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RESEARCH ARTICLE

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Revision of the genus *Protadelomys*, a middle Eocene theridomyoid rodent: evolutionary and biochronological implications

Monique Vianey-Liaud*  and Lionel Hautier

Abstract

The generic status of the species referred to *Protadelomys* has long been problematic. Most *Protadelomys* species are now considered paraphyletic, except for the type species *P. cartieri* and for *P. lugdunensis*. Here, we revised these two species from their type locality, Egerkingen (Swiss Jura) for *P. cartieri* and Lissieu (Rhône, France) for *P. lugdunensis*. For the latter species, we also consider the locality of Laprade (Tarn-et-Garonne, Quercy, France). Additionally, we revised the material attributed to *Protadelomys* species that is now considered paraphyletic: *?P. alsaticus* from Bouxwiller (Bas-Rhin, France) and Cuzal (Lot, Quercy, France), *?P. maximini* from St-Maximin (Gard, France), and *?P. nievesae* from Casa Ramon (Huesca, Spain). Our detailed morphological analysis enables us to better characterize the extent of the morphological and size variability in all *Protadelomys* and *?Protadelomys* species. We show that both *P. cartieri* and *P. lugdunensis* co-existed in Egerkingen, Lissieu, and Laprade. We also erected a new genus and species, *Homœtreposciurus egerkingensis*, and reported the presence of *Euelfomys* from Egerkingen. *Euelfomys* is here described as a new genus and species from Laprade. Size and morphological comparisons enabled us to detect large intraspecific variation in the material of *?P. alsaticus* from Bouxwiller, as well as in the type population of *?P. maximini*. The co-occurrence of the two *Protadelomys* species, at least in two localities, in addition to the revision of the features characterizing the three species of *?Protadelomys*, led us to question the existence of a single evolutionary lineage (chronospecies), as previously recognized from *?P. maximini* to *P. lugdunensis*.

Keywords: Theridomorphs, *Protadelomys*, Dental morphologic and size variability, Systematics, Lutetian biochronology

Introduction

The adaptive radiation of the Theridomorpha occurred during a limited time window (Eocene to late Oligocene) and in a restricted area (Western Europe). Throughout their evolutionary history, these rodents showed a relatively wide range of sizes and adaptations, both locomotory and dietary (e.g., Hartenberger, 1971; Schmidt-Kittler 1971; Vianey-Liaud 1979, 1976; Vianey-Liaud et al. 2015; Vianey-Liaud & Marivaux 2016). Their

skulls are characterized by a large infra-orbital foramen (hystricomorphous condition), a sciurognathous mandible, a dental formula with 1–2/0 premolars and 3/3 molars, upper molars with a hypocone as robust as the protocone, and various cases of parallelisms and convergences in the structure and dental patterns.

Until recently, the early occurrence and diversification of Theridomorpha were considered to occur during the late middle Eocene, with four species of the genus *Protadelomys* (Hartenberger, 1969; Peláez-Campomanes 1995; Escarguel, 1998) and two putative pseudosciurid species (Hartenberger, 1969, 1970, 1990) being recognized from a time interval comprised between MP11–12 to MP14 (Early to Late middle Eocene). Vianey-Liaud

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and Marivaux (2021) recently showed that a number of lower Eocene ischyromyoid species display typical theridomorph features, such as a wide infraorbital foramen, a strong oblique mesiolingual to distobuccal postprotocristid on lower teeth, and the development of the hypocone and endoloph on upper DP4 and molars.

The generic status of the species now referred to *Protadelomys* has long been problematic. This is exemplified by the generic attribution of type species *P. cartieri*, which was first included in the genus *Adelomys* (Stehlin & Schaub, 1951). When clarifying the systematics of the wastebasket genus *Adelomys*, Thaler (1966: 24–26) decided to place *cartieri* within the genus *Masillamys* Tobien, 1954, together with two other species, *M. lousisi* and *M. tobieni*, later attributed to different genera (i.e., *Meldimys lousisi* Michaux, 1968; *Elfomys tobieni* Hartenberger, 1971). Hartenberger (1969) created the genus *Protadelomys* to generically distinguish the species "*Adelomys*" *cartieri* (Stehlin & Schaub, 1951) from the Upper Eocene species of the genus *Adelomys* (e.g., Thaler, 1966: 30–50). For Hartenberger, the dentition as well as some anatomical features of the sphenoidal region should be considered as primitive. He then rejected Thaler's proposal to attribute the species *cartieri* to the genus *Masillamys*, since its skull was hystricomorphous (Hartenberger, 1968, 1969) while that of *Masillamys* was so far considered as sciuriformous (Tobien, 1954). The concise original diagnosis of *Protadelomys* proposed by Hartenberger (1969), with *P. cartieri* as type-species, partly hindered the assessment of intraspecific variability in the assemblage of *Protadelomys* from Egerkingen, in which we detected important variability. A revision of all the species formerly included in the genus *Protadelomys* seemed essential to better understand the relationships between the different species of the "*Protadelomys* complex". This work represents the third part of a morphological and phylogenetic analysis of Eocene theridomorphs. The first part proposed a revision of the genus *Masillamys* from Messel (Vianey-Liaud et al. 2019). The second part (Vianey-Liaud & Marivaux, 2021) focused on theridomorph early diversification using phylogenetic analyses that included middle Eocene species of *Masillamys* and *Protadelomys*.

Recent phylogenetic advances on theridomorphs (Vianey-Liaud & Marivaux, 2016) and European Eocene rodents (Vianey-Liaud & Marivaux, 2021) pushed back

the origin of Theridomorpha to the lower Eocene. These studies mainly included lower Eocene rodents previously considered as Ischyromyoidea, as well as several middle Eocene theridomorphs. The retrieved tree topologies suggested that *Protadelomys* was paraphyletic, with only the most recent species, *P. lugdunensis* and *P. cartieri* being considered as monophyletic (Vianey-Liaud & Marivaux, 2021: Fig. 2–4). Vianey-Liaud & Marivaux (2016) then suggested that the three basal branches (*P. alsaticus*, *P. maximini*, and *P. nievesae*) could represent evolutionary grades, but refrained to attribute different generic names to each of them in order to avoid an unnecessary complexification of the clade taxonomy. These species were then questionably kept in the genus *?Protadelomys*.

Here, we first revise the material attributed to two species of the clade *P. cartieri*/*P. lugdunensis* from their type localities and other localities, then revise *Protadelomys* species now considered as paraphyletic: *?P. alsaticus*, *?P. maximini*, and *?P. nievesae* (Fig. 1). Our new morphological descriptions led us to describe new theridomyoid taxa as well as to discuss previously considered differential features between *Protadelomys* and three other Eocene genera (*Masillamys*, *Pantrogna*, and *Hartenbergeromys*).

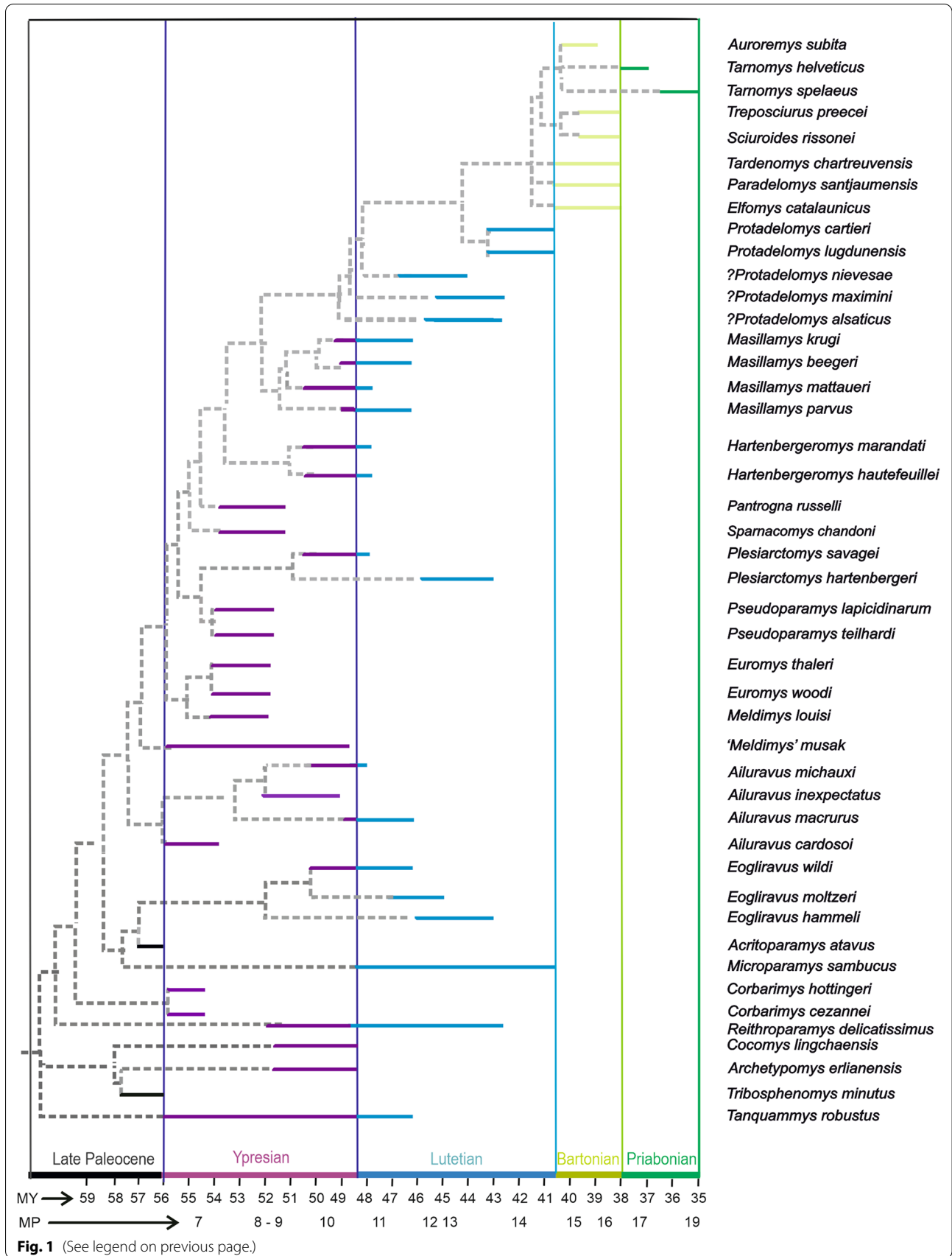
Material and methods

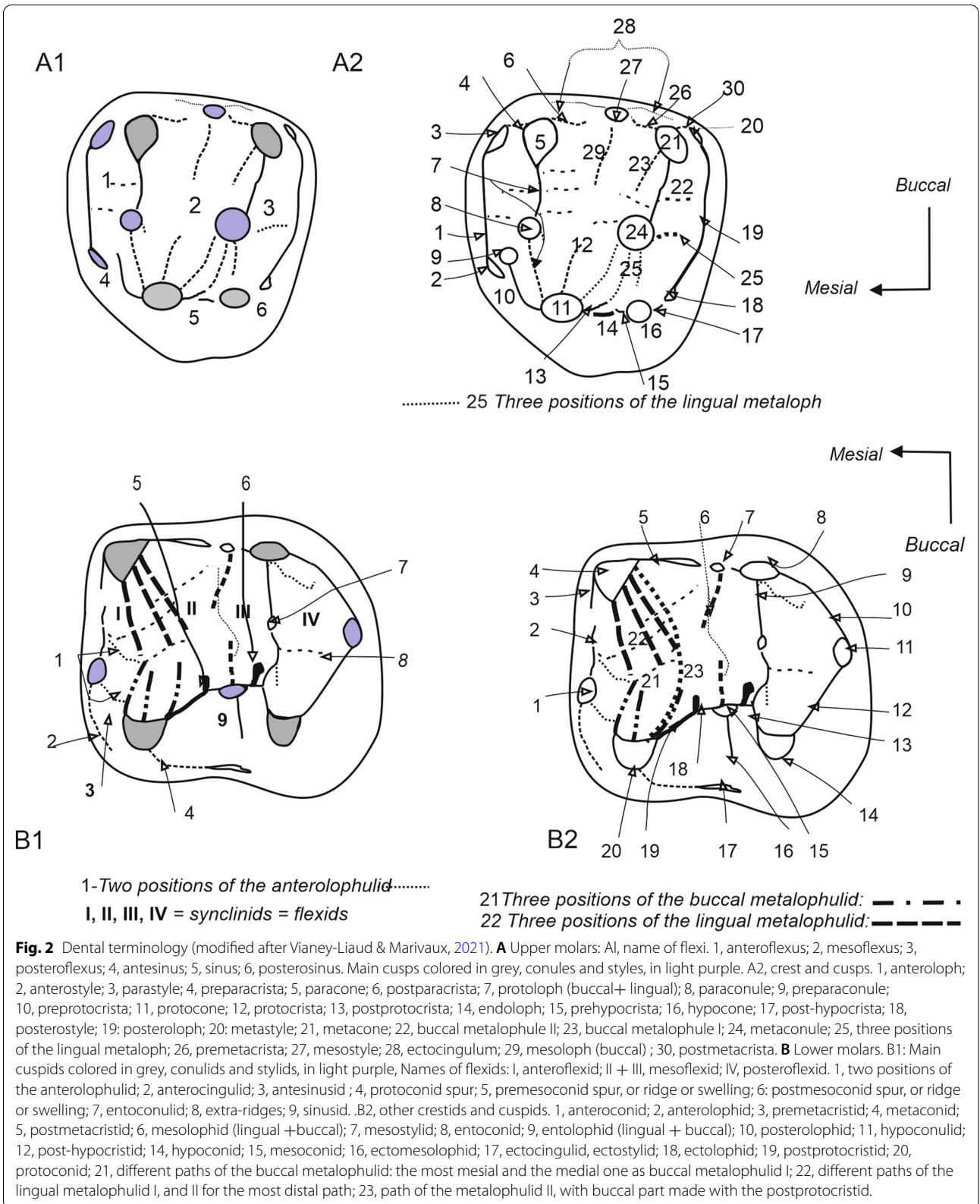
Studied specimens

The material and their measurements are listed in Additional file 1: S1, Additional file 2: S2, Additional file 3: S3, Additional file 4: S4, Additional file 5: S5, and Additional file 6: S6). We revised the assemblages of *Protadelomys* from Egerkingen (Swiss Jura), Lissieu (Rhône, France), Bouxwiller (Bas-Rhin, France), St-Maximin (Gard, France), Casa Ramon (Huesca, Spain), Laprade (Tarn et Garonne, France), and from Cuzal (Lot, France). The studied material is housed in the collections of the Naturhistorisches Museum Basel (Switzerland; NHMB) for the Egerkingen localities, in the collections of the Université de Lyon and of the Musée des Confluences for *Protadelomys* from Lissieu, and the collections of the Université de Montpellier (France; UM) for all other localities. The material studied has been compared to casts of *P. nievesae* (Museo Nacional de Ciencias Naturales, Madrid), mainly composed of isolated teeth, with a few partial jaws. We described the dental morphology

(See figure on next page.)

Fig. 1 Place of the species belonging to the genus *Protadelomys* and *?Protadelomys* on the phylogenetic tree from Vianey-Liaud and Marivaux (2021, Fig. 4), replaced on a stratigraphic scale. In that paper, the species *marandati* and *hautefeuillei* makes a clade, separated from their sister species, *russelli*. For this reason, and the reevaluation of their morphological features, they are both referred to the genus *Hartenbergeromys*. In the cited paper, the generic attribution of several other species has been changed because of morphology and phylogenetic relationships (*cezannei* has been changed from *Pseudoparamys* to *Corbarimys*; *inexpectatus* from *Euromys* to *Ailuravus*, *lapicidinarum* from *Plesiarctomys* to *Pseudoparamys*)





using the terminology of Vianey-Liaud et al. (2019, Fig. 1) modified in Vianey-Liaud and Marivaux (2021; Fig. 1), and slightly modified again here (Fig. 2). In the following descriptions, we use the term “typical” to indicate the type population of a species. For some species (notably *?P. alsaticus* and *?P. maximini*), we found an important morphological and dimensional variability. Therefore, we defined several morphotypes, which deviate from the characters (cf.) of the considered typical species.

Measurements and statistical analyses (Table 1)

All measurements were made with a Nikon Measuring microscope for the material from St-Maximin, Bouxwiller, Cuzal, Laprade and Lissieu, and the casts from Casa Ramon. All the teeth studied from Egerkingen were drawn at the NHMB, (magnification $\times 31, 5$) and their measurements calculated from the drawings (protocol tested for the specimens of *alsaticus*, available from Bouxwiller or Cuzal and the casts of *nievesae*). The teeth are weakly and unilaterally hypsodont; the walls of the crowns are generally vertical, but sometimes curved, the corresponding cusps being bulged. Therefore, the dimensions slightly vary from the top to the bottom of the crown. As often as possible, we measured maximal mesiodistal length and buccolingual width. To avoid any bias, we decided to measure all teeth without taking into account data from the literature. When both normality and homoscedasticity are assumed and tested, we perform multivariate analyses of variance (MANOVAs) to compare dental measurements (i.e., length and width) between the different species of *Protadelomys* and *?Protadelomys*. We perform statistical analyses with Past 4.04 (Hammer et al., 2001).

Geographical and geological context

Localization of the rodents from Egerkingen fillings (Additional file 1: S1)

We recognized several rodent taxa among the Egerkingen specimens, with a noticeable variability in the dental morphology. The question of their origin from the different “Egerkingen” fissures is crucial, as biochronological differences have been reported since Stehlin (1903). Hartenberger (1969, 1970) cited Stehlin (1903) and then Hürzeler (1963, cited in Hartenberger, 1969) who proposed age differences between the numerous fissure fillings in the karstic complex of Egerkingen based on primates and ungulates. The oldest localities would correspond to Egerkingen γ and Huppersand (“lower–middle Lutetian”), the youngest to Egerkingen α and β (“Upper Lutetian”). However, Wood (1962, cited in Hartenberger, 1969) and Franzen (1968) considered that the specimens of *Plesiarctomys* (from fissures Ef, Eg, Eh, Ek, and He) and *Palaeotherium* show a “relative homogeneity”. During

the symposia around the mammalian biochronology of the European Tertiary (Schmidt-Kittler 1987, Aguilar et al. 1997), Egerkingen $\alpha + \beta$ were considered as type locality for the standard level MP14. Faunal lists of these localities included the rodent taxa *Protadelomys cartieri*, *Paradelomys* sp. (EK H003), and *Treposciurus* sp. (EK H004). It was only during the second symposium, known as BiochroM’ meeting, that Egerkingen γ and Huppersand were considered to be close to the level MP13, but without associated faunal list. Among the material stored in the Basel Museum, we observed that five specimens were labeled Huppersand, six Egerkingen γ , and all the others, Egerkingen only, except Em 21 (mandible) which is labelled Egerkingen α . For Hartenberger, Ek H003 (Hartenberger, 1969, pl. I, Fig.3) would come from Egerkingen α and Ek H004 (o.c. pl.I, Fig.4), from Egerkingen γ . However, in the NHMB collection, these two specimens are labeled “Egerkingen”, without precision on the fissure. No rodents are indicated as coming from Egerkingen β . Therefore, it is impossible to relate the observed morphological and size variations to stratigraphical levels or to timing of faunal changes.

Hartenberger (1969) identified all theridomyid specimens from Egerkingen as *Protadelomys cartieri*, except for three specimens: Ek 592 was determined as *?Protadelomys* sp., Ek H003 and Ek H004 as *Pseudosciuridae* gen. and sp. indet 1 and 2., later as *Paradelomys* sp. and *Treposciurus* sp (Escarguel, 1999). *Plesiarctomys* from Egerkingen has been described in Wood (1970).

Among the 50 observed specimens including jaws and isolated teeth, 44 upper teeth and 45 lower teeth were found in different fillings (Ef, Eg, Ek or He) (see Additional file 1: Data S1). We considered as difficult to distinguish species using upper teeth since the morphological differences between *P. cartieri* and *P. lugdunensis* only involve degrees of individualization of the same structures (e.g., mesoloph, metalophules I and II). In contrast, differential structures on the lower teeth are discrete and more easily identifiable (mesoconid present or absent, orientation and length of the posprotocristid, occurrence of protocristid on p4). Eleven specimens display features similar or compatible with that of the holotype of *P. cartieri*. Fourteen are questionably approached to this species, but could represent another species (see descriptions below). For the lower teeth, because Eg 587 is considered to belong to *P. cartieri*, as proposed by Stehlin and Schaub (1951), seven specimens (Ek 67, 69, 81, 70, 76, H002, H004) sharing numerous characters with this specimen, especially the absence of mesoconid and very short ectolophid, are here also referred to this species. Some (Ek 248, Ek 250, and He6) share some characters but there are a few differences, described below.

Table 1 Range of the size variations (length and width: min., max.; average \pm Sm = σ/\sqrt{n} ; $v = 100 \sigma/\text{average L or W}$): A. of the different loci of teeth of *Protadelomys cartieri* Hartenberger, 1969 and B. length and width for some loci only *Protadelomys lugdunensis* Hartenberger, 1969 from Egerkingen (MP 14; Swiss Jura). For A: equations (Y) of the regression lines and correlation rates (R^2) between length and width of the different loci of teeth

A. *Protadelomys cartieri* from Egerkingen

Length							Length/width	
	n	min	mean \pm Sm	max	σ	v	Regression	correlation
DP4	0	–	–	–	–	–	Y	R^2
P4	8	1.45	1.555 \pm 0.028	1.68	0.080	5.13	1,0684x + 0.0499	0.6673
M1	12	1.61	1.774 \pm 0.027	1.90	0.095	5.34	0.3713x + 1,2456	0.2301
M2	13	1.64	1.716 \pm 0.013	1.77	0.048	2.79	1,06x + 0.0888	0.334
M3	7	1.61	1.734 \pm 0.044	1.90	0.116	6.68	–0.2367x + 2,1062	0.0684
dp4	2	1.50	1.545 \pm 0.045	1.59	0.064	4.14	–	–
p4	8	1.56	1.676 \pm 0.027	1.81	0.077	4.59	0.0291x + 1,0697	0.0255
m1	6	1.70	1.810 \pm 0.046	2.00	0.112	6.19	0.5343x + 0.404	0.8011
m2	10	1.72	1.866 \pm 0.020	2.00	0.076	4.07	0.8502x + 0.0012	0.8915
m3	4	1.95	2.120 \pm 0.064	2.22	0.129	6.08	0.5102x + 0.5783	0.8824
Width								
	n	min	mean \pm Sm	max	σ	v		
DP4	0	–	–	–	–	–		
P4	8	1.55	1.711 \pm 0.037	1.84	0.104	6.08		
M1	12	1.74	1.903 \pm 0.027	2.00	0.082	4.31		
M2	13	1.74	1.902 \pm 0.023	2.05	0.083	4.36		
M3	7	1.53	1.696 \pm 0.040	1.87	0.105	6.19		
dp4	2	1.09	1.110 \pm 0.020	1.13	0.028	2.55		
p4	8	1.25	1.318 \pm 0.031	1.50	0.081	6.15		
m1	6	1.38	1.538 \pm 0.058	1.72	0.143	9.29		
m2	10	1.53	1.651 \pm 0.033	1.88	0.110	6.66		
m3	4	1.56	1.640 \pm 0.034	1.72	0.067	4.09		

B. *Protadelomys lugdunensis* from Egerkingen

Upper molars	Length	Width
M1	1,88	2
M2	1,78	2,06
Lower teeth	Length	Width
p4	1,94	1,48
m1	2	1,72
m1	1,66	1,25
m2	2,22	1,88
m2	1,91	1,68
m3	2,19	1,59
m3	2,25	1,75

The lower jaw Em 21 more largely differs from Eg 587 in having a mesoconid aligned mesially with the long oblique postprotocristid, and distally with the distal very short ectolophid, this resulting long oblique lophid making an angle with the prehypocristid, and in having a well-defined antesisinid–anterocingulid. These

features are found in some specimens of *P. lugdunensis* from Lissieu, like LIS 2628. Three specimens belong to very different taxa: Ek H004 and Ek 79 belong to *Homœtreposciurus inexpectatus*, a new genus and species; the third and smallest one, Ek H003, is here identified as a new genus *Eoelfomys*, described below from the Laprade locality. A few molars were too worn or

damaged to be identified and were described separately as *gen* and *sp. indet.*

Locality of Lissieu (Rhône), middle Eocene, MP14

Contrary to Egerkingen, for which the sedimentary origin of the various rodent fossils can be questioned, the Eocene vertebrates of Lissieu have been collected in a single fissure containing only four to five m³ of sediment (Depéret, 1894). This fact supports the co-occurrence of the taxa *P. lugdunensis* and *P. cartieri*.

Locality of Laprade (Tarn-et-Garonne, Quercy), middle Eocene, MP14

The fissure filling from Laprade (Tarn-et-Garonne, Quercy) has yielded 21 mammalian taxa (Sudre et al., 1990). The fauna has been biostratigraphically positioned between those from Egerkingen and Lissieu and consequently, close to the MP 14 reference-level of the European Mammalian biochronological scale, based notably on mammalian taxa such as artiodactyles like *Mixotherium priscum* and *Pseudamphimeryx schlosseri*, the primate *Nannopithec cf. filholi*, and the rodent *Protadelomys*.

Locality of Bouxwiller (Bas-Rhin), middle Eocene, MP13.

Protadelomys alsaticus has been defined from this locality (Hartenberger, 1969). The rodents studied below, stored in the UM collections, have been extracted by washing and screening green marls outcropping at the base of the quarry of Bouxwiller (Jaeger, 1971). This base has been dated as lower part of middle Lutetian (e.g., Schuler & Ollivier-Pierre, 1981).

Locality of Cuzal, middle Eocene, MP13

The Cuzal fossiliferous beds occupies the section of a fissure filling of a few meters in diameter, the base of which communicates with a cavity of larger dimensions. The upper part of the filling is a yellow ochre clay rich in iron pisoliths, fine quartzes, and phosphate nodules that can reach a decimetric size. The base of the filling shows reddish, relatively homogeneous and finely bedded clays, overlying a sandy level, with rolled elements of fine and homogeneous granulometry, mainly siliceous with some pebbles of reworked pisolite clays.

Locality of Saint-Maximin (Gard); middle Eocene, MP13/14

The history of the discovery and presentation of the vertebrate fossils from the Saint-Maximin fissure fillings were reported in the proceedings of the Congress Biochrom'97 (Remy et al. 1997). Escarguel (1998) attributed most of the rodent remains from Saint-Maximin to *Protadelomys maximini*. Here, these rodents are included

in the paraphyletic *Protadelomys*. In this sample, we observed important morphological variation, possibly intraspecific one, especially among the dp4 and M1–M2, which allowed us to distinguish several morphs. The deciduous teeth are abundant in the material. One small lower molar (SMX1-299) displays morphological similarities with *Sparnacomyx* (Remy et al. 1997).

Locality of Casa Ramòn (Huesca, Spain) middle Eocene (MP12?)

This fossiliferous locality is an approximately 30-cm-thick subhorizontal bed of grey marl belonging to the Escanilla Formation. This formation was first dated as late Eocene on the based on comparison with the faunas from the localities Capella and Laguarres (Crusafont 1967; Hartenberger, 1971; Cuevas, 1990), and then considered as middle Eocene (MP12?) based on the association of primates and rodents displaying primitive features (Peláez Campomanes 1995).

Systematics

Super Family Theridomyoidea Alston, 1876

Genus *Protadelomys* Hartenberger, 1968

Type species. *Protadelomys cartieri* Stehlin & Schaub, 1951

Type locality. Egerkingen Huppertsand (Swiss Jura); middle Eocene (MP13? or 14?).

Referred species;

Protadelomys cartieri Stehlin & Schaub, 1951 and *Protadelomys lugdunensis* Hartenberger, 1969.

Questionably referred: *Protadelomys alsaticus* Hartenberger, 1969; *Protadelomys maximini* Escarguel, 1968; *Protadelomys nievesae* Peláez-Campomanes, 1995. Their features are not taken into account in the emended diagnosis of the genus.

Original diagnosis of *Protadelomys*. (Translation from French, in Hartenberger 1968).

"Small sized middle Eocene Adelomyinae with primitive cheek teeth"

Emended diagnosis. Hystricomorphous i.o.f; dentary with long diastema and mental foramen opening anterior to the p4, below the diastema.

Unilaterally and weakly hypsodont teeth; combining primitive (i), and more derived (ii) dental features. i) P4 with the hypocone absent or reduced, much smaller than the protocone. Upper molars with the hypocone slightly smaller than the protocone on M2, and the endoloph present, being short and slightly lower than the protocone and hypocone apices; short buccal mesoloph variably present; paraconule and metaconule present, slightly

protruding. Lower p4 and molars with relatively high metaconid, higher than the protoconid when present; mesolophid absent, mesoconid variably present; and hypoconulid present.

ii) Hypocone and protocone similar in size on M1; relatively high endoloph, lingual metaloph connected to the hypocone; metalophule I reduced or absent; paraconule smaller than the metaconule. Constant extra-ridges along the protoloph and metaloph absent. Complete metalophulid I distinct from the anteroconid–anterolophid; buccal antesisinid and anterocingulid variably present; thick and long postprotocristid with a premesoconid swelling; mesoconid absent to strongly reduced; very low mesiodistal ectolophid, interrupted on unworn or weakly worn teeth; complete entolophid, linked to the prehypocristid.

Differs, from:

- *Masillamys*, *Pantrogna*, and *Hartenbergeromys*: In the constant more distal attachment of the metaloph–metaconule, with the hypocone; in the absence of constant extraridges along the protoloph and metaloph; in the protoconid often present on p4; on lower molars, in the variable absence of mesoconid and in a sinusid deeper buccolingually; the entolophid always complete and higher than granules and extraridges.

- *Homœtreposciurus*: In its less basined lower teeth, less ornamented; in its higher and more continuous entolophid, and metalophulid I more distal, developed from the metaconid apex to the apex of the protoconid; in its p4 shorter than m1; in the short anterolophid, limited at the buccal half of the mesial edge, not connected to the protoconid.

- *Protadelomys* in the absence of constant extraridges along the protoloph and metaloph, the enamel surface of lower and upper teeth basins much less ornamented; in the variable absence of mesoconid and the shorter ectolophid.

***Protadelomys cartieri* (Stehlin & Schaub, 1951)**

Holotype. Ef 1002: right P4–M3.

Type locality. Egerkingen (Swiss Jura), Huppensand?; middle Eocene, MP14.

Original diagnosis. Stehlin & Schaub, 1951 (translation from German).

Upper teeth subtriangular to quadrangular; pseudypoconus (=hypocone) still directly connected to the protocone; sinus absent; conules well present; transverse crests of lower molars low or incomplete; no indication of a mesoconid.

Remarks about the diagnosis of *Protadelomys cartieri*.

Hartenberger defined the genus *Protadelomys* for the species *cartieri* from Egerkingen previously referred to the genus *Adelomys* (type: right P4–M3; Fig. 25, in Stehlin & Schaub, 1951), then to *Masillamys* (Thaler, 1966). Stehlin and Schaub (1951) provided some dental features in their diagnosis, (e.g., the lack of the mesoconid on lower teeth), which were not taken into account in the definition of the species *P. cartieri* by the following authors (Escarguel, 1998; Hartenberger, 1969; Peláez-Campomanes, 1995).

Emended diagnosis. Species of *Protadelomys* with slender lower jaw. Upper teeth with buccal protoloph and metaloph slightly lower than the paracone and metacone; buccal metalophule I variably present; buccal metalophule II free or fused to the metaconule; lingual protoloph connecting protocone and lingual metaloph absent or very low and connecting hypocone; short high endoloph; sinus shallow and short linguobuccally; paraconule smaller than the metaconule. On lower p4, protoconid weak and stretched in the protoconid ridge; on lower molars, metalophulid I and entolophid are low, complete or interrupted buccally; no indication of a mesoconid.

Differential diagnosis. *Protadelomys cartieri* differs from *P. lugdunensis*:—in its relatively slender dentary; on lower teeth, in the presence of a thicker protoconid on p4, in the absence of mesoconid and anterolophulid, and in its weak antesisinid and anterocingulid; on upper teeth, it differs in its narrower P4 and smaller M2.

Material from Egerkingen and Measurements

S1; Tables 1, 8; Fig. 3

A few lower molars are too worn (Ek 68, 44, 75, 76) or damaged (Ek 73) to be identified with certainty. The length and width of upper teeth, except that of P4 (Fig. 3, Table 1) are poorly correlated, whereas these dimensions are better correlated on the lower teeth, except p4. These p4 are far smaller than m1, which are smaller than m2. The m3 are longer but not wider than m1–m2. The M1 are generally longer than M2 (not on the type, on which both have same length. The M3 are narrower and as long as M1–2.

Description. Figures 4, 5, 6, 7, 8, 9 and 10

Skull. The specimen Ek 245, described and figured in Hartenberger (1969: 38–41) is now badly damaged. The remaining parts include a fragment with left P4 and M1. The casts of the two dental rows with P4 to M3 are still available. A fragment of the left maxillary He 14, bearing M1–M2, shows the base of the hystricomorphous infraorbital foramen.

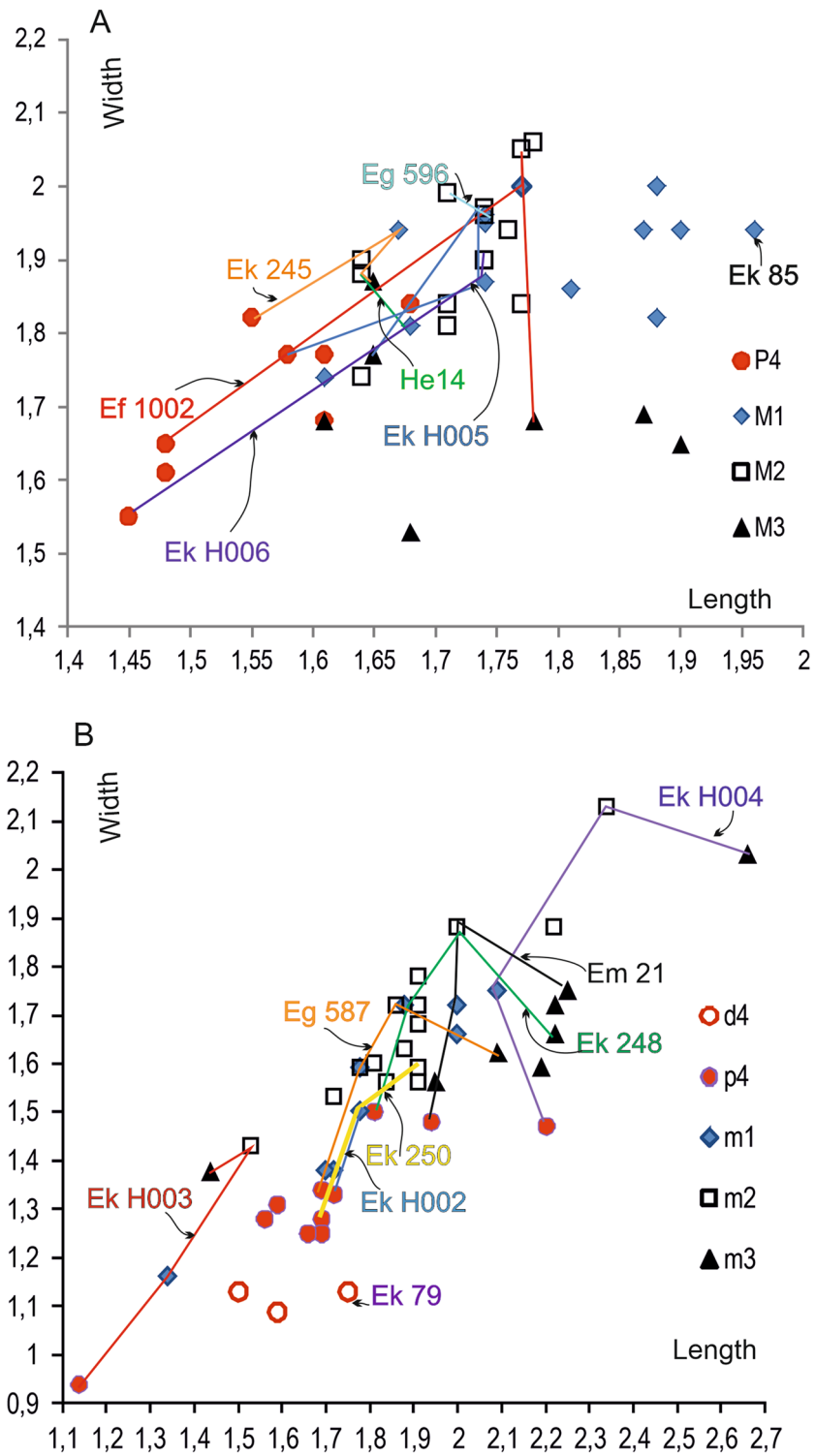
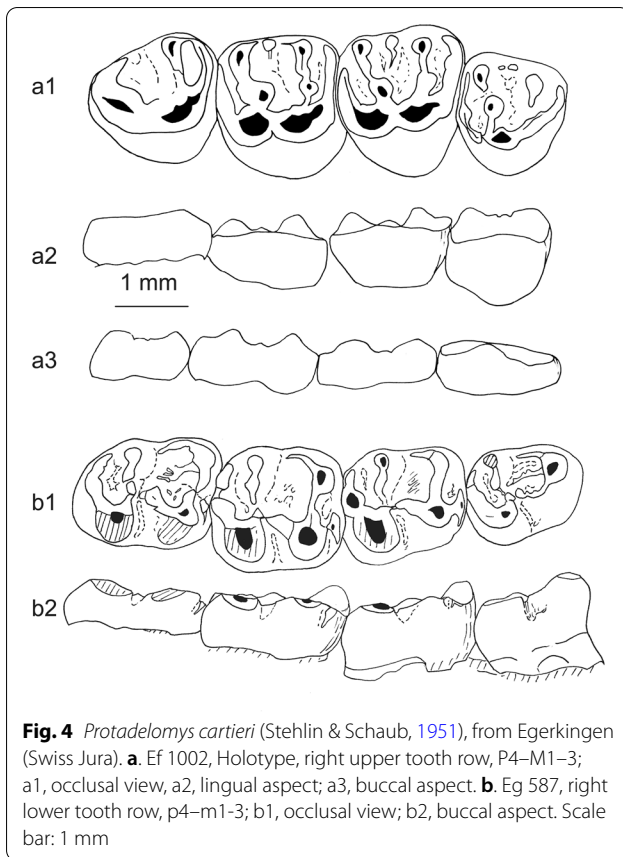


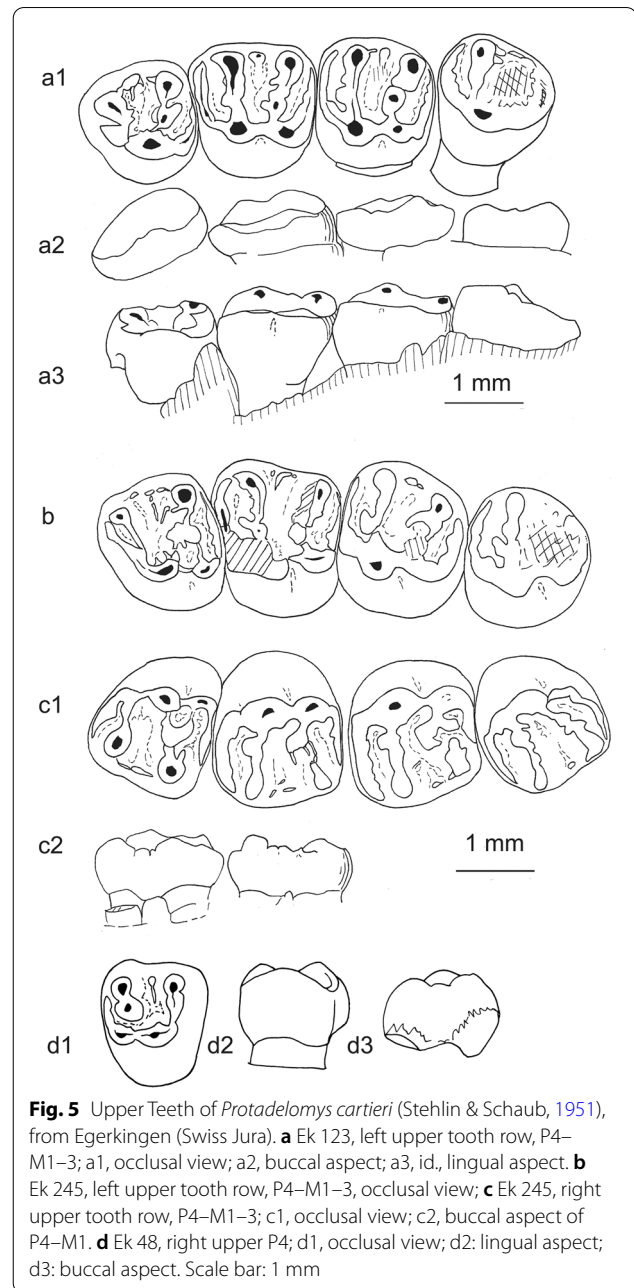
Fig. 3 Bivariate graph of the size (width/length) of the upper (A) and lower (B) teeth of the rodent's species from Egerkingen (Swiss Jura). The colored lines joins the different loci on a same jaw. **A** upper teeth. *Protadelomys cartieri* (Stehlin & Schaub, 1951): Ef 1002, Holotype, P4 to M3, red line; Ek 245, M1 to M3, orange line; Ek H006, P4 to M2, purple line; Ek H005, M1 to M3, blue line; He 14, M1–M2, green line; Eg 596, M1–M2, turquoise line. *Homætreposciurus egerkingensis* nov. gen, nov. sp.: Ek 85, M1, black circle. **B** lower teeth. *Protadelomys cartieri* (Stehlin & Schaub, 1951): Ek H002, p4–m1, blue line; Ek 250, p4–m2, yellow line; Ek 587, p4–m3, orange line; Ek 248, p4–m3, green line. *Protadelomys lugdunensis* Hartenberger, 1969: Em 21, p4 to m3. *Homætreposciurus egerkingensis* nov. gen, nov. sp.: Ek H004, p4 to m3, purple line; Ek 79, dp4, purple circle. *Eoelfomys* nov. gen. nov. sp: Ek H003, p4 to m3, red line



Upper teeth

Description of the type Ef 1002 (Fig. 4a). The P4 is smaller than the M1–2 (Fig. 3A; Additional file 1: S1). It is triangular since the hypocone is nearly absent. A weak parastyle connects to the preparacrista, which swells at the level of an anterostyle. The parastyle is lingually connected to a distinct anteroloph. There is no distinct paraconule. The paracone is bulged, prolonged in a short protoloph oriented anteriorly to the anteroloph. The enamel of the mesoflexus is smooth. A low ridge and mesostyle a little higher than this ridge terminates the mesoflexus buccally. The metacone and the paracone are at the same level. A short buccal part of the metalophule II ends at the base of the metaconule, which is rounded and strong. This metaconule connects to the postprotocrista through a well-distinct lingual metalophule. The buccal metalophule I is absent. The posteroloph is long and ends against the postprotocrista. The hypocone is indistinct.

The curved parastyle is longer and stronger on M1 than on M2. The anteroloph ends at the anterostyle. A short antesinus marks the anterostyle at its junction



with the preprotocrista, which is more distinct on M1 than on M2. The paracone and metacone are swollen, little prominent, and prolonged lingually in complete transverse buccal protoloph and metalophule II. Paraconule and metaconule are slightly protruding, the paraconule being smaller than the metaconule. Protocone and hypocone are equal on M1, the hypocone being a little smaller than the protocone on M2. The protoloph

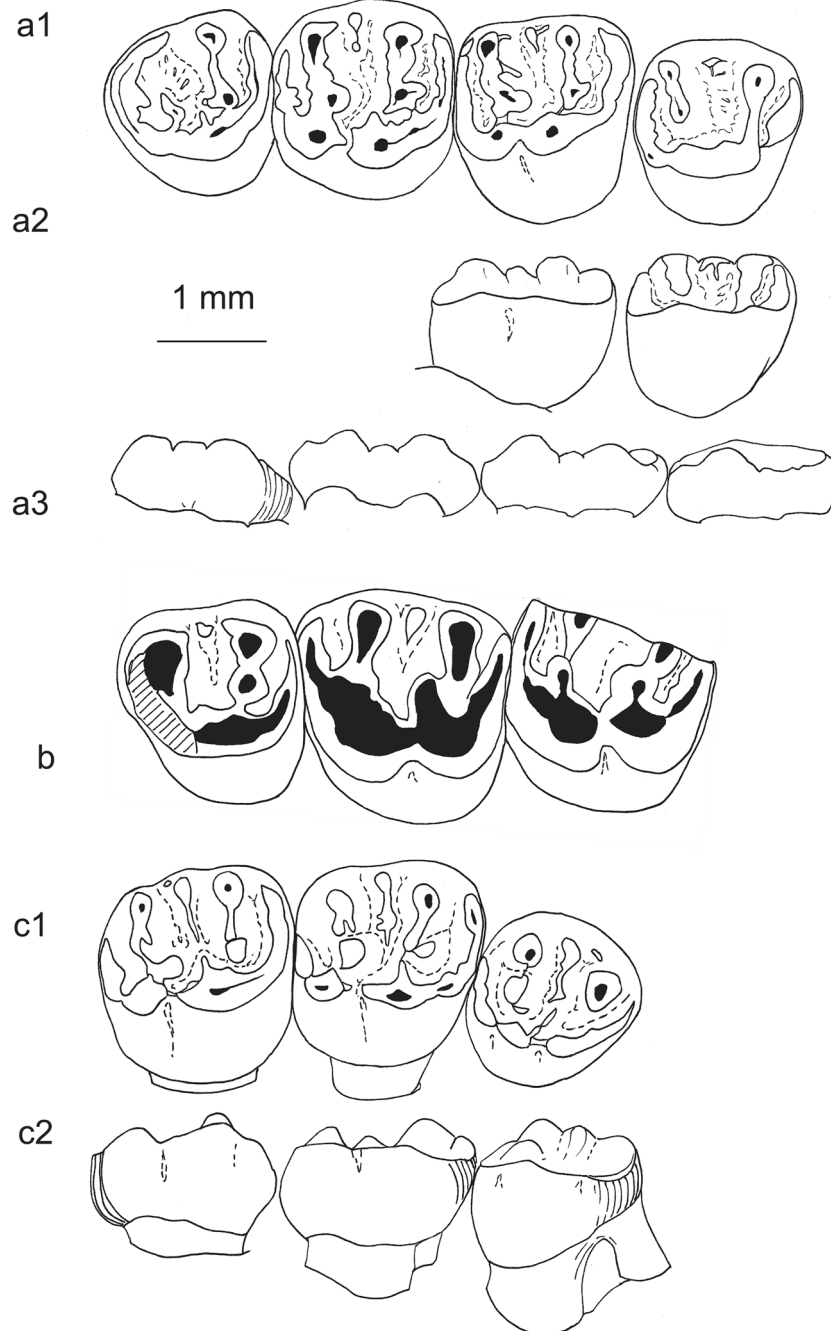


Fig. 6 Upper teeth of *Protadelomys cartieri* (Stehlin & Schaub, 1951), from Egerkingen (Swiss Jura). **a** Ek H005, right upper tooth row, P4–M1–3; a1, occlusal view; a2, lingual aspect of M1–P4; a3, buccal aspect of P4–M1–3. **b** Eg 601, left upper tooth row, P4–M2, occlusal view. **c**: Ek H006, right upper tooth row, P4–M2; occlusal view, teeth worn. Scale bar: 1 mm

connects to the protocone. The metalophule joins the hypocone slightly mesially to its center. On the three molars, a distinct mesostyle extends lingually in a short mesoloph. A short premetacrista is present on M1–2.

The posteroloph is long; it extends from the post-hypocrista to the base of the metacone, without merging with the latter.

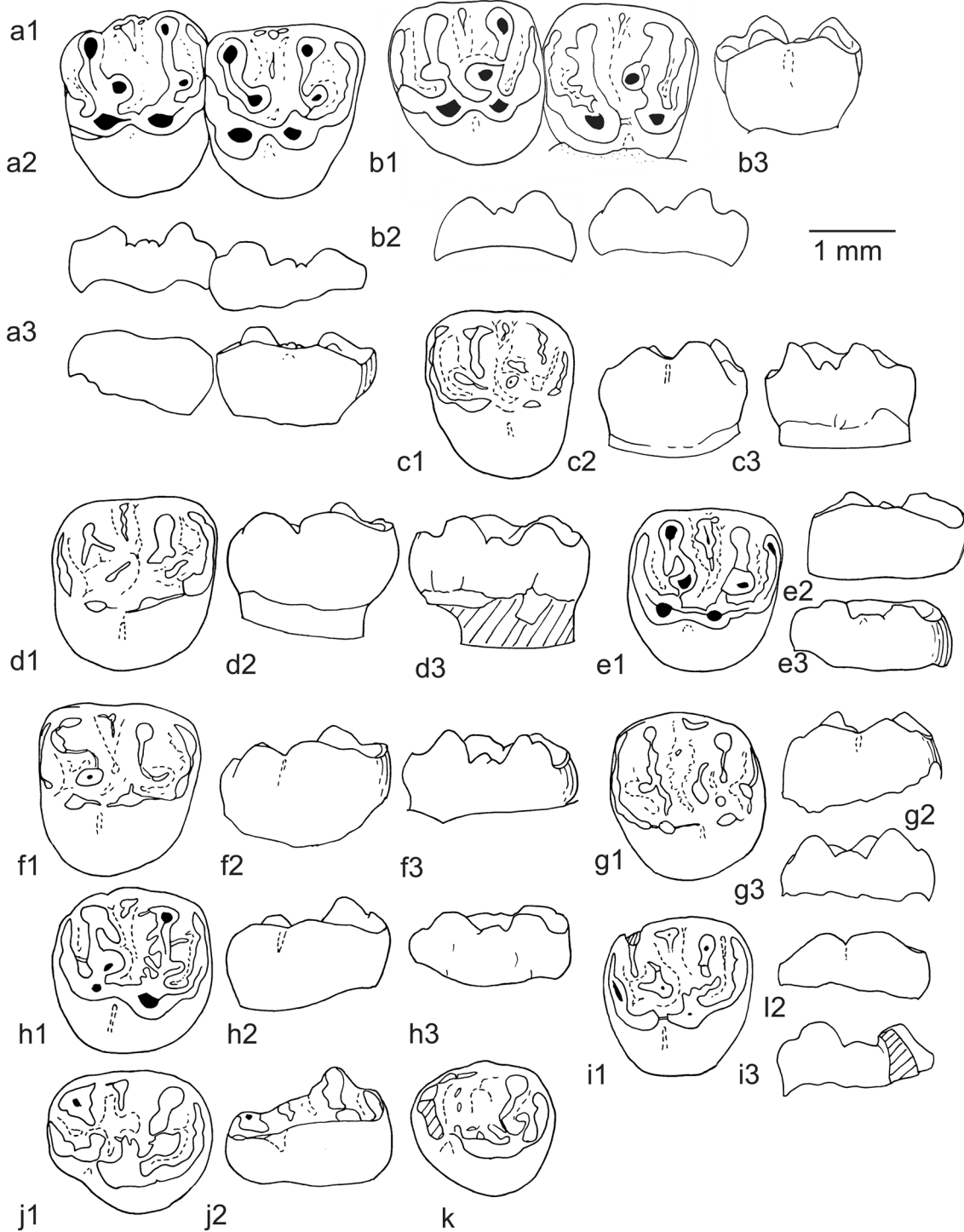
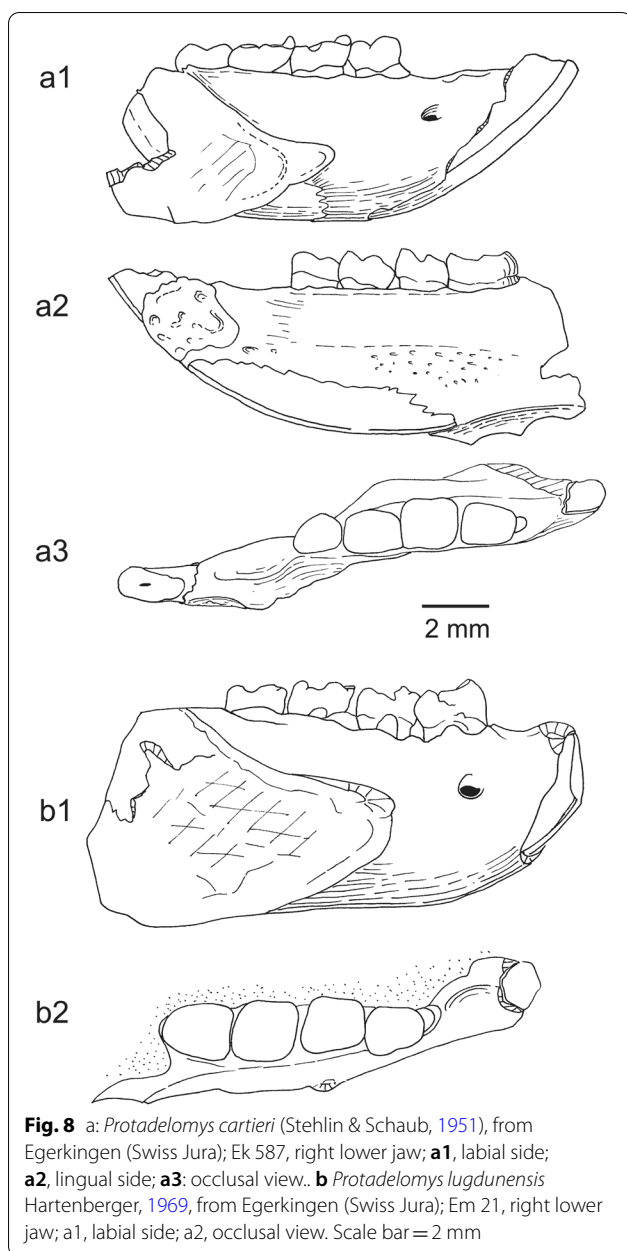


Fig. 7 Upper teeth of *Protadelomys cartieri* (Stehlin & Schaub, 1951), from Egerkingen (Swiss Jura). **a** Eg 596, right M1–M2; a1, occlusal view; a2, buccal aspect; a3, lingual aspect. **b** Ek 249, left M1–M2; b1, occlusal view; b2, buccal aspect; b3, lingual aspect of M1. **c** Ek 87, left M1, nearly unworn; c1, occlusal view, c2: lingual aspect; c3, buccal aspect. **d** Ek 45, right M1, nearly unworn; d1, occlusal view; d2, lingual aspect; d3, buccal aspect. **e** Ek 125, right M1, moderately worn; e1, occlusal view; e2, lingual aspect; e3, buccal aspect. **f** Ek 124, right M1, nearly unworn; f1, occlusal view; f2, lingual aspect; f3, buccal aspect. **g** Ek 86, left M2, nearly unworn; g1, occlusal view; g2, lingual aspect; g3: buccal aspect. **h** Ek 87, right M2, weakly worn; h1, occlusal view; h2, lingual aspect; h3, buccal aspect. **i** Ek 88, right M2, weakly worn; i1, occlusal view; i2, lingual aspect; i3, buccal aspect. **j** Ek 46, right M3, weakly worn; j1, occlusal view; j2, lingual aspect. **k** Ek 84, right M3, occlusal view. Scale bar: 1 mm



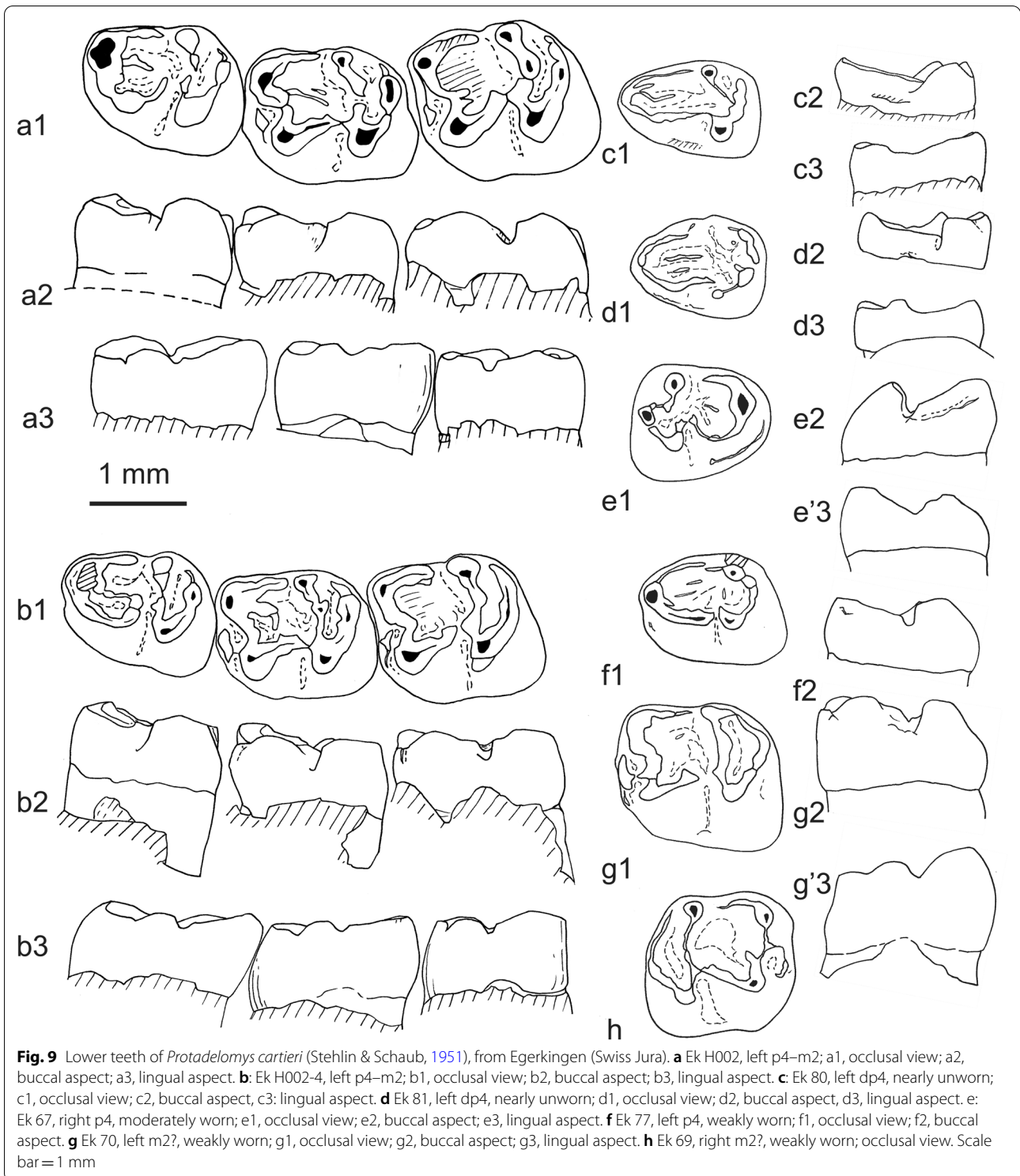
The M3 is badly preserved, with the cusps and lophes less visible than on the M1–2. It is triangular and lacks a distinct hypocone.

