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ARTICLE

Enigmatic rodents from Lavergne, a late middle Eocene (MP 16) fissure-filling of the Quercy Phosphorites (Southwest France)

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Abstract: Two somewhat "odd" taxa of theridomyid rodents, one formerly known (*Bernardia marandati* Vianey-Liaud, 1991) and the other new (*Idicia vidalenci* gen. et sp. nov.) are discussed from a taxonomical and taphonomical perspectives. These two rodents were found at Lavergne, a late middle Eocene (MP16) "*phosphatière*" from the Quercy (Southwest France). The genus *Bernardia*, being preoccupied by a scale insect (*Bernardia* Ashmead, 1881), is here renamed *Burgia*. We benefit from this nomenclatural change to describe additional new dental specimens of this patriotheridomyine species, including a previously undescribed locus (P4). The other theridomyid from Lavergne, *Idicia vidalenci* gen. et sp. nov., so far documented by a mandible preserving two teeth (m2-m3) is a new taxon of peculiar occlusal morphology, and whose subfamilial affinities remain unknown. These two peculiar theridomyids recorded at Lavergne are found nowhere else, whether in coeval localities in Quercy or elsewhere in Western Europe. We discuss the possible causes of their unique presence at Lavergne.

Keywords: Rodentia, Theridomyidae, late Bartonian, diversity, taxonomy.

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INTRODUCTION

The rich fossil-bearing locality of Lavergne (Quercy, Southwest France) yielded 52 species of mammals (Table 1), which allowed establishing a relative biochronological age estimate: Bartonian (MP 16; e.g., Crochet *et al*., 1981; Remy *et al*., 1987). Despite the richness and taxonomic interest of this locality, little material has been studied and published to date. Of the ten species of rodents recognised, most (eight species) are members of the Theridomyoidea. This Bartonian site is particularly attracting because it documents odd taxa, otherwise unknown in the rich subcontemporaneous or coeval deposits from the Quercy and other localities in Western Europe. Among them, a species showing a singular morphology and a very strong degree of hypsodonty of the crown, was described as a new genus and new species (*Bernardia marandati* Vianey-Liaud, 1991). However, it turns out that the genus name of this taxon needs to be changed as the name *Bernardia* is preoccupied by Ashmead (1891) (Insecta, Hemiptera, Coccidae) (Christian Kammener's personal communication). This alpha taxonomy issue about this strange rodent from Lavergne has been raised because another *Bernardia* has just been named for a Brazilian tangle-veined fly (Pujol-Luz and Lamas, 2023a). The latter has already been renamed recently (Pujol-Luz and Lamas, 2023b). The purpose of this paper is to change the name of this theridomyid rodent and to describe three additional isolated teeth of that rodent, recently recovered at Lavergne, and that document one previously undescribed dental locus. We also take this opportunity to describe another enigmatic rodent from Lavergne, based on a new mandible fragment preserving a portion of incisor and m2-m3, the morphology of the latter is also unusual.

MATERIAL AND METHODS

Fossil recovery and extraction. A large amount of sediment from the Lavergne fossil-bearing locality has been washed and sieved over several decades. This was the work of various teams of palaeontologists, including some amateurs, until the site was protected in the framework of the "*Réserve naturelle nationale d'intérêt géologique du département du Lot*", then more recently, in the framework of the "*Causses du Quercy* UNESCO Global Geopark" for the "*Phosphatières*". The fossil-yielding sediments at Lavergne are largely the result of phosphate mining over the nineteenth century. These sediments were deposited away from the fissure filling, but nevertheless near to its opening. Most of the first specimens of "*Bernardia*" (here *Burgia* gen. nov.) were found by teams from the University-CNRS during the end of the twentieth century, among hundreds of rodent teeth collected at Lavergne. In contrast, the new specimens of this taxon, as well as the mandible of the new genus we described here, were found by Dominique Vidalenc, after several years of sediment processing, and hundreds of mammalian specimens found. His collection was recently donated to the *Université de Montpellier*.

Fossil repository. The fossil material described in this paper is permanently housed in the palaeontological collections of the *Université de Montpellier* (UM), *Laboratoire de Paléontologie, Institut des Sciences de l'Évolution de Montpellier* (ISE-M), France.

Nomenclature, dental loci and measurements. The terminology for the rodent dentition (Fig. 1) follows Vianey-Liaud and Schmid (2009) (see also Vianey-Liaud and Marivaux, 2017, 2021; Marivaux and Boivin, 2019). Upper-case letters are used for the upper dentition (P, for premolar; M, for molar) and lower-case letters for the lower dentition (p, for premolar; m, for molar). Teeth were measured (maximum mesiodistal length [MDL], maximum buccolingual width [BLW], and maximum crown height [H]; Fig. 1) using a measuroscope (Nikon 10), coupled with a digital counter (CM-6S). Measurement values are expressed in millimetres (mm) in the following text.

