *Romanella boriesi*, can also be found. These levels correspond to a brief regressive phase occurring during the Middle Ilerdian (Berger et al. 1997). As in the Fordones section, a marine recurrence overlies the mammal-bearing layers at Le Clot. The total thickness of the section exposed here is more reduced and more clastic than those observed eastwards, near the “Moulin d’Albas” which consist of 400 m thick marly limestones and marls (Massieux 1973). Such lateral lithological and thickness variations are probably due to different environmental depositional conditions (see Plaziat 1984, p. 1079–1086). In this eastern part of the Corbières, the Ilerdian regression probably occurred earlier than in the western part.

3 Systematic palaeontology

Institutional Abbreviations: MNHN: Museum National d’Histoire Naturelle de Paris; RI: Rians locality (MNHN collections); M prefix: Palaeontology Department, Natural History Museum, London (BMNH collections); PU: Princeton University Collections; AV: Avenay Locality (MNHN

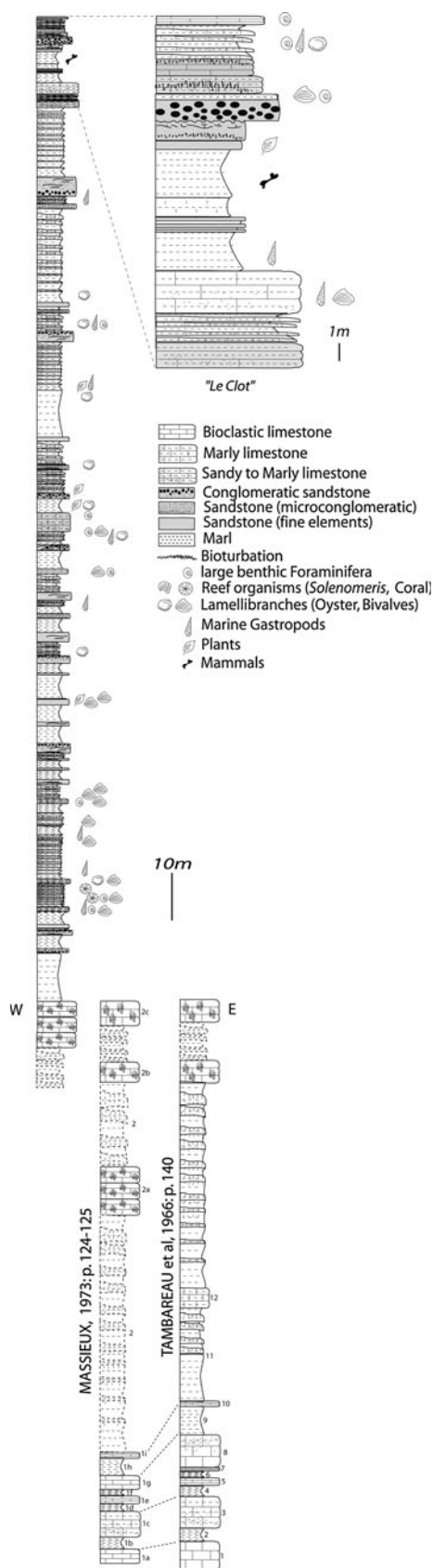


Fig. 2 Geological section Albas/Le Clot (Corbières area) and position of the Le Clot locality at the top of the section

Collections); UM/CLO: Le Clot locality (University of Montpellier Collections).

3.1 Multituberculata COPE, 1884

Neoplagiulacidae AMEGHINO, 1890

Ectypodus MATTHEW and GRANGER, 1921

Type species: *Ectypodus musculus* MATTHEW and GRANGER, 1921

The species described below is tentatively referred to *Ectypodus* because the generic diagnoses from Sloan (1981) are mainly based on variable characters of the P/4. The species *E. childei* has been erected from Abbey Wood as typifying a new genus (*Charlesmooria* KÜHNE, 1969). This genus was later synonymized with either *Ectypodus* (Godinot 1981) or *Parectypodus* (Sloan 1981) and finally referred to *Ectypodus* (Krause 1982a). Some North American specimens from the Four Mile area of northwestern Colorado, considered as *Parectypodus childei* by Sloan (1981, text.Fig. 6–8A) were subsequently attributed to *Ectypodus tardus* (Krause 1982a). Krause (1982a) identified four P/4 referred to cf. *E. childei* in the Despair and Kent Quarries in the Four Mile area, and he described a new species of *Parectypodus* (*P. lunatus*). Since that time, the taxonomy of the two genera has remained unclear (see discussion in Vianey-Liaud 1986, p. 88–91 and p. 15–159) especially when only isolated teeth are available.

Measurements Cusp numbers in cusp formulae as well as dental measurements follow Vianey-Liaud (1986). The cusp formulae are scored for each row from labial row to lingual row (on upper teeth: n1: n2: n3; on lower teeth: n1: n2).

?*Ectypodus riansensis* nov. sp.

(Figs. 3, 4, 5a–f)

Synonymy. *Ectypodus* aff. *childei* (KÜHNE 1960), GODINOT 1981.

Holotype. Right P/4, RI 273, coll. MNHN.

This specimen, the most complete P/4 from Rians or Le Clot, has been selected as holotype as the neoplagiulacid diagnosis are generally established on the last premolars (P/4 and P4/).

Type locality. Rians (Provence, France)

Type material RI 348, anterior part of left P/4; RI 363, posterior part of left P/4; RI 393, complete left M/1; RI 422, anterior fragment of damaged M/1; RI 414, right P4/; RI 393, anterior fragment of left P4/; RI 413, damaged left P4/; RI 394, best preserved P1/; RI 376 and RI 418, damaged P1/.

Age Early Eocene (near MP7)

Other localities Le Clot (Corbières)

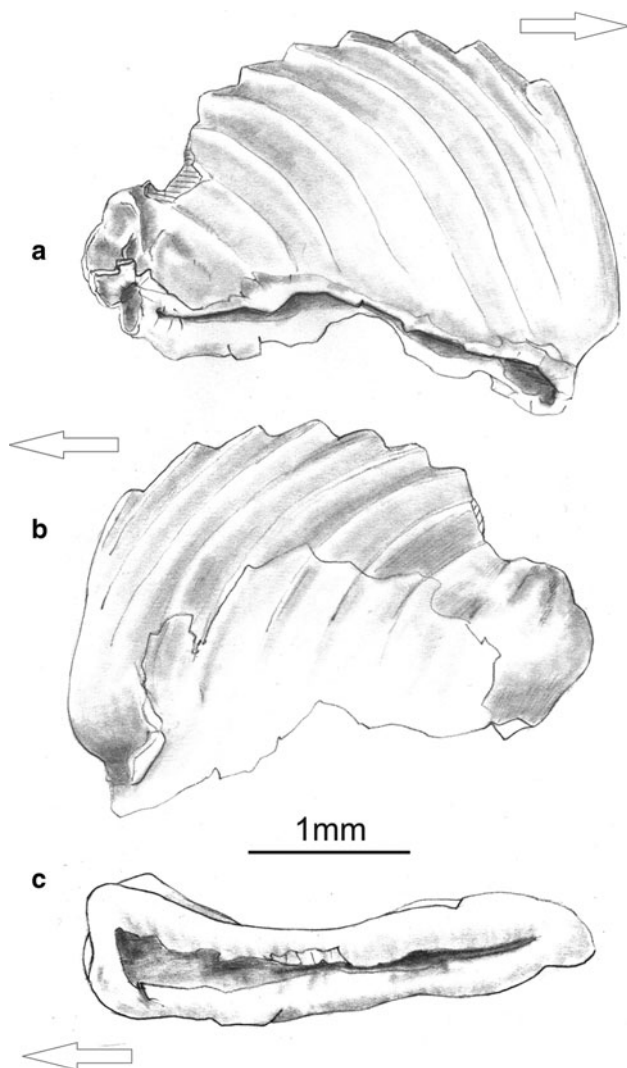


Fig. 3 Holotype of ?*Ectypodus riansensis* nov. sp. (RI363), right P4; **a** labial side, **b** lingual side and **c** inferior view