Other teeth

P4. The teeth are triangular on the type Ef 1002 and on Ek H006 (Fig. 6c), due to the absence of hypocone. The hypocone can, however, be small [Ek 48, Ek 123, (Fig. 5a, d) Ek 601 (Fig. 6b)], more developed [Ek 245 (Fig. 5, b, c), Ek H005 (Fig. 6a)], or as robust as the protocone (Ek 35). The size of the P4 is independent of the presence/absence of the hypocone. The anteroloph is long (holotype Ef

1002, and EK H005, EK H006, Ek 35, Ek 245), short (Ek 123, EK 601), or absent (EK 48). Paracone and metacone are swollen and similar in size. The paraconule is generally absent, and can be absent, or indistinguishable from the anterostyle on Ek 245, at the level of the connection with the protoloph. The paracone is isolated, without buccal protoloph, the protoloph being reduced to its low lingual ridge on Ek H006 (Fig. 6c); it is more generally short and directed or connected to the anteroloph at the anterostyle level; it is transverse and joins the anterior arm of the protocone on Ek H005 (Fig. 6a). The mesoflexus is narrow, buccally edged by a more or less swollen mesostyle; the latter being lengthened mesiodistally (Ek 245), or swollen (3/8). In Ek 48, Ek H006, and Ek 123, the mesostyle is connected to a mesoloph, which is short or nearly reaching the metaconule level. On Ek 123, a short postparacrista connects the paracone with the mesostyle. On four teeth (Ek 35, Ek 245 (left and right), Ef 1002), the mesostyle is twofold; it is unique on the others. The paraconule is absent (Ek 48, Ek 35) or pulled forward, merging with the anterostyle. The buccal metalophule I is reduced or absent. The metaconule, swollen, is in line with the metacone through the metalophule II. The lingual metalophule is oriented towards the posterior part of the protocone, joining it only on two specimens (Holotype and Ek 245). The P4 Ek 245 shows a short sinus, a metaconule connected to the hypocone and to the postprotocrista. Furthermore, there is a weak ridge marking the buccal metalophule I, several wrinkles around the metaconule, in the mesoflexus and the posteroflexus. On Ek 35, there is a sinus separating protocone and hypocone; a short thin remnant of the lingual protoloph connected with the protocone is visible, separated from the thick buccal protoloph, which turns forwards.

M1 and M2. The molars display close dimensions, M2 being a little shorter than M1, and M3 much narrower (Table 1). The M2 differs from the M1 in their narrower and shorter distal area: the hypocone is more buccal and a little smaller than the protocone, whereas the protocone and hypocone are equal in size on M1. The lingual flank of the crowns is higher than the buccal one. The cusps are bulbous and their apex is acute on juveniles. In adults, the buccal cusps merge within the thick buccal parts of the protoloph and metaloph. These lophes are slightly less high than these cusps. The lingual parts of these lophes are very low or absent. Lingually, the protocone merges within its pre- and post-cristae, which are aligned mesiodistally; it is the same for the hypocone that displays shorter and weaker anterior and posterior arms. The postprotocrista prolongs through the endoloph. The endoloph is short and high. The sinus is barely marked; its height is less than one-third of the crown height, so that it is often indistinguishable on worn teeth.



M1 are easily distinguished from M2 due to their strong parastyle, which lengthens the buccal edge of the tooth as opposed to the lingual edge and gives it a trapezoidal outline. The protocone and hypocone are closer

on M1 than on M2. On M2, the parastyle elongates as an extension of the anteroloph; it is sometimes swollen [Eg 596 (Fig. 7a), Ek 123 (Fig. 5a), holotype (Fig. 4a), and Ek H006 (Fig. 6c)]. Moreover, M2 mostly show a metacone

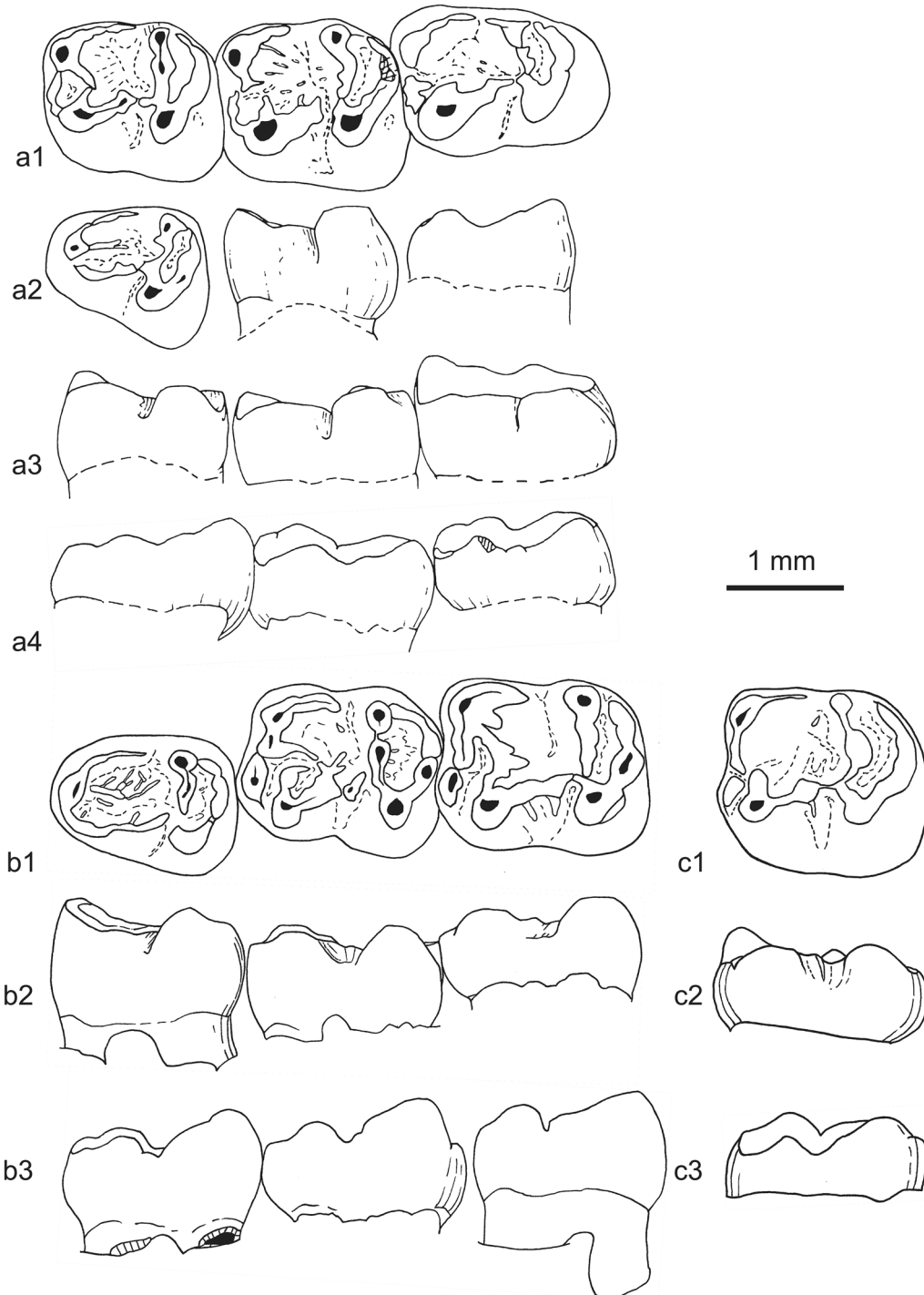


Fig. 10 **a** Lower tooth row of *Protadelomys cartieri* (Stehlin & Schaub, 1951), from Egerkingen (Swiss Jura); Ek 248, left p4–m3; a1, m2–m3, occlusal view; a2, p4, first, occlusal view, second buccal aspect; third, lingual aspect. **b** Lower tooth row, *Protadelomys* sp. indet., from Egerkingen (Swiss Jura); Ek 250, left p4–m2; b1, occlusal view; b2, buccal aspect; b3, lingual aspect. Scale bar = 1 mm

lingual to the paracone and the hypocone more buccal than the protocone, both making the posterior lobe of the tooth narrower buccolingually than the anterior lobe, and the posteroloph shorter.

The anteroloph is lower and thinner than the anterostyle and the preprotocrista. The paraconule, merged in the protoloph, can be variably stretched distomesially, more or less swollen. The protoloph ensures the connection from the paracone to the middle of the protocone, this connection being weak on unworn or weakly worn teeth.

The mesostyle is always present and can be constituted by one or two (mesial and/or distal) small low cusps (e.g., Fig. 5c) (9/29). It is nearly in line with the paracone and metacone, e.g., on the holotype and EK H005 (Fig. 3a, 6a), but it is more buccal on Ek 45 (Fig. 7d). A short premetacrista can be present (9/29) and exceptionally, a postparacrista. A mesoloph is often observed (20/29), reaching the level of the metaconule only in three specimens. On Ek 124, the top of the arched metacone is doubled (Fig. 7f1, f3). The metaconule is strong and bulged, a little lower than the metacone; its position is slightly mesial to that of the metacone and hypocone. The buccal metalophule I is variably present (19/29), sometimes highly reduced; it is lower and thinner than the buccal metalophule II and rarely connects the metaconule (4/29). The buccal metalophule II can be free or join the metaconule (12/29). The ridge connecting the metaconule and the hypocone is very low, therefore these two cusps appear separated on unworn teeth. The enamel surface is generally smooth. Some rare low wrinkles are present at the bottom of the flexi (10/29) (Fig. 5c, 6a, 7g,h). The unworn specimen Ek 87 (Fig. 7h) displays unusual features, which might be related to wear differences. The protocone and hypocone are a little closer than on the other molars, both being acute. The mesostyle is slender, without mesoloph. The lingual parts of the protoloph and metaloph are absent; therefore, the paraconule and the twinned metaconule are isolated. The buccal metalophule II is short and transverse. The paraconule and metaconule are isolated.

M3. The strongly reduced hypocone sometimes separates from the protocone (4/7) with a shallow sinus. On weakly worn teeth, this sinus communicates with the opposite flexus (2/4) (Fig. 7j, k). The paracone represents the only salient cusp, on unworn teeth. The metacone is weakly prominent from the buccal ridge it forms with the mesostylar area. The paraconule and metaconule are present, but low. The hypocone is isolated on one weakly worn tooth (Eg 597) and appears connected to the postprotocrista on more worn teeth. The posteroloph usually connects to the metacone and the hypocone.

Dentary. The body of the mandible Eg 587 (Fig. 8a) is slender than that of Em 21 [*P. cf. lugdunensis* (Fig. 8b)].

The diastema of Eg 587 is longer and the radius of curvature of the incisor larger than that of Em 21. The mental foramen opens anteriorly to the p4, at the level of the posterior part of the diastema. The masseteric crest is strong and starts ventral to the mesial root of m1.

Lower teeth (Figs. 9, 10). Among the observed materials from Egerkingen, a few specimens (Ek 67, 69, 70, 76, 81, Ek 248, Ek H002, and Ek H002-4) display the dental morphological features of the lower jaw of *Protadelomys cartieri* figured by Stehlin and Schaub (1951, Eg 587) such as the absent mesoconid and the broken distal ectolophid. The mandible Ek 248 is slightly larger than Eg 587, but the size ratio between the different dental loci is similar (see lines connecting p4, m1, m2, and m3 in both specimens, in Fig. 3B).

dp4. Only three teeth can be identified as dp4 based on the low crown and of the morphology of cusps and ridges, and we can confidently refer Ek 81 to *Protadelomys cartieri*. It differs from the dp4 Ek 80 in its wider and shorter crown. The metaconid is mesiomedian. The low protoconid is more arcuate than in Ek 80 (Fig. 10c). The low ectocingulid is present and long. The strong bulbous hypoconulid is more buccal, connected to the entolophid, making it oblique posteriorly. The posterolophid is long. The dp4 Ek 80 is slender and less bulbous than Ek 81 (Fig. 9d). We cautiously refer this dp4 to *P. cartieri*. Two mesiodistal extra-ridges develop from the distolingual side of its metaconid to the talonid basin. Its entolophid, similarly posteriorly oriented and linked to the hypoconulid, is shorter. Its posterolophid is very short lingually to the hypoconulid.

p4. The p4 are smaller than the m1 and m2 (Table 1, Fig. 3B, Additional file 1: S1). A weak and low anteroconid is present only on Ek H002 (Fig. 9a). The metaconid, the highest cusp, shows two symmetrical cristids, the postmetacristid lingually and the premetacristid buccally, the latter being curved towards the protoconid area. Present on EK H002 and Ek 127, the protoconid is almost absent on Eg 587 (Fig. 4b), Ek 248, H002-4, and Ek 67 (Fig. 9). A low ectocingulid is visible on Ek 67 only (Fig. 9e). The postprotocristid angles at its end, bearing a short spur or a swelling, considered here as a kind of “premesoconid”, as there is neither a distinct mesoconid nor a mesolophid or an ectomesolophid. It connects to the short mesiodistal ridge descending from the metaconid on Ek H002-4; it is free on the others and reduces to a low wrinkle on Ek 67. The ectolophid interrupts distal to the premesoconid and before its connection with the entolophid and the prehypocristid. The entolophid is not continuous showing breaks at its center, close to the mesial end of the prehypocristid. On Ek 67, the entolophid connects also with the hypoconulid. The hypoconulid is usually bulbous. The posterolophid is short and reduced; it is absent on Ek 67.

The two p4 (Ek 67, 127) are variants of *P. cartieri*. They differ from the one described above in their more lengthened mesiodistally postprotocristid, and Ek 127 (Fig. 9f) shows a swelling at the protoconid level, when its sinusid is less deep buccolingually than on Ek 67. The ectolophid is very short and interrupted shallowly at the hypoconid level. There is no prehypocristid on Ek 127, but the hypoconid area appears worn here. The lingual part of the entolophid is present on Ek 127 only, the entolophid being reduced to a short low ridge on Ek 67. The posthypocristid is long and the hypoconulid is moderately swollen. The posterolophid is thin and join the entoconid on Ek 127, closing the posterosynclinid lingually.

m1–m2. These teeth display a bulbous and low anteroconid, which individualizes from the protoconid flank on unworn and weakly worn molars. A short anterocingulid can be present, and the anteroflexid is narrower on m2.

A very short anterolophid directs lingually from the apex of the anteroconid. It is separated from the metalophulid I by a shallow anteroflexid, which is open buccally and lingually (Fig. 9 a, b). An anterolophulid is distinct on the worn m1 of Eg 587, or on the unworn Ek 70 (Fig. 9g). On Ek 248, the anteroflexid closes buccally, whereas it remains open on Eg 587. The lingual and buccal parts of the metalophulid I does not connect on m2 and m3; therefore, the anteroflexid communicates with the basin. On the other teeth, a low and postwardly angled metalophulid I extends from the metaconid to the apex of the protoconid. The thick postprotocristid slightly swells at its distal end, and rarely bears a premesoconid spur on m2 (Ek H002 and H002-4, Ek 70). The mesial ectolophid and the mesoconid cannot be distinguished from the oblique postprotocristid, except on the weakly worn m1 of Ek 250 (Fig. 10a1). The distal ectolophid, very short and low, appears interrupted on the occlusal surface. Very low and rare extra-ridges are present on the posterior slope of the metalophulid I to the basin (Figs. 9a, b; 10a2). The distal part of the ectolophid is much lower than the occlusal surface, and only a short crest joins the very low prehypocristid.

The entolophid is almost straight and only slightly angled. It is interrupted at its buccal part, before joining the prehypocristid. The entoconulid is variably present and slightly swollen. The salient hypoconulid separates shallow notches from the post-hypocristid and from the posterolophid on the less worn specimen (m1 of Ek H002). The short posterolophid does not reach the summit of the entoconid leaving the posteroflexid opened lingually. The weakly worn m2 Ek 70 differs from Ek H002, H002-4, and Eg 587 in having a longer buccal anterocingulid, a strong anterolophulid, and a weak ectomesostylid. Ek H002 is not the specimen figured pl.I, Fig.2 under this number *in* Hartenberger, 1969. We noticed

that the latter actually corresponds to Ek 250 (NHMB collections).

m3. One weakly worn m3 of the tooth row Eg 587 (Fig. 4b), one on Ek 248 (Fig. 10a) and two isolated much worn m3 (Ek 68, 76) are available. The anteroconid is small, not connected to the premetacristid, bearing a short buccal cingulid. A few low and short extra-ridges are visible in the basin. The thick postprotocristid ends in a short lingual spur. The very short ectolophid shows the break observed on m1–m2.

Material from Lissieu (Rhône) referred here to *Protadelomys cartieri* (Stehlin & Schaub, 1951)

Description. Among the smallest m1 and m3 of the Lissieu assemblage, five lower teeth stand out from the material assigned to *P. lugdunensis*: one right m1 (LIS 54, Fig. 11b), one weakly worn right m2 (LIS 60, Fig. 11c), and three strongly worn m3 (LIS 30, 33, (Fig. 11d) and 45–3). These teeth present some similarities with the typical lower teeth of *P. cartieri* from Egerkingen, based on the characteristics of the ectolophid, the mesial area, and of the relative proportions of the synclinids.

p4. One p4, LIS 41 (Fig. 11a), has a size compatible with the p4 of *P. lugdunensis* LIS 42, 37 and 40, but its crown is higher. The anteroconid, which is buccally displaced, is stretched mesiodistally, connects to a short metalophulid, and joins buccally the protoconid ridge. The mesiodistally stretched protoconid is more distinct on LIS 41 than on the other p4 from Lissieu, and the postprotocristid is higher than the ectolophid and makes an obtuse angle with the stretched protoconid. The postprotocristid is stretched along a mesiolingual to distobuccal axis, and bears distobuccally a bulged postmesoconid spur. The lingual entolophid is distally oriented from the entoconid, and not connected to its buccal part, reduced to a spur. As the protoconid is present and the ectolophid angles at the level of the mesoconid, which is indistinct, this p4 is referred to as *P. cartieri*.

m1. On LIS 54 (Fig. 11b), the low anteroconid separates from the protoconid, and nearly connects the plunging premetacristid. The metalophulid I is complete, low, and curved distally. The postprotocristid is almost as high as the protoconid, and its distal end is swollen; no distinct mesial ectolophid is observed. The ectolophid is very low, interrupted, and reaches the base of the postprotocristid swelling and of the prehypocristid. The entolophid, swollen at the level at the base of an entoconulid, attaches directly to the hypoconid. The hypoconulid is present and small. The posterolophid joins the base of the entoconid.

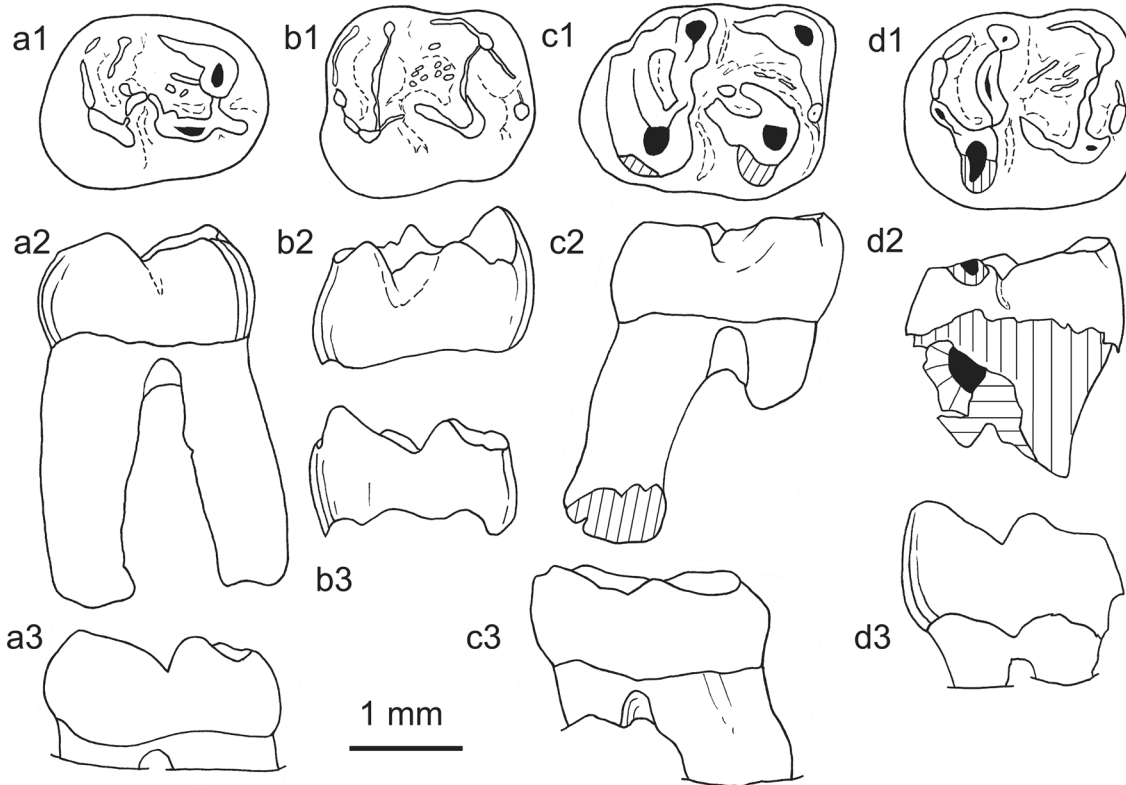


Fig. 11 Lower molars of *Protadelomys cartieri* (Stehlin & Schaub, 1951), from Lissieu (Rhône), **a** LIS 41, right p4; a1, occlusal view; a2, buccal aspect; a3, lingual aspect. **b** LIS 54, right m1; b1, occlusal view; b2, buccal aspect; b3, lingual aspect. **c**: LIS 33, right m3; c1, occlusal view; c2 buccal aspect; c3, lingual aspect. **d** LIS 60, right m2; d1, occlusal view; d2, buccal aspect; d3, lingual aspect. Scale bar = 1 mm

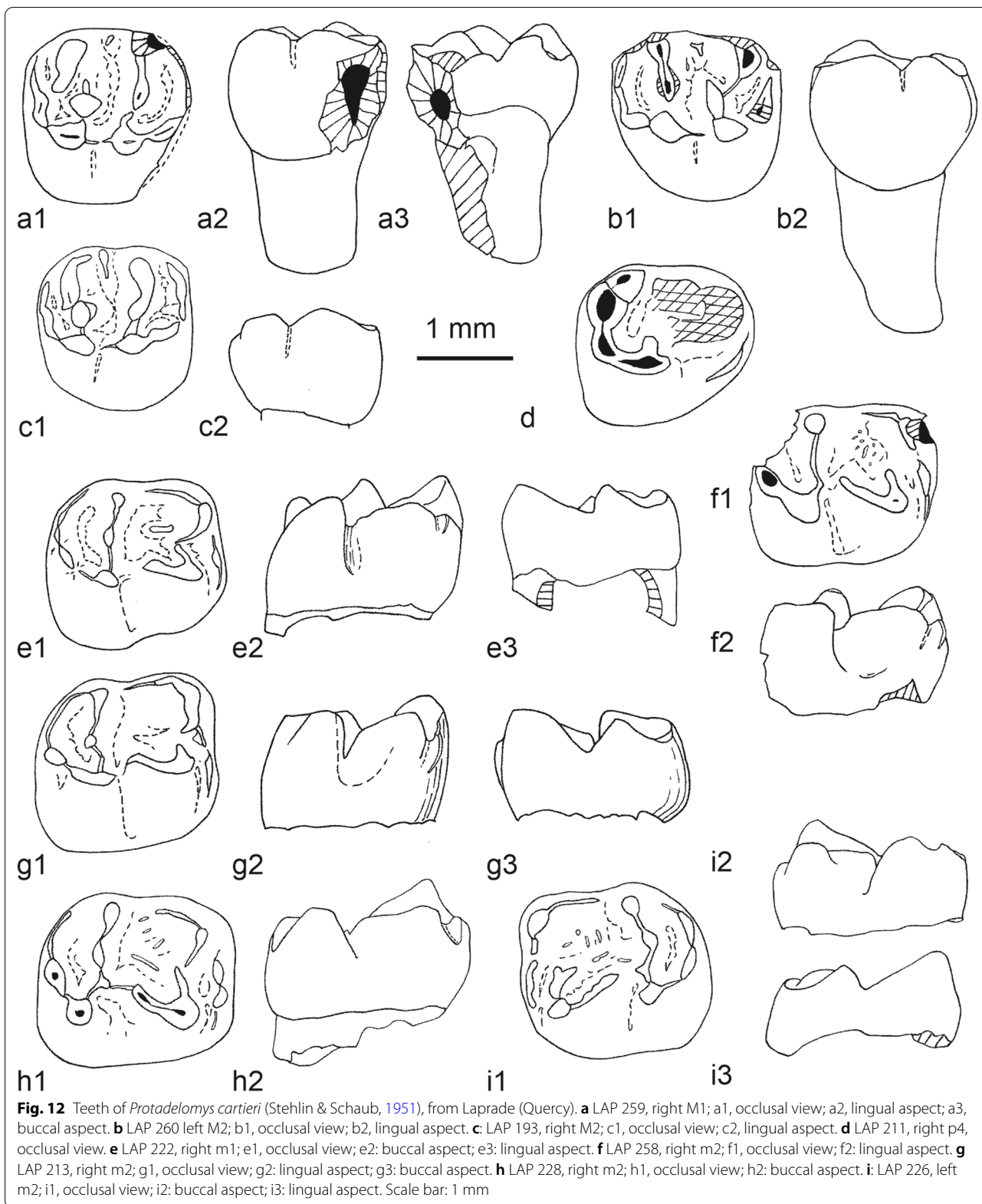
m2. On LIS 60 (Fig. 11d), the anteroconid, low, is closer to the metalophulid I (anteroflexid narrower) than on the m1, the anterolophid is hardly distinct and the premetacristid is absent. The ectolophid is interrupted and very short and the entolophid distally attaches to a short prehypocristid.

m3. Among the three m3 ($L = 1.8$ to 1.95 mm) that are smaller than those of *P. lugdunensis* ($L = 2.2$ to 2.4 mm), only one (LIS 33) is unworn enough to permit the identification of possible relationships between the cusps and crests (Fig. 11c). However, on the m3, the mesosynclinid is not elongated relative to the posterosynclinid, as is the case in *P. lugdunensis*. LIS 33 shows a small anteroconid connected to the mesial metalophulid (premetacristid). The distal metalophulid I is not visible due to wear; only its thick buccal part is distinguishable and distally bent like on the m3 of *P. lugdunensis*. Apart from this case, the postprotocristid is short, located just in front of the mesoconid. The quite short ectolophid shows the break observed on m1–m2, like in typical specimens of *P. cartieri*.

Material referred to *Protadelomys cartieri* (Stehlin & Schaub, 1952) from Laprade

Upper teeth

M1–2. One M1 (LAP 259: Fig.12a) and two M2 (LAP 193: Fig.12c, 260: Fig.12b) are referred to *Protadelomys cartieri*. They differ from *P. lugdunensis* from the same locality in their smaller size (but this is not statistically significant, owing to the limited sample, Table 8), in their higher crowns, as well as in the following features: the paraconule does not protrude forwards and swells within the protoloph on the M1, less on the M2; the metalophule II is short and can be posteriorly directed (LAP 193, 259); the metalophule I is very reduced; the metaconule is closer to the hypocone than to the metaloph and connects at mid-hypocone by a short low ridge; only a small mesostyle on LAP 259 is present, which is a little stronger and prolonged in a short mesoloph on LAP 260 and LAP 193.



Lower teeth (Fig. 12 d to i)

The teeth, especially the molars, display somewhat higher crowns than that of *P. lugdunensis* (see buccal aspects in Fig. 12). The highest unworn *P. lugdunensis* m2 reaches 1.19 mm in height for 1.98 mm in length, whereas the highest unworn m2 of *P. cartieri* is more than 1.23 mm in height for 1.86 mm in length. However, the low number of teeth and their poor states of preservation preclude any evaluation of the whole variability of these features.

p4. (Fig. 12 d) One p4 is shorter but as posteriorly wide as the p4 of *P. lugdunensis*. However, as it is worn mesially, its identification remains uncertain. It shows a low buccal ectocingulid and a buccolingually deep sinusid.

m1. (Fig. 12 e) One tooth is identified as an m1 of *P. cartieri*. This unworn LAP 222 has a small anteroconid prolonged in a very short anterolophid lingually and a short anterocingulid descending buccally. A small circular shallow basin separates these two ridges from the metalophulid I. The two parts of the metalophulid I (lingual and buccal) are distally oriented but not joined, their directions making an acute angle. The postprotocristid is oblique and shorter than in *P. lugdunensis*. A short edge marks its distal end into the mesoflexid. The ectolophid is deeply interrupted, making the sinusid communicate with the mesoflexid, which is a little shorter than in *P. lugdunensis*. The entolophid is swollen at the level of the entoconulid, and lowers at the junction with the ectolophid. The hypoconulid is strong, the posterolophid low and short.

m2. (Fig. 12 g, h) A few m2 resemble the m1, apart from their mesial border, which is less reduced compared to the distal one. On four m2 (LAP 213, 228, 229, 258), the anterocingulid is longer than on the other m2; it is also pinched. One m2, LAP 226 (Fig. 12 i), is difficult to refer either to *P. cartieri* or to *P. lugdunensis* as it displays a combination of features of the former (anterolophid absent, distal ectolophid and mesoconid missing), and the latter (relatively long postprotocristid, lingual metalophulid I in line with the anterolophid).

Protadelomys lugdunensis Hartenberger, 1969 (Figs. 13, 14, 15, 16, 17, 18 and 19).

Holotype. L 2627: left M1–M2; Fig. 15a.

Type locality. Lissieu (Rhône); middle Eocene, MP14.

Original diagnosis (Hartenberger, 1969); translation from French. “*Protadelomys* more evolved than *P. cartieri* and *?P. alsaticus*; lower p4 more important in the tooth row than for these two species; mesoconid always well-developed; on upper teeth sinus nearly reaching the base of the crown”.

Emended diagnosis. *Protadelomys* larger than *?Protadelomys alsaticus* and *?P. maximini*; nearly similar in size as *Protadelomys cartieri*. *P. lugdunensis* differs from *P. cartieri* in the higher and more robust mandible with

relatively short diastema and incisor, the longer and oblique mesiobuccal to distolingual postprotocristid encompassing the mesial ectolophid and a more or less strong mesoconid, the reduced distal ectolophid, the asymmetrical sinus, which is a little deeper (reaching half height of the crown).

P. lugdunensis differs from *?P. alsaticus* in displaying less ornamented enamel, more bulbous cusps, simpler ridges and lophids on lower teeth, DP4 more molarized (hypocone as robust as protocone on the only one known DP4), P4 less triangular, buccal mesoloph often longer, higher buccal protoloph and metaloph, and sinus generally marked by a higher groove (but still shallow and narrow).

P. lugdunensis differs from *?P. maximini* and *?P. nievesae* in its stronger hypocone, and in the composition of the lingual wall of the upper teeth (i.e., association of pre- and post-protocristae, protocone, endoloph, pre- and post-hypocristae, and hypocone), which is not stretched mesiodistally.

Material and measurements from Lissieu. (L: Collections of the “*Université de Lyon*”; LIS: collections of the “*Musée des confluences de Lyon*”) (Sup data, S 2). Like for *P. cartieri* from Egerkingen, we observed that the dimensions of upper molars in Figures 13A and 14A are more scattered than those of the lower teeth (Table 2). The deciduous and premolar teeth are smaller than the molars, both on the lower and upper tooth row. The M1 and M2 are of similar size and the M3 are clearly narrower than the first two molars. The lower m1 are moderately larger than the m2. The m3 are longer than the m1 and m2 (see Figs. 13B, 14B; Table 2A). All the teeth are significantly larger than those of typical *?P. alsaticus*, *?P. maximini*, and *?P. nievesae* (Table 8).

Description

Maxillary. A few maxillary fragments are represented (L45 and L45-2). The infraorbital foramen is hystricomorphous. The premaxilla–maxilla suture is located in front of the mesial root of the zygoma.

Upper dentition (Figs. 15, 16).

DP4. There is only one isolated upper deciduous premolar (LIS11, Fig. 15b); [The tooth n°2629 (Pl.4 Fig. 1, in Hartenberger, 1969) is likely a P4, even if it shows a mesial buccal root oblique forwardly. Its hypocone is not lingual and quite smaller than the protocone. The anteroflexus and anteroloph are reduced and the protoloph connects to the mesial end of the preprotocrista].

This DP4, moderately worn, is molariform and trapezoidal. The hypocone is as robust as the protocone, and lingually displaced relative to the protocone. The parastyle, standing at the same level as the paracone, is weakly swollen. The anteroloph links lingually to the anterostyle, which connects to the short preprotocrista. The four

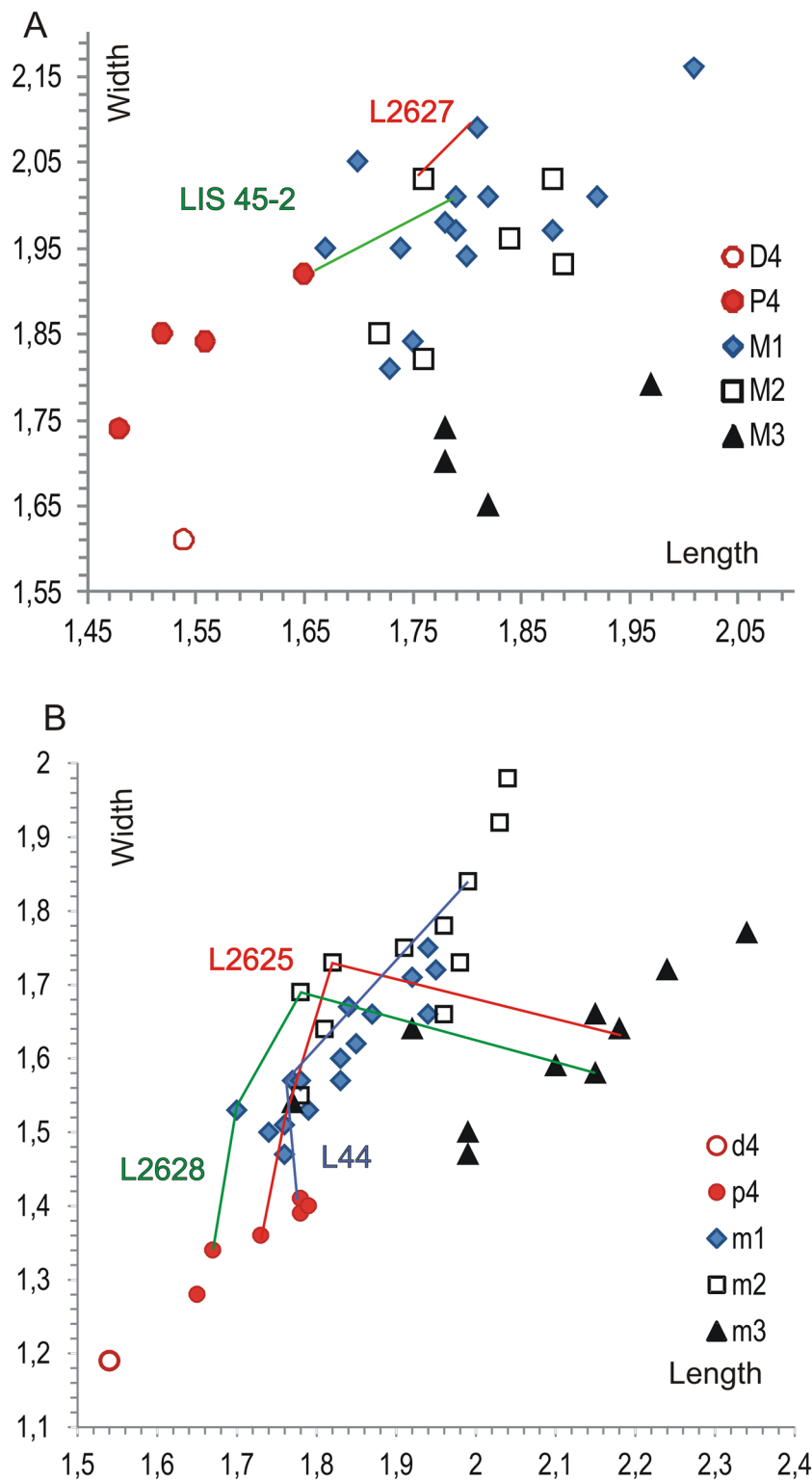


Fig. 13 Bivariate graph of the size (width/length) of the upper (A) and lower (B) teeth of *Protadelomys lugdunensis* Hartenberger, 1969 from Lissieu (Rhône). The colored lines joins the different loci on a same jaw. **A** upper teeth. L2627, Holotype, M1–M2, red line; LIS 45–2, P4–M1, green line. **B** lower teeth. L2625, p4–m3, red line; L2628, p4–m3, green line; L44, p4–m2, blue line

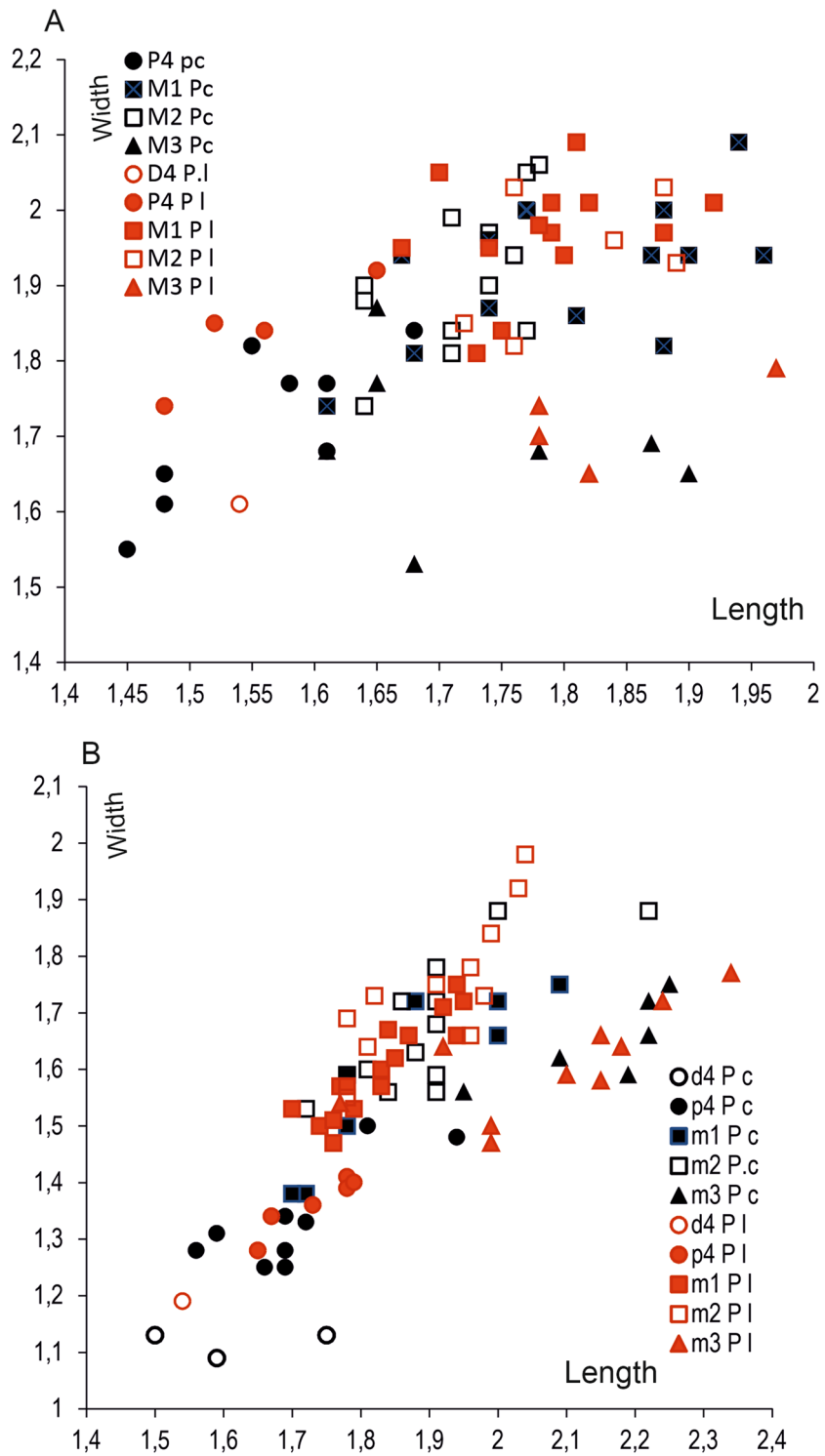


Fig. 14 Bivariate graph of the size (width/length) of the upper (A) and lower (B) teeth of *Protadelomys lugdunensis* Hartenberger, 1969 from Lissieu (Rhône) (red marks) compare to the size of the teeth of *Protadelomys cartieri* (Stehlin & Schaub, 1951), from Egerkingen (Swiss Jura) (black marks)

main cusps are bulbous. The protoloph attaches towards the middle of the protocone. The paraconule stretches mesially from the protoloph to the anterostyle. The mesostyle stands at the level of the lingual flanks of the paracone and metacone; it is buccolingually compressed and stretched mesiodistally. Some isolated wrinkles form a mesoloph. The protocone and hypocone connects through a high and short endoloph. The sinus is very weak and low. The metacone and the paracone are similar in size, like for *P. cartieri*. The metalophule I is present but very low. It does not join the metaconule, contrary to the metalophule II, which is thicker and higher. The metaconule is bulbous and separated from the hypocone. The post-hypocrista connects to the posteroloph. The thickening (worn area) observed at their junction is probably the posterocone. The posteroflexus opens buccally.

P4. (Fig. 15c to f). The P4 are triangular due to the weak development of the hypocone. The anteroloph is short and the parastyle is weakly swollen; it is free (1/4) or connected to the flank of the paracone (3/4). The mesoflexus is narrow, buccally closed by a more or less swollen mesostyle; the latter is lengthened mesiodistally (2/4), reduced (1/4) or swollen (1/4). In L2629, the mesostyle connects to a mesoloph, which nearly reaches the metaconule level. In the other cases, the mesoloph is absent or reduced to rare wrinkles. The paraconule is absent. The protoloph connects to the preprotocrista (3/4) or the anteroloph (L2629). The metalophule I is reduced or absent. The metaconule, swollen, connects to the protocone (L45-2) or the postprotocrista (L2629). It aligns with the metacone through the metalophule II. Both are oriented towards the posterior part of the protocone, joining only on the most worn specimen (LIS13). The hypocone is small (L45-1 and 2, L 2629, LIS13) or indistinct (LIS10), connecting the posteroloph. The latter does not connect to the metaconule, leaving the posteroflexus opened buccally.

M1 and M2. (Fig. 15a, f to j; Fig. 16a to e). The crowns are unilaterally and moderately hypsodont, like in *P. cartieri*. The cusps are bulbous and their apex is acute on juveniles (i.e., weakly or unworn teeth). In adults, the buccal cusps extend within the buccal parts of the protoloph and metaloph, which are slightly less high. In contrast, the lingual parts of the lophes are very low or absent. Lingually, the protocone merge within its pre- and

post-protocristae, aligned mesiodistally. The endoloph prolongs the postprotocrista mesiodistally. The hypocone shows a similar pattern, but the pre- and post-hypocristae are shorter and weaker. The endoloph is short and high, but lower than the apexes of the protocone and hypocone. The sinus is barely marked; its height is less than half the crown height, and it is almost completely absent on worn teeth.

The M1 can be quite easily distinguished from M2 due to the strong development of its parastyle, its trapezoidal outline consecutive to the lengthening of its buccal edge compared to the lingual one. On the M2, this parastyle elongates in an extension of the anteroloph. Moreover, they mostly show a metacone lingual to the paracone, so that the posterior lobe of the tooth appears narrower buccolingually than the anterior lobe, with the posteroloph being shorter than on M1.

The anteroloph is lower and thinner than the strong anterostyle and the preprotocrista. The paracone can be rarely divided (1/20: L45-1: Fig. 15 g) into a bigger half displaced lingually and a stylar one developed between the end of the parastyle and the mesostyle. The paraconule attaches to the protoloph and protrudes mesially. The protoloph ensures the connection from the paracone to the middle of the protocone. The mesostyle is stretched mesiodistally or bulbous. A low mesoloph reaches the level of the metaconule (9/19); it can be shorter (6/19) or absent (4/19). The strong metaconule is slightly lower than the metacone; its position is slightly mesial to that of the metacone and hypocone. Only one specimen (LIS5) displays a duplicated metaconule. The metalophule I is always present, sometimes much reduced, lower and thinner than the metalophule II. The latter is generally free and rarely joins the metaconule (2/20). The metaconule weakly connects to the hypocone. The enamel surface is generally smooth. Some rare low wrinkles are visible at the bottom of the flexi (LIS1, 2, 8, 26); in one case (L45-1), they are present as surface folds of the lingual flanks of the protocone and hypocone.

M3. (Fig. 16 f to h). The hypocone is strongly reduced. It often separates from the protocone (3/4) with a shallow sinus. On weakly worn teeth, this sinus communicates with the opposite flexus (2/4). The paracone constitutes the only salient cusp. The metacone is only slightly higher than the buccal ridge it forms with the mesostylar area.

(See figure on next page.)

Fig. 15 Upper teeth of *Protadelomys lugdunensis* Hartenberger, 1969 from Lissieu (Rhône). **a** L2627, left M1–M2, Holotype; a1, occlusal view; a2, lingual aspect. **b** LIS 11, left DP4; b1, occlusal view; b2, lingual aspect; b3, buccal aspect. **c**: L2629, left P4; c1, occlusal view; c2, lingual aspect; c3, buccal aspect. **d** LIS 13, right P4, occlusal view. **e** LIS 10, right P4; e1, occlusal view; e2, lingual aspect; e3, buccal aspect. **f** LIS 45–2, left P4–M1; f1, occlusal view; f2, buccal aspect of P4; f3, lingual aspect of P4. **g** L 45–1, left M1; g1, occlusal view; g2, lingual aspect; g3, buccal aspect. **h** LIS 14, left M1, occlusal view. **i**: LIS 6, left M1, worn; i1, occlusal view; i2, lingual aspect; i3, buccal aspect. **j**: LIS 22, right M1, strongly worn; j1, occlusal view; j2, lingual aspect; j3, buccal aspect. Scale bar: 1 mm

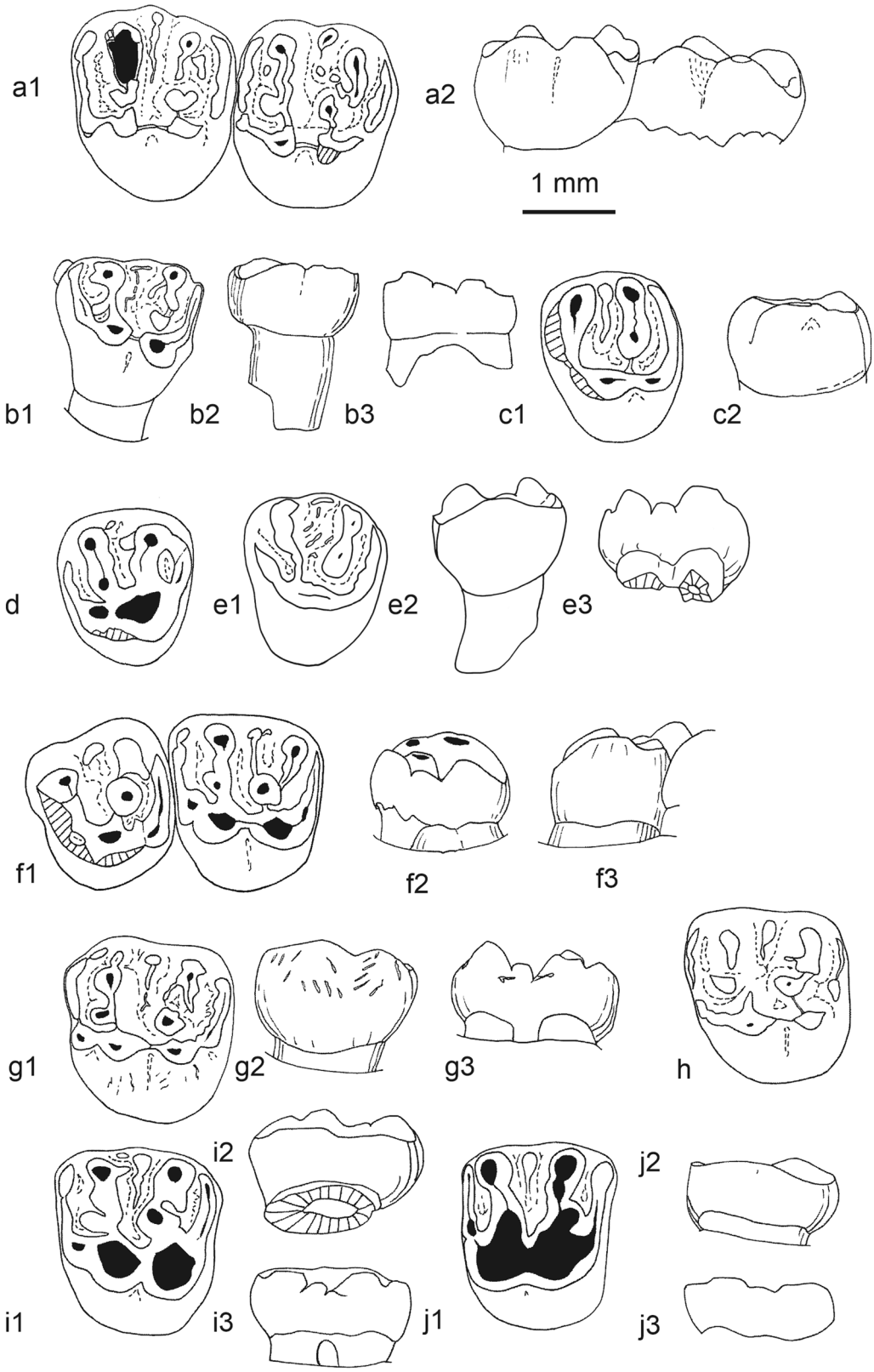
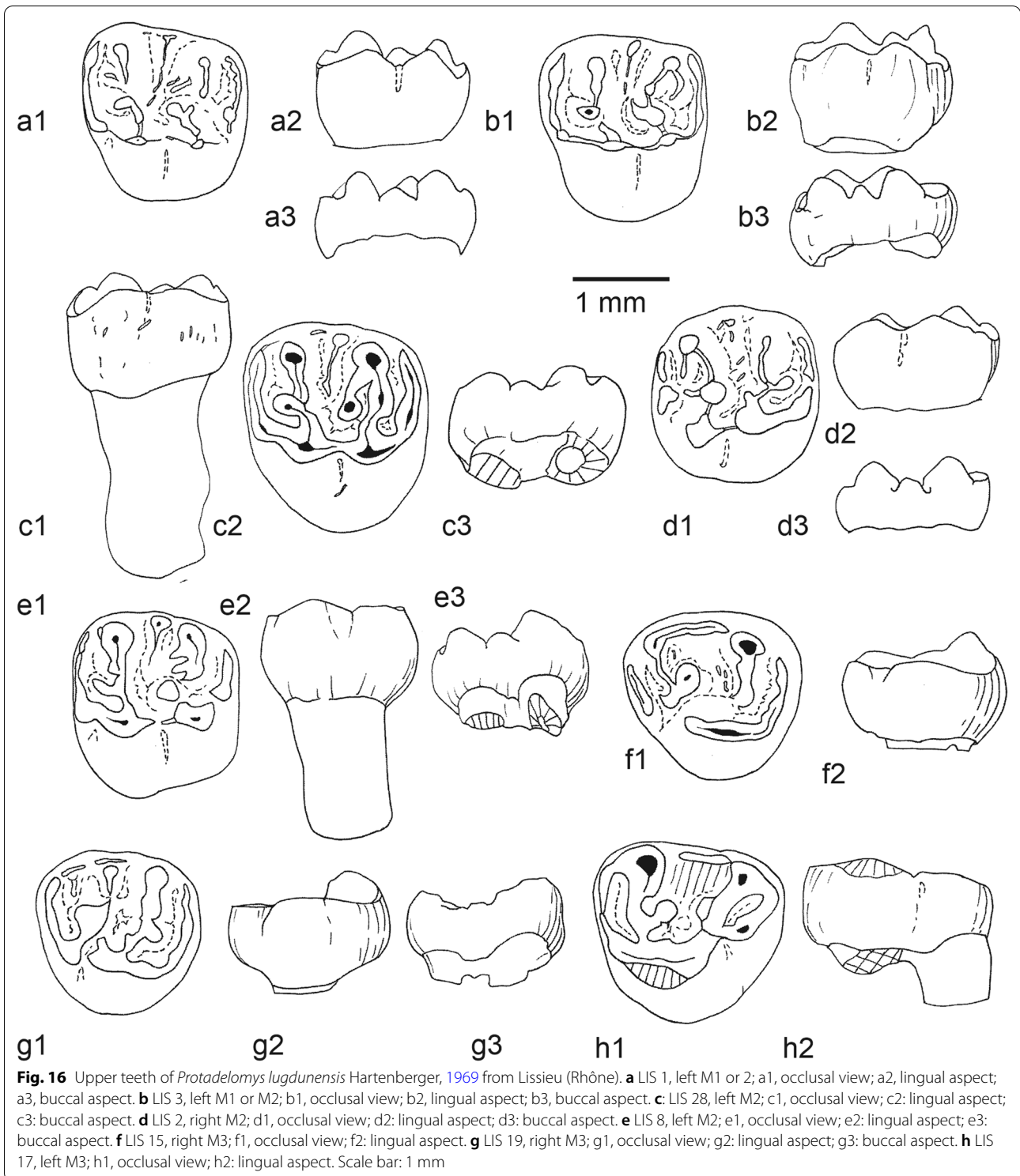


Fig. 15 (See legend on previous page.)



The paraconule and metaconule are present, although low. The posteroloph can be either distinct from the metaconule (1/4) or connected to it (3/4).