Drawings. The line drawings of the specimens presented in this work (Fig. 2D, G, I, K, M) were made by hand (MV-L) using a stereomicroscope (Leica MZ8), coupled with a camera lucida (Wild 308/00).

Optical photography. Some of the tooth pictures (Fig. 2A–C, E–F, J, H, L and Fig. 3H) are photographs of original specimens. These views are the result of the fusion of multifocus images obtained with an optical stereomicroscope (Leica M205 C) connected to a digital camera (Leica DFC420 C).

High-resolution µCT scan. The three-dimensional (3D) data presented in this work (Fig. 3A–G) were produced through the technical facilities of the Montpellier RIO Imaging (ISE-M, Montpellier, France). We used X-ray microtomography (µCT scan) for obtaining a 3D digital model (3D surface rendering) of the fossil mandible (UM-LAV 1700). The specimen was scanned with a resolution of 7 µm using a µCT-scanning station EasyTom 150 / Rx Solutions. The elements of the mandible (enamel of the tooth crowns and the tooth roots, as well as the bone structure of the dentary) were virtually delimited by manual segmentation under AVIZO 2020.2 (Visualization Sciences Group). The specimen was prepared within a “Label Field” module of AVIZO, using the segmentation threshold selection tool.

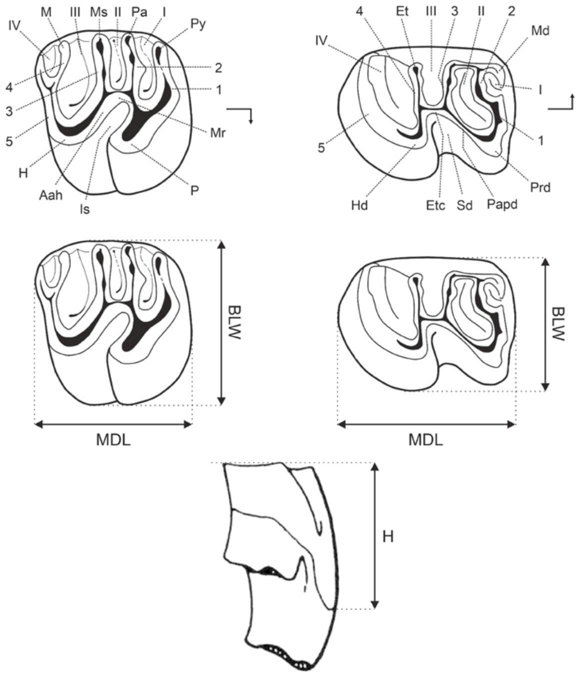

Figure 1. Dental nomenclature used for the Theridomyidae, with indication of the linear measurements taken (after Vianey-Liaud and Schmid, 2009; Vianey-Liaud and Marivaux, 2017, 2021; Marivaux and Boivin, 2019). **Nomenclature abbreviations - A, Upper teeth**: **1–5**, anticlines (A); **A1**, anteroloph (or anterocingulum); **A2**, protoloph; **A3**, mesoloph (and/or mesolophule); **A4**, metaloph; **A5**, posteroloph (or posterocingulum); **I–IV**, synclines (S); **SI**, paraflexus; **SII**, mesial mesoflexus; **SIII**, distal mesoflexus; **SIV**, posteroflexus; **Aah**, anterior arm of the hypocone; **H**, hypocone; **M**, metacone; **Mr**, mure; **Ms**, mesostyle; **P**, protocone; **Pa**, paracone; **Py**, parastyle; **Is**, internal sinus (or hypoflexus). **B, Lower teeth**: **1–5**, anticlinids (a); **a1**, anterolophid (or anterocingulid); **a2**, metalophulid II (lingual); **a3**, mesolophid; **a4**, entolophid (and/or hypolophid); **a5**, posterolophid; **I–IV**, synclinids (s); **sI**, anteroflexid (or paraflexid); **sII**, mesial mesoflexid; **sIII**, distal mesoflexid; **sIV**, metaflexid; **Et**, entoconid; **Etc**, ectolophid; **Hd**, hypoconid; **Md**, Metaconid; **Papd**, posterior arm of the protoconid (or postprotocristid); **Prd**, protoconid; **Sd**, sinusid (or hypoflexid). **Measurement abbreviations: MDL**, maximum mesiodistal length; **BLW**, maximum buccolingual width; **H**, maximum crown height. The black arrows indicate the tooth orientation on the jaw (i.e., mesiolingual).

Abbreviations. LAV, Lavergne; MP, (European) Mammal Palaeogene; UM, *Université de Montpellier*.

