A new late Paleocene micromammal fauna from Montchenot (Paris Basin). Preliminary results

Article *in* Palaeobiodiversity and Palaeoenvironments · December 2012

DOI: 10.1007/s12549-012-0100-x

Martin Jehle
Ecole Pratique des Hautes Etudes

Marc Godinot
Ecole Pratique des Hautes Etudes

Dominique Delsate
Musée national d'histoire naturelle de Luxembourg

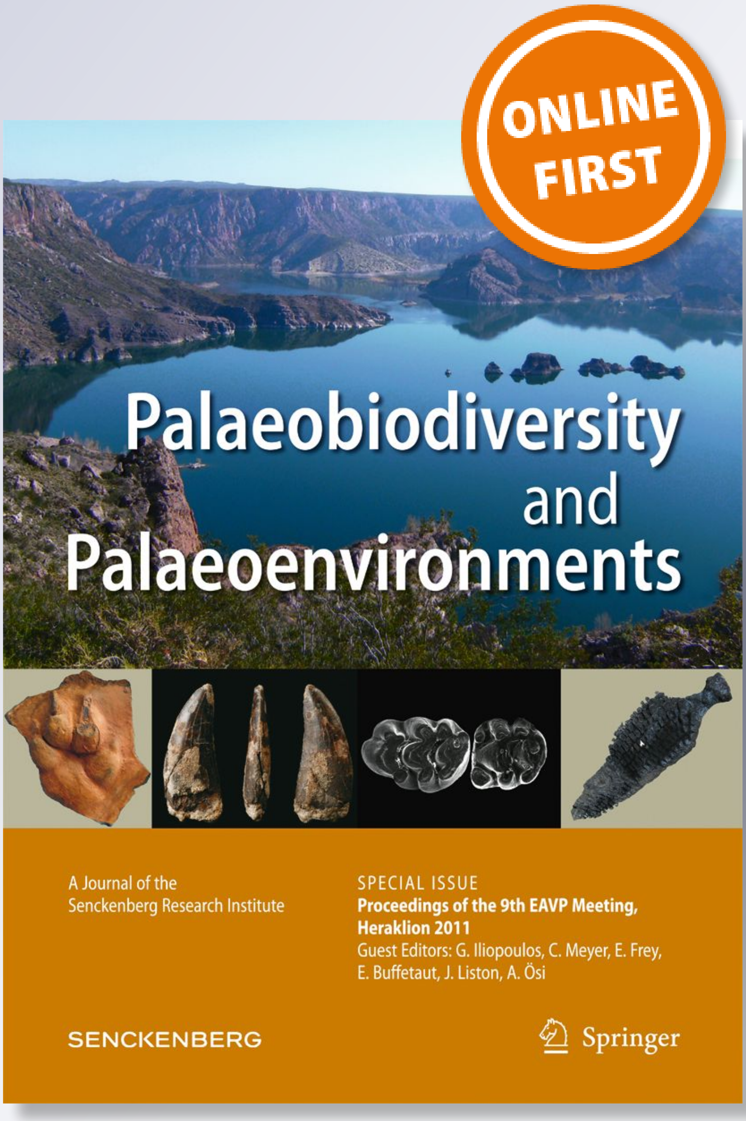
A new late Paleocene micromammal fauna from Montchenot (Paris Basin). Preliminary results

Martin Jehle, Marc Godinot, Dominique Delsate, Alain Phélizon & Jean-Louis Pellouin

Palaeobiodiversity and Palaeoenvironments

ISSN 1867-1594

Palaeobio Palaeoenv
DOI 10.1007/s12549-012-0100-x



Palaeobio Palaeoenv
DOI 10.1007/s12549-012-0100-x

SENCKENBERG

ORIGINAL PAPER

A new late Paleocene micromammal fauna from Montchenot (Paris Basin). Preliminary results

Martin Jehle · Marc Godinot · Dominique Delsate ·
Alain Phélizon · Jean-Louis Pellouin

Received: 31 March 2012 / Revised: 3 July 2012 / Accepted: 23 July 2012

Abstract A diversified fauna of fossil mammals is described from the Thanetian Marnes de Montchenot near Reims (France, Paris Basin). The new fauna is composed mainly of micromammals, which are represented by isolated teeth and a few more complete dental remains. Multituberculates, insectivore-like mammals and louisinine "condylarths" are particularly common at Montchenot, and tiny toliapinid plesiadapiforms are relatively well represented. In contrast, the larger-sized plesiadapiform *Plesiadapis* and pleuraspidotheriid "condylarths" are less abundant than at Cernay or Berru. Special attention is paid to *Neoplagiaulax nicolai*, the most common species of multituberculate at Montchenot. The new sample of this species allows to reconsider the composition of its upper premolar series and the orientation of isolated deciduous anterior upper premolars in neoplagiaulacids. Insectivore-like mammals from Montchenot include a previously unrecognised adapisoriculid, known by the complete upper and lower molar series, which combines an *Afrodon*-like morphology with strong posterior cingula on its upper molars. Mammal fossils indicate an age of the Montchenot fauna close to Cernay (European mammalian reference level MP6), confirming previous age determinations based on mollusks and charophytes. Preservational biases including selective predation and hydrodynamic sorting, possibly in combination with specific palaeoenvironmental conditions related to deposition in a quiet freshwater milieu, seem to be responsible for the peculiar composition of the mammalian fauna from Montchenot compared to other late Paleocene localities in the Paris Basin.

Keywords Thanetian · Paris Basin · Marnes de Montchenot · Fossil mammals · Biochronology · Taphonomy

Introduction

Fossil faunas from the Paris Basin provide the best window into the composition and structure of tetrapod and particularly mammal faunas in Europe prior to the Paleocene/Eocene boundary. Late Paleocene mammals of the Paris Basin are mainly known from Cernay and Berru near Reims (Louis 1996). A new Thanetian mammal fauna is described here from marls accessible in two localities at Montchenot[1] near Reims (Marne). One of these, the abandoned quarry "Les Monts-Martin", has been previously known for its well-preserved freshwater mollusk fauna (Laurain and Henry 1968). The occurrence of mammals and other vertebrates in the Marnes de Montchenot was announced by Laurain and Meyer (1986), who listed 8 species of mammals from this locality based on data of the late P. Louis (*Neoplagiaulax eocaenus* (Lemoine, 1880), *Liotomus marshi* (Lemoine, 1882), *Adapisorex gaudryi*

This article is a contribution to the special issue "Messel and the terrestrial Eocene—Proceedings of the 22nd Senckenberg Conference"

M. Jehle (✉) · M. Godinot
EPHE, Laboratoire d'Evolution des Primates, UMR 7207 CR2P,
Muséum National d'Histoire Naturelle, Département d'Histoire de la Terre,
CP 38, 8, rue Buffon,
75005 Paris, France
e-mail: majehle@paleocene-mammals.de

