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## Parallelism in the evolution of dental pattern and systematic implications: The case of *Protechimys major* Schlosser, 1884 (Theridomyinae, Rodentia, Mammalia) and its associated rodents



*Parallélisme évolutif du pattern dentaire, implications systématiques : le cas de Protechimys major Schlosser, 1884 (Theridomyinae, Rodentia, Mammalia) et son cortège de rongeurs*

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## ABSTRACT

Abundant remains of *Protechimys major* Schlosser (1884) (Rodentia, Theridomyinae) from Mas-de-Pauffié (Lot, France; standard-locality MP26, e.g., Biochrom'1997; Early Chattian) are described and their morphological and dimensional variability are analyzed. At this locality, and also at Les-Milles (Bouches-du-Rhône), *P. major* is associated with a few teeth of *Archaeomys-Blainvillimys* sp. Due to this scarcity and to similar evolutionary trends in the pattern of lower molars, it is not possible to find accurate features likely to distinguish *Protechimys* from *Archaeomys* or advanced *Blainvillimys*, but lines of research are given. Their co-occurrence with *Issiodoromys pauffiensis* Vianey-Liaud (1976) is documented at localities with different depositional conditions; together with the analysis of precise and focused samples made in the limited outcrop, it contributes to demonstrate the temporal homogeneity of the MP26 rodent assemblage from Mas-de-Pauffié.

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## RÉSUMÉ

Le gisement du Mas-de-Pauffié (Lot, France ; localité-type du niveau repère MP26, par exemple, Biochrom'1997 ; Chattien inférieur) a livré d'abondants restes de *Protechimys major* Schlosser (1884) (Rodentia, Theridomyinae). La variabilité morphologique et dimensionnelle de cette espèce est décrite et analysée. Dans ce gisement, et dans celui des Milles (Bouches-du-Rhône), *P. major* est associé avec quelques dents d'*Archaeomys-Blainvillimys* sp. Du fait de cette rareté, et parce que ces genres montrent des tendances évolutives convergentes, il n'est pas encore possible de proposer des critères évidents pour

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distinguer les molaires inférieures de *Protechimys* de celles d'*Archaeomys* ou des *Blainvillimys* les plus évolués, mais quelques pistes sont ouvertes. À ces deux espèces est aussi associé *Issiodoromys pauffiensis* Vianey-Liaud (1976). La même association faunique dans ces deux localités formées dans des milieux de dépôts différents, ainsi que l'analyse des dents fournies par des prélèvements ciblés, contribuent à démontrer l'homogénéité temporelle de l'assemblage MP26 des rongeurs du Mas-de-Pauffié.

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## 1. Introduction

During the Early Tertiary, the rodent family Theridomyidae underwent a remarkable adaptive radiation that occurred in a geographical context restricted to Western Europe for a period covering more than 20 million years (Middle Eocene up to Late Oligocene). Theridomyids likely appeared in southwestern Europe during the Middle Eocene, possibly as the result of an evolution from some paramyids (e.g., Escarguel, 1999; Marivaux et al., 2004). They occupied this area until they became extinct by the end of the Oligocene, after a series of adaptive radiations and extinction crises (e.g., Schmidt-Kittler, 1971; Vianey-Liaud, 1979; Vianey-Liaud and Michaux, 2003). Strong environmental changes occurred during this period: from a tropical warm and humid climate, in which forest environments dominated, to the Late Eocene/Early Oligocene cooling (33.8 My) that contributed to install an arid climate during the Early Oligocene (Rupelian). Warmer and wetter conditions marked the Late Oligocene, but brief cooling episodes (glaciations) also occurred during the Early Chattian (Cramer et al., 2009; Vandenberghe et al., 2012). These rodents show a diversification reflecting the colonization of diverse habitats, ranging from closed to open environments, or even sub-desertic environments (e.g., Thaler, 1966; Vianey-Liaud, 1991).

Among these rodents, the sub-family Theridomyinae was the most diversified and it is the only one within Theridomyidae that shows episodes of radiation characterized by strong changes in tooth morphology in the arid and open Oligocene environments. Many cases of evolutionary parallelisms have been demonstrated in this group, which make it difficult to decipher the lineages and phylogenetic relationships (e.g., Mödden, 1993; Thaler, 1966; Vianey-Liaud, 1972, 1979, 1998). Among them, the most hypsodont species – belonging to the genera *Blainvillimys*, *Taeniodus*, *Archaeomys*, and *Protechimys* – were particularly studied. The strong increase in crown height together with clear occlusal surface changes characterizing these genera could help to discriminate the species and evolutionary stages, but also amplify the variability of the occlusal patterns. This could have led to the typological taxonomic interpretations and erroneous definitions of new genera, when the concept of interspecific variability was misunderstood (e.g., Mayo, 1983, 1987). Mödden (1993) rejected such typological interpretations, by reviewing the material of *Archaeomys* and *Protechimys* mainly from old collections. Abundant and/or well stratigraphically localized populations are very rare in the Upper Oligocene, except that of *Archaeomys laurillardii* Gervais, 1848 from Coderet (e.g., Huguéney, 1969; Mammalian Paleogene level MP30),

and *Protechimys* from more recently discovered localities from Quercy (MP24: Lébratières 14; MP25, Belgarric1, Rigal-Jouet1; and Belgarric IV [Mödden, 1993]; MP26: Mas-de-Pauffié [Vianey-Liaud, 1998]) and from Languedoc (Saint-Privat-des-Vieux, Bonnet et al., 2011) (Fig. 1). *Protechimys major* Schlosser (1884) is present in these MP26 localities and also in Les-Milles (Bouches-du-Rhône) from which 37 specimens have been collected. Here, we report on abundant and well preserved fossil remains of this species collected from the MP 26 standard-locality Mas-de-Pauffié (Lot, France) since 1987, together with all the species characterizing this level, such as *Issiodoromys pauffiensis* (Vianey-Liaud, 1976) (Table 1). This new and abundant material allows a better description of the dental, mandibular and maxillary variability of this species, and a comparison with the contemporaneous species of *Archaeomys*–*Blainvillimys*. Furthermore, we examine new data on the rodent-assemblage from the fissure-filling of Mas-de-Pauffié, thanks to the analysis of precise and focused samplings made on the limited outcrop, and comparisons to contemporaneous assemblages.

## 2. Material: (List of studied material: supplementary info)

**Material from Mas-de-Pauffié:** The samples of theridomyids (*Protechimys major* and

	m.y.	MP	Standard localities	Other localities, considered in this paper	
OLIGOCENE	CHATTIAN	24	Coderet		
		29	Rickenbach		
		25	28b	Pech-du-Fraysse	
		28a		Pech-Desse	
		26	27	Boningen	Ehrenstein7 St-Henri/St-André,
	RUPELIAN	26	26	Mas-de-Pauffié,	St-Privat-des-Vieux, Les Milles, Oensingen
		27	25c		Rigal-Jouet1
		25b		Garouillas	Antoingt
		25a		Belgarric1 BelgarricIV	
		28	24	Heimersheim	Mas-de-Gaston Lebratières 14, Valenc
29	23/24		Saint-Martin-de-Castillon		
30					
31	23	Itardies	Pech-Crabit		

**Fig. 1.** Biochronologic position, and correlation with the geochronologic timescale (following Cramer et al., 2009 and Vandenberghe et al., 2012), of the Oligocene localities considered in this paper. m.y.: million year; MP: European Mammalian Paleogene standard-level.

**Fig. 1.** Position biochronologique, et corrélation avec l'échelle géochronologique globale (d'après Cramer et al., 2009 et Vandenberghe et al., 2012), des gisements fossilifères oligocènes considérés dans ce travail. m.y.: million d'années; MP: niveau-repère mammalien de l'Oligocène d'Europe.

**Table 1**

List of rodents from lower Chattian localities: Mas-de-Pauffié (Lot, France), standard-locality of MP26, and from six other localities close to MP26.

**Tableau 1**

Liste des rongeurs des localités du Chattien inférieur : Mas-de-Pauffié (Lot, France), gisement-repère de MP26 et de six autres localités rapportées à ce niveau MP26.

	SPV	StM	MPF	LMilles	StH/StA	Oen11	MüH
<i>Gliravus bruijini</i> (Hugueney, 1967)	x	x	x				
<i>Gliravus bravoii</i> (Hugueney, 1985) (? = <i>G. bruijini</i> )						cf	
<i>Gliravus majori</i> (Stehlin & Schaub, 1951) (? = <i>G. garouillensis</i> ) (Vianey-Liaud, 1994)						cf	cf
<i>Microdyromys praemurinus</i> (Freudenberg, 1941)		x			cf	sp.	
<i>Peridyromys</i> sp.						x	
<i>Bransatoglis</i> sp.						x	
<i>Glirudinus</i> sp.			x			x	
<i>Bransatoglis planus</i> (Bahlo, 1975)		x			cf		
<i>Eomys zitteli</i> (Schlosser, 1884)	aff	x	x		x		
<i>Eomys molassicus</i> (Engesser, 1987)						x	x
? <i>Eomys minor</i> (Comte & Vianey-liaud, 1987)			x				
<i>Eomys</i> sp.							x
<i>Eucricetodon</i> sp. 1, 2					x	x	
<i>Eucricetodon huerzeleri</i> (Vianey-liaud, 1972)	x	aff	x			x	x
<i>Eucricetodon huberi</i> (Schaub; 1925)			x			x	x
<i>Eucricetodon murinus</i> (Schlosser, 1884)							x
<i>Eucricetodon dubius</i> (Schaub, 1925)		aff	x		x		
Cricetidae indet	x						
<i>Pseudocricetodon thaleri</i> (Hugueney, 1969)			?			cf	cf
<i>Pseudocricetodon incertus</i> (Schlosser, 1884)	x	x	x		x	x	x
<i>Pseudocricetodon philippi</i> (Hugueney, 1971)					aff		
<i>Pseudocricetodon moguntiacus</i> (Bahlo, 1975)			x			x	cf
<i>Heterocricetodon hausi</i> (Engesser, 1987)							x
<i>Heterocricetodon gaimersheimensis</i> (Freudenberg, 1941)	cf					x	
<i>Heterocricetodon helbingi</i> (Stehlin & Schaub, 1951)		cf	cf		x	x	
<i>Heterocricetodon schlosseri</i> (Schaub, 1925)							
<i>Paracricetodon spectabile</i> (Schlosser, 1884)						x	x
<i>Paracricetodon</i> sp.						x	
<i>Melissiodon schaubi</i> (Dehm, 1935)		aff	aff				
<i>Heteroxerus costatus</i> (Freudenberg, 1941)		x					
<i>Heteroxerus</i> sp.			x				
<i>Comtia bernardi</i> (Vianey-Liaud, in press)	x						
Sciuridae indet.						x	
<i>Issiodoromys pauffiensis</i> (Vianey-Liaud, 1976)	x	x	x	x	x	x	sp
<i>Blainvillimys stehlini</i> (Mayo, 1987)							x
<i>Protechimys major</i> (Schlosser, 1884)	x		x	x	?	aff	x
<i>Archaeomys</i> - <i>Blainvillimys</i> sp. / "huerzeleri" (Thaler, 1966)		x	x	x	x	x	
<i>Archaeomys-Blainvillimys robustus</i> (Lavocat, 1952)			?		x		
<i>Archaeomys</i> "ehrensteini" (Mödden, 1993)		x					
<i>Plesiosminthus</i> sp.			x				x
<i>Steneofiber</i> sp. aff. <i>butselensis</i> (Misonne, 1957)					x		
Indeterminate rodent family							x
? Aplodontidae indet	x						
<b>Number of species</b>	<b>10</b>	<b>13</b>	<b>18</b>	<b>3</b>	<b>13</b>	<b>21</b>	<b>16</b>

SPV: Saint-Privat-des-Vieux (Gard, France); StM: Saint-Menoux (Allier, France); LMilles: Les-Milles (Bouches-du-Rhône, France); StH/StA: Saint-Henri/Saint-André (Bouches-du-Rhône, France); Oen11: Oensingen11 (Switzerland); MüH: Mümliswyl-Hardberg (Switzerland).

*Archaeomys-Blainvillimys* sp.) studied here come from the whole sampling (see geological context). The teeth and jaws are well-preserved, not worn-out and only a few are digested. All can be easily observed and measured.

**Material from Les-Milles:** Because the fossiliferous sediment is clayey and highly oxidizing, the bones of rodents are somewhat corroded and crushed, although a few specimens are relatively complete (mandibles and fragments of skulls, with dental rows). The teeth of *P. major* themselves are very fragile, the dentine being badly or not preserved, leaving the enamel only. Insofar as one of the characteristics of these teeth is to have the enamel layer strongly thinned on certain structures, it still increases the fragility.

It is almost impossible to prepare these specimens mechanically.

**Methods:** The material from Mas-de-Pauffié was observed (and drawn) under a Leica MZ8 binocular microscope. X-ray  $\mu$ CT was used to acquire 3D data from Les-Milles. Ten specimens were scanned at a resolution of 36  $\mu$ m, using a Skyscan 1076  $\mu$ CT equipment, which is part of the Montpellier RIO Imaging (MRI) platform. 3D surfaces representing the cranial bones and the teeth were produced with Avizo 7.0.1 (Visualization Sciences Group) via thresholding and manual segmentation. Due to the relatively poor contrast between the bone and the sediment and the bad preservation of the fossils, only the general shape of the cranial bones and that of the enamel blades

could be extracted. Dentine areas could not clearly be distinguished in the CT images.

**Terminology** Fig. 2: For theridomyids, due to the strong modifications of the tribosphenic pattern of their teeth, Stehlin and Schaub (1951) initiated the use of specific nomenclatural terms, as synclines (synclinids) (I to IV), anticlines (anticlinids) (1 to 5) and sinus (sinusid) for upper (and lower) molars, avoiding the questions of homologies. Here, that terminology is combined with the classical terminology of Wood and Wilson (1936), in order to follow homologies. On much advanced species, additional synclines (ids) can be present.