Dentary. (Fig. 17). The body of the mandible is robust and high (L44). The diastema and incisor are short. The mental foramen opens close to the mesial root of p4. The

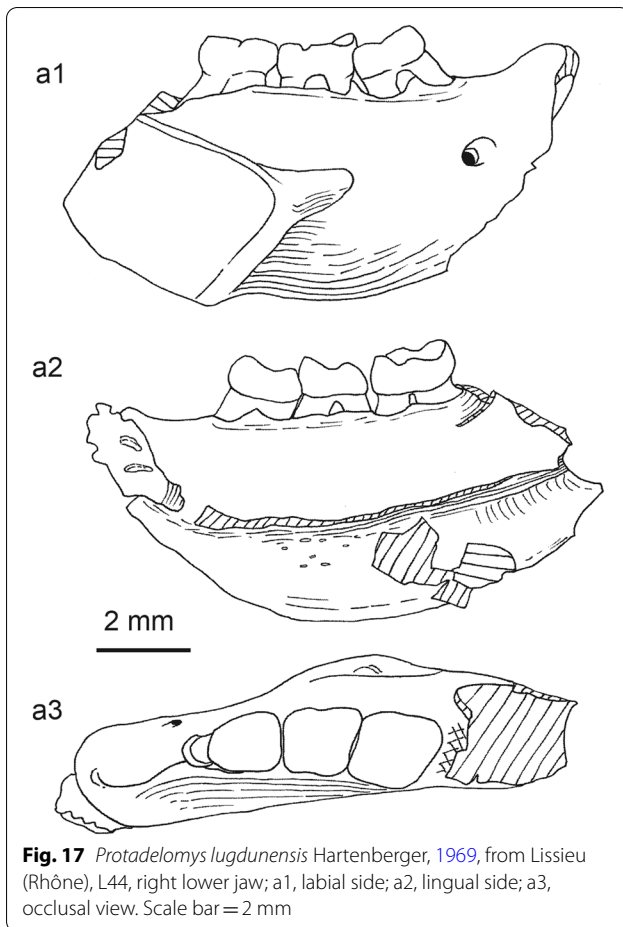


Fig. 17 *Protadelomys lugdunensis* Hartenberger, 1969, from Lissieu (Rhône), L44, right lower jaw; a1, labial side; a2, lingual side; a3, occlusal view. Scale bar = 2 mm

masseteric crest is strong and begins below the mesial root of m1.

Lower dentition. (Figs. 18, 19).

dp4. Only one tooth (LIS 40; Fig. 18b), smaller than the p4, could be identified as a dp4. Its posterior buccal root is inclined distally. The metaconid is mesiolingual. The enamel has weak and rare wrinkles along the lingual flank of the long postmetacristid. A short mesiodistal anterolophid attaches to the metaconid. A bulged anteroconid is present buccally. A short transverse metalophulid I connects the metaconid to the protoconid, from which a low mesiodistal ridge descends in the basin. The lophid constituted by the stretched protoconid, the postprotocristid and the mesial part of the ectolophid is

weakly oblique, almost mesiodistal. The short distal part of the ectolophid links the anterior arm of the hypoconid with the entolophid. The latter makes an angle oriented distally at the level of a small entoconulid. The hypoconid is higher than the hypoconulid, which is swollen. The long posterolophid reaches the mesiolingual edge of the entoconid. A small ectostylid is present at the base of the sinusid.

p4. The p4 is slightly shorter than m1, and clearly narrower (Table 2A).

An anterior tooth is listed as a dp4 in the collection from Lissieu (LIS47). However, the height and robustness of the crown and roots rather evoke a p4. Four isolated p4 (LIS 42, 37, 39, and 41) are similar in size with p4 included in dental rows (L 2625, L 2628, and LIS 44). However, the crown of LIS 41 is slightly higher than the others are and displays some peculiar features, which enable us to reattribute it to *P. cartieri* (see below).

LIS 32, LIS 37, and L 2625 (Fig. 18 d, e, f) show neither an anteroconid nor an anterolophid. The metaconid is the only cuspid of the mesial border of the crown, which is then narrower than the other p4. On L 2628 (Fig. 18a), the anteroconid is buccal and isolated; a short buccal cingulid descends from the mesial end of the preprotocristid. A short mesiobuccal anterolophid is visible on L44 (Fig. 18e).

The metaconid is the highest cusp of the tooth; it connects to the protoconid, which is low, weak and stretched in a mesiodistal protocristid including its pre- and post-protocristae. A very low ectocingulid sometimes interrupts an asymmetrical sinusid (LIS 32, 37, and 44). On the lingual side, the postmetacristid descends to the lingual notch. A low crestid extends from the metaconid apex to the mesioflexid; it can be continuous or not and composed of two to three very low crestules. The mesostylid is absent. The ectolophid is very short and distally interrupted superficially, separating the postprotocristid from the prehypocristid (LIS 37 and L44). On L 2628, the entolophid reduced to its lingual half is posteriorly oriented, connected to the mesial end of the prehypocristid. On the others, the entolophid is complete from the entoconid to the junction prehypocristid–ectolophid. The posterolophid is well separated from the entoconid, so that the posterosynclinid opens lingually.

m1. The m1 are smaller than the m2, the protoconid–metaconid width is lower than the hypoconid–entoconid

(See figure on next page.)

Fig. 18 Lower teeth of *Protadelomys lugdunensis* Hartenberger, 1969, from Lissieu (Rhône), **a** L2628, right p4–m3; a1, occlusal view; a2, buccal aspect. **b** LIS 40, left dp4; b1, occlusal view; b2, buccal aspect; b3, lingual aspect. **c**: LIS 32, right p4; c1, buccal aspect; c2 occlusal view; c3, lingual aspect. **d** L2625, right p4–m3; d1, occlusal view; d2, lingual aspect. **e** L44, right p4–m2; e1, occlusal view; e2, buccal aspect; e3, lingual aspect. **f** LIS 37, right p4; f1, occlusal view; f2, buccal aspect; f3, lingual aspect. Scale bar = 1 mm

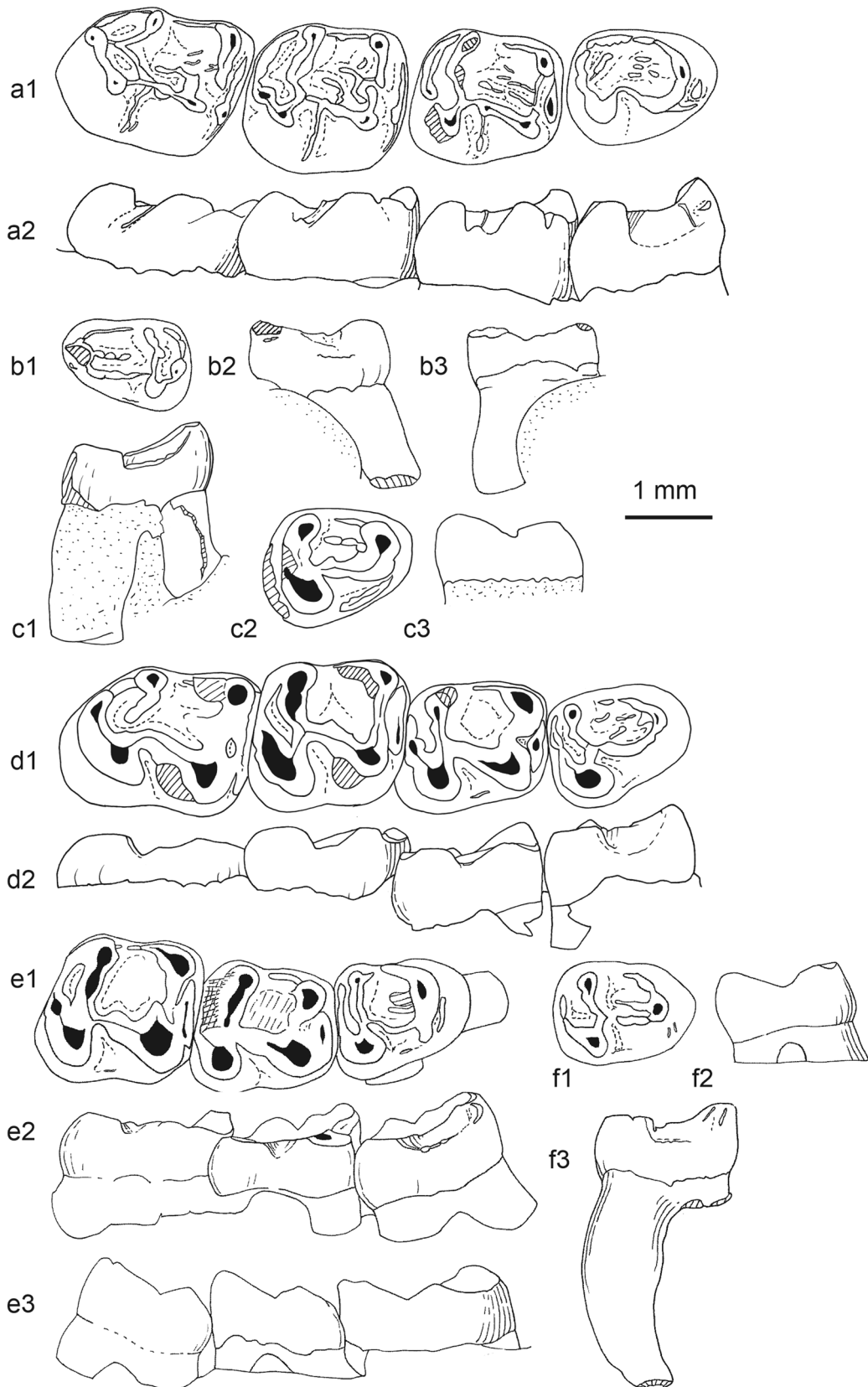


Fig. 18 (See legend on previous page.)

width. The lingual side is only slightly shallower than the buccal side. The anteroconid is individualized on unworn or weakly worn teeth (LIS 67 and 66; Fig. 19a), and the anterolophid is short. The lingual anterocingulid and the anterosinusid are weakly marked or absent. The anterolophulid is rarely visible, mainly on worn teeth, low and connects the anterior flank of the protoconid to the anteroconid. The metaconid represents the highest cusp, from which the postmetacristid steeply descends. The metalophulid I is generally angled, its lingual and buccal parts distally oriented; the latter is connected to the protoconid apex. On weakly worn teeth, the enamel surface of the mesoflexid bears short mesiodistal wrinkles and granules (LIS 67, 68, and 72). Exceptionally, these wrinkles merge into longer mesiodistal ridges, which are connected to the metalophulid I (L 2628, Fig. 18a). The postprotocristid is thick and oblique; it extends to a more swollen area that corresponds to the mesoconid. Both are discernible on slightly worn teeth (LIS 53, 55, 67, and 68, Fig. 19a, c, h), while they appear in continuity in a long oblique lophid on more worn teeth. Some teeth have a bulbous and low anteroconid and the buccal cingulid is reduced to absent (LIS 68, 69, and 71); but their size and other features are not different of the other teeth of *P. lugdunensis*.

A short ridge on its lingual side indicates the mesoconid area; there is no well-individualized mesolophid. Some teeth have an ectomesolophid connected to an ectostylid (LIS 55 and L 2628), while other specimens only display an ectostylid more or less swollen (L 2625, LIS 53, 68, and perhaps on badly preserved LIS 70). The distal part of the ectolophid is very short and low. It appears interrupted on unworn or weakly worn teeth (LIS 53, 68, and 70). The distal part of the ectolophid ensures the connection with the mesial end of the short prehypocristid and the buccal part of the entolophid. This buccal part is lower than the lingual one and it is partly missing on two teeth (LIS 67 and 68); both parts make a distally oriented angle. The lingual half of the entolophid is swollen at its base, his swelling being reminiscent of an entoconulid.

The post-hypocristid is connected to the hypoconulid; it is always well defined and higher than the posterolophid, which is short. If the lingual border of the posterosynclinid is rather high, the posterolophid itself does not merge with the entoconid. This cusp is lower than the hypoconid on weakly worn teeth, but the lingual side is higher than the

buccal one on worn teeth: wear affects more the buccal half of the tooth than its lingual counterpart does.

m2. (Fig. 19 e to i) The m2 differ from the m1 in showing a larger size, a rectangular outline due to the equal protoconid–metaconid and hypoconid–entoconid widths, a longer anterolophid and sometimes a longer anterocingulid, as well as different connections with the metalophulids. The anteroconid is less bulbous than on the m1; the anterolophulid is lingual, often linking the anterolophid with the lingual metalophulid I, thereby forming a longer antesisinusid. Other features are more similar between m1 and m2: secondary wrinkles on LIS 42, 59, 66, and 69 (Fig. 18); long low mesiodistal crestids and ectomesostylid on L 2628; the presence of an ectostylid on LIS 42, 56, 57. As wear increases, the posterolophid can reach the apex of the entoconid (LIS 51, 59; L 2625 and L 2628), even on a moderately worn m2 (LIS 42).

m3. The m3 are clearly longer than the m2 (x about 1.15), due to the lengthening of the mesosynclinid area, they are as wide as to slightly wider as the m1 (Table 2A). The posterior area is narrower than the anterior one. The lingual metalophulid I is more mesial, it is thus closer to the anterolophid (L 2628, LIS 29; Fig. 18a, 19 k) with which it is often connected (LIS 46, 39; Fig. 19 l). The connection between the lingual metalophulid I and the buccal metalophulid I can be disrupted, or reduced to weak short ridges. The anterolophid is buccal when present (LIS 29, 36, 39). The low mesiodistal ridges arising from the buccal metalophulid I extremity are more frequent and more visible on weakly worn teeth (LIS 29, 36, 39, and L 2628). The entoconid is reduced, which puts the metaconid in relief. The entolophid makes an angle pointing posteriorly at the level of the entoconulid, when the latter is present (LIS 49, 46). The buccal part of the entolophid is sometimes absent (L 2625 and LIS 46). On L 2628, the apex of the angle defined by the lingual and buccal parts of the entolophid connects to the hypoconulid by a thin mesiodistal ridge; ditto for LIS 46 but the entolophid is very incomplete on this tooth. The hypoconulid is bulged while the posterolophid is lower, short, and does not reach the entoconid.

(See figure on next page.)

Fig. 19 Lower molars of *Protadelomys lugdunensis* Hartenberger, 1969, from Lissieu (Rhône), **a** LIS 67, right m1; a1, occlusal view; a2, buccal aspect. **b** LIS 55, right m1; b1, occlusal view; b2, buccal aspect; b3, lingual aspect. **c** LIS 53, left m1; c1, occlusal view; c2, buccal aspect; c3, lingual aspect. **d** LIS 66, left m1; d1, occlusal view; d2, buccal aspect; d3, lingual aspect. **e** LIS 56, left m1 or m2, occlusal view. **f** LIS 59, left m2; f1, occlusal view; f2, buccal aspect; f3, lingual aspect. **g** LIS 42, left m2, occlusal view. **h** LIS 69, left m2; h1, occlusal view; h2, buccal aspect; h3, lingual aspect. **i** LIS 57, left m2, occlusal view. **j** LIS 36, left m3; j1, occlusal view; j2, buccal aspect; j3, lingual aspect. **k** LIS 29, right m3; k1, occlusal view; k2, buccal aspect; k3, lingual aspect. **l** LIS 39, left m3; l1, occlusal view; l2, lingual aspect; l3, buccal aspect. Scale bar = 1 mm

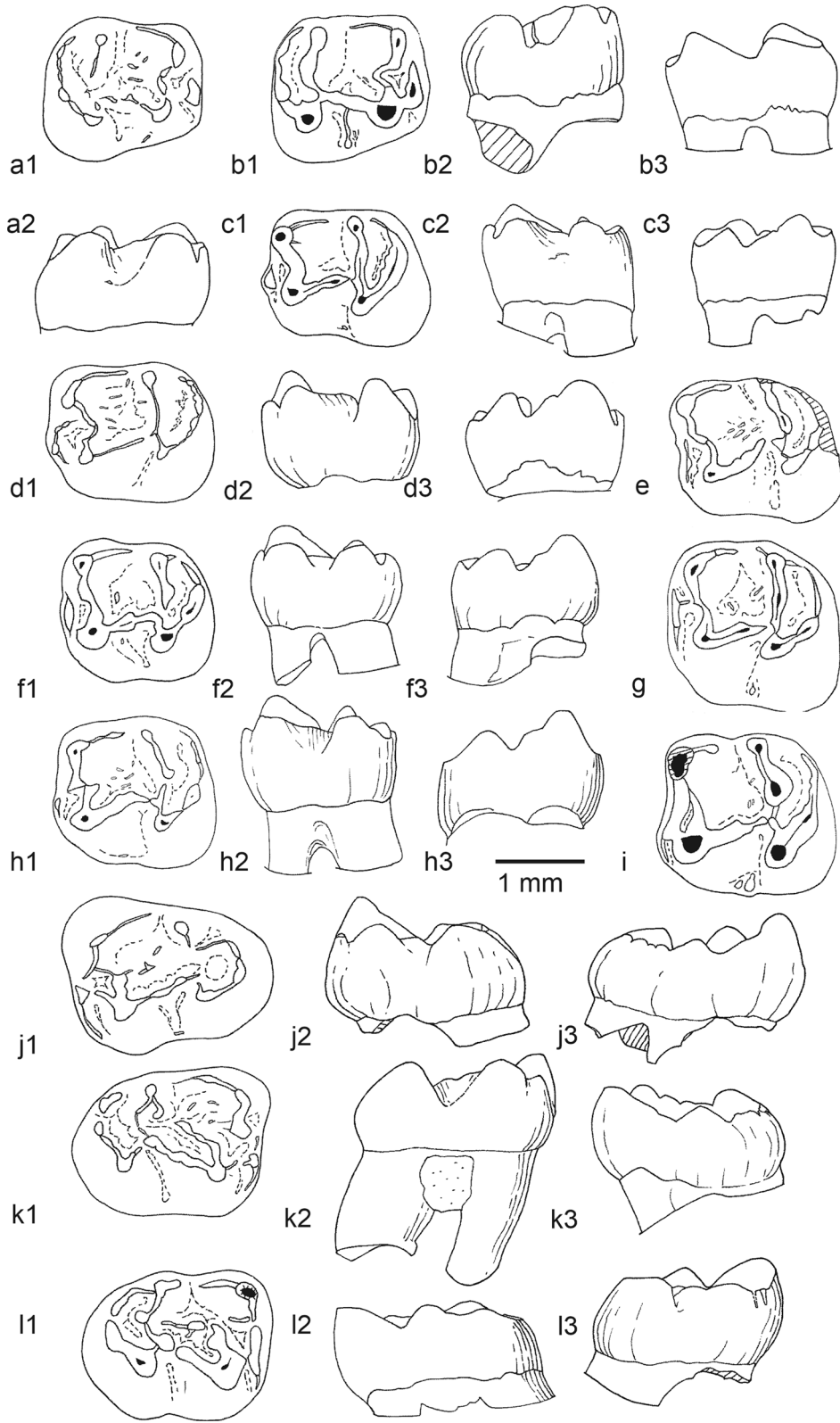


Fig. 19 (See legend on previous page.)

Table 2 Range of the size variations (length and width: min., max.; average \pm Sm = σ/\sqrt{n} ; v = 100 σ /average L or W): A. of the different loci of teeth of *Protadelomys lugdunensis* Hartenberger, 1969 and B. length and width for some loci only of *Protadelomys cartieri* Hartenberger, 1969 from Lissieu (MP 14; Rhône, France)

A. <i>Protadelomys lugdunensis</i> from Lissieu							
Length	n	min	mean \pm Sm	max	σ	v	
DP4	1	–	1,54	–	–	–	–
P4	4	1,48	1,553 \pm 0.036	1,65	0.073	4.69	
M1	14	1,67	1,799 \pm 0.024	2,01	0.090	4.95	
M2	6	1,72	1,808 \pm 0.029	1,89	0.071	3.94	
M3	4	1,82	1,838 \pm 0.045	1,97	0.090	4.91	
dp4	1	–	1,54	–	–	–	–
p4	5	1,65	1,722 \pm 0.027	1,78	0.061	3.54	
m1	15	1,7	1,835 \pm 0.020	1,95	0.077	4.20	
m2	9	1,78	1,924 \pm 0.033	2,04	0.099	5.14	
m3	7	1,99	2,164 \pm 0.041	2,34	0.109	5.04	
Width	n	min	mean \pm Sm	max	σ	v	
DP4	1	–	1.61	–	–	–	–
P4	4	1,74	1,838 \pm 0.037	1,92	0.074	4.03	
M1	14	1,81	1,98 \pm 0.024	2,16	0.090	4.52	
M2	6	1,82	1,937 \pm 0.036	2,03	0.089	4.57	
M3	4	1,65	1,720 \pm 0.030	1,79	0.059	3.45	
dp4	1	–	1,19	–	–	–	–
p4	5	1,28	1,356 \pm 0.023	1,41	0.050	3.71	
m1	15	1,47	1,609 \pm 0.022	1,75	0.084	5.22	
m2	9	1,64	1,784 \pm 0.037	1,98	0.110	6.17	
m3	7	1,47	1,633 \pm 0.037	1,77	0.099	6.06	
B. <i>Protadelomys cartieri</i> from Lissieu							
Length	n	min	mean \pm Sm	max	σ	v	
p4	1	–	1.79	–	–	–	–
m1	1	–	1.74	–	–	–	–
m2	2	1,78	1,870 \pm 0.090	1,96	0.127	6.81	
m3	3	1,77	1.893 \pm 0.065	1.99	0.112	5.94	
Width	n	min	mean \pm Sm	max	σ	v	
p4	1	–	1.40	–	–	–	–
m1							
m2	2	1,55	1,610 \pm 0.055	1,66	0.078	4.85	
m3	3	1,50	1,560 \pm 0.042	1,64	0.072	4.62	

Material referred to *Protadelomys lugdunensis* Hartenberger, 1969 from Egerkingen

Remarks

Together with the mandible Em 21 (Fig. 8b, Fig. 20b) and a few isolated molars, we tentatively refer the specimen Ek 592 (right M1–M2), identified as ? *Protadelomys* in Hartenberger (1969) to ? *P. lugdunensis*. The ratio between M1 and M2 width is different from that of the holotype of *cartieri* in which M1 and M2 have same length, whereas here the M2 is well shorter than the M1 (Fig. 19a), the cusps more acute and higher, and looks

like the holotype of *P. lugdunensis* from Lissieu, LIS 2627. Among the lower teeth from Lissieu, we detected similar variation as that observed in the lower teeth of specimens previously identified as *P. cartieri* from Egerkingen (Hartenberger, 1969), which led us to find both species in Egerkingen and Lissieu (see below and discussion). *P. cartieri* is more abundant than *P. lugdunensis* in Egerkingen, whereas the opposite is true in Lissieu.

Material referred. Em 21, right lower jaw, with p4–m3; Ek 71, weakly worn right m2, Ek 126, right m1, Ek 72, right m3; EK 592, right M1–M2; all in Fig. 20.

Locality. Egerkingen ? α and fissure indet., upper middle Eocene (MP14 ?).

Description

Upper teeth

Ek 592, M1–M2, (Fig. 20a) the paracone and metacone are relatively high and acute. The parastyle is present and swollen on M1, less on M2. The anteroloph extends between the parastyle and the anterostyle. The paraconule, a little less robust than the metaconule, is protruding from the protoloph, the latter being sinuous at this level. The protoloph connects lingually at the center of the protocone. The preprotocrista, the protocone, and the postprotocrista are aligned mesiodistally, the protocrista being relatively short and slightly separated from the anterostyle by a shallow notch. A strong mesostyle is present, linked to a thin low ridge, as a lingual mesoloph. A few low and thin extra-ridges are visible and restricted in the center of the mesoflexus. A clear but low metalophule I connects the metacone and the strong metaconule, which is mesially protruding. The buccal part of the metalophule II, more distal, is short and high. A deep notch separates the metalophule II from the metaconule, which is free from a very short lingual spur of the metaloph visible at the level of the mid-hypocone. The endoloph is relatively low compare to the hypocone. A shallow, narrow, and short sinus is marked between the two lingual main cusps. The hypocone is nearly as robust as the protocone. The posteroloph is long on M1, reaching the base of the mesiobuccal corner of the metacone. It is much shorter on M2, on which it stops at the level of the lingual end of the buccal metalophule II.

Lower jaw with p4 to m3. The body of the mandible Em 21 (Fig. 8b) is wider and higher than that of *Protadelomys cartieri* Eg 587 (Fig. 8a). The diastema is shorter and the radius of curvature of the incisor is smaller. The mental foramen opens more distally, below the anterior root of the p4. The masseteric crest is strong and begins below the mesial root of m1. The incisor is thicker.

p4. (Fig. 20b) The metaconid is mesiolingual and a small anteroconid is mesiobuccal, both separated by a well-marked notch. A short metalophulid connects the metaconid and a low incipient protoconid. The posprotocristid is long and oblique, bearing a short lingual premesoconid spur. In the continuity of the posprotocristid, the ectolophid bears a stretched mesoconid, associated to a short mesolophid and ectomesolophid. The asymmetrical sinusid (ectoflexid) is limited buccally, at its base,

by a strong ectostylid. The distal part of the ectolophid connects to the mesial end of the prehypocristid. A buccal short lophid joins more mesially this ectolophid; it corresponds to the buccal part of the entolophid of the molars. On p4, the lingual part of the entolophid turns postwardly to the junction hypoconulid–posterolophid. The latter is short and does not join the entoconid.

Molars. m1 is a little wider than p4, and shorter and narrower than m2 and m3 (Additional file 1: S1, Fig. 3, Table 1B). The anteroconid extends buccally through a clear anterocingulid; it lingually joins the mesial branch of the lingual metalophulid (premetacristid). Another lingual branch, close to the former, turns posteriorly and joins the transverse buccal metalophulid I (Fig. 20b1). The anteroflexid is defined between the anteroconid and the elements constitutive of the metalophulid I; it is limited buccally by an anterolophulid. The metaconid is clearly higher than the entoconid, resulting in a steep postmetacristid (Fig. 20b3). One short mesiodistal spur descends in the basin located at the buccal end of the lingual metalophulid I, the enamel of which bears low and weak extra-ridges. The postprotocristid, the ectolophid and mesoconid are in line obliquely. The mesoconid displays two short spurs, one lingual (mesolophid) and one buccal (ectomesolophid). Like on p4, the strong ectostylid limits the sinusid buccally. The entolophid, complete, connects to the junction ectolophid–prehypocristid. An entoconulid is more visible on m2 than on m1 and m3. The hypoconulid is bulged at the end of the posthypocristid, and the posterolophid is short, distinct from the entoconid, leaving the posteroflexid opened lingually.

Other lower teeth. The m1 Ek 126, m2 Ek 71 and the m3 Ek 72 (Fig. 20 c, d,e) shares some features with Em 21, like the reduced or absent lingual metalophulid I, the long oblique postprotocristid bearing a more or less distinct mesoconid, an ectomesolophid, the posteroflexid closed lingually, the long postmetacristid. However, the entolophid is not connected buccally, and these teeth do not display an ectostylid. On the m?1 Ek 126, the anteroconid is connected to the preprotocristid, closing the anteroflexid buccally, whereas it is stretched and free and developed more lingually and buccally on the others. The buccal metalophulid I is transverse on Ek 71 and Ek 72, it is oblique distobuccally on Ek 126. The mesoconid is barely distinguishable; it corresponds to the ectolophid area located at the end of the thick oblique posprotocristid. A small mesoconid seems to be present on the m3.

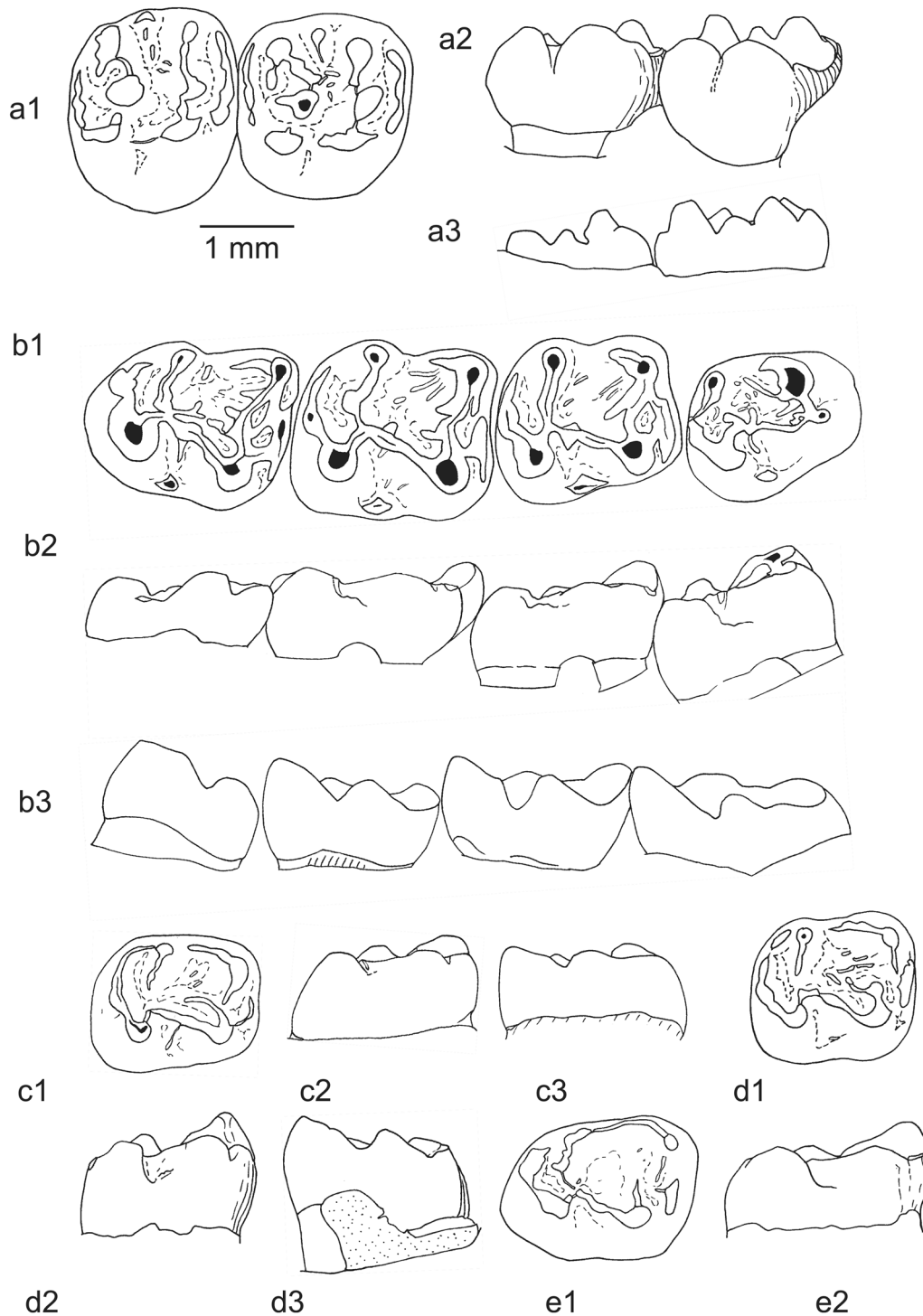


Fig. 20 Lower teeth of *Protadelomys lugdunensis* Hartenberger, 1969, from Egerkingen (Swiss Jura). **a** Ek 592, right P4–M2; a1, occlusal view; a2, lingual aspect; a3, buccal aspect. **b** Em 21, left right tooth row with p4–m3; b1, occlusal view; b2, buccal aspect; b3, lingual aspect. **c**: Ek 126, right m1, weakly worn; c1, occlusal view; c2: buccal aspect; c3: lingual aspect. **d** Ek 71, right m2, weakly worn; d1, occlusal view; d2: buccal aspect; d3: lingual aspect. **e** Ek 72, right m3, weakly worn; e1, occlusal view; e2: buccal aspect. Scale bar = 1 mm

Material referred to *Protadelomys lugdunensis* (Hartenberger, 1969) from Laprade (Tarn-et-Garonne, Quercy)

List of material and measurements: Additional file 3: S3;

The size of the teeth from Laprade does not differ significantly from that of the teeth of *Protadelomys lugdunensis* from Lissieu (Tables 2, 3, 8; Fig. 21).

Remarks

Sudre et al. (1990) have identified the larger theridomorphs from Laprade as *Protadelomys* cf. *lugdunensis*. A smaller species was referred to *Elfomys* nov. sp. (Marandat et al., 1993; Comte et al., 2012). Here, we reassess these species and also distinguish a few teeth that could be referred to *P. cartieri*, and possibly another species differing from both *P. lugdunensis* and *P. cartieri*. The co-occurrence of *P. cartieri* and *P. lugdunensis* has been reported above, both from Egerkingen and Lissieu.

Description

Maxillary. Two maxillary fragments are present in the collection (Fig. 22). LAP 224 is an incomplete right hemi-maxillary, showing the alveolus of DP3; DP4 is broken and a fragment of an erupting P4 is present in the mesiobuccal alveolus; only the nearly unworn M1 is present associated with damaged alveoli of M2 and M3. The mesial end of the zygomatic process of the maxilla is preserved, which enables to characterize the wide opening of the infra-orbitary foramen in frontal view.

In palatal view, the maxillary part of the palate is flat and wide, showing the edge for the insertion of the superficial masseter between the level of the alveolus of DP3 and the premaxillary–maxillary suture. Medial to that, there is a trace of the distal closure of the anterior palatine foramen (f.p.a.). Posteriorly, the palate is damaged, but the maxilla–palatine suture can be distinguished at the level between M1 and M2.

LAP 83 is a fragmentary left maxilla, broken at the level of the mesial alveoli of M2. On this specimen, a longer part of the zygomatic arch is preserved, showing the ridge of the insertion of the anterior deep masseter, and the posterior edge of the f.p.a.. LAP 83 shows the alveoli of P4 and a remnant of the alveolus of D3. The only molar preserved, the M1, is more worn than those of LAP 224.

Upper teeth

DP4. Only one unworn DP4 is present in the material from Laprade (LAP 191; Fig. 23a). It is molariform, very similar to LIS 11 from Lissieu. Because it is unworn, the anterostyle is superficially separated from the short preprotocrista. The paraconule is displaced mesially from the protoloph. The mesostyle weakly protrudes buccally;

it is located closer to the metacone than to the paracone and associated to a weak premetacrista. A very low ridge is reminiscent of the presence of a mesoloph. The metalophule I is weak, low, and does not join the metaconule, unlike the metalophule II, which is thicker and higher. A minute additional conule is present between the bulbous metaconule and the metacone. The hypocone, more lingual than the protocone, is separated from the posteroloph by a shallow notch.

P4. There are four well preserved and two damaged P4.

A first group of three P4 is very similar to the P4 known from Lissieu. They (LAP 84, (Fig. 23d), 192 (Fig. 23b), 223, L 45–2) are characterized by a weak development of the hypocone. The parastyle is absent. On a weakly worn P4 (LAP 192), the anterostyle is slightly swollen, separated from the protocone and connected to the short anteroloph. Their mesostyle is swollen and not connected to a mesoloph. Some low wrinkles are present in the mesoflexus; they can be in line with the mesostyle forming a kind of mesoloph (LAP 84, Fig. 23d), or directed towards the metaconule (LP 223) or the protoloph (LAP 192). The protoloph does not reach the protocone on LAP 84, 192, and 269; LAP 223 is worn at this level. The metalophule I is absent. The metaconule is strong and isolated on unworn teeth (LAP 84, 192 and 269), or connected to the metacone and the hypocone on worn teeth (LAP 223).

The two other specimens, weakly worn (LAP 235: Fig. 23c, and LAP 272) display different features. The anteroloph is much reduced and low. A short distomesial crest (anterolophule) links the buccal part of the protoloph to the anteroloph on LAP 235 (Fig. 23c). On both teeth, the protoloph connects to the preprotocrista. The protoloph makes an angle pointing anteriorly at the middle of the occlusal surface of the crown. The mesostyle is twinned, the main part being prolonged in a mesoloph directed towards middle of the mesoflexus. The strong bulbous metaconule shows a short buccal ridge, ending free on LAP 235, and extended to the metacone mesial flank on LAP 272. On the latter, there is also a short lingual ridge, which is oblique mesially. These ridges may constitute remnants of the metalophule I. The short metalophule II is distally oriented. The P4 L45-2 from Lissieu shows a similar orientation of the short branch of the metalophule II, but the other features resemble more those of the first group of P4.

M1 and M2. (Fig. 23e to m) Their features are very close to those of *P. lugdunensis* from Lissieu. The paracone is never divided on the M1–2 (contra in a few specimens from Lissieu: e.g., L45-1). The paraconule is developed mesially to the protoloph. The latter ensures the connection from the paracone to the middle of the protocone, which is bulbous at its base and pinched at its upper part from the preprotocrista to the postprotocrista. The low

Table 3 Range of the size variations (length and width: min., max.; average $\pm Sm = \sigma/\sqrt{n}$; $v = 100 \sigma/\text{average L or W}$): A. of the different loci of teeth of *Protadelomys lugdunensis* Hartenberger, 1969 and B. length and width for some loci only of *Protadelomys cartieri* Hartenberger, 1969 from Laprade (MP 14; Tarn et Garonne, France)

A. *Protadelomys lugdunensis* Laprade

Length	n	min	mean $\pm Sm$	max	σ	v
DP4	1	–	1,58	–	–	–
P4	4	1,38	1,548 \pm 0,058	1,63	0,116	7,49
M1	9	1,6	1,803 \pm 0,036	1,87	0,079	4,40
M2	6	1,73	1,762 \pm 0,008	1,79	0,020	1,11
M3	3	1,68	1,723 \pm 0,023	1,76	0,040	2,34
dp4	3	1,53	1,547 \pm 0,017	1,58	0,029	7,11
p4	4	1,65	1,788 \pm 0,049	1,88	0,097	5,43
m1	11	1,79	1,895 \pm 0,037	2,23	0,121	6,39
m2	6	1,83	1,940 \pm 0,031	2,03	0,075	3,89
m3	4	2,03	2,098 \pm 0,058	2,27	0,115	5,50
Width	n	min	mean $\pm Sm$	max	σ	v
DP4	1	–	1,61	–	–	–
P4	4	1,66	1,723 \pm 0,022	1,76	0,043	2,52
M1	9	1,69	1,920 \pm 0,037	2,09	0,111	5,76
M2	6	1,62	1,827 \pm 0,060	1,99	0,146	8,00
M3	3	1,64	1,697 \pm 0,052	1,80	0,040	2,34
dp4	3	1,04	1,073 \pm 0,018	1,10	0,031	2,85
p4	4	1,25	1,370 \pm 0,046	1,47	0,092	6,72
m1	11	1,51	1,590 \pm 0,019	1,73	0,642	4,04
m2	6	1,55	1,717 \pm 0,043	1,85	0,106	6,18
m3	4	1,56	1,625 \pm 0,027	1,67	0,115	5,50

B. *Protadelomys cartieri* Laprade

Length	n	min	mean $\pm Sm$	max	σ	v
M1	4	1,68	1,700 \pm 0,011	1,73	0,022	1,29
M2	1	–	1,68	–	–	–
p4	1	–	1,66	–	–	–
m1	5	1,78	1,826 \pm 0,020	1,90	0,046	2,50
m2	7	1,81	1,880 \pm 0,020	1,96	0,054	2,85
m3	2	2,1	2,105 \pm 0,005	2,11	0,007	0,34
Width	n	min	mean $\pm Sm$	max	σ	v
M1	4	1,74	1,833 \pm 0,043	1,94	0,085	4,64
M2	1	–	1,8	–	–	–
p4	1	–	1,47	–	–	–
m1	5	1,59	1,638 \pm 0,024	1,70	0,054	3,27
m2	7	1,51	1,654 \pm 0,042	1,86	0,112	6,78
m3	2	1,66	1,725 \pm 0,065	1,79	0,092	5,33

mesoloph reaches the level of the metaconule (2/19); it is often shorter (15/19) and rarely absent (2/19). The strong metaconule is swollen, a little lower than the metacone; it is slightly mesial to the metacone and hypocone.

One specimen (LAP 196) displays a duplicated metaconule. The buccal part of the metalophule I is absent or reduced to a low and short ridge. The metaconule is

sometimes more mesial; the metalophule II is directed distally from the metacone, but does not reach the posteroloph. Among these teeth, three (LAP 85, 86, and 203) are a little smaller than the abovementioned specimen, but shows very similar features, with a metalophule I being well present for LAP 85 and 203.

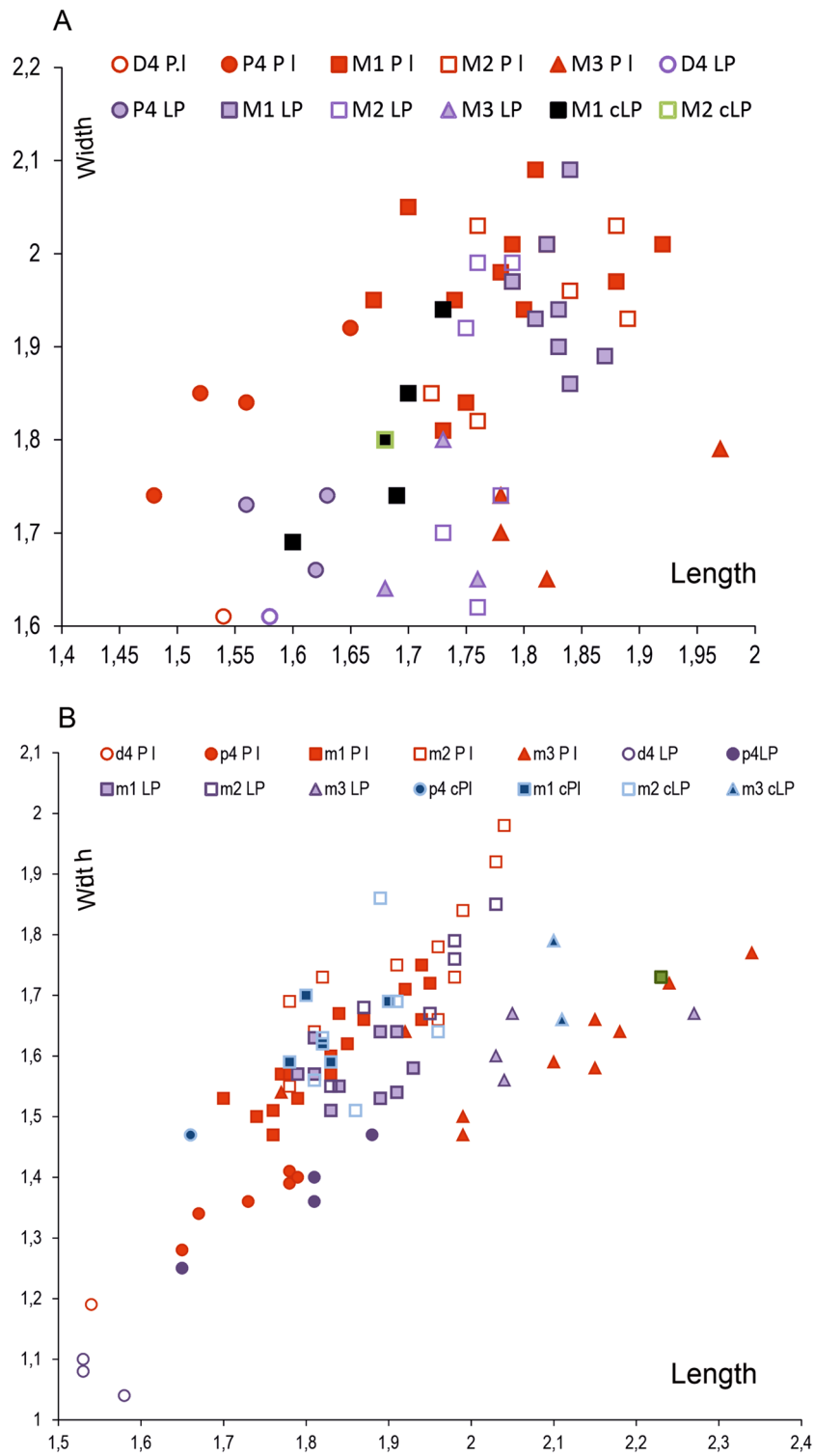


Fig. 21 Bivariate graph of the size (width/length) of the upper (A) and lower (B) teeth of *Protadelomys lugdunensis* Hartenberger, 1969 from Laprade (Quercy) (LP, light violet marks) compare to the size of the teeth of *Protadelomys lugdunensis* from Lissieu (Rhône) (PL, red marks). Some teeth from Laprade are *Protadelomys cartieri* (Stehlin & Schaub, 1951) (cLP, black and green marks on A; blue marks on B)

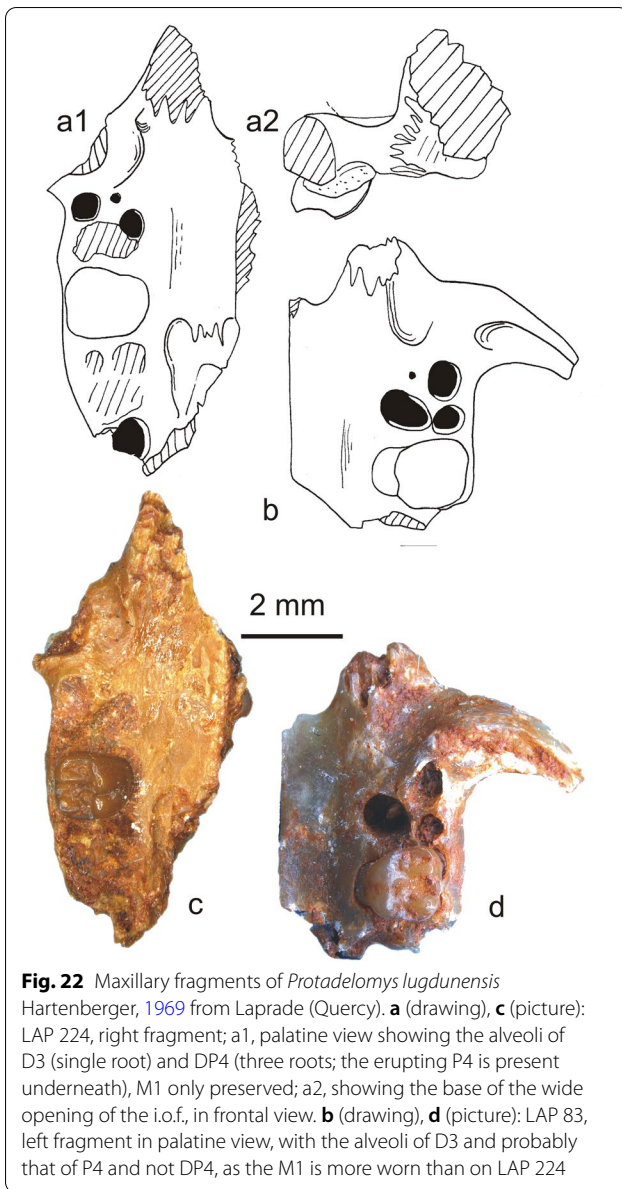


Fig. 22 Maxillary fragments of *Protadelomys lugdunensis* Hartenberger, 1969 from Laprade (Quercy). **a** (drawing), **c** (picture): LAP 224, right fragment; a1, palatine view showing the alveoli of D3 (single root) and DP4 (three roots; the erupting P4 is present underneath), M1 only preserved; a2, showing the base of the wide opening of the i.o.f., in frontal view. **b** (drawing), **d** (picture): LAP 83, left fragment in palatine view, with the alveoli of D3 and probably that of P4 and not DP4, as the M1 is more worn than on LAP 224

M3. The hypocone is strongly reduced, separated from the protocone (LAP 206: Fig. 23n) by a shallow sinus or connected by a low and short curved endoloph (LAP 25: Fig. 23o).

Dentary. (Fig. 24) The body of the mandible (LAP 246) is robust and dorso-ventrally deep, as in typical *P. lugdunensis*. Even if the mandible is fragmentary, the preservation of a posterior part of the symphysis indicates that the diastema is short. The mental foramen opens a little anterior to the mesial root of p4 as for typical *P. lugdunensis*. The masseteric crest is strong and begins below the mesial root of m1 as for *P. lugdunensis* from Lissieu and *P. cartieri* from Egerkingen.

Lower teeth. The lower p4, m1, and m2 are significantly larger than those of *P. lugdunensis* from Lissieu (Fig. 21B; Tables 2, 3, 8).

dp4. (Fig. 25 a,b,c) Three specimens are deciduous teeth on the bases of the low crown, low profiles and shape of cusps, low ridges and diverging roots. We attributed these teeth to *P. lugdunensis*, even if dp4 are poorly documented in Lissieu, because the crown is higher than that of *P. cartieri*. The metaconid is mesiolingual and constitutes the highest cusp. The protoconid is low but well distinct from the metaconid due to the presence of a shallow mesiobuccal notch. A very short and low anterolophid (LAP 208–209) or anteroconid (LAP 207) limits this notch mesially.

The sinusid is asymmetrical and short buccolingually. One slender long ridge descends from the premetacristid in the trigonid basin: it nearly reaches the bottom of the mesosynclinid. The hypoconid, entoconid, and hypoconulid display similar height, but the latter is weakly swollen. The entolophid is continuous, transverse, and connected to the junction ectolophid–prehypocristid. The ectolophid is low when compared to the hypoconid. The posterolophid is longer than that of *P. cartieri* (Ek 80).

p4. (Fig. 24 a1; Fig. 25 d to g) p4 are represented by four isolated teeth (LAP 210, 212, 251, and 256) and one damaged on the mandible LAP 246. The p4 are shorter than m1 (Table 3).

Two p4 have a reduced buccal anteroconid. The metaconid is strong and mesiolingual. The protoconid is poorly developed and merged in the protocristid. The enamel shows low wrinkles along the protocristid and/or the median crestid. The ectolophid is weakly swollen within the mesoconid. An ectocingulid is present and long, joining the protocristid to the buccal edge of the sinusid (LAP 212: Fig. 25f). There is no mesostylid. The ectolophid is very short and interrupted shallowly, and sometimes separates the ends of the postprotocristid from the prehypocristid (LAP 251: Fig. 25g; LAP 256: Fig. 25e). The orientation and position of the entolophid vary. On LAP 251, from its lingual part, a short ridge is posteriorly oriented to the hypoconulid while another ridge is directed anteriorly to the ectolophid, near the mesoconid. On LAP 256, the lingual part of the entolophid is longer and oblique postwards to the hypoconulid. A narrow, shallow slit separates this lingual part of the entolophid from its very short buccal part. On LAP 256, the low entolophid joins the extremity of the prehypocristid. The posterolophid reaches the entoconid posterior flank, closing the posterosynclinid lingually.

m1. The m1 are smaller than the m2 (Fig. 21B; Table 3) the protoconid–metaconid width is lower than the hypoconid–entoconid width. As often seen on weakly

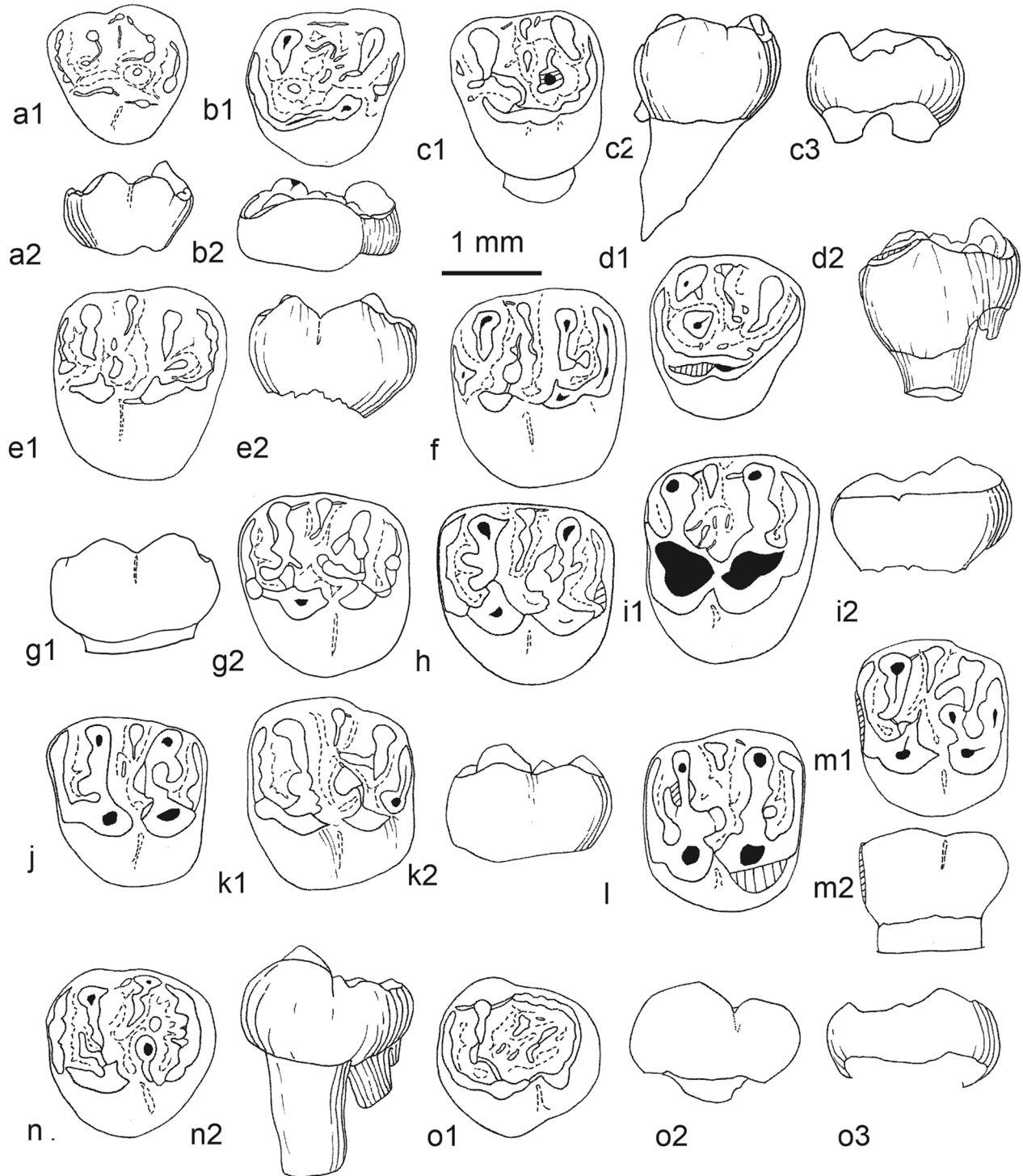


Fig. 23 Upper teeth of *Protadelomys lugdunensis* Hartenberger, 1969 from Laprade (Quercy). **a** LAP 191, left DP4; a1, occlusal view; a2, lingual aspect. **b** LAP 192, right P4; b1, occlusal view; b2, lingual aspect. **c**: LAP 235, left P4; c1, occlusal view; c2: lingual aspect; c3: buccal aspect. **d** LAP 84, left P4; d1, occlusal view; d2: lingual aspect. **e** LAP 200, right M1; e1, occlusal view; e2: lingual aspect. **f** LAP 224, right M1, occlusal view. **g** LAP 205, left M1 or 2; g1, lingual aspect; g2, occlusal view. **h** LAP 83, left M1; occlusal view. **i** LAP 198, right M1, worn; i1, occlusal view; i2: lingual aspect. **j**: LAP 85, left M1; occlusal view. **k**: LAP 88, left M2; k1, occlusal view; k2, lingual aspect. **l**: LAP 86, right M1–2; occlusal view. **m**: LAP 203, left M1–2; m1, occlusal view; m2, lingual aspect. **n**: LAP 206, left M3; n1, occlusal view; n2, lingual aspect. **o**: LAP 255, left M3; o1, occlusal view; o2, lingual aspect; o3, buccal aspect. Scale bar: 1 mm

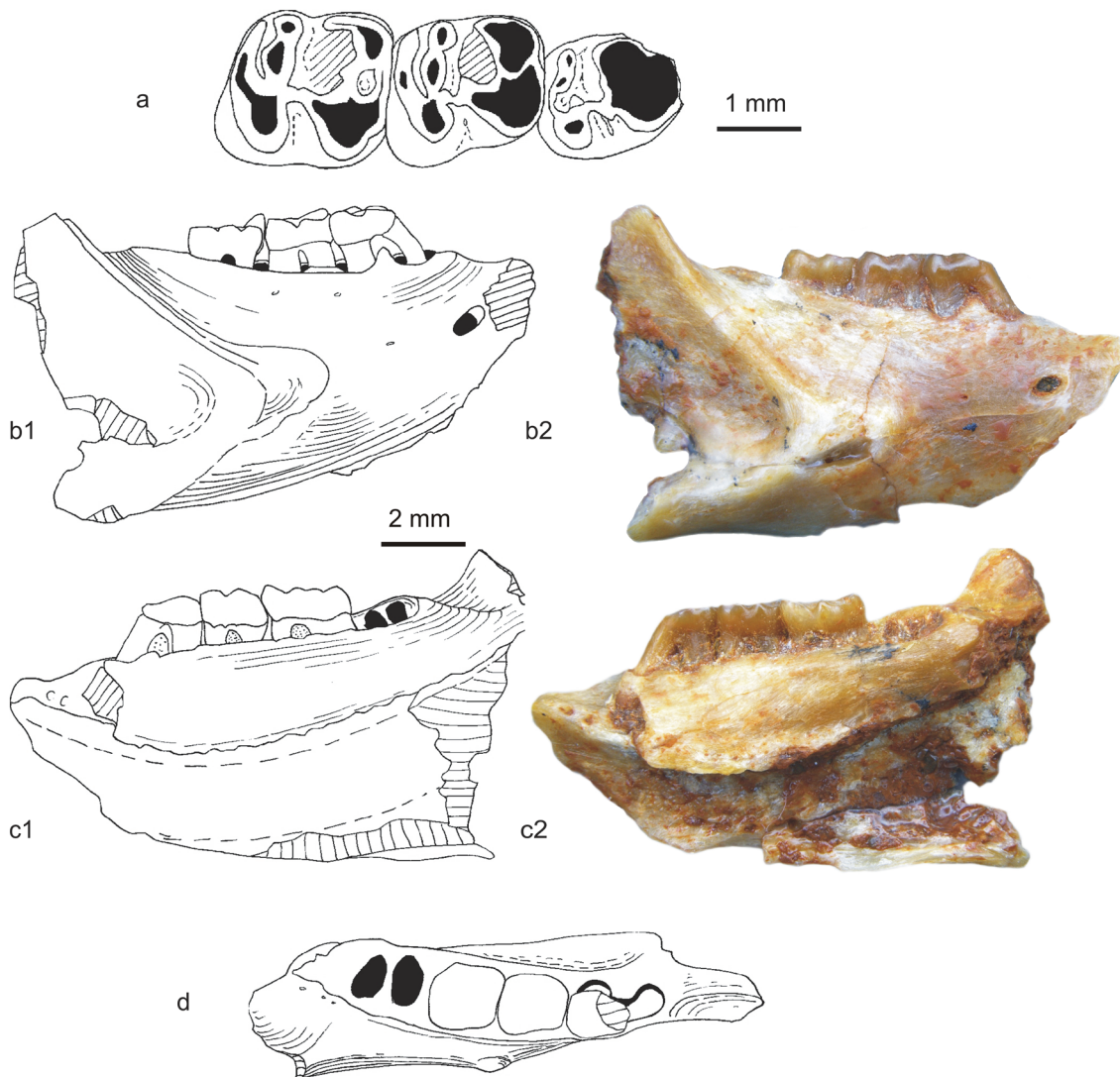


Fig. 24 *Protadelomys lugdunensis* Hartenberger, 1969, from Laprade (Quercy), LAP 246, right lower jaw; **a**, occlusal view of the tooth row, p4–m2, worn. Scale bar = 1 mm. **b**, b1 (drawing), b2 (picture): labial side of the dentary + teeth; **c**, c1 (drawing), c2 (picture), lingual side; **a4**, occlusal view. Scale bar = 2 mm

worn teeth, the lingual side is as high as the buccal side. The anteroconid is bulbous on unworn to weakly worn teeth and the anterolophid is short. The lingual anterocingulid and the anterosingulid are weak or absent. The anterolophulid is low, rarely visible, mainly on worn teeth on which it connects the anterior flank of the protoconid to the anteroconid. On LAP 87 (Fig. 26e), a metastylid is distinct on the postmetacristid. The buccal and lingual parts of metalophulid I often make an obtuse angle open mesially; the lingual part is weak to absent (LAP 87), distally oriented (LAP 215, 254: Fig. 25h, LAP 217: Fig. 25i, LAP 218: Fig. 26j) or mesially (LAP 216:

Fig. 25k, LAP 220); the buccal part is connected to the center of the protoconid.