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Order RODENTIA Bowdich, 1821

Suborder ISCHYROMYIFORMES Marivaux, Vianey-Liaud and Jaeger, 2004

Infraorder THERIDOMORPHA Lavocat, 1955

Family THERIDOMYIDAE Alston, 1876

Subfamily PATRIOTHERIDOMYINAE Vianey-Liaud and Marivaux, 2017

Genus ***Burgia*** gen. nov. = *Bernardia* Vianey-Liaud, 1991 (*nec* Ashmead 1891; *nec* Pujol-Luz and Lamas, 2023).

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Derivatio nominis. From Pierre Burg, who was the mayor of the village of Bach for several decades, and who has always helped palaeontologists with their research in the phosphorite fissure-fillings (« *phosphatières* »).

Type and only known species. *Burgia marandati* comb. nov. (= *Bernardia marandati* Vianey-Liaud, 1991).

Diagnosis. As that of the type species (by monotypy).

Burgia marandati Vianey-Liaud, 1991, comb. nov.

Figure 2

Holotype. UM-LAV 1501, a left m1 or 2 (Fig. 2A–B). See also Vianey-Liaud (1991, fig. 1a).

Type locality and age. Lavergne (Quercy) MP 16, late middle Eocene (Bartonian; Crochet *et al*., 1981; Remy *et al*., 1987).

Emended Diagnosis. Middle sized Theridomyidae, strongly semi-hypsodont; lower teeth tetralophodont with mesolophid complete or incomplete, absence of hypoconulid on the posterolophid; tetralophodont to pentalophodont upper teeth; longitudinal crest absent either on upper (mure) and lower (ectolophid) teeth: deep transverse communication between the sinus with the opposite syncline (SIII) on upper teeth, as well as between the sinusid and the opposite synclinid (sIII) on lower teeth (i.e., internal sinus and sinusid remaining transversely/buccolingually open, respectively); P4 larger than M1-2.

New material and measurements. UM-LAV 1510, a slightly worn right P4 (Fig. 2F–I; MDL × BLW × H: 2.56 × 2.93 × 2.93), UM-LAV 1509 a pristine left M1 or 2 (Fig. 2J–M; 2.31 × 2.18 × 3.59), UM-LAV 1512 a right m1 or 2 (Fig. 2C–E; 2.42 × 1.97 × 3.00).