**Measurements** Fig. 2: In order to compare with previous literature, the measurements were taken both on the occlusal surface and from the edges of the crown (mesio-distal and bucco-lingual). The heights of the sinus and sinusid (HSin) were measured to estimate a degree of wear, and the maximal height of weakly worn teeth (H) measured when possible. The angle  $\alpha$  (formed by the bucco-lingual projection of the postprotocristid, and the oblique length of the postprotocristid) was estimated from  $\cos \alpha$  (ratio between the two dimensions). Isolated teeth and jaws were measured with a “Nikon Measuroscope”.

**Collections:** The material is housed in the ISE-M (Institut des Sciences de l'Évolution), Montpellier 2 University Collections.

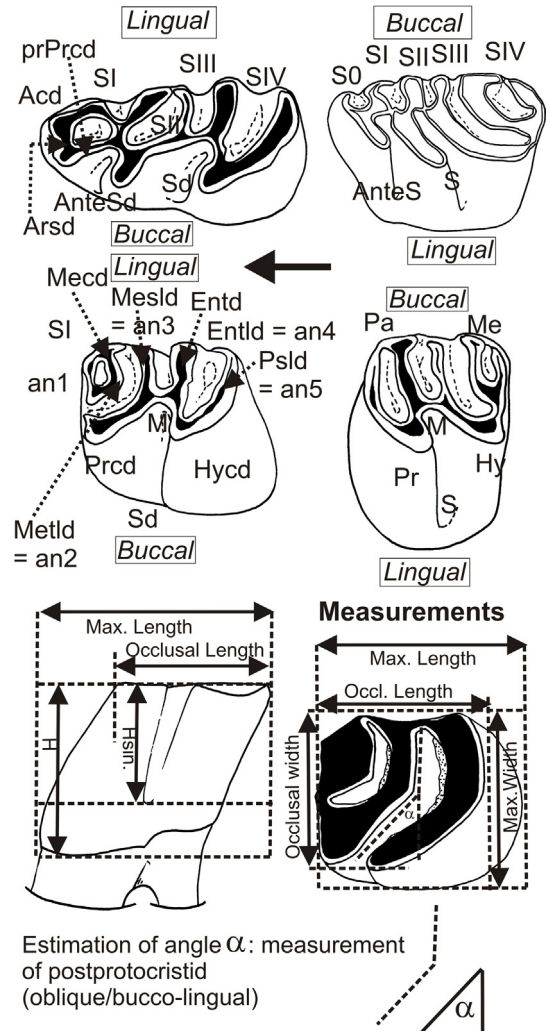
**Abbreviations:** MNHN: Muséum national d'histoire naturelle, Paris; NMB: Naturhistorisches Museum, Basel; BSPG: Bayerisches Staatssammlung für Paläontologie und Geologie, München; UMA: Musée de l'université de Marseille.

### 3. Geological context of localities and historical background

#### 3.1. Les-Milles (Bouches-du-Rhône, France)

The “Les-Milles” locality is located in a quarry (Les Tuilières, near Aix-en-Provence) that has been exploited for many years to provide clay for manufacturing roof tiles. No real concentration of bones had been found, but isolated remains of three rhinocerotid species (e.g., Ménouret and Guérin, 2009; Répelin, 1916) have been found over the years, their precise location in the quarry being unknown. Small mammals were limited to a rodent of “*Archaeomys* type” (Huguenev and Truc, 1976) until the discovery by X. Valentin and D. Roggero in 1988 of a small fossiliferous lens including several remains of *Issiodoromys pauffiensis* and *Archaeomys-Blainvillimys* sp. Later, in 2006, the regular survey of the quarry by X. Valentin and G. Garcia was successful and another lens was discovered close to the first locus, with remains of *Protechimys major* and *Archaeomys-Blainvillimys* sp. The exposure is about 18 m thick with variously colored clays intercalated with more or less coarse detrital and pedogenetic layers (see Nury, 1988, fig. 96). The rodents described here come from a level located about 3 m from the bottom. The lenses were interbedded within thick layers of red clays, in the lower beds of the quarry. The quarry is now backfilled.

#### dp4 and lower molar DP4 and upper molar



**Fig. 2.** Dental terminology used for the descriptions. The arrow indicates the mesial direction. *Lower teeth* ( $dp_4$  and  $m_{1-2}$ ). Accl: anteroconid; AnteSd: antésinusid; Arsd: antérosinusid; an1: anticlinid 1; anterolophid; an2: métalophid; an3: mésolophid; an4: entolophid; an5: posterolophid; Entd: entoconid; Hycd: hypoconid; Mecl: métaconid; Mesld: mésolophid; prPrccd: préprotoconid; Prcd: protoconid; Sd: sinusid; SI to SIV: synclines I to IV. *Upper teeth* ( $DP^4$  and  $M^{1-2}$ ). AnteS: antésinus; Hy: hypocone; Me: métacone; Pa: paracone; Pr: protocone; S: sinus; S0 to SIV: synclines 0 à IV. The dimensions measured are indicated on a lower tooth, and same are measured on upper teeth, except the angle  $\alpha$ .

**Fig. 2.** Terminologie dentaire utilisée pour les descriptions. La flèche indique la direction mésiale. *Dents inférieures* ( $dp_4$  et  $m_{1-2}$ ). Accl: antéroconide; AnteSd: antésinuside; Arsd: antérosinuside; an1: anticlinide 1; antérolophide; an2: métalophide; an3: mésolophide; an4: entolophide; an5: postérolophide; Entd: entoconide; Hycd: hypoconide; Mecl: métaconide; Mesld: mésolophide; prPrccd: préprotoconide; Prcd: protoconide; Sd: sinuside; SI to SIV: synclines I à IV. *Dents supérieures* ( $DP^4$  et  $M^{1-2}$ ): AnteS: antésinus; Hy: hypocone; Me: métacone; Pa: paracone; Pr: protocone; S: sinus; S0 to SIV: synclines 0 à IV. Les dimensions mesurées sont indiquées sur une molaire inférieure et elles ont été prises de la même façon sur les dents supérieures, excepté l'angle  $\alpha$ .

Nury (1988) considered that the Les-Milles deposits are contemporaneous with the St-Henri-St-André formation (Marseille, Bouches-du-Rhône), i.e., Lower Chattian in age.

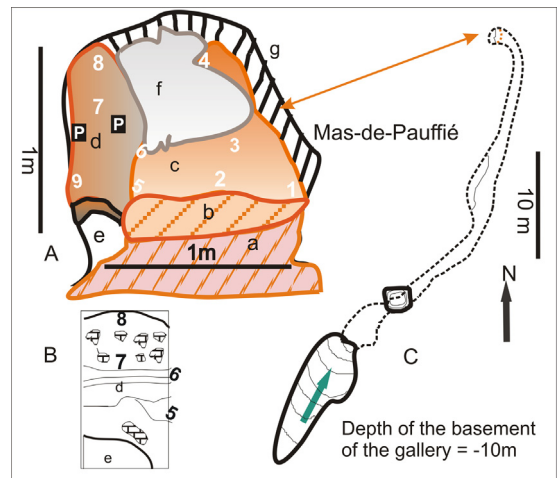
### 3.2. Mas-de-Pauffié (Lot, Quercy, France)

Paleontological investigations have been undertaken in the Quercy phosphorites since 1965 by Montpellier and Paris teams, joined by the Poitiers and Lyon teams, and are currently still in progress together with the association “Les phosphatières du Quercy” (e.g., Peigné et al., 2014). These investigations discovered richly fossiliferous fissure-fillings, with diverse and abundant vertebrates, which were the basis of numerous evolutionary studies. At least one hundred homogeneous and well dated fossiliferous fissure-fillings were documented, with very rare occurrences of presumable contact of two distinct fillings (e.g., Legendre et al., 1997), such as Mas-de-Pauffié (appearing to be one by the end of 1987). As this locality was retained “faute de mieux” (half a year earlier) as the standard locality MP26 (Biochro'M, 1997), taphonomic studies were involved to understand the genesis of the filling, but this work proved to take much longer than expected. It was not finished before the end of a PhD thesis (Laudet, 2000), and before new collections and their processing, which for multiple reasons took more than 20 years.

Filling of a karst does not work as accumulations in fluvio-lacustrine basins. Fluvio-lacustrine deposits are often but not always set horizontally, superposed and time-ordered, sometimes reworked, sometimes complicated by episodes of emersion, erosion or pedogenesis, and followed by diagenesis. In these, the trapping of remains of organisms can be very short on the scale of seasonal events, but can also work over a much longer scale. A fissure is also rapidly filled and the filling (containing fossils) is stable after diagenesis until another karstic event occurs. Generally, such events are rare, and much more so in the deepest underground parts of fillings, which constitute the main remains of ancient paleokarsts. When they occur, they do not inevitably affect the whole previous filling, but some peculiar areas can be “reactivated”. Thus sampling in fissure fillings, as in any type of continental fossiliferous deposit, requires careful examination of the sediments and taphonomy of fossils. It is the reason why the different steps of the exploitation of Mas-de-Pauffié are analyzed here.

Mas-de-Pauffié is a small fissure-filling at the bottom of a subterranean gallery, the section of which is about 1.5 m<sup>2</sup> (Fig. 3). The right side of the filling shows red-yellow clays without any stratification, whereas the re-entrant on the left side displays irregular stratifications, underlined by sandy layers, its upper part being brecciated. A thin recent calcitic crust covers the passage between these two sides.

Three phases can be distinguished in the exploitation of this site. First, small quantities of sediment were sampled from the small outcrop, and also on the surface of excavated-sediment on the ground level. The mammal assemblage is that classically defined from the Mas-de-Pauffié locality, the standard locality for the European mammal Paleogene level MP26 (e.g., Biochro, 1997: 792; Brunet and Vianey-Liaud, 1987: 187–188). The sampling operations were limited through time (from 1969 to 1972)



**Fig. 3.** Diagram of the Mas-de-Pauffié fossiliferous locality. A. Different parts of the outcrop at the extremity of the underground gallery, with location of the samples; a+b+c: right side of the filling, without stratification; a+b: spoil from the excavation in 1987; c: red clay; d: “niche”, hollowed at the left side of the outcrop; e: low and shallow small cavity; f: thin recent calcitic crust covering the filling; g: enclosing jurassic limestone. 1 to 9: samples locations. P: location of sampling for palaeomagnetic analysis (Lévêque, 1993). B. Detail of d, with breccia on top, and below, irregularly stratified yellow and red clays with graded sandy inputs. C. Diagram of the caves and gallery leading to the outcrop.

**Fig. 3.** Schéma de la localité fossilifère de Mas-de-Pauffié (Lot, France). A. Différentes zones de l’affleurement, situé à l’extrémité de la galerie souterraine, montrant l’emplacement des prélèvements ciblés; a+b+c: côté droit du remplissage dépourvu de stratification; a+b: déblais du prélèvement important de 1987; c: argiles rouges; d: renforcement du côté gauche de l’affleurement; e: petite niche basse et peu profonde; f: couverture calcitique récente masquant partiellement les argiles rouges; g: calcaire jurassique encaissant. 1 to 9: localisation des prélèvements de 1993. P: localisation des échantillons analysés pour le paléomagnétisme (Lévêque, 1993). B. Détail de d, montrant une brèche irrégulière à ciment argileux au sommet, et, au-dessous, des argiles jaunes et rouges irrégulièrement stratifiées par des lits sableux granoclassés. C. Schéma du réseau karstique d’accès au gisement (en fond de galerie souterraine).

and quantity (less than 100 kg) due to the accumulation of CO<sub>2</sub>, because the air was not renewed at the bottom of the gallery. Fossils were abundant despite the limited quantity of processed sediment, and they never show any sign of transport. Second, after the installation of an efficient pumping system, it was then possible to sample more substantially during summer field work in 1987. About 200 kg of sediment were extracted from the outcrop (Fig. 3a–b), and processed (screen/washing operations) directly in the field, which revealed the occurrence of unexpected rodents (see below). Third, in 1993, a new campaign was carried out to analyze the outcrop precisely, as it has been left after the samplings in 1987, and to take precise and localized samples in the different loci of the filling. Nine small samples (about 1 kg each) were collected by the author (see acknowledgements) and then processed separately. Each locus yielded small mammals (Fig. 3).

### 4. Taphonomic control and validity of the rodent assemblages

**Les-Milles:** only three rodent species are known, from the lower layers in the quarry. They all

represent evolutionary stages of three theridomyoid lineages, *Issiodoromys pauffiensis*, *Protechimys major* and *Archaeomys-Blainvillimys* sp. (Table 1).

**Mas-de-Pauffié:** Recognition of the locality Mas-de-Pauffié as a new standard-level of the European Mammal Paleogene scale, between Garouillas (=Antoingt) chosen for MP25, and Böningen (MP27), was accepted “faute de mieux”, because no other locality including well-identified evolutionary stages of theridomyoids, with a well-defined variability, were found. Unlike Garouillas, also a fissure-filling, which includes diversified and well characterized small and large mammals, the whole fauna of Mas-de-Pauffié was relatively poor in large mammals. Other MP26 sites, such as Oensingen (fossils collected in 1916, cf. Engesser and Mödden, 1997) or St-Menoux (e.g., Hugueney, 1980; theridomyids poorly documented), which had yielded fossils for decades, did not have more “qualities” than Mas-de-Pauffié. But because the scientific community would have preferred such sites from fluvio-lacustrine basins rather than a karstic one, the geometric relationships with older or more recent sites, and with marine formations, would have been (in theory) more obvious. But it is a long way from dream to reality for the Oligocene of western Europe, which often consists of small and independent basins and also of more extended basins but widely concerned by the alpine tectonics. Their geometric relationships are not obvious, and geochronologic or magnetostratigraphic dates are rare (e.g., Legendre and Lévêque, 1997; Schlunegger et al., 1996; Vianey-Liaud, 1998). Thus, paleomammalogists in the last decades needed to overcome these difficulties, developing innovative methods of research focused on the evolution of existing and new mammals in this case. Further independent data (new geochronologic datations, new localities, new well-studied species) will test their results.