On weakly worn teeth, the enamel surface of the mesoflexid bears short wrinkles and granules. The postprocristid is oblique and extends to the mesoconid, which is swollen. The lingual side of the mesoconid is rarely prolonged by a short edge on its lingual side. Buccally, the ectomesolophid is absent. The short ectolophid connects together to the mesial extremity of the short prehypocristid and to the buccal end of the entolophid, which is complete. The entolophid weakly angles at the junction of its lingual and buccal parts. The entoconulid and the

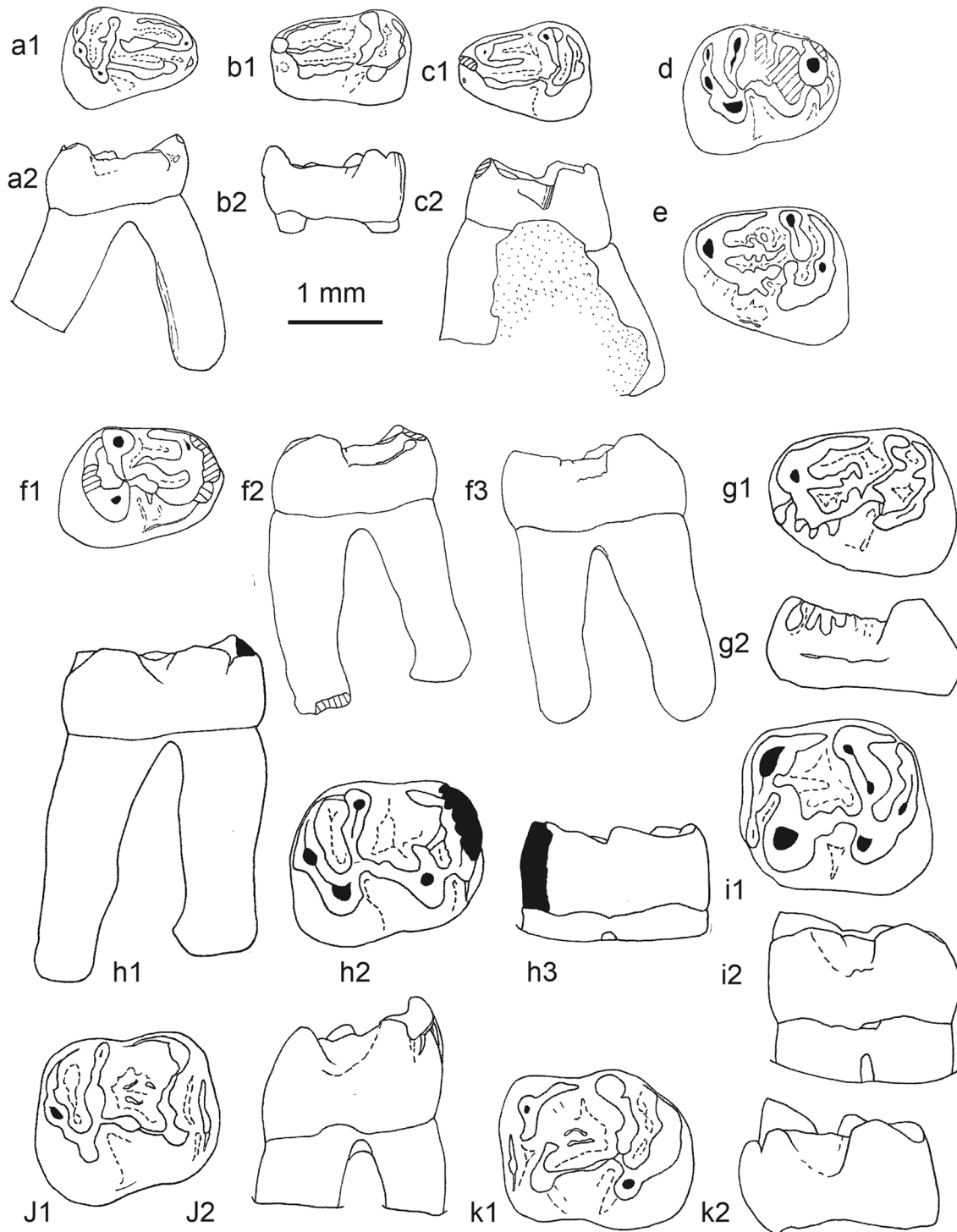


Fig. 25 Lower teeth of *Protadelomys lugdunensis* Hartenberger, 1969, from Laprade (Quercy), **a** LAP 207, right dp4; a1, occlusal view; a2, buccal aspect. **b** LAP 208, left dp4; b1, occlusal view; b2, lingual aspect. **c**: LAP 209, left dp4; c1, occlusal view; c2, lingual aspect. **d** LAP 210, right p4; occlusal view. **e** LAP 256, left p4, occlusal view. **f** LAP 212, right p4; f1, occlusal view; f2, buccal aspect; f3, lingual aspect. **g** LAP 251, left p4; g1, occlusal view; g2, buccal aspect. **h** LAP 254, right m1; h1, buccal aspect; h2, occlusal view; h3, lingual aspect. **i** LAP 217, left m1?; i1, occlusal view; i2, buccal aspect. **j**: LAP 218, right m1; j1, occlusal view; j2, buccal aspect. **k**: LAP 216, left m1; k1, occlusal view; k2, buccal aspect. Scale bar = 1 mm

hypoconulid are more or less swollen. The posterolophid is short.

m2. (Fig. 26 a to d) Their morphology is similar to that of *P. lugdunensis* from Lissieu, apart from their size, which is larger, and their rectangular outline due to the equal protoconid–metaconid and hypoconid–entocoid widths. The m2 differ from m1 in their longer anterolophid. When present, the anterolophid has a more lingual position, often joining the anterolophid to the lingual metalophid I, thereby forming a longer antesisinusid. On LAP 249 (Fig. 26b), the metalophid I is not angulated, but rectilinear and continuous from the metaconid to the protoconid; on this unworn tooth, the wrinkles and granules are numerous, but still very low. The posterolophid is always short.

m3. (Fig. 26 f, g, h) The m3 are longer and narrower than the m2 (Table 3A). The lingual metalophid I is mesially oriented and joins the anterolophid. On unworn LAP 233 the buccal metalophid I is forked, (Fig. 26g) a part oriented distally, like on the other m3, and a short edge oriented mesially. The anteroconid is swollen on LAP 233 and LAP 230; it is stretched as a longer anterolophid on the other teeth. The connection between the lingual and the buccal metalophulids is broken.

Granules are rare on the enamel surface. The entolophid is very low; its buccal part is also very low or absent (LAP 232, 233, 252: Fig. 26 h, and 253: Fig. 26g). The hypoconulid is poorly inflated. The posterolophid is short and does not reach the entoconid.

Comparisons between *P. lugdunensis* from the different localities and *P. cartieri*

As the materiel of *P. lugdunensis* from Egerkingen most of the lower teeth of *P. lugdunensis* from Lissieu display obliquely aligned postprotocristid–ectolophid. The main difference with the lower teeth of *P. cartieri*, as defined by Stehlin and Schaub (1951), corresponds to the absence of a mesoconid associated to a disruption of the distal ectolophid distally in *P. cartieri*. The P4 are only slightly less reduced in *P. lugdunensis* than in *P. cartieri*, and the m3 are only slightly longer.

We have not confirmed that the lower p4 of *P. lugdunensis* from Laprade are less molarized than those of *P. lugdunensis* as previously considered (Sudre et al., 1990: 20). They have similar length and the protoconid is weak as in typical *P. lugdunensis* from Lissieu. The P4 are not significantly narrower than typical *P. lugdunensis* (Table 8), but similar in size to *P. cartieri*. Extra-ridges and granules are variably present as for the teeth from Lissieu, and the M3 are not significantly smaller than the M3 from Lissieu (Tables 2, 3, 8). These features cannot support the idea that the teeth from Laprade, are more “primitive” than

those from Lissieu (Sudre et. al.: 20), bearing in mind their limited number. It would rather be the opposite, some dental categories (p4, m1, m2) in Laprade being actually significantly larger than specimens from Lissieu (Table 8), while dental size increase was often observed through the evolutionary history of these lineages (e.g., Escarguel, 1998; Vianey-Liaud & Marivaux, 2017).

In addition with the differential development of extra-ridges and granules, most of the morphological differences observed between *P. lugdunensis* and *?P. alsaticus* involve the lower teeth: in *P. lugdunensis*, the cusps seem more bulged, the entolophid is more continuous, the postprotocristid is fused to the mesoconid area (no distinct pre, meso and postmesoconid elements).

Protadelomys sp. indet

Material. Two specimens from Egerkingen [Ek 250, p4–m2 (Fig. 10b) and He 6, m2 (Fig. 10c)] differ from *P. cartieri* in the anteroconid more buccally positioned, the more mesial lingual metalophid I, and the occurrence of a mesoconid. They also differ from *P. lugdunensis* in the weaker and mesiodistally oriented distal ectolophid, making the sinusid shallower buccolingually, and more symmetrical.

Description

p4. Ek 250. This tooth is slightly shorter than m1. The high metaconid is mesial, the postmetacristid high and long, the protoconid very low and hardly distinct from the postprotocristid and the ectolophid. The ectolophid interrupts in front of the hypoconid. The prehypocristid is absent and the entolophid ends free buccally. There is a shallow notch between the post-hypocristid and the hypoconulid, which connects the posterolophid. The posterolophid joins the entoconid, closing the posterosynclinid lingually. Several extra-ridges are visible in the talonid basin, the main ridge being more or less mesiodistal.

molars. Ek 250 and He 6. On EK250, the m1 is shorter and narrower than the m2, its protoconid–metaconid width being lower than the hypoconid–entoconid width. The m1 and m2 have a low bulbous anteroconid. The anteroflexid opens buccally and closes lingually due to the contact of the anteroconid against the lingual metalophid I (=premetacristid). The lingual metalophid I is double on the m2 Ek 250: a mesial thick and short part is observable on the three teeth, to which a short and low more distal lophid is added, oriented mesiolingual to distobuccal on the m2 Ek 250. On the m1 and m2 of Ek 250, a short mesiodistal ridge is joining the buccal metalophid (on m2) or parallel to it (on m1); it is absent on He 6. The postprotocristid is oblique and thick, longer in Ek 250 than in He 6. The mesial ectolophid is poorly

individualized and short; it is weakly separated from the mesoconid on m1. A weak ectomesolophid is present on He 6 and on the m1 Ek 250. The distal ectolophid is short, lower than the short prehypocristid. On these two specimens, the attachment of the entolophid varies. It is more mesial and located at the junction ectolophid–prehypocristid or a little more distal on Eg 250 m1–m2. In He 6 the entolophid is angled, it is transverse in Ek 250. The entoconulid is bulged on the m1 Ek 250 and the m2 He 6. The posterolophid is long and joins the entoconid.

?Protadelomys alsaticus (Hartenberger, 1969)

Remarks

On the bases of the observation of “two upper jaws” of the Naturhistorisches Museum Basel, Hartenberger (1969, p.46) wrote that the M2 are stronger than the M1, their posteroloph being longer on M2. For this reason, he assigned the specimen BUX 67–2 (The holotype) to an M1. However, on this specimen, the metacone–hypocone width is reduced compared to the paracone–protocone

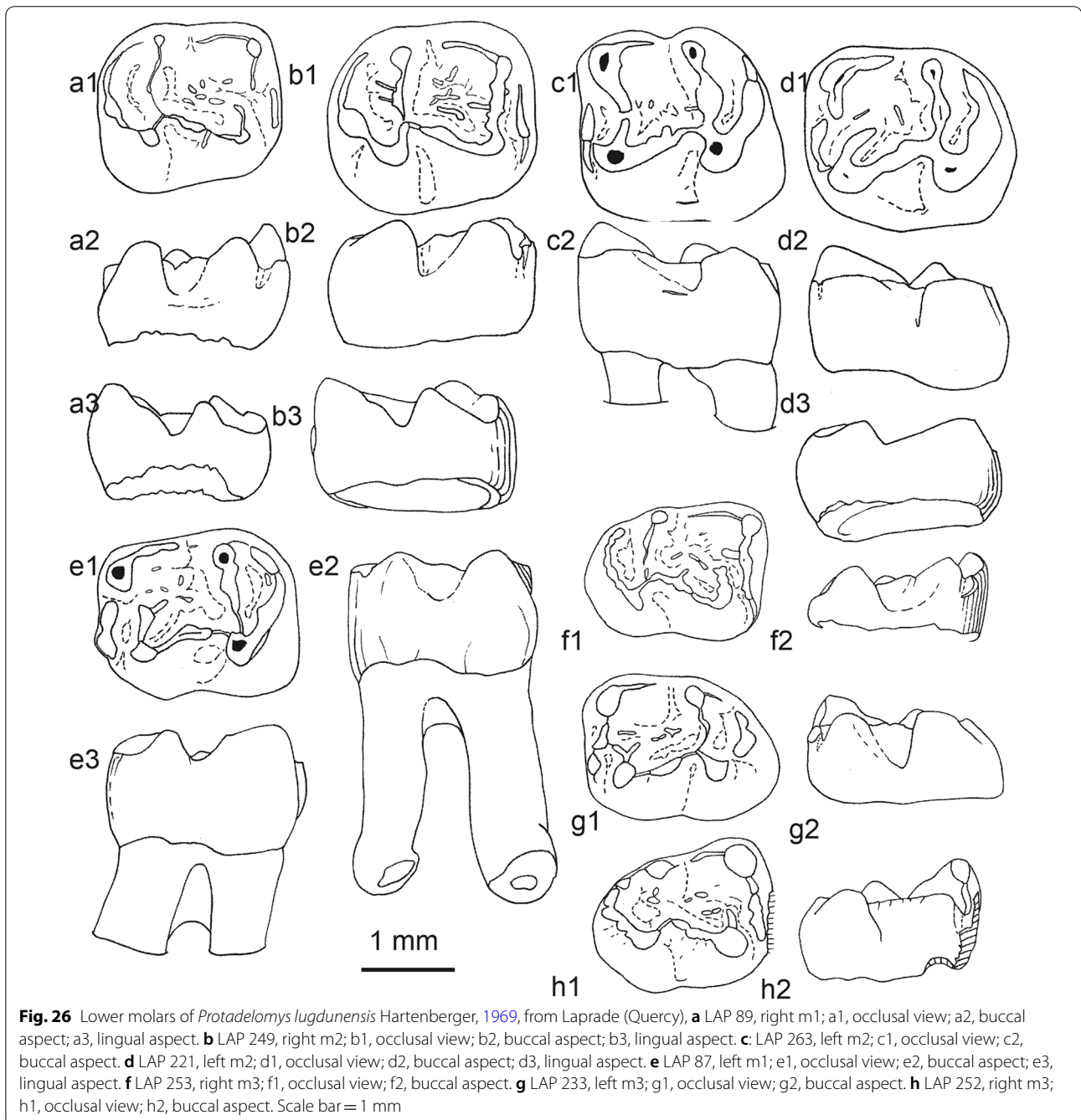


Table 4 Range of the size variations (length and width: min., max.; average \pm Sm = σ/\sqrt{n} ; $v = 100 \sigma/\text{average L or W}$): A. of the different loci of teeth of *?Protadelomys alsaticus* Hartenberger, 1969 and B. length and width for some loci only of *?Protadelomys cf. alsaticus* nov. sp.1,2,3, from Bouxwiller (MP 13; Bas Rhin, France)

A ? <i>Protadelomys alsaticus</i> from Bouxwiller								
Length	n	min	mean \pm Sm	max	σ	v		
DP4	6	1.28	1.347 \pm 0.022	1.43	0.055	4.46		
P4	10	1.4	1.529 \pm 0.038	1.7	0.120	7.85		
M1	35	1.50	1.691 \pm 0.012	1.86	0.071	4.20		
M2	24	1.58	1.680 \pm 0.011	1.78	0.052	3.12		
M3	18	1.54	1.683 \pm 0.020	1.87	0.084	4.99		
dp4	9	1.30	1.429 \pm 0.026	1.53	0.077	5.38		
p4	9	1.44	1.569 \pm 0.022	1.68	0.066	4.23		
m1	27	1.66	1.794 \pm 0.013	1.96	0.066	3.68		
m2	32	1.74	1.819 \pm 0.010	1.96	0.059	4.22		
m3	22	1.79	1.947 \pm 0.016	2.09	0.076	4.62		
Width	n	min	mean \pm Sm	max	σ	v		
DP4	6	1.31	1.388 \pm 0.030	1.52	0.076	4.46		
P4	10	1.38	1.587 \pm 0.036	1.79	0.114	7.18		
M1	35	1.64	1.748 \pm 0.013	1.98	0.076	4.37		
M2	24	1.67	1.762 \pm 0.018	1.87	0.011	3.11		
M3	18	1.46	1.594 \pm 0.024	1.84	0.102	6.37		
dp4	9	0.98	1.089 \pm 0.022	1.16	0.066	6.19		
p4	9	1.12	1.279 \pm 0.039	1.46	0.118	3.93		
m1	27	1.40	1.516 \pm 0.013	1.67	0.070	4.60		
m2	32	1.5	1.609 \pm 0.013	1.76	0.059	4.20		
m3	22	1.47	1.536 \pm 0.016	1.63	0.049	3.18		
B ? <i>Protadelomys cf. alsaticus</i> morphotypes 1, 2, 3, Bouxwiller								
Morphotype 1			Morphotype 2			Morphotype 3		
cat	Length	width		Length	width	Length	width	
P4	1.58	1.43	M1	1.61	1.64	D4	1.45	1.53
M1	2.01	1.99	M1	1.61	1.68	D4	1.41	1.48
M1	1.80	1.98	M1	1.58	1.65	P4	1.49	1.71
M2	1.85	2.01	M1	1.61	1.54	P4	1.50	1.60
dp4	1.46	1.07	M2	1.61	1.63	M2	1.95	2.06
dp4	1.35	1.32	M2	1.60	1.62	M3	4.76	1.80
p4	1.72	1.37	M3	1.62	1.45	m1	1.80	1.67
m1	1.86	1.68	M3	1.49	1.44	m2	2.02	1.81
m1	1.78	1.65	d4	1.21	0.89	m2	1.89	1.59
m2	2.00	1.70	p4	1.72	1.22	m3	2.08	1.68
m2	2.00	1.70	p4	1.45	1.31	m3	2.11	1.75
m2	1.94	1.67	p4	1.45	1.19			
m3	2.18	1.79	m1	1.75	1.52			
			m3	1.98	1.40			

width, and the posteroloph is short, like for the M2 of the species of *Protadelomys* (*P. cartieri* or *P. lugdunensis*) and more generally of the basal Theridomorpha. The holotype rather represents an M2. Moreover, the

size distribution (L x w) of the M1 overlaps that of M2 (Fig. 27A and Table 4), which indicates that M2 are not typically larger than M1. Furthermore, the two specimens from the NHMB (Buchs 660) are for one an upper

jaw with M1–M3 and the other one a lower jaw with p4–m2. They are not “two upper jaws with P4–M1–M2” (Hartenberger, 1969: 46).

Holotype. M2 (not M1) sup. (Hartenberger, 1969: Pl. 2, Fig. 6; this paper: Fig. 31a).

Type locality. Bouxwiller (green marls), France; middle Eocene, MP13.

Original diagnosis (translation from French). “*Protadelomys* more primitive than *P. cartieri*. Upper molars with sinus less pronounced. Paraconule, metaconule, and mesostyle variable in volume. Short lower fourth premolars. Numerous wrinkles.”

New diagnosis. Dental morphology “intermediate” between *Masillamys* and *Protadelomys*. Unilaterally weakly hypsodont teeth; almost the entire teeth bear more or less low extra-ridges and granules, and enamel surface of the outskirts of the crown (mainly lingual for upper teeth or buccal for lower teeth) displaying faint and oriented ornamentations from the base to the edge of the crowns.

Upper teeth: DP4 a little smaller than P4 and more molarized, with the hypocone lingually displaced. P4 with paracone and metacone more bulbous than on DP4; paraconule mesially displaced and fused with the anterostyle; small hypocone variably present. On molars, the hypocone is slightly smaller, to nearly equal in size, than the protocone. The M2 posterior width is shorter than the M1 posterior width. The postparacrista and premetacrista variably present. The mesostyle is always present; the mesoloph sometimes reaches the mediobuccal ridge of the metaconule. A small hypocone is generally present on M3.

Lower teeth: the anteroconid is buccally located on molars; it is more or less lingually stretched, and sometimes joins the linguobuccal premetacristid. The anterocingulid is absent. The mesial metalophulid I often corresponds to the premetacristid, which sometimes bifurcates or is parallel to a more distal branch of the metalophulid I. The latter sometimes turns distally to join the buccal transverse branch of the metalophulid I. The postprotocristid is thick, long and oblique; its distal end is often swollen with a premesoconid spur. The short mesiodistal ectolophid bears a small mesoconid. The ectomesolophid and mesolophid spurs are variably developed or absent; the postmesoconid swelling and/or spur is present and variably developed. The entolophid lowers buccally, and attaches either to the postmesoconid spur/swelling or to the junction of the distal part of the ectolophid and the prehypocristid, which is short. The hypoconulid is bulged and sometimes duplicated.

?*Protadelomys alsaticus* differs from:

- *Protadelomys cartieri* in a few ancestral features as the sometimes slightly more reduced hypocone, the P4 shorter relative to M1, or the presence of a mesoconid. *?P. alsaticus* also displays more numerous specialized characters such as the small hypocone frequent on P4; the buccal mesoloph longer, the strong metaconule more protruding in the mesoflexus, the thick high endoloph on upper molars; the protoconid stronger on dp4 with the entolophid connected to the prehypocristid + ectolophid on lower molars.

- *Protadelomys lugdunensis* in the absence of anterocingulid on lower teeth, and the enamel ornamentations more numerous and frequent.

- *?Protadelomys maximini* in the often longer and more frequent mesoloph, the less reduced hypocone, and the thicker lingual wall.

- *Tardenomys*. **On upper teeth:** In the constant presence of a high endoloph, a thick prehypocrista and well-distinct metaconule, isolated from the hypocone; in the absence of a fully developed mure. **On lower teeth:** in the less frequent and weaker oblique extra-ridge from the lingual extremity of the buccal metalophulid I, and in the absence of buccal cingulid developed from the anterolophid together with the buccal closing of the anteroflexid.

Material and measurements: (Additional file 4: S4, Table 4A). Numerous isolated teeth (6 DP4, 11 P4, 69 M1–M2, 21 M3; 9 dp4, 9 p4, 64 m1 and m2, 21 m3) come from the green marls at the base of the Bouxwiller Quarry. Most of the teeth belong to the species *?P. alsaticus* here revised. They are provisionally attributed to the paraphyletic genus *?Protadelomys*. The congruence between the size and some morphological features makes it possible to distinguish several morphotypes within the assemblage from Bouxwiller that are plotted on the Figure 27 (morphotype 1: light violet; morphotype 2: turquoise; morphotype 3: light green). Like for *P. cartieri* and *P. lugdunensis* *?P. alsaticus* displays DP4, P4, dp4 and p4 smaller than the molars. M1 and M2 are similar in size and the M3 are clearly narrower than the other molars, but are close in length. The m1 are moderately smaller than the m2. The m3 are longer than the m1 and m2, but less than in *P. lugdunensis*. The teeth are a slightly smaller than *P. cartieri* (Fig. 28; Tables 1, 4), and significantly smaller than *P. lugdunensis* (Table 8).

Description. Most of the teeth bear more or less low additional ridges and granules, and the enamel surface of the crown displays faint and oriented ornamentations

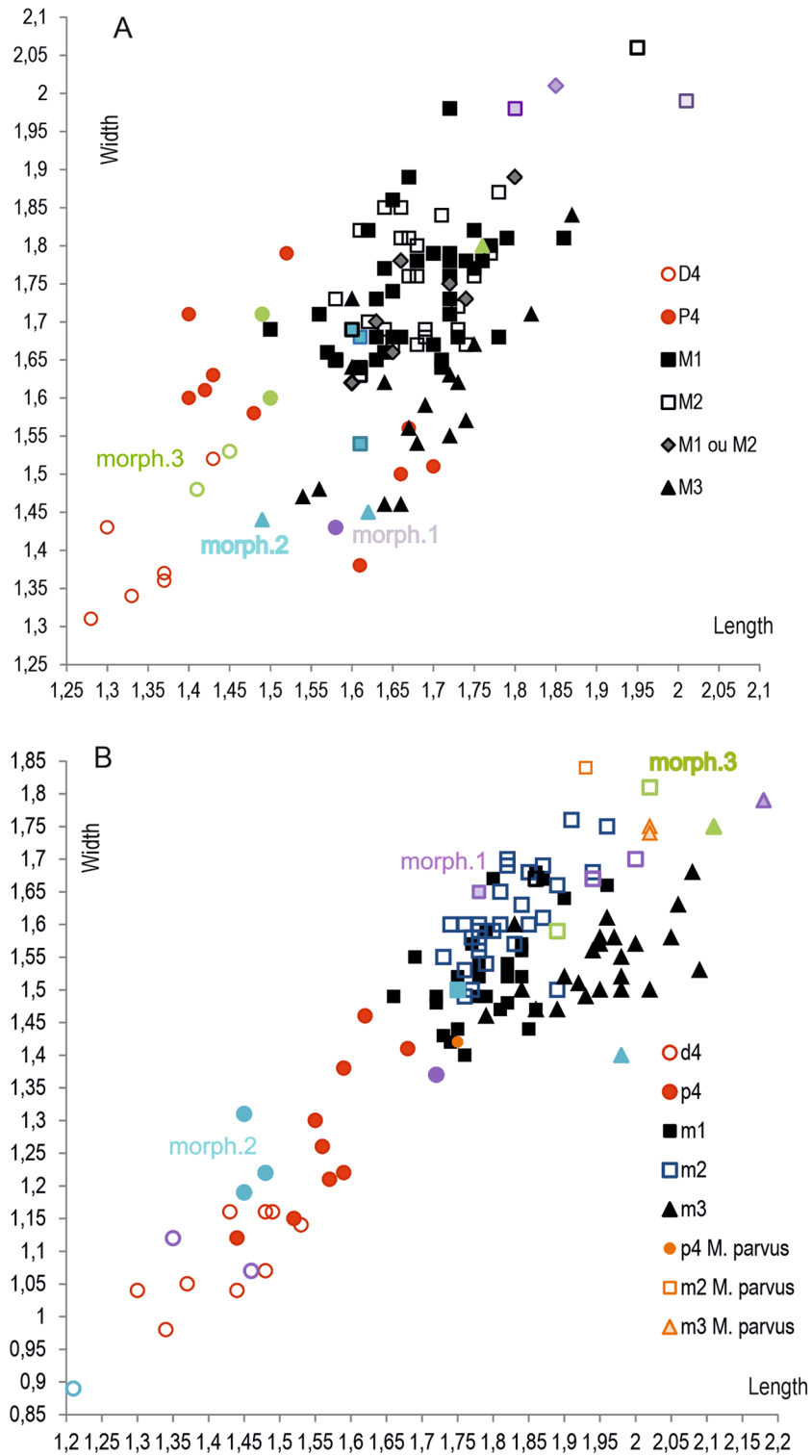


Fig. 27 Bivariate graph of the size (width/length) of the upper (A) and lower (B) teeth of *Protadelomys alsaticus* Hartenberger, 1969 from Bouxwiller (Bas-Rhin) (dp4/DP4 and p4/P4: red marks; upper and lower molars: black marks). From Bouxwiller, a few teeth are identified as *?P. cf. alsaticus* sp. indet 1 (purple marks), sp. indet 2 (turquoise blue marks) and sp. indet 3 (green marks). On B, four teeth (orange marks) are *Masillamys parvus* from Messel (Germany)

from the base to the edge of the crowns, which are mainly lingual for upper teeth and buccal for lower teeth.

Description of the type (BUX67-2) (Fig. 31a).

The type specimen corresponds to an M2 that displays a long and thin buccolingual anteroloph, in the extension of a thick and high preprotocrista, swollen at its mesial extremity in an anterostyle. The bulged paracone and metacone are similar in size. The buccal part of the protoloph is straight, until its low connection to the paraconule. The latter is bulged and protruding mesially from the protoloph. Lingually to the paraconule, the very thin and low lingual part of the protoloph weakly connects the apex of the protocone. A thin postparacrista and a thicker premetacrista are present and descend towards but do not fuse with the bulged mesostyle. The latter prolongs lingually in a buccal mesoloph, for which the distal end faces but does not fuse with the metaconule. The buccal metalophule II is strong, first parallel to the buccal protoloph, then turns mesially; it joins a high distolingually to distobuccally stretched metaconule, which reaches the center of the tooth. Several extra-ridges descend mesially from the buccal protoloph and the metalophule II, around the mesiobuccal extremity of the metaconule, and on the buccal flank of the association of the protocone and endoloph. The metalophule I is not distinct among these extraridges. The hypocone is nearly equal in size to the protocone; both cusps are a little stretched, mesiodistally for the protocone and mesiolingual to distobuccal for the hypocone. This stretching of the protocone and hypocone prolongs in their anterior and posterior arms. The metaconule is stretched and prolonged mesiobuccally to distolingually to join the hypocone via a high lingual metaloph. The postprotocrista and prehypocrista are short and linked by a thick and high endoloph. The posteroloph is short and lowly connected to a short posthypocrista; it begins lingually in a bulged posteroconule, and ends at the base of the metacone, the posteroflexus being opened buccally.

Upper teeth. The teeth of *P. alsaticus* are unilaterally and weakly hypsodont. Thereby, the occlusal surfaces vary with wear, but not strongly. The cusps are bulged; the conules and associated ridges are sharp on unworn teeth, but blunt and rounded on worn teeth. The breaks along the lophs as well as the extra-ridges and granules sometimes disappear with wear.

DP4 (Fig. 29a to d). Eight teeth correspond to DP4 in our sample; among them six only are referred to this species, and the two largest (CSBX2 and 3) to *?Protadelomys cf. alsaticus* morphotype 3. In all cases, DP4 are smaller than P4 (Fig. 27 A; Table 4A). Their contour is triangular due to the presence of a small hypocone.

The parastyle is present and the anteroloph relatively long and low. The anteroloph links with the

preprotocrista. The anterostyle is not clearly distinct, due to wear. The paraconule is smaller than the metaconule and slightly protruding from the protoloph, the latter being weakly linked to the preprotocrista. The mesostyle is slightly more buccal than the paracone and metacone; it is closer to the metacone and is separated or connected to a short mesoloph. The metalophule I is sometimes absent, often present but short, low, discontinuous, directed or connected to the mediobuccal crest of the metaconule. The metaconule is strong, isolated from the hypocone, and weakly connected to the postprotocristid. The hypocone is conical and much smaller than the protocone; it is lingual when compared to the protocone. The endoloph is very short and high. The sinus is absent or barely marked. The posteroloph is generally short and swollen at the level of the posteroconule. The hypocone–posteroloph connection is either low and short, or weak or absent.

P4 (Fig. 29e to l). Thirteen teeth correspond to P4. On a length x width diagram (Fig. 27), two groups are identifiable. The first gathers the longest and narrowest teeth (CSBX5, 6, 7, 8, 9), and the second the shortest and longest ones. However, their morphological variation is partly independent of this grouping. Moreover, their lengths and widths show a coefficient of variation v compatible with a single population (Table 4A) (Legendre & Vianey-Liaud, 1986). Among the largest P4, CSBX8 is morphologically simpler and can be referred to *?Protadelomys cf. alsaticus* morphotype 1; CSBX12 displays a sharp and strong preparacrista and a mesoflexus closed buccally, it can be referred to *?Protadelomys cf. alsaticus* morphotype 3. All the other P4 are attributed to *?Protadelomys alsaticus*.

All P4 are triangular with a reduced hypocone (12/13). Only CSBX 9 displays a hypocone nearly as strong as the protocone; it is more squared, with parallel anteroloph and posteroloph but its other features are similar to those of the other P4 (Fig. 29i). The endoloph is very short to absent, and the sinus is generally absent or barely marked. The paracone is isolated (9/13) or lowly connected to the paraconule (4/13). The anteroloph is very short and slender. The paraconule is generally indistinct from the anterostyle, as a strong mesiolingual conule, lower than the paracone and protocone. The mesostyle prolongs in a mesoloph; on CSBX 6 (Fig. 29f) the buccal openings of the mesoflexus, on either sides of the mesostyle, are blocked by short ectocingulids. A premetacrista is generally present. The metalophule I is short and weak. The metaconule is strong, isolated from the lingual cusp on the less worn P4 and, on the others, it is connected either to the postprotocrista by a very low ridge on CSBX 7, 9, 12, or to the hypocone (CSBX 13, 29) or to the posteroloph (CSBX 28). The strong bulbous metaconule bears

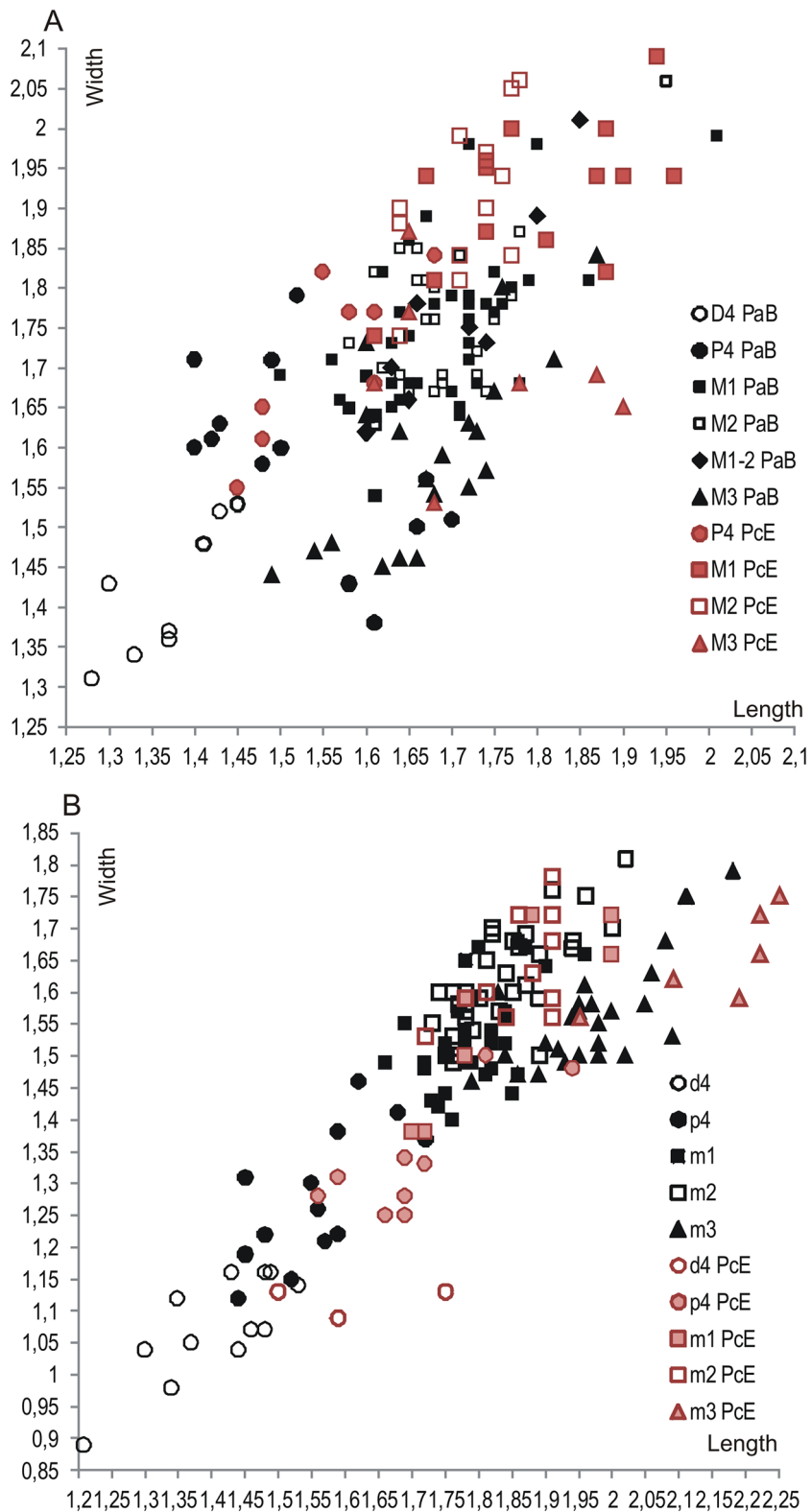
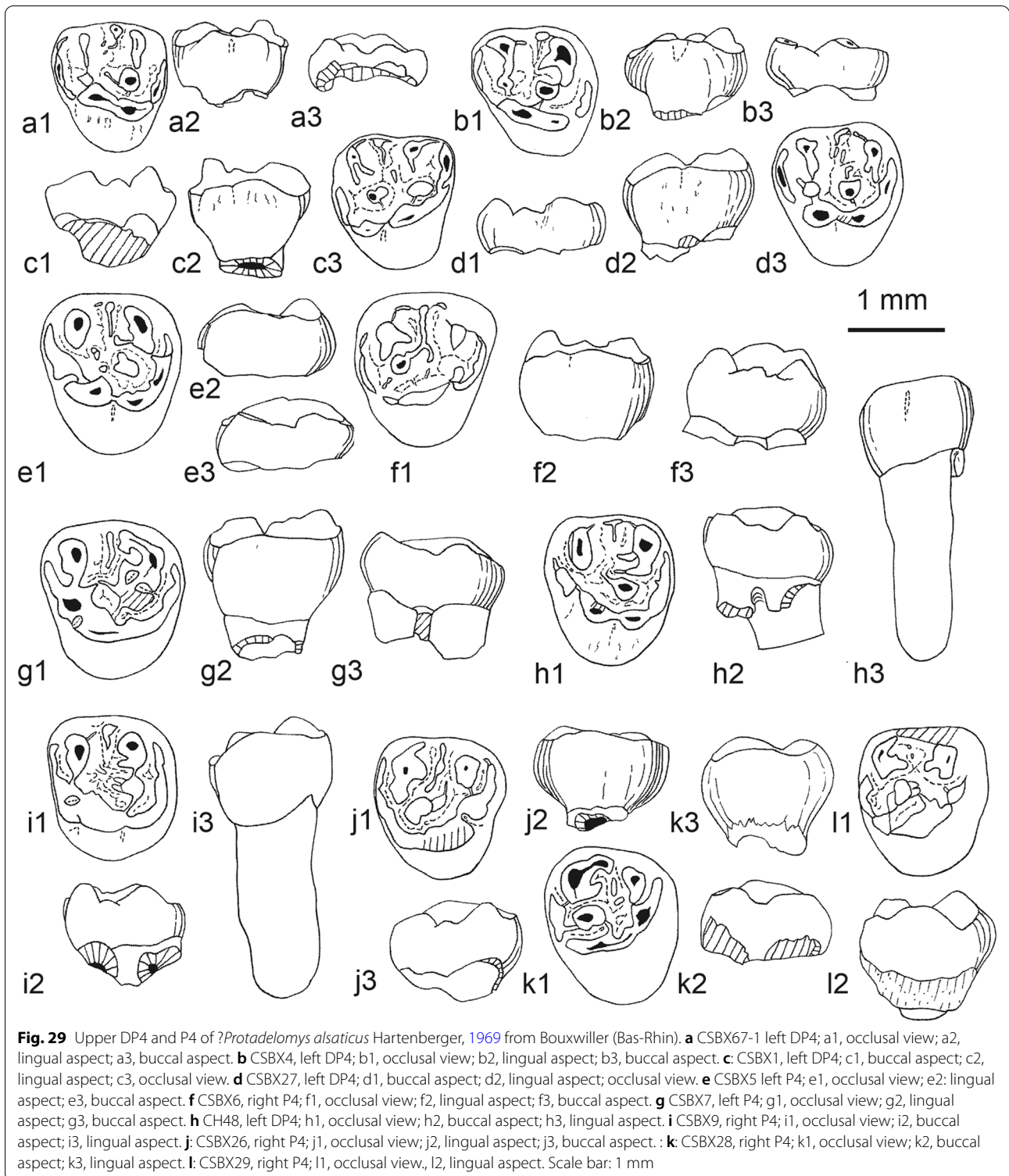


Fig. 28 Bivariate graph of the size (width/length) of the upper (A) and lower (B) teeth of *Protadelomys alsaticus* Hartenberger, 1969 from Bouxwiller (Bas-Rhin) (black marks, PaB) compared to the size of the teeth of *Protadelomys cartieri* (Stehlin & Schaub, 1951), from Egerkingen (Swiss Jura) (red marks, PcE)



a short mesiobuccal ridge, ending free or connected to the metalophule I. There are more or less numerous low extra-ridges or granules in the mesoflexus.

M1 (Fig. 30) and **M2** (Fig. 31). If M1 and M2 display a strong morphological variability, a common pattern is recognizable. All these teeth are pentalophodont, with a short mesoloph. The paracone and metacone are salient;

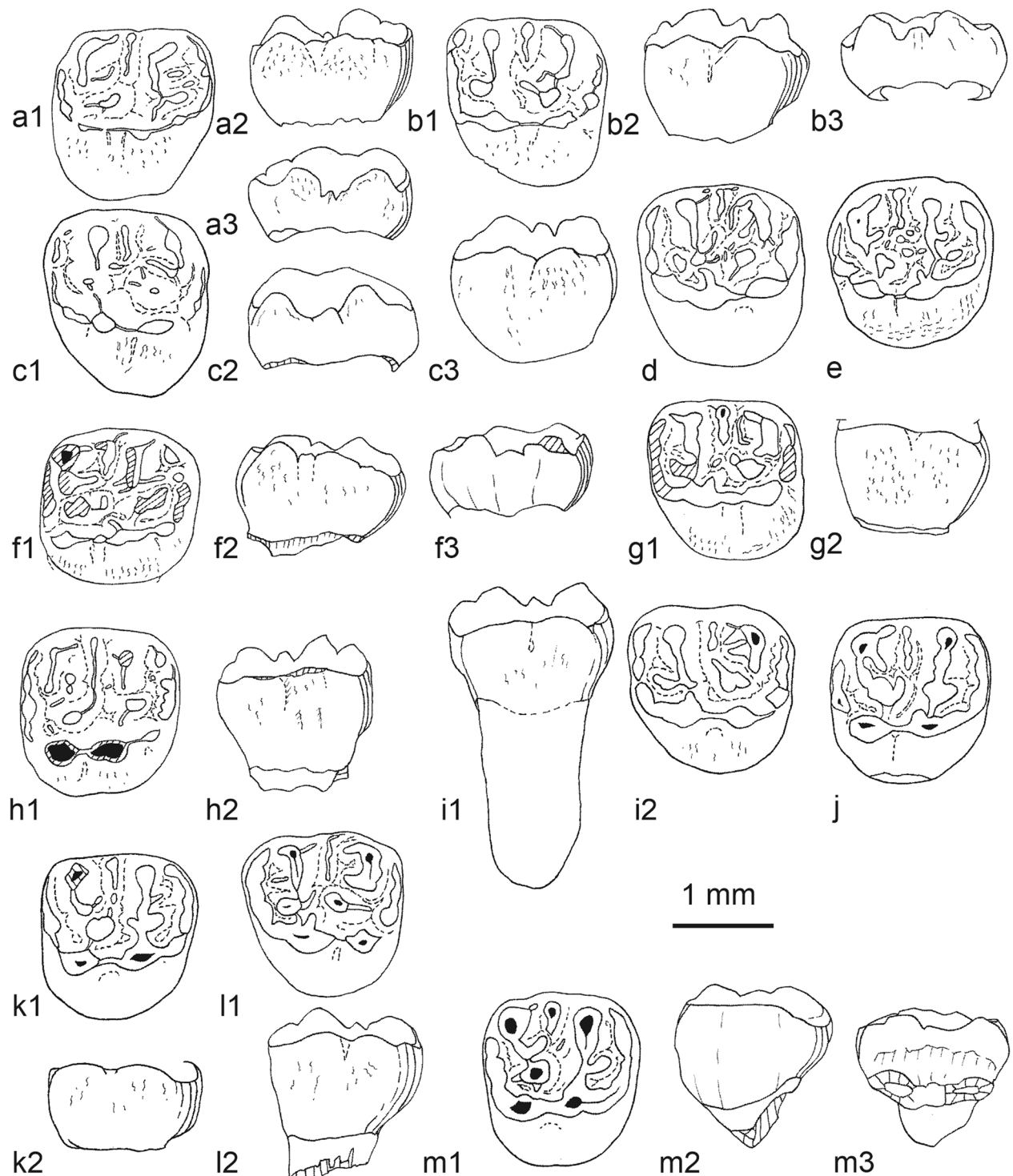


Fig. 30 Upper M1 of *Protadelomys alsaticus* Hartenberger, 1969 from Bouxwiller (Bas-Rhin). **a** CSBX32, right M1; a1, occlusal view; a2, lingual aspect; a3, buccal aspect. **b** CSBX67, left M1; b1, occlusal view; b2, lingual aspect; b3, buccal aspect. **c**: CH41, right M1; c1, occlusal view, c2, buccal aspect; c3, lingual aspect. **d** BUX67-24, left M1, occlusal view. **e** BUX67-66, right M1, occlusal view. **f** BUX67-61, right M1; f1, occlusal view; f2, lingual aspect; f3, buccal aspect. **g** BUX67-68, left M1; g1, occlusal view; g2, lingual aspect; g3: buccal aspect. **h** BUX67-54, right M1; h1, occlusal view; h2, lingual aspect. **i** BUX67-47, left M1; i1, lingual aspect; i2, occlusal view; **j**: BUX67-53, right M1, weakly worn, occlusal view. **k**: BUX67-43, right M1; k1, occlusal view; k2, lingual aspect. **l**: CH49, left M1; l1, occlusal view; l2, lingual aspect. **m**: BUX67-46, right M1; m1, occlusal view; m2, lingual aspect; m3: buccal aspect. Scale bar: 1 mm

the protocone and hypocone are sharp on weakly worn teeth and blunt when worn. The protocone is stretched mesiodistally with its pre- and post-protocristae. The hypocone is smaller than the protocone, with lower and weaker arms. Mesiodistally, the endoloph is short, thick, and high but a little lower than the protocone and hypocone summits (as seen on lingual views of unworn teeth; Fig. 30a2, b2, c3, f2). The sinus is barely marked or absent. The paraconule is protruding mesially from the protoloph; it is rounded or a little stretched distomesially, and generally nearly as strong as the metaconule. The metaconule is generally more bulbous than the paraconule, except on the holotype where it is stretched obliquely. The connection between the protoloph and the center of the protocone, as well as the connection between the metaconule and the prehypocrista, are generally weak and very low, except on the holotype. The buccal metaloph is generally absent, the metaconule being separated from the hypocone.

The main variation involves the development of the parastyle and anterostyle, the shape and thickness of the mesostyle, the length and development of the mesoloph, the relationships of the latter with the mediobuccal crest of the metaconule, the development of metalophule I, the connection between the metaconule and the posteroconule, the extra-ridges and granules, and the enamel ornamentation. The parastyle is often more swollen on M1 than on M2, but not always. It generally fuses with the anteroloph; except on some unworn specimens like CSBX 67: Fig. 30b, CH 41: Fig. 30c, BUX 67–28, and BUX 67–54: Fig. 30h. The anteroloph is higher than the posteroloph and located between the parastyle and the anterostyle. The latter is generally swollen and connected to the end of the preprotocrista, which is more or less oblique linguo-mesially. On BUX 67–61: Fig. 30f, the preprotocrista is slightly mesiodistally oriented. The anteroloph is more or less crenulated, with very short mesiodistal wrinkles. One of these wrinkles sometimes joins an extra-ridge from the protoloph. This extra-ridge can be present, absent, or duplicated and parallel to the paraconule. The distal flank of the paracone rarely shows a short postparacrista (M1: BUX 67–61: Fig. 30f, BUX 67–54: Fig. 30h, CH49, Fig. 30l; M2: BUX 67–44: Fig. 31e, BUX 67–2, BUX67-56: Fig. 31l, CSBX 36). The premetacrista is thick and always present. The metalophule II is short and rarely connected to the metaconule. The metalophule I is absent or reduced to weak extraridges. The surface of the mesostyle can be underlined by a hawk-shape ridge (BUX 67–59, 64), which disappears with wear in a thick mesostyle. Short mesiodistal ectocinguli rarely frame the mesostyle (Fig. 30d). When present, the granules and short low extra-ridges are located in the mesoflexus, from the base of the protocone to the

mesoloph and metaconule. The mediobuccal crest of the metaconule is generally weak, and sometimes directed towards the lingual extremity of the mesoloph, without merging with it. BUX 67–70 departs from other molars by its more triangular shape. It probably corresponds to an M1, as the posteroloph and the hypocone are not really reduced. The preprotocrista is relatively short and the anterostyle small. The parastyle is not salient. The protruding paraconule is small. All the other features are close to those described above.

On the M2 CSBX 30, the post-hypocrista is absent and the posteroconule is linked to a short lingual part of the metaloph, which descends from the hypocone; the posteroloph is reduced to a short crest.

M3. (Fig. 32). Most of the M3 are unworn or weakly worn (17/21); they display a wide range of size variation (Fig. 27 A), but their lengths and widths show a coefficient of variation v compatible with a single population (Table 4A) (Legendre & Vianey-Liaud, 1986). Among the three biggest teeth, BUX 67–27 could belong to *?Protadelomys* cf. *alsaticus* morphotype 3. We have not found singularities for the two other large M3 (BUX 67–85, 86), which could justify to exclude an attribution to *?Protadelomys alsaticus*. Among the smallest specimens, BUX 67–88 and BUX 67–87 are referred to *?Protadelomys* cf. *alsaticus* morphotype 2.

The remaining 18 specimens display a long anteroloph and a distinct parastyle. The paracone represents the higher cusp. The metacone is salient from the buccal ridge it forms with the mesostylar area and the metalophule II. The paraconule is small and protruding. The development of the metaconule is variable; it is salient on unworn teeth and otherwise usually weaker than the paraconule, but not always (BUX67-84). The central basin is wide and filled with extra-ridges as strong as in the M1–2, in the area close to the mesostyle and metaconule. These extra-ridges are more or less numerous. The distal part of the teeth is highly variable. The metalophule II is short, connected to the metacone and oriented distomesially. It can be separated from the metacone or absent, with the metacone connecting with the posteroloph. The hypocone, more or less strongly reduced, is more buccal than the protocone. The posteroloph always joins the post-hypocrista. The sinus is often present but weakly marked; it rarely communicates with the opposite synclines. Wrinkles can be present on the lingual slope of the crown.