Diagnosis Teeth larger (LP4/ = 2.6 mm, LP4 = 3.5 mm, LM/1 = 2.31 mm) than those of *Ectypodus tardus*; Straight anterior margin of P4, above a short ventral projection, the posterior slope more curved than straight; ratio height of the first serration/standard length (H2/L in Vianey-Liaud 1986) about 0.41, and apogee of the crown at the third serration (type specimen); cutting edge bearing ten serrations, plus that of the labial cuspid; from the first serration, the first ridge along the anterior margin cuts the second ridge only, the other ridges run parallel and do not converge to the margin ridge; M/1 longer than in *E. tardus*, with cusp formula 8:10; posterior slope of P4/long, steep and straight, with weak posterolingual cuspsule; P4/formula 3:7:0; main cusps on P4/wrinkled by enamel ridges, from the top to the base of each cusp. Differs from *E. childei* in its longer and higher serrations on the cutting edge, in the different pattern of the anterior ridges of the labial side: at least three ridges

cross the first one in *E. childei* (and more in *E. tardus*). Differs also from *E. tardus* in its steeper P4/anterior slope, longer and higher P4/and in its longer M/1.

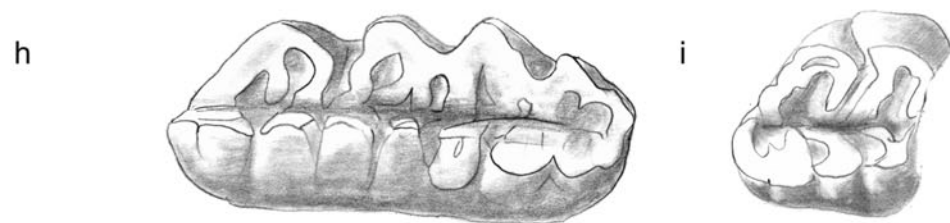
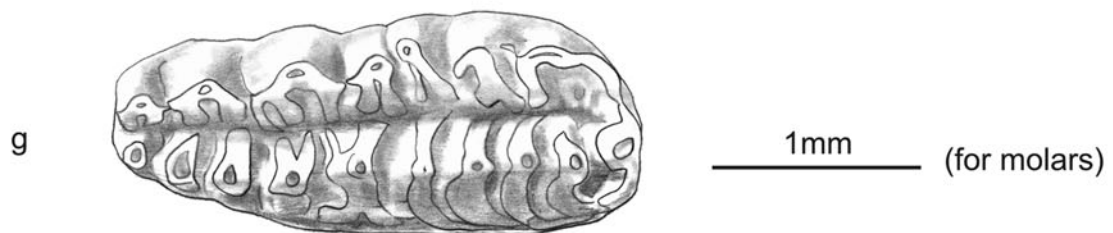
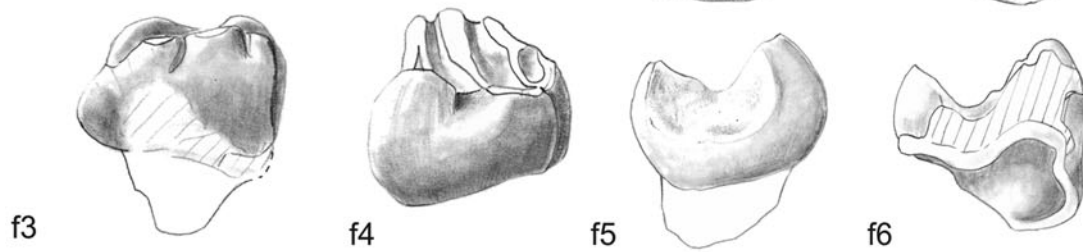
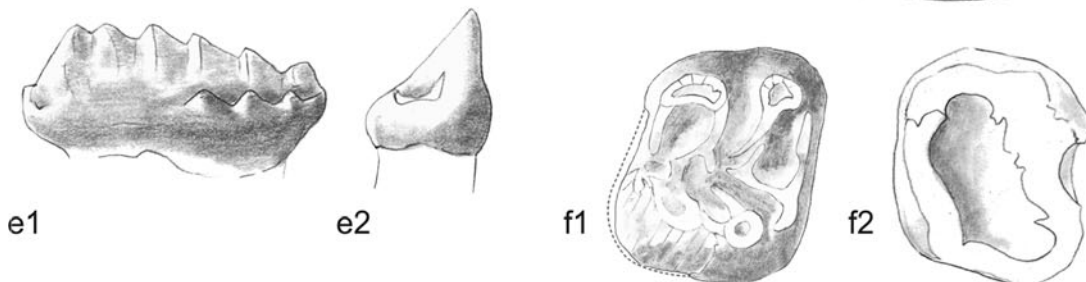
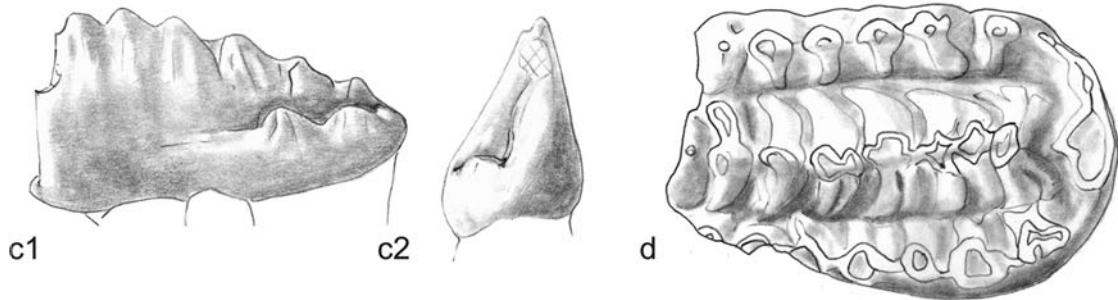
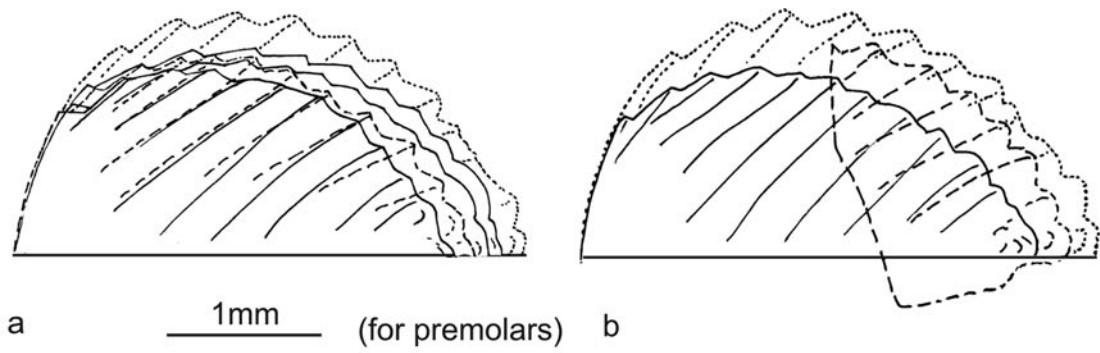
3.1.1 Nomenclatural remark

This new species must be referred to ?*Ectypodus riansensis* VIANEY-LIAUD 2012, following the article 50.1 and the “recommendation 50A concerning multiple authors” of the International Code of Zoological Nomenclature (ICZN, 1999: 52, 182).