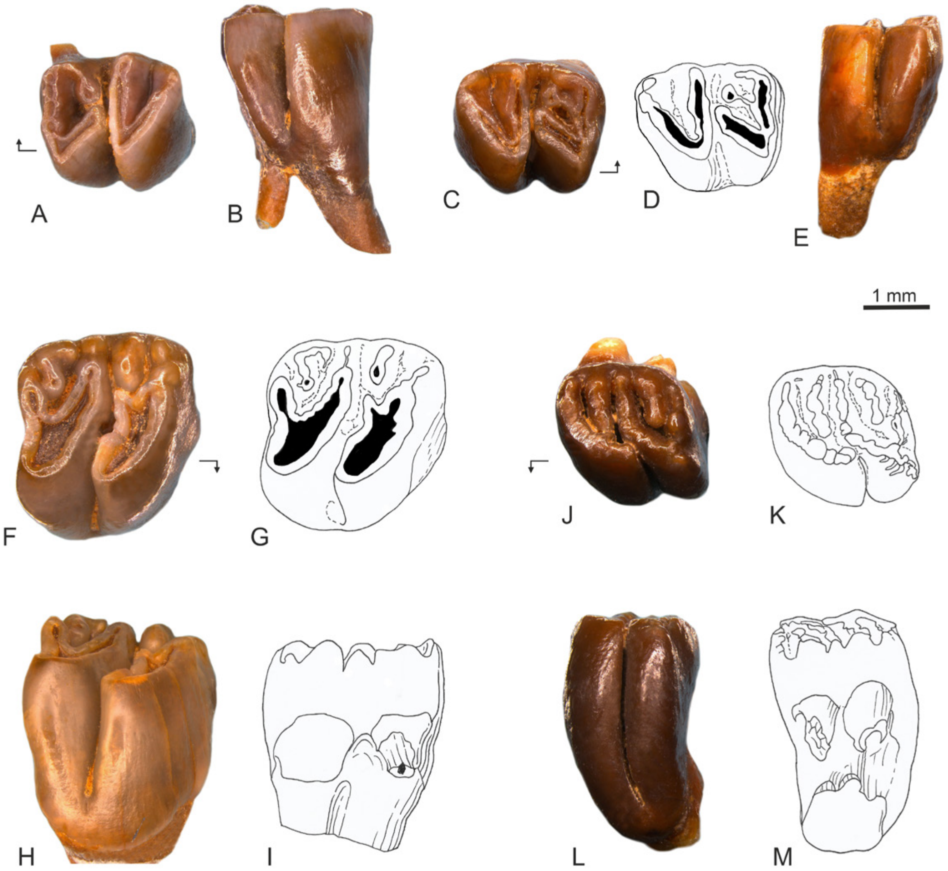

Figure 2. ***Burgia marandati*** Vianey-Liaud, 1991, comb. nov. **A−B**, UM-LAV 1501, left m1 or 2 (Holotype, Vianey-Liaud, 1991, fig. 1a) in occlusal (A) and buccal (B) views; **C−E**, UM-LAV 1512, right m1 or 2 in occlusal (C−D) and buccal (E) views; **F−I**, UM-LAV 1510, right P4 in occlusal (F−G), lingual (H), and buccal (I) views; **J−M**, UM-LAV 1509, left M1 or 2 in occlusal (J−K), lingual (L), and buccal (M) views. Images A-C, E-F, H, J and L are the result of the fusion of multifocus images obtained with an optical stereomicroscope connected to a digital camera. Line drawings D, G, I, K and M were made by hand (MV-L) using a stereomicroscope coupled with a camera lucida. The black arrow next to each specimen indicates the tooth orientation on the jaw (i.e., mesiolingual).

Description

The upper P4, unknown until now, is longer than M1 and M2 (see Vianey-Liaud, 1991), but displays a similar pattern then these molars (Fig. 2F−I) characterized by primers for syncline IV (SIV) and anticline 4 (A4), a short SV, the A3 (mesoloph) and A6 (posteroloph) connected to the hypocone, and internal sinus confluent with SII (i.e., there is no mure, and the internal sinus remains buccolingually open). We interpret this UM-LAV 1510 tooth as a P4 rather than a DP4, because its crown is particularly high, whereas in hypsodont theridomyids, the DP4 has a crown that is significantly lower than on premolars and molars. The pristine M1 or 2 (Fig. 2J−M) has four synclines and five anticlines, the tops of these unworn ridges are not smooth, but mammellated due to the granules that make them up, from which a few crestules can be seen on the internal aspect of the hypocone. As for P4, the SII and the internal sinus are confluent on upper teeth (i.e., there is no mure, and the internal sinus remains buccolingually open), a confluence which is also observed on the lower molars (at least m1 and m2) between sIII and the sinusid. On the UM-LAV 1512 m1 or 2 (Fig. 2C−E), a small cuspid fills the sII. This cuspid is connected distomesially to the first anticlinid (a1). The other features are like those of the previously described lower molars (see Vianey-Liaud, 1991). Notably on upper molars, the SI is short whereas the stretched protocone is long, in the continuation of the anteroloph. Lingually, the internal sinus is confluent with the SII, due to the absence of a central longitudinal crest (i.e., mure). The stretched hypocone, connected to the mesoloph (A3), joins a bulged mesostyle. The syncline SIV is very short, delimited by a short metaloph (A4) and the posteroloph (A5), which is broken in its lingual region. On the worn LAV 1508 M1 or 2, a structural elevation is distinct at the confluence between the internal sinus and the mesosyncline (SII). This elevation could correspond to a very low mure. The lower molars display two small mesial roots and one strong distal root. On the weakly worn lower molars, there is no indication of an anteroconid or a sI: the mesialmost synclinid is the sII, limited mesially by the metalophid. It is limited lingually by a postmetaconid cristid (posterior arm of the metaconid). The central anticlinid (a3) is a mesolophid, which displays a median angle and often bears an enamel swelling (cuspid-like structure).

Subfamily indet.

Genus ***Idicia*** gen. nov.

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Derivatio nominis. From the Latin « *idic* » that means particular, special.

Type and only known species. *Idicia vidalenci* gen. and sp. nov.

Diagnosis. As that of the type species (by monotypy).

Idicia vidalenci sp. nov.
Figure 3

Derivatio nominis. Epithet in honour of Dominique Vidalenc, who discovered the specimen.

Holotype. UM-LAV 1700, a left dentary preserving a portion of incisor and m2-m3 (Fig. 3).

Type locality and age. Lavergne (Quercy), MP 16, late middle Eocene (Bartonian; Crochet *et al*., 1981; Remy *et al*., 1987).

Diagnosis. Medium sized Theridomyidae, brachydont with bulbous main cuspids; ectolophid absent (i.e., sinusid remaining lingually open, being confluent with the sIII); entoconid markedly displaced mesially and bent forwardly; entolophid strong and oblique, distobuccally directed; no trace of a hypoconulid on the particularly thick posterolophid, which is prolonged lingually by a crenulated cristid.

Material and measurements. Only the UM-LAV 1700 holotype, a left dentary with incomplete incisor (proximal *versus* distal diameters = 1.81 and 2.14), m2 (MDL × BLW × H: 2.29 × 2.12 × 1.24) and m3 (2.30 × 1.88 × 1.09) (Fig. 3A−G).