Since the definition of the MP26 standard-level, its rodent association –including marker species such as *Issiodoromys pauffiensis*, *Protechimys major* and *Eucricetodon huerzeleri* Vianey-Liaud (1972)– has since been found in new fluvio-lacustrine localities, such as Oensingen11 (Engesser and Mödden, 1997) and St-Privat-des-Vieux (Vianey-Liaud et al., 2015) for the richest, or Les-Milles (this paper) and Puycelsi (Astruc et al., 2003) for the poorest. Attempts to enrich the fauna of Mas-de-Pauffié have both met expectations and provided an additional challenge.

The fossils discovered in 1987 (Phase 2 of exploitation) included several teeth of *Issiodoromys limognensis* Vianey-Liaud, 1976, together with the much more abundant *I. pauffiensis*. Now these two species are considered two successive evolutionary stages of the same lineage (e.g., Schmidt-Kittler et al., 1997; Vianey-Liaud, 1976). Two hypotheses can consequently be proposed: 1- The evolutionary lineage is not valid, and there are two synchronous species; 2- Or was there a more recent (MP28) reactivation of the fissure-filling (MP26) and a mixture of two different faunas in the collected sample, with successive evolutionary stages of *Issiodoromys*? The fact that no other locality –stratified or karstic– has ever yielded the two species simultaneously does not argue in favor of the first alternative (Table 1; and e.g., Mödden, 1994).

The rodents collected from the samples 1 to 9 are listed in Table 2. Five of the nine samples (1, 2, 3, 4, 6) have yielded a few teeth of *Issiodoromys limognensis*, 6 teeth of *Eomys gigas* Comte and Vianey-Liaud (1989) and *E. quercyi* Comte and Vianey-Liaud (1989) known in the same MP level (MP28), three species in all. The other small samples have yielded 11 species known from the MP26 level (from the initial samplings in Mas-de-Pauffié –the standard locality–, or from palustrine-fluviatile localities close to MP26 [Table 1]). Altogether, there are 45 teeth of *I. limognensis*, the main part being worn out, and 181 well-preserved teeth of *I. pauffiensis* and only a few show traces of digestion. These traces are easily recognizable on teeth (see e.g., Bonnet et al., 2011; Laudet, 2000). The first collections from Mas-de-Pauffié (phase 1) were made in a portion of the filling where the fossils never show any sign of transport, some being digested. In other Quercy localities where *I. limognensis* is present alone (i.e. MP 28, Pech-Desse, Pech-du-Fraysse), teeth are well preserved, not worn out, some can be digested, and they are very abundant (up to several thousands). In the Mas-de-Pauffié sample processed in 1987 there are about 3450 isolated teeth of *I. pauffiensis* and more than 100 jaws, whereas it contains 250 isolated teeth of *I. limognensis*. It seems that the sampling made in 1987, and the targeted samplings in 1993 under the calcitic concretion (No. 4 and 6), or on the right side of the outcrop (No. 1, 2, 3) reached a locus in the fissure-filling that was subsequently re-activated. This part is clayey, without any trace of stratification (contra the left side of the outcrop where some stratification is visible, Fig. 3B): it is therefore difficult to identify precisely the features of the re-activated sediment. Fortunately, the re-activation occurred long enough after the MP26 filling (more than one million years to MP28a, see Fig. 1). Thus, it is quite possible to differentiate its faunal intakes, as at least seven MP26 localities are now documented (Table 1).

If species undoubtedly younger (*I. limognensis*, *Eomys gigas* and *E. quercyi*) are not taken into account, the rodents assemblage from Mas-de-Pauffié –encompasses 18 species (Table 1). Among them, three markers (evolutionary stages restricted to the level)– *Issiodoromys pauffiensis*, *Protechimys major*, *Archaeomys/Blainvillimys* sp. – are common to six of these localities. Nine species are shared at least by three “MP26” localities, but not restricted to MP26 (*Gliravus bruijni* Hugueney, 1967, *Microdyromys praemurinus* [Freudenberg, 1941], *Eomys zitteli* Schlosser, 1884, *Eucricetodon huerzeleri* Vianey-Liaud, 1972, *E. huberi* [Schaub, 1925], *E. dubius* [Schaub, 1925], *Pseudocricetodon incertus* [Schlosser, 1884], *P. moguntiacus* [Bahlo, 1975], *Heterocricetodon helbingi* Stehlin and Schaub, 1951). In the future, the joint presence of same species (markers and others) is expected to be even more, when a review of the fossils will be made, with direct comparisons between specimens reported. It is the case for the species of *Gliravus*, *Glirudinus*, *Heterocricetodon* and cricetids other than *Eucricetodon huerzeleri*, undetermined sciurids and rodent of undetermined affinity. The question of the identification of *Archaeomys*/advanced *Blainvillimys* species is still open (since Mödden and Vianey-Liaud, 1997 and this paper, p.xx), but the species represented in Mas-de-Pauffié is different from the species of *Archaeomys* recorded in MP28.

**Table 2**

Number of teeth of each species of rodents in the focused samples 1 to 9 (Fig. 1) from the Mas-de-Pauffié locality (Lot, France), collected in 1993.

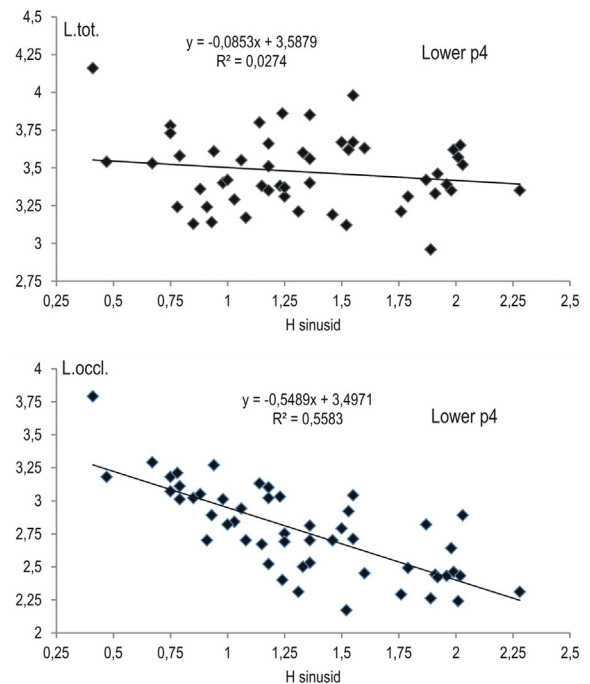
**Tableau 2**

Nombre de dents de rongeurs livrées par chacun des 9 échantillons collectés dans les loci ciblés 1 à 9 en 1993 à Mas-de-Pauffié (Lot, France).

Taxa sample	1	2	3	4	5	6	7	8	9
<i>Issiodoromys pauffiensis</i>	31	27	8	11	40	16	59	4	12
<i>Issiodoromys limognensis</i> (Vianey-Liaud, 1976)	10	6	9	5	0	2	0	0	0
<i>Protechimys major</i>	3	6	0	0	6	2	5	0	0
<i>Archaeomys</i> ( <i>Blainvillimys</i> ) sp.	0	0	0	0	17	0	6	0	0
<i>Eucricetodon huerzeleri</i>	10	7	0	2	14	6	3	1	1
<i>Eucricetodon dubius</i>	0	0	2	0	0	0	0	0	0
<i>Pseucricetodon incertus</i>	0	2	0	0	2	0	3	2	0
<i>Pseudocricetodon montalbanensis</i>	0	2	0	0	6	0	0	0	0
<i>Eomys</i> aff. <i>zitteli</i>	2	4	3	6	2	0	1	0	0
<i>Eomys minor</i>	2	0	0	0	0	0	0	0	0
<i>Eomys gigas</i> (Comte & Vianey-Liaud, 1989)	0	0	2	0	0	0	0	0	0
<i>Eomys ?quercyi</i> (Comte & Vianey-Liaud, 1989)	0	?1	4	1	0	0	0	0	0
<i>Plesiosminthus</i> sp.	0	1	1	0	0	0	0	0	0
<i>Gliravus bruijni</i>	0	0	0	0	0	0	4	0	0

## 5. Results of measurements

Since the 1970s, the question has remained how to measure the semi-hypsodont (asymmetrical growth of the crown) teeth of evolved theridomyines, like *Archaeomys*, or evolved issiodoromyines (*Issiodoromys*). The occlusal pattern changes with growth, and much more when this growth is accompanied by tilting of the crown and variations of the orientation of the wear plane. Stages of wear were defined (e.g., Vianey-Liaud, 1979) or morphometrical parameters were established (e.g., Vianey-Liaud, 1998 or Schmidt-Kittler, 1984, for issiodoromyines) to figure or quantify hypsodonty. Besides the measurements of length and width of the occlusal surface, and those from the edges (mesio-distal and bucco-lingual) of the crown, other dimensions have been proposed (e.g., diagonal of P<sup>4</sup>; Mödden, 1993). Here, we measured the occlusal surface, but also the length and width from the edges of the crown (supplementary info). Several jaws with teeth were available, and it was not possible to measure the complete height of their crowns, thus the sinus (sinusid) height was measured for the whole teeth. Until now, it was not possible to differentiate morphologically the lower teeth of advanced *Protechimys* from those of advanced *Archaeomys* and *Blainvillimys*, whereas clear differences appeared in their upper teeth (e.g., Mödden, 1993). This paper does not provide clear answers. The angle  $\alpha$  shows an important variation (between 20° and 58° for *P. major*), but this variation is widely independent of the size (total length of m1-2/angle  $\alpha$ ;  $y = -1.6812x + 45.271$ ,  $R^2 = 0.0038$ : insignificant because  $< 0.0529$ , for  $n = 70$ ). The total length is independent of wear (wear estimated by the height of sinusid; see Fig. 4 for p<sub>4</sub>), whereas the occlusal length is correlated with the sinusid height, i.e., with wear (lower graph on Fig. 4). The measurement of such an angle could be extended to abundant populations of *Archaeomys*, and multivariate analysis involved. The teeth of *P. major* are wider than that of *P. blainvillei* (Fig. 5, for M<sup>1-2</sup>), but their lengths do not differ. Differences of width are mainly due to differences in hypsodonty: the effects of wear on more hypsodont teeth increase the occlusal surface bucco-lingually (Figs. 4 and 5).

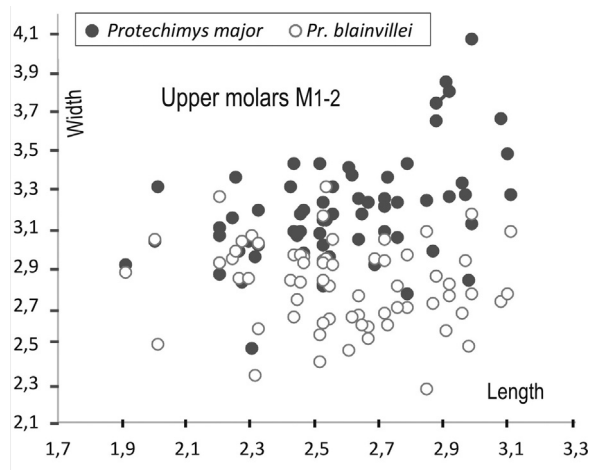


**Fig. 4.** A. Variation of the occlusal length of lower molars ( $m_{1-2}$ ) of *Protechimys major* Schlosser from Mas-de-Pauffié correlated with the sinusid height ( $n = 51$ ;  $R^2 > 0.1225$ ; significant  $P = 0.99$ ). B. Variation of their total length, widely independently of the sinusid height ( $n = 51$ ;  $R^2 < 0.0729$ ; no correlation).

**Fig. 4.** A. Variation de la longueur occlusale des molaires inférieures ( $m_{1-2}$ ) de *Protechimys major* Schlosser de Mas-de-Pauffié corrélée avec la hauteur du sinuside (pour  $n = 51$ , corrélation significative à  $p = 0,99$ , pour  $R^2 > 0,1225$ ). B. Variation de leur longueur totale, largement indépendante de la hauteur du sinuside (pour  $n = 51$ , pas de corrélation, car  $R^2 < 0,0729$ ).

## 6. Taxonomic context

A short historical background is necessary, following the vicissitudes of theridomyine genera and species names, in order to explain why two species belonging to two different genera, following convergent evolution of their lower teeth, could have the same specific name: *Blainvillimys*



**Fig. 5.** Bivariate graph of dimensions of upper molars ( $M^{1-2}$ ) of *Protechimys major* Schlosser from Mas-de-Pauffié (Lot, France; MP26) and *Protechimys blainvillei* Gervais from Rigal-Jouet1 (Tarn-et-Garonne, France; MP25). Length: total length; Width: total width.

**Fig. 5.** Diagramme bvarié des dimensions des molaires supérieures ( $M^{1-2}$ ) de *Protechimys major* Schlosser de Mas-de-Pauffié (Lot, France; MP26) et de *Protechimys blainvillei* Gervais de Rigal-Jouet1 (Tarn-et-Garonne, France; MP25). Length : longueur totale ; Width : largeur totale.

*blainvillei* Gervais, 1852 and *Protechimys blainvillei* Lavocat, 1952.

Among the Latest Eocene and Oligocene Theridomyidae Alston, 1876, four genera were first distinguished: *Theridomys* Jourdan, 1837, *Taeniodus* Pomel, 1853, *Trechomys* Lartet, 1869 and *Archaeomys* Laizer and Parieu, 1839. Pomel (1853) distributed the species previously attributed to *Theridomys* between *Theridomys* for the type-species (*T. lembronicus* Bravard in Gervais, 1848) and *Isoptychus* for the “primitive” ones (e.g., *I. aquatilis* [Aymard, 1849]). As new material became more and more abundant and diverse, notably from French localities (Auvergne, as a result of quarrying and civil engineering; Quercy, as a result of mining activities for phosphate extraction), a new genus, *Protechimys* (Schlosser, 1884), and several new species were described. Until that time, all along the successive discoveries and re-evaluation of older ones, the uncertainties of the generic allocation of the different recognized species as well as the different phylogenetic relationships rapidly emerged.