3.1.2 Description of the type material

Godinot (1981, Plate 1; Fig. 2) has described the P4 RI 273 from Rians as *E. aff. childei*. Two other fragmentary P4 show 10 or 11 serrations like in *Ectypodus tardus* or *E. childei*. It has been named *E. aff. childei* (Godinot 1981), on the basis of its size, slightly longer than that of *E. childei*, its similar profile shape and its low number of serrations (9–10 for Godinot). But there are some striking differences between the Rians specimens and those of Abbey Wood. The profile of the most complete P4 of ?*E. riansensis* (RI363, L = 3.53 mm, H2 = 1.75 mm) is slightly higher than that of *E. childei* from Abbey Wood.

The serrations are higher and longer on the Rians specimens than on those of Abbey Wood. On the labial side of the Rians P4, the first serration-ridge is secant only to the first following ridge, whereas in *E. childei* from Abbey Wood, or in the type of *E. tardus* from the Willwood Formation, the first serration-ridge is secant to at least the three following serrations. We can also stress some peculiarities of the other teeth of Rians. One M/1 from Rians is fairly preserved (RI347, L = 2.31 mm, W = 1.00 mm). It is clearly longer and a little wider than the M/1 from the type of *Ectypodus tardus*. These species differ by their cusp formula (?*E. riansensis*, 10:7; *E. tardus*, 7:4). The more numerous lingual cusps, on the M/1 from Rians, seem less mesiodistally expanded than in *E. tardus*. The first lingual cusp is conical; its two lingual arms are close to each other. The 2nd and the 3rd ones are crescentic with two lingual arms, the posterior being double. The 4th lingual cusp, as well as the 5th and the 6th, have only one labial arm, these cusps being twinned. The last lingual cusp is crescentic, with two labial arms, the posterior connected with the posterior cingulum, the anterior being free. The four anterior labial cusps are pyramidal, increasing in size from the first to the fourth, with an inclined labial facet on the 1st to the 3rd, and two labial arms on the 4th. The 5th labial cusp has an intermediate morphology between them and the 6th to 9th, which are crescentic, with one lingual arm and one labial arm both curved backwardly. The 5th displays also



◀ **Fig. 4 a** Lower P/4 profiles of the holotype of *Ectypodus tardus* (dashed line), of the three specimens of *Ectypodus childei* from Abbey Wood (M26617, M15131, and M60309), and of the holotype of *?Ectypodus riansensis* nov. sp. (dotted line, RI363). The profiles are aligned from the anterior-most point to the posterior-most point. **b** Profiles of the holotypes of *?Ectypodus riansensis* nov. sp. (dotted line) and of *Ectypodus tardus* (Jepsen, PU 13265). The fragment of P/4 from Le Clot (UM/CLO33) is tentatively inserted between them. **c** P4/of *?Ectypodus riansensis* nov. sp. from Rians (RI414): **c1** labial view, **c2** anterior view. **d** M1/of *?Ectypodus riansensis* nov. sp. from Le Clot (UM/CLO43), occlusal view. **e** P4/of *Ectypodus tardus* (PU 17674): **e1** labial view, **e2** anterior view. **f** M2 of *?Ectypodus riansensis* nov. sp. from Le Clot (UM/CLO38): **f1** occlusal view; **f2** inferior view; **f3** labial view; **f4** lingual view, a little inclined; **f5** anterior view; **f6** posterior view. **g** M1 of *?Ectypodus riansensis* nov. sp. from Rians (RI347), occlusal view, slightly inclined. **h** M1 of *Ectypodus tardus* (PU 13265), Holotype from the Willwood Formation, occlusal view, slightly inclined. **i** M2 of *Ectypodus tardus* (PU 13265), holotype from the Willwood Formation, occlusal view

an anterolingual arm. The 10th labial cusp is fused within the posterior cingulid.

The P4/of *E. tardus* ($C = 6:1-3$; $L = 1.9-2.0$ mm; $W = 0.7-0.8$ mm) is quite smaller than those known from Rians ($C = 7:3$; $L = 2.51$ mm; $h = 1.34$ mm/ $W = 1.00$ mm). The posterior slope of the latter is nearly vertical and high, whereas it is forwardly reclined and low in *E. tardus*. The best preserved fragmentary P1/ $(L = 1.34$ mm/ $W = 1.14$ mm) among those described by Godinot (1981) is clearly larger than that of *E. tardus* (i.e. PU 17674, $L = 0.81$ mm/ $W = 0.70$ mm).

Description of the material from Le Clot

Material 1 fragment of a right P/4, UM/CLO 33; 1 right M/2, UM/CLO 38; 1 fragment of P4/, with 3 cusps, UM/CLO 44; 1 left M1/, UM/CLO 43.

P/4: Only one fragment displaying seven or eight serrations is preserved. The preserved fragment corresponds to the posterior serrations, because the two last serrations display the wrinkles generally linked with the posterolabial cingulid. This fragmentary P/4 has been compared to the three specimens of Abbey Wood (Hooker 2010, Text-fig. 7) and the specimen RI363 from Rians. This fragment can be tentatively inserted within the variation of these specimens (Fig. 4b). The outlines and size of the serrations are more similar to those from Rians than those from Abbey Wood (Table 1). The features shown by this fragment reasonably match the new species, knowing full well, however that the position of the higher serration, as well as the total number of serrations, the expansion of the exodaenodont lobe, and the complete length of the blade cannot be established.

M/2 ($L = 0.84$ mm, $W = 1.00$ mm) (Figs. 4f, 5e, f). This tooth is more reduced than in any known neoplagiaulacid, clearly wider than long (as seen from the base of the crown, Fig. 4f2). There are three labial cusps as in other neoplagiaulacids, but here the anterior one is reduced

and cingulid-like: it is mesiodistally pinched and connected to a bifurcate plunging lophid with the two arms of the first lingual cuspid (Figs. 4f1, f3, 5e). The central and posterior labial cusps are larger than the first one. The lophid originating from the second labial cuspid joins posteriorly the anterior arm of the posterior lingual cuspid. The third labial cuspid is reduced and fused to the short posterolabial cingulid (here with worn enamel cover; Fig. 4f6). The anterior and posterior lingual cusps are mesiodistally crescentic, but in a lesser degree than in any other neoplagiaulacid. The tooth is therefore mesiodistally compressed.

P4/The fragment (Fig. 5b) displays two complete cusps and two incomplete ones, one posterior and one anterior. The lack of accessory labial cusps indicates that it is a posterior fragment, may be from the 2nd to the 4th cusp. The height of the crown (1.13 mm under the supposed 3rd cusp), the size (Table 1) and ornamentation of the cusps fits with the P4/from Rians (Figs. 4c, 5a).

M1/ $(L > 1.94$ mm, $W = 1.24$ mm) (Figs. 4d, 5c). The lingual row is complete, with seven cusps all being connected by mesiodistal spurs of their occlusal surfaces. Only cusps $n^{\circ}3$ to $n^{\circ}7$ show flat lophs, down from the top to the lingual gutter. The central row displays eight cusps, which appear crescentic together with their lingual and labial flat lophs curved forwardly. The ultimate cusp is well separated from the others by a valley; it is connected with low lingual and labial posterior cingula. The other cusps occur in tight succession. The 4th, 5th, 6th and perhaps 7th before the ultimate are twinned, that being underlined by the bifid lingual flat lophs. The three other central cusps (and lophs) are isolated. The labial row preserves six cusps, a 7th is incipient in the swollen anterior end of the posterolabial cingulum. The five cusps before the last one are vertically sharpened by wear and connected to each other, whereas the 6th is widely separated from the 5th.