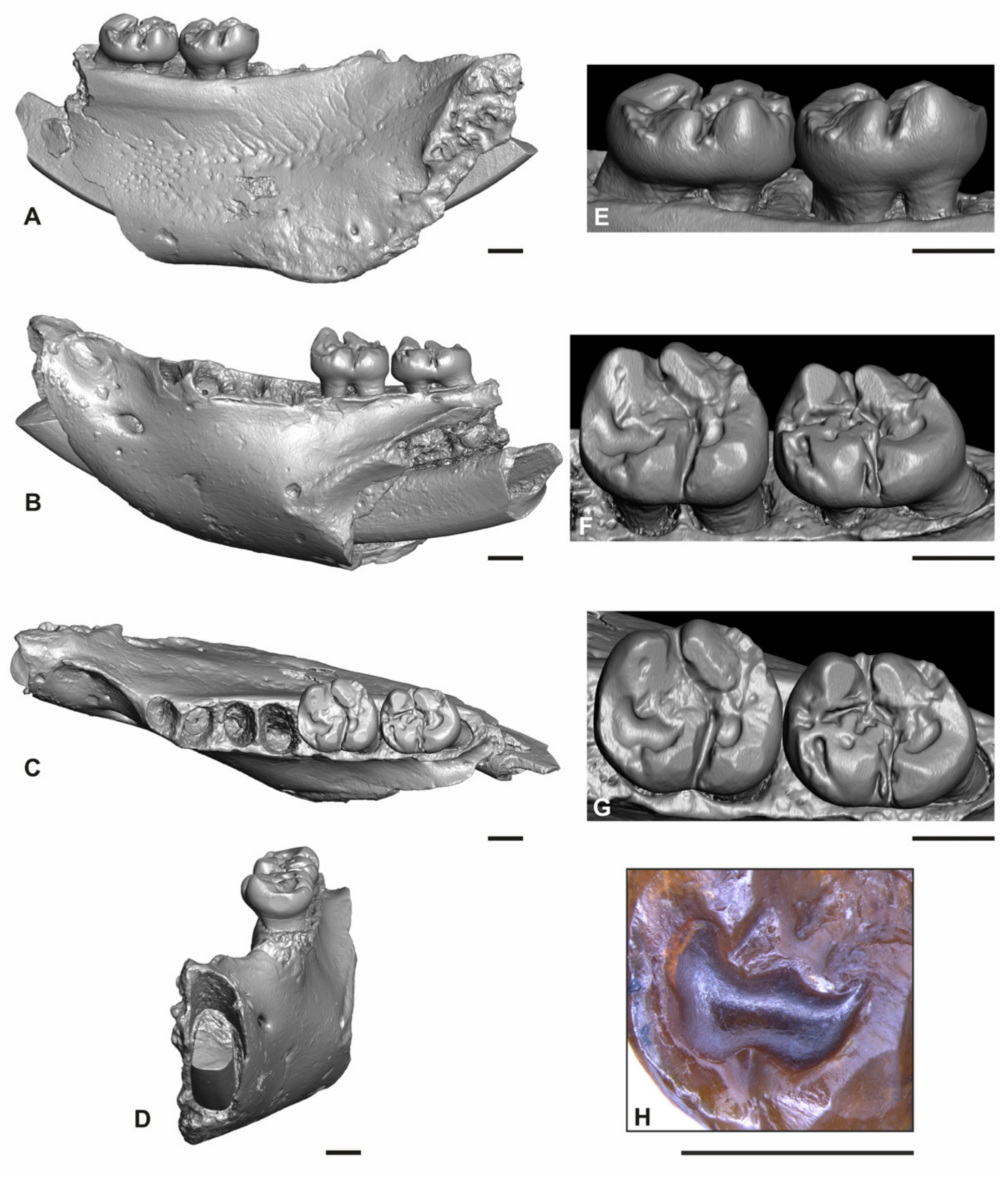

Figure 3. ***Idicia vidalenci*** gen. et sp. nov. **A−H**, UM-LAV 1700 (Holotype), a left mandible preserving a portion of incisor and the second and third molars. **A**, lingual view of the jaw; **B**, buccal view; **C**, occlusal view of the jaw, showing the diastema, the p4 and m1 alveoli, and the m2 and m3; **D**, mesial view of the dentary showing the incisor section inside its alveolus, and the mesial profile of the diastema and that of m2-m3; **E**, zooming of the lingual aspect of m2-m3; **F**, zooming of m2-m3 in occluso-buccal view; **G**, zooming of the occlusal view of m2-m3; **H**, zoom of the mesio-buccal region of m2, showing a large open pit of dentine, which is likely the result of a caries. Images A−G are renderings of the 3D digital model of the fossil specimen, obtained by a X-ray micro-computed (µCT) surface reconstruction (segmented enamel surface), whereas the image H is the result of the fusion of multifocus images obtained with an optical stereomicroscope connected to a camera. Scale bars = 1 mm.

Description

Dentary. Dentary with the foramen mentale located below the diastema, directly below the front of the p4 anterior root (Fig. 3B), masseteric crests ending below the posterior alveolus of the root of m1 (Fig. 3B), robust symphysis, ending below the level of the p4 roots (Fig. 3A).