Schlosser (1884) distributed the Latest Eocene and Oligocene theridomyoids genera into two families, the Theridomyidae and Archaeomyidae, the latter including the genera *Archaeomys* and *Protechimys*. Freudenberg (1941) thought that *Protechimys* was a possible “ancestor” for *Archaeomys*. Among Theridomyidae, Stehlin and Schaub (1951) described the new genus *Blainvillimys* for the species *blainvillei* (pl. 47, fig. 17 and 18–18A, in Gervais, 1852) from Antoingt (Allier, France). They re-introduced the “primitive” species included in *Isoptychus* within the genus *Theridomys*. Finally, they included the species named into the genus *Protechimys* by Freudenberg within the genus *Archaeomys*. This option was based on the erroneous definition of *Protechimys* by Schlosser (see Mödden, 1993).

Around the same time, Lavocat (1952) divided the specimens referred to the species *blainvillei* from Antoingt in Gervais (1852) between the genera *Theridomys* (subgenus *Blainvillimys*) and *Archaeomys*, both keeping the same specific name *blainvillei*, thus not contravening the Code of Zoological Nomenclature (Mödden, 1993). *Archaeomys blainvillei* later got a new specific name (*A. gervaisi*, Thaler, 1966) in order to try to avoid confusion. However, this attempt was not successful and it led to long nomenclatural debates. *A. gervaisi* was then used in several works (e.g., Vianey-Liaud, 1979; Vianey-Liaud et al., 1995) before returning to the option of Lavocat (1952). For a detailed argument on these nomenclature changes, see Mödden (1993: 27–31). Mödden (1993) made a very thorough and relevant analysis of these problems of species synonymies and their generic attributions among *Blainvillimys*, *Protechimys* and *Archaeomys* and particularly the typological definitions of other new genera and species proposed by Mayo (i.e. 1983, 1987).

The genus *Theridomys* sensu Lavocat (1952), i.e., including the subgenus *Blainvillimys*, was then used (Vianey-Liaud, 1972). Later on, the generic attribution of the subgenus *Blainvillimys* changed to the genus *Archaeomys*, as it appeared that the features of the most derived species of *Blainvillimys* were closer to *Archaeomys* than to *Theridomys* (Vianey-Liaud, 1979). Mödden assessed the validity of the genus *Protechimys* (Mödden, 1993: 21–22) as that of the Archeomyini Schlosser tribe within the subfamily Theridomyinae for *Protechimys* and *Archaeomys*. In this tribe, the mesoflexid (synclinid III) disappeared due to the lingual penetration of the hypoflexid (sinusid), i.e., the lingual displacement of the ectolophid. However, this morphological trend can be observed in the genus *Blainvillimys* to different degrees. Otherwise, the first representatives of *Protechimys* [*Protechimys truci* (Hugueney, 1994) or *P. lebratierensis* Vianey-Liaud, 1998] at least, do not show the main characters given by Mödden (1993) to define the tribe – i.e., the lack of synclinid III on lower molars (Mödden and Vianey-Liaud, 1997: Table 1) or the absence of synclinid I, which can be present on weakly worn  $p_4$  and  $m_{1-2}$ . For the time being, it is better to use the subfamily, and not the tribes Archeomyini and Theridomyini. A comprehensive phylogenetic analysis of Theridomyoidea is currently in progress.

## 7. Systematics

**Theridomyinae** (Miller and Gidley, 1918).

*Protechimys* Schlosser (1884).

**Type-species.** *Protechimys gracilis* Schlosser (1884).

**Species included.** *P. truci* (Hugueney, 1994), MP23/24; *P. lebratierensis* Vianey-Liaud (1998), MP24; *P. variabilis* Vianey-Liaud (1998), MP24/25; *P. gracilis* Schlosser (1884), MP25 a-b; *P. blainvillei* (Gervais, 1848), MP25b; *P. major* Schlosser (1884), MP26.

**Differential diagnosis.**

Teeth of *Protechimys* differ from:

- *Blainvillimys* in: - the weaker enamel thickness differentiation on the opposite sides of lophids and lophids, - the shorter and transverse (not oblique) syncline II (= SII),



**Table 3**Measurements and elementary statistics of the population of teeth of *Protechimys major* from Mas-de-Pauffié (Lot, France).**Tableau 3**Mesures et statistiques élémentaires de la population de dents de *Protechimys major* de Mas-de-Pauffié (Lot, France).

Protechimys major Schlosser, 1884, Mas-de-Pauffié: lower teeth									Upper teeth							
	L	OL	W	OW	Lmsl	Lmsl/Lpcd	cos a	H-sin		L	OL	W	OW	H-sin	H	
dp4									DP4							
n	19	19	19	19	17	17	16	9	n	10	10	10	10	10	9	
min	3.43	3.4	1.81	1.75	0.93	0.636	0.348	0.03	min	3.09	2.84	1.89	1.65	0.62	0.3	
aver.	3.89	3.61	2.15	1.98	1.04	0.738	0.519	0.228	aver.	2.39	3.24	2.57	1.89	0.82	1.25	
max	4.22	3.96	2.65	2.82	1.17	0.833	0.647	0.53	max	3.7	3.42	2.88	2.2	0.98	1.55	
sd	0.186	0.121	0.169	0.219	0.064	0.043	0.088	0.166	sd	0.164	0.173	0.276	0.2	0.124	0.37	
p4									P4							
n	52	52	52	52				51	n	26	26	26	25	24	22	
min	2.96	2.17	1.9	1.27				0.41	min	2.63	2.05	2.6	1.57	0.15	0.81	
aver.	3.48	2.77	2.39	1.86				1.32	aver.	3.24	2.56	3.08	2.2	1.37	2.08	
max	4.16	3.79	2.8	2.47				2.28	max	3.61	3.04	3.5	2.83	2.42	3.81	
sd	0.234	0.333	0.237	0.273				0.458	sd	0.234	0.285	0.274	0.393	0.769	0.817	
m1-2: maximum Height: 3,57									M1-2							
n	116	117	115	113	70	70	70	107	n	67	67	67	65	62	48	
min	2.3	1.55	2.22	1.36	0.62	0.461	0.575	0.08	min	1.91	1.65	2.48	1.55	0.31	0.89	
aver.	3.01	2.19	2.73	2.18	0.89	0.589	0.765	1.17	aver.	2.59	2.09	3.18	2.18	1.68	2.41	
max	3.77	2.77	3.22	2.72	1.21	0.818	0.974	2.5	max	3.1	2.64	4.07	2.89	3	3.76	
sd	0.281	0.258	0.208	0.289	0.149	0.068	0.083	0.625	sd	0.273	0.231	0.273	0.359	0.833	0.956	
m3: maximum Height: 2,27									M3							
n	23	23	23	23	16	16	16	23	n	22	22	22	22	19	16	
min	2.21	1.48	1.79	1.44	0.56	0.441	0.695	0.37	min	1.96	1.34	2.19	1.44	0.46	1.14	
aver.	2.67	1.86	2.23	1.88	0.73	0.547	0.87	0.87	aver.	2.38	1.89	2.67	1.85	1.25	1.98	
max	3.19	2.19	2.6	2.02	0.94	0.707	0.975	1.44	max	2.71	2.51	3.3	2.48	2.24	3.17	
sd	0.259	0.202	0.217	0.221	0.123	0.079	0.088	0.313	sd	0.194	0.299	0.254	0.281	0.49	0.628	

protoloph and mesoloph (anticlines 2 and 3) on upper molars, - the occurrence of a well-marked antesisinus on DP<sup>4</sup> together with the SII reduced or absent; in the oldest species (*P. truci* and *lebratierensis*) the mure still present, interrupted then lost after strong reduction of the SII on the others.

- *Archaeomys* in the loss of SII before SI with wear on P<sup>4</sup>, whereas SI is lost before SII in *Archaeomys*; in the absence of an additional posterosyncline 5 (SV) on DP<sup>4</sup>.

### *Protechimys major* Schlosser (1884).

**Holotype.** Left maxillary bearing DP<sup>4</sup> to M<sup>2</sup> (1879 XV 518, BSPG, Munchen).

**Type-Locality.** Quercy, Old Collections.

**Emended diagnosis.** (after Vianey-Liaud, 1976: 55; Mödden, 1993; Mödden and Vianey-Liaud, 1997, 1998).

Evolutionary stage more evolved than *Protechimys blainvillei* (Gervais, 1848) (= *Archaeomys gervaisi* Thaler, 1966): wider teeth and higher hypsodonty. Occurrence of a thin layer of cement at the bottom of flexids even on deciduous teeth. *Lower teeth*: Fusion between synclinid I and presynclinid on dp<sub>4</sub>. *Upper teeth*: On P<sup>4</sup>-M<sup>3</sup>, syncline I present only in very slightly worn teeth, or missing. Syncline II absent.

**Material and measurements.** (See supplementary info and Table 3).

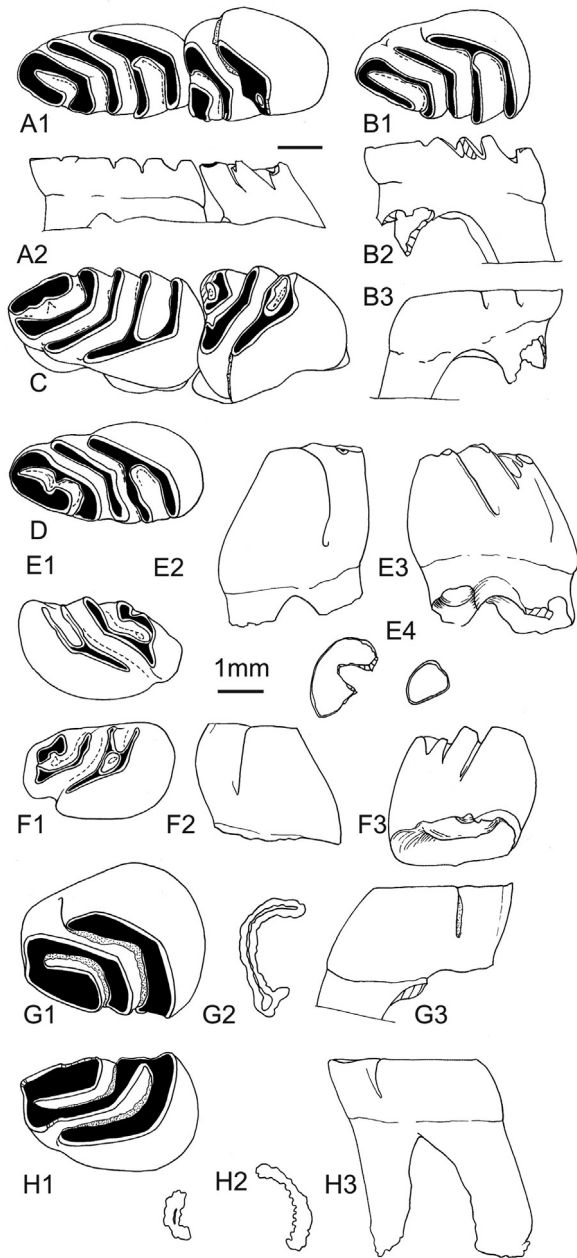
### Description and comparisons.

*Dentary and lower incisor*: On its medial side, the horizontal ramus bears a strong and horizontal zygomatic plate, and the lower masseteric crest is strong; the foramen mentale is located slightly mesially to the hollow portion

of the diastema. This ramus is lower and shorter than on the younger species from Pech-Desse (*Archaeomys quercyi* Mödden, 1993), and a little higher and stronger than on the older species *P. blainvillei*, *P. lebratierensis* and *P. variabilis*, but all with similar proportions. *P. gracilis* from Belgarric1 (BEL84) shows different proportions: the mesial edge of the horizontal zygomatic plate reaches the mesial alveolar edge of p<sub>4</sub>, and its horizontal ramus is higher than that of *P. blainvillei*. All these species (except *P. gracilis*) have a relatively slender horizontal ramus, with a strong and nearly horizontal zygomatic plate, wider than on *Blainvillimys* on which the plate is less horizontal, diving distally. On the buccal side, the mesial-most edge of the masseteric fossa lies below the anterior part of m<sub>3</sub>; distally to m<sub>3</sub>, the foramen incisivum open in line with the alveolar surface.

The lower incisor starts below and lingual to the anterior half of m<sub>3</sub>, whereas it starts slightly distally in *P. variabilis* from Mas-de-Gaston, and clearly more mesially (below m<sub>2</sub>) in *Archaeomys quercyi* Mödden, 1993 from Pech-Desse or *A. intermedius* Vianey-Liaud, 1979 from Pech-du-Fraysse. The incisor is longer in *Blainvillimys helmeri* Vianey-Liaud, 1972 (i.e., from Itardies and Pech-Crabit) ending posteriorly to m<sub>3</sub>; in *Blainvillimys blainvillei* (from Orsonnette or Rigal-Jouet1) it ends just behind m<sub>3</sub>. It is triangular in cross section as seen in Mas-de-Pauffié and Les-Milles material.

dp<sub>4</sub> (Fig. 6A-D). The lower deciduous molars of *P. major* are morphologically close to that of *P. blainvillei* (Vianey-Liaud, 1979: fig. 26 a), but larger. The new material allows their variability to be described. Five synclinids are present, the SI is open lingually and limited antero-lingually by the pre-metalophid anticlinid. This strongly oblique anticlinid (anticlinid 1) can be regularly straight (11/19) or more or less bilobate (8/19). The metaconid is prolonged



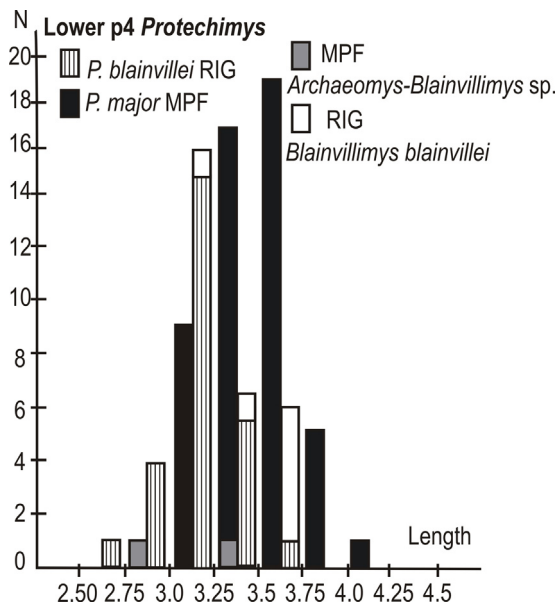
**Fig. 6.** *Protechimys major* Schlosser from Mas-de-Pauffié (Lot, France; MP26). A. MPF244, fragment of right lower jaw, with  $dp_4$  and  $m_1$ , A1, occlusal view, A2, lingual view. B. MPF19, right  $dp_4$ , B1, occlusal view, B2, lingual view, B3, buccal view. C. MPF253, fragment of left lower jaw, with  $dp_4$  and  $m_1$  erupting, occlusal view. D. MPF226, right  $dp_4$ , occlusal view. E. MPF277, right  $p_4$ , E1, occlusal view, E2, buccal view, E3, lingual view, E4, curved distal (left) and mesial (right) roots seen ventrally, widely open (juvenile). F. MPF295, left  $p_4$ , F1, occlusal view, F2, buccal view, F3, lingual view (juvenile). G. MPF284, right  $p_4$ , G1, occlusal view, G2, curved distal root still open but thickened, seen ventrally, G3, buccal view (adult). H. MPF287, left  $p_4$ , H1, occlusal view, H2, curved distal root closed and nearly closed mesial root, seen ventrally, H3, buccal view (old adult).