3.1.3 Discussion

The multituberculate fossil record in Europe is rather limited, aside the rich Paleocene localities of Hainin, Cernay and Berru (Vianey-Liaud 1979, 1986). European Eocene multituberculates have been described, or only reported, from essentially a scarce and fragmentary material from a few Ypresian localities: Abbey Wood (Kühne 1969; Hooker 2010), Rians (Godinot 1981), Le Quesnoy (Nel et al. 1999), Mutigny, Saint-Pol (Soissons) and Avenay (Sloan 1981; Russell et al. 1982; Louis 1996). Hooker (2010) split the three specimens from Abbey Wood into two species: *E. childei* (M26617, M15131) and *E. cf. tardus* (M60309), mainly on the basis of the height of the first serration and on some differences in width among the three specimens. However, these measurements of the width of

Fig. 5 *?Ectypodus riansensis* nov. sp. from Rians. **a** P4/ (RI414) in labial view. *?Ectypodus riansensis* nov. sp. from Le Clot, **b** P4/ fragment (UM/CLO44) in labial view, **c** M1/ (UM/CLO43) in occlusal view, **d** P4/ fragment (UM/CLO33) in labial view, and **e–f** M2/ (UM/CLO38) in occlusal and posterior views. *Corbarimys hottingeri* from Le Clot, **g** P4/ (UM/CLO05), **h** M1/ (UM/CLO2), **i** M2/ (UM/CLO19), **j** P4/ (UM/CLO17), **k** M1/ (UM/CLO18) and **l** M2/ (UM/CLO11), in occlusal views (j and l are reversed views). Paramyidae gen. et sp. indet from Le Clot, **m**: M2? (UM/CLO31) in occlusal view. *Lessnessina praecipuus* from Le Clot, **n–o** P/2 (UM/CLO37) in occlusal and lingual views, **p–q** dentary with M/1 and M/2 (UM/CLO35) in occlusal and labial views, and **r–s** M/3 (UM/CLO36) in occlusal and labial views. *Paschatherium plazati* from Le Clot, **t** M2/ (UM/CLO32), and **u** M3/ (UM/CLO41) in occlusal views. Scale bar 1 mm

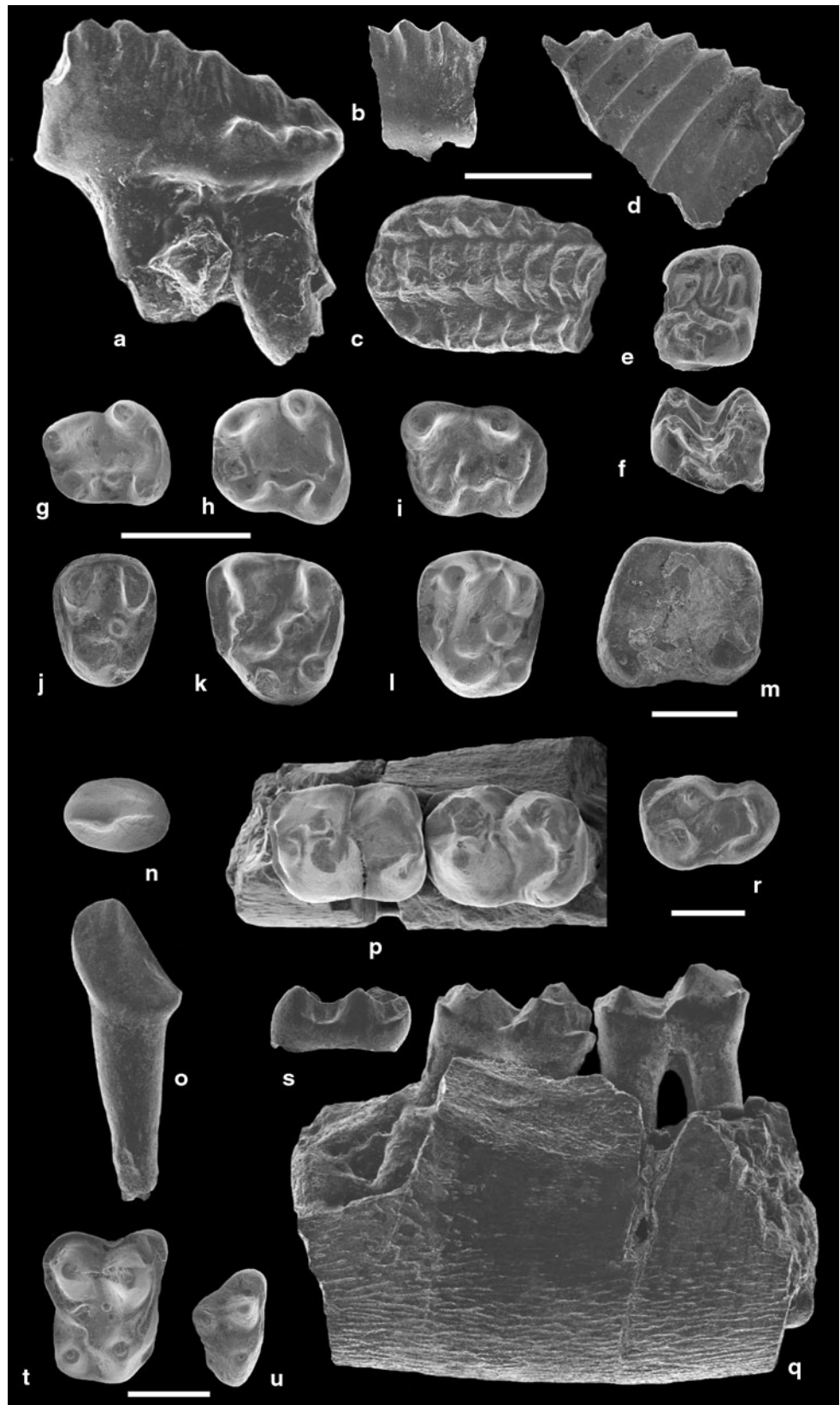


Table 1 Measurements in millimeters of the premolar's cusps (main row, on P4/) and serrations (on P4/) of *Ectypodus* from various Early Eocene European localities

P4/	<i>?E. riansensis</i> nov. sp. RI 273		<i>?E. riansensis</i> nov. sp. UMCLO 33		<i>Ectypodus childei</i> M26617	
	Length (mm)	Height (mm)	Length (mm)	Height (mm)	Length (mm)	Height (mm)
Serration 2	0.52	0.14			0.40	0.07
Serration 3	0.40	0.11			0.27	0.05
Serration 4	0.39	0.12	0.39	0.13	?0.40	0.04
Serration 5	0.34	0.14	0.37	0.13	0.25	0.04
Serration 7	0.33	0.14	0.35	0.11		
			0.32	0.10	0.23	0.07
			0.29	?0.9		
			0.39	0.13		

P4/	<i>?E. riansensis</i> nov. sp. RI 414 (mm)	<i>?E. riansensis</i> nov. sp. UM CLO44 (mm)	<i>Ectypodus tardus</i> PU 17 674 (mm)
Cuspules 2	0.28		0.28
3	0.31	0.30	0.28
4	0.36	0.34	0.28
5	0.42		0.26
6	0.36		0.28
7	0.41		

the P4/, of first serration height, as well as the drawings of profiles depend on the state of preservation of the tooth and on its orientation. Moreover, this height is variable as it has been defined within populations of the same species (i.e. Krause 1982b; Vianey-Liaud 1986; Scott 2005; Scott and Krause 2006). Of course, this has not yet been established for the poorly documented European species of *Ectypodus*. The superimposed profiles of the three Abbey Wood P4 (oriented as in Jepsen 1940 or Vianey-Liaud 1986) do not show a high level of variation (Fig. 4a). The direction and slope of the striations on the three specimens are compatible with each other, and with that of *Ectypodus tardus* (Fig. 4a). The outline of the serrations on the P4/ of *E. childei* fits better with those of *Ectypodus tardus* than with the P4/ from Rians. The M/2 from Le Clot is as wide as the posterior part of the M/1 of *?E. riansensis* from Rians. If these lower molars belong to the same species, as hypothesized here, they highlight a peculiar feature of *?E. riansensis*, i.e. its long M/1 and reduced M/2. In *E. tardus*, where M/1 is relatively short (L = 1.74 mm, W = 0.83 mm), the M/2 is not much reduced (L = 1.03 mm × W = 0.86 mm). It is the same for the Early Eocene Chinese low-crowned neoplagiaulacid *Mesodmops dawsonae* (Tong and Wang 1994). Moreover, among the three labial cuspids of the M/2 from Le Clot, the most anterior one is reduced (crestiform) and the posterior one is smaller by comparison with *Ectypodus tardus* and other Neoplagiaulacidae. In addition, the M/2 from Le Clot differs from all other neoplagiaulacids by its crescentic lingual cuspids which are more mesiodistally compressed in shape.