Lower molars. The two teeth preserved on the dentary (m2 and m3) are double-rooted (one mesial root and one distal root, both being mesiodistally compressed), as is also the case for the teeth that precede them (i.e., p4 and m1), judging by the number of root sockets.

m2: The mesiobuccal area is particularly worn, revealing a large open pit of dentine, which could be the result of a caries (Fig. 3F–H). The protoconid and buccal anterolophid wears result in a single area, with a short remain of the antesinusid. The metaconid is strong, prolonged into a thick and short transverse lingual metalophulid I connecting to the protoconid area, from which runs the oblique (distolingually directed) posterior arm of the protoconid. The distal extremity of the latter is free due to the absence of ectolophid. The sinusid is narrow and deep, being confluent with the mesoflexid (sIII). It remains transversely open and appears as an arched furrow. A weak and short cristid runs between the posterior arm of the protoconid and the lingual metalophulid I. The entoconid is smaller than the metaconid, and is inclined forward (tilts forward). It seems to be somewhat displaced mesially, thereby appearing very close to the metaconid. The close proximity of the two latter cuspids reduce the mesoflexid (sIII) lingual opening, thereby appearing as a narrow and deep notch (Fig. 3E). A mesiodistally oblique and large entolophid prolongs the entoconid distobuccally and connects to the transverse and thinner hypolophid. The attrition wear on the two main lingual cuspids is strongly internal, generating almost steep-sided wear facets on the buccal aspects of the metaconid and entoconid-entolophid. The posterolophid is thick and extends from the hypoconid to the level of the buccal end of the entolophid. Distally, the posterolophid is prolonged lingually by a thin and discontinuous cingulid bearing weak cristulids. In addition, there are also cristulids in the posteroflexid and along the distal flank of the entoconid/entolophid.

m3: It is shorter and narrower than m2, and its mesiobuccal area shows no signs of pathology, thereby enabling structures to be better distinguished (Fig. 3F–G). The buccal part of the anterolophid is strong and long, and separated from the protoconid flank by a narrow and long antesinusid. The latter is limited by a long cingulid, and connected to the buccal metalophulid by a clear anterolophulid. The lingual anterolophid is very short, reduced to an isolated tiny enamel swelling (cuspid-like structure). The lingual metalophulid I is short and attached to a thin mesiodistal lophulid running into the mesoflexid. The metalophulid I is parallel to a short cristid derived from the buccal metalophulid and having the same direction as the anterolophulid. The strong postprotocristid (i.e., posterior arm of the protoconid) is well defined, with a bulging at its distolingual end. There is no ectolophid, only a weak enamel elevation between the distal extremity of the postprotocristid and the mesial border of the hypolophid. A thin additional cristid descends from the distal flank of the protoconid into the sinusid and obstructs its buccal opening. Lingually, unlike on m2, there is a low and small but well-defined and isolated mesostylid, which is situated between the metaconid and the entoconid, but not in line with the metaconid-entoconid long axis, being slightly external on the lingual aspect of the crown; the distal cristulids are fused between the entolophid and the posterolophid, thereby closing the lingual end of the posteroflexid.

Comparisons and discussion

The affinities of *Burgia marandati* have been extensively discussed when it was first described (Vianey-Liaud, 1991, p. 81-88). A suite of anatomical details depicted on the available dental material allowed to support its status as a Theridomyidae rather than a Ctenodactylidae. This conclusion was confirmed by our previous cladistic assessment of the dental evidence (Vianey-Liaud and Marivaux, 2017), which placed *B. marandati* close to *Patriotheridomys*, both sharing the strong hypsodonty and lophodonty, the oblique postprotocristid, the metalophulid I, the absence of both mure and ectolophid. The new material does not contradict this conclusion, which is further reinforced by the large size and morphology of the P4, like in *Patriotheridomys*. The latter genus is relatively frequent in Quercy localities dating from the Priabonian (from Gousnat, MP 18a, to Tabarly, MP 20), but neither *Burgia* nor *Patriotheridomys* have been found in the only relatively well-known other Bartonian "*phosphatières*", such as Le Bretou (seven known species of rodents, while there are eleven species from Lavergne). *Patriotheridomys* is so far primarily recorded from Priabonian localities, the older species, *P. sudrei*, being found in Gousnat (Vianey-Liaud and Ringeade, 1993; Vianey-Liaud and Marivaux, 2017).