**Fig. 6.** *Protechimys major* Schlosser de Mas-de-Pauffié (Lot, France; MP26). A. MPF244, fragment de mandibule droite, avec  $dp_4$  et  $m_1$ , A1, face occlusale, A2, profil lingual. B. MPF19,  $dp_4$  droite, B1, face occlusale, B2, profil lingual, B3, profil buccal. C. MPF253, fragment de mandibule gauche, avec  $dp_4$  et  $m_1$  en cours d'éruption, face occlusale. D. MPF226,

in a short metalophid, which is connected mesially to a preprotoconid crestid, with which it makes an angle. This metalophid (anticlinid 2) is separated from the protoconid cuspid, then the synclinid II continues into an oblique antesisinid, both crossing the tooth. The mesolophid, transverse to slightly oblique, is connected to the obliquely elongated protoconid (anticlinid 3), at the level of a well-marked angle, parallel to the preprotoconid crestid. This angle is located at midline of the tooth, or a little buccally. The sinusid crosses the tooth from the labial to the lingual edges. Thus, the mure is absent. In this context, the synclinids II and III are not individualized. The hypoconid is obliquely elongated and parallel to the protoconid, its anterior arm being connected to the transverse to slightly oblique entolophid (anticlinid 4). Its posterior arm is linked to a short and transverse posterolophid. They delimit the synclinid IV, which is open lingually. These  $dp_4$  are similar or slightly smaller in size than those of *A. quercyi* and smaller than those of *A. intermedius* Vianey-Liaud, 1979. They are clearly less hypsodont than these species, with less deep lingual openings of the synclinids, shallower antesisinids and sinusids, and the SIV longer and wider. The angle on the anticlinids 2 and 3 are situated more lingually (metalophid and mesolophid shorter) and the buccal parts are longer as a result.

$p_4$  (Fig. 6E–H). They appear longer than those of *P. blainvillei* (e.g., from Rigal-Jouet1; Fig. 7). They are smaller and less variable in size than those from Pech-Desse (Vianey-Liaud, 1979), likely related to their lower hypsodonty. Variations in the occlusal pattern can be seen mainly on weakly worn teeth. On these, it appears that SI is absent, or if present, it appears as a small and shallow indentation of the pre-metacoid (anterolophid) crestid. The metaconid may appear swollen in early stages of wear, but ends up being indistinguishable from the anterolophid with stronger wear. It is clearly less swollen and more merged with the anterolophid in *A. quercyi* and *A. intermedius*, in which the protoconid and hypoconid are more elongated than in *P. major*. The anterolophid can be tightly joined to the protoconid, or separated by a more or less deep anterosinusid on two specimens (see below: *Archaeomys-Blainvillimys* sp.). In strongly worn teeth, the occlusal surface reaches the frequent vertical mesial fold of the crown, drawing a more or less protruding angle. SII is open lingually until advanced stages of wear. The sinusid crosses the tooth transversally up to significant stages of wear, but it is closed lingually in more advanced stages of wear, and SIII is absent. SIV is present and shallow, and disappears soon with wear; however, it is wider mesiodistally and longer buccolingually than in *A. intermedius*. It can be divided by a short mesio-distal crestid. The two roots,

$dp_4$  droite, face occlusale. E. MPF277,  $p_4$  droite, E1, face occlusale, E2, profil buccal, E3, profil lingual, E4, racine distale à section incurvée (à gauche) et racine mésiale à section arrondie (à droite) vues ventralement, largement ouvertes (juvénile). F. MPF295,  $p_4$  gauche, F1, face occlusale, F2, profil buccal, F3, profil lingual (juvénile). G. MPF284,  $p_4$  droite, G1, face occlusale, G2, racine distale encore ouverte mais épaissie, vue ventralement, G3, profil buccal (adulte). H. MPF287,  $p_4$  gauche, H1, face occlusale, H2, racine distale close, et racine mésiale presque complètement obturée, H3, profil buccal (individu âgé).



**Fig. 7.** Histogram of total length (L) of lower  $p_4$  of *Protechimys major* Schlosser (Mas-de-Pauffié: median L between 3.5 and 3.75 mm) and *P. blainvillei* Lavocat (Rigal-Jouet1: median L between 3.0 and 3.25 mm), on which are added the known 7  $p_4$  of *Blainvillimys blainvillei* Gervais from Rigal-Jouet1, and two  $p_4$  from Mas-de-Pauffié tentatively considered as *Archaeomys-Blainvillimys* sp.

**Fig. 7.** Histogramme des longueurs totales (L) des  $p_4$  inférieures de *Protechimys major* Schlosser (Mas-de-Pauffié: L médiane comprise entre 3,5 et 3,75) et *P. blainvillei* Lavocat (Rigal-Jouet1: L médiane comprise entre 3,0 et 3,25), sur lequel sont ajoutées les 7  $p_4$  connues de *Blainvillimys blainvillei* Gervais de Rigal-Jouet1 et deux  $p_4$  de Mas-de-Pauffié attribuées avec doute à *Archaeomys-Blainvillimys* sp.

first widely open and thin, thicken and close to their lower extremities during the ageing process of the animal. The distal root is the strongest. Its deep end is arched, ensuring the reinforcement of the attachment on the jaw.

**Lower molars** (Fig. 8). SI, as an islet closed lingually, and SIV open lingually, are shallow. Thus, they are present on unworn or weakly worn teeth, and then SI (14/117) is lost before SIV (22/117). SII is open lingually up to strongly worn teeth, in which it is closed by the lingual junction between the metaconid and mesolophid. It occurs generally when the pattern of  $p_4$  shows a protruding mesial angle. With wear progress, the patterns of protoconid and hypoconid appear more and more oblique and long, and the angle between the postprotocristid and mesolophid is more distinct. The sinusid crosses the tooth up to strongly worn teeth, in which it is closed lingually by the mesolophid-entolophid junction. SIII is absent. Due to the loss of SIV, the entolophid and posterolophid are indistinct. The roots become completely ossified, closed or nearly closed when the sinusid and SII are lingually enclosed. The small buccal mesial root is closer to the arched strong distal root than the small buccal root. The same kind of morphological variation is observed in the smaller and less hypsodont *P. blainvillei* from Garouillas and Rigal-Jouet1. It is also similar for *A. quercyi* from Pech-Desse and *A. intermedius* from Pech-du-Fraysse, the teeth of these two species reaching higher size and higher hypsodonty. Their ratio – length of

mesolophid/length of stretched protoconid – is lower than in *P. major*. One can notice that higher are the crowns, greater is the amount of variation of the dimensions, whatever the lengths, widths or heights of the teeth. This fact is related to the strong disto-mesial tilting of the teeth, combined with the possible variations in the orientation of the occlusal plane with wear, which reveal the top down shape changes of the structures (anticlinids, synclinids and sinusids), which constitute the crown.

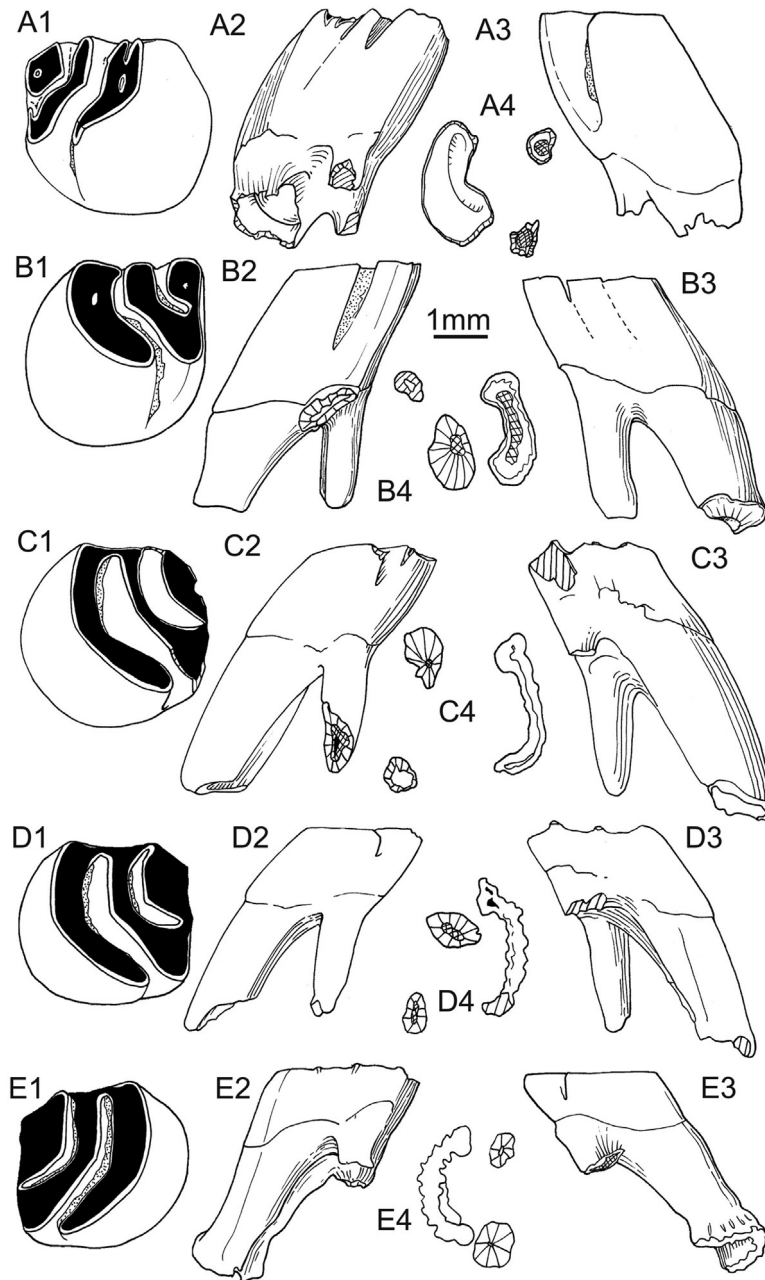
The third molar is quite smaller than the  $m_{1-2}$ , as well in *P. blainvillei*, *P. major* as in *A. quercyi* and *A. intermedius*.

**Material from Les-Milles** (Fig. 9A-C): Although the enamel blades (distal for lower teeth and mesial for the upper ones) of the lophids and lophs are often the sole structures visible, it is enough to identify the pattern characterizing *P. major* from Mas-de-Pauffié. For instance, on LM01 the same oblique shape of the anterolophid, the lingual opening of SI, the crossing sinusid and antesinusid, and the well-developed SIV. The following  $m_1$ , weakly worn, shows a SI and SIV, traits confirmed on LM20-21.