D. Delsate
Musée national d'Histoire naturelle de Luxembourg,
25, rue Münster,
2160 Luxembourg, Luxembourg

A. Phélizon · J.-L. Pellouin
Société d'Etude des Sciences Naturelles de Reims,
122 bis, rue du Barbâtre,
51100 Reims, France

---

[1] Also known as Mont-Chenot (Laurain et al. 1981)

Lemoine, 1883, *Plesiadapis tricuspidens* Gervais, 1877, *Arctocyon primaevus* Blainville, 1841, *Arctocyonides arenae* Russell, 1964, *Orthaspidotherium edwardsi* Lemoine, 1885 and *Dipavali petri* (Russell, 1964)), but no detailed description of this fauna has been published up to now. Nevertheless, the Montchenot fauna has been mentioned in discussions of faunal successions in the Paris Basin. For instance, Hooker (1998) regarded Montchenot as the most recent fauna of mammalian reference level MP6 (used by him as a zone instead of a level). Similarly, Hooker and Millbank (2001) have postulated a superposition of the Marnes de Montchenot/Calcaire de Rilly over the Sables supérieurs de Châlons-sur-Vesle and of the latter above the Conglomérat de Cernay (reference locality of MP6)—a succession apparently not directly observable in a single site. Thus, the relative age of Montchenot compared to the classic localities of Cernay and Berru remains to be demonstrated, and the study of the mammalian faunal composition has a high potential of resolving these relationships.

Fossil localities and material

The study of the mammal fauna from "Les Monts-Martin" is partly based on collections previously made by D. Delsate, M. Duchamplecheval and J.-L. Pellouin (approximately 100 identifiable mammal teeth). Attempts to locate the specimens constituting the basis of the original faunal list compiled by P. Louis have not been successful. Additional specimens come from excavations at Montchenot carried out by the Laboratoire d'Evolution des Primates (EPHE) with the support of A. Phélizon. A total of 320 kg of sediment were screen-washed in 2009, yielding about 40 identifiable mammal teeth. Further increases of the sample size are expected from ongoing sorting of the residue obtained by screen-washing of 670 kg of matrix in 2010.

Excavations at "Les-Monts-Martin" in 2009 and 2010 exposed the upper part of the section described by Laurain and Henry (1968) (Fig. 1). Yellow-grey argillaceous sands at the bottom of the exposed section correspond to Level D of Laurain and Henry (op. cit.). A marked indurated surface occurs near the upper end of this level, followed by about 45 cm of variegated marls becoming increasingly less sandy towards the top. Above these, approx. 45 cm of grey argillaceous marls represent Level E of Laurain and Henry. On top of these darker grey marls, about 50 cm of light grey marls rich in algal concretions are the equivalent of level F of Laurain and Henry. Sediments strongly altered by influences from the surface form the end of the exposed section. Most fossil mammals come from levels E and F of Laurain and Henry, which were also sampled most extensively, but fossils still occur further down in the section, including the top of level D.

A second fossiliferous locality has meanwhile been discovered at Montchenot in immediate vicinity of Les Monts-Martin, west of highway D951 which separates the two sites. Mammal specimens from this new locality have been collected by J.-L. Pellouin. Both localities appear to be closely similar in faunal content and show a comparable lithology. Fossils recovered from both sites are therefore considered as forming part of the Montchenot fauna. For clarity, the original locality Les Monts-Martin east of D951 is here referred to as Montchenot East, while the new

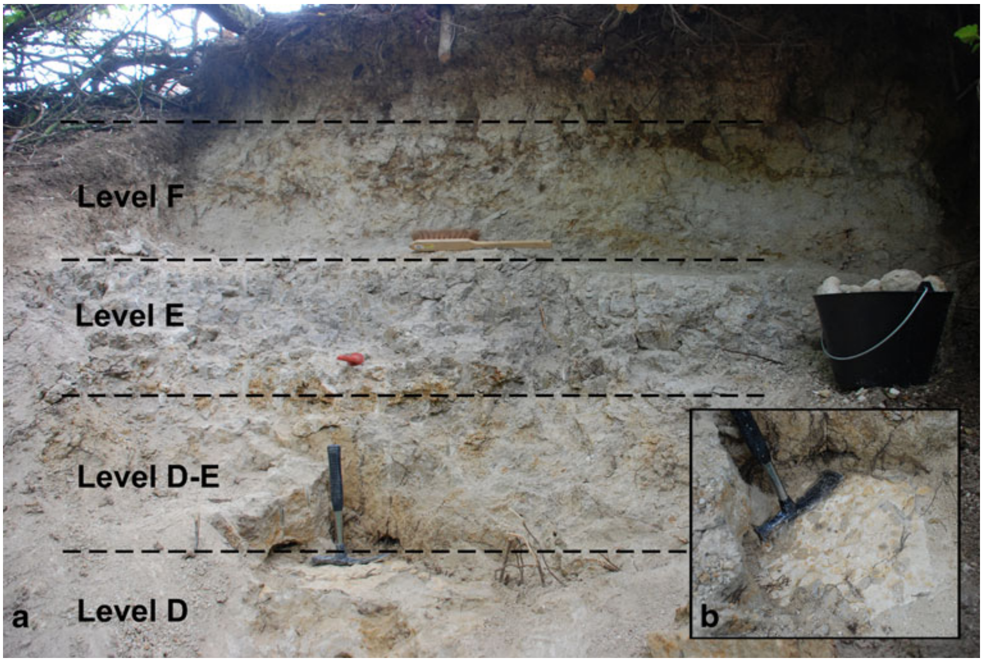


Fig. 1 **a** Section at Les Monts-Martin (Montchenot) during excavations in 2010, with nomenclature of Laurain and Henry (1968). *Level D* yellow-grey argillaceous sands. *Level D-E* (transition) variegated marls becoming increasingly sandy below. *Level E* grey argillaceous marls. *Level F* light grey marls rich in concretions (piled up in bucket). Length of hammer 30 cm. **b** Detail of indurated surface on top of level D. Photos A. Phélizon

locality west of D951 will be referred to as Montchenot West in this paper.

Almost all mammal specimens found at Montchenot are isolated teeth, mainly of micromammals. A maxillary with P^3–M^3 of a louisinine "condylarth" and a few other specimens with associated dental remains demonstrate the potential of these sites for delivering more complete fossil remains. More than 400 dental mammal specimens identifiable at least to genus level are currently available. Only few mammalian postcranial remains have been recovered up to now.

Catalogue numbers in this paper refer to specimens in the collections of the Muséum National d'Histoire Naturelle (MNHN), Paris, with the prefix MTC used for Montchenot, CR for Cernay-lès-Reims and BRL for Lentille de Berru.

