A diverse rodent fauna from the middle Bartonian (Eocene) of Les Alleveys, Switzerland: snapshot of the early theridomyid radiation

JERRY J. HOOKER[1],[*] & MARC WEIDMANN[2]

ABSTRACT

A fossiliferous fissure filling at Les Alleveys, Mormont (Canton de Vaud, Switzerland), sampled in 1986 and representing part of the same fissure system as that excavated by Chavannes and Morlot in 1852, contains an Eocene mammal fauna of 27 species-group taxa, dominated by micromammals. Unlike the 1852 collection, thanks to screenwashing techniques, there