#### Cranial anatomy:

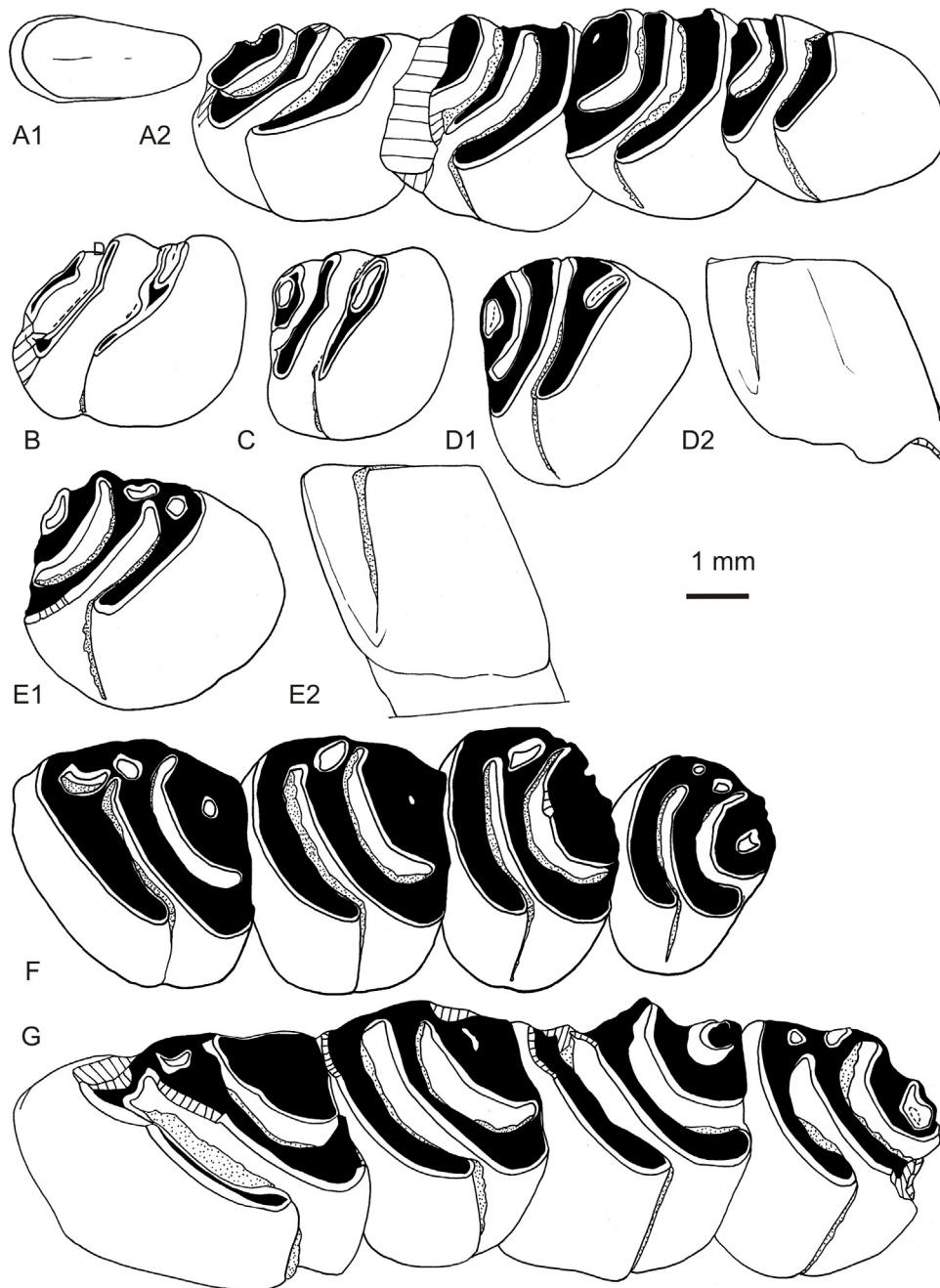
General data on the skull shape are provided by the scan of LM06 (Les-Milles; Fig. 10) and exact information about the maxillary and palate by the specimens from Mas-de-Pauffié (MPF407, 412). The bones of LM06 have been crushed and displaced from one another, but the wide infra-orbitary foramen (f.i.o.) is distinct, as well as the triangular palate, with mesially converging upper tooth rows. The zygomatic arch, parallel to the buccal edge of the molars, is closer to the skull than in *Archaeomys*, a condition which is confirmed with the maxillaries from Mas-de-Pauffié; the radius of curvature of the anterior root of the zygomatic arch is smaller than in *Archaeomys quercyi*, *A. intermedius*, or *A. laurillardii*. In frontal view, the base of the f.i.o. is flat, and it shows a clear infra-orbitary gutter at its lingual corner, whereas it is shorter and flat in *Archaeomys*. The isolated maxillaries of *P. major* from Mas-de-Pauffié show the openings of anterior palatine foramina close to the mesial edge of  $P^4$  or  $DP^4$ . The maxillary part of the palate is long, up to the mesial half of  $M^2$ , with the opening of the posterior palatine foramina. The palate (maxillary part) is thick on its whole length, contra *P. blainvillei*, where it is shorter and thick below  $P^4$  and  $M^1$  only. The palate is longer anteriorly in *Archaeomys robustus* Lavocat, 1952, *quercyi* and *intermedius* – in front of  $P^4$  – and slightly shorter and thinner posteriorly, after the distal edge of  $M^2$ .

$DP^4$  (Fig. 11A-G, I). They are characterized by the absence of SII, going with the sinus which crosses the whole width of the tooth, by a long SIII and a SIV always present. SI is always present but shorter than SIV. The main variation occurs at the level of the antesinus and the presence of the S0, anterior to SI. When S0 is present (5/11), it is separated from the antesinus by a short mesiodistal anterolophule. It can disappear with wear, but some weakly worn  $DP^4$  lack S0. The posteroloph is generally swollen obliquely, and it is bicuspid on one tooth. The shape is very similar to that of *P. blainvillei*, the teeth being slightly larger, and the lophs a little more oblique, the protocone being more stretched obliquely disto-mesially. They differ from the two  $DP^4$  referred to *Archaeomys-Blainvillimys* sp. in Mas-de-Pauffié. The latter have a well-developed S0, but



**Fig. 8.** *Protechimys major* Schlosser from Mas-de-Pauiffié (Lot, France; MP26). A. MPF34, left  $m_{1-2}$ , A1, occlusal view, A2, lingual view, A3, buccal view, A4, the curved distal (left) and the two mesial (right) roots seen ventrally, widely open (juvenile). B. MPF35, right  $m_{1-2}$ , B1, occlusal view, B2, buccal view, B3, lingual view, B4, the curved distal (right) and the two mesial (left) roots seen ventrally, less open (young adult). C. MPF356, right  $m_{1-2}$ , C1, occlusal view, C2, buccal view, C3, lingual view, C4, the curved distal (right) and the two mesial (left) roots seen ventrally (adult). D. MPF363, right  $m_{1-2}$ , D1, occlusal view, D2, buccal view, D3, lingual view, D4, the curved distal (right) and the two mesial (left) roots seen ventrally (adult). E. MPF365, left  $m_{1-2}$ , E1, occlusal view, E2, buccal view, E3, lingual view, E4, the curved distal (right) and the two mesial (left) roots seen ventrally, distal root closed (old adult).

**Fig. 8.** *Protechimys major* Schlosser de Mas-de-Pauiffié (Lot, France; MP26). A. MPF34,  $m_{1-2}$  gauche, A1, face occlusale, A2, profil lingual, A3, profil buccal, A4, la racine distale (à gauche) et les deux racines mésiales (à droite) en vue ventrale, largement ouvertes (juvénile). B. MPF35,  $m_{1-2}$  droite, B1, face occlusale, B2, profil buccal, B3, profil lingual, B4, la racine distale (à droite) et les deux racines mésiales (à gauche) en vue ventrale, moins ouvertes (jeune adulte). C. MPF356,  $m_{1-2}$  droite, C1, face occlusale, C2, profil buccal, C3, profil lingual, C4, la racine distale (à droite) et les deux racines mésiales (à gauche) en vue ventrale (adulte). D. MPF363,  $m_{1-2}$  droite, D1, face occlusale, D2, profil buccal, D3, profil lingual, D4, la racine distale (à droite) et les deux racines mésiales (à gauche) en vue ventrale (adulte). E. MPF365,  $m_{1-2}$  gauche, E1, face occlusale, E2, profil buccal, E3, profil lingual, E4, la racine distale (à gauche) et les deux racines mésiales (à droite) en vue ventrale, racine distale close (individu âgé).

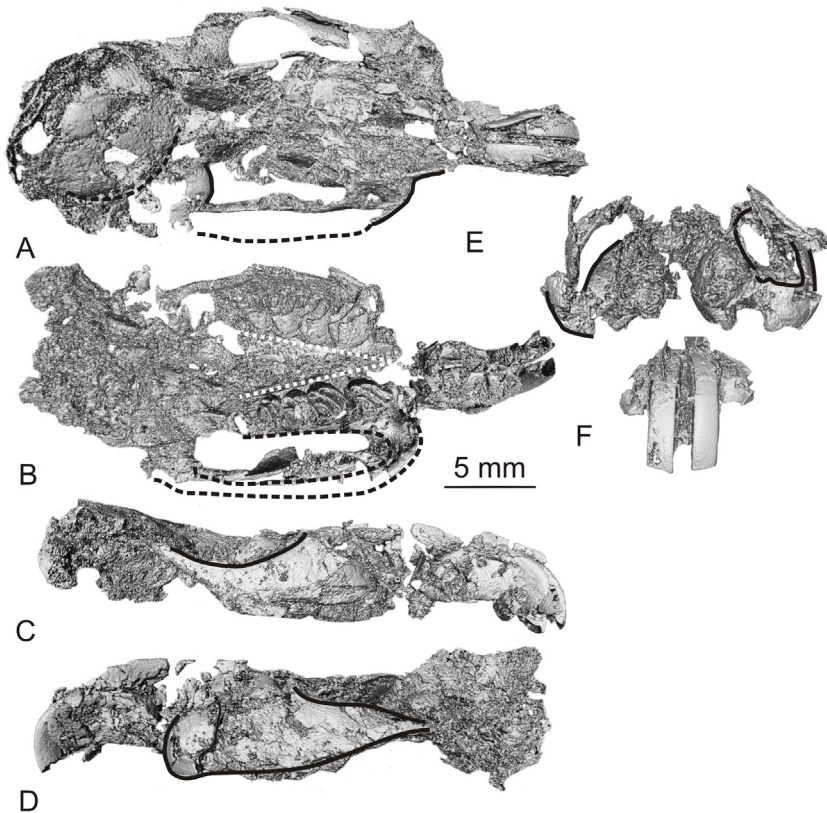


**Fig. 9.** Theridomyinae from (A–E) Les-Milles (Bouches-du-Rhône, France; MP26) and (F) Saint-Henri (Bouches-du-Rhône, France; ?MP26-MP27). A–D. *Protechimys major* Schlosser. A. LM10, left lower jaw, with A1, I, A2, m<sub>1-3</sub>. B. LM18, left p<sub>4</sub>. C. LM20, left m<sub>1-2</sub>. D. LM11, right P<sup>4</sup>, D1: occlusal view, D2: lingual view. E. *Archaeomys-Blainvillimys* sp., LM12, right P<sup>4</sup>, E1: occlusal view, E2: lingual view. F. LM36, left upper jaw, with P<sup>4</sup>-M<sup>3</sup>, occlusal view. G. *Archaeomys robustus* Lavocat, UMA13712, left P<sup>4</sup>-M<sup>3</sup>.

**Fig. 9.** Theridomyinae des gisements: (A–E) Les-Milles (Bouches-du-Rhône, France; MP26) et (F) Saint-Henri (Bouches-du-Rhône, France; ?MP26-MP27). A–D. *Protechimys major* Schlosser. A. LM10, rangée dentaire gauche, A1, I, A2, m<sub>1-3</sub>. B. LM18, p<sub>4</sub> gauche. C. LM20, m<sub>1-2</sub> gauche. D. LM11, P<sup>4</sup> droite, D1: face occlusale, D2: profil lingual. E. *Archaeomys-Blainvillimys* sp., LM12, P<sup>4</sup> droite, E1: face occlusale E2: profil lingual. F. LM36, maxillaire gauche avec P<sup>4</sup>-M<sup>3</sup>, face occlusale. G. *Archaeomys robustus* Lavocat, UMA13712, left P<sup>4</sup>-M<sup>3</sup>, face occlusale.

less than SI, with a relatively short sinus and a mure, i.e., a SII present (reduced to an islet in the worn and partly digested specimen), and SIII and SIV shorter. They differ from younger species of *Archaeomys* in the absence of SV.

P<sup>4</sup> (Fig. 9D; 11H, J, L, N). All the P<sup>4</sup> allocated to *P. major* display a SI, open or as an islet, and SII is absent contra *Archaeomys-Blainvillimys* sp. in which both are present, SII being stronger than SI. It is the same for the material from



**Fig. 10.** *Protechimys major* Schlosser from Les-Milles, reconstruction of the scanned skull LM06. A. Dorsal view. B. Ventral view. C. Right side. D. Left side. E. Front view, at the level of the infra-orbital foramen. F. Front view, at the level of incisors.

**Fig. 10.** *Protechimys major* Schlosser de Les-Milles, reconstruction du crâne scanné LM06. A. Vue dorsale. B. Vue ventrale. C. Vue du côté droit. D. Vue du côté gauche. E. Vue frontale, au niveau du foramen infra-orbitaire. F. Vue frontale, au niveau des incisives.

Les-Milles, the SI being distinct even on scan reconstructions. The SIV is open or closed only on weakly worn teeth (8/26), and absent on more worn teeth. SII is absent even on unworn teeth, and the sinus crosses the tooth, contra *P. blainvillei*, in which a short SII is still present up to worn teeth. They are stronger than that of *P. blainvillei*.

**Upper Molars** (Fig. 11M–N). SI is short and shallow when present on unworn to weakly worn ( $n = 20$ )  $M^{1-2}$  (7/63). SII is absent. The sinus crosses the tooth and it is limited buccally by the elevated crown margin. On more worn  $M^{1-2}$ , there is a buccal junction between the two main anterior lophes (fused anticline1+2 and anticline 3). The SIII remains open buccally and longer than the sinus. It joins the metaloph-metacone in late stages of wear. SIV occurs more frequently than SI (24/63).  $M^3$  are smaller than  $M^{1-2}$ , with its reduced anticlines 3, 4, 5, but display the same pattern as  $M^{1-2}$ . The main and strong root is arched, which follows the curve of the anteroloph, whereas the two small roots remain buccal, the mesial one below SI, the distal one below SIV positions.

They differ from the molars of *Archaeomys-Blainvillimys* sp. from the same locality in the lack of SII. They are wider and higher than that of *P. blainvillei* (Fig. 5).

**Archaeomys** de Laizer and de Parieu, 1839 or **Blainvillimys** Stehlin and Schaub, 1951.

**Type species of *Archaeomys*.** *A. arvernensis* de Laizer and de Parieu, 1839.

**Neotype.** Cod. 137 (NMB), left  $P^4-M^3$ , Coderet (Allier, France); Latest Oligocene (MP30).

**Type species of *Blainvillimys*.** *B. blainvillei* (Lavocat, 1952).

**Holotype.** Right lower jaw, bearing  $m_1-m_3$ , (MNHN), Antoingt (old coll., Auvergne, France); early Late Oligocene transition (MP 25).