Faunal composition

Small-sized mammals are dominating the assemblage (see Fig. 2 for examples), and none of the largest-sized species known from the Thanetian of the Paris Basin have been recovered up to now. A preliminary list of mammalian species from the combined Montchenot fauna is given in Table 1. Figure 3 shows the relative abundances of the different taxa at Montchenot East based on the total number of specimens; available mammal specimens from Montchenot West have only in part been studied up to now. Total sample size is not yet sufficient for allowing a meaningful evaluation in terms of minimum number of individuals. Since multituberculate teeth except P^4 and P_4 are not always unambiguously determinable to species, these specimens have been grouped as *Neoplagiaulax* sp. in this diagram.

Multituberculates form an abundant and diversified part of the Montchenot assemblage (Fig. 2a, b). At least 4 species of *Neoplagiaulax* ranging from the smallest (*N. sylvani*) to the largest one (*N. nicolai*) known from Cernay and Berru (Vianey-Liaud 1986) have been determined, with *N. nicolai* being the most frequent. In addition, the rare Cernaysian species *Cernaysia manueli* is also present. Although *Liotomus marshi* is among the few species from Montchenot listed by Laurain

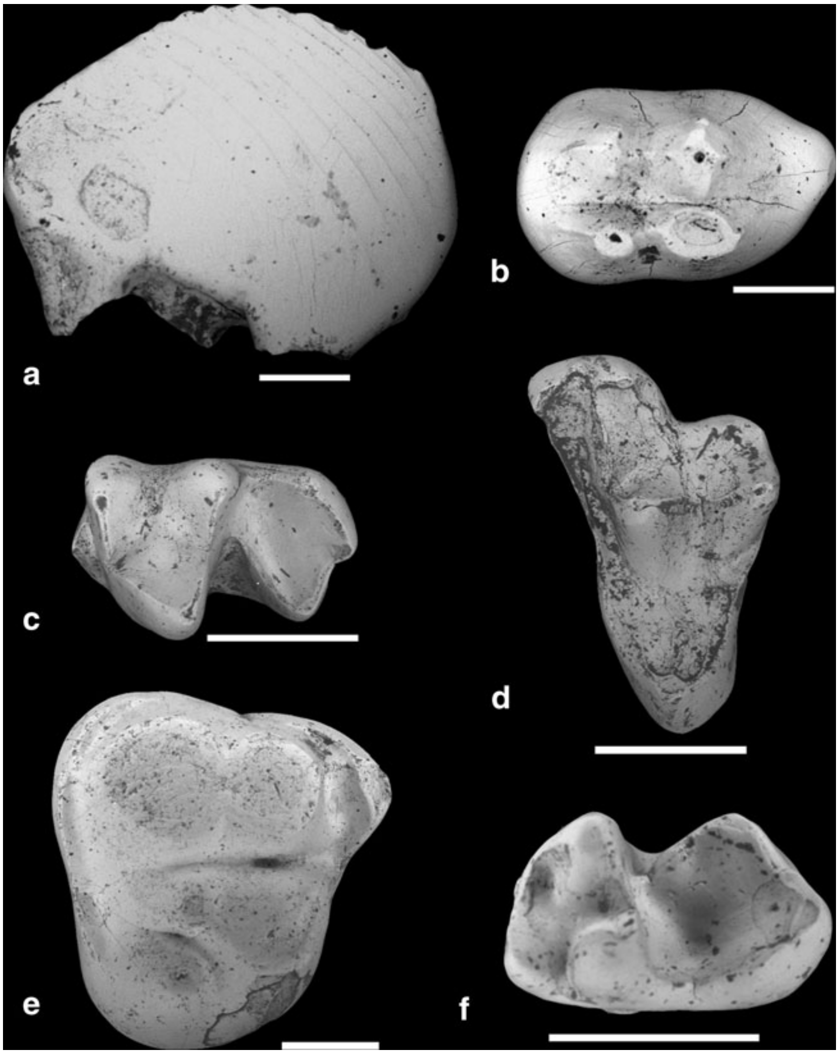


Fig. 2 SEM photographs of mammalian fossils from Montchenot. *Scale bar* 1 mm. **a** *Neoplagiaulax eocaenus*, right P_4, labial view (MNHN.F.MTC 33); **b** *Neoplagiaulax nicolai*, right P^3, occlusal view (MNHN.F.MTC 66); **c** cf. *Nosella* sp., left M_2, occlusal view (MNHN.F.MTC 29); **d** cf. *Nosella* sp., left M^3, occlusal view (MNHN.F.MTC 18); **e** *Gigarton meyeri*, right M^1, occlusal view (MNHN.F.MTC 114); **f** *Sarnacius gingerichi*, right M_3, occlusal view (MNHN.F.MTC 15). Specimens figured in (**c**), (**d**) and (**f**) collected by D. Delsate

Table 1 Preliminary combined faunal list of Montchenot East and West

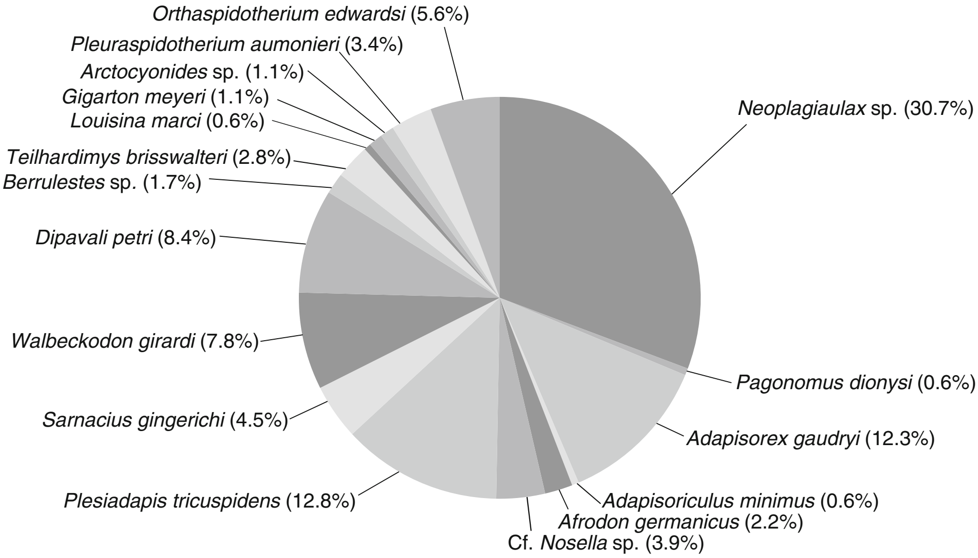
- Order Multituberculata
  - Family Neoplagiaulacidae
    - *Neoplagiaulax sylvani* Vianey-Liaud, 1986
    - *N. eocaenus* (Lemoine, 1880)
    - *N. copei* Lemoine, 1885
    - *N. nicolai* Vianey-Liaud, 1986
    - *Cernaysia manueli* Vianey-Liaud, 1986
- Order Pantolesta
  - Family inc. sed.
    - *Pagonomus dionysi* Russell, 1964
- Order Lipotyphla?
  - Family Erinaceidae?
    - *Adapisorex gaudryi* Lemoine, 1883
- Euarchonta?, order inc. sed.
  - Family Adapisoriculidae
    - *Adapisoriculus minimus* (Lemoine, 1883)
    - *Afrodon germanicus* (Russell, 1964)
    - Cf. *Nosella* sp. Peláez-Campomanes, 1999
- Order Plesiadapiformes
  - Family Plesiadapidae
    - *Plesiadapis tricuspidens* Gervais, 1877
  - Family Toliapinidae
    - *Sarnacius gingerichi* (Russell, 1981)
    - *Berruvius lasseroni* Russell, 1964
- "Condylarthra"
  - Family Apheliscidae, Subfamily Louisininae
    - *Walbeckodon girardi* Hooker and Russell, 2012
    - *Dipavali petri* (Russell, 1964)
    - *Berrulestes pellouini* Hooker and Russell, 2012
    - *B. phelizoni* Hooker and Russell, 2012
    - *Teilhardimys brisswalteri* Hooker and Russell, 2012
    - *Louisina marci* Hooker and Russell, 2012
    - *Gigarton meyeri* Hooker and Russell, 2012
  - Family Arctocyonidae
    - *Arctocyonides trouessarti* (Lemoine, 1891)
    - *A. arenae* Russell, 1964
  - Family Pleuraspidotheriidae
    - *Pleuraspidotherium aumonieri* Lemoine, 1878
    - *Orthaspidotherium edwardsi* Lemoine, 1885