Lower teeth. (Figs. 33, 34, 35, 36, 37) six specimens are considered as dp4 of *?Protadelomys alsaticus*. The size distribution (Fig. 27 B; Table 4A) is large, dp4 being the smallest, then p4 smaller than molars, the m2 being slightly larger than the m1. The crowns of all the teeth are as high buccally as lingually, but their lingual flank is

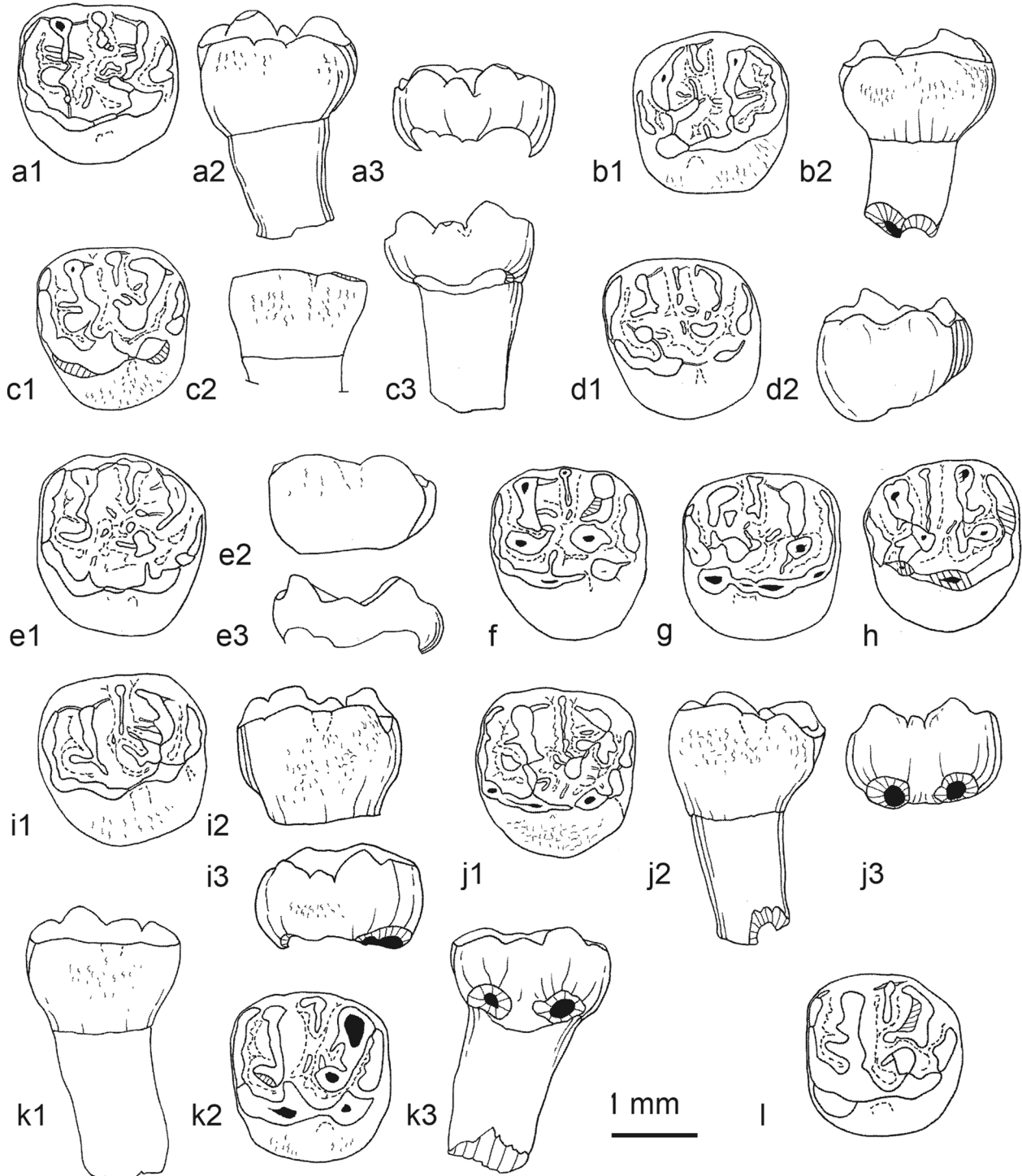
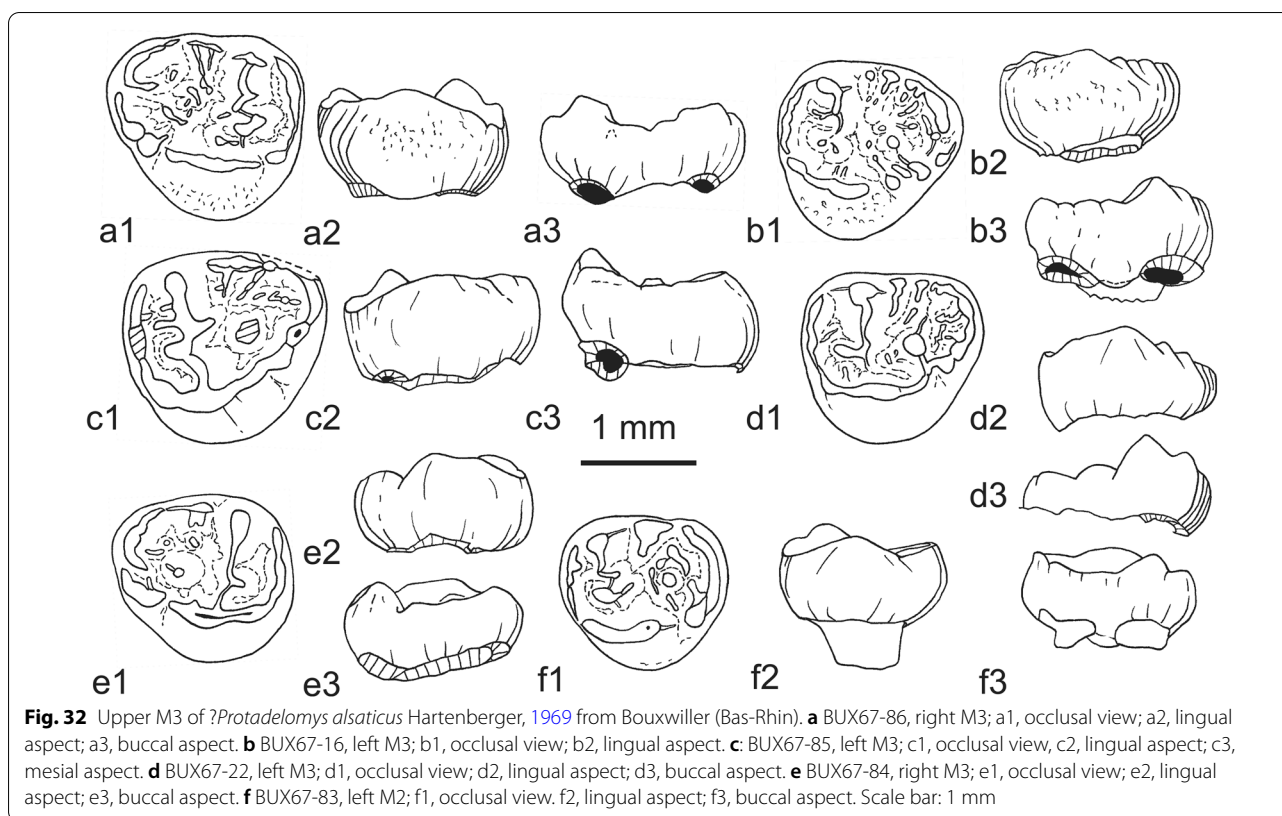


Fig. 31 Upper M2 of *Protadelomys alsaticus* Hartenberger, 1969 from Bouxwiller (Bas-Rhin). **a** BUX67-2, left M2, Holotype; a1, occlusal view; a2, lingual aspect; a3, buccal aspect. **b** CH43, right M2; b1, occlusal view; b2, lingual aspect. **c**: CH41, left M2; c1, occlusal view, c2, lingual aspect; c3, buccal aspect. **d** CH32, left M2; d1, occlusal view; d2, lingual aspect. **e** BUX67-44, left M2; e1, occlusal view; e2, lingual aspect; e3, buccal aspect. **f** CSBX69, left M2; occlusal view. **g** CSBX33, right M2; occlusal view. **h** BUX67-6, right M2; occlusal view. **i** BUX67-56, left M2; i1, occlusal view; i2, lingual aspect; i3, buccal aspect. **j**: BUX67-72, left M2; j1, occlusal view; j2, lingual aspect; j3, buccal aspect. **k**: BUX67-52, left M2; k1, lingual aspect; k2, occlusal view; k3, buccal aspect. **l**: BUX67-79, left M2; occlusal view. Scale bar: 1 mm



relatively flat whereas the buccal flanks of the protoconid and hypoconid are bulged. Wrinkles, weak ridges or granules are variably present in the basins.

dp4. (Fig. 33a to f) The metaconid is the highest and mesial-most cusp. It separates from the protoconid, which is smaller. The anteroconid is absent; a weak and short mesiobuccal ridge (preprotocristid) is only visible on two teeth (CSBX 50: Fig. 33f, and BW 56–55; Fig. 33e). A short buccal metalophulid I is only visible on CH 55. The metaconid prolongs distally in a high postmetacristid. A small mesostylid is isolated at the distal extremity of this crest on two specimens (CSBX 50 and BW 56–54). All specimens display a low mesiodistal extra-ridge, descending from the metaconid to the mesoflexid. This extra-ridge is high on CSBX 43 (Fig. 33a) less on the others, discontinuous on CSBX 50, CH 55 and BW 56–55, and almost erased on BW 56–54. There are a few granules and/or low ridges in the basins (meso- and posteroflexids). The postprotocristid is nearly mesiodistal and connected to the mesoconid; the latter is a little swollen and the ectolophid can be more lingually located, after making an angle distal to the mesoconid (CSBX 43). This ectolophid lowers between the mesoconid and the short prehypocristid. The entoconid is salient and isolated from the postmetacristid–mesostylid. The entolophid is complete and very low (6/9), joining the extremity of the

short prehypocristid; it is incomplete on BUX 67–100 and 104. On one specimen only (CSBX 43), the lingual half of the entolophid is distally directed towards the posterolophid. The hypoconulid is swollen and connected to a long post-hypocristid and to a short posterolophid. The latter ends at the level of the distal flank of the entoconid, and closes the posteroflexid lingually.

p4. (Fig. 33g to m) The posterior root of p4 is vertical and strong. The length between the entolophid and the mesial border is only a little longer than to the distal border; it is shorter than in the other *Protadelomys* species. The metaconid is the highest and mesial-most cusp, and extends in a long lingual postmetacristid. The metaconid separates from the protoconid, which is smaller and weaker. The protoconid is usually low and less distinct than that of dp4; it is rarely well distinct from the metaconid (CH 26, BW 56–57, and BUX 67–97). The anteroconid is absent; there is only a weak short mesiobuccal ridge on BW 56–55, and a shallow anterossinus on BUX 67–103 (Fig. 33k). The wrinkling of the enamel is stronger on the latter than on the other eight p4. The mesiodistal ridge is usually low, continuous or more or less interrupted. The granules and extra-ridges are rare. BUX 67–103 and 107 are the most ornamented p4. The mesoconid is weak, the mesial ectolophid is indistinct from the postprotocristid–mesoconid, and the distal ectolophid is short and broken

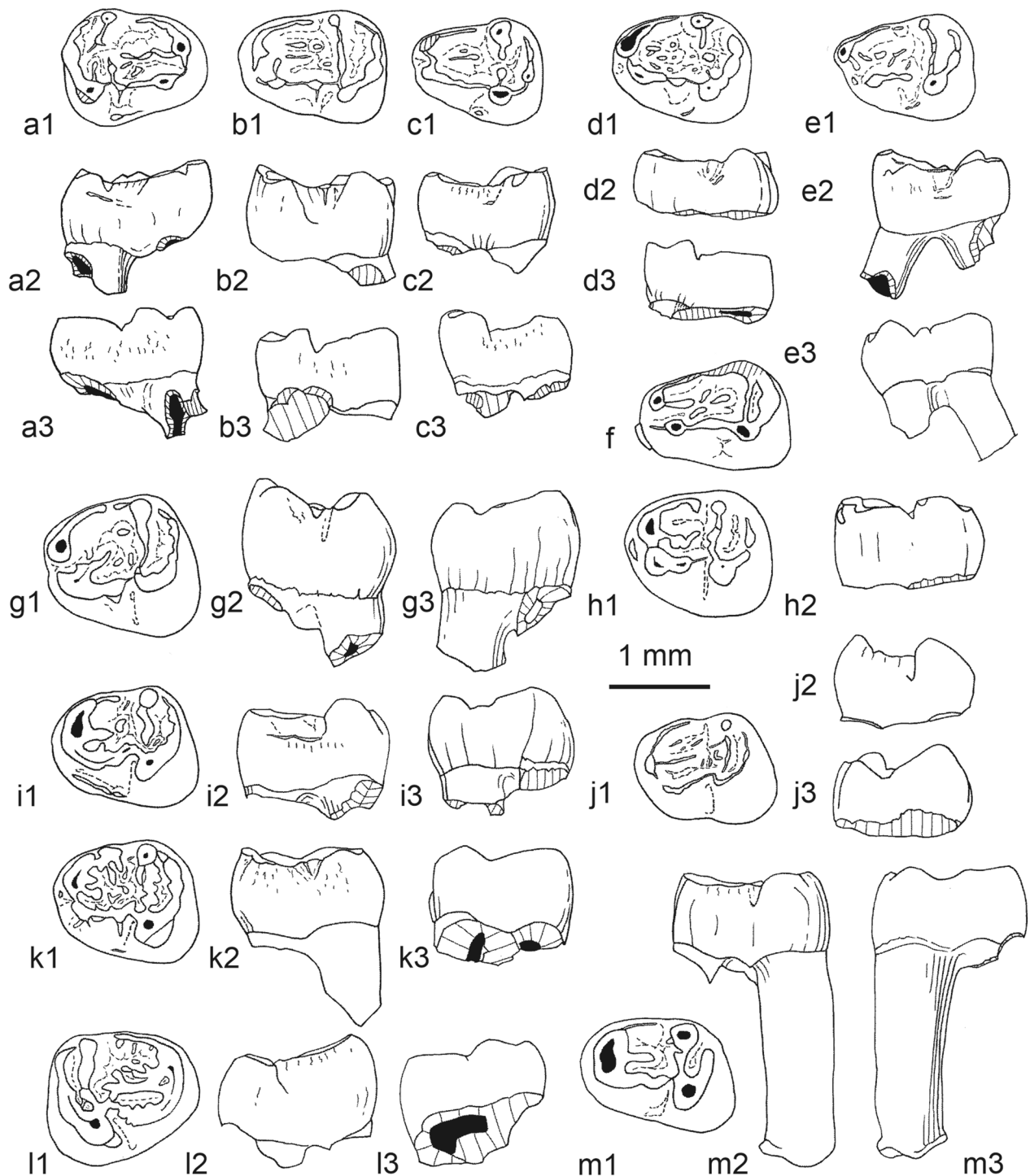


Fig. 33 Lower dp4 and p4 of *Protadelomys alsaticus* Hartenberger, 1969 from Bouxwiller (Bas-Rhin). **a** CSBX43, right dp4; a1, occlusal view; a2, buccal aspect; a3, lingual aspect. **b** CH55, left dp4; b1, occlusal view; b2, buccal aspect; b3, lingual aspect. **c** BUX67-100, left dp4; c1, occlusal view; c2, buccal aspect; c3, lingual aspect. **d** BUX67-104, left dp4; d1, occlusal view; d2, buccal aspect; d3, lingual aspect. **e** BW56-55, left dp4; occlusal view. **f** CSBX50, left dp4; f1, occlusal view; f2, buccal aspect; f3, lingual aspect. **g** CH26, left p4; g1, occlusal view; g2, buccal aspect; g3, lingual aspect. **h** BW56-57, left p4; h1, occlusal view; h2, lingual aspect. **i** BUX67-101, left p4; i1, occlusal view; i2, buccal aspect; i3, lingual aspect. **j** BUX67-102, left p4; j1, occlusal view; j2, buccal aspect; j3, lingual aspect. **k** BUX67-103, left p4; k1, occlusal view; k2, buccal aspect; k3, lingual aspect. **l** BUX67-107, right p4; l1, occlusal view; l2, buccal aspect; l3, lingual aspect. **m**: BUX67-105, left p4; m1, occlusal view; m2, buccal aspect; m3, lingual aspect. Scale bar = 1 mm

at the level of the prehypocristid, as seen on unworn or weakly worn teeth (CH26: Fig. 33g; BW59-57: Fig. 33h). An ectostylid is present buccally at the base of the sinusid on BUX 67–101 and 103. The sinusid is asymmetrical and pinched. The entolophid is low and rarely continuous (BUX 67–103 and 105), directed to or connected to the short prehypocristid. The hypoconulid is not well individualized; the posterolophid ends at the base of the entoconid.

m1 (Fig. 34)–**m2**. (Fig. 35). The two loci can be distinguished by a set of morphological characters. The hypoconid is as strong as the protoconid, and slightly placed more buccally on m1 than on m2. The distal root is generally more vertical on m1 than on m2, where it is oblique posteriorly and a little twisted buccally. On m1, the metaconid–protoconid width is lower than the entoconid–hypoconid width, the anteroconid is usually less stretched and shorter, and the anterolophid is most often absent.

For both m1 and m2, the morphological variation is important. We did not identify clear-cut groupings among the molars, but by combining size variation and a few discrete features, a characterization of three different tooth morphotypes was made possible (see below).

On all m1 and m2, the metaconid is the higher cusp, followed lingually by a high and strong postmetacristid descending more or less steeply towards the lingual opening of the mesoflexid. The mesostylid is absent on the m1, except on CSBX 48, and present on a few m2 as a swelling at the distal end of the postmetacristid (BSK-A28, BUX 67–110: Fig. 35 h, 127: Fig. 35d, 132, ?134, BUX 68–44: Fig. 35k) or as a separated small cuspid (BUX 67–116, CSBX 46). The valley between the postmetacristid and the entoconid is generally obtuse but it appears more constricted, acute, on BUX 67–136, 137, CSBX 47, and BUX 68–33, or even reduced when the mesostylid is present. An anterolophid is present, as a short lingual prolongation of the anteroconid, on m1 BUX 136 only. On m2, the anteroconid is generally slightly bulbous, more or less stretched buccolingually. It disappears in the slender anterolophid on BUX 68–44 and 46, BUX 67–112: Fig. 35f, 117, 118, and 141. On BUX 67–141, the anterolophid is longer than on the other m2, whereas the thick lingual metalophulid I is not mesial and runs obliquely (mesiobuccally) from the top of the metaconid

to meet the transverse buccal metalophulid I. The complete metalophulid I usually closes the anteroflexid distally (m1: BUX 67–25, CSBX 67–52; m2: BUX 67–110: Fig. 35 h, 116, 119: Fig. 35i, 120) at least at its base; but sometimes it is open distally when the connection does not exist (m1: BUX 68–33, 39; CSBX 42, BUX 67–11; m2: BSK-A21, A28; BUX 67–15, 112: Fig. 35f, 118, 121, 139; CH 13; CSBX 49). The anteroflexid is reduced when the lingual metalophulid I is mesial, as a premetacristid (m2: BUX 67–19 and 133). The anteroflexid is slightly opened buccally on weakly worn teeth, but a low buccal elevation of enamel is present on its floor.

If the buccal half of the metalophulid I always retains the same cuspid arrangement and buccolingual orientation, a strong variation is observed on the lingual metalophulid I. The buccal metalophulid I always starts from the apex of the protoconid to run linguobuccally towards the midwidth of the crown. The main variation occurs at the connection with the lingual metalophulid I. They generally separates with a mesiodistal narrow groove, more or less wide or deep. In these cases, the lingual metalophulid I can be short and regularly thin (e.g., BUX67-33: Fig. 35l) or thick (e.g., 130: Fig. 35c, 132: Fig. 35b, 133, 141; CH 22), or bulbous at its buccal end (e.g., BUX 68–39; BUX 67–129). The lingual and buccal parts of the metalophulid I can, in some cases (CSBX 40, 44, 46, 52; BUX 67- 113, 132, 140), be strongly connected.

The lingual metalophulid I is usually mesial, and occupies the position of the premetacristid (e.g., m1: BUX 68–39; BSK-A24, 25, 27; BUX 67–25, 114, 128, 135, 136, CSBX48; m2: BUX 67–110, 112, 113, 116, 117, 120, 133, 140; BUX 98–44; BSK-A21, A28, A29; CSBX 40, 41, 49, 53). It can be slightly displaced or angled distally (m2: BUX67-11, 15, 115, 121,132, 134; BSK-A26; CSBX 42, 46, 47, 54), or splitted in two branches more or less separated (e.g., m1: BSK-A22; BUX 67–5, 19; BW 56–59; CH 13, 17, 24; CSBX 44, 52, 56; m2: BUX 67–127, 130). On BUX 67–141, the strong lingual metalophulid I is transversely in line with the buccal metalophulid I. When distinct from the buccal metalophulid I, the lingual metalophulid I can be long (half-width of the metalophulid I length) or short (e.g., m1: BUX 67–115, 123; CH 22; m2: CSBX 54; BUX 67–115). The overall shape of the lingual and buccal metalophulids I makes an angle open mesially (e.g., BUX 67–124, 126, 132, 140; CSBX 46), but it can be

(See figure on next page.)

Fig. 34 Lower m1 of *Protadelomys alsaticus* Hartenberger, 1969 from Bouxwiller (Bas-Rhin). **a** BUX67-136, right m1; a1, occlusal view; a2, buccal aspect; a3, lingual aspect. **b** CSBX52, left m1; b1, occlusal view; b2, buccal aspect. **c** BUX67-135, left m1; c1, occlusal view; c2, buccal aspect; c3, lingual aspect. **d** BUX68-39, right m1; d1, buccal aspect; d2, lingual aspect; d3, occlusal view. **e** BUX67-5, left m1; e1, occlusal view; e2, buccal aspect; e3, lingual aspect. **f** BUX68-33, right m1; f1, occlusal view; f2, buccal aspect. **g** BUX67-128, left m1; g1, buccal aspect; g2, occlusal view; g3, lingual aspect. **h** CH22, left m1; h1, occlusal view; h2, buccal aspect. **i** BSK-A24, left p4; i1, occlusal view; i2, buccal aspect. **j** BUX67-111, right m1; j1, occlusal view; j2, buccal aspect; j3, lingual aspect. **k** BUX67-114, right m1; k1, occlusal view; k2, buccal aspect; k3, lingual aspect. **l** BUX67-115, right m1; l1, occlusal view; l2, buccal aspect. Scale bar = 1 mm

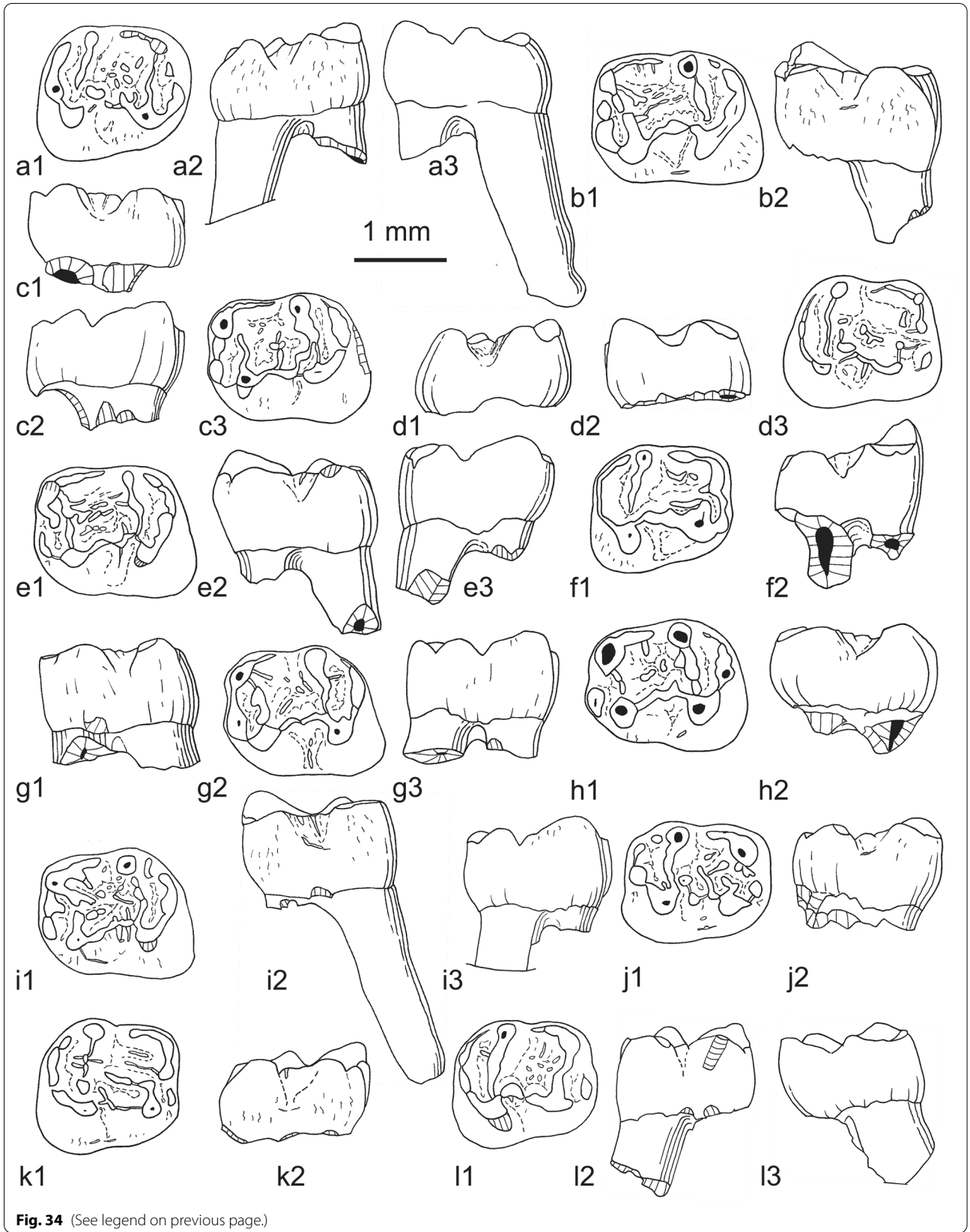


Fig. 34 (See legend on previous page.)

strictly transverse (e.g., BUX 67–113, 131, CSBX 44, 52). A lower and generally weaker ridge descends from the apex of the metaconid, distally to the main lingual metalophulid I (CSBX41, 47, 48; BSK-A21, A29; BUX 67- 127, 128, 130, 135, 136, 140; CH 17, 22). It is generally slender, weak, and short, but can also be absent. In few cases, the connection of this ridge with the buccal metalophulid I occurs through this distal lingual metalophulid I. It is the case for instance on BUX 67–25,123, where the metalophulid I is complete and angles medially; or on BUX 67–116: Fig. 35a, 136, 137, and BUX 68–44: Fig. 35k, where it is straight and transverse.

The postprotocristid is strong, thick distally and oblique mesio Buccal to distolingual; it is always longer than the prehypocristid.

The ectolophid area, defined from the distal end of the postprotocristid to the mesial end of the prehypocristid, appears variable. The Figure 36 illustrates this variation with schematized drawings of the buccal area of the m1–m2 from Bouxwiller. The mesoconid can occupy most of the ectolophid (BUX 67–19, 111; BUX 68–33). On both sides of this mesoconid, the ectolophid is short. Its mesial part is generally in the continuity of the postprotocristid, and hardly distinct. Its distal part is lower, which interrupts on weakly worn or unworn teeth. However, the path of this ectolophid + mesoconid varies. The postprotocristid is thick and frequently swollen at its end in a “premesoconid”-like structure (BUX 67–11, 25, 141; BSK-A26, A28). This structure prolongs in a lingual spur of variable size (BUX 67–25, 110, 111, 112, 123, 130, 132, 136; CH 22, 24; CSBX 40, 41, 44, 46, 47, 48), two lingual spurs (BUX 67–132, 140), or one buccal spur (CH 13). On the m1 BW56-59, this spur is long at the end of the postprotocristid but does not present any lingual swelling. It is indistinct or absent on the m2 BUX 67–116, 117, and 129. On worn teeth, the swelling or the spur of the premesoconid are not visible (BSK-A27: Fig. 36, BSK-A29 BUX 67–23, 120, 139). The short mesial part of the ectolophid is higher than the distal one, and rarely distinct from the junction premesoconid–mesoconid. The shape of the mesoconid varies with wear: it can be bulbous, reduced or stretched. BUX 67–115 display a peculiar morphology, with bulbous cuspids, conids (mesoconid, premesoconid at the extremity of the postprotocristid, postmesoconid spur, anteroconid, and

hypoconulid), and even ridges (posterolophid and extra-ridges), which are all thick and low. The mesial part of the ectolophid is mesiodistally oriented and very short and weak; its distal part is directed buccolingually to connect the postmesoconid, and is linked to the extremity of the prehypocristid. In only a few cases (BUX 67–19 and CSBX 52), the mesolophid is facing the lingual flank of the mesoconid, and is reduced to a spur. The other molars do not show a true mesolophid. A postmesolophid-like structure is sometimes visible (BUX 67–5, 114, 115, 123, 124, 125, 126, 135: Fig. 34c, 136, 137, BSK-A27, BW 56–59, CH 17, 22, 24; CSBX 47), the postmesoconid spur, which is more or less bulged or elongated obliquely. The mesoconid and postmesoconid are, in some cases, undistinguishable (CSBX 47, 54; CH 24; BUX 67–116).

The entolophid can be almost transverse or slightly curved distally. It usually joins the mesial end of the prehypocristid, together with the low distal ectolophid. It lowers at the level of this junction, sometimes interrupts. On BUX 67–133, the entolophid is not continuous and formed only by small isolated oblique ridges. The buccal junction of the entolophid often occurs either more lingually, to the postmesoconid or the postmesoconid spur; or more distally, to the anterolingual wall of the hypococone (BUX 67–130, 132; BUX 68–39; BW 56–59; CSBX 54). The entolophid usually bears an entoconulid, which is however frequently worn and difficult to identify; it is only visible on BUX 67–5, 19, 25, BW 56–59, CH 24, CSBX 40, 47, 56. One, rarely two, distomesial spur(s) or ridge(s) frequently descend(s) from the entoconulid in the central basin.

A few extra-ridges, wrinkles or granules are present in the central basin, but often erased by wear. Some of these are organized in oblique ridges from the distal extremity of the lingual metalophulid I, or/and from the lingual extremity of the buccal metalophulid I to the basin floor. There are two well-distinct oblique extra-ridges (BSK A22, 24), one on BUX 67–19, 128, 137, CSBX 40, 47, 52, 56, and CH 22, three on BUX 67–114, 136, BUX 68–36, 39, and BW 56–59. The extra-ridges are numerous on BUX 67–114, 137, and BW 56–59; CSBX 52.

m3. (Fig. 37). Among the measured m3, three are much larger than the others are, and are described below as *?P. cf. alsaticus* morphotype 1 and *?P. cf. alsaticus* morphotype 3 (Table 4B). If another teeth is much shorter (BUX

(See figure on next page.)

Fig. 35 Lower m2 of *Protadelomys alsaticus* Hartenberger, 1969 from Bouxwiller (Bas-Rhin). **a** BUX67-116, right m2; a1, occlusal view; a2, buccal aspect; a3, lingual aspect. **b** BUX67-132, left m2; b1, occlusal view; b2, buccal aspect; b3, lingual aspect. **c** BUX67-130, right m2; c1, occlusal view; c2, buccal aspect; c3, lingual aspect. **d** BUX67-127, left m2; d1, occlusal view; d2, buccal aspect; d3, lingual aspect. **e** CSBX49, right m2; e1, occlusal view; e2, buccal aspect; e3, lingual aspect. **f** BUX67-112, right m2; f1, buccal aspect; f2, lingual aspect; f3, occlusal view. **g** CSBX56, left m2; g1, occlusal view; g2, buccal aspect; g3, lingual aspect. **h** BUX67-110, left m2; h1, occlusal view; h2, buccal aspect; h3, lingual aspect. **i** BUX67-119, right m2; i1, buccal aspect; i2, lingual aspect; i3, occlusal view. **j** BUX67-141, right m2; j1, buccal aspect; j2, occlusal view; j3, lingual aspect. **k** BUX68-44, left m2; k1, occlusal view; k2, buccal aspect; k3, lingual aspect. **l** BUX67-33, left m2; l1, occlusal view; l2, buccal aspect; l3, lingual aspect. **m** BUX67-133, right m2; m1, occlusal view; m2, buccal aspect; m3, lingual aspect. **n** BUX67-140, left m2, occlusal view. Scale bar = 1 mm

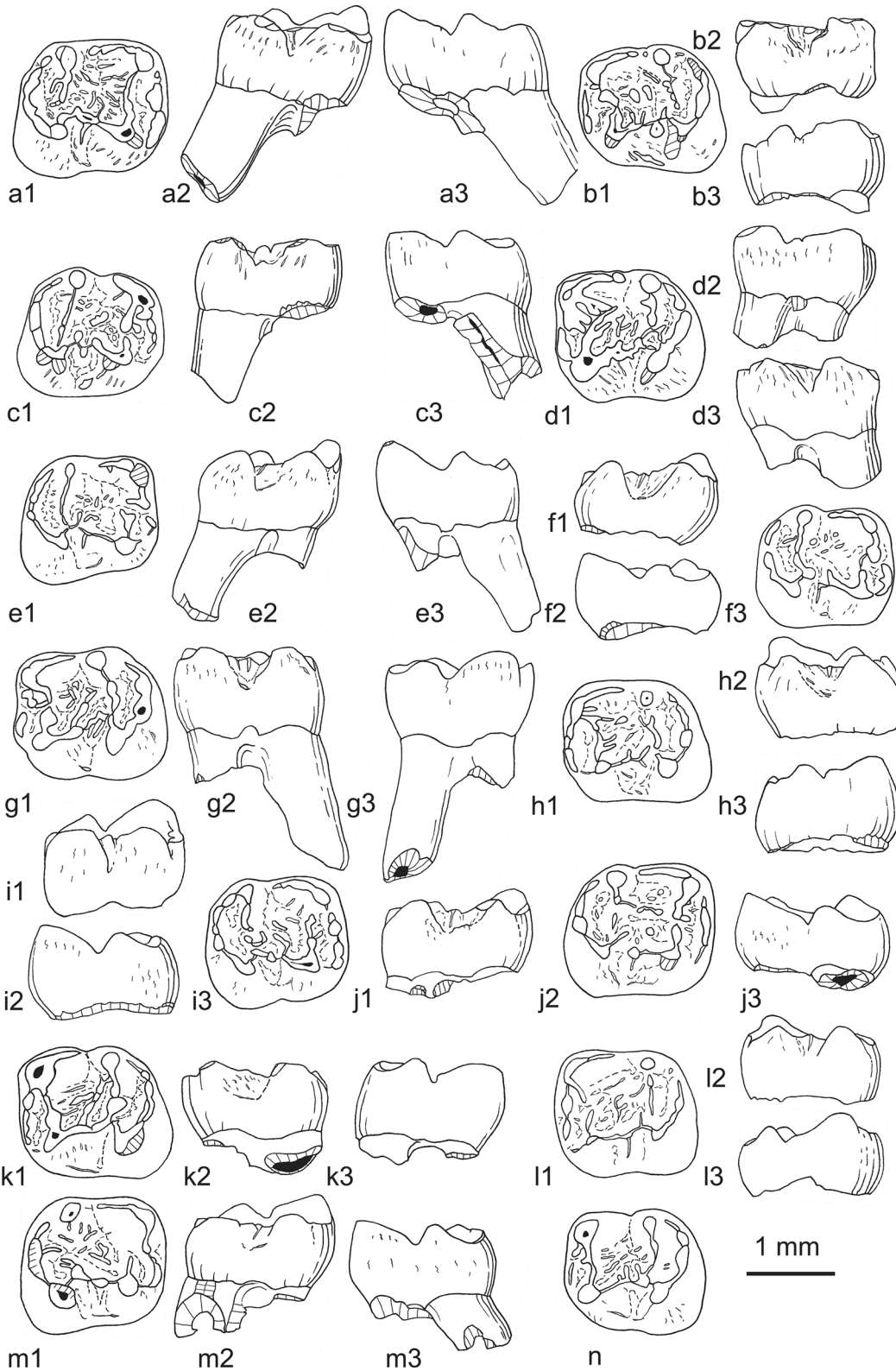


Fig. 35 (See legend on previous page.)

67–155), its features seem to enter the whole variability. BUX 68–37, is here referred to *?P. cf. alsaticus* morphotype 2. It has a relatively short oblique postprotocristid, a low mesial ectolophid; the mesoconid is strong and prolonged in a thick postmesoconid. The distal ectolophid is higher than the mesial one; the prehypocristid is thin and short. It differs from BUX 67–155 and from all the other specimens in the absence of a thick postprotocristid and of a premesoconid spur or ridge.

In all m3, the lingual metalophulid is mesial, except on BUX 67–160, where it is distally oriented. The occurrence and strength of the ectomesolophid and of a more or less mesiodistal ridge from the lingual metalophulid are variable among all the m3. The ectomesolophid is long on BSK-A25, BUX 67–151, 153, 159, 165, and 168. A mesostylid, more or less distinct from the postmetacristid, occurs on CSBX 45, BUX 67–14, 151, 152, 157, 159, 160, and 165. On BSK-A29 and BUX 67–168, the mesostylid prolongs buccally in a short lingual mesolophid, the metaconid appears more massive, thicker at its base, than on the other specimens.

We observed the same main variation along the postprotocristid–ectolophid area, but less pronounced than on m1–2. The post-hypocristid is relatively short up to the hypoconulid area. The hypoconulid is weakly bulged, single or often duplicated (e.g., BUX 68–37; 67–53, 151, 154, 155, 158, 164, 168). The posterolophid is short, generally ending at the distal base of the entoconid.

Remarks and comparisons Even if *?P. alsaticus* has its postprotocristid thick, long and oblique with its distal end often swollen with a premesoconid spur, like in *P. lugdunensis*, morphological differences involving the lower teeth are observed, together with the differential development of extra-ridges and granules: in *P. lugdunensis*, the cusps are more bulged, the entolophid is more continuous, the postprotocristid is fused to the mesoconid area (no distinct pre, meso and postmesoconid elements).

?Protadelomys cf. alsaticus

Several teeth deviate from the typical morphology of *?Protadelomys alsaticus*. They are here named *?P. cf. alsaticus*. We distinguish three morphotypes (1, 2, 3) among them, which are described below.

***?Protadelomys cf. alsaticus* morphotype 1**

Material and measurements (Additional file 4: S4, Table 4B). We refer two P4, one M1, two M2, two dp4, one p4, two m1, two m2, one m3, to this morphotype.

Description

Upper teeth

P4. (Fig. 38a) One P4 (CSBX 8) displays a simpler occlusal morphology than other specimens, and cusps more bulbous. The paracone and metacone are very close to one another, and the mesoflexus is narrow. The mesostyle is small, adjacent to the metacone, and the mesoloph is absent. Another P4 (CSBX 29) could be close to CSBX 8, with its bulbous cusps and small hypocone, but it is too damaged, especially in the area between the paracone and metacone.

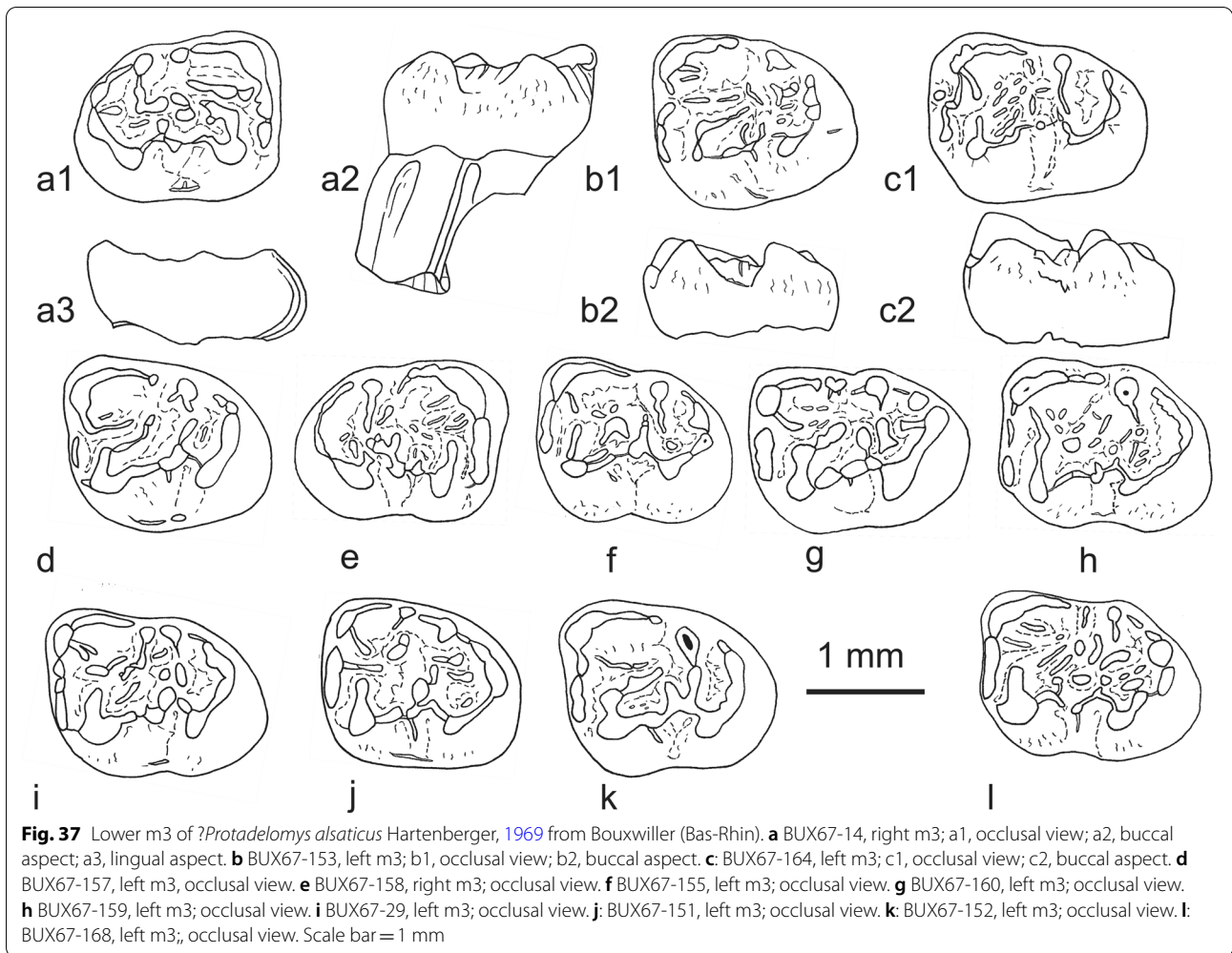
M1. (Fig. 38b) One tooth (CSBX 35) has been questionably referred to an M2 of *?P. alsaticus* (Hartenberger, 1969: pl.2, Fig. 7). This weakly worn M1 displays an anterosyncline wider than that of the other M1. The parastyle is strong, slightly separated from the anteroloph, and weakly connected to a sloping preparacrista. The anteroloph is weakly worn, whereas the parastyle is unworn. The anterostyle is strong, connected to both the preprotocrista and the anteroloph. The endoloph is short and thick, nearly as high as the lingual main cusps. The hypocone is slightly smaller than the protocone, its anterior and posterior arms being short. The parastyle presents one additional ridge connected to the anteroloph in the anterosyncline. The paracone is slightly swollen. The buccal part of the rectilinear protoloph is as high as the paracone, and its lingual part is lower. The protoloph connects to the protruding paraconule and to the middle of the protocone (protocrista). The paraconule is mesial to the protoloph and slightly less swollen than the metaconule. The paracone is framed by the pre- and post-paracristae. The latter is strong, and interrupted anterior to the mesostyle. The mesostyle prolongs in a strong mesoloph, joining a low cusp (mediobuccal) against the metaconule. A short ectocingulum is present on the distal flank of the mesostyle. The premetacrista is strong and the metacone a little thicker than the paracone. The metalophule II is high and the metalophule I is low, descending mesially from the latter to the base of the metaconule. The connection between the metalophule II and the metaconule is low as is the one between the latter and the mid-hypocone. There is a strong posteroconule,

(See figure on next page.)

Fig. 36 Schematic representations of the variations of the outer wall components of the lower molars of *?Protadelomys alsaticus* Hartenberger, 1969 from Bouxwiller (Bas-Rhin). Color caption: the colors represent different cusps, cristids or lophids: 1: Brown = protoconid; 2: buccal part of the metalophulid I = pale violet; 3: postprotocristid = brown like the protoconid; 4: premesoconid swelling (spur or ridge) = brown, at the distal end of the postprotocristid; 5: mesial ectolophid = green; 6: mesoconid = blue; 7: ectomesolophid = blue; 8: postmesoconid ridge and swelling = ochre; 9: distal ectolophid = Green; 10: prehypocristid = black; 11: hypoconid = black; 12: entolophid = black; 13: poshypocristid = black



Fig. 36 (See legend on previous page.)



lowly attached to the metaconule and to the mesiodistal post-hypocrista. The sinus forms only a very shallow depression below the endoloph. Some rare very low ridges, present on the floor of the flexi, connect the main structures.

M2. (Fig. 38c) Among the largest M2, BUX67-37 and 67-77 are referred to this morphotype. They show distinct and swollen conules. The metaconule is simple. If the thick buccal metalophule II is transverse on BUX 67-37, it thickens lingually and curves distally on BUX 67-77 to join the posteroconule. The mesostyle and the buccal mesoloph are present but their width seems to vary: on BUX 67-37, it is thicker and longer and reaches the metaconule.

Lower teeth

dp4. (Fig. 38d, e) Two dp4 differs from the others by having a transverse metalophulid I, as well as a short anterolophid closing a small anteroflexid. On BUX 67-96, the mesiodistal ridge is barely marked, as is the buccal half

of the entolophid. The lingual part of the latter is short and distally oriented towards the posterolophid. CH 25 is much worn with a damaged mesial flank, but the “trigonal” area is preserved and similar to that of BUX 67-96.

p4. (Fig. 38f) On CH 18, the metaconid is strong and prolonged buccally in a high and short anterolophid up to the preprotocristid. A short transverse metalophulid I runs parallel to the anterolophid, both being separated by a minute anteroflexid. The short postmetacristid descends abruptly towards the lingual opening of the mesoflexid, mesially to the entoconid, which is massive. This lingual opening is V shaped and the vertical surface of enamel is concave at the junction of the lingual flanks of metaconid and entoconid. This is due to the bulging of the buccal flanks of the metaconid + postmetacristid, and the bulging of the buccal flanks of the entoconid. One thick mesiodistal ridge runs from the metaconid to the premesoconid spur; lingual to it, there is an additional parallel crest, more discontinuous. Three short extraridges fill the space between the main ones. The

ectolophid makes an angle behind the mesoconid; the latter is slightly stretched mesiolingual to bucco-distal. A short and strong ectomesolophid curves and its buccal end connects a hypoconid spur, which is mesiobuccal. The lophids, ridges, and conids appear thick when worn.

m1–2. The peculiar shape of the buccal wall of the p4 and m3 is not so easy to distinguish on the m1–2: the recess between the bulging flanks of the metaconid and the entoconid is not strongly marked, and varies with wear. Among the largest m2, BUX 67–138, 139; Fig. 38i, 142, and CSBX 53 show these features; BUX 67–121 does not. We found this character on the m1 BUX 67–125 and 137. BUX 67–125 has a short and swollen anteroconid; the lingual metalophulid I is mesial then turns distally in a short ridge, which meets the distomesial hook located at the end of the transverse buccal metalophulid I. The weak and low additional lingual metalophulid I makes a long mesiodistal ridge up to the center of the basin, where it meets a few low and slender extra-ridges. Another extra-ridge runs on the buccal flank of the metaconid lingually to this additional metalophulid I. A short premesoconid spur is present. The mesoconid is a little stretched obliquely (mesiolingual to bucco-distal); it bears a barely marked ectomesolophid and a weak mesiobuccal spur of the hypoconid. Its distal end is linked to a thick postmesoconid. The distal ectolophid is low and very short, and this is especially clear on unworn and weakly worn teeth. The entolophid is almost straight and connected to the prehypocristid. The post-hypocristid is short, the hypoconulid strong, and the posterolophid displays two successive bulges. The occlusal face of BUX-137 is damaged and all occlusal structures are worn.

BUX 67–138 is a pristine m2, reduced to its enamel cap (Fig. 38h). At its lingual end, the stretched anteroconid connects with a thin discontinuous mesiodistal ridge running towards the center of the basin. The lingual metalophulid I is mesial and short as a premetacristid. The buccal metalophulid I is longer, being transversely oriented at its most buccal part then turning slightly backwards. An additional lingual metalophulid I is thin and low, like the extra-ridges located in the basin. The postprotocristid ends in a premesoconid spur. It strongly connects to the mesoconid, which is stretched buccomesial to linguodistal. A strong ectomesolophid descends mesiodistally along the buccal flank of the mesoconid, while a thin mesiobuccal spur climbs on the hypoconid flank. Two postmesoconid spurs emerge from a unique point at the distal end of the mesoconid. The distal ectolophid is low, and connects to the short prehypocristid. The entolophid is almost straight and complete; it is linked to the extremity of the prehypocristid. The hypoconulid swells at the extremity of the post-hypocristid, and

the posterolophid is long, relative to the post-hypocristid length.

m3. (Fig. 38j) BUX 68–23 is the larger m3 of the theriomorph assemblage from Bouxwiller. Its morphology is relatively simple when compared to other m3, and the extra-ridges are very low and rare. Its metaconid and entoconid are more massive. The lingual metalophulid I is mesial as it is the case on nearly all the m3 from Bouxwiller; it is short and its buccal end joins the anterolophid lingual end. The additional more distal lingual metalophulid I is slender and low; it descends in the direction of the transverse buccal metalophulid, without connecting it. There is no mesostylid. The postprotocristid is long and thick, and connects to the mesoconid by a low mesial part of the ectolophid. The mesoconid is a little stretched mesiodistally, with two tiny mesial and distal bulges with short lingual spurs. A thick linguodistal short ridge starts in front of the distal bulge. We interpret this ridge as the postmesoconid ridge. Indeed, there is no trace of a lingual part of the entolophid. The entoconid is free from the posterolophid. The latter is very short, making a short and thick curve with the hypoconulid and the post-hypocristid. The hypoconulid is unique and not swollen.

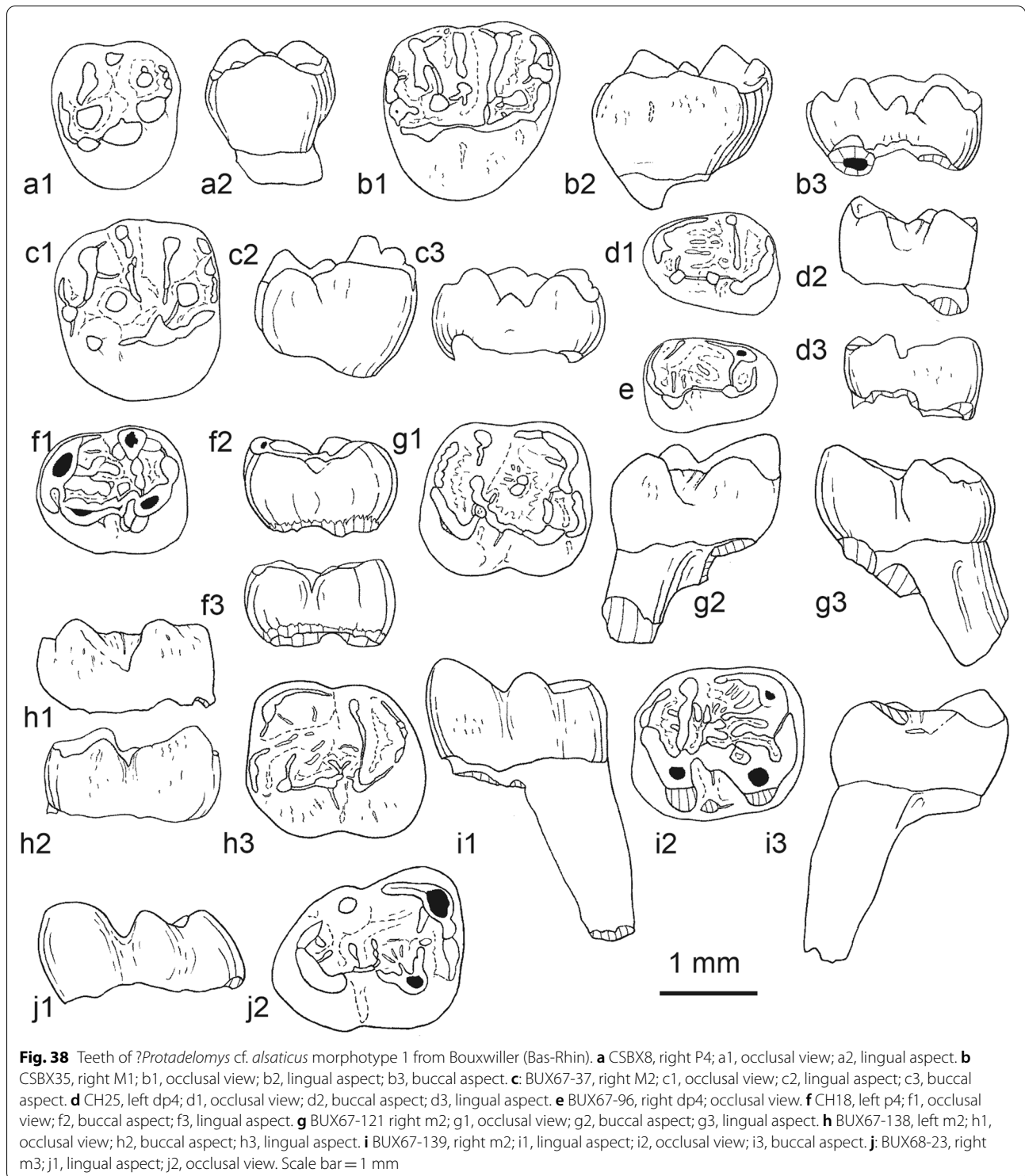
?*Protadelomys cf. alsaticus* morphotype 2

Material and measurements. (cf. Additional file 4: S4; Table 4B) We refer six M1–M2, two M3, one dp4, three p4, one m1, one m3 to this morphotype.

Description

Upper teeth

M1. (Fig. 39a, b, c). The smaller M1 of the assemblage (BUX 67–78; Fig. 39a) has a relatively simple occlusal pattern, without wrinkles of the enamel on the outskirts of the crown, only very small and tiny roughnesses. The parastyle is weakly swollen. The main cusps and conules, as well as the anterostyle and posteroconule, are bulbous. The metacone bears a premetacrista. The mesostyle is strong and placed a little more buccally than the paracone and metacone. The paraconule prolongs mesially in a short thick ridge; it is a little smaller than the metaconule, which is bulbous and strong. The mesoloph reaches the center of the mesoflexus but its lingual part is discontinuous and low. The protoloph is strong only in its buccal part; its lingual part is very low and slender, and connects with the center of the protocone. The buccal part of the metalophule II is strong; it ends lingually in a distomesial spur, which could represent a vestigial metalophule I. The lingual metalophule is as weak as the very low distal connection between the metalophule II and the metaconule, and the low distal connection between the metaconule and the center of the hypocone. The other M1 (BUX 67–48; Fig. 39c, BUX67-49; Fig. 39b,



BUX67-63: Fig. 39d = M1 or M2; BUX67-78: Fig. 39a) are small but display the same occlusal pattern, with some variations in the mesoloph length (shorter in BUX 67–48) and in its lingual connection: to the metaconule

mesial spur (BUX67-48, 49), or free (BUX 67–63). The parastyle is more swollen on BUX 67–48 and 49.

M2 (Fig. 39d, e). The M2 show the same features as the M1, but the connection between the mesoloph and

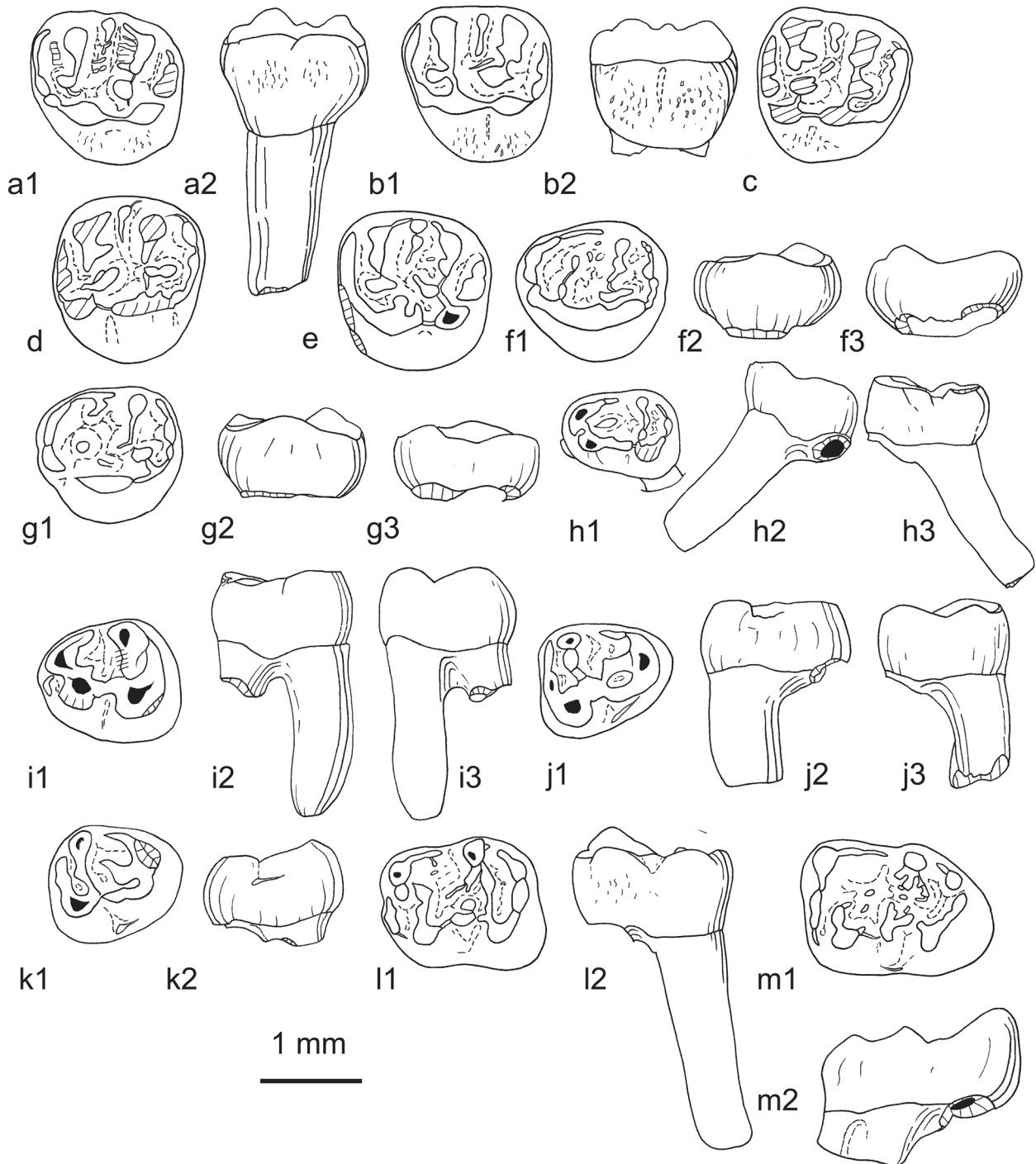


Fig. 39 Teeth of *Protadelomys cf. alsaticus* morphotype 2 from Bouxwiller (Bas-Rhin). **a** BUX67-78, left M2; a1, occlusal view; a2, lingual aspect. **b** BUX67-49, left M1; b1, occlusal view; b2, lingual aspect. **c**: BUX67-48, right M1; occlusal view. **d** BUX67-63, right M1 or M2; occlusal view. **e** BUX67-41, left M2; occlusal view. **f** BUX67-87, right M3; f1, occlusal view; f2, lingual aspect; f3, buccal aspect. **g** BUX67-88 right M3; g1, occlusal view; g2, buccal aspect; g3, lingual aspect. **h** BUX67-95, left dp4; h1, occlusal view; h2, lingual aspect; h3, buccal aspect. **i** BUX67-106, left p4; i1, occlusal view; i2, buccal aspect; i3, lingual aspect. **j**: BW56-54bis, right p4; j1, occlusal view; j2, buccal aspect; j3, lingual aspect. **k**: BUX67-98, right p4; k1, occlusal view; k2, buccal aspect. **l**: BSK-A27, left m1; l1, occlusal view; l2, buccal aspect. **m**: BUX68-37, left m3; m1, occlusal view; m2, lingual aspect. Scale bar = 1 mm

the buccal ridge of the metaconule is stronger on BUX 67–26, which also shows a stronger distal spur on the paraconule. The mesoloph is short and ends free in the mesoflexus on BUX 67–41. BUX 67–26 shows a short ectocingulum on the distal flank of the mesostyle. BUX 67–41 has both postparacrista and premetacrista while BUX 67–26 has only the premetacrista, like on the M1.