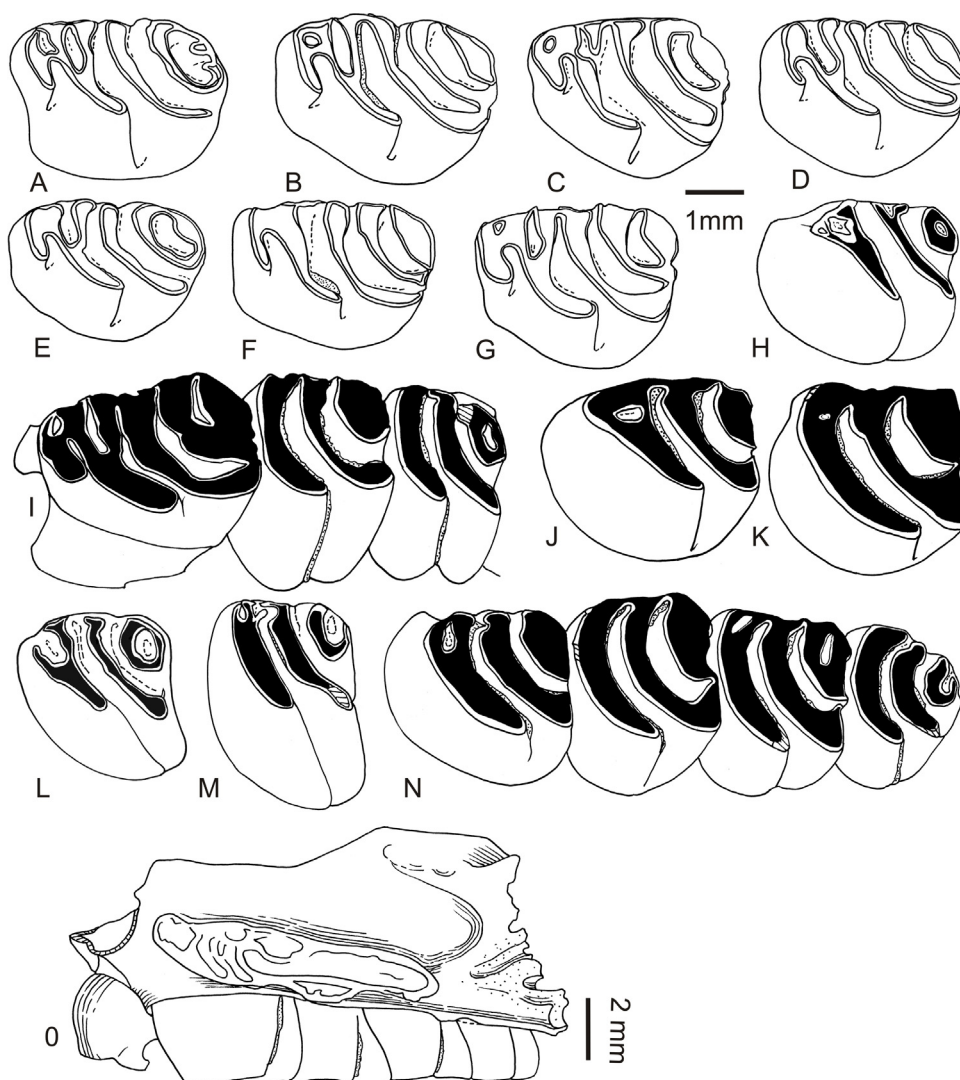
***Archaeomys-Blainvillimys* sp.**

**Description and comparisons.**

**Mas-de-Pauffié** (Figs. 12–14).

The locality has yielded one left upper jaw with  $P^4-M^3$ , 13 upper teeth (2  $DP^4$ , 5  $P^4$ , 6  $M^{1-2}$ , 1  $M^3$ ), one  $dp_4$ , and probably some  $p_4$  and lower molars within the lower teeth of *P. major*. The teeth display cement except in deciduous molars. It fills the flexids, but does not reach the occlusal plane on weakly to moderate worn teeth.

We compare this small population of *Archaeomys-Blainvillimys* sp. to *A. huerzeleri* Thaler, 1966 from Boningen and *A. robustus* Lavocat, 1952 from St-Henri/Saint-André. $dp_4$ . One  $dp_4$  differs from the *P. major* ones. It is slightly smaller and the lophids are less angular. There is a short spur (vestigial mure?) distal to the mesolophid junction with the postprotocristid. The metalophid is connected both to the anterior arm of the protoconid and the preprotoconid lophid. Therefore, there is a closed antesinusid,



**Fig. 11.** *Protechimys major* Schlosser from Mas-de-Pauffié (Lot, France; MP26), upper teeth. (A–N: occlusal views) A. MPF427, left DP<sup>4</sup>. B. MPF428, right DP<sup>4</sup>, reversed. C. MPF423, right DP<sup>4</sup>, reversed. D. MPF424, right DP<sup>4</sup>, reversed. E. MPF420, right DP<sup>4</sup>, reversed. F. MPF426, right DP<sup>4</sup>, reversed. G. MPF418 left DP<sup>4</sup>. H. MPF438, right P<sup>4</sup> weakly worn, occlusal view, reversed. I. MPF416, right DP<sup>4</sup>-M<sup>2</sup>, reversed. J. MPF431, right P<sup>4</sup> worn, occlusal view, reversed. K. MPF433, right P<sup>4</sup> strongly worn, occlusal view, reversed. L. MPF441, left P<sup>4</sup> weakly worn, occlusal view. M. MPF461, left M<sup>1-2</sup> weakly worn, occlusal view. N. MPF407, right P<sup>4</sup>-M<sup>3</sup>, moderately worn, reversed. O. MPF407, lingual profile of the maxillary.

**Fig. 11.** *Protechimys major* Schlosser de Mas-de-Pauffié (Lot, France; MP26), dents supérieures. (A–N: faces occlusales) A. MPF427, DP<sup>4</sup> gauche. B. MPF428, DP<sup>4</sup> droite, inversée. C. MPF423, DP<sup>4</sup> droite, inversée. D. MPF424, DP<sup>4</sup> droite, inversée. E. MPF420, DP<sup>4</sup> droite, inversée. F. MPF426, DP<sup>4</sup> droite, inversée. G. MPF418 DP<sup>4</sup> gauche. H. MPF438, P<sup>4</sup> droite peu usée. I. MPF416, DP<sup>4</sup>-M<sup>2</sup> droites, inversées. J. MPF431, P<sup>4</sup> droite usée, inversée. K. MPF433, P<sup>4</sup> droite très usée, inversée. L. MPF441, P<sup>4</sup> gauche peu usée. M. MPF461, M<sup>1-2</sup> gauche peu usée. N. MPF407, P<sup>4</sup>-M<sup>3</sup> droite, modérément usée, inversée. O. MPF407, profil lingual du maxillaire.

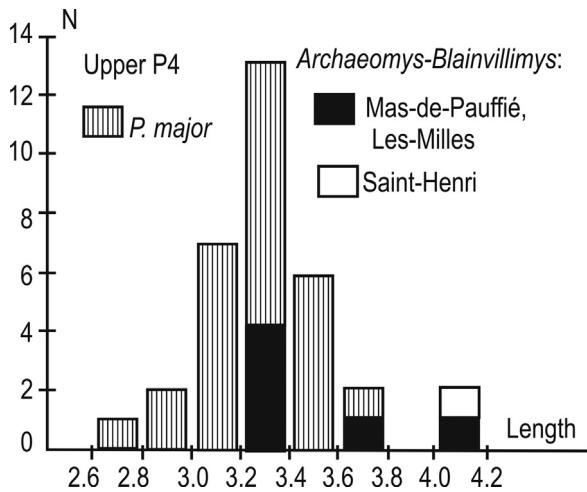
separated from the SII and SI. All the synclinids are open lingually.

**Lower premolars and molars.** Criteria for distinguishing *Archaeomys-Blainvillimys* sp. lower teeth are still to be defined. The measurements of the angle  $\alpha$  have not provided discriminant information until now. On two weakly worn p<sub>4</sub>, larger than the others, the anterolophid is separated by an anterosinusid more (Fig. 13B) or less (Fig. 13C) deep, whereas the other unworn p<sub>4</sub> have no anterosinusid. They may belong to *Archaeomys-Blainvillimys*.

The upper jaw (MPF17) is stronger than that of *P. major* and the maxillary thicker above the palate. The maxillary

part of the palate ends less distally with the posterior palatine foramen at the mesial border of M<sup>2</sup>. The radius of curvature of the anterior root of the zygomatic arch is larger than in *P. major*. In frontal view, the base of the f.i.o. shows a flat and shallow infra-orbitary gutter in its lingual corner.

**DP<sup>4</sup>.** One is partly digested and worn, the two others are well-preserved. Both shows S0, SI, SII and SIII; SIV is present only on the weakly worn tooth, as seen in *A. ehrensteini* (Mödden, 1993, Fig. 28). They differ from *Protechimys* and *A. huerzeleri* Thaler, 1966 in the presence of SII and from the Late Oligocene *Archaeomys* (*quercyi*, *intermedius*,



**Fig. 12.** Histogram of total length of upper P<sup>4</sup> of *Protechimys major* Schlosser (Mas-de-Pauffié: median L between 3.2 and 3.4 mm), on which are added five P<sup>4</sup> of *Archaeomys-Blainvillimys* sp. from Mas-de-Pauffié, and the P<sup>4</sup> of the specimen UMA of *Archaeomys robustus* Lavocat from St-Henri/St-André.

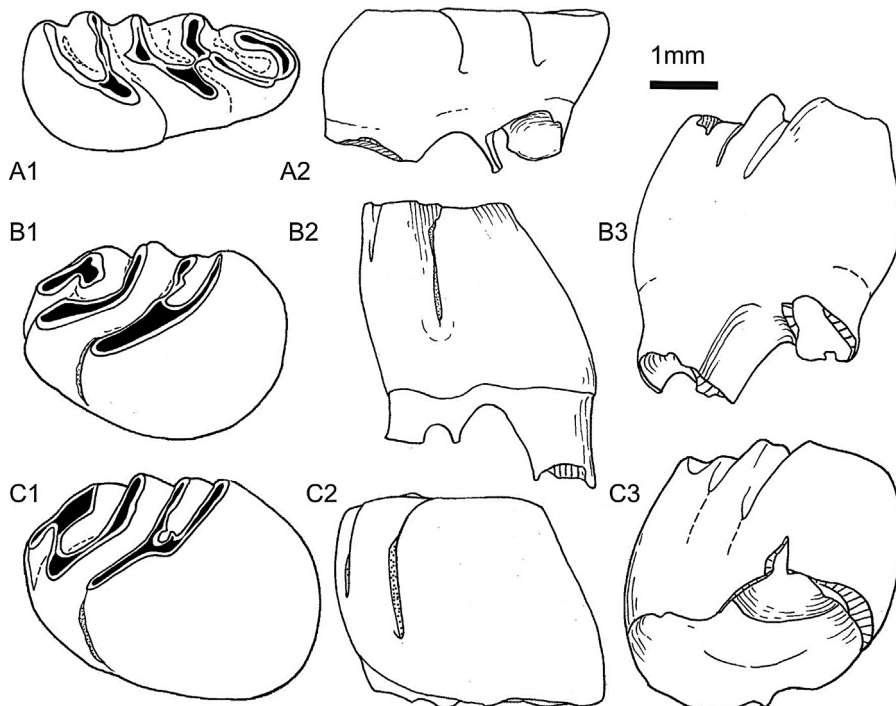
**Fig. 12.** Histogramme des longueurs totales des P<sup>4</sup> de *Protechimys major* Schlosser (Mas-de-Pauffié : L médiane entre 3,2 et 3,4 mm), auquel sont ajoutées les cinq P<sup>4</sup> d'*Archaeomys-Blainvillimys* sp. de Mas-de-Pauffié, la P<sup>4</sup> du spécimen UMA d'*Archaeomys robustus* Lavocat de St-Henri/St-André.

*helveticus* [Vianey-Liaud, 1977], *laurillardii* and *arvernensis*) in the absence of SV.

P<sup>4</sup>. One unerupted and one weakly worn P<sup>4</sup> show the well-developed SI, transversely longer than SII. With wear progress, SII appears longer than SI. The mure is therefore present. SIV is shallow, open buccally or closed on weakly worn teeth, it is reduced on worn teeth. The P<sup>4</sup> of the upper tooth row is more worn than those described above, and slightly longer. Only one isolated P<sup>4</sup> is larger than the others. The four P<sup>4</sup> of *Archaeomys-Blainvillimys* were placed on the same histogram of length of P<sup>4</sup> of *P. major*. Three appear to be close together on it, and far from the P<sup>4</sup> of *A. robustus* (type from Saint-André), one is intermediate from both. P<sup>4</sup> of the specimen determined as *Blainvillimys geminatus* Thaler, 1966 from Saint-Henri (UMA coll.) has the same size as that of *A. robustus* (Fig. 12).

M<sup>1-2-3</sup>. All the buccal synclines are present, but SI and SII are more reduced than in *B. blainvillei* and *B. stehlini*. SII and SIII remain only on heavily worn molars. The main root is arched parallelly to the anteroloph curve, as for *P. major*, but it seems slightly more mesially twisted: the bottom of the sinus is at the distal limit of the root, whereas it is slightly more mesial in *Protechimys*. It is not possible to check this character on the other molars of *A.-B.* sp., because their roots are poorly preserved.