If *Burgia* can be related to younger lineages of Theridomyidae, it is substantially distinct from *Idicia*, even if the available teeth (lower molars) of *Idicia* display undeniable features characterizing Theridomyoidea. This is particularly shown with the oblique postprotocristid, which is oriented distolingually, and the metalophulid connecting directly the protoconid to the metaconid (metalophulid I), other features being somewhat unusual. Due to the entoconid placed close to the metaconid, the entolophid makes an angle with its hypolophid component, whereas it is generally straight among the Theridomyoidea. These features are found in older species: it can be angulated in some teeth of primitive Theridomyoidea, such as *Hartenbergeromys* (Vianey-Liaud and Marivaux, 2021; MP 10), or in more advanced ones such as *Protadelomys lugdunensis* from Lissieu (but the mesoconid is present in the latter) or *P. cartieri* from Egerkingen (MP 14; see Vianey-Liaud and Hautier, 2022) among other theridomyid features. This angular entolophid-hypolophid is common in ctenodactyloids, such as for instance *Tataromys* or *Yindirtemys* (Schmidt-Kittler *et al.*, 2007), but these rodents have a metalophulid II, due to the postprotocristid connecting to the metaconid, neither free in the talonid basin nor connected to the ectolophid. The condition of the ectolophid (i.e., very low to absent) is also found in different brachydont Theridomyoidea, notably in the Theridomyidae such as *Estellomys*, the Issiodoromyinae *Elfomys* and *Pseudoltinomys*, or in the Pseudosciuridae such as *Treposciurus* and in some *Protadelomys* (like *P. cartieri*). Finally, several features of *Idicia* are common with some theridomyids, which tempers the originality of this taxon. Its affinities will be further tested with phylogenetic analyses.

Table 1. List of mammals from the fossil-bearing locality of Lavergne (Bartonian, MP 16).

Metatheria
Amphiperatherium fontense
Amphiperatherium minutum
Peratherium lavergnense

Pseudorhyncocyonidae
Leptictidium sigei

Nyctitheriidae
Euronyctia grisollensis
Saturninia mamertensis

Primates
Necrolemur cf. *antiquus*
Necrolemur sp.
Pseudoloris parvulus

Rodentia
Burgia marandati
Elfomys cf. *engesseri*
Glamys robiacensis
Idicia vidalenci
Paradelomys crusafonti
Pseudoltinomys nov. sp.
Remys minimus
Sciuroides cf. *romani*
Sciuroides siderolithicus
Suevosciurus minimus

Chiroptera
Carcinipteryx trassounius
Hipposideros morloti
Vaylatsia cregolensis
Vaylatsia astruci
Vespertiliavus gracilis

Hyaenodonta
Allopterodon minor
Paracynohyaenodon schlosseri
Cynohyaenodon cayluxi

Carnivoramorpha
Cynodictis sp.
Quercygale angustidens
Paramiacis exilis
Paramiacis teilhardi

Artiodactyla
Acotherulum campichii
Catodontherium robiacense
Cebochoerus minor
Dacrytherium elegans
Dichobune sigei
Dichodon frohnstettense
Haplomeryx euzetensis
Haplomeryx picteti
Leptotheridium lugeoni
Mixtotherium nov sp.
Mouillacitherium elegans
Pseudamphimeryx pavloviae
Pseudamphimeryx renevieri
Robiacina lavergnensis
Tapirulus schlosseri
Xiphodon castrense

Perissodactyla
Anchilophus jeanteti
Eurohippus parvulus
Metanchilophus gaudini
Palaeotherium siderolithicum
Plagiolophus annectens

Table 2. List of mammals from the fossil-bearing locality of Le Bretou (Bartonian, MP 16).

Metatheria
Amphiperatherium bourdellense
Amphiperatherium fontense
Amphiperatherium minutum
Peratherium bretouense
Peratherium lavergnense

Pseudorhyncocyonidae
Leptictidium sigei

Nyctitheriidae
Cryptotopos woodi
Saturninia gracilis
Saturninia mamertensis

Primates
Anchomomys cf. *quercyi*
Necrolemur cf. *antiquus*
Pseudoloris parvulus

Rodentia
Elfomys cf. *tobieni*
Glamys robiacensis
Paradelomys crusafonti
Plesiarctomys huerzeleri
Pseudoltinomys aff. *mamertensis*
Remys minimus
Sciuroides sp.
Sciuroides romani

Chiroptera
Carcinipteryx trassounius
Hipposideros morloti
Hipposideros schlosseri
Hipposideros tenuis
Palaeophyllophora quercyi
Vaylatsia astruci
Vespertiliavus disjunctus
Vespertiliavus cf. *schlosseri*

Hyaenodonta
Allopterodon minor
Paracynohyaenodon magnus
Paracynohyaenodon schlosseri

Carnivoramorpha
Quercygale cf. *angustidens*
Paramiacis exilis
Simamphicyon helveticus

Artiodactyla
Acotherulum campichii
Catodontherium robiacense
Cebochoerus helveticus
Cebochoerus lacustris
Dacrytherium elegans
Dichobune sigei
Dichodon cervinum
Dichodon frohnstettense
Haplomeryx picteti
Leptotheridium lugeoni
Leptotheridium traguloides
Mouillacitherium elegans
Pseudamphimeryx pavloviae
Pseudamphimeryx renevieri
Robiacina minuta
Robiatherium cournovense
Tapirulus schlosseri
Xiphodon castrense