and Meyer (1986) based on data of P. Louis, no unambiguous specimens of *Liotomus* have been identified in available collections from Montchenot (see below). Figure 4 shows relative abundances of the different species of multituberculates at Montchenot East and West based on P^4 and P_4 counts, the only dental elements which are unambiguously identifiable for all species of Cernaysian multituberculates.

Insectivore-like eutherians are also well represented at Montchenot, especially the abundant *Adapisorex gaudryi*, which has often been regarded as an erinaceomorph lipotyphlan (e.g. López-Martínez and Peláez-Campomanes 1999). A smaller possibly lipotyphlan form, also present at Cernay and tentatively assigned by Russell (1964) to *Adunator lehmani* Russell, 1964, but described by Hooker and Russell (2012) as a new species, *Walbeckodon girardi*, also regularly occurs. Comparisons of specimens from Montchenot with a cast of the type of *Adunator lehmani* from Walbeck confirm that there are significant differences in lower molar morphology and that a different species is represented in the Paris Basin. Hooker and Russell (op. cit.) include *Walbeckodon* in their concept of the Louisinidae, and they regard the latter, together with *Adapisorex* and probably *Adunator*, as stem members of the Macroscelidea.

Much rarer insectivore-like teeth from Montchenot are those of a comparatively large form, *Pagonomus dionysi*, belonging to the extinct order Pantolesta. In contrast, the smallest insectivore-like forms from Montchenot belong to the Adapisoriculidae, a family recently brought into the focus of research because of their possible relationships with plesiadapiforms (Storch 2008) or Euarchonta (Boyer et al. 2010; Smith et al. 2010). Among described species, at least *Afrodon germanicus* and *Adapisoriculus minimus* are present at Montchenot. Of particular interest are several specimens of an adapisoriculid first described as *Aboletylestes?* sp. Russell, 1964 on the basis of a single upper molar from the Lentille de Berru (MNHN.F.BRL 121; Russell et al. 1966). Szalay (1968) attributed this tooth to a possible apatemyid close to *Jepsenella* Simpson, 1940. Together with a second specimen from Cernay (MNHN.F.CR 11 Bn), the Berru specimen was subsequently assigned to *Nosella europaea* Peláez-Campomanes, 1999 (López-Martínez and Peláez-Campomanes 1999), a species of uncertain affinities based on material from the Thanetian of the Tremp Formation in the Spanish Pyrenees. The additional sample from Montchenot allows reconstitution of the complete upper molar series of this hitherto unrecognised adapisoriculid (Figs. 2d, 5a). It further includes lower molars of all positions suitable in size and morphology for assignment to this species (Figs. 2c, 5b), which are apparently conspecific with lower molars from Cernay described as Erinaceoidea gen. indet. by Russell et al. (1966). Teeth of this form closely resemble *Afrodon*, but $M^{1–2}$ can be distinguished from described species of this genus by a pronounced posterolingual cingulum. Like *Proremiculus lagnauxi*, an adapisoriculid described by de Bast et al. (2012) from the early Paleocene of Hainin (Belgium) and considered as sister taxon of *Remiculus* Russell, 1964 by these authors, the species from the Paris Basin combines a straight centrocrista with a distinct postcingulum and a weaker precingulum. It differs from the Hainin species in showing, among other differences, wider upper molars with deeper ectoflexus and lower molars with a narrower talonid.

Fig. 3 Relative abundances of mammalian taxa at Montchenot East based on the total number of specimens for each taxon. Total sample size $n=179$



Further comparisons will allow for evaluation of the species' identity with *Nosella europaea* and for determination of its systematic position within the Adapisoriculidae.

Among definitive plesiadapiforms, *Plesiadapis* is common at Montchenot but not as dominant as, e.g. at Cernay, where it accounts for about one-third of the mammal specimens (Russell et al. 1966). Available specimens indicate close similarity with *Plesiadapis tricuspidens*, the species also represented at Cernay and Berru. In addition, the tiny toliapinid plesiadapiform *Sarnacius gingerichi* is surprisingly well represented (Fig. 2f), and at least one tooth of the even smaller *Berruvius lasseroni* is known from Montchenot West. Additional collecting will show whether this unusual structure of the plesiadapiform component of the fauna can be confirmed for larger sample sizes.

As is typical of the European late Paleocene faunas, "condylarth" mammals are well represented at Montchenot. Small-sized Apheliscidae of the subfamily Louisininae[2] are the most common and diverse "condylarths" in this assemblage, especially if the insectivore-like *Walbeckodon girardi* is included here. Since the detailed revision of the group by Hooker and Russell (2012) was published only shortly before submission of this paper, taxonomic determinations presented here must be regarded as preliminary. Besides specimens of *Walbeckodon girardi, Berrulestes pellouini, B. phelizoni* and the particularly common *Dipavali petri* (which is even more frequent in the combined sample for Montchenot East and West than shown in Fig. 3), several specimens from Montchenot fall inside the large range of variation of teeth described by Russell (1964) as *Louisina mirabilis*. Hooker and Russell (op. cit.) have removed the majority of Russell's original specimens of *Louisina mirabilis* to different species or even genera. Among these, *Louisina marci* and *Teilhardimys brisswalteri* seem to be represented at Montchenot, including the most complete associated upper dentition of the latter species, a well-preserved maxillary with P^3–M^3 which first documents P^3 in this form. Relatively large, unusually bunodont teeth (Fig. 2e) belong to a louisinine first figured by Russell (1964, pl. XVI, fig. 5) and Russell et al. (1966, pl. XXI, fig. 4 left) and described as *Gigarton meyeri* by Hooker and Russell (op. cit.). Taxonomic determination of the remaining Louisininae from Montchenot may still further increase the group's diversity at this site.