Several P4/are known from Rians, whereas, unfortunately, no P4/is known from Abbey Wood, and only one poorly preserved fragment with three cusps is documented from Le Clot. Similarly, there is a nearly complete M1/in le Clot, but neither in Abbey Wood nor in Rians. The size of the M1/from Le Clot is quite comparable to that of *Ectypodus tardus* but is larger (PU17674: L = 2.20 mm, W = 1.08 mm) and, even though it is incomplete, it seems to have a similar cusp formula. However, there are differences in the arrangements of their respective cusps. The ante-penultimate cusp is tightly connected to the preceding cusp in the M1/from Le Clot, while they are well-separated in *Ectypodus tardus* from the Willwood Formation (Bighorn Basin). The cusps of the medial row are crescentic on the M1/from Le Clot, while they are not in *E. tardus*. Finally, taking into account the intraspecific variability observed in well-documented neoplagiaulacid populations, we can reasonably hypothesize that the same species occurs in Le Clot and Rians, tentatively referred to the new species *?E. riansensis*, which is different from *E. childei*. If the latter shares similarities with the North American *E. tardus* (p4' size, p4' serration number...), the differences with *?E. riansensis* are more important.

In the other Early Eocene localities such as Saint-Pol, Avenay and Mutigny, it seems that one (or more) different species are documented. In these localities, multituberculates have been reported, named either *Parectypodus* or *Ectypodus* (i.e. Sloan 1981; Russell et al. 1982; Louis 1996). Among them, several specimens from Mutigny have been referred to *Neoplagiaulax* aff. *sylvani* (Vianey-Liaud

1986, text-fig. 57). Some specimens from Avenay (P4: AV26BN, or fragments of P4: AV5659, AV671BN) can be referred to the same species. The teeth figured by Louis (1996, Pl.2, fig. 1–3) from Saint-Pol could also belong to this species of *Neoplagiaulax*.

To summarize and with great caution because the material is scarce, the three P/4 of the species from Abbey Wood probably belong to a single species. This species, *E. childei*, is very close to the North American *Ectypodus tardus*. The material from Rians and Le Clot display particular characters, and they belong to a new species ?*E. riansensis* currently not recorded in Early Eocene Northern European faunas. Finally, the multituberculates from Avenay, Mutigny and Saint-Pol share at least one species, referred to *Neoplagiaulax* aff. *sylvani*, which has been formerly described from the Late Paleocene of Cernay (Vianey-Liaud 1986).

3.2 Rodentia BOWDICH, 1821

Paramyidae MILLER and GIDLEY, 1918

Corbarimys hottingeri MARANDAT, 1989 (Fig. 5g–l)

Material 1 right DP4/, UM/CLO 21; 3 right P4/, UM/CLO 17, UM/CLO 23, UM/CLO 28; 1 left P4/, UM/CLO 24; 4 left M1/, UM/CLO 08, UM/CLO 09, UM/CLO 22, UM/CLO 27; 1 right M1/, UM/CLO 20; 1 right M1–2/, UM/CLO 10; 2 left M2/, UM/CLO 06, UM/CLO 26; 5 right M2/, UM/CLO 07, UM/CLO 11, UM/CLO 15, UM/CLO 29, UM/CLO 30; 1 right M3/, UM/CLO 18; 1 right P/4, UM/CLO 12; 4 left M/1, UM/CLO 02, UM/CLO 05, UM/CLO 13, UM/CLO 14; 2 right M/1, UM/CLO 03, UM/CLO

25; 1 right M/2, UM/CLO 04; 2 left M/3, UM/CLO 16, UM/CLO 19.

3.2.1 Comments

We will not describe in detail the new specimens of *Corbarimys hottingeri* from Le Clot because most of the characters that characterize this small rodent, initially described from Fordones (Marandat 1989, 1991), are also found in the population from Le Clot: trigonid widely open posteriorly, short anterior cingulid lacking a contact with the protoconid, transversely elongated hypoconulid on M/1 and M/2, and large metacone and hypocone on M1/ and M2/. Also, the teeth from Le Clot match the size of their counterparts from Fordones. As in this latter locality, *C. hottingeri* is the most abundant species recorded in the Le Clot fauna. Two small rodents had been formerly recorded in Rians, *Sparnacomys* cf. *chandoni* (Godinot, 1978) and in Silveirinha, *Microparamys paisi* (Estravis 1994) but Escarguel (1999) has referred these two rodents to *Corbarimys*. As such, this genus is now recorded from the South European localities of Fordones (*Corbarimys hottingeri*; Marandat 1989, 1991), Rians (*Corbarimys* cf. *hottingeri*) and Silveirinha (*Corbarimys paisi*). Interestingly, this small rodent has so far never been recorded in the Early Eocene localities from the Paris/London/Belgian Basins, which are rich and well diversified (more than 10 species in Dormaal). On the other hand, a small rodent close to *Corbarimys* (*Corbarimys?* *nomadus*) has been recently reported from the Early Wasatchian Red Hot Local Fauna (Mississippi) by Beard and Dawson (2009) (Table 2).

Table 2 Measurements in millimeters of the jugal teeth of rodent *Corbarimys hottingeri* from Le Clot, Early Eocene of Southern France

N° specimen	Teeth	Length	Width	N° specimen	Teeth	Length	Width
UM/CLO 05	P/4 g	0.97	0.85	UM/CLO 22	M1/ g	0.96	1.11
UM/CLO 25	P/4 d	0.93	0.79	UM/CLO 08	M1/ g	1.06	1.21
UM/CLO 01	M/1 d	1	0.94	UM/CLO 09	M1/ g	0.97	1.11
UM/CLO 03	M/1 d	1.07	1.06	UM/CLO 27	M1/ g	1.04	1.19
UM/CLO 13	M/1 g	1.09	1.02	UM/CLO 07	M2/ d	0.98	1.21
UM/CLO 14	M/1 g	1.06	1.05	UM/CLO 11	M2/ d	0.99	1.13
UM/CLO 02	M/1 g	1.10	1.07	UM/CLO 15	M2/ d	1.07	1.18
UM/CLO 04	M/2 d	1.07	1.09	UM/CLO 29	M2/ d	0.94	1.05
UM/CLO 19	M/3 g	1.20	0.92	UM/CLO 26	M2/ g	0.95	1.17
UM/CLO 16	M/3 g	1.15	1.02	UM/CLO 30	M2/ d	0.99	1.06
UM/CLO 21	DP4/ d	0.85	1.06	UM/CLO 10	M1–2/ d	1.03	1.20
UM/CLO 17	P4/ d	0.82	1.07	UM/CLO 23	M3/ d	0.91	1.07
UM/CLO 28	P4/ d	0.79	1.09	UM/CLO 18	M3/ g ?	0.98	0.97
UM/CLO 24	P4/ g	0.82	1.03				

Paramyidae gen. and sp. indet. (Fig. 5m)

Material: right M/2?, UM/CLO 31 (1.99 × 1.81)

3.2.2 Comments

Because the enamel of this tooth is unfortunately worn, it is difficult to discuss its affinities. This lower molar is much larger than those referred to *Corbarimys hottingeri* and even larger than *Pseudoparamys cezannei* from Fordones and Palette. In this latter locality, there is also an unidentified rodent documented by a worn upper molar (M1/or M2/), significantly larger than those referred to *Pseudoparamys cezannei*, the only rodent recorded to date at Palette.