Perissodactyla
Anchilophus jeanteti
Eurohippus parvulus
Leptolophus stehlini
Lophiodon sp.
Metanchilophus castrensis
Metanchilophus gaudini
Pachynolophus bretovensis
Palaeotherium siderolithicum
Plagiolophus annectens

DISCUSSION AND CONCLUSIONS

Why have *Idicia* and *Burgia* never been found before in Quercy or elsewhere during the late Bartonian? Does this represent a collection bias, a taphonomic bias or an ecological bias?

Except for the two rodents reported in this paper, the numerous other orders of mammals recorded at Lavergne (see the taxa list in Table 1) does not include unique taxa, but taxa recorded in other coeval fossil-bearing localities of the Quercy, such as for instance Le Bretou (Table 2). The presence of these two unique taxa at Lavergne is perhaps a matter of sampling bias, due to the exceptional long-term processing of a very large quantity of sediment, which led to the discovery of rare species.

Only one other sub-contemporaneous or coeval locality has been exploited in Quercy phosphorite, e.g., Le Bretou (Hartenberger *et al*., 1974). The latter is a restricted locality where less abundant and harder sediment had to be processed by acid-etching. Due to the difficulties of the process, it has not benefited from such sustained exploitation. Despite this, a monograph of the whole vertebrates has been published in 1988 encompassing the Rodentia (Hartenberger, 1988) and ecological analyses (Legendre, 1988). The faunal list is updated in the present study (see Table 2). Eight species of rodents were identified, encompassing one Gliridae, one Remyinae, and five Theridomyidae. The whole mammalian fauna of Le Bretou is characterized by a continuous body-size distribution of species from the highest to the lowest weights, without intermediate weight gaps (and an abundance of species in all weight categories, small, medium and large; Legendre, 1988; Sudre, 1988). In the current absence of palynological and/or paleobotanical data, the palaeoenvironmental reconstruction derived from the cenogram of Le Bretou indicates a forested environment with an equatorial climate, with alternating rainy and dry seasons, the latter (two per year), being variable and not very marked (Legendre, 1988, p. 180). Such a monograph and ecological inferences for Le Bretou have not yet been drawn for Lavergne. The diversity of Artiodactyla is high (16 species) at Lavergne, while the diversity of the other mammals is lower (five Perissodactyla, three Metatheria, two Nyctitheriidae, five Chiroptera, three Hyaenodonta, four Carnivoramorpha, and three Primates) (see Table 1). Among the ten rodent species from Lavergne, one is a glirid and one a remyine; eight are theridomyids including the two *Idicia* and *Burgia*. The two latter, somewhat "odd", rodents from Lavergne were likely very rare in the palaeoenvironments of the Quercy region during the Bartonian, and as such their chance of fossilisation was low, insofar it is possible to extrapolate based on so few localities. Alternatively, the rarity of *B. marandati*, as an early hyspodont taxon, could also be related to the scarcity of suitable open habitats at that time in this region. Basically, hypsodont forms appeared later in the Eocene, and so it is intriguing to find a hypsodont species identified in a locality close to the MP 16, particularly present at Lavergne but absent at Le Bretou. A noticeable elevation of the crown, selected in other theridomorph rodents, is indeed only recorded in the fossil record later, during the Priabonian (i.e., MP 18 to MP 20), when habitats began to become patchier and more open. This could suggest specific environmental conditions at Lavergne, possibly less forested.

Concerning the more or less rich stratified localities close to MP 16, such as the well-known Robiac (Depéret and Carrière, 1901; then Sudre, 1969; Hartenberger, 1973a, b; Remy, 2015) and Grisolles (Hartenberger and Louis, 1976), rodents are not numerous. The mammal fauna from Robiac and its associated flora indicate a hot, wet and forested environment, palaeoenvironmental conditions which are corroborated by the structure of its cenogram (Legendre and Sudre, 1984). The same is true for Le Bretou (Legendre, 1988). The fossil assemblage from Lavergne is not quite different except the lower diversity of perissodactyls and the greater diversity of rodents, with the occurrence of *Idicia* and *Burgia*. Lavergne is among the richest fossil-bearing locality for rodents and the most diversified one at MP 16. There are no birds of prey documented to date that could indicate an unusual predation phenomenon (linked to a larger hunting area), and which could have led to a taphonomic bias, implying a fossil record not representative of the true local conditions at Lavergne. There is no difference between the Lavergne and Le Bretou bird fossil records (Mourer-Chauviré, 1988). In sum, considering the large amount of sediment treated, the occurrence of rare taxa is not surprising, or even expected, and can therefore be considered a characteristic feature.

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