M3. BUX 67–87: Fig. 39f, and 88: Fig. 39g, are small, their occlusal outline is almost circular in shape with rare extra-ridges and small conules. The metaconid is weakly protruding from the bucco-distal cingulum.

Lower teeth

dp4. (Fig. 39h). BUX 67–95 is much smaller than the other dp4. Despite an important mesial wear, it is possible to distinguish a mesial junction between the metaconid and the protoconid (anterolophid), closely followed distally by the metalophulid I. The mesiodistal ridge is incomplete and low. The postprotocristid makes a short low lingual spur at its distal extremity. The mesoconid is barely marked on the short mesiodistal ectolophid. The latter lowers at the level of its junction with both the prehypocristid and the buccal end of the entolophid. The hypoconulid is slightly protruding above the prehypocristid and posterolophid. There is no distinct extra-ridge or granule, and the enamel is smooth.

p4. (Fig. 39i, j, k). The three p4 are shorter than but almost as wide as those of *?Protadelomys alsaticus*. The extra-ridges are absent, apart from a short mesiodistal ridge, which connects to the metaconid (BUX 67–98 and BW 56-54bis) or to the protoconid (BUX 67–106). The latter and BUX 67–98 show a small mesial notch (not visible for BW 56-54bis); it is limited linguo-mesially by a short cingulid on BUX 67–106.

molars. On the smallest lower molars previously referred to as *P. alsaticus*, no peculiar morphological characters can justify an attribution to *P. cf. alsaticus* morphotype 2. However, we tentatively refer two teeth to this morphotype: one m1 (BSK-A27: Fig. 39l) and one m3 (BUX 68–37: Fig. 39m), which are clearly narrower than the other m3.

?Protadelomys cf. alsaticus morphotype 3

Material and measurements. (Additional file 1: S4; Table 4B). We refer two DP4, one P4, one M2, one M3; one m1, two m2, and three m3 to this morphotype.

Description

Upper teeth

DP4. The larger DP4 (CSBX 2: (Fig. 40a).) of the Bouxwiller assemblage displays a more intricate pattern than the other DP4 (Fig. 40b). The paraconule is relatively

reduced and aligned with the straight protoloph, while the metaconule is duplicated, as are the mesostyle and the mesoloph. The metalophule I joins the mediobuccal ridge of the metaconule, together with the main mesoloph. The outskirts of the crown display irregular wrinkles, thicker than the thin ornamentation of *?P. alsaticus*.

P4. (Fig. 40c, d). CSBX 12 and 13 show common features with the P4 of *?P. alsaticus*, but still differs from them in some aspects. They show a longer anteroloph with a preparacrista, which is stronger; the connection between the postparacrista, the small mesostyle, and the long premetacrista limits the shallow mesoflexus buccally. The metalophule I is reduced or almost absent. The hypocone is almost as large as the protocone.

M2. (Fig. 40e). BUX 67–3 is weakly worn, especially in its medial part. The extra-ridges are more numerous than on the M1 BUX 67–35 (morphotype 1). The paracone is bulged and the postparacrista is present. The protoloph turns a little distally, buccal to the paraconule. The latter separates from the protoloph by an oblique notch; it is stretched forward, inside the anteroflexus. The paraconule attaches to the short transverse lingual part of the protoloph, linked at mid-protocone, just mesially to a low protocrista. The premetacrista, the metacone, and the metalophule II merge into a loph, which is arcuate up to the metaconule level. The metaconule is complex, which makes it difficult to identify a swollen conule present in this area alongside at least three very close ridges. The mesostyle is complex, prolonged by a bifurcated mesoloph. A ridge extends from the end of the buccomesial border of the metacone and runs parallel to the mesoloph. Another ridge descends from the metalophule II in the basin; it could constitute a remnant of the metalophule I. The endoloph is high and thick. The hypocone is more buccal than the protocone. It separates from a distinct posteroconule by a shallow and narrow slot. The posteroloph is very short.

M3. (Fig. 40f). The unworn M3 BUX 67–27 appears more concave than the other molars, as the cusps and the surrounding bucco-distal ridge or the lingual one are not high or thick. The paracone is not much prominent, and only slightly higher than the protoloph. The mesially protruding slender paraconule is oriented towards the anterostyle. The latter, not well individualized, only represents a swelling at the extremity of the preprotocrista. The extra-ridges and the granules are numerous on the mesoflexus floor. The metacone is low, not salient, and located above the bucco-distal crest joining the mesostyle area. This metacone is similar in height as the posteroloph, which is short. The protocone is a little elongated mesiodistally from the preprotocrista to the postprotocrista. A thickening, which actually corresponds to the high and strong endoloph observed on the M2, prolongs the

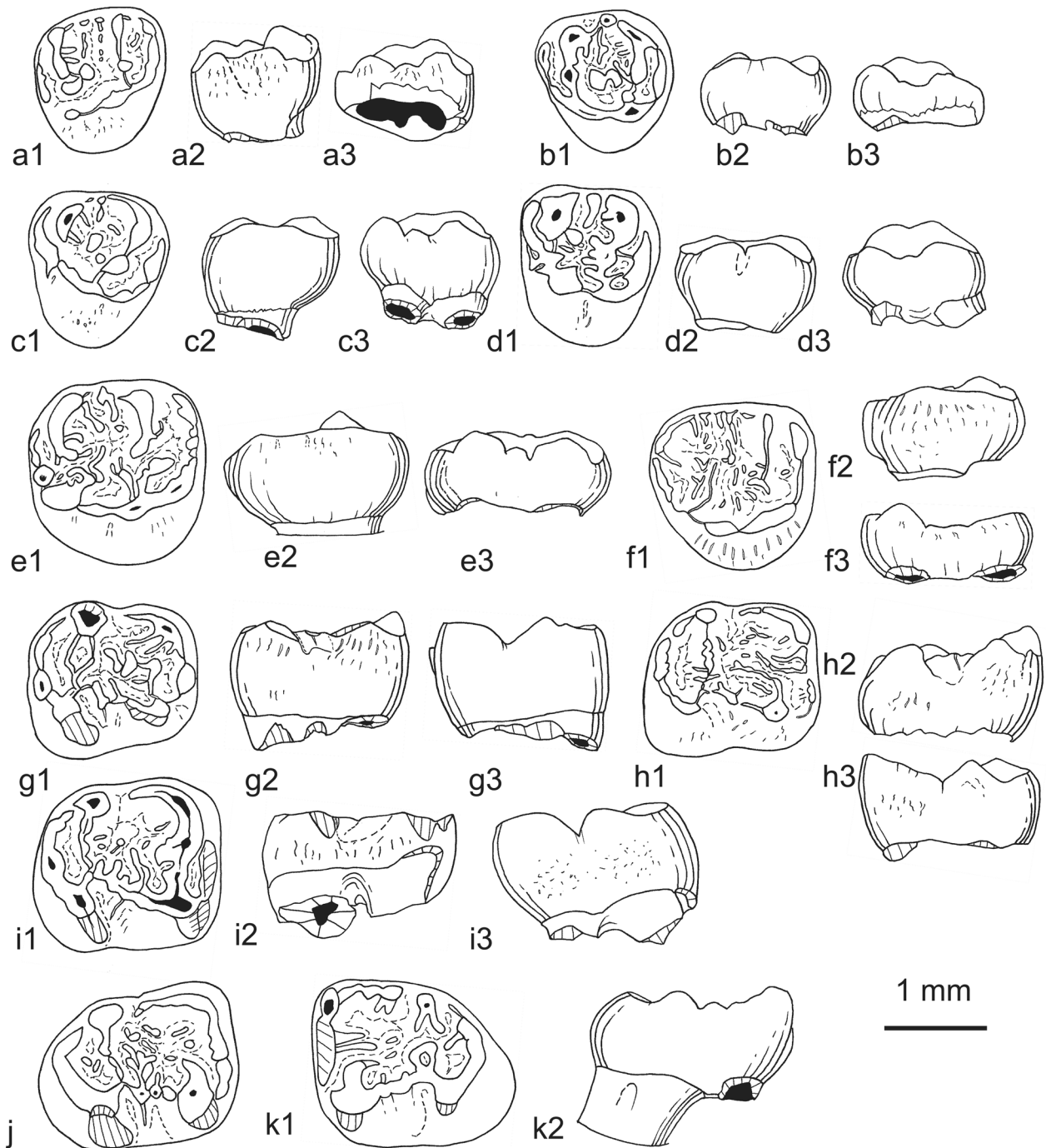


Fig. 40 Teeth of *Protadelomys cf. alsaticus* morphotype 3, from Bouxwiller (Bas-Rhin). **a** CSBX2, right DP4; a1, occlusal view; a2, lingual aspect; a3, buccal aspect. **b** CSBX3, left DP4; b1, occlusal view; b2, lingual aspect; b3, buccal aspect. **c** CSBX12, left P4; c1, occlusal view; c2, lingual aspect; c3, buccal aspect. **d** CSBX13, left p4; d1, occlusal view; d2, lingual aspect; d3, buccal aspect. **e** BUX67-3, right M2; e1, occlusal view; e2, lingual aspect; e3, buccal aspect. **f** BUX67-27, right M3; f1, occlusal view; f2, lingual aspect; f3, buccal aspect. **g** BW56-59, right m1; g1, occlusal view; g2, buccal aspect; g3, lingual aspect. **h** BUX67-129, right m1 or m2; h1, occlusal view; h2, buccal aspect; h3, lingual aspect. **i** BUX67-142, right m2; i1, occlusal view; i2, buccal aspect; i3, lingual aspect. **j**: BSK-A25, right m3; occlusal view. **k**: BUX67-169, left m3; k1, occlusal view; k2, lingual aspect. Scale bar = 1 mm

postparacrista (BUX67-3). A linguobuccal lophid, as high as the paraconule, faces the protocone and reaches the central extra-ridges. The hypocone is not clearly identifiable, as it is not swollen; it is strongly linked to the postprotocrista. There is no trace of a sinus. The metaconule is lower than the paraconule, and reduces to a thin ridge postwardly oriented. Smooth vertical wrinkles, diverging from its occlusal surface, adorn the lingual surface of the protocone.

Lower teeth

m1–m2. (Fig. 40g, h, i). The m1 BW 56–59 has numerous extra-ridges and wrinkles. The elements of the postprotocristid + ectolophid area are in line obliquely, mesio-buccal to distolingual, like on the two m2 (BUX 67–129 and 142). BUX 67–129 is little worn, as are their short anteroconid whereas the premetacristid (mesial lingual metalophulid I) is longer than on the m1 and it bears two long mesiodistal ridges, parallel to the one starting at the lingual end of the buccal metalophulid I. The postmetacristid is steep and long. On BUX 67–142 (Fig. 40i), which is not too much worn but a little damaged, the premesoconid–mesoconid–postmesoconid elements are obliquely in line with the postprotocristid, like on the m1. The ectomesolophid is faint. The lingual metalophulid I, transverse, is almost in line with the buccal one, without any break. Even worn, it is possible to distinguish numerous low extra-ridges in the central basin and a few wrinkles descending from the postprotocristid and mesoconid area in the sinusid.

m3. (Fig. 40j, k). BUX 67–169 differs from the other large m3 BUX 68–23 (morphotype 1) in its mesial part that is relatively wider than the distal one. It also differs from it in the presence of a mesostylid at the extremity of the postmetacristid closing lingually the mesoflexid, and in the presence of an entolophid. A few wrinkles descend buccally from the postmetacristid and from the mesostylid; some granules are visible in the basin, even if the tooth is worn. The lingual metalophulid I is mesial (premetacristid) and bears two long low mesiodistal ridges running in the basin, parallel to the short ridge emitted by the lingual end of the transverse buccal metalophulid I. A premesoconid spur is well distinct, directed lingually from the end of the postprotocristid. The lophid developed from the postprotocristid to the prehypocristid is mesially oblique and then oriented mesiodistally, with the distal part of the ectolophid. The ectomesolophid is absent (contra on BSK-A25 where it is well present). The buccal part of the entolophid connects to the strong postmesoconid ridge and to the prehypocristid. The lingual entolophid is duplicated and the distal one is slightly directed distally. While worn, the hypoconulid seems to be also duplicated, with a distomesial ridge

running towards the buccal entolophid. The extra-ridges and granules are numerous in the low basins of BSK-A25.

Remarks and comparisons

The larger lower molars of *?Protadelomys* cf. *alsaticus* morphotype 3 are similar in size as the ones of *Masillamys parvus* from Messel. They share the numerous extra-ridges and the organization of the lingual metalophulid I area. However, the oblique postprotocristid + ectolophid is longer, the sinusid is deeper linguobuccally. Moreover the trigonid of p4 in this species is better developed than in p4 of *Masillamys parvus*, with a distinct protoconid, and the entolophid and extraridges are thicker in the species from Bouxwiller than in *M. parvus*.

?Protadelomys cf. *alsaticus* from Cuzal (Lot, Quercy)

Remarks

These rodents have been referred to as *Protadelomys* (cf.) *alsaticus* (Marandat et al. 1993) based on the presence of frequent enamel wrinkles and size similarities, which are smaller than that of the teeth of *P. lugdunensis*.

Material and measurements (Additional file 5: S5, Fig. 41 Table 5).

Most of the teeth, except the two lower dp4, are slightly larger than the teeth of *P. alsaticus* from Bouxwiller (Table 4). The difference is only statistically significant for the m1 (Table 8).

Morphological comparison

Upper teeth. (Fig. 42a to m). The two DP4 from Cuzal display some differences with *P. alsaticus* from Bouxwiller. On the DP4 from both localities, the protoloph is oriented forward and connects to the junction anteroloph–preprotocrista. The paraconule is absent in the species from Cuzal whereas it is always present in *P. alsaticus* from Bouxwiller. Two mesostyles and mesolophes are present on the two DP4 like in Bouxwiller. Contrary to *P. alsaticus* from Bouxwiller, the hypocone is as strong as the protocone, which is more lingual. The metalophule I is not distinct, while it is on a few DP4 from Bouxwiller. The metaconule is not bulged and reduced to extraridges, which join the hypocone and the posteroloph (CUZ 176). In *P. alsaticus*, the metaconule is strong with no lingual connection or junction with the postprotocrista. The P4 from Cuzal are triangular with a reduced hypocone, whereas the hypocone is less reduced in Bouxwiller. The floor of the mesoflexus of the P4 is flatter and more wrinkled than in *P. alsaticus*. On CUZ 188, the anteroloph is very short and weakly swollen at the level of the anterostyle, which joins the preprotocrista, not on CUZ 177 and CUZ 189. The paracone is slightly smaller than the metacone. A thin postparacrista plunges to the mesostyle area. On CUZ 188 (Fig. 42d), the buccal

Table 5 Range of the size variations (length and width: min., max.; average \pm Sm = σ/\sqrt{n} ; $v=100 \sigma/\text{average L or W}$). of the different loci of teeth of *?Protadelomys alsaticus* Hartenberger, 1969, from Cuzal (MP3/14, Lot, Quercy)

A. <i>Protadelomys alsaticus</i> from Cuzal (Lot, Quercy)						
Length	<i>n</i>	min	mean \pm Sm	max	σ	<i>v</i>
DP4	2	1.37	1.425 \pm 0.055	1.48	0.078	5.46
P4	3	1.67	1.703 \pm 0.132	1.74	0.035	2.06
M1	8	1.59	1.816 \pm 0.052	2.03	0.148	8.15
M2	2	1.82	1.85 \pm 0.015	1.88	0.042	2.27
M3	3	1.90	1.96 \pm 0.03	2.00	0.053	2.70
dp4	2	1.51	1.525 \pm 0.015	1.54	0.021	1.39
p4	2	1.81	1.835 \pm 0.025	1.86	0.035	1.93
m1	7	1.82	1.940 \pm 0.034	2.05	0.089	4.59
m2	8	1.93	1.966 \pm 0.013	2.04	0.036	1.83
m3	2	2	2.025 \pm 0.025	2.05	0.0354	1.75
Width	<i>n</i>	min	mean \pm Sm	max	σ	<i>v</i>
DP4	2	1.38	1.380 \pm 0	1.38	0	0
P4	3	1.66	1.720 \pm 0.06	1.84	0.104	6.05
M1	8	1.62	1.781 \pm 0.049	1.99	0.148	8.15
M2	2	1.75	1.762 \pm 0.018	1.84	0.064	3.50
M3	3	1.72	1.733 \pm 0.009	1.75	0.015	0.88
dp4	2	1.04	1.060 \pm 0.020	1.08	0.028	2.67
p4	2	1.34	1.345 \pm 0.005	1.35	0.007	0.53
m1	7	1.41	1.561 \pm 0.038	1.69	0.099	6.34
m2	8	1.62	1.676 \pm 0.014	1.71	0.040	2.39
m3	2	1.57	1.575 \pm 0.025	1.58	0.007	0.45

protoloph is forked, one part oriented forwards to the anterostyle, the other backwards, directed to the lingual metaloph. They are less distinct on the other P4 and correspond to low extraridges. The P4 lack a paraconule. The mesostyle prolongs in a mesoloph on CUZ 188 and 189, it is duplicated mesially on the former, and interrupted on CUZ 177. A short metalophule I joins the distal mesoloph on CUZ 188. The metaloph II is thicker and directed towards (CUZ 177) or connected (CUZ 189) to the robust metaconule. The latter is more (CUZ 188) or less (CUZ 177, 189) fused with the postprotocrista. A small ridge connects the metaconule to the hypocone, which is weak and stretched on CUZ 188.

The upper molars of cf. *?P. alsaticus* from Cuzal display some variable features. On all of them, as well on the M1 as on the M2, the hypocone is only slightly less robust than the protocone. The smallest M1 (CUZ 154: Fig. 42 k, and 155: Fig. 42j) have shorter protocone + pre- and post-protocristae, but the other features vary like in the other M1 from Cuzal (CUZ 178, 181, 182, 186) and like in *?P. alsaticus* from the type locality, Bouxwiller, with numerous extraridges. Elsewhere, we noted a few differences with *?P. alsaticus* from Bouxwiller. The size difference

between the two main lingual cusps, the protocone and hypocone, is more important in typical *alsaticus*. The paraconule and metaconule are present but less bulged than in the type population. In the upper molars from Cuzal, the protoloph connects the preprotocrista or the protocone; the buccal metaloph II is nearly always present and connects the hypocone and often both the posteroloph through mesiodistal extraridges (CUZ 156, 178, 182); the extraridges are more numerous in the flexi; a metalophule I is present or sketched (6/8). A mediobuccal crest of the metaconule is generally present, merging with various extraridges. A narrow pinched sinus is more frequently present, below the endoloph. The morphology of upper M3 (at least CUZ 180) is close to that of the large M3 from Bouxwiller.

Lower teeth. (Fig. 42n to x). The lower dp4 have a narrower pre-lobe, due to the absence of the protoconid and metalophulid I. The protocristid is low, and an ectostylid limits the base of the sinusid on CUZ 187 (Fig. 42n). The entolophid is low and weak. The posterolophid is absent on CUZ 161 and replaced by a linguodistal notch. Like the dp4, the p4 differs from typical *?P. alsaticus* in the

absence of protoconid and in the ratio of the length of the anterior lobe, markedly longer than the posterior lobe. The anterior is delimited lingually by the metaconid + the postmetacristid and buccally by the mesiodistal protocristid + the postprotocristid + the ectolophid and mesoconid, the posterior lobe extends from the hypoconid, through the post-hypocristid + the hypoconulid + the posterolophid to the entoconid.

Unlike typical *?without ?P. alsaticus*, the anterolophid is more often present as a lingual prolongation of the relatively bulbous anteroconid on m1 and m2. It is generally distinct from the premetacristid, which is generally absent. It connects to the metaconid flank only on a few worn teeth (m1, m2: CUZ 164). Like in typical *alsaticus*, the anteroflexid is closed distally by a complete (buccolingual) metalophulid I on lower molars. A low anterolophid can divide the anteroflexid (m1–2: CUZ 168, 169, 170, 175; m3: CUZ 164).

The path of the metalophulid I is more constant than in typical *?without ?P. alsaticus*. It is complete in all cases, rectilinear from the anterior part of the metaconid to the protoconid, and slightly oblique mesiolingual to distobuccal. Its lingual part is never completely mesial, as it is typically in *? without ?P. alsaticus*. Additional thin ridges (one to three) descend from the lingual metaconid flank to the talonid basin.

The postprotocristid is strong, thick distally and oblique buccomesio-distolingually; it is always longer than the prehypocristid, like in typical *?P. alsaticus*. There is less variation in the ectolophid area, from the distal end of the postprotocristid to the mesial end of the prehypocristid. The mesoconid occupies most of the ectolophid, which is short. The direction of the ectolophid mesial part generally makes an angle with that of the postprotocristid. Similarly, its short distal part makes an angle with the prehypocristid; it is slightly lingual than the mesial one. The mesial and distal parts are similar in height but low, seeming interrupted on unworn teeth. The premesoconid, mesolophid, and postmesoconid ridges are always distinct, more or less long. At least one ectomesolophid is present (13/15 m1–2), but it can be duplicated (CUZ 170). The entolophid is more or less continuous, connecting the entoconid to the prehypocristid or to the postmesoconid ridge. Two m3 only are present; their morphology is similar to that of m1–2, but with a reduced posterior lobe.

Comparison. Overall, we found more similarities between the species of Cuzal and *?P. alsaticus* than with the other species of *Protadelomys* (*P. cartieri*, *P. lugdunensis*) and *?Protadelomys* (*?P. maximini* and *?P. nievesae*), notably in its size, the organization of the postprotocristid–ectolophid, the connections between the lophs and the lingual cusps, the alignment of the pre- and

post-cristae, and the numerous extra-ridges. Among the differences, some could indicate a more progressive grade than typical *?P. alsaticus*, like the more robust hypocone, the less bulged conules, and the transverse lophs and metalophulid I that are better defined than in typical *alsaticus*. However, the evolutionary significance of the absence of the protoconid on p4 and dp4 remains unclear, as it is present on p4 and dp4 of *?P. nievesae*, *?P. alsaticus*, and *P. cartieri*. In contrast, it is poorly developed or absent on p4 and dp4 of *?P. maximini* and *P. lugdunensis*. The weak morphological variation of the lower molars is also noticeable.

?Protadelomys maximini (Escarguel, 1998)

Holotype. M2 (or M1?); SMX1-28.

Type locality. Saint-Maximin “Grand Chantier” = SMX1 (Gard, France).

Other localities. Loci SMX2 (surface sampling) and SMX3 (Grand chantier, gallery entrance, alveolus), from Saint-Maximin (Gard); middle Eocene, MP13/14.

Original diagnosis. Escarguel, 1998: 372–373; translated from French. “Size similar to *P. alsaticus*. Low crowned cheek teeth, with low ridges and cusps. Sinus weak or absent on upper molars. Small hypocone; reduced conules, especially the paraconule; small mesostyle; mesoloph much reduced or absent; reduced protoloph and metaloph, especially at the level of the connection with the lingual cusps. Lower molars with: reduced anterolophid occupying a buccal position; very weak metalophid and hypolophid, often separated from buccal cuspids; mesoconid and hypoconulid very underdeveloped, even absent; posterolophid relatively little reduced”.

Emended diagnosis A species of *?Protadelomys*, about the same size as *?P. alsaticus*, but with slightly longer dp4, wider DP4 and significantly larger M1; larger than *?P. nievesae*.

Enamel of the teeth generally ornamented with weak and low extra-ridges and granules.

Upper teeth. DP4 with anteroloph occupying half-width of the mesial edge and protoloph attached to the junction anteroloph-mesial end of the preprotocrista; Anteroflexus generally wide, protruding and short buccolingually. Protoloph high and continuous, with a small paraconule either distinct or indistinct from the anterostyle. Small hypocone, rarely lingual to the protocone. P4 as length as and slightly wider than the DP4. On molars, complex mesostyle area; anterostyle, pre- and post-protocristae, protocone, thick endoloph and small hypocone aligned mesiodistally; mesoloph short when present; para- and meta-conule often crestiform; anterostyle as strong as the hypocone, symmetrical with respect of the protocone; one or two lingual metalophules attached to

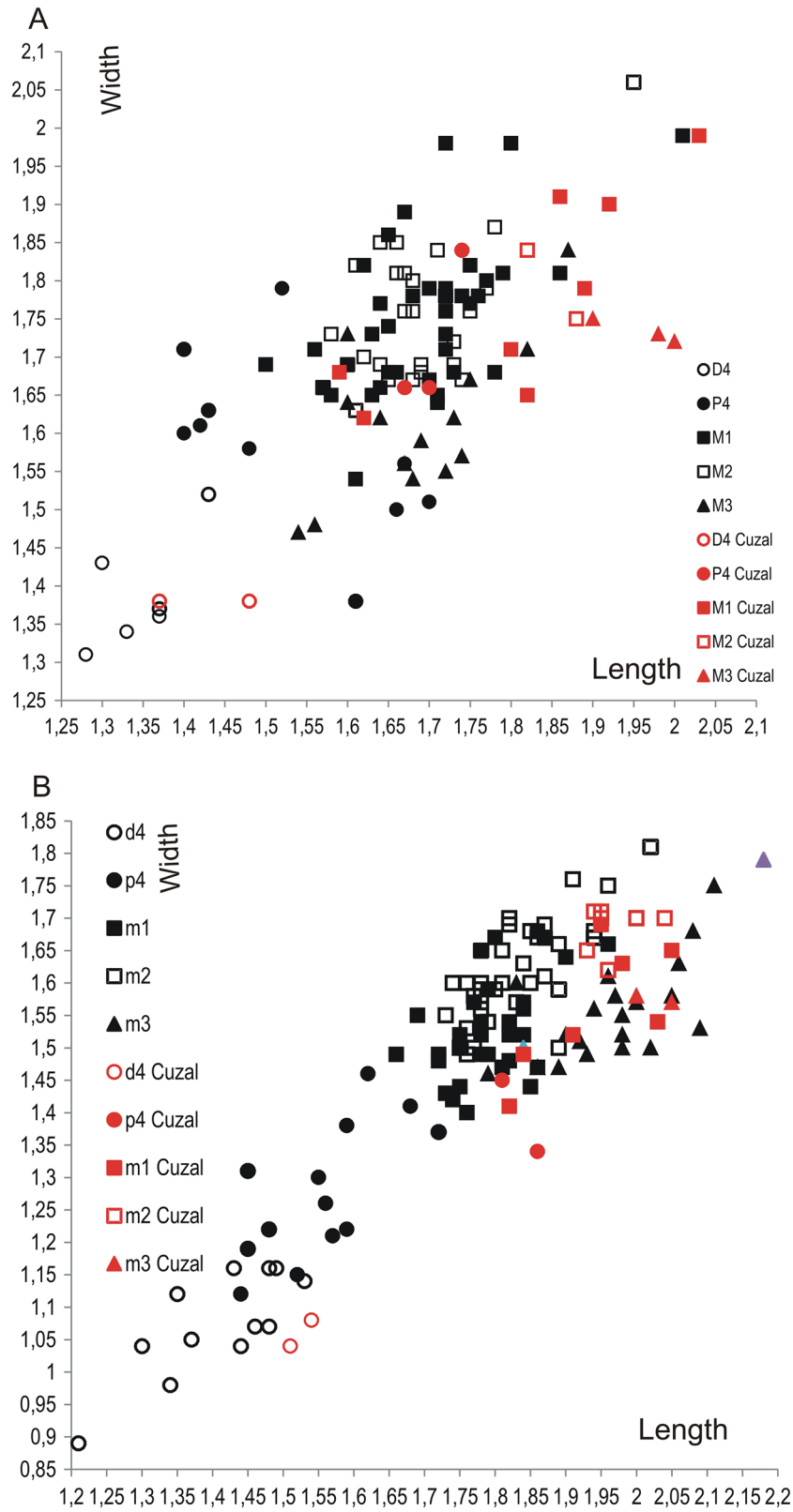


Fig. 41 Bivariate graph (width/length) of the size of the upper (A) and lower (B) teeth of *Protadelomys alsaticus* Hartenberger, 1969 from Cuzal (Quercy) (red marks) compared to the size of the teeth of *Protadelomys alsaticus* Hartenberger, 1969 from Bouxwiller (Bas-Rhin) (black marks)

the hypocone; m3 with metacone slightly prominent; paraconule protruding and metaconule crestiform.

Lower teeth. All the lophids and ridges are thin. On dp4, anteroconid absent, and anterocingulid variably present; protoconid small, and lower than the metaconid; no strong mesiodistal ridge descending in the mesoflexid. On p4, weak, nearly indistinct protoconid. On molars, the metaconid is the higher cuspid, with a long post-metacristid, often joining a preentocristid; the metalophid I is generally complete; the mesoconid is small and slightly swollen, often bearing mesolophid or ectomesolophid, The entolophid is always very low, and often discontinuous and incomplete; it is rarely connected to the postmesoconid or to the prehypocristid. Hypoconulid weak. Floor of the mesoflexid relatively flat.

?*P. maximini* differs from:

- ?*P. alsaticus* in showing: less bulbous main cusps; thinner lophids, lophids and ridges, generally more numerous but weaker and lower extra-ridges and granules; less rough and less wrinkled crown outskirts; relatively longer (mesiodistally) and flatter mesoflexus and mesoflexids; slightly more mesial protoconid on dp4; protoconid absent or indistinct from the metaconid on p4; reduced hypoconulid; upper molars with longer postparacrista and premetacrista, longer and higher endoloph, smaller hypocone, weaker paraconule, metaconule and mesostyle.

- ?*P. nievesae* in showing: the DP4 with a more mesiodistally stretched protocone and hypocone, a longer pre- and post- protocristae and hypocristae, a more reduced hypocone, and lower crown; the upper molars with less bulged cusps and conules that are distinct from the lophids, a higher endoloph, and the sinus nearly absent; the dp4 with a flat basin; the p4 with an underdeveloped protoconid; the lower molars with a more discontinuous and low entolophid.

Material and measurements. (Additional file 6: S6; Tables 6, 8; Figs. 43, 44).

Upper teeth: Probably due to different taphonomic conditions, the DP4 from Saint-Maximin are numerous (14), while they are rare in Bouxwiller. If their length variation (1.30–1.58) is close to that observed in Bouxwiller (1.30–1.53), where several species are distinguished; their width (1.30 to 1.58) is somewhat larger (1.28–1.45). The M1 varies in size from 1.51 × 1.62 mm, to 1.94 × 1.88 mm, and the M2 from 1.63 × 1.65 mm to 1.92, to 2.03 mm (i.e., the type) (Table 6A, Additional file 6: S6). Only two M3 (SMX1-291 and SMX2-226) are well preserved, and a few are broken, probably due to the overrepresentation of juveniles in the Saint-Maximin locality (Escarguel, 1998, Fig. 5–11, 12).

Lower teeth: Fourteen dp4 are present in the sample from Saint-Maximin. They appear slightly larger than the

dp4 of ?*P. alsaticus* from Bouxwiller (Tables 4A, 6A). The size of the p4 of ?*P. maximini* is only slightly smaller than that of ?*P. alsaticus* from Bouxwiller (Tables 4A and 6A). It is larger than that of ?*P. nievesae* from Casa Ramon (Additional file 7: S7, Table 7). There are 16 m1, 12 m2 and 8 m3, and their size is not much different from that of ?*P. alsaticus* (Fig. 44), but they are significantly larger than those of ?*P. nievesae* from Casa Ramon (Table 8).

Description

Upper teeth

DP4. (Fig. 45a to i). Probably due to different taphonomic conditions, the DP4 from Saint-Maximin are numerous (14), while they are rare in Bouxwiller. Like for ?*P. alsaticus* from Bouxwiller, their features display a strong variation, which we consider as intraspecific (see below, morphotypes).

The largest DP4 are morphologically homogeneous, with an anteroloph occupying half-width of the mesial edge and a protoloph that is attached to the junction anteroloph-mesial end of the preprotocrista (=endoloph *in* Escarguel, 1998). The anteroflexus is relatively wide, protruding, and short buccolingually. One DP4 (SMX1-253; Fig. 45a) has a discontinuous anteroloph, with a short stretched parastyle, separated from the anterostyle, which is prolonged in a short lingual ridge; its anteroflexus is clearly narrower than that of other DP4. The postparacrista of SMX1-253 is high and ends in a swelling, which is reminiscent of a premesostyle, followed buccodistally by a strong mesostyle. The short premetacrista is separated from the latter by a shallow valley. The protoloph is high and continuous; its lingual end turns mesially to join the anteroloph at the level of the anterostyle (=protostyle *in* Escarguel, 1998), which is indistinct from the paraconule. A tiny paraconule is sometimes distinct on the protoloph (SMX1-254; Fig. 45b, 259, 260; Fig. 45 g, 264; SMX2-216; Fig. 46 h, 217; Fig. 45j). On the unworn SMX1-255; Fig. 45c and weakly worn SMX1-256; Fig. 45d, the paraconule is strong and indistinct from the anterostyle. The protoloph is discontinuous on SMX1-255. On the latter specimen, like on SMX1-260, the hypocone is not displaced lingually to the protocone as in all other specimens; therefore, the arms of these two lingual cusps are more mesiodistal than oblique. On SMX1-258 and 259, a low connection of the protoloph with the preprotocrista is present more distally than in the specimens described above. The two arms of the protocone are here aligned obliquely, and the conical hypocone does not display any arm.

A postparacrista, more (SMX1-256, 258; SMX2-216) or less strong, is usually present, while a strong premetacrista is always present. Between the two cristae, two adjacent styles are often present: a premesostyle smaller

Table 6 Range of the size variations (length and width: min., max.; average \pm Sm = σ/\sqrt{n} ; $v = 100 \sigma/\text{average L or W}$): A. of the different loci of teeth of *?Protadelomys maximini* Escarguel, 1998 and B. length and width for some loci only of *?Protadelomys cf. maximini* nov. sp.1, 2, from Saint Maximin (MP 13?; Gard, France)

A. <i>Protadelomys maximini</i> . Saint–Maximin (Gard)						
Length	n	min	mean \pm Sm	max	σ	v
DP4	13	1.28	1.404 \pm 0.024	1.58	0.093	6.62
P4	4	1.39	1.455 \pm 0.036	1.55	0.072	4.94
M1	14	1.69	1.803 \pm 0.029	1.94	0.076	6.88
M2	12	1.62	1.736 \pm 0.031	1.94	0.108	6.19
M3	5	1.61	1.734 \pm 0.038	1.84	0.084	4.87
dp4	10	1.37	1.480 \pm 0.025	1.62	0.095	6.63
p4	6	1.49	1.563 \pm 0.023	1.62	0.057	5.82
m1	14	1.67	1.785 \pm 0.019	1.89	0.077	4.76
m2	13	1.63	1.822 \pm 0.020	1.97	0.240	12.88
m3	8	1.95	2.024 \pm 0.099	2.23	0.099	4.89
Width	n	min	mean \pm Sm	max	σ	v
DP4	15	1.25	1.425 \pm 0.026	1.58	0.100	7.00
P4	4	1.48	1.605 \pm 0.052	1.73	0.010	6.49
M1	14	1.65	1.786 \pm 0.026	2.03	0.104	6.04
M2	12	1.65	1.767 \pm 0.022	1.89	0.076	4.31
M3	5	1.63	1.676 \pm 0.017	1.73	0.039	2.30
dp4	10	1.02	1.073 \pm 0.017	1.15	0.048	5.84
p4	6	1.18	1.312 \pm 0.031	1.38	0.031	5.70
m1	14	1.37	1.476 \pm 0.018	1.60	0.065	5.31
m2	13	1.44	1.585 \pm 0.004	1.74	0.184	11.66
m3	8	1.63	1.687 \pm 0.064	1.91	0.191	11.32
B. <i>?Protadelomys cf. maximini</i> morph.1 and morph.2 from Saint-Maximin						
morph.1			morph.2			
Upper teeth	Length	Width	Upper teeth	Length	Width	
DP4	1.33	1.25	D4	1.28	1.55	
M1	–	–	M1	1.51	1.62	
M1	–	–	M1	1.57	1.67	
M1	–	–	M1	1.57	1.69	
Lower teeth	Length	Width	Lower teeth	Length	Width	
dp4	–	–	dp4	1.34	1.06	
dp4	–	–	dp4	1.36	1.02	
dp4	–	–	dp4	1.37	1.01	
dp4	–	–	dp4	1.41	1.09	
dp4	–	–	dp4	1.60	1.23	
m1	1.69	1.45	m1	1.64	1.30	
m1	1.86	1.57	m1	1.65	1.42	
m2	1.79	1.62	m1	1.71	1.36	
m3	1.82	1.43	m2	1.62	1.41	
m3	2.25	1.75	m3	–	–	

and lower than the mesostyle, the latter being more buccal and often linked to the premetacrista. A very short or medium-length buccal mesoloph is also present; it can be

sometimes duplicated (SMX1-253, 254, 260). The buccal part of the metaloph (metalophule II) runs parallel to the protoloph, and ends at the level of a strong metaconule

(metaconule 2). The latter can be bulbous (SMX1-253, 254, 258, 259, 260, 264), or more or less stretched in its mesiodistal ridges. There is no clear metalophule I, but a distomesial ridge, which can be short (SMX1-256, 259, 260) or vestigial. The metaconule generally separates from the lingual cusps, except on SMX1-253, 258, 259, and 264 where it is linked to the mid-hypocone via a low ridge. The posteroloph is low and variably long, from the base of the hypocone to the base of the metacone. Faint wrinkles are visible on weakly worn teeth along the anteroloph and/or the posteroloph, and rare extra-ridges or granules are present in the central basin. One of the largest DP4 (SMX1-264: Fig. 45k) shows a long low ridge from the mid-protocone (=protocrista), directed towards the buccal mesoloph; on this specimen, the extra-ridges are more numerous. Similar observations can be made on SMX1-260: Fig. 45g, which is smaller. The SMX1-252 is a pristine DP4 reduced to an enamel cap with no dentine and roots; it is particularly small. On this tooth, the unworn lophids and extra-ridges are low and discontinuous. The paraconule is bulged, whereas, the metaconule is ridge-like. The anteroloph is long, ending in an anterostyle, which connects the preprotocrista. The protocone and the smaller hypocone are lingually aligned; they are linked through a well-distinct endoloph. The posteroloph is very short and well separated from the hypocone. A buccal premesostyle weakly separates from the postparacrasta, and connects to the more buccal mesostyle. This ridge is symmetrical to the premetacrasta, on each side of the mesostyle. A well-distinct short mesoloph descends in the mesoflexus from the mesostyle. A few slender and short extra-ridges occupy the mesoflexus.

P4. (Fig. 45j to n). Only five upper premolars are present in the sample, one being far stronger and more quadrate than the three others and showing more robust roots (SMX2-218: Fig. 45j). This tooth is worn and the anteroloph cannot be distinguished. The paracone prolongs in a short thick protoloph, which is linked mesially to a very short anteroloph. The latter is hardly distinguishable and linked to the thick preprotocrista. A low central conule is connected to the distal flank of the protoloph. A thick short postparacrasta is visible. A small and shallow valley separates the distal extremity of this postparacrasta

from the mesostyle, which is closer to the premetacrasta mesial extremity. A short buccal mesoloph prolongs the mesostyle lingually. The premetacrasta is thick. The metaloph is buccal and as short as the protoloph. Its posterior part (metalophule II) links to an almost indistinct posterolophid, which is fused to the buccal extremity of the post-hypocristid. The hypocone is present, even if shorter than the protocone. A short metalophule I is directed from the buccal metaloph to the metaconule. The latter is swollen, strong, isolated and slightly mesial when compared to the metaloph. Low ridges and granules are present in the central basin.

The three others P4 differ from SMX2-218 in their smaller size and slender roots. Their shape is more trapezoidal (SMX1-262: Fig. 45l, and 263: Fig. 45m) or rounded (SMX1-265: Fig. 45n), with a very small to absent hypocone, longer (although short) anteroloph and posteroloph (except SMX1-263 where the anteroloph is as reduced as on SMX2-218). A strong conule widens the mesial end of the preprotocrista on SMX1-262 and could correspond to a mesially displaced paraconule. A weak and low connection is present between this conule and the protoloph–anteroloph. The metaconule is absent on SMX1-263 and present on SMX1-262 and 265. On the latter, a narrow and shallow break separates the mesostyle from the postmetacrasta.

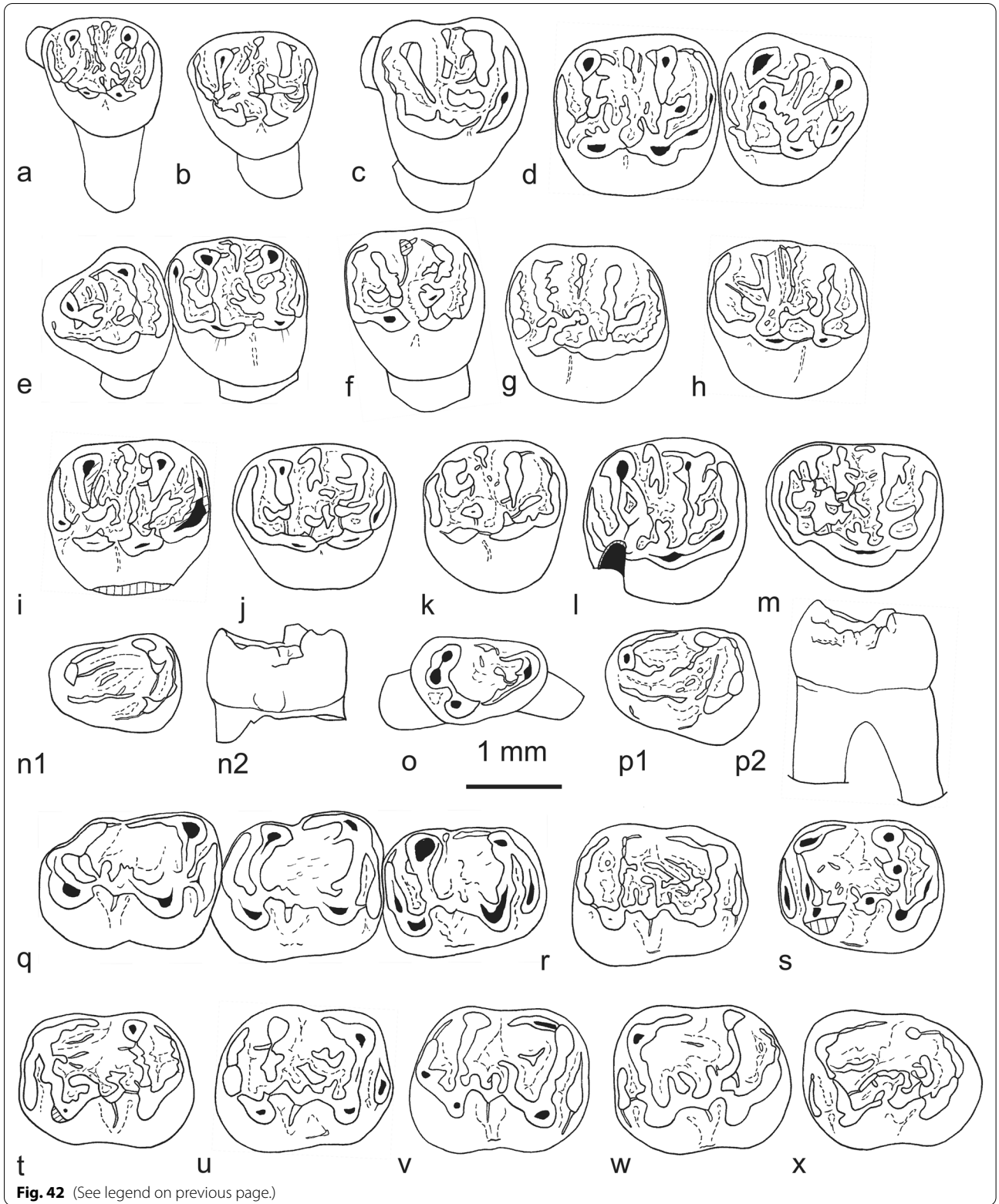
M1–2.

Description of the type SMX1-281. (Fig. 46a).

The type is the largest upper molar of the sample (1.91 × 2.02 mm; Figure 5–8 in Escarguel, 1998). It could represent an M2, as the hypocone is slightly less lingual than the protocone, and the metacone less buccal than the paracone. The anteroloph is long, from the stretched parastyle to its junction with the preprotocrista. The paracone is conical and bears a mesiodistal postparacrasta. The buccal part of the protoloph is relatively high and transverse buccolingually; it is sinuous at the level of the protruding paraconule, and lowers lingually where it connects to the protocone apex. The mesostyle is duplicated and more buccal than the paracone and metacone; it separates from the premetacrasta and prolongs lingually into a short buccal mesoloph. The metacone is arched together with its curved premetacrasta and the short

(See figure on next page.)

Fig. 42 Teeth of *Protadelomys alsaticus* from Cuzal (Quercy). **a** CUZ183, left DP4; occlusal view. **b** CUZ176, left DP4; occlusal view. **c** CUZ177, left P4; occlusal view. **d** CUZ188, right P4–M1; occlusal view. **e** CUZ189, left P4–M1; occlusal view. **f** CUZ155, left M1; occlusal view. **g** CUZ156, right M1; occlusal view. **h** CUZ182, left M1; occlusal view. **i** CUZ178, right M1; occlusal view. **j** CUZ155, left M1; occlusal view. **k** CUZ156, right M1; occlusal view. **l** CUZ182, left M1; occlusal view. **m** CUZ178, right M1; occlusal view. **n** CUZ186, left M1; occlusal view. **o** CUZ154, right M2; occlusal view. **p** CUZ179, right M2; occlusal view. **q** CUZ180, right M3; occlusal view. **r** CUZ187, left dp4; n1, occlusal view; n2, buccal aspect. **s** CUZ161, right dp4; occlusal view. **t** CUZ152, left p4; p1, occlusal view; p2, buccal aspect. **u** CUZ164, right m1–m2–m3; occlusal view. **v** CUZ168, right m1; occlusal view. **w** CUZ163, left m1; occlusal view. **x** CUZ153, left m1; occlusal view. **y** CUZ167, right m1; occlusal view. **z** CUZ172, right m2; occlusal view. **aa** CUZ169, left m2; occlusal view. **ab** CUZ173, left m3; occlusal view. Scale bar = 1 mm



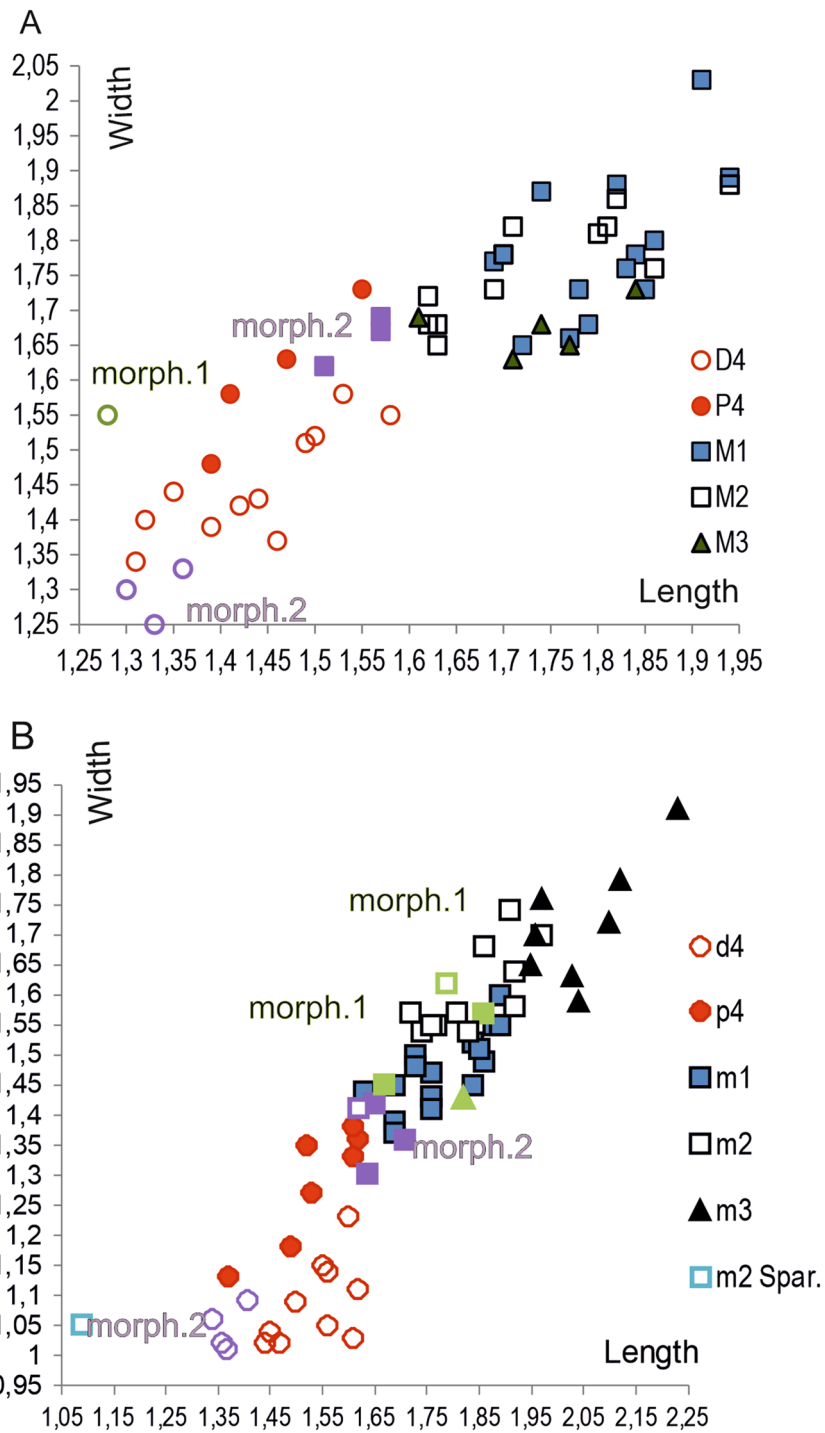


Fig. 43 Bivariate graph (width/length) of the upper (A) and lower (B) teeth of *?Protadelomys maximini* Escarguel, 1998 from Saint-Maximin (Gard) (dp4/DP4 and p4/P4: red marks; upper and lower molars: black and blue marks). From Saint-Maximin, a few teeth are identified as *?P. cf. maximini* sp. indet. 1 (green marks) and sp. indet. 2 (light purple). On B, a turquoise blue mark corresponds to the small m2 identified as *Sparnacomys* (Remy et al. 1997)

Table 7 Range of the size variations (length and width: min., max.; average $\pm Sm = \sigma/\sqrt{n}$; $v = 100 \sigma/\text{average L or W}$). of the different loci of teeth of *Protadelomys nievesae* Peláez-Campomanes, 1995, from Casa Ramon (MP 12?, Huesca, Spain)

A. <i>Protadelomys maximini</i>. Saint-Maximin (Gard)						
Length here	n	min	mean $\pm Sm$	max	σ	v
DP4	13	1.28	1.404 \pm 0.024	1.58	0.093	6.62
P4	4	1.39	1.455 \pm 0.036	1.55	0.072	4.94
M1	14	1.69	1.803 \pm 0.029	1.94	0.076	6.88
M2	12	1.62	1.736 \pm 0.031	1.94	0.108	6.19
M3	5	1.61	1.734 \pm 0.038	1.84	0.084	4.87
dp4	10	1.37	1.480 \pm 0.025	1.62	0.095	6.63
p4	6	1.49	1.563 \pm 0.023	1.62	0.057	5.82
m1	14	1.67	1.785 \pm 0.019	1.89	0.077	4.76
m2	13	1.63	1.822 \pm 0.020	1.97	0.240	12.88
m3	8	1.95	2.024 \pm 0.099	2.23	0.099	4.89
Width	n	min	mean $\pm Sm$	max	σ	v
DP4	15	1.25	1.425 \pm 0.026	1.58	0.100	7.00
P4	4	1.48	1.605 \pm 0.052	1.73	0.010	6.49
M1	14	1.65	1.786 \pm 0.026	2.03	0.104	6.04
M2	12	1.65	1.767 \pm 0.022	1.89	0.076	4.31
M3	5	1.63	1.676 \pm 0.017	1.73	0.039	2.30
dp4	10	1.02	1.073 \pm 0.017	1.15	0.048	5.84
p4	6	1.18	1.312 \pm 0.031	1.38	0.031	5.70
m1	14	1.37	1.476 \pm 0.018	1.60	0.065	5.31
m2	13	1.44	1.585 \pm 0.004	1.74	0.184	11.66
m3	8	1.63	1.687 \pm 0.064	1.91	0.191	11.32

B. ? *Protadelomys cf. maximini* morph.1 and morph.2 from Saint-Maximin

morph.1			morph.2		
Upper teeth	Length	Width	Upper teeth	Length	Width
DP4	1.33	1.25	D4	1.28	1.55
M1	–	–	M1	1.51	1.62
M1	–	–	M1	1.57	1.67
M1	–	–	M1	1.57	1.69
Lower teeth	Length	Width	Lower teeth	Length	Width
dp4	–	–	d4	1.34	1.06
dp4	–	–	d4	1.36	1.02
dp4	–	–	d4	1.37	1.01
dp4	–	–	d4	1.41	1.09
dp4	–	–	d4	1.60	1.23
m1	1.69	1.45	m1	1.64	1.30
m1	1.86	1.57	m1	1.65	1.42
m2	1.79	1.62	m1	1.71	1.36
m3	1.82	1.43	m2	1.62	1.41
m3	2.25	1.75	m3	–	–

metalophule II. The extremity of the latter links with a short and low distomesial ridge, which can represent a kind of metalophule I. It separates from the metaconule

by a narrow furrow. The metaconule is equally strong as the paraconule and lowly connects to the hypocone, through a lingual metalophule. The protocone is only

Table 8 Multivariate analyses of variance (MANOVA) of dental measurements (length and width) between different species of *Protadelomys* and *?Protadelomys*