3.3 “Condylarthra” COPE, 1881

Louisinidae SUDRE and RUSSELL, 1982 (sensu HOOKER & RUSSELL, 2012)

Paschatherium RUSSELL, 1964

Paschatherium plaziati MARANDAT, 1989 (Fig. 5t–u)

Material: 2 right M2/, UM/CLO 32 (1.59 × 1.90) and UM/CLO 39 (1.56 × 1.81), left M1/, UM/CLO 40 (1.67 × 2.17); right M3/, UM/CLO 41 (0.97 × 1.38); left M1–2, UM/CLO 42 (1.68 × 1.27).

3.3.1 Comments

A few teeth document a small louisinid condylarth in which are found many features shown by the different species referred to the genus *Paschatherium*. The measurements of the Le Clot specimens are smaller than those of *P. dolloi* from Dormaal (López-Martinez et al. 2006) but are similar to those of the corresponding specimens of *Paschatherium plaziati* from Fordones (Marandat 1991) or *P. marianae* from Silveirinha (Estravís and Russell 1992). The two M2/ from Le Clot show a strong and continuous postmetaconulecrista, unlike in those of *P. yvetteae* from Dormaal and Claret (López-Martinez et al. 2006) but like in the upper molars of *P. marianae* and *P. plaziati*. The two M2/ from Le Clot, like those of Fordones referred to *P. plaziati*, are however more quadrate and less transversely elongated than those of *P. marianae*. Therefore, we attribute the specimens from Le Clot to *P. plaziati*.

Hyopsodontidae TROUËSSART, 1879

Lessnessina HOOKER, 1979

Lessnessina praecipuus (RUSSELL, 1987) (Fig. 5n–s)

Referred material: UM/CLO37, right P/2; UM/CLO35, right fragmentary dentary bearing M/1 and M/2; UM/CLO36 left M/3.

3.3.2 Description

The P/2 is oval in shape in occlusal view, uniradicated and very simple in morphology; there is neither paraconid and metaconid nor cingulum. The protoconid, which is mesially projected, bears a distolabially oriented postprotocristid as well as a shorter and higher preprotocristid.

On the fragmentary dentary, the depth of the horizontal ramus under M/2 is 4.3 mm. The M/1–2 are rectangular in outline; the mesial cingulum is strong, notably in its buccal part. On M/1, the paracristid is short and swollen in front of the protoconid, the paraconid is isolated and situated mesially to the metaconid. The latter is larger than the protoconid, there is no postmetacristid. Distolingually to the protoconid, the postprotocristid joins a longer postmetacristid; these two crests form a deep V-shaped notch, at the bottom of which the cristid obliqua reaches the trigonid. The difference in height between the trigonid and talonid is moderate. A dominant hypoconid occupies approximately the two-thirds of the talonid. The talonid basin is reduced to a simple mesiolingual furrow lingually opened in front of the cusped entoconid. This cuspid is connected to the hypoconid by a curved postcristid without any trace of hypoconulid. M/2 differs from M/1 in having a trigonid wider than the talonid, a protoconid more distant from the metaconid, a vestigial paraconid fused with the metaconid, a closed trigonid basin, a more marked inflation on the paracristid at the base of the protoconid, a mesoconid with a lingual bump, a more labially oriented cristid obliqua, and in having a minute enamel swelling (hypoconulid?) twinned with the hypoconid on the postcristid.

The M/3 is reduced in size. The strong mesial cingulum is limited to the labial edge of the crown. The metaconid and protoconid are subequal in size and height, and very distant from each other; the metaconid is distally offset. The paracristid is short and reaches an elongated mesiolingually oriented premetacristid. The cristid obliqua links the ends of the postmetacristid in a more labial position than in M/1–2. From this point, another cristid emerges and joins the base of the protoconid (this cristid does not appear to be homologous of the protocristid). The talonid basin is wider and the hypoconid is reduced, more labial and distal than in M/1–2. The entoconid is robust and mesiodistally elongated. The postcristid is strong and embraces the distal edge of the talonid.

3.3.3 Discussion

The genus *Lessnessina* (with its synonym *Midiagnus* RUSSELL, 1987) includes a primitive Asian species, *L. khushuensis* HOOKER and DASHZEVEG, 2003 from the Bumbanian of Tsagan Khushu, Mongolia (see Kondrashov

2004; Hooker 2010), as well as two European species only known from the earliest Eocene, *L. packmani* HOOKER 1979 from Lessness Shell Bed, Abbey Wood and *L. praecipuus* (RUSSELL 1987) from Palette.

The two European species are diversely documented: *L. praecipuus* is represented by its holotype only which associates left and right dentaries bearing worn premolars and molars; and *L. packmani* is essentially known by a maxillary bearing P2/-M3/as well as by few isolated teeth among them a P/4 and only one lower molar, identified as a M/2. As a result, direct comparison between both species is difficult and limited, especially as the molars of *L. praecipuus* are somewhat worn. The well-preserved lower molars from Le Clot give thus the opportunity to reassess some characters that were proposed by Hooker and Dashzeveg (2003) for differentiating *L. praecipuus* from *L. packmani*. For these authors, *L. packmani* differs notably from *L. praecipuus* in having weakly crested M/2, with a strong mesial cingulid, a cusped entoconid, and the occurrence of a low bump that virtually joins the hypoconid to the mesoconid; the latter being considered as missing in *L. praecipuus*. On the P/4, *L. packmani* has a lower hypoconid and a more mesially sloping paracristid (instead of high, nearly horizontal in *L. praecipuus*).

Showing a mesoconid, the incipient low bump on the talonid and a cuspidate entoconid the M/2 from Le Clot is similar to that of *L. packmani*. Based upon these features alone, the specimens from Le Clot seem to belong to *L. packmani*. However, these differences on the M/2 of *L. packmani* and *L. praecipuus* could be due to the worn condition of the molars of the type specimen of *L. praecipuus*. On the latter, the entoconid appears somewhat reduced and crestiform due to important wear on its labial side, and we cannot exclude the presence of a mesoconid fully twinned with the hypoconid considering the large size of this cusp. Besides, relative to *L. packmani*, the M/2 from Le Clot is similar to those of the holotype of *L. praecipuus* in having a weaker mesial cingulid and stronger crests (less bunodont cusps). Moreover, although the dentary from Le Clot is less robust and lower than that of the holotype of *L. praecipuus* from Palette, their dental measurements are similar. The dental measurements of the holotype of *L. praecipuus* given by Russell in Godinot et al. (1987) were a little underestimated, it remains however smaller than *L. packmani*. The occlusal outline of the latter is also more transversally developed and quadrate than on the holotype of *L. praecipuus* and the Le Clot specimen.

L. khushuensis is similar in size with *L. praecipuus* (Palette and Le Clot specimens) but it is clearly apart in having a paraconid separated from (not fused to) the metaconid, a shorter talonid, a weaker cristid obliqua on M/1–3, a well distinct hypoconulid on M/2, and M/3 longer than M/1 with a robust entocristid that bears a small cuspid

in front of the entoconid. *L. khushuensis* differs also from *L. praecipuus* in the position of the mental foramina, which are positioned more distally in the Asian species, and in the absence of the small cuspid at the mesial base of the protoconid on M/1–3. Kondrashov (2004) noted also that the P/4 of *L. khushuensis* differs from that of *L. praecipuus* by the lack of metaconid and the occurrence of two cusps on the talonid. In our opinion, however, these features on the P/4 of *L. praecipuus* cannot be checked due to wear and breakage.

3.4 Additional material

Some fragmentary specimens show the presence in the Le Clot fauna of a lipotyphlan insectivore maybe close to *Saturninia* sp. or *Leptacodon* sp. from Fordones (Marandat 1991).

Some other fragments of upper molars testify to the occurrence of a tiny marsupial. These specimens match both in size and morphology some specimens referred to *Peratherium constans* from Fordones.