Concerning the larger "condylarths", members of the Pleuraspidotheriidae (cf. Ladevèze et al. 2010) are much less common at Montchenot than at Cernay and Berru where they form a dominant part of the mammalian fauna. While the smaller *Orthaspidotherium* still occurs frequently, the larger *Pleuraspidotherium* is present but comparatively rare at Montchenot. Arctocyonids, most of which are likewise larger-sized, are documented by a few specimens representing the two Cernaysian species of *Arctocyonides, A. trouessarti* and *A. arenae*. It should be added that Laurain and Meyer (1986) cited the presence of *Arctocyon primaevus* at Montchenot following observations of P. Louis, but this large form has not yet been identified in collections available for study (more than 400 identifiable mammal specimens).

Other vertebrate fossils discovered to date include fish remains, urodeles and anurans, anguid and necrosaurid lizards (determination by J.-C. Rage), choristoderes and crocodiles.

---

[2] Following Zack et al. (2005), the Louisininae are here considered as members of the Apheliscidae. This family name has been revived for forms previously placed in the Hyopsodontidae excluding the type genus *Hyopsodus* Leidy, 1870. The latter seems in fact more closely related to forms traditionally considered as Mioclaenidae, which are now placed in the redefined Hyopsodontidae (ibid.). Hooker and Russell (2012) have raised the Louisininae to family rank and consider them, together with the Apheliscidae, as basal Macroscelidea. Evaluating these systematic changes is beyond the scope of this paper, and Louisininae are here retained as a subfamily within the "condylarth" family Apheliscidae.

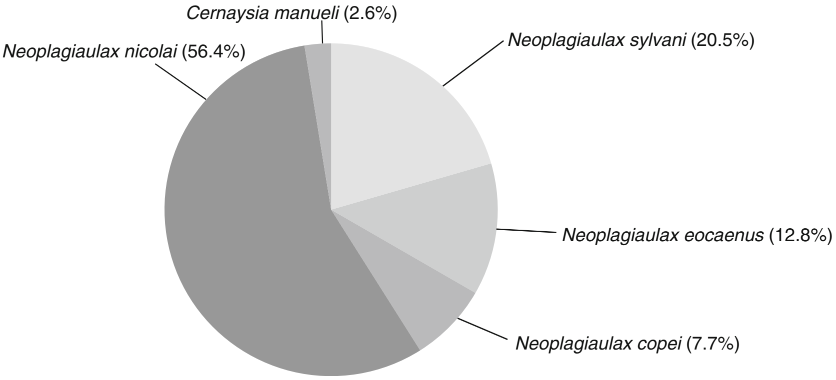


Fig. 4 Relative abundances of multituberculate species at Montchenot East and West based on total number of P^4 and P_4 specimens for each taxon. Total sample size $n=39$

Remarks on Cernaysian multituberculates

Study of the multituberculates from Montchenot also provides the opportunity to reassess previous hypotheses on Cernaysian members of the group. Eight species of multituberculates from Cernay and Berru have been established mainly on the basis of the diagnostic P^4 and P_4. Isolated molars as well as permanent and deciduous anterior upper premolars have been tentatively assigned to these species (Vianey-Liaud 1986). While no unambiguously diagnostic elements (P^4 or P_4) of *Liotomus marshi* and none of the P^{1-2} tentatively attributed to this species have been identified in the collections from Montchenot available for this study, isolated P^3s similar to those assigned to *L. marshi* by Vianey-Liaud (op. cit.) are common in the Montchenot fauna (Fig. 2b). These P^3s are here reinterpreted as belonging to *Neoplagiaulax nicolai*, the most common multituberculate species at Montchenot, and the species of Cernaysian multituberculates closest to *L. marshi* in size.

Fig. 5 Reconstructed upper and lower molar series of a new adapisoriculid (cf. *Nosella* sp.) from Montchenot in occulusal view. **a** Left M^{1-3}, M^1 MNHN.F.MTC 17, M^2 MNHN.F.MTC 91 (reversed), M^3 MNHN.F.MTC 18 (see also Fig. 2d); **b** left M_{1-3}, M_1 MNHN.F.MTC 30 (reversed), M_2 MNHN.F.MTC 29 (see also Fig. 2c), M_3 MNHN.F.MTC 22. Specimens MNHN.F.MTC 17, 18, 22, 29 and 30 collected by D. Delsate, MNHN.F.MTC 91 collected by J.-L. Pellouin. *Scale bar* 1 mm

This identification is also supported by morphological criteria (Fig. 6). Teeth identified as P^{1-2} of *L. marshi* by Vianey-Liaud (op. cit.) are characterised by little separated anterolabial and labial cusps and by a lower posterolingual cusp, even if the difference in height is less distinct on P^2. In contrast, P^{1-2} of *N. nicolai* have better separated anterolabial and labial cusps, and the posterolingual cusp is typically higher than these. Teeth previously interpreted as P^3 of *L. marshi* are consistent in morphology with P^{1-2} of *N. nicolai* in having better separated cusps in the labial row and higher cusps in the lingual row, especially the posterolingual cusp. It should be noted that the few isolated premolars previously identified as P^3 of *N. nicolai* are quadrate or triangular in occlusal shape (ibid.), unlike the more elongated P^3 of most other Cernaysian species of *Neoplagiaulax*, and may represent more anterior premolar positions. Teeth hitherto interpreted as P^2 of *L. marshi* (ibid.) show considerable variation in shape and may include P^3 of this species.

The recognition of characteristic traits in the anterior premolar morphology of *Liotomus* may also allow testing systematic questions. Vianey-Liaud (op. cit.) assigned several North American species of multituberculates [*Anconodon russelli* (Simpson, 1935), *Parectypodus sinclairi* (Simpson, 1935), and tentatively *Parectypodus vanvaleni* Sloan, 1981] to *Liotomus* based on morphology of P_4 / P^4 and inferred a North American origin of the genus with subsequent dispersal to Europe. If these systematic attributions are correct, appropriately sized anterior premolars of a morphotype similar to P^{1-2} of *Liotomus marshi* should co-occur with the diagnostic posterior premolars of the North American species assigned to *Liotomus*, a hypothesis which could be tested on the basis of adequate samples from localities delivering these species.