	<i>P. car. Eg</i>	<i>P. lug. Lis,</i>	<i>P. lug. Lapr</i>	<i>P. car. Lapr</i>	<i>?P.alsa. Boux</i>	<i>?P.alsa. Cuz</i>	<i>?P. maxi. Smx</i>	<i>?P. niev. CasRam</i>
<i>P. cartieri</i> Egerkingen	/	0.01,463	–	–	0.0800	–	0.1874	8,79E–06
<i>P. lugdunensis</i> Lissieu	0.3911	/	0.1371	–	3,86E–03	–	0.0133	2,17E–04
<i>P. lugdunensis</i> Laprade	–	0.4517	/	–	0.0518	–	0.2179	1,02E–03
P4 <i>P. cartieri</i> Laprade	–	–	–	/	–	–	–	–
<i>?P.alsaticus</i> Bouxwiller	0.7141	0.3641	0.5837	–	/	–	0.5677	–
<i>?P.alsaticus</i> Cuzal	–	–	–	–	–	/	–	–
<i>?P. maximini</i> St. Maximin	0.6893	0.1777	0.5436	–	0.9022	–	/	3,41E–03
<i>?P. nievesae</i>	0.1895	0.185	0.2521	–	–	–	0.321	/
	<i>P. car. Eg</i>	<i>P. lug. Lis</i>	<i>P. lug. Lapr</i>	<i>P. car. Lapr</i>	<i>?P.alsa. Boux</i>	<i>?P.alsa. Cuz</i>	<i>?P. maxi. Smx</i>	<i>?P. niev. CasRam</i>
<i>P. cartieri</i> Egerkingen	/	0.08,397	0.771	–	2,05E–03	3,11E–03	2,13E–03	1,36E–04
<i>P. lugdunensis</i> Lissieu	0.8062	/	0.1868	0.03,368	4,85E–08	4,85E–11	6,48E–06	1,23E–05
<i>P. lugdunensis</i> Laprade	0.9715	0.8455	/	0.09,811	5,19E–06	7,08E–03	6,78E–03	6,95E–04
M1 <i>P. cartieri</i> Laprade	–	0.6363	0.6285	/	0.5002	–	–	–
<i>?P.alsaticus</i> Bouxwiller	0.5513	0.3561	0.5523	0.9716	/	–	6,52E–05	7,21E–05
<i>?P.alsaticus</i> Cuzal	0.5071	0.3561	0.4931	–	–	/	0.8887	0.0145
<i>?P. maximini</i> St. Maximin	0.5856	0.3845	0.6069	–	0.6577	0.9877	/	4,61E–05
<i>?P. nievesae</i>	0.2543	0.2215	0.2336	–	0.5887	0.3903	0.2641	/
	<i>P. car. Eg</i>	<i>P. lug. Lis</i>	<i>P. lug. Lapr</i>	<i>P. car. Lapr</i>	<i>?P.alsa. Boux</i>	<i>?P.alsa. Cuz</i>	<i>?P. maxi. Smx</i>	<i>?P. niev. CasRam</i>
<i>P. cartieri</i> Egerkingen	/	0.01,356	–	–	8,01E–06	–	–	2,12E–07
<i>P. lugdunensis</i> Lissieu	0.5842	/	–	–	2,15E–06	–	1,15E–03	6,41E–05
<i>P. lugdunensis</i> Laprade	–	–	/	–	–	–	–	–
M2 <i>P. cartieri</i> Laprade	–	–	–	/	–	–	–	–
<i>?P.alsaticus</i> Bouxwiller	0.5014	0.3803	–	–	/	–	–	6,62E–09
<i>?P.alsaticus</i> Cuzal	–	–	–	–	–	/	–	–
<i>?P. maximini</i> St. Maximin	–	0.4054	–	–	–	–	/	–
<i>?P. nievesae</i>	0.1289	0.08,949	–	–	0.2349	–	–	/
	<i>P. car. Eg</i>	<i>P. lug. Lis</i>	<i>P. lug. Lapr</i>	<i>P. car. Lapr</i>	<i>?P.alsa. Boux</i>	<i>?P.alsa. Cuz</i>	<i>?P. maxi. Smx</i>	<i>?P. niev. CasRam</i>
<i>P. cartieri</i> Egerkingen	/	0.3566	–	–	0.1062	–	0.9299	3,60E–03
<i>P. lugdunensis</i> Lissieu	0.7728	/	–	–	0.0161	–	0.3016	5,89E–03
<i>P. lugdunensis</i> Laprade	–	–	/	–	–	–	–	–
M3 <i>P. cartieri</i> Laprade	–	–	–	/	–	–	–	–
<i>?P.alsaticus</i> Bouxwiller	0.8156	0.6473	–	–	/	–	0.2560	4,96E–03
<i>?P.alsaticus</i> Cuzal	–	–	–	–	–	/	–	–
<i>?P. maximini</i> St. Maximin	0.984	0.6706	–	–	0.8726	–	/	0.0137
<i>?P. nievesae</i>	0.3915	0.3195	–	–	0.6304	–	0.4241	/
	<i>P. car. Eg</i>	<i>P. lug. Lis</i>	<i>P. lug. Lapr</i>	<i>P. car. Lapr</i>	<i>?P.alsa. Boux</i>	<i>?P.alsa. Cuz</i>	<i>?P. maxi. Smx</i>	<i>?P. niev. CasRam</i>
<i>P. cartieri</i> Egerkingen	/	0.5743	0.1184	–	8,83E–03	–	7,65E–03	8,19E–05
<i>P. lugdunensis</i> Lissieu	0.895	/	0.04,769	–	1,02E–03	–	1,30E–03	8,75E–05
<i>P. lugdunensis</i> Laprade	0.6224	0.3627	/	–	3,04E–04	–	6,26E–04	1,49E–04
p4 <i>P. cartieri</i> Laprade	–	–	–	/	–	–	–	–
<i>?P.alsaticus</i> Bouxwiller	0.5088	0.2857	0.198	–	/	–	0.5151	1,38E–03
<i>?P.alsaticus</i> Cuzal	–	–	–	–	–	/	–	–
<i>?P. maximini</i> St. Maximin	0.4122	0.1897	0.1215	–	0.8953	–	/	0.0143
<i>?P. nievesae</i>	0.2084	0.1254	0.1104	–	0.3629	–	0.4274	/
	<i>P. car. Eg</i>	<i>P. lug. Lis</i>	<i>P. lug. Lapr</i>	<i>P. car. Lapr</i>	<i>?P.alsa. Boux</i>	<i>?P.alsa. Cuz</i>	<i>?P. maxi. Smx</i>	<i>?P. niev. CasRam</i>
<i>P. cartieri</i> Egerkingen	/	0.2005	–	–	–	2,79E–02	–	6,06E–05
<i>P. lugdunensis</i> Lissieu	0.8365	/	0.01,898	0.2442	1,23E–03	7,34E–06	7,19E–06	7,59E–09
<i>P. lugdunensis</i> Laprade	–	0.7084	/	0.0291	4,99E–03	0.2006	1,17E–03	1,42E–06

Table 8 (continued)

		<i>P. car. Eg</i>	<i>P. lug. Lis</i>	<i>P. lug. Lapr</i>	<i>P. car. Lapr</i>	? <i>P. alsa. Boux</i>	? <i>P. alsa. Cuz</i>	? <i>P. maxi. Smx</i>	? <i>P. niev. CasRam</i>	
m1	<i>P. cartieri</i> Laprade	–	0.8472	0.5803	/	2,83E-03	2,56E-03	–	2,99E-06	
	? <i>P. alsaticus</i> Bouxwiller	–	0.7091	0.7387	0.6672	/	6,85E-05	0.1442	9,232E-11	
	? <i>P. alsaticus</i> Cuzal	0.4889	0.2881	0.8072	0.2656	0.5387	/	2,84E-03	6,78E-08	
	? <i>P. maximini</i> St. Maximin	–	0.4021	0.5413	–	0.9031	0.5213	/	–	
	? <i>P. nievesae</i>	0.1982	0.1685	0.2051	0.09,898	0.2465	0.0789	–	/	
		<i>P. car. Eg</i>	<i>P. lug. Lis</i>	<i>P. lug. Lapr</i>	<i>P. car. Lapr</i>	? <i>P. alsa. Boux</i>	? <i>P. alsa. Cuz</i>	? <i>P. maxi. Smx</i>	? <i>P. niev. CasRam</i>	
m2	<i>P. cartieri</i> Egerkingen	/	0.03,983	0.2002	0.9011	0.118	–	0.2878	7,08E-06	
	<i>P. lugdunensis</i> Lissieu	0.6844	/	0.0445	0.09,994	–	–	1,88E-04	–	
	<i>P. lugdunensis</i> Laprade	0.7947	0.5953	/	0.3198	4,49E-04	–	0.03,481	5,54E-06	
	<i>P. cartieri</i> Laprade	0.9862	0.7016	0.7961	/	0.0541	0.01,161	0.2877	5,63E-06	
	? <i>P. alsaticus</i> Bouxwiller	0.8987	–	0.6438	0.8504	/	1,18E-07	–	5,444E-10	
m3	? <i>P. alsaticus</i> Cuzal	–	–	–	0.4759	0.4222	/	–	1,138E-08	
	? <i>P. maximini</i> St. Maximin	0.8882	0.4053	0.6572	0.8637	–	–	/	2,27E-04	
	? <i>P. nievesae</i>	0.1613	–	0.04,852	0.06,816	0.2851	0.02,578	0.3267	/	
			<i>P. car. Eg</i>	<i>P. lug. Lis</i>	<i>P. lug. Lapr</i>	<i>P. car. Lapr</i>	? <i>P. alsa. Boux</i>	? <i>P. alsa. Cuz</i>	? <i>P. maxi. Smx</i>	? <i>P. niev. CasRam</i>
	m3	<i>P. cartieri</i> Egerkingen	/	0.2547	–	–	1,65E-03	–	0.03,643	3,18E-03
<i>P. lugdunensis</i> Lissieu		0.7104	/	–	–	–	–	1,97E-04	2,80E-04	
<i>P. lugdunensis</i> Laprade		–	–	/	–	–	–	–	–	
<i>P. cartieri</i> Laprade		–	–	–	/	–	–	–	–	
? <i>P. alsaticus</i> Bouxwiller		0.5727	–	–	–	/	–	–	–	
? <i>P. alsaticus</i> Cuzal	–	–	–	–	–	/	–	–		
? <i>P. maximini</i> St. Maximin	0.479	0.2413	–	–	–	–	/	4,28E-05		
? <i>P. nievesae</i>	0.2786	0.2557	–	–	–	–	0.2127	/		

Wilk's lambda values are presented in the bottom left and *p*-values of the corresponding comparisons are presented in the top right. Significant differences and *p*-values according to $p \leq 0.05$ are bolded

slightly protruding above its pre- and post-protocristae. The endoloph is long and thick, in line with the postprotocrista. The hypocone is clearly smaller than the protocone, and do not display distinct arms. The posteroloph, short, starts by a swelling, probably a posteroconule, and ends at the base of the metacone flank. Some extra-ridges are visible in the mesial and central flexi, and along the posterior slope of the protoloph. The outer surface of enamel is rough.

Other M1–M2. (Fig. 46b to o).

The molars (SMX1- 269, 270, 271, 272, 275, 278, 279, 282, 284, 285, 286, 288; SMX2- 220, 221, 222, 223, 224) have a well-ornamented enamel, as well as well-defined lophs, which are sharp and often thin. The posterior part of the M2 is shorter than the anterior part, the hypocone and metacone being closer than on M1.

On these molars, the antero- and mesoflexi are wide, filled with low granules and/or ridges. The paraconule and metaconule are more often crestiform than bulged. The parastyle is stretched. The anteroloph is long and wrinkled distally. The protoloph is thin and angles at the level of the paraconule, which is protruding, and then connects to the preprotocrista or to the anterostyle. This anterostyle, as seen on weakly or unworn molars, is nearly as strong as the hypocone. The paraconule can connect mesially to the anteroloph via a small ridge (SMX2-223). The anterostyle, the protocone, the pre- and post-protocristae, the endoloph, and the hypocone are mesiodistally aligned, the anterostyle and hypocone being symmetrical with respect to the protocone. The mesostyle area is relatively complex: a mesostyle is present; it is more or less shifted buccally, bulged

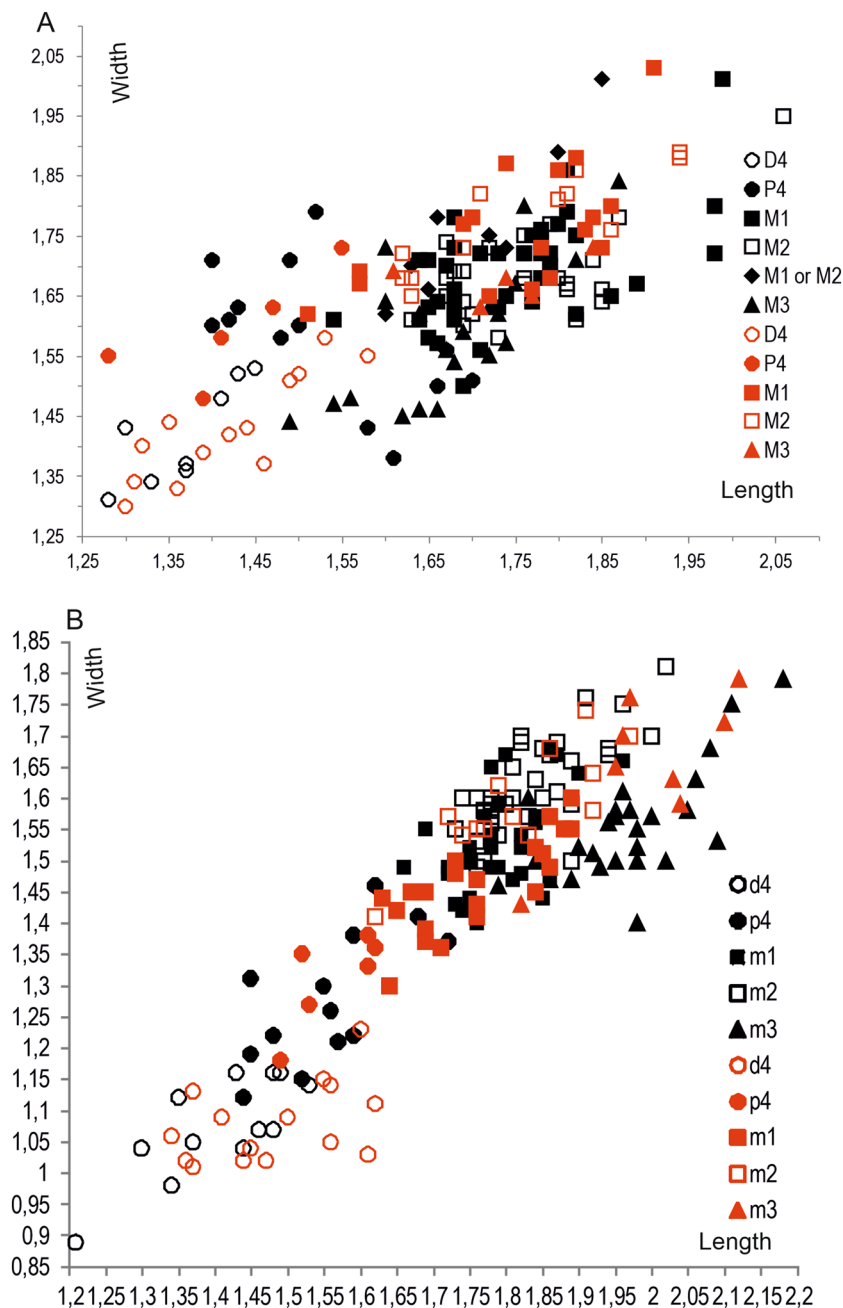


Fig. 44 Bivariate graph (width/length) of the size of the upper (A) and lower (B) teeth of *Protadelomys maximini* Escarguel, 1998 from Saint-Maximin (Gard) (red marks), compared to the size of teeth of *Protadelomys alsaticus* Hartenberger, 1969 from Bouxwiller (Bas-Rhin) (black marks)

or stretched mesiodistally, and framed by swellings of the distal extremity of the thin postparacrista and the mesial extremity of the strong premetacrista. The three swellings can prolong lingually into low and short ridges; the medial swelling can even do so as a lingual mesoloph. Premetacrista + metacone + metaloph make an arcuate loph (thin on unworn or weakly worn teeth), which is

usually separated from the metaconule area. This area is complex and can be filled with several conules and ridges (e.g., on SMX1-275: Fig. 46f3). One or two (e.g., SMX1-275) lingual metalophules attach to the hypocone. The endoloph is thick and high. On SMX1-278: Fig. 46h, a low entostyle is located below the endoloph. The posteroloph

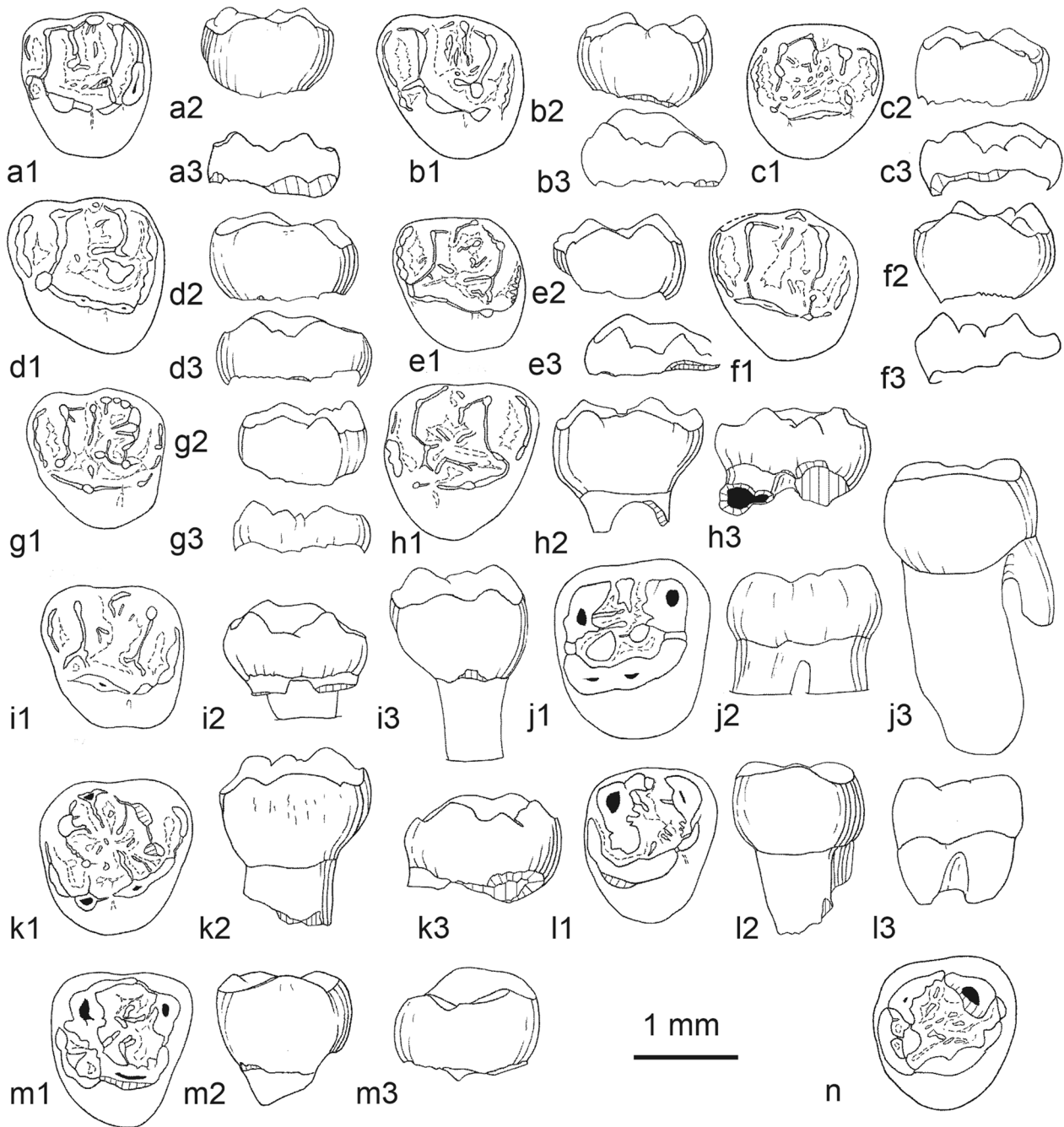


Fig. 45 Upper DP4 and P4 of *Protadelomys maximini* Escarguel, 1998 from Saint-Maximin (Gard). **a** SMX1-253 left DP4; a1, occlusal view; a2, lingual aspect; a3, buccal aspect. **b** SMX1-254, left DP4; b1, occlusal view; b2, lingual aspect; b3, buccal aspect. **c**: SMX1-255, right DP4; c1, occlusal view; c2, lingual aspect; c3, buccal aspect. **d** SMX1-256, left DP4; d1, occlusal view; d2, lingual aspect; d3, buccal aspect. **e** SMX1-257, left DP4; e1, occlusal view; e2, lingual aspect; e3, buccal aspect. **f** SMX1-258, left DP4; f1, occlusal view; f2, lingual aspect; f3, buccal aspect. **g** SMX1-260, left DP4; g1, occlusal view; g2, lingual aspect; g3, buccal aspect. **h** SMX2-216, right DP4; h1, occlusal view; h2, lingual aspect; h3, buccal aspect. **i** SMX2-217, right DP4; i1, occlusal view; i2, buccal aspect; i3, lingual aspect. **j**: SMX2-218, right P4; j1, occlusal view; j2, buccal aspect; j3, lingual aspect. **k**: SMX1-264, right DP4; k1, occlusal view; k2, lingual aspect; k3, buccal aspect. **l**: SMX1-262, right P4; l1, occlusal view; l2, lingual aspect; l3, buccal aspect. **m**: SMX1-263, right P4; m1, occlusal view; m2, lingual aspect; m3, buccal aspect. **n**: SMX1-265, right P4; occlusal view. Scale bar: 1 mm

is short and rarely reaches the distolingual corner of the metacone (SMX1-271: Fig. 46e).

Some M1 (SMX1-273) and M2 (SMX1-276, 280), similar in size, share features, such as the extra-ridges in the synclines, with the teeth described above. However, they also display some morphological variations. The M1 show a more swollen parastyle, anterostyle, and posterocone, as well as thicker loph, especially the protoloph. As such, the synclines appear narrower and the granules and ridges are less numerous. This arrangement occurs in the M2 SMX1-276: Fig. 46o, which however displays numerous extra-ridges. The M2 SMX1-280, (Fig. 5–5, in Escarguel, 1998: Fig. 46m) is slightly different, with its longer and transverse buccal metaloph, which is parallel to the protoloph, its bulged paracone and metacone, and its mesocone developed on the endoloph.

M3. (Fig. 46p). The metacone is present but little prominent from the arcuate cingulum encompassing the premetacrista + posteroloph + low hypocone + protocone + pre- and post-protocristae + endoloph, to the anteroloph. The only break on this “pericingulum” is located between the parastyle and the paracone. The paracone is protruding and the metacone is crestiform. Low granules and extra-ridges fill the basin.

Lower teeth

dp4. (Fig. 47a to g). Their morphology is relatively homogeneous, but a few features are only present in the smallest dp4, which are here attributed to *?Protadelomys cf. maximini* morphotype 2.

The two roots diverge, as usual on dp4. The protoconid is present, small, and lower than the metaconid. A mesial notch separates the two cusps mesially (except on SMX1-203), but a short metalophulid I can be present. The latter is absent on SMX1-201 and SMX2-205, and interrupted on SMX1-206. A short anterocingulid descends from the protoconid on some teeth (SMX2-204, 205: Fig. 47e, f). On all the dp4s, the postmetacristid is high and sharp. No strong mesiodistal ridge descends from the metalophulid I to the center of the basin; only one isolated short ridge is visible (SMX1-203, 206: Fig. 47b, d). The long post-protocristid is nearly mesiodistal, aligned with the lower

ectolophid; the latter bears a small salient mesoconid. On some teeth, the hypoconid displays a spur at its mesial base (Fig. 47b1, d2), which is linked to a short ectocingulid that closes the base of the sinusid (SMX1-203, 206). This cingulid can be simply a flat and not a ridge (SMX1-201; SMX2-205: Fig. 47a, f). The short prehypocristid descends towards the ectolophid. The entoconid is small and conical. When present, the entolophid is low, complete (SMX1-203; SMX2-204) or incomplete (SMX1-202, 204, 206; SMX2-205; SMX3-26). It is connected, or directed, to the junction prehypocristid – ectolophid, or to the hypoconid (SMX1-205). The posterolophid is high, reaching the distal slope of the entoconid. It bears a weakly salient hypoconulid. In the basin, the granules and small extraridges are rare (SMX1-202, 203; SMX2-202, 204, 205) to numerous (SMX1-206: Fig. 47d).

p4. (Fig. 47h to k). There are seven p4 from Saint-Maximin, only four of them can be described in details, the others being too much worn or damaged. On p4, the main cusps are more bulbous and robust than on dp4. The protoconid is weak, nearly indistinct of a protocristid mesiodistal ridge and lower than the metaconid, which is more mesially placed. The protoconid is slightly more distinct on one p4 only (SMX1-208). The metaconid is not much higher than the hypoconid and entoconid. The postprotocristid is oblique; it joins the very short mesiodistal ectolophid, which bears a swollen mesoconid. A mesiodistal ridge descends from the metaconid, which is only strong on SMX1-208. The thick and short postmetacristid ends at a notch, which is the lingual opening of the central basin. The entolophid is discontinuous and low. Extra-ridges are visible in the basin of SMX1-208. A spur on the protoconid distal flank prolongs in an ectostylid on SMX1-210. A short ectomesolophid is noticeable on SMX1-208 and 210.

m1–m2. (Fig. 48a to g). Like in Bouxwiller, we observed a large morphological variation among the 34 m1–m2 from Saint-Maximin, which it is worth comparing to the size variation. For both m1 and m2, the morphological variation is not as important as in *?P. alsaticus*, but they are half less numerous than in Bouxwiller. Two molars are more “bulbous” and are described as *?Protadelomys*

(See figure on next page.)

Fig. 46 Upper molars of *?Protadelomys maximini* Escarguel, 1998 from Saint-Maximin (Gard). **a** SMX1-281, left M1, Holotype; a1, occlusal view; a2, lingual aspect; a3, buccal aspect. **b** SMX1-269, left M1 or 2; b1, occlusal view; b2, buccal aspect. **c**: SMX1-287, left M1, enamel cover only; occlusal view. **d** SMX1-273, right M1; d1, occlusal view; d2, buccal aspect; d3, lingual aspect. **e** SMX1-271, left M1; e1, occlusal view; e2, lingual aspect; e3, buccal aspect. **f** SMX1-275, right M1; f1, lingual aspect; f2, buccal aspect; f3, occlusal view. **g** SMX2-224, right M1; g1, occlusal view; g2, lingual aspect; g3, buccal aspect. **h** SMX1-278, right M1; h1, occlusal view; h2, lingual aspect; h3, buccal aspect. **i** SMX2-221, left M1; i1, occlusal view; i2, lingual aspect; i3, buccal aspect. **j**: SMX2-222, right M1 or M2; j1, occlusal view; j2, lingual aspect; j3, buccal aspect. **k**: SMX2-220, left M1; k1, lingual aspect; k2, occlusal view; k3, buccal aspect. **l**: SMX1-223, left M2; l1, occlusal view; l2, lingual aspect; l3, buccal aspect. **m**: SMX1-280, left M2; m1, occlusal view; m2, lingual aspect; m3, buccal aspect. **n**: SMX1-268, right M2; occlusal view. **o**: SMX1-276, left M2; o1, occlusal view; o2, lingual aspect. **p**: SMX1-291, left M3; p1, occlusal view; p2, buccal aspect. Scale bar: 1 mm

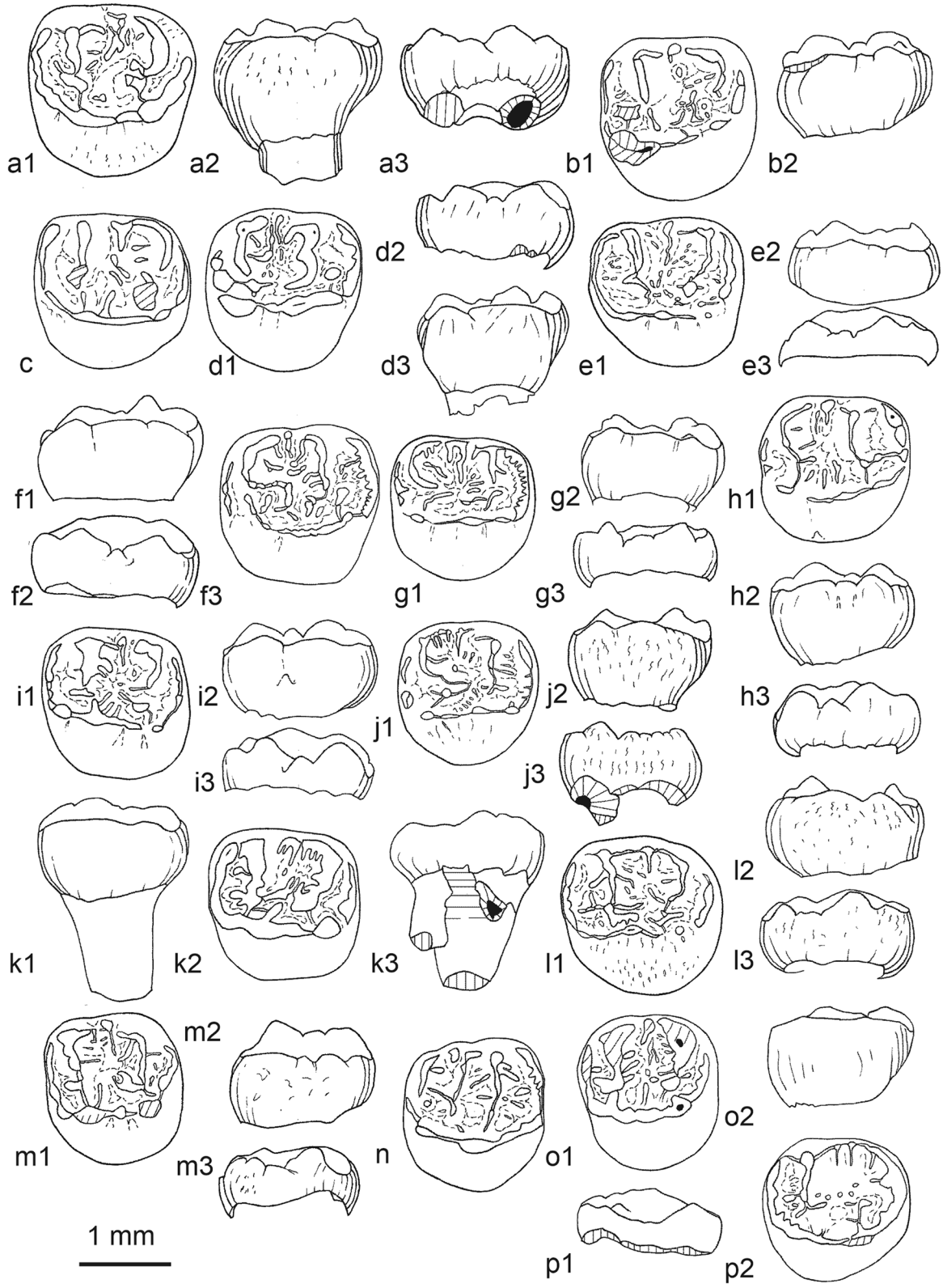


Fig. 46 (See legend on previous page.)

cf. *maximini* morphotype 1. The m2 SMX1-400 is by far the smallest, and is attributed here to *?Protadelomys* cf. *maximini* morphotype 2, alongside four small other teeth. Therefore, 27 lower molars (m1–m2) are considered as typical *?P. maximini*.

On all the teeth, the metaconid represents the higher cusp, followed lingually by the high and acute postmetacristid. The latter is as long as in *?P. alsaticus*, and longer than in *?P. nievesae*. The mesostylid is absent. The valley between the postmetacristid and the entoconid is generally obtuse; the postmetacristid joins a preentocristid, nearly closing the valley, on SMX1-230. All the lophids and ridges are thin. The anteroconid (mainly distinct on m1) and the anterolophid are present but are thinner than in *?P. alsaticus*. The anteroflexid is generally closed distally by a complete (buccolingual) metalophulid I (SMX1-213, 214, 216, 218, 220, 221, 227, 228, 229, 230, 246, 250; SMX2-212); it is rarely opened distally when there is no connection between the buccal and the lingual halves of the metalophulid I (SMX2-208, 209, 213, 215; SMX1-232, 238 (=298 in Escarguel, 1998, Fig. 4–9), 241, 248). The anteroflexid slightly opens buccally on weakly worn teeth, but closes through a buccal elevation of enamel of its floor.

The buccal half of the metalophulid I always displays the same arrangement and buccolingual orientation, starting always from the apex of the protoconid, and running linguobuccally to midwidth of the tooth. As for *?P. alsaticus*, the main variation is observed at the level of the lingual metalophulid I. The latter arises completely mesial, and its buccal end slightly turns distobuccally to join the buccal metalophulid I; it can be more distal, descending from the middle of the metaconid (SMX1-216, 218).

The postprotocristid is strong, thick distally and oblique mesiobuccal to distolingual; it is always longer than the prehypocristid. The variation observed along the ectolophid area is less large than in *?P. alsaticus*. The mesoconid can occupy most of the ectolophid area. On both sides of the mesoconid, the ectolophid is short. Its mesial and distal parts are low and distinct on weakly worn molars. The path of this ectolophid + mesoconid varies less than in *?P. alsaticus*. The postprotocristid is thick and swollen at its end, this thickening could represent an incipient “premesoconid”, frequently marked by a lingual spur or ridge (e.g., SMX1-227, 238, SMX2-209, 212). The shape of the mesoconid only slightly varies with wear. It is generally small and slightly swollen, and can bear a short ridge towards the mesoflexid (mesolophid) or an ectomesolophid (e.g., SMX1-227, 230; SMX2-209). A postmesoconid spur is present on some specimens (e.g., SMX2-212, SMX1-233) and can be linked to extra-ridges oriented towards the entolophid. The entolophid is always very low, and often discontinuous and incomplete; it is rarely connected to the postmesoconid or to the prehypocristid. The floor of the mesoflexid

is relatively flat. The thick and long post-hypocristid ends with the hypoconulid, which is weakly or not bulged. The hypoconulid prolongs in a thinner posterolophid, ending at the level of the entoconid, which is small.

Low extra-ridges, wrinkles, and granules are numerous in the anteroflexid, mesoflexid and posteroflexid. A few of these ornamentations organize in very low oblique ridges in the basin; some converge from the metaconid flank to the mesoflexid.

m3. (Fig. 48h, i). All eight m3 are quite larger than the m1–2. They show the same features as the other molars.

***?Protadelomys* cf. *maximini* morphotype 1**

Upper teeth. Only one upper tooth, the DP4 SMX1-261, is here referred to as *?P. cf. maximini* morphotype 1. It corresponds to one of the shortest DP4 from St-Maximin, but it is as wide as the large DP4 from this locality.

DP4. (Fig. 49a). This DP4 is more bunodont than the other DP4 from St-Maximin. Its short anteroloph starts close to the paracone flank, and then curves mesiodistally. It then interrupts lingually to make a weak anterostyle. The latter is linked to a short mesiodistal ridge, parallel to a more buccal paraconule, which fills the anteroflexus. The protoloph is short and only linked to the protruding paraconule. The paracone bears a weak postparacrista. A shallow valley separates the latter from a strong mesostyle, which could correspond to a metastyle, attached to the premetacrista. Two short metalophules (I and II) descend from the metacone, the distal one (metalophule II) being stronger. The metaconule is duplicated; its mesial part is stronger than its more distal one, which is accompanied by a small granule located at the floor of the posteroflexus. The posteroloph is short, free from the metacone, and weakly and lowly attached to the hypocone. The latter cusp is conical and small, as on the other DP4, but it is much more lingual. The arms of the protocone are in line obliquely, as on other DP4, but they are also clearly shorter. The extra-ridges are absent.

Lower teeth. (Fig. 49b to e). (2 m1: SMX1-220, 224; 1 m2: SMX2-210, 1 m3: SMX1-401).

m1–2–3. Four lower teeth differ from typical *?P. maximini* and from the molars described below as *?P. cf. maximini* morphotype 2. The m1 SMX1-220, 224, the m2 SMX2-210, and the m3 SMX1-401 are among the smallest teeth. SMX1-224 is worn, but its main cusps are still more bulbous and its mesoflexid less flat than in typical *?P. maximini*. Extra-ridges and granules are rare on SMX1-224, like on the m2 SMX1-210. The latter displays a swelling at the distal end of the postmetacristid, which does not completely close the lingual opening of the mesoflexid. The m3 SMX1-401 shows bulbous protoconid and hypoconid, and rare low extra-ridges. They are here only tentatively associated with the small DP4 SMX1-261, because they share a more bulbous cusp pattern.

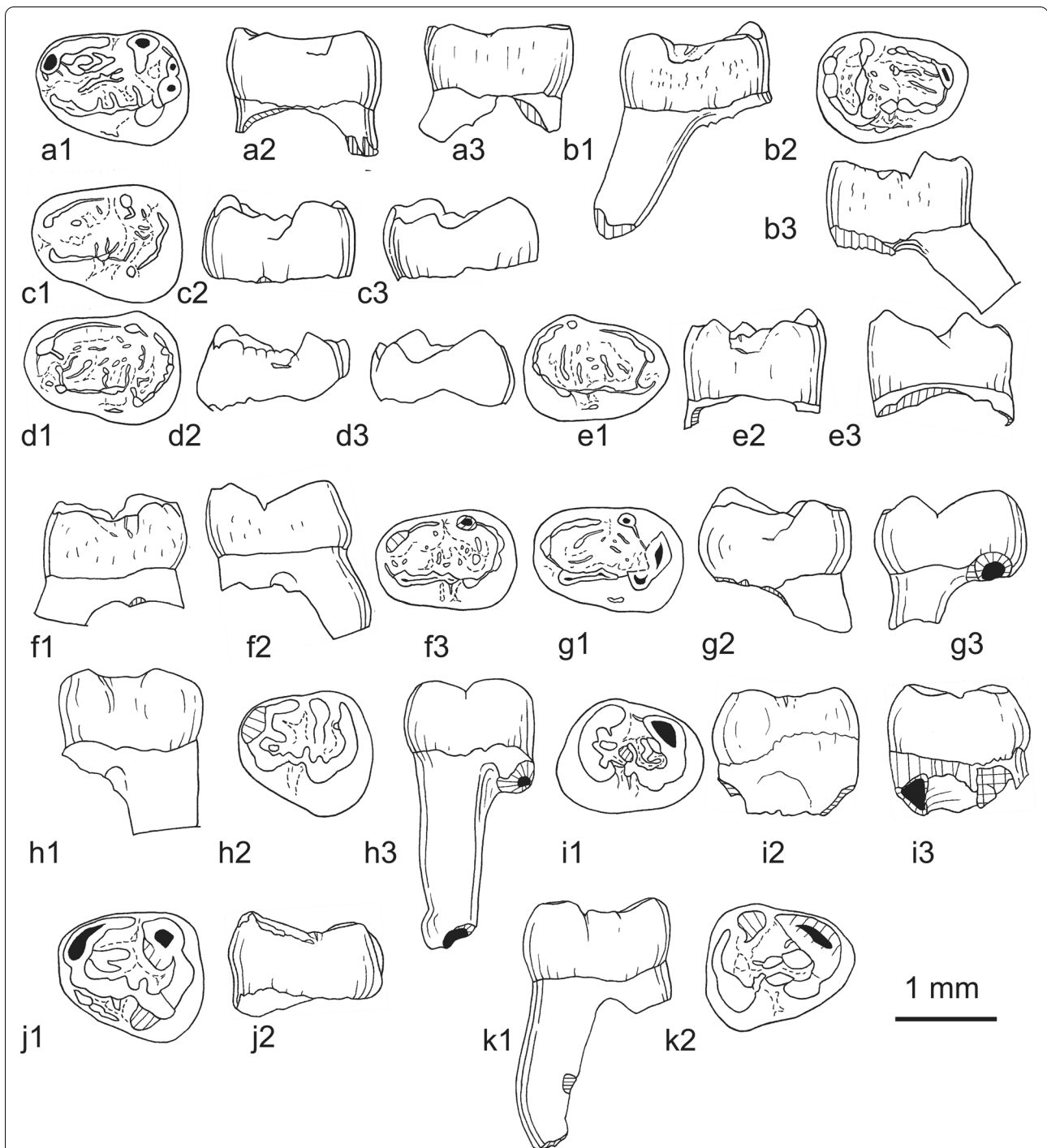
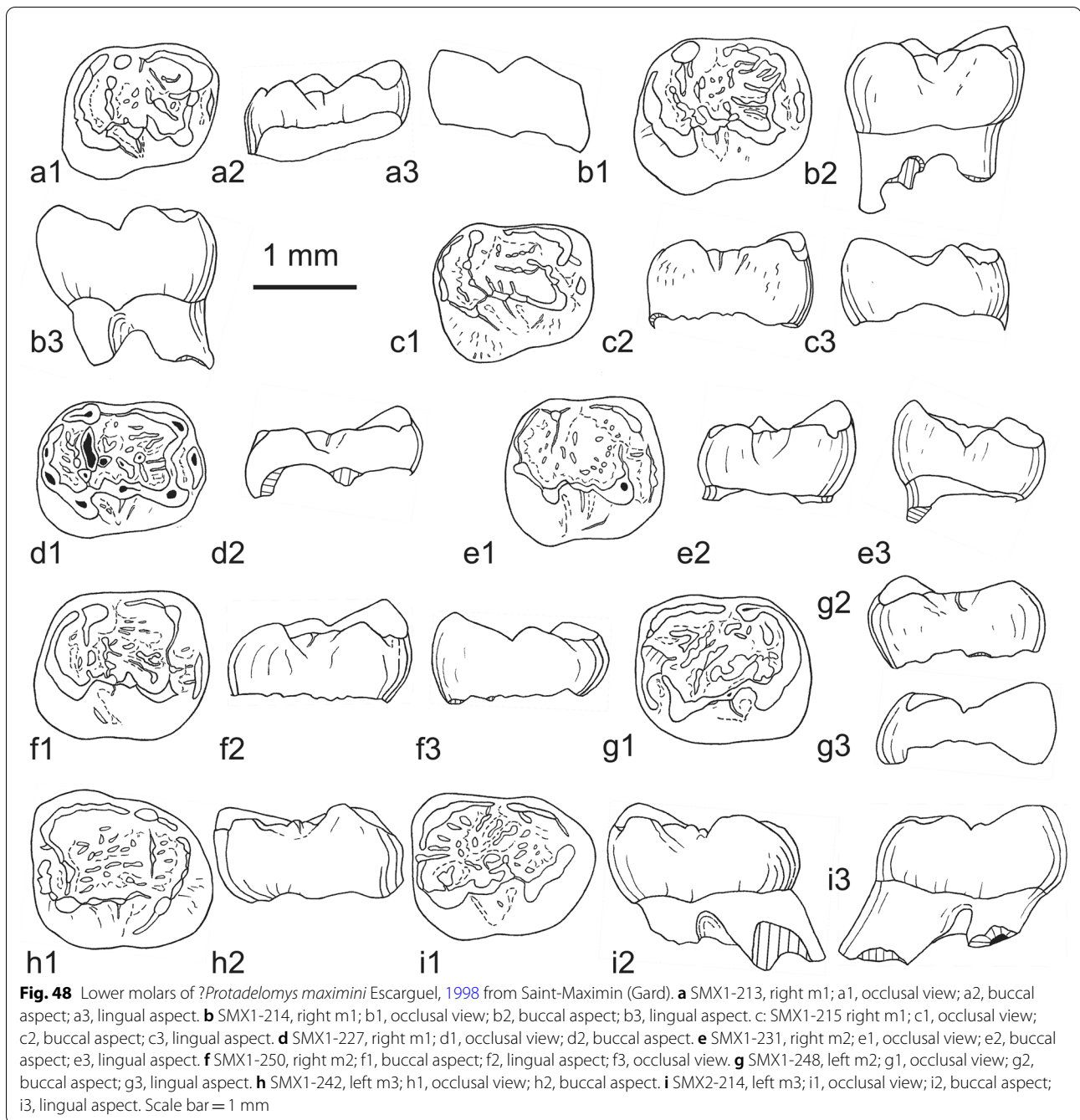


Fig. 47 Lower dp4 and p4 of *Protadelomys maximini* Escarguel, 1998 from Saint-Maximin (Gard). **a** SMX1-201, left dp4; a1, occlusal view; a2, buccal aspect; a3, lingual aspect. **b** SMX1-203, right dp4; b1, buccal aspect; b2, occlusal view; b3, lingual aspect. **c** SMX1-202, left dp4; c1, occlusal view; c2, buccal aspect; c3, lingual aspect. **d** SMX1-206, left dp4; d1, occlusal view; d2, buccal aspect; d3, lingual aspect. **e** SMX2-204, right dp4; e1, occlusal view; e2, buccal aspect; e3, lingual aspect. **f** SMX2-205, left dp4; f1, buccal aspect; f2, lingual aspect; f3, occlusal view. **g** SMX3-26, left p4; g1, occlusal view; g2, buccal aspect; g3, lingual aspect. **h** SMX1-209, left p4; h1, buccal aspect; h2, occlusal view; h3, lingual aspect. **i** SMX1-208, right p4; i1, occlusal view; i2, buccal aspect; i3, lingual aspect. **j** SMX1-210 left p4; j1, occlusal view; j2, buccal aspect. **k** SMX2-206, right p4; k1, buccal aspect; k2, occlusal view. Scale bar = 1 mm



?*Protadelomys* cf. *maximini* morphotype 2

Upper teeth

DP4. (Fig. 50a). The smallest DP4 from Saint-Maximin (SMX3-44), trapezoidal, differs from the small DP4 attributed to *?P. cf. maximini* morphotype 1, in its narrower size, and relatively longer anteroloph. Its hypocone occupied a very lingual position when compared to the protocone, whereas the two cusps are roughly located

at the same lingual level on typical *?P. maximini*, and slightly less lingual in *?P. cf. maximini* morphotype 1.

M1–M2. (Fig. 50b, c). Three M1–2 (SMX3-46, 47, and 48) are smaller than the molars of typical *?P. maximini*. The enamel surface is slightly ornamented, with only a few granules. The hypocone is conical. The arms of the protocone are mesiodistal, the posterior one being short and ending at the level of the short endoloph. The

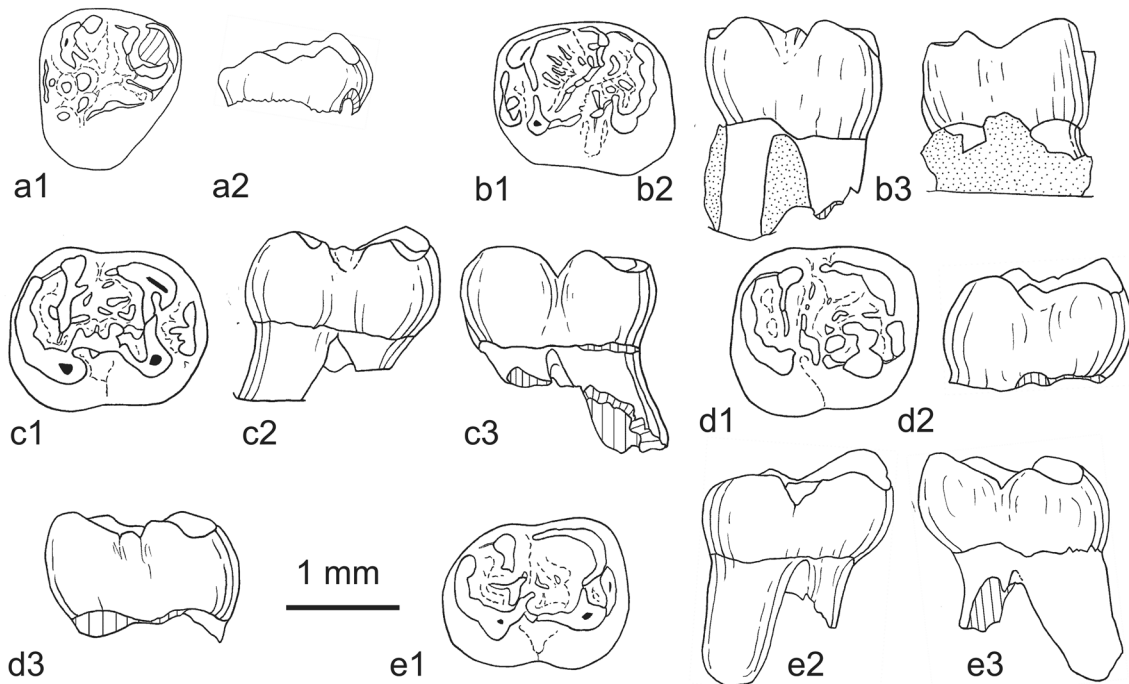


Fig. 49 Teeth of *Protadelomys cf. maximini* morphotype 1, from Saint-Maximin (Gard). **a** SMX1-261, right DP4; a1, occlusal view; a2, buccal aspect. **b** SMX1-220, left m1; b1, occlusal view; b2, buccal aspect; b3, lingual aspect. **c** SMX1-224, right m1; c1, occlusal view; c2, buccal aspect; c3, lingual aspect. **d** SMX2-210, right m2; d1, occlusal view; d2, buccal aspect; d3, lingual aspect. **e** SMX1-401, right m3; e1, occlusal view; e2, buccal aspect; e3, lingual aspect. Scale bar = 1 mm

postparacrista is weak while the premetacrista is slightly stronger and frames a small mesostyle, which prolonged in a short and slender buccal mesoloph. Paraconule and metaconule are protruding and nearly equal in size. The metaconule is linked to the apex of the hypocone. There is a mid-protocone ridge (protocrista) directed towards the paraconule on SMX3-47 (Fig. 50c). On the latter, unworn, the metalophule II is straight, and does not connect to the metaconule. Short ridges represent vestigial metalophule I, which is directed towards, on the unworn M1 or joining the mesoloph on SMX3-48.

Lower teeth

dp4. (Fig. 50d to f). The specimen SMX1-207 previously considered as a p4 (Escarguel, 1998: 372), is here considered as a dp4 due to the distal direction of its posterior root and to a distinct low protoconid close to the metaconid. This specimen is one of the shortest dp4 (1.13 × 1.37 mm), with SMX3-40: Fig. 50d, SMX3-41: Fig. 50f, SMX3-42: Fig. 50e, and SMX2-202 (the latter being figured as *P. maximini*: Fig. 4–3, in Escarguel, 1998). The metaconid and protoconid are almost unworn on SMX1-207, the second being much lower and slender than the metaconid, and placed a little more distally, which indicates that this tooth likely corresponds to a dp4 rather

than a p4; a mesial notch separates the protoconid from the metaconid. The long posprotocristid ends with a weak premesoconid swelling, before joining the mesiodistal ectolophid, which is small. The mesoconid is tiny. The center of the basin is not well distinct on SMX1-207, but a long mesiodistal ridge, a short mesolophid, and an entolophid nearly complete are perceivable. The posterolophid does not reach the entoconid and the hypococonid. SMX3-42 display similar features as SMX1-207. SMX2-202 and SMX3-41 have neither a long mesiodistal ridge, nor a long entolophid, but show small low granules and ridges in the basin. On SMX3-40, the entolophid is better individualized.

m1–m2. (Fig. 50g, h). The m1 SMX1-222 and 226 have the anterolophid reduced to the anteroconid, whereas it is longer on SMX-225. This anteroconid–anterolophid does not connect the short premetacristid (= mesial metalophulid I) on SMX1-222 and 226; but it does on SMX1-225. A more distal lingual metalophulid I descends from the metaconid and joins the transverse buccal metalophulid I on the three m1. The thick oblique postprotocristid develops from the protoconid apex; it bears a low premesoconid swelling or a spur, in front of the mesoconid, which is slightly stretched and in line with the postprotocristid. A postmesoconid spur is present at the

junction with the distal ectolophid, which is lower than the postprotocristid. The prehypocristid is low and short. Some elements of the entolophid join this spur. There are low and thin extra-ridges in the basins. The posterolophid is long, connecting the distal flank of the entocoid, through a postentocristid. The hypoconulid is small. The entolophid is low, variably long and incomplete and does not reach the hypoconid or ectolophid. SMX1-225 also presents a short ectomesolophid.

The unique m2 SMX1-400 displays a similar morphology to that of the m1, but the anterolophid is longer, slender, and connected to the premetacristid. Its lingual metalophulid I does not fuse the buccal metalophulid I. The weak entolophid is reduced to its lingual part.

?*Protadelomys nievesae* (Peláez-Campomanes, 1995).

Type locality. Casa Ramòn (Huesca, Spain); middle Eocene (MP 12?).

Remarks. P. Peláez-Campomanes described the new species *Protadelomys nievesae* (1995) from Casa Ramòn (Huesca, Spain). Here we provide a specimen list with their measurements as Additional file 7: Data S7 and compare them with *?P. maximini* (Escarguel, 1998),

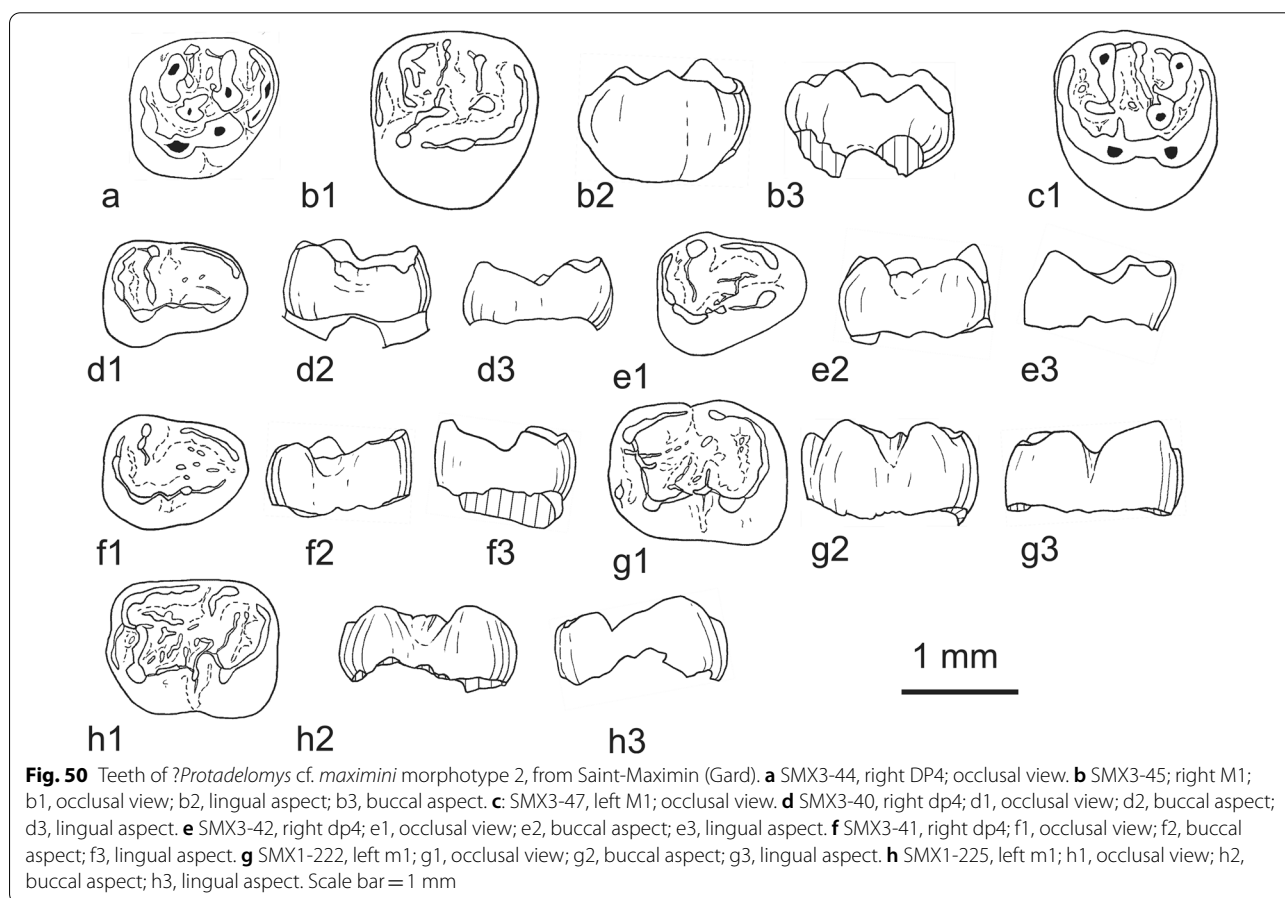
?P. alsaticus, *Protadelomys cartieri*, and *P. lugdunensis* (Hartenberger, 1969).

Original diagnosis. Peláez-Campomanes, 1995: 301. “The cheek teeth are small. The permanent and the deciduous premolars are smaller than the molars. The metalophule is directed towards the protocone instead of towards the hypocone in DP4 and P4. The anterior lobe of P4 is slightly larger than the posterior one. The lower molars do not have a mesoconid”.

“*P. nievesae* differs from *P. cartieri* by its smaller premolars and its P4 which has a poorly developed anterior part.

P. nievesae differs from *P. alsaticus* by the following features: DP4 with well-developed mesostyle and the metaconule and the paraconule connected to the adjacent cusps; P4 and DP4 with the metalophule directed towards the protocone; P4 with the anterior lobe poorly developed and lower molars without mesoconid.

P. nievesae differs from *P. lugdunensis* by its smaller size, its lower molars without ectomesolophid and its P4 with the anterior lobe poorly developed”.



Material and measurements. (Additional file 7: S7; Fig. 51; Table 7). The holotype RP022 is probably an m2, because the mesial (trigonid) and distal (talonid) sides show similar widths.

The teeth are significantly smaller than those of the other species of *?Protadelomys* as well as from *Protadelomys cartieri* and *P. lugdunensis*. (Bivariate graphs in Figs. 3, 14, 28, 44, 51; Tables 6, 7, 8.)