4 Discussion

4.1 Biochronology of the earliest Eocene southern Europe localities

The provisional faunal list of Le Clot could be as follows: *?Ectypodus riansensis* nov. sp.; *?Peratherium constans*; *?Saturninia* sp. or *Leptacodon* sp. indet.; *Corbarimys hottingeri*; Paramyidae indet.; *Paschatherium plaziati*; *Lessnessina praecipuus*. From these data, it appears that the Le Clot fauna provides important faunal elements of correlation with Fordones, particularly *Corbarimys hottingeri* and *Paschatherium plaziati*. As such, it is likely that Fordones and Le Clot—both interbedded in the Middle Ilerdian lagoonal/marine levels—have roughly the same age.

Lessnessina is a very rare genus which—except its Asian occurrence—has been found in only three localities from the earliest Eocene of Western Europe (Le Clot, Abbey Wood and Palette). The presence of *L. praecipuus* in Le Clot and Palette suggests a correlation with both localities. Likewise, such a correlation between Fordones and Palette had been formerly proposed (Marandat 1991). These two localities and Le Clot can therefore be considered as contemporaneous but their relative biochronological position with regard to Rians and Silveirinha has long remained unclear (Godinot et al. 1987; Marandat 1991; Hooker 1998; Hooker and Dashzeweg 2003).

The small paromomyid primate *Arcius* lineage, *A. rougeri*–*A. cf. fuscus*, suggests a succession: Palette,

Rians/Fournes (Godinot 1984). *Arcius zbyzewski* from Silveirinha is the smallest species referred to this genus (Estravis 2000) and if it belongs to the same evolutionary lineage as *A. rougieri* and *A. fuscus*, the locality of Silveirinha would be older than those of Palette and Rians/Fournes. In what concerns the diacodexid artiodactyl *Diacodexis*, *D. antunesi* from Silveirinha would be the smallest and the most primitive artiodactyl known to date according to Estravis and Russell (1989), even more primitive than *D. gazini* from Rians. In both lineages, a size increase through time is hypothesized. But a decisive breakthrough could be found in the rodent lineage of *Corbarimys*. Escarguel (1999) has indeed developed arguments to establish a phyletic lineage within the different species referred to the paramyid rodent *Corbarimys*: *Corbarimys paisi*–*Corbarimys hottingeri*–*Corbarimys* cf. *hottingeri* and therefore a biochronological sequence Silveirinha–Fordonnes–Rians.

From all these data, we can hence here propose the following sequence for the earliest Eocene of Southern Europe: (1) Silveirinha, (2) Fordones/Palette/Le Clot, (3) Rians/Fournes. This sequence of South Western Europe localities is thus characterized by the presence of shared lineages and moreover likely represents a relatively important span of time during the early Early Eocene. It is therefore legitimate to wonder which part of the Northern European mammalian sequence it could correspond to.

In the course of the Mainz Symposium in 1987, principally devoted to the mammalian biochronology of the European Paleogene, a series of mammalian reference levels (MP, i.e. Mammal Paleogene standard level) have been established by participants (Schmidt-Kittler 1987). Each of these reference levels is defined by the whole fauna of a reference locality. Within this reference fauna, evolutionary stages reached by mammalian lineages constitute the most reliable biochronological elements of correlation. So, a given locality can be situated with regard to the reference fauna: it may be older or more recent and thus situated in the interval between two reference levels, or closer to one than the other (BiochroM'97 1997). Three reference levels have been chosen and defined in the European early Eocene (MP7, MP8+9, MP10; Schmidt-Kittler 1987).

Some localities from the Paris/London/Belgian Basins (Le Quesnoy, Suffolk Pebble Beds) and from Southern Europe (Silveirinha, Palette, Fordones, Rians) are considered to be located close to the earliest Eocene reference level (i.e. Dormaal, MP 7). But the question of the relative biochronological position of these European localities has been and is still a disputed topic (Gingerich 1989; Hooker 1998; Godinot and Lapparent de Broin 2003). Although there is a strong consensus for considering Dormaal (locality reference level of MP7) as the oldest locality of

the European Eocene, it is worth mentioning here that, based on geochemical data alone, the earliest Eocene age of Dormaal is unfortunately only inferred by correlation with the Doel borehole, about 30 km away (Smith et al. 2006). Anyway, some authors have suggested (see Sect. 1) that some of the Southern Europe faunas were older than the Belgian locality based on concepts of primitive evolutionary grades in some lineages, for example *Diacodexis antunesi* from Silveirinha (Estravis and Russell 1989) or *Palettia* (formerly *Donrussellia*) sensu Godinot (1992), from Palette (Godinot et al. 1987). Both cases have been disputed by Gingerich (1989). In order to resolve problems of correlations concerning these reference levels MP7 to MP8+9 within the Neustrian ELMA (European land mammal age), Hooker (1998) proposed to use a combination of parsimony analysis and links to other biostratigraphies. This led him to propose five concurrent range biozones to replace the Reference levels MP7 to MP8+9. They are from the oldest to the most recent: (1) *Platychoerops georgei*–*Cymbalophus cuniculus* Biozone (Zone PE I), (2) *Platychoerops russelli*–*Teilhardina belgica* Biozone (Zone PE II), (3) *Platychoerops daubrei*–*Cantius eppsi* Biozone (Zone PE III), (4) *Cantius savagei*–*Arcius fuscus* Biozone (Zone PE IV), (5) *Donrussellia gallica*–*Apatemys sigogneui* Biozone (Zone PE V).

The localities corresponding to these biozones are the following: PE I: Try, Erquelinnes, Suffolk Pebble Beds, and Dormaal, PE II: Meudon, Soissons, and Sinceny, PE III: Abbey Wood and Pourcy, PE IV: Mutigny, PE V: Avenay

If this sequence of mammalian biozones can be useful for the earliest Eocene of Northern Europe for which it was originally exclusively established (Hooker 1996), i.e. as an alternative to the unclear definition of MP8+9, it does not solve the question of the correlation with Southern Europe Faunas. Indeed, a great majority of taxa (for example *Cymbalophus*, *Platychoerops*, *Teilhardina*...) used to define these biozones are absent in Southern Europe faunas, at least for zones PE I to PE III. Despite this, Hooker (1998) tried to correlate Southern Europe Faunas with his PE biozones and he concluded that these faunas are not older than PE II for the oldest (Silveirinha). But, aside the absence of several northern taxa in southern Europe, the fact that key Southern genera like *Lophiaspis* and *Donrussellia* are first recorded in zones PE IV and PE V in the Bassin de Paris does not necessarily mean that South Western Europe faunas are younger. Hooker (1998) himself suggests that these genera could have originated earlier in the south and later dispersed northwards.

Moreover, the earliest Eocene from Northern Europe has been in a recent past better documented by the discovery of new localities such as Le Quesnoy (Nel et al. 1999) or very recently, Sotteville-sur-Mer (Smith et al. 2011). The first one

is generally considered of the same age as Dormaal but taxa such as, *Cantius* sp. and an undetermined multituberculate (taxa which remain unrecorded in Dormaal) have been collected at Le Quesnoy.

According to Smith et al. (2011), the mammal assemblage of Sotteville-sur-Mer is best correlated with MP7 but is slightly younger than Dormaal based on geochemical data. It has yielded two species of *Peradectes* and a small species of *Arcius* (Smith et al. 2011) but both families Peradectidae and Paromomyidae are absent in zone PE I and appear only in zone PE II (Hooker 1998). However, the Sotteville-sur-Mer fossils come from the Mortemer Formation and predate the oldest known records of these families from the Soissonais and Vaugirard Formation (Smith et al. 2011). In other words, it appears that taxa absent in Dormaal are now recorded in some new localities (Le Quesnoy and Sotteville-sur-Mer) contemporaneous or slightly younger than the Belgian locality.