The abundance of *Neoplagiaulax nicolai* at Montchenot also provides the opportunity to identify its deciduous upper premolars, which are similar to those tentatively assigned to *N. nicolai* and *N. copei* by Vianey-Liaud (op. cit.) (Fig. 7), and to readdress the question of their orientation in the jaw. This issue has been problematic for isolated deciduous upper premolars of Late Cretaceous and Early Tertiary multituberculates (Krause 1977; Lillegraven 1969), and only a single relevant case of associated teeth has been described

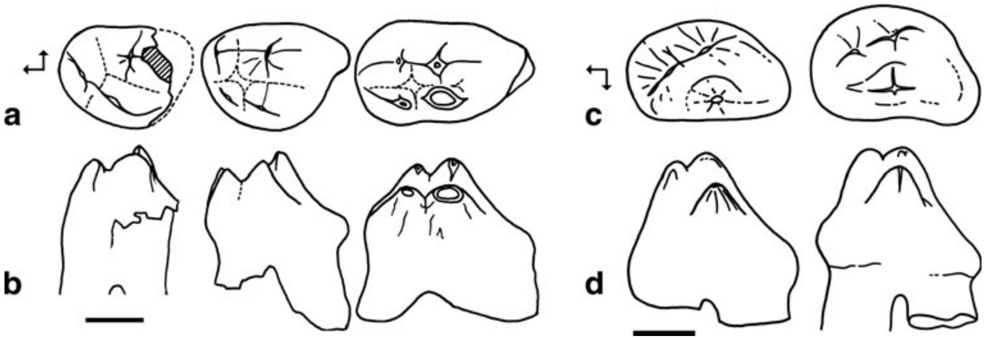


Fig. 6 Reconstructed upper anterior premolars of Cernaysian multituberculates, with *arrows* indicating anterior and lingual direction in occlusal view. **a**, **b** Right P$^{1-3}$ of *Neoplagiaulax nicolai* from Montchenot in occlusal and labial view, anterior towards left, showing low, well-separated labial cusps. P^1 MNHN.F.MTC 63 (reversed), P^2 MNHN.F.MTC 71, P^3 MNHN.F.MTC 66, all collected by D. Delsate; **c**, **d** Left P$^{1-2}$ of *Liotomus marshi* from Cernay in occlusal and lingual view, anterior towards left, showing high, little separated labial cusps. P^1 MNHN.F.CR 11918, P^2 MNHN.F.CR 14426, (both reversed) modified after Vianey-Liaud (1986). *Scale bar* 1 mm

for the cimolodontid *Cimolodon* sp. Marsh, 1889 (Szalay 1965). Nevertheless, detailed structural similarities between deciduous and permanent anterior premolars of *N. nicolai* allow inferences concerning tooth orientation. As already observed by Vianey-Liaud (op. cit.), deciduous premolars of Cernaysian neoplagiaulacids show one row of cusps with longitudinally oriented crests, like the labial cusps of permanent premolars, suggesting that this row is located on the labial side. Also, like the lingual row of permanent premolars, the second cusp row of deciduous premolars exhibits more strongly expressed transverse crests (ibid.). In addition, blades of cusps on the labial side of deciduous premolars are more obliquely oriented towards one end of the tooth, and a single transversely oriented cusp (sometimes doubled) exists in dP^3 at this end of the tooth. This pattern closely matches the increasingly transverse orientation of crests towards the front of P$^{1-3}$, indicating that the oblique labial crests and the median cusp in dP^3 occur towards the anterior side (unlike the dP^2 of *Cimolodon* sp. described by Szalay 1965, which shows a median cusp in the back of the tooth). Assuming this orientation, cusp height is increasing posteriorly in dP^2 and dP^3, like in P$^{2-3}$, and lingual cusps tend to be higher than labial ones in deciduous anterior premolars like in their permanent successors. This interpretation is consistent with that of Vianey-Liaud (op. cit.) but is in contrast with the proposal of Lillegraven (1969) who interprets the low median cusp of deciduous anterior premolars assigned to the early neoplagiaulacid *Mesodma* sp. Jepsen, 1940 as posterior. Excellently preserved associated dentitions of North American species of *Neoplagiaulax* have recently been described (Scott 2005), and fossils preserving deciduous teeth in place may ultimately become available for testing the proposed tooth orientations.

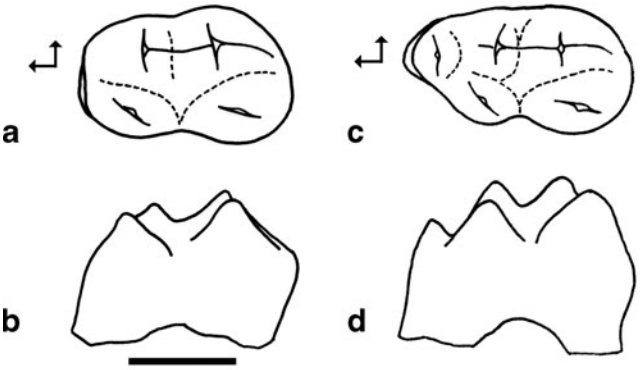


Fig. 7 Deciduous right upper premolars of *Neoplagiaulax nicolai* from Montchenot, with *arrows* indicating anterior and lingual direction in occlusal view. **a**, **b** dP^2 MNHN.F.MTC 62 in occlusal and labial view. **c**, **d** dP^3 MNHN.F.MTC 75 (reversed) in occlusal and labial view. All specimens collected by D. Delsate. *Scale bar* 1 mm

Taphonomy and palaeoenvironment

Fossil mammal teeth from Montchenot are apparently easily broken, but otherwise are often well preserved, with no or little signs of abrasion by postmortem transport. Different stages of chemical alteration or removal of enamel (and in some cases also dentine) are frequent, however. While some of these cases can be explained by factors like metabolic activities of plants, other teeth showing extensive to complete loss of enamel, or areas of massive chemical erosion of enamel and dentine, are apparently the result of digestion by predators (cf. Andrews 1990; López-Martínez and Peláez-Campomanes 1999). Accumulation of micromammal remains by predators may therefore have been an important factor at Montchenot, as has been proposed for the formation of microvertebrate concentrations in general (Mellett 1974). Digestion of bone by predators may also explain the unusual rarity of mammalian postcranial remains at Montchenot.

In another Paleocene micromammal fauna, the Shotgun local fauna from Wyoming, loss of enamel without visible erosion of dentine has been linked to digestion by crocodiles on the basis of investigations on preservation and histology of tooth tissues, together with the results of feeding experiments with living crocodilians (Fisher 1981). Although no such detailed analysis has been carried out in the case of Montchenot, this is at least a plausible possibility for similarly preserved teeth from this locality. Interestingly, Fisher (op. cit.) described a state of preservation in the Shotgun specimens in which patches of enamel only remain where adjacent teeth were once in contact, presumably due to restricted circulation of the digestive fluids when these teeth were still located in the jaw. Such interdental patches of enamel have also been observed on the anterior and posterior end of an otherwise enamel-less lower molar of *Walbeckodon girardi* (MNHN.F.MTC 155) from Montchenot.