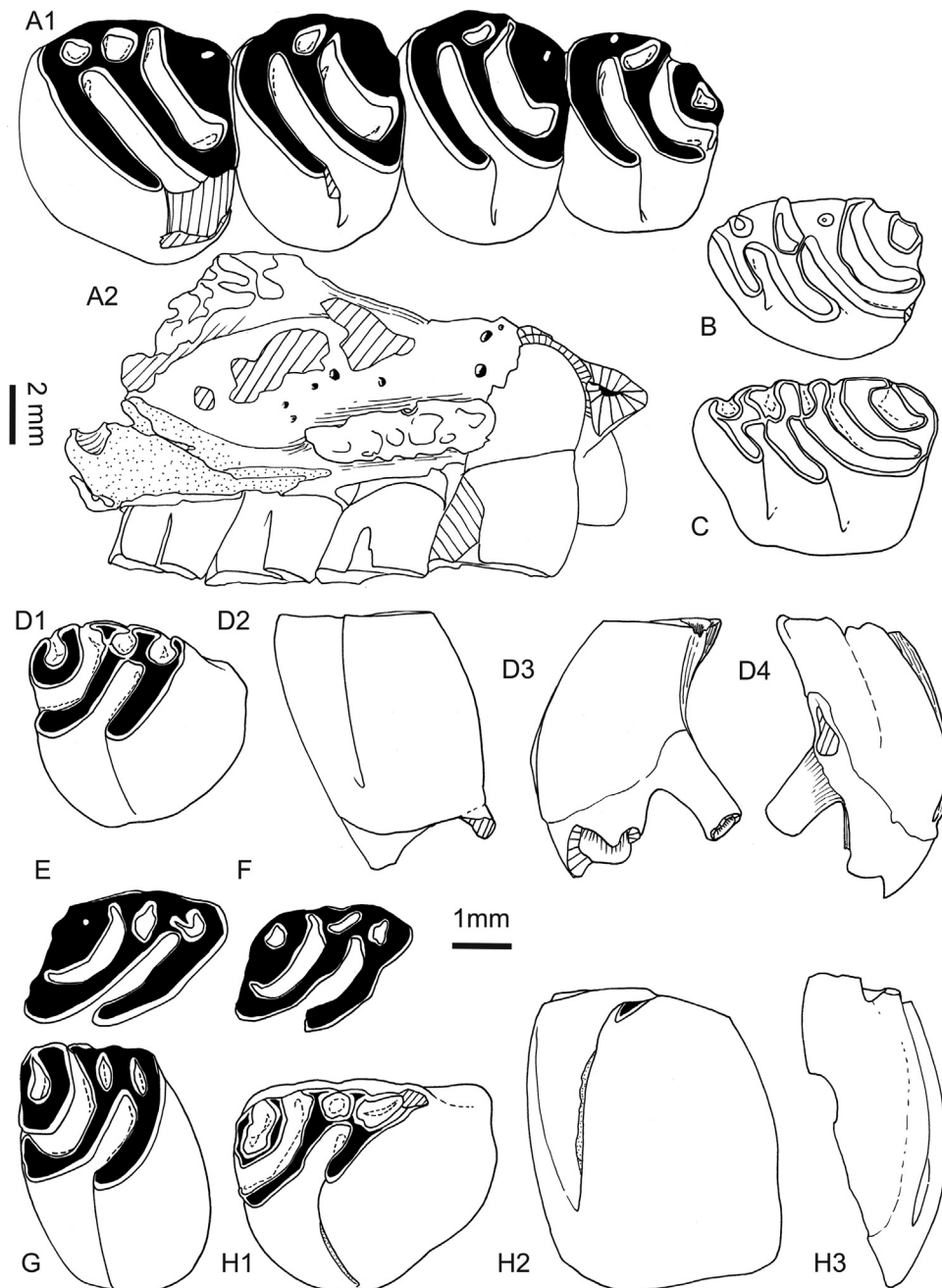
**Les-Milles** (Fig. 9E-F). Three P<sup>4</sup> and one left upper jaw with P<sup>4</sup>-M<sup>3</sup> are allocated to this genus (LM08, LM12, LM36). They show the same features as in Mas-de-Pauffié, with SI, SII, SIII and SIV, and the mure present.



**Fig. 13.** *Archaeomys-Blainvillimys* sp. from Mas-de-Pauffié, lower teeth. A. MPF530, right dp<sub>4</sub>, A1, occlusal view, A2, buccal view. B. MPF273, left p<sub>4</sub>, B1, occlusal view, B2, buccal view, B3, lingual view. C. MPF278, left p<sub>4</sub>, C1, occlusal view, C2, buccal view, C3, lingual view.

**Fig. 13.** *Archaeomys-Blainvillimys* sp. de Mas-de-Pauffié, dents inférieures. A. MPF530, dp<sub>4</sub> droite, A1, face occlusale, A2, profil buccal. B. MPF273, p<sub>4</sub> gauche, B1, face occlusale, B2, profil buccal, B3, profil lingual. C. MPF278, p<sub>4</sub> gauche, C1, face occlusale, C2, profil buccal, C3, profil lingual.





**Fig. 14.** *Archaeomys-Blainvillimys* sp. from Mas-de-Pauffié, upper teeth. A. MPF17, left row with P<sup>4</sup>-M<sup>3</sup>, A1, occlusal view, A2, maxillary lingual profile. B. MPF532, left DP<sup>4</sup>, worn, occlusal view. C. MPF540, left DP<sup>4</sup>, weakly worn, occlusal view. D. MPF34, right P<sup>4</sup>, weakly worn, D1, occlusal view, D2, lingual view, D3, mesial view, D4, distal view. E. MPF535, right P<sup>4</sup>, occlusal surface. F. MPF536, right P<sup>4</sup>, occlusal surface. G. MPF541, right M<sup>1-2</sup>, occlusal view. H. MPF539, right P<sup>4</sup> stronger than the other P<sup>4</sup>, H1, occlusal view, H2, lingual view, H3, distal view.

**Fig. 14.** *Archaeomys-Blainvillimys* sp. De Mas-de-Pauffié, dents supérieures. A. MPF17, left P<sup>4</sup>-M<sup>3</sup>, A1, face occlusale, A2, profil lingual du maxillaire. B. MPF532, DP<sup>4</sup> gauche usée, face occlusale. C. MPF540, gauche peu usée, face occlusale. D. MPF34, P<sup>4</sup>, peu usée, D1, face occlusale, D2, profil lingual, D3, profil mésial, D4, profil distal. E. MPF535, P<sup>4</sup> droite, surface occlusale. F. MPF536, P<sup>4</sup> droite, surface occlusale. G. MPF541, M<sup>1-2</sup> droite, face occlusale. H. MPF539, P<sup>4</sup> droite plus grande que les autres P<sup>4</sup>, H1, face occlusale, H2, profil lingual, H3, profil distal.

## 8. Remarks and discussion

Why use two generic names *Archaeomys* - *Blainvillimys* for this species? The type species of *Archaeomys* is a Latest Oligocene taxon (from Cournon or Pérignat, old collections

from Auvergne), which is characterized by strongly hypodont and tenodont teeth: oblique and long parallel lophs, with long oblique synclines (especially SIII, but also SIV) and sinus, SI and SII absent, long and deep antesinus, additional SO and SV on DP<sup>4</sup>, and cement filling all the

sinus (sinusid) and synclines (synclinids). The lower jaw bears strongly hypsodont teeth and short lower incisor. The premolar and molars are without SI and SIII, with two flexids only (SII and sinusid). Another species, of greater size, is identified in the same (?) locality, *A. laurillardii*, defined from Auvergne (Cournon or Pérignat?), which displays about the same morphological features. Several species have been referred to *Archaeomys*, on the basis of the same lower tooth pattern, and differing in their upper tooth pattern. The differences have been interpreted as signs of less advanced evolutionary stages (e.g., Mödden, 1993; Vianey-Liaud, 1979). Some of their upper teeth display a SII alone on P<sup>4</sup> and not on molars (*A. helveticus* – MP29, *A. intermedius* – MP28), for another a SII on P<sup>4</sup> and molars (*A. quercyi* – MP28a), for others (*A. robustus* – MP277, *A. ehrensteini* Mödden, 1993 – MP27) a SI and SII on P<sup>4</sup> and only SII on molars and then (*A. huerzeleri* Thaler, 1966 – MP26, “A.” *stehlini* Mayo, 1987 – MP25) SI and SII on P<sup>4</sup> and molars. The problem is that such a pattern is also found in *Blainvillimys blainvillei* Lavocat, 1952 (MP25), very close to that of “A.” *stehlini*. Moreover, when Mayo (1987) defined the species *stehlini*, it was referred to the genus *Blainvillimys*. The issue was reviewed by Mödden and Vianey-Liaud (1997), in order to disentangle the problems. In fact, the species *stehlini* was referred again to *Blainvillimys*, but the question of the generic attribution of species with small buccal synclines remained. Although we wrote “no common ancestor of *Protechimys* and *Archaeomys* is known at present”, the relationships between the different species of *Blainvillimys* and those referred to different species of *Archaeomys* were still unsolved. The type of *Blainvillimys blainvillei* displays lower teeth with reduced buccal synclinids, but SIII and mure vary from well distinct to weak. In *B. stehlini*, the SIII is strongly reduced either absent, but the mure is present on some. The trend to the reduction of the lingual synclines in *Blainvillimys* lineages (and also some *Theridomys*) is now well known (e.g., Vianey-Liaud, 1972, 1979, 1998), and the lineage from *Blainvillimys langei* Vianey-Liaud, 1972 – *Blainvillimys gregarius* Schlosser, 1884 – *Blainvillimys helmeri* Vianey-Liaud, 1972 to *B. blainvillei* is very well documented in numerous localities. Moreover, other species of early Oligocene *Blainvillimys* have been described like *B. heimersheimensis* Bahlo, 1975, *B. gemellus* Vianey-Liaud, 1989 or? *B. avus* (Stehlin and Schaub, 1951) (Bahlo, 1975; Vianey-Liaud, 1989, 1998), in which differences are sometimes observed only after a thorough analysis and measurements of all dental loci and their morphological and size variability. Whereas in Rupelian western European localities, *Blainvillimys* is the dominant theridomyine genus, from the end of this period (MP24) until the beginning of the Chattian (MP25–26) *Protechimys* is dominant, followed in the time by “*Archaeomys*” (MP28 to MP30), of which the relative abundance is not well known from MP27. However, we must keep in mind that the most abundant theridomyid in these localities – from late Rupelian to Late Chattian – is the issiodoromyine *Issiodoromys* (e.g., Schmidt-Kittler and Vianey-Liaud, 1987; nearly 4000 teeth of *Issiodoromys pauffiensis* from Mas-de-Pauffié).

The only way to understand the possible relationships between the morphologically converging genera *Blainvillimys* and *Archaeomys* (and *Protechimys*), is to analyze

and compare well documented populations. It is now possible for *P. major*, abundant from Mas-de-Pauffié, more difficult for the rare *Archaeomys-Blainvillimys* teeth from the localities in which *P. major* is found.

The specimen MPF17 from Mas-de-Pauffié was previously referred to *Blainvillimys geminatus*, a species named by Thaler (1966) for the specimen UM 2940 (Oensingen-Ravellen, Switzerland, MP26), on the basis of its size and the presence of small buccal synclines; he also referred another specimen, from Saint-Henri (coll. UMA; Fig. 9F), to this species. Mödden and Gad (1992) synonymized *Blainvillimys geminatus* with *Archaeomys huerzeleri* Thaler, 1966 from Boningen (UM 5068, Switzerland, MP27), both showing similar morphology, and close size. All the specimens described from Saint-Henri/Saint-André (same quarry near Marseille), of larger size than *A. huerzeleri*, are included in *A. robustus*.

Moreover, the Mas-de-Pauffié material probably includes at least one theridomyine species besides *Protechimys major*, showing attributes of both *Archaeomys* (absence of SIII on lower teeth) and of *Blainvillimys* (presence of small buccal synclines), close to *A. huerzeleri*, but showing differences at least in the DP<sup>4</sup> morphology. Two theridomyines are also reported together from Oensingen, in the same MP level (MP26), or three from Ehrenstein7 (Germany, MP27) and Boningen (Switzerland, MP27), Pech-Desse (France MP28a) Pech-du-Fraysse (France MP28b), and Rickenbach (Switzerland, MP29). In order to make clear definitely the question of the synonymy of the species *geminatus* and *huerzeleri*, the relative place of *robustus*, and their generic affiliation, it would be necessary to get and study new and better documented material, their variability remaining badly known. Until now, there are not abundant samples of these taxa, and, although more recent excavations have been done and new material collected from Oensingen (Oensingen11; Engesser and Mödden, 1997), it has not been described until now.

## 9. Results and conclusions

This paper provides evidence for defining morphological and size variability of *Protechimys major* Schlosser, known so far by poor material. The sample of Mas-de-Pauffié appears homogeneous. The width of teeth is larger and hypsodonty is higher than in *P. blainvillei*; the maxillary part of the palate is longer.

This species appears to be the most derived *Protechimys*. *P. mayoi*, defined (Mödden, 1993) on only one upper jaw from old collections (Quercy; stratigraphic position and variability unknown), cannot be considered here. It has been possible to trace the origins of the *Protechimys* lineages (Vianey-Liaud, 1998), from Late Rupelian species (*truci*, *lebratierensis*, *variabilis*), to Lower Chattian species (*gracilis*, *blainvillei*), and now *P. major*. At the beginning of the Chattian (MP25a), one lineage is identified, *P. gracilis* (Belgarric1, MP25a) considered the possible “ancestor” of *P. blainvillei* (MP25b and c), with transitional morphotypes of lower molars identified from Garouillas (MP25b) and the two lineages in Rigal-Jouet1 (MP25c) The succession of these three evolutionary stages permits the identification of a level older than the reference MP25 level (Garouillas),

and a level younger: it is the reason for the MP25 a, b (standard-locality) and c (e.g., Vianey-Liaud, 1998). The lower tooth features of the Chattian species, i.e., the lingual closure of the SII, the characters of DP<sup>4</sup>, like the transversely long S0, and the relatively short SIV, are still present in *P. gracilis*. The features of *P. blainvillei* (SII of lower teeth open lingually; on DP<sup>4</sup>, short S0 and long SIV) are accentuated in *P. major*.

In addition to the abundant *Protechimys major*, *Archaeomys-Blainvillimys* sp. is rare but present, and their co-occurrence in the small fossiliferous concentration from Les-Milles or from St-Privat-des-Vieux strengthens the hypothesis of their co-occurrence in Mas-de-Pauffié. The specimens of *Archaeomys-Blainvillimys* sp. from this locality are also different from those of *Archaeomys* from Pech-Desse (MP28a), smaller and less hypsodont, their DP<sup>4</sup> without a mure. It is still difficult to name this species. The size and morphological variation of the contemporaneous or sub-contemporaneous named species (*A. huerzeleri*, *A. robustus*) are not known and not very important.

Although the Rupelian and Early Chattian history of *Protechimys* was successful, it seems to have changed shortly thereafter. It is a paradox that this species realized a specialized dental pattern of the lower molars until MP25b, which was then extended to almost all surviving theridomyines (except *Theridomys*), but no link can be drawn between these theridomyines and *P. major*. The upper molars of all the younger species show an upper dental pattern more complicated than in *P. major*, which is found on one or two rare contemporaneous/sub-contemporaneous species (*Archaeomys-Blainvillimys* sp., *Archaeomys huerzeleri*). Their lower teeth are quite indistinguishable from those of *P. major*. In the context of this work, it was not possible to carry out a morphometric and multivariate analysis of these teeth, but some perspectives have been opened. It would be necessary to conduct such investigations, along with abundant populations of the Upper Chattian interval, like those of Pech-Desse, Pech-du-Fraysse or Coderet. In these localities, several species of theridomyines are recorded, which have replaced *Protechimys* at the MP26/MP27 transition.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crpv.2014.12.008>.

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