Dormaal is the standard fauna of the reference level of MP7, as it is characterized by a very rich and varied fauna including 50 taxa (Smith 2000). However, can we totally rule out that there are some taphonomic bias and/or adverse environmental conditions in the Belgian locality? It is currently premature to tell, and answer this question requires first the complete study of the Le Quesnoy fauna. Interestingly, Nel et al. (1999) have pointed out that the diversity and quality of the Le Quesnoy material suggest that the mammal association is not very much biased.

For the time being, it seems thus very difficult to intercalate the Southern sequence (1—Silveirinha, 2—Fordones/Palette/Le Clot, 3—Rians/Fournes) in the Neustrian series established by Hooker (1998) (Table 3). Smith et al. (2011) note, however, that the new data from Sotteville-sur-Mer indicate that some South Western European localities could be older than originally suggested by Hooker (1998). To solve the question of the age of the Southern sequence, the use of chemostratigraphy appears as an excellent tool. To date, the identification of the CIE in the Southern European province was only investigated at

Palette where the CIE was recorded about 80 m below the mammalian site (Cojan et al. 2000). This result indicates that the fauna from Palette is younger than the Dormaal one which is situated at the base of the Tienen Formation. Really, according to Steurbaut et al. (2003) and Smith et al. (2006), the base of the Tienen Formation corresponds to the onset of the CIE. In a near future, it will be therefore necessary to determine the position of the CIE in the Corbières for Fordones/Le Clot, in Provence for Rians, but also for Silveirinha, likely the oldest locality of the Southern European sequence.

4.2 The Southwestern European province: An earliest Eocene intra-European provincialism

If the Middle Ilerdian faunas from the Corbières are near the reference level recognized as the oldest one, MP7, it implies that these faunas must have an age near the oldest faunas from the Sparnacian of the Bassin de Paris or in equivalent facies in Belgium (Dormaal Sands) or in England (Woolwich Beds).

The comparative studies of the earliest Eocene faunas from Northwestern Europe and North America show that the Neustrian faunas of Dormaal and Erquelinnes (Belgium), Try (France), Kyson (England) have strong affinities with those from the Earliest Wasatchian. These similarities have been long known (Savage 1971) and about 11 species of land mammals (*Pachyaena gigantea*, *Ectypodus childei*, *Arfia junnei*, *Dipsalidictis transiens*, *Oxyaena gulo*...) were considered common to North America and Northwestern Europe (Hooker 1998). Although some of these apparent similarities between the Wasatchian and Early Eocene Northwestern European faunas have been reconsidered (Smith and Smith 2001; Solé et al. 2011), these faunas still present strong affinities. In contrast, Marandat (1997) has pointed out that, except *Peratherium constans* and *Arcius fuscus*, there was no named species in common between Neustrian localities from Northern and Southern France. This is quite remarkable for localities

Table 3 Hypothetical correlations between the two mammalian successions of the Northern and Southern Western European provinces during the earliest Eocene

Ma	ELMA	Bio zones	MP	Standard locality	Northern Province	Southern Province
	Neustrian	PE V	8+9	Avenay	Avenay	
		PE IV			Mutigny	
55.12 ^a		PE III			Abbey Wood, Pourcy	
		PE II			Meudon, Soissons, Sinceny	Rians/Fournes ? Fordones/Palette/Le Clot ?
55.8		PE I	7	Dormaal	Sotteville-sur-Mer Try, Erquelinnes, Suffolk Pebble Beds, Le Quesnoy	Silveirinha ?

^a Hooker (2010)

from the same continental area, which are moreover currently referred to the same reference level MP7.

From the 37 mammalian genera recorded in the Belgian locality, 25 are also present in other Northern European localities close to MP7 and interestingly, only 12 are known in the earliest Eocene from Southern Europe while 22 genera are common with the earliest Wasatchian of North America (Smith 2000). Among others, some of these Euramerican taxa are the following: *Plesiadapis*, *Teilhardina*, *Arfia*, *Coryphodon*, *Pachyaena*, *Palaeosinopa* and *Palaeonictis*. Marandat (1997) had already noticed the absence of these genera in Southern Europe. This could be interpreted as the absence of this faunal stratum in the earliest Eocene of southern Europe. But the high number of endemic taxa (*Mondegodon*, *Eurodon*, *Russellmys*, *Ilerdoryctes*, *Merialus*, *Fordonia*, *Spaniella*, and *Parvagula*) recorded in the Southern Europe province (Table 1), but which are still unrecorded so far in Northwestern European faunas, rather suggests the coexistence of two different provinces at the dawn of the European Eocene. Such a biotic provincialism has been pointed out for early Wasatchian mammalian faunas from North America (Beard and Dawson 2009).

4.3 Provincialism and climatic change

The recognition of two different European Mammalian provinces at the beginning of the Eocene does not solve the question as to determine if the earliest Neustrian Northern and Southern faunas are contemporaneous or not. If so, how to explain these disparities in their faunal compositions? From some palaeogeographic reconstructions of the Early Eocene of Europe (Fig. 1) (Andeweg 2002; Barrier and Vrielinck 2008), it seems difficult to invoke an efficient physical barrier between Northern and Southern Europe. A climatic barrier could be a more plausible explanation. Indeed, we suggest that there was a latitudinal zonation of temperature from the South to the North in Western Europe before, during (?), and after the PETM. This hypothesis is supported by the study of the pollen and Dinophyceae of the Middle Ilerdian from Fordones (Gruas-Cavagnetto 1991). For this author, the pollen assemblage indicates the presence of a subtropical to tropical forest at Fordones; and she also emphasized the presence of latitudinal zonation of the vegetation during the earliest Eocene between North western and Southwestern European provinces. Such an Early Paleogene latitudinal zonation of temperature has been also notified based on floras by Wing et al. (2005) in North America. The Fordones flora can be distinguished from the warmest flora from the Paris Basin by the presence of numerous pollen of Apocynaceae and Loranthaceae, and of many different caesalpinoid palynomorphs which are unknown in Northern Europe (see

however the occurrence of wood and a flower of a Caesalpiniaceae in the Sparnacian of central Bassin de Paris; De Franceschi and De Ploëg 2003).

Consequently, the Rians fauna, that we place here in the youngest part of our Southern European sequence and which includes a number of Euramerican elements, could eventually represent the beginning of the recovery of significant faunal exchanges between the two European areas. As such it must be noted that the new Southern European mammalian fauna of La Borie close to the level MP8+9 according to Laurent et al. (2010) includes taxa such as the condylarth *Phenacodus* and the tillodont *Plesiasthonyx*. It is the first mention of tillodonts in a Southern European fauna which are otherwise known since the early Neustrian of Le Quesnoy (Nel et al. 1999). Phenacodontids are recorded in the early Neustrian of Dormaal (Smith and Smith 1995) but are not represented in the Southern European faunas before Rians (Ginsburg and Mennessier 1973).

Also, the persistence of a climatic gradient may explain why after the recovery of the West European faunal interchange between the MP7 and the MP8+9, a certain number of Neustrian forms, eventually adapted to a less warm and more humid environment (pantodonts, plesiadapids, arctocyonids, palaeonictines...), have not colonized the Southern province. Therefore, the environmental data concur with the mammalian ones to reinforce our assumption of two distinct palaeobiogeographical provinces—corresponding to the Northern and Southern European faunas—during the earliest Eocene of Western Europe.

Acknowledgments We first wish to thank Mr. Raymond Roche, owner of the site, who kindly authorized our field work, Mikaël Antiocco for his help in the field as well as screen-washing and careful picking of sediments from le Clot and preliminary study of the Le Clot fauna in the frame of a Master Degree, Jerry Hooker for the loan of casts and publications and Pierre-Olivier Antoine for discussions. We are also indebted to Christopher Beard and Thierry Smith for their contributions to improve the manuscript. Financial supports for recent palaeontological studies in Le Clot area have been generously supported by the “Institut des Sciences de l’Evolution de Montpellier” (J.-C. Auffray). Publication ISE-M n° 2012–172.

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