Deciduous teeth are common at Montchenot, especially those of the larger species. Of the collected specimens of *Plesiadapis*, 14 % are deciduous teeth, and the corresponding fraction among pleuraspidotheriid specimens is about 20 %. In both cases, deciduous teeth occur more frequently at Montchenot than in a sample of mammalian teeth from the Conglomérat de Cernay (collection D. Delsate). As in permanent teeth, some of the deciduous teeth from Montchenot show alteration or destruction of enamel and sometimes also dentine.[3]

While various stages of dental wear are represented by mammal specimens from Montchenot, unworn or little worn teeth are common. Together with the high proportion of deciduous teeth, this seems to indicate preferred preservation of teeth from young individuals, which are especially prone to predation. It should be added that a number of teeth from Montchenot show almost exaggerated sharpness of cusps and crests, without any evidence of wear. Enamel in these fossils is unusually thin and shows little brilliance. These specimens apparently represent tooth germs still in development in the jaws at the time of death of the animal.

Predation produces death assemblages that are highly selective (Andrews 1990) and may thus, at least in part, be responsible for differences in faunal composition between Montchenot and other Cernaysian mammal localities near Reims. Other possible explanations of these differences are hydrodynamic sorting leading to preferred preservation of micromammal remains, or differences in the original faunal composition due to a different environmental setting. While the Conglomérat de Cernay has been described as a fluvial–deltaic deposit and the Berru deposits as fluviatile (Laurain et al. 1981, Laurain and Meyer 1986), sediments at Montchenot have been interpreted as deposited in a calm, yet not completely stagnant, freshwater milieu (Laurain and Henry 1968). Such an environment can also be deduced from the characteristic algal concretions frequently occurring at Montchenot, since regular formation of layers around all sides of the encrusted object requires a certain limited amount of water current (ibid.). Freytet et al. (2001), who describe in detail the algal concretions from Montchenot, interpret them to have formed "… in a relatively quiet environment, probably a pond behind a dune belt … where the slow movement of waves on the shorelines induced the regular turning over of the oncolithes" (p. 7). The molluscs and charophytes preserved in the Marnes de Montchenot also support a quiet freshwater milieu and are suggestive of coastal marshes (Laurain et al. 1981). Such an environment may have sheltered a mammalian fauna different in composition from that of Cernay or Berru, an idea already expressed by Russell et al. (1966) for the Marnes de Rilly (see below).

Even if final deposition of sediments at Montchenot occurred under low energy conditions, hydrodynamic sorting before deposition cannot be ruled out as another factor contributing to the peculiar composition of the Montchenot fauna, and in particular to the abundance of micromammals and absence of large-sized forms. Yet hydraulic sorting cannot adequately explain all aspects of the particular composition of the Montchenot fauna. *Neoplagiaulax nicolai* is abundant at Montchenot even if it is the largest species of Cernaysian multituberculates except *Liotomus marshi*, whereas it is apparently only a moderately common species at Cernay and Berru based on specimen lists in Vianey-Liaud (1986). If hydraulic sorting alone was responsible for the particular composition of the Montchenot fauna, small-sized tooth elements of *N. nicolai* like its upper anterior premolars would be expected to be more common than large elements like P_4, a tooth significantly larger than most mammal teeth from Montchenot. However, teeth of *N. nicolai* are dominating among multituberculates in tooth categories of different sizes, from upper anterior premolars to P_4. This indicates a biological reason (abundance in the original fauna or selective predation) for at least this aspect of the Montchenot fossil assemblage.

Biochronological results and conclusions

The fossil mammals recovered from the Marnes de Montchenot appear very close to those of Cernay (European mammalian reference level MP6). All mammal species identified up to now (including the adapisoriculid cf. *Nosella* sp.) are also known from Cernay, and the majority of these also occur at the Lentille de Berru, a deposit similar to the Conglomérat de Cernay in several regards (Russell et al. 1966). The number of species in common with the main

---

[3] Andrews (1990) found the proportion of mammalian molars showing signs of digestion in pellets of different birds of prey and scat of different mammalian predators to vary strongly with the predator species (between 0 % and close to 100 % for avian predators). In almost all cases, a significant part of ingested molars had no visible signs of digestion. Absence of evidence for digestion in individual fossil teeth can thus not be interpreted as evidence against these teeth having been ingested by a predator.

fauna from Berru (bed 5 in Hooker and Russell 2012 and Laurain and Meyer 1986) is lower, apparently because micromammals are less well known from this fauna. Resemblance of the Montchenot mammal fauna to Cernay, Lentille de Berru and the Berru main fauna clearly confirms the Late Thanetian age previously determined on the basis of molluscs (Laurain and Henry 1968) and charophytes (Riveline 1976).

López-Martínez and Peláez-Campomanes (1999) have proposed renaming MP6 into MP6a and insertion of a new level, MP6b, with Claret 4 from the Spanish Pyrenees as reference locality. According to these authors, MP6b is characterised by the first appearance of the otherwise typically Eocene taxa *Paschatherium* cf. *dolloi* (Teilhard de Chardin, 1927) (*P. yvettae* Gheerbrant et al., 1997 in López-Martínez et al. 2006) and *Microhyus* cf. *musculus* Teilhard de Chardin, 1927 (*Teilhardimys musculus* in Hooker and Russell 2012) as well as by abundance of *Paschatherium* cf. *dolloi* (similar to several Neustrian localities). Absence of typically Eocene taxa and missing abundance of *Paschatherium* (if present at all) might support reference of Montchenot to level MP6a in the biochronological proposal of López-Martínez and Peláez-Campomanes (1999). Except for the possible common occurrence of *Nosella europaea* and ubiquitous Cernaysian mammals (*Adapisorex* sp., cf. *Pleuraspidotherium* sp.), no species are shared between Montchenot and the still poorly known fauna from Claret 4.

The Montchenot fauna differs from the faunas of Cernay and Berru mainly in being dominated by small mammal species, with less common occurrence of *Plesiadapis* and pleuraspidotheriid "condylarths". Also, the largest members of the MP6 fauna, the mesonychian *Dissacus* Cope, 1881 and the "condylarths" *Tricuspiodon* Lemoine, 1885 and *Arctocyon,* are not present in available collections from Montchenot, although the presence of the latter genus at Montchenot has been observed by P. Louis (Laurain and Meyer 1986). In these respects, the Montchenot fauna resembles the small collection of Thanetian mammals from the Marnes de Rilly (3 km east of Montchenot) briefly described by Russell et al. (1966), apparently a close stratigraphic correlative (Laurain et al. 1981; Laurain and Meyer 1986). In fact, patterns of abundance mentioned above match closely those described by Russell et al. (op. cit.) for the Marnes de Rilly, and with the exception of *Liotomus marshi*, all nine mammal species documented for the latter fauna are well represented at Montchenot.[4] As discussed above, the composition of the Montchenot fossil assemblage may be the combined result of palaeoenvironmental conditions leading to a peculiar faunal structure and of taphonomic biases, including selective predation, for which there is direct evidence, and hydrodynamic sorting.