Remarks about differential diagnosis, and comparisons

?Protadelomys nievesae differs from *?P. maximini* and *?P. alsaticus* in its DP4 showing a less stretched protocone and hypocone, shorter pre- and post-protocristae and hypocristae. DP4 of *?P. nievesae* and *?P. maximini* share well-developed buccolingually transverse protoloph and metaloph. The DP4 and molars of *?P. nievesae* and of *?P. alsaticus* differ from *?P. maximini* in showing a less reduced hypocone. The reduced anterior part of the P4 (anteroloph short to absent and reduced anteroflexus) is present in 7/9 teeth of *?P. nievesae*; the anteroloph is otherwise long and presents a narrow anteroflexus on 2/9. The reduced anterior part is not a unique feature of *?P. nievesae*, but mainly characterizes *?P. maximini* (5/5 P4). The number of P4 with reduced anterior part varies also in *P. cartieri* (5/9) and *P. lugdunensis* (3/5). Owing to the weak number of P4, we consider that these differences are not significant.

On the upper molars of *?P. nievesae* and *?P. alsaticus*, the cusps and conules are more bulged and distinct from the loph than in *?P. maximini*, and the endoloph is lower. The sinus is variably present in *?P. nievesae* and less individualized in *?P. alsaticus*, whereas it is nearly absent in *?P. maximini*. The hypocone is generally distinct on unworn P4 of *?P. nievesae*. On upper molars, a lingual metaloph is not always distinct. When present, it joins the hypocone or the endoloph in *?P. maximini*, although more rarely. In the latter, it is very low as on molars of *?P. nievesae*. In *?P. nievesae*, the metaloph is sometimes oriented towards the protocone on DP4 (2/5) and on P4 (1/8), towards the hypocone on DP4 (2/5) and more frequently on P4 (5/8) and towards the posteroloph on P4 (2/8). This lingual metaloph is more often distinct on molars of *P. cartieri* and *P. lugdunensis* even if these teeth are only moderately worn; on these molars it connects the hypocone, or the endoloph. In *Protadelomys* and *?Protadelomys* species, the size of the mesostyle is variable, and the mesoloph is variably long, although it never bypasses the metaconule level.

The dp4 basin floor of *?P. maximini* is flatter than that of the dp4 of *?P. alsaticus* or *?P. nievesae*. The p4 protoconid is often absent, exceptionally present and well distinct in *?P. nievesae* (2/7) whereas it is present only on one

p4 of *?P. maximini*, on which it is low. On lower molars, the entolophid is generally relatively high and complete (11/15) or shortly interrupted (4/15) in *?P. nievesae*, whereas it is more often discontinuous and low in *?P. maximini*. It is generally complete in *P. cartieri*, *P. lugdunensis*, and *?P. alsaticus*.

Genus *Homætreposciurus* nov. gen

Genus and species indet 1 (in Hartenberger, 1969);

Treposciurus sp. in Hartenberger (1990)

Etymology. From Latin *Homæ*, looks like, *Treposciurus*.

Type species. *Homætreposciurus egerkingensis* nov. gen. nov. sp.

Diagnosis. That of the type-species (see below).

***Homætreposciurus egerkingensis* nov. gen. nov. sp.**

Holotype. Ek H004, lower left tooth row, with p4–m3.

Type locality. Egerkingen γ (Swiss Jura); middle Eocene (MP14).

Diagnosis. The lower molars display some features considered derived for theridomyids (e.g., Vianey-Liaud & Marivaux 2016; 2021): p4 longer than m1, with metaconid and protoconid mesially positioned; long thick postprotocristid; high ridges on the lingual (postmetacristid) and distal (post-hypocristid + posterolophid) edges of the teeth; numerous granules and low extraridges and granules in the basin; metalophulid I complete, developed from the mesial edge of the metaconid (premetacristid) to the preprotocristid.

They also show: dp4 shorter than p4. Lower molars lengths increasing from m1 to m3. Anteroconid absent on p4 and mesiobuccally situated on molars; short on molars but extending buccolingually more and more from m1 to m3, reaching the middle of the mesial border on m3. Entolophid low and discontinuous. Ectolophid mesiodistal from p4 to m2 (nearly aligned with the postprotocristid on p4, a little oblique on m3), with mesoconid weakly marked. Ectomesolophid present on p4.

The molar morphological features differs from that of *Treposciurus* in showing lower crowned and more concave occlusal surface of teeth, less individualized lophids (metalophulid I and entolophid), the metaconid fused in a curved and high crest with the postmetacristid, a smaller mesostylid, and smaller granules on enamel surface.

Material. The holotype Ek 1004 (p4 to m3); Ek 79, a right lower dp4, and possibly a left M1 (Ek 85). Even if the material is poor, it is possible to erect a new taxon, due to the peculiar features of the lower teeth.

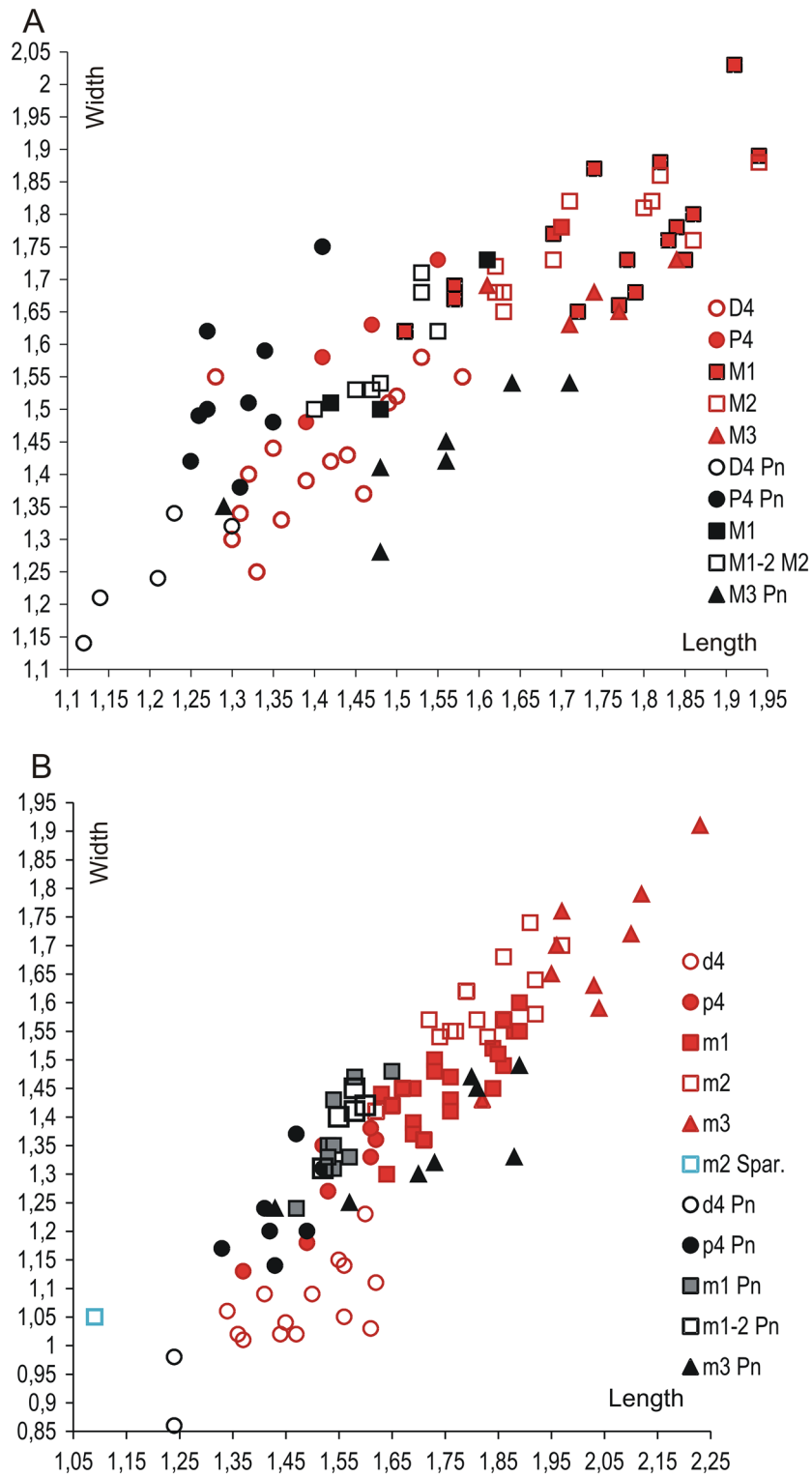


Fig. 51 Bivariate graph (width/length) of the size of the upper (A) and lower (B) teeth of *Protadelomys nievesae* Peláez Campomanes, 1995 from Casa Ramòn (Huesca, Spain) (black marks) compared to the size of teeth of *Protadelomys maximini* Escarguel, 1998 from Saint-Maximin (Gard) (red marks)

Upper tooth

M1 (Fig. 52c). Compared to *Protadelomys* of the same locality, the weakly worn M1 Ek 85 displays some peculiar features. It is larger, its paraconule and metaconule showing similar size and being both isolated. The parastyle is mesiobuccal; the anterostyle is present. The protoloph reduces to a short thin buccal ridge posteriorly oriented; it is followed lingually by the distinct paraconule. A well-marked protocrista is present, its mesial end being free. The strong mesostyle stretched mesiodistally and surrounded by two small cusps, closes the mesoflexus buccally. The metacone shows a short premetacrista; the buccal metalophule II is present, but short. Two small granules could constitute the remnants of the buccal metalophule I. The metaconule, not larger than the paraconule, is isolated both from the buccal metalophule I and from the lingual cusps, protocone and hypocone. The mesoflexus displays a few extra-ridges. The hypocone appears smaller than the protocone. The endoloph is relatively long, thin and high. It is slightly marked lingually by a shallow and short sinus.

Lower teeth

dp4 (Fig. 52b). The base of the crown EK 79 is poorly preserved and partly covered with glue. Despite these facts, at the metaconid level, the crown is clearly higher than that of dp4 of the other species of the same locality. The postmetacristid is high and buccodistally compressed, overhanging the lower central basin; a tiny mesostylid is distinct. The protoconid is merged in the oblique protocristid, which ends in a weak mesoconid. The distal ectolophid is interrupted in front of the hypoconid. The prehypocristid is long and oblique bucco-mesially. The hypoconid and entoconid are equally robust, bulbous with their upper part tapered. Wrinklins are numerous on the enamel surface, some making a kind of ectocingulid at the buccal opening of the sinusid.

p4. The specimen Ek H004 (Fig. 52a) was first described and figured by Hartenberger (1969, p. 54; pl. 1, Fig. 4) as gen. and sp. indet, close to *Suevosciurus*; then as *Treposciurus* in Hartenberger (1990) and Escarguel (1999: 246). It is a little longer (2.20 mm) than m1 (2.09 mm). The protoconid is close to the metaconid, but it is somewhat lower and separated by a shallow and narrow groove. The metaconid curves mesio-lingually and prolongs in the high and narrow mesiodistal postmetacristid. The postmetacristid ends at the base of a low and small entoconid, leaving the wide mesosynclinid opened lingually. Several ridges run obliquely in both the mesosynclinid and the posterosynclinid. The lophids are crenulated by short wrinkles. The postprotocristid is slightly oblique, long, and marked at the base of its distal end by a short edge. The sinusid is shallow, and the crown high below. The

ectolophid is located in the continuity of the postprotocristid; it is long and bears a long ectomesolophid reaching the floor of the sinusid. The ectolophid joins a short prehypocristid. The entolophid is low and interrupted between its buccal and lingual halves. One thin ridge connects the lingual half with the posterolophid, which does not join the apex of the entoconid.

Lower molars. The lower molars have a concave talonid, with low and discontinuous transverse lophids and high edging ridges. The basin enamel surfaces are strongly wrinkled, with short ridges and granules, while the lophids are crenulated. The antesinusid–anteroflexid always opens buccally and lingually.

m1–m2. The m1 (2.09 × 1.75 mm) differs from the m2 (2.34 × 2.13 mm) in displaying a smaller size, a metaconid closer to the protoconid than the entoconid to the hypoconid, a smaller anteroconid located closer to the protoconid than to the metaconid. On the m2 and m3, the anteroconid is equidistant from the protoconid and metaconid, and stretched in a short and low anterolophid. In both cases, the anteroconid does not connect with the metalophulid I; the anterolophulid is lacking but two to four low mesiodistal wrinkles are present in the anteroflexid. The metalophulid I is rectilinear due to the alignment of its lingual and buccal halves; it connects to the preprotocristid. The postprotocristid is thick, long, oblique, and its end bears a short premesoconid spur on the m1, but not on the m2–3. The ectolophid is mesiodistally oriented, long, and swollen at the level of the mesoconid; it makes an obtuse angle with the postprotocristid. Its distal extremity is lower than the level of the connection between the prehypocristid and the entolophid. The latter angles at an entoconulid level and it is low and incomplete lingually. The post-hypocristid and the posterolophid are continuous. The hypoconulid is not distinct or salient.

m3 (2.66 × 2.03 mm) is longer than m2. This elongation affects the anterior part of the tooth; while the posterior lobe width is slightly reduced with respect to m2. Consequently, its anterolophid is longer than that of the m2, ditto for the postmetacristid and the postprotocristid. The short ectolophid is lower than the postprotocristid.

Comparison with *Treposciurus mutabilis* [from Ehrenstein 3 (MP18, upper Eocene)]

Because these specimens have been previously referred to *Treposciurus*, we compared them to a (younger) species of this genus, *T. mutabilis*, whose teeth are highly ornamented. The major similarities between *Homætreposciurus* and *Treposciurus* lie in the ornamentation of the enamel surface, with numerous wrinkles and granules. However, the wrinkles and ridges are more continuous and reticulated in *Treposciurus*. We also found

a number of differences between the two genera. Compared to *Homætreposciurus*, *Treposciurus mutabilis* is characterized by higher crown and higher main cusps; a p4 smaller than or equal to m1, whereas m3 is equal or smaller than m2; better defined and higher transverse lophids (metalophid I and entolophid), even if the anterolophid remains low; a longer and lingually developed anterolophid, while the anteroconid remains buccal and close to the protoconid; a higher metaconid that is tapered at its apex and not fused in a curved and high crest with the postmetacristid; a less oblique postprotocristid; a more salient mesoconid, with the ectomesolophid present on all the molars; a mesostylid often distinct and sometimes extending in a short lingual mesolophid; a less reduced posterior lobe of m3. Similar differences were observed with older species of *Treposciurus*, such as *T. preecei* from Creechbarrow (Bartonian), even if their teeth are smaller, with less ornamented enamel.

Theridomyoidea gen. and sp. indet. 1

Two teeth from Laprade (LAP 197 and LAP 214) can be distinguished from the teeth of *Protadelomys lugdunensis* or *P. cartieri*.

Description

M1. Figure 52a LAP 197 is probably an M1, as the width of the posterior area is not reduced. However, the parastyle is not strongly thickened. The preprotocrista is long, thick, and does not show any swelling (anteroconule) at its mesial extremity. The small paraconule is slightly protruding mesially. Buccal to the paraconule, two opposite mesiodistal ridges descend from the protoloph. The protoloph reaches the apex of the protocone. The endoloph is short and low. The hypocone is as robust as the protocone. The metacone is as strong as the paracone.

The mesostyle connects to the mesoloph, which ends mid-way through the mesoflexus. Two small extra-mesostyles lie on each side of the main one. Two low ridges are present in the mesial part of the mesoflexus. The metalophule II bears two successive small metaconules. The stronger metaconule stands mesially to the lingual part of the metalophule II, which connects to the apex of the hypocone. The post-hypocrista extends posteriorly to join the posteroconule, which is swollen. The posteroloph is low and swollen at its buccal end.

m1. The anteroconid of LAP 214 (Fig. 52b) is close to the protoconid, as in *P. lugdunensis*. It is underlined by the anterocingulid and a well-marked antesinusid. A very low anterolophid does not quite reach the occlusal surface. The anterolophid connects the anteroconid to the mesial base of the metaconid, which corresponds to the highest cuspid. The lingual metalophid I extends linguodistally

along the metaconid buccal flank, and then forms an angle open mesially when connecting the buccal metalophid I, which is oblique buccodistally. The latter is connected to the ventral summit of the protoconid. A very low more or less mesiodistal ridge, ornamented with wrinkles, develops posteriorly from the angle of the metalophid I towards the thin mesolophid. The oblique postprotocristid is long, but shorter than in *P. lugdunensis*. Its distal end forms an angle with the mesial ectolophid, which is mesiodistal and longer than in *P. lugdunensis*. The mesoconid is merged in the ectolophid, slightly swollen and elongated mesiodistally. It displays a long and thin low ridge buccally, like an ectomesolophid. The prehypocristid connects to the ectolophid and to the buccal end of the entolophid. The latter is nearly straight and without any entoconulid, lowering from the entoconid to its buccal end. The mesoflexid appears longer than other flexids when compared to *P. lugdunensis*. The hypoconulid is weak and stretched into the posterolophid.

Comparison

The M1 LAP 197 displays some original features compare to *P. lugdunensis* from Laprade. Despite this molar is nearly unworn, the protoloph appears continuous; bearing a small and slightly protruding paraconule. There are extraridges, absent in *P. lugdunensis*, especially two opposite mesiodistal ridges descending from the protoloph, buccal to the paraconule, and short and thin ridges in the mesoflexus, one mesial close to the mesoloph, one more distal, joining the most lingual metaconule. Two small extra-mesostyles lie on each side of the main one. The metacone is as robust as the paracone. There are two slender buccal metalophs, the mesial one connecting two successive small metaconules. The strongest of these metaconules lays mesially to the lingual part of the metaloph, which connects to the center of the hypocone. The preprotocrista, like the post-hypocrista are longer and thicker. The long posteroloph is low and swollen at its buccal end.

The m1 LAP 214 is larger than the other m1 from Laprade, and differs from the two species of *Protadelomys* in the lophids slender and higher. The height of its roots implies a high mandibular horizontal ramus, much higher than that of *P. lugdunensis*.

Genus *Eoelfomys* nov. gen.

(Fig. 53c to g).

Type species. *Eoelfomys lapradensis* nov. gen. nov. sp.

Type locality. Laprade (Lot, Quercy), middle Eocene (MP14).

Diagnosis. That of the type species *Eoelfomys lapradensis* nov. gen. nov. sp.

Remarks

The smallest teeth from Laprade were referred to *Elfomys* nov. sp. by Hartenberger (in Sudre et al., 1990) and this identification was taken over by Comte et al. (2012). However, even if these teeth display some morphological and length similarities with *Elfomys engesseri* Hooker & Weidmann, they are larger and show unique feature combination, which justifies the creation of a new taxon, to which the mandible Ek H003 from Egerkingen could belong.

Eoelfomys from the type locality Laprade

Eoelfomys lapradensis nov. gen. nov. sp.

Elfomys nov. sp. Hartenberger, in Sudre et al., 1990, p. 20.

Elfomys sp. in Comte et al., 2012: Fig. 17; Pl.8, Fig. x to z

Holotype. LAP 243, unworn right upper M1. (Fig. 53c).

Diagnosis. Size close to that of the large *Elfomys engesseri* Hooker & Weidmann, 2007; smaller than *E. catalaunicus* Bonilla-Salomon et al., 2016.

Differs from the Eocene *Elfomys* species in:

- The occurrence of a strong and high endoloph, which prevents the communication between the sinus and the mesoflexus;
- The absence of connection between the metalophule II and the posteroloph on the upper teeth, the absence of a long prehypocrista connecting a mesiobuccal metaconule crest, the presence of a strong metaconule;
- The occurrence of a long low mesolophid on m2–m3.

Material and measurements. Appendix, S3: two M1, one M2, one m2, one m3. (cf. Figure 17, in Comte et al., 2012). Their size is close to that of *Elfomys engesseri* Hooker & Weidmann, 2007, and larger than *E. catalaunicus* Bonilla-Salomon et al., 2016.

Description. The crowns are unilaterally hypsodont but low.

M1–2. The parastyle of the two M1 is slightly curved towards the paracone. LAP 243, the holotype (Fig. 53c), shows a premetacrista, not easily distinguishable on the other two upper molars (LAP 244 and 245), which are worn. The posterior area is narrower on the M2 (LAP 244) than on the M1 (LAP 243, 245). The three teeth have a high endoloph separating the shallow sinus from the mesoflexus. The paraconule stretches forward and protrudes mesially. The attachment of the protoloph to the mid-protocone is weak. The mesostyle is present. The mesoloph either reaches the buccal flank of the metaconule (LAP 245: Fig. 53d), or is shorter (LAP 244: Fig. 53e) or replaced by a low ridge reaching the buccal base of the metaconule (LAP 243). On the latter, a very low short ridge is reminiscent of a vestigial metalophule I. The metalophule II

is short and weakly connected to the base of the metaconule. The latter also weakly attaches to the mid-hypocone. There are scarce granules on the enamel surface.

The main differences with the late Eocene species of *Elfomys* are the strong endoloph together with the absence of communication between the sinus and the mesoflexus, the absence of relationship of the metalophule II with the posteroloph, the absence of a long prehypocrista connecting to the mesiobuccal metaconule crest.

m2–3. The teeth are flatter than that of the late Eocene *Elfomys*, the metaconid less salient, the anteroconid smaller.

On m2 (LAP 242; Fig. 53f), the anterolophid is very short, the anteroflexid reduced, and the anterocongulid absent. The two parts of the metalophulid I are continuous, even if their extremities are not completely fused. The long and oblique postprotocristid makes an angle with the short mesiodistal ectolophid. From the junction between the postprotocristid and the ectolophid, a few low granules punctuate the path of a mesolophid. The mesoconid is weak. The entolophid is straight and connects the junction of the prehypocristid to the ectolophid. The sinusid and mesoflexid do not communicate.

On m3 (Fig. 53g), the anterolophid is a little longer and it is weakly attached to the short lingual part of the metalophulid I. The buccal part of the metalophulid I is free and distally oriented. Small and very low granules trace the mesolophid path. The posterior lobe is reduced.

Remarks and comparisons

As for basal Theridomorpha and the middle Eocene species of *Masillamys* or *Protadelomys*, this genus displays a high endoloph. *Eoelfomys* could represent an early stage preceding *Elfomys*, genus in which the endoloph disappears, the prehypocrista lengthens to the mesoloph, and the distal ectolophid reduces. The size and morphology of its lower molars is similar to those of the mandible Ek H003 from Egerkingen.

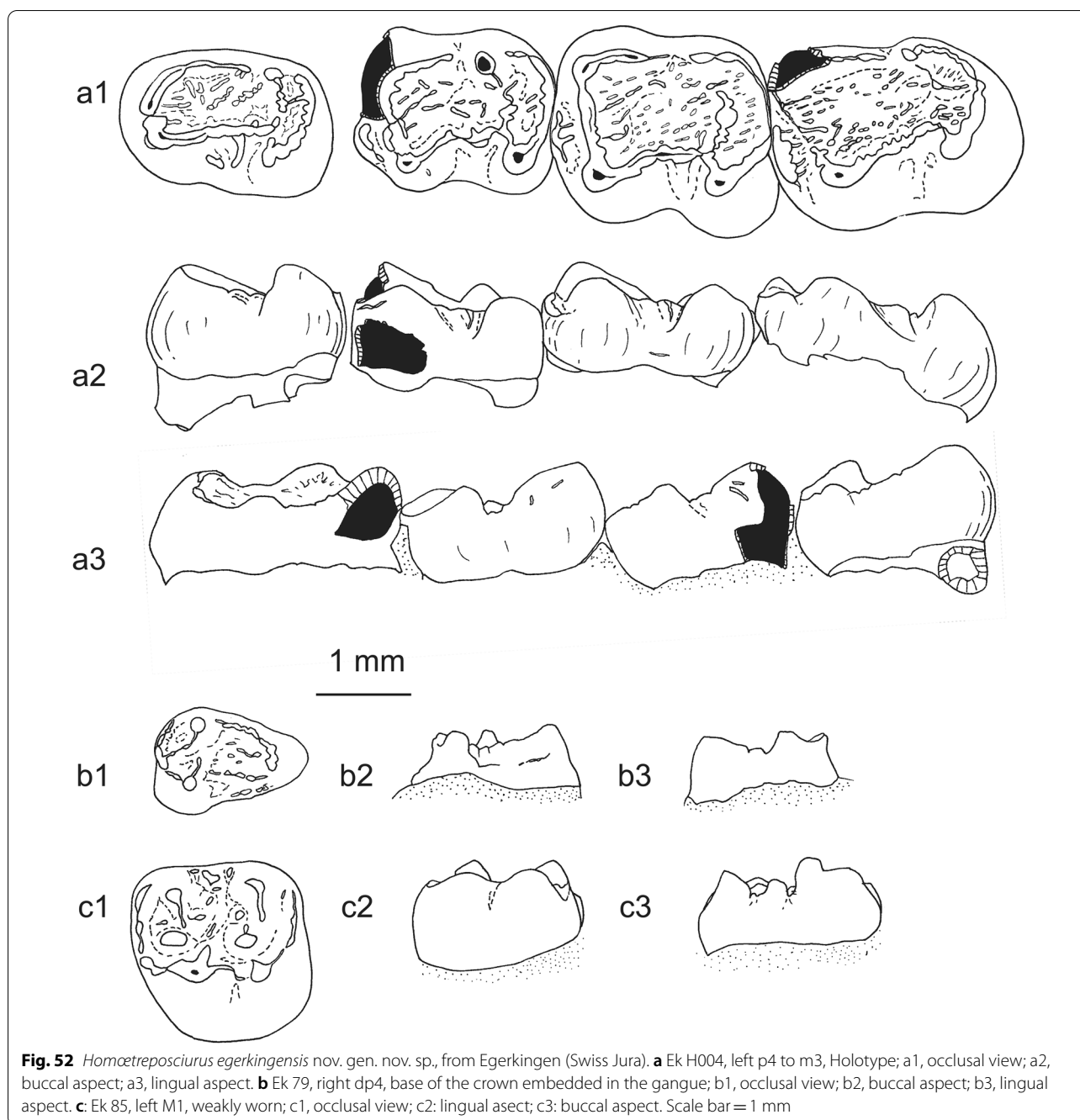
Eoelfomys from Egerkingen

Eoelfomys nov. gen., nov sp. indet

Genus and species indet 2, in Hartenberger (1969); ?
Paradelomys sp. in Hartenberger (1990)

Material. Ek H003, one fragment of right lower jaw bearing p4–m3; from Egerkingen α , (Swiss Jura); middle Eocene, MP14.

Remark. According to Hartenberger (1969: 54–55), "this lower jaw is very small; with a reduced p4 indicating a primitive character, while the long hypolophid and the metaconid and entoconid equally robusts seem more evolved. The anteroconid connected to the metaconid from



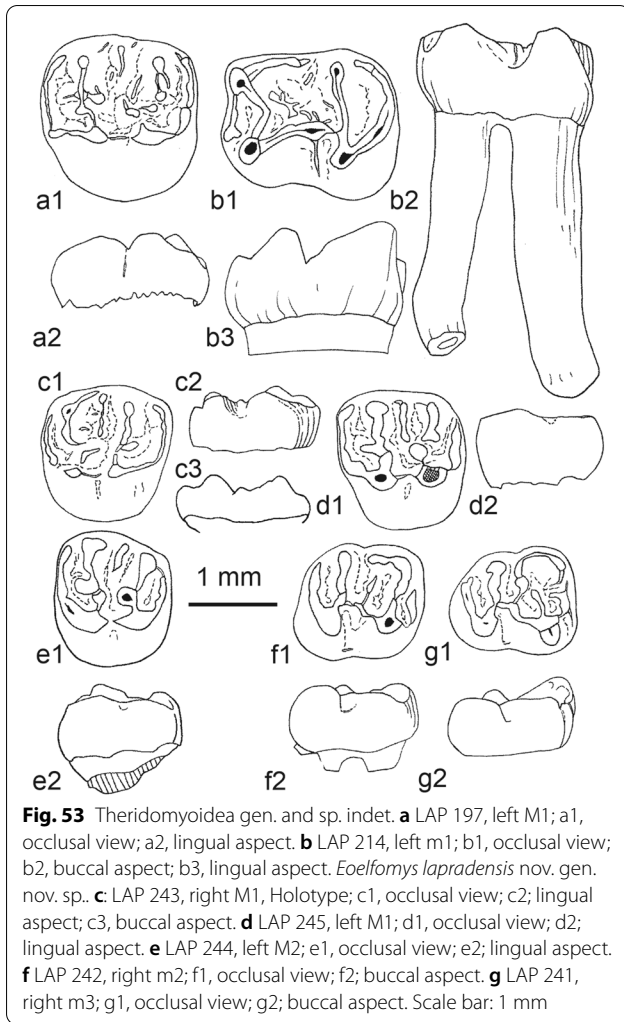
the anterolophid (“cingulum antérieur”), the deep sinusid and the rather square shape of m1–m2 evoke *Paradelomys*” (translation from French). He considered this as the most probable hypothesis given the absence of upper teeth.

Description of Ek H003. (Fig. 54).

Dentary. The body of the mandible is fragmentary, but the upper masseteric crest and the masseteric tubercle are preserved. The position of the latter is much mesial,

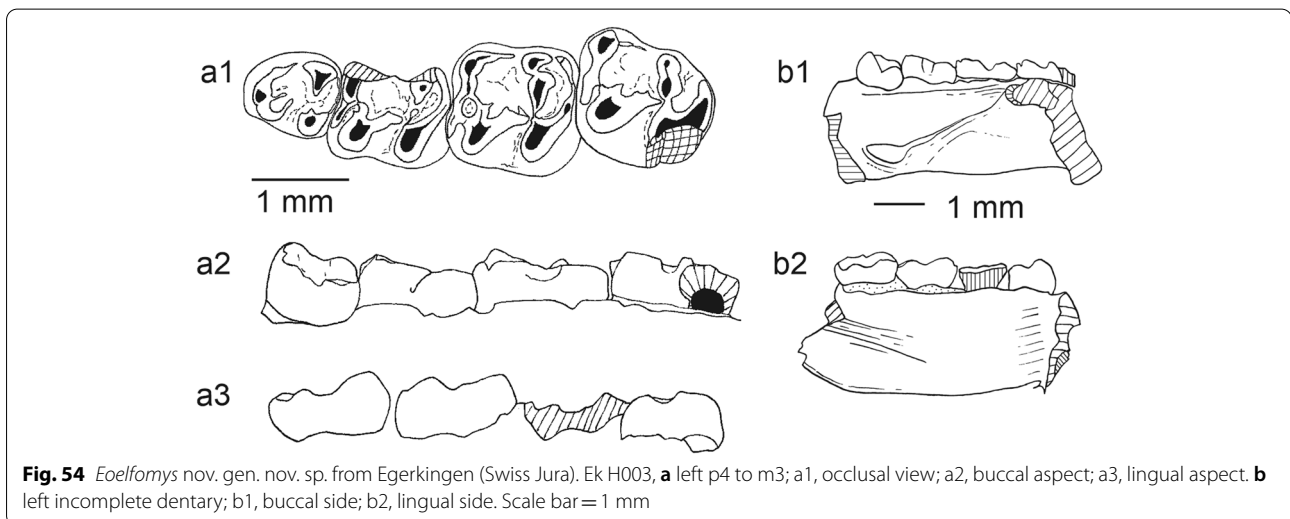
below the p4, while it is clearly more distal on *Protadelomys cartieri* and *P. lugdunensis*. The ascending ramus starts between m2 and m3, while it is more posterior (after m3) on *Protadelomys*. Comparatively, on the lower jaws of *Paradelomys crusafonti* (MP16), the masseteric tubercle is below m1, and the uplift of the ascending ramus recalls the situation observed in *Protadelomys*.

p4. This tooth is much smaller (1.14×0.94 mm) than the molars ($m1 = 1.34 \times 1.16$ mm). The metaconid is



mesial. The protoconid is leaning against the metaconid buccally, being slightly lower as can be estimated on this moderately worn tooth. The postprotocristid is relatively short. A weak mesiodistal extra-ridge descends distally from the metaconid. The postmetacristid is well marked and short. The asymmetrical sinusid is rather deep buccolingually. The ectolophid is interrupted and lies low below the wear surface; it allows a communication between the sinusid and the mesoflexid. The entoconid and hypoconid are isolated and relatively bulbous. The entolophid is reduced to a short ridge from the entoconid and the prehypocristid is minute.

m1–m2–m3. The m1 (1.34 mm) is shorter than the m2 (1.53 mm); its buccal border is damaged. The m3 is a little shorter than the m2 (1.44 mm) but this length could be underestimated, as the buccal part of the posterior lobe is missing. The anteroconid is located close to the mesial border of the protoconid from which it separates by a narrow antesisinusid. This antesisinusid separates from the anteroflexid on m2, due to the presence of an anterolophid. The latter is very low and does not reach the occlusal surface on m1 and m3. The anterolophid prolongs the anteroconid and can be distinguished from the lingual part of the metalophid I (premetacristid). This premetacristid connects, through an angle, to the buccal part of the metalophid I. This buccal metalophid I reaches the top of the protoconid. The postprotocristid is oblique and long, ending with a short spur/ridge directed buccolingually towards the basin; there is no distinct mesoconid. The ectolophid is short, interrupted at the level of the hypoconid mesial flank. The entolophid bears an entoconulid, well distinct on m2 and



m3. It is shrunken or discontinuous at the junction with the mesial end of the prehypocristid. The posterolophid is continuous and follows the post-hypocristid. The hypoconulid is not particularly swollen between the posterolophid and the post-hypocristid. The posterolophid fuses with the distal flank of the entoconid on the m1 and m2, while it is more distinct on m3 due to the reduction of the posterior lobe. On the m3, the anterolophid runs straighter towards the lingual part of the metalophulid I. Its buccal part is not as well preserved and distinct as in the other molars.

Comparisons

Elfomys catalaunicus from Frontyana 1 (MP15; Bonilla-Salomón et al., 2016) most resembles this new taxon. Many similarities were observed between the two taxa: the shape of the postprotocristid, the short mesiodistal ectolophid, the absence of mesolophid, the deep sinusid, as well as the relationships between the anterolophid, metalophulid I, metaconid, and protoconid. However, *E. catalaunicus* is slightly smaller, whereas the p4 and m3 are longer than in the new species from Egerkingen.

This species differs from *Paradelomys santjaumensis* (Bonilla-Salomón et al., 2016) a contemporaneous species of *E. catalaunicus*, even if they share a deep oblique sinusid together with a long postprotocristid. The ectolophid is oblique, aligned with the postprotocristid in *Paradelomys*, whereas it is mesiodistal in *Elfomys* and in Ek H003.

The morphology of these worn lower teeth could be compatible with that of the two weakly worn m2 and m3 from Laprade, previously referred to as *Elfomys* sp. (Hartenberger, in Sudre et al., 1990), but differs in the absence of a mesolophid.

Discussion and conclusion

An extensive phylogenetic analysis (Vianey-Liaud & Marivaux, 2021, Fig. 2–4) retrieved *Pantrogna russelli* as the sister species of the whole Theridomyoidea, among which *Hartenbergeromys* constitute a basal clade, including the two species *H. marandati* and *H. hautefeuillei*. Two groups differentiated successively, the *Masillamys* clade, then the successive offshoots of *Protadelomys*, the most basal being *?P. alsaticus*, then *?P. maximini*, then *?P. nievesae*, and followed by the clade *P. cartieri*—*P. lugdunensis*, sister group of the other Theridomyoidea, including the Pseudosciuridae (Fig. 2). This analysis established the paraphyly of the genus, the genus name being kept for *P. cartieri* and *P. lugdunensis*. Here, we revised this material in order to better characterize the extent of the morphological and size variability in all *Protadelomys* and *?Protadelomys* species as well as to re-evaluate the theridomyoid diversity in a number of middle Eocene sites.

Variability in the *Protadelomys* and *?Protadelomys* species

We revisited the intraspecific variation among the species of *Protadelomys* and *?Protadelomys* and proposed that the morphological and size changes are not as linear as previously considered (Escarguel, 1997, 1998; Hartenberger, 1969). We analyzed and described the high variability of the original material of *?P. alsaticus*, especially with regard to the morphological characters of the buccal wall of the lower teeth. Among this material, three morphotypes can be recognized based on their size and morphology: *?Protadelomys* cf. *alsaticus* morphotype 1 with more bulbous cusps, the smaller *?Protadelomys* cf. *alsaticus* morphotype 2, and the larger *?Protadelomys* cf. *alsaticus* morphotype 3 with a size similar to that of *Masillamys parvus*. The comparison of typical *?P. alsaticus* with the specimens of *?P. cf. alsaticus* from Cuzal shows a number of similarities. The weak morphological variation of the lower molars from Cuzal is also striking, when compared to that observed in *?P. alsaticus* specimens from Bouxwiller. Among the differences observed between specimens of *?P. alsaticus* from the two localities, some could indicate more derived features in Cuzal specimens than in typical *?P. alsaticus*, such as the larger teeth, the hypocone generally stronger, the conules less bulged, the well-defined transverse lophs on upper teeth and a well-defined metalophulid I on lower teeth. The ratio Lp4/Lm1 (1.94) is stronger than that of *?P. alsaticus* and similar to that of *P. lugdunensis*, but only two p4 and seven m1 were identified in the sample. In addition, the evolutionary significance of the absence of the protoconid on the few p4 and dp4 from Cuzal remains unclear, as it is present on p4 and dp4 of *?P. nievesae*, *?P. alsaticus*, and *P. cartieri* and weak or absent on p4 and dp4 of *?P. maximini* and *P. lugdunensis*. The morphological variation in *?P. maximini* enabled us to define two morphotypes in addition to the typical *?P. maximini*, the morphotype 1 differs from typical *maximini* in the more bulbous cups pattern, and the morphotype 2 is quite smaller.

In contrast, more discrete morphological differences could be described within the genus *Protadelomys*, and justify the recognition of the two species *P. cartieri* Hartenberger and *P. lugdunensis* Hartenberger. We show that these two species can be in fact contemporaneous, as they were found in association in the three Lutetian localities of Egerkingen, Lissieu and Laprade.

New named taxa and evolution of rodent diversity during the middle Eocene

In this paper, we also described and named two new genera. The first one, *Homætreposciurus egerkingensis* from Egerkingen, was previously included in the

Pseudosciuridae *Treposciurus*. However, we consider its morphology to clearly depart from that of the latter in displaying a combination of derived features, such as the p4 longer than m1 and the complete metalophid I, with more primitive features such as the low crowns and concave lower teeth with flat floor bearing numerous granules, and lacking complete high entolophid. The other new genus and species, *Eoelfomys lapradensis*, was described from Laprade deposits where it was found associated with *P. lugdunensis*, *P. cartieri* and a possible *Theridomyoidea* nov. gen. nov. sp.. A specimen from Egerkingen, Ek H003, is also likely attributable to *Eoelfomys*, but its poor state of preservation prevents any definite specific attribution.

The diversity in rodent species found in association with *Protadelomys* and *?Protadelomys* is listed in Table 9. The rodent diversity of Lutetian species (MP11 to M P14) is lower than that found in older Eocene localities (Ypresian: MP8-9 and MP10) and much lower than in the early Bartonian localities (MP 15). This decrease in diversity could be correlated to climatic changes, this period corresponding to a long decrease in temperature between the Ypresian (EECO) and lower Bartonian (MECO) climatic optima (Vandenberghé et al., 2012). On the contrary, from MP12 to MP15, the time extension of the *?Protadelomys* and *Protadelomys* species and morphotypes, the diversity seems to decrease.

Differential features between *Protadelomys*, *Masillamys*, *Pantrogna*, and *Hartenbergeromys*

Our new descriptions of species previously referred to *Protadelomys* enable us to discuss previously proposed differential features between the genus *Protadelomys* and three other Eocene genera: *Masillamys*, *Pantrogna*, and *Hartenbergeromys*. In order to identify shared character states between these genera and *Protadelomys*, Escarguel (1999: Table 5) provided a list of 16 characters (numbered below in italics) either present, absent or intermediate in these genera, which we discuss hereafter based on our reevaluation of the morphological variation observed in *Protadelomys*.

1- *Hystricomorphous infraorbital foramen*. For Escarguel, only *Protadelomys* is hystricomorphous, the size of the i.o.f. of *Hartenbergeromys* being intermediate in size between protrogomorphous (small) and hystricomorphous (large). We recently showed that a large i.o.f. is recognized in the four genera (Vianey-Liaud, Marivaux, Lehman 2019; Vianey-Liaud & Marivaux, 2021).

2- *P3 absent*. The third premolar is present in all genera (Vianey-Liaud & Marivaux, 2021) and at least in one species of *Protadelomys*, i.e., *P. lugdunensis* from Laprade. Moreover, compared to the P3/D3 of *Masillamys* and *Hartenbergeromys*, the P3 in *Protadelomys* is quite small.

Table 9 Lists of rodents' species from middle and upper Ypresian (MP8–9–10), Lutetian (MP 13–14), and lower Bartonian (MP15) European fossiliferous localities

Mutigny MP 8–9	Saint–Maximin (MP /13 ?)
<i>Meldimyslouisi</i>	? <i>Protadelomys maximini</i> + 2 morphotypes
<i>Euromysthaleri</i>	? <i>Sparnacomys</i> indet
<i>Pseudoparamys teilhardi</i>	Bouxwiller (MP 13)
<i>Sparnacomys chandoni</i>	<i>Ailuravus picteti</i>
<i>Pantrogna russelli</i>	<i>Plesiarctomys hartenbergeri</i>
<i>Euromys woodi</i>	? <i>Protadelomys alsaticus</i> + 3 morphotypes
Avenay (MP 8–9)	<i>Eogiliravus hammeli</i>
<i>Meldimys louisi</i>	Egerkingen (MP 14)
<i>Euromys thaleri</i>	<i>Ailuravus picteti</i>
<i>Pseudoparamys teilhardi</i>	<i>Plesiarctomys spectabilis</i>
<i>Sparnacomys chandoni</i>	<i>Protadelomys cartieri</i>
<i>Pantrogna russelli</i>	<i>Protadelomys lugdunensis</i>
<i>Euromys woodi</i>	<i>Homœotreposciurus egerkingensis</i>
Saint–Agnan (MP 10)	<i>Eoelfomys</i> nov. sp.
<i>Ailuravus michauxi</i>	Lissieu (MP 14)
<i>Ailuravus inexpectatus</i>	<i>Protadelomys lugdunensis</i>
<i>Meldimys louisi</i>	<i>Protadelomys cartieri</i>
<i>Pseudoparamys teilhardi</i>	Laprade (MP 14)
<i>Plesiarctomys savagei</i>	<i>Protadelomys lugdunensis</i>
<i>Pantrogna russelli</i>	<i>Protadelomys cartieri</i>
<i>Hartenbergeromys hautefeuillei</i>	<i>Theridomyoidea</i> gen. and sp. indet. 1
<i>Masillamys mattaueri</i>	<i>Eoelfomys lapradensis</i> nov. gen nov. sp
<i>Euromys woodi</i>	Chery-Chartreuve (MP 15)
Messel (MP 11)	<i>Glamys</i> aff. <i>robiacensis</i>
<i>Ailuravus macrurus</i>	<i>Plesiarctomys huerzeleri</i>
<i>Masillamys parvus</i>	<i>Suevosciurus</i> sp.
<i>Masillamys krugi</i>	<i>Treposciurus</i> sp
<i>Masillamys beegeri</i>	<i>Auroremys subita</i>
<i>Eogiliravus wildi</i>	<i>Protadelomys</i> sp
Casa Ramon (MP 12 ?)	<i>Tardenomys chartreuvensis</i>
<i>Plesiarctomys</i> cf. <i>hartenbergeri</i>	<i>Elfomys engesseri</i>
? <i>Protadelomys nievesae</i>	<i>Pseudoltinomys</i> sp
<i>Eogiliravus moltzeri</i>	<i>Remys major</i> nov. sp
	<i>Estellomys</i> sp.

3- *P4 with large paracone, more buccal than the metacone*. This situation occurs variably in *Masillamys*, *Hartenbergeromys* or in *Protadelomys*; the paracone is often slightly more buccal than the metacone in *Pantrogna* (Vianey-Liaud et. al. 2019; Vianey-Liaud & Marivaux, 2021).

Upper molars:

4- *Paraconule extending mesially from the protoloph*. It is the case in all four genera (Vianey-Liaud & Marivaux, 2021).

5- *Connection between the metaconule and the hypocone.* This distal connection of the metaconule–buccal metaloph with the hypocone is always present in Pseudosciuridae, Theridomyidae, and *Protadelomys*; it is more mesial and often indistinct from the prehypocrista in *?Protadelomys*. The connection is variable, from the postprotocrista to the endoloph or the hypocone in *Masillamys*, more mesial (protocone or post-hypocrista) in *Hartenbergeromys* and *Pantrogna* (Vianey-Liaud et al. 2019; Vianey-Liaud & Marivaux, 2021).

6- *Sketch of a mesoloph.* This is the case in all species of the four genera, including *Pantrogna russelli* (contra Escarguel, 1999: Table 5) (Vianey-Liaud et al. 2019; Vianey-Liaud & Marivaux, 2021).

7- *Increase of the hypocone and “centralization” of the sinus.* These features (enlargement of the hypocone to reach the size of the protocone; consequently, the sinus defined between these two similarly robust cusps occupies a central position on the lingual flank) are observed at least on the M1 of *Masillamys* and *Protadelomys*, and are intermediate in *?Protadelomys*, in which the hypocone is generally smaller than the protocone on M1 and M2. However, this sinus is never deep linguobuccally in these theridomorphs, which have an endoloph.

Lower molars:

8- *Anteroconid present on lower molars.* The anteroconid is variably distinct from the anterolophid in *Protadelomys* and *?Protadelomys*. It is indistinct from the anterolophid in *Masillamys*, *Pantrogna*, and *Hartenbergeromys* (Vianey-Liaud et al. 2019; Vianey-Liaud & Marivaux, 2021).

9- *Developed postprotocristid.* The postprotocristid is present and strong not only in *Hartenbergeromys* and *Protadelomys*, but also in *Masillamys* and *Pantrogna*. It is the case for all the genera included in the Theridomorpha and corresponds to a synapomorphy of the group (e.g., Vianey-Liaud & Marivaux, 2021).

10- *Sketch of a mesolophid.* Present not only in *Hartenbergeromys* and *Protadelomys* but also in *Pantrogna* and *Masillamys*.

11- *Mesoconid merged in the ectolophid.* The mesoconid is generally merged in the ectolophid in the four genera.

12- *Hypolophid (=entolophid) complete or nearly complete.* This is the case in *Hartenbergeromys*, *Masillamys*, and *Protadelomys*.

13- *Strong break between the hypoconulid and the entoconid.* This break is variably observed in the four genera.

14- *Connection mesoconid–hypoconid reduced in Protadelomys and Hartenbergeomys.* If this feature involves the height of the distal ectolophid, we observed that it could be variably interrupted in the four genera.

15- *Hypoconid stretched obliquely, that produces a “reverse” sinus.* In these genera, the shape of the sinus results not only from a weak stretching of the hypoconid and prehypocristid, but also from the strong lengthening of the mesiobuccal to distolingual oblique postprotocristid. The latter occurs in some species of *Masillamys* (*M. krugi*, *M. mattaueri*), as well as in *Hartenbergeromys*, *Pantrogna*, *Protadelomys*, and *?Protadelomys*.

16- *Hypoconulid merged in the posterior cingulum.* The hypoconulid is more or less merged in the “posterior cingulum” in the four genera, possibly slightly more in *Protadelomys*.

Phyletic relationships and morphological changes

Based on the characters discussed above, Escarguel (1999: 231–232) proposed phyletic relationships between *Pantrogna russelli*, *Hartenbergeromys marandati*, *H. hautefeuillei* and *Masillamys* on one side, and between *Pantrogna russelli*, the two species of *Hartenbergeromys* and the “primitive” Theridomyidae (*Protadelomys*) on the other side. Both clades convergently evolve transverses lophs and lophids and display a larger hypocone. Escarguel (1998) and Hartenberger (1969, 1973, 1990) considered that the four *Protadelomys* species (*maximini*, *alsaticus*, *cartieri*, and *lugdunensis*) represent grades of an evolutionary lineage (= a chronospecies sensu Simpson, 1951) showing the following evolutionary trends: the increase in size of P4, a more transversely oriented metaloph, the development and increase of the hypocone together with the deepening of the lingual sinus, a lengthening of the mesoloph, or a relative elongation of lower p4 (Hartenberger, 1969: 55; Escarguel, 1997: 66; 1998: 380). According to Escarguel (1998: 380), these trends are also deduced from the biochronological anteriority of Bouxwiller compared to the different fissures from Egerkingen, anteriority that was previously admitted by several authors (Hartenberger, 1969; Jaeger, 1972; Biochro'M, 1997). Escarguel (1998: 379) also considered *?P. nievesae* to represent the most “primitive” species, even if belonging to another lineage endemic from Spain and distinct from the *Protadelomys maximini–alsaticus–cartieri–lugdunensis* lineage.

We discuss hereafter the morphological features supposed to characterize these morphological changes (Escarguel, 1998):

1- *Increase in size of P4.* The ratio between the mean lengths of P4/M1 of *P. lugdunensis* is 0.87 in Lissieu, and 0.86 in Laprade; it is 0.88 for *P. cartieri* from Egerkingen, 0.90 and 0.94 for *?P. alsaticus* from Bouxwiller and Cuzal, respectively; *?P. maximini* shows the lowest ratio of 0.81; the ratio in *?P. nievesae* is 0.86 like that of *P. lugdunensis*

from Laprade. Consequently, the ratio between P4 and M1 lengths appears fairly similar between the supposed successive taxa *?P. maximini*, *?P. alsaticus*, *P. cartieri*, and *P. lugdunensis*. Our dataset does not attest a relative size increase of P4 in the supposed lineage, bearing in mind the low sample sizes.

2- *Linguobuccal deepening of the lingual sinus and increase in size of the lingual cusps of upper molars.* This sinus is reduced to absent in *?P. nievesae*, *?P. maximini*, and *?P. alsaticus*. It is usually present in these taxa but weak, narrow, shallow, and never significantly deepened linguobuccally. On molars, size increase mainly involves the hypocone, which is clearly smaller than the protocone in *?P. nievesae* and in *?P. maximini* and to a lesser extent in *?P. alsaticus*. In contrast, the two cusps are almost equal in size in *P. cartieri* and *P. lugdunensis*. The endoloph is present in all these species, at the same lingual level as the apex of the protocone and hypocone; it is variably long, high and thick, and always separates the lingual slope from the mesoflexus. A short sinus appears with wear on the occlusal surface when the endoloph, the postprotocrista, and prehypocrista are relatively short, as well as when the protocone and hypocone lingual flanks are bulged. A “true” sinus is visible only in younger theriodomyids, in which the postprotocrista and the prehypocrista lengthen obliquely and buccally towards the mesoflexus or when a mure replaces the endoloph (e.g., Comte et al. 2012).

3- *Increase in size of p4.* The p4/m1 average lengths ratio of *P. cartieri* is 0.93, those of *P. lugdunensis* from Lissieu and Laprade are very similar (around 0.94); the ratio in *?P. alsaticus* from Bouxwiller is lower (0.87); the ratio of *?P. maximini* is 0.86, close to that of the species from Bouxwiller, that of *?P. nievesae* is higher (0.93). The highest ratios are observed in the oldest species *?P. nievesae* and the two youngest *P. cartieri* and *P. lugdunensis*. The only increase in size involves the species of *?Protadelomys* from St-Maximin–Bouxwiller and the *Protadelomys* from Egerkingen–Lissieu. As for the P4, we consider that the sample sizes remain too low to confirm any clear tendency in size increase.

4- *Increase in size of the anteroconid and development of the lophodonty on lower molars.* The anteroconid is present and never strongly bulged in all species. A short anterocingulid can develop buccally from the anteroconid, especially in *P. lugdunensis*. The development of the lophodonty on lower molars evolved in concert with the development of a continuous metalophulid I and entolophid. A better individualization and simplification of the lingual metalophulid I, coupled with a better individualization of its junction with the buccal metalophulid I, is observable

in the two *Protadelomys* species when compared to *?Protadelomys* species. The entolophid is complete or nearly complete (i.e., with interruptions) in the five species; it is particularly incomplete and low in *?P. maximini*.

Peláez-Campomanes (1993, 1995) proposed additional features to characterize the morphological changes along the inferred evolutionary lineage (*P. nievesae*–*P. alsaticus*–*P. cartieri*–*P. lugdunensis*), *P. maximini* being unknown at this time.

1—*Acquisition of a metalophule I on upper M1–2.* We noted that low elements of metalophule I can be identified variably in all species.

2—*Relative increase of the anterior lobe of lower p4.* The anteroconid of p4 is always absent in *?P. nievesae* or *?P. maximini*, and exceptionally present in *?P. alsaticus*, *P. cartieri* or *?P. lugdunensis*. When present, the anteroconid does not significantly increase the length of the p4. Similarly, the occurrence and size of the protoconid vary; it is absent in *?P. maximini*, only rare in *P. lugdunensis*, variably present in *?P. nievesae* and *P. cartieri*, and frequent in *?P. alsaticus*. However, we noted a variation of the lengths defined from the mesial edge of the tooth up to the entolophid relative to the length defined from the entolophid up to the distal edge of the p4. This ratio is shortest in *?P. alsaticus*, *?P. maximini* and *?P. nievesae*, and longest in *P. cartieri* and *?P. lugdunensis*. The latter species and specimens of *Masillamys* from Messel (nov. gen. nov. sp.: Fig. 5a, 6b) exhibit very similar ratio values.

This work has confirmed the need for the use of a precise and unified nomenclature to objectively analyze and describe dental morphological variation of ancient theriodomorphs. The terminology proposed here, also applicable to all Eocene rodents, enabled us to discuss the long assumed phylogenetic relationships between the different species grouped in the genera *Protadelomys*, notably with regard to *Masillamys* species. Our morphological comparisons demonstrate the co-occurrence of the two species of the clade *P. cartieri*/*P. lugdunensis* in their type localities. Therefore, these species can hardly be considered as successive evolutionary grades of a single evolutionary lineage, as previously conceived (Hartenberger, 1969). This co-occurrence, and the possible occurrence of several morphotypes or taxa in the paraphyletic assemblage of *?Protadelomys*, also question their use as biochronological markers (Escarguel, 1997; tab. 1). If more than a single evolutionary lineage possibly exist, *?P. nievesae* represents the last diverging branch of the paraphyletic genus *?Protadelomys*, sister species of the *Protadelomys* clade *P. cartieri*/*P. lugdunensis*, and not the earliest offshoot, as previously proposed by Escarguel (1997).

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13358-022-00245-3>.

Additional file 1: Supdata S1. Listing of rodents from Egerkingen: Table row with blue background: holotype of *Protadelomys cartieri*; table rows with yellow background: *Homotropeosciurus egerkingensis* n.g.n.s.; table rows with light green background: *Protadelomys lugdunensis*; table rows with light green background: table rows with salmon pink color background: *Eoelfomys* nov. gen.sp. indet. (measurements ; mm).

Additional file 2: Supdata S2. Listing and measurements of the Material of *Protadelomys* from Lissieu. (LIS = Collections of the Lyon University; L: collections of the Museum of Lyon) (measurements ; mm).

Additional file 3: Supdata S3. Listing and measurements of Material of rodents from Laprade. (LAP = Collections of the Montpellier University) (measurements ; mm).

Additional file 4: Supdata S4. Listing and measurements of ?*Protadelomys* material from Bouxwiller (coll. UM) ?*Protadelomys alsaticus* and ?*Protadelomys* cf. *alsaticus* morphs. 1, 2, 3. (measurements ; mm).

Additional file 5: Supdata S5. Listing and measurements of Material from Cuzal (Lot, France). (CUZ) Collections of the Montpellier University) (measurements ; mm).

Additional file 6: Supdata S6. Listing and measurements of Material from Saint Maximin (Gard, France). (SMX1 = "Grand chantier, main sampling", SMX 2 = Grand chantier, déblais en surface; SMX3 = Grand chantier, hall d'entrée, avéole) Collections of the Montpellier University) (measurements ; mm).

Additional file 7: Supdata S7. Listing and measurements of Material of ? *Protadelomys* from Casa Ramon (Huesca, Spain). (RP0xx) Museo de Ciencias Naturales, Madrid. (measurements ; mm).

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Authors' contributions

Concepts and approaches were developed by M V-L. M V-L described and measured the material, as well as made all the illustrations. Data analyses were performed by LH and M V-L. The manuscript was written by M V-L, and edited by L.H. Both authors read, discussed and approved the entire text, prior to submission. Both authors, M V-L and LH declare no competing interests. This work was carried out within the "Institut des Sciences de l'Évolution de Montpellier", and M V-L got a travel funding from the "ISEM" to visit the collections of the Naturhistorische Museum, Basel (NMHB). Both authors read and approved the final manuscript.

Data availability

The materials are available in the ISEM and NMHB collections and the data in the additional data.

Declarations

Ethics approval and consent to participate

Not applicable.

Competing interests

The authors declare that they have no competing interests

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