Even if interpretations of the Montchenot fauna must take into account these possible biases, the mammal fauna from Montchenot provides the opportunity to improve our knowledge of the small mammals existing in Europe before the large-scale faunal exchanges linked to the advent of the Eocene, and possibly to gain insight into a hitherto rarely sampled habitat. Further study of the new fauna, based on increased sample sizes, may allow for its more detailed placement in the succession of fossil localities in the Paris Basin close to the Paleocene–Eocene boundary.

Acknowledgements The authors thank M. Laurain for helpful discussions of local geology, M. Duchamplecheval, E. Herbomel (EPHE) and several residents of Villers-Allerand for support during excavations at Montchenot. The Marguet Champagne (B. Marguet) provided a washing and screening site in Ambonnay. E. Zoukouba (EPHE) and the staff of the Musée national d'Histoire naturelle de Luxembourg helped in sorting residue. J.-C. Rage kindly provided first determinations for the herpetofauna of Montchenot. M. Vianey-Liaud and E. Gheerbrant provided helpful comments for improving this paper.

References

Andrews P (1990) Owls, caves and fossils. Natural History Museum, London

Bast E de, Sigé B, Smith T (2012) Diversity of the adapisoriculid mammals from the early Paleocene of Hainin, Belgium. Acta Paleontol Pol 57:35–52

Boyer DM, Prasad GVR, Krause DW, Godinot M, Goswami A, Verma O, Flynn JJ (2010) New postcrania of *Deccanolestes* from the Late Cretaceous of India and their bearing on the evolutionary and biogeographic history of euarchontan mammals. Naturwissenschaften 97:365–377

Fisher DC (1981) Taphonomic interpretation of enamel-less teeth in the Shotgun local fauna (Paleocene, Wyoming). Contrib Mus Paleontol Univ Mich 25:259–275

Freytet P, Duringer P, Koeniguer J, Lablanche G, Laurain M, Pons D (2001) Distribution and paleoecology of freshwater algae and stromatolithes: IV, some examples from the Tertiary of the Paris Basin and the Alsace Graben (France). Ann Paleontol 87:143–205

Hooker JJ (1998) Mammalian faunal change across the Paleocene-Eocene transition in Europe. In: Aubry M, Lucas SG, Berggren WA (eds) Late Paleocene-early Eocene climatic and biotic events in the marine and terrestrial records. Columbia University Press, New York, pp 428–450

Hooker JJ, Millbank C (2001) A Cernaysian mammal from the Upnor Formation (Late Paleocene, Herne Bay, UK) and its implications for correlation. Proc Geolog Assoc 112:331–338

Hooker JJ, Russell DE (2012) Early Palaeogene Louisinidae (Macroscelidea, Mammalia), their relationships and north European diversity. Zool J Linn Soc 164:856–936

Krause DW (1977) Paleocene multituberculates (Mammalia) of the Roche Percée local fauna, Ravenscrag Formation, Saskatchewan, Canada. Palaeontograph Abt A 159:1–36

Ladevèze S, Missiaen P, Smith T (2010) First skull of *Orthaspidotherium edwardsi* (Mammalia, "Condylarthra") from the Late

---

[4] Based on the faunal list of Russell et al. (1966), mammals known from the Marnes de Rilly include *Neoplagiaulax eocaenus*, *N. copei*, *N. nicolai* [=*Neoplagiaulax* sp. A (ibid.)], *Liotomus marshi, Walbeckodon girardi* [=*Adunator lehmani?* (ibid.)], *Adapisorex gaudryi, Plesiadapis tricuspidens, Dipavali petri* and *Orthaspidotherium edwardsi*.

Paleocene of Berru (France) and phylogenetic affinities of the enigmatic European family Pleuraspidotheriidae. J Vertebr Paleontol 30:1559–1578

Laurain M, Meyer R (1986) Stratigraphie et paléogéographie de la base du Paléogène champenois. Geolog Fr 1986:103–123

Laurain M, Henry P (1968) Montchenot: Gisement accessible de la faune thanétienne du calcaire lacustre de Rilly. Ann Univ ARERS Reims 6:127–132

Laurain M, Guérin H, Barta L, Montciardini C, Neiss R (1981) Carte géologique à 1/50 000, feuille de Reims, no. 132. Bureau de Recherches Géologiques et Minières, Orléans

Lillegraven JA (1969) Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. University of Kansas paleontological contributions 50

López-Martínez N, Smith R, Peláez-Campomanes P, Smith T (2006) The acme of the micromammal *Paschatherium* across the Paleocene-Eocene boundary in continental Europe. Micropaleontology 52:267–280

López-Martínez N, Peláez-Campomanes P (1999) New mammals from south-central Pyrenees (Tremp Formation, Spain) and their bearing on late Paleocene marine-continental correlations. Bull Soc Geol Fr 170:681–696

Louis P (1996) Recherches de mammifères paléogènes dans les départements de l'Aisne et de la Marne pendant la deuxième moitié du vingtième siècle. Palaeovertebrata 25:83–113

Mellett JS (1974) Scatological origins of microvertebrate fossil accumulations. Science 185:349–350

Riveline J (1976) Étude floristique des niveaux marneux de la carrière de Montchenot (Marne). Mise en évidence d'une nouvelle association de Characées d'âge thanétien. C R Acad Sci Paris ser D 283:25–28

Russell DE (1964) Les mammifères paléocènes d'Europe. Mém Mus Natl Hist Nat ser C 13:1–324

Russell DE, Louis P, Poirier M (1966) Gisements nouveaux de la faune cernaysienne (Mammifères paléocènes de France). Bull Soc Geol Fr 7e ser 7:845–856

Scott CS (2005) New neoplagiaulacid multituberculates (Mammalia: Allotheria) from the Paleocene of Alberta, Canada. J Paleontol 79:1189–1213

Smith T, de Bast E, Sigé B (2010) Euarchontan affinity of Paleocene Afro-European adapisoriculid mammals and their origin in the Late Cretaceous Deccan Traps of India. Naturwissenschaften 97:417–422

Storch GD (2008) Skeletal remains of a diminutive primate from the Paleocene of Germany. Naturwissenschaften 95:927–930

Szalay FS (1965) First evidence of tooth replacement in the subclass Allotheria (Mammalia). Am Mus Novit 2226:1–12

Szalay FS (1968) Origins of the Apatemyidae (Mammalia, Insectivora). Am Mus Novit 2352:1–11

Vianey-Liaud M (1986) Les multituberculés thanétiens de France, et leurs rapports avec les multituberculés nord-américains. Palaeontograph Abt A 191:85–171

Zack SP, Penkrot TA, Krause DW, Maas MC (2005) A new apheliscine "condylarth" mammal from the late Paleocene of Montana and Alberta and phylogeny of "hyopsodontids". Acta Paleontol Pol 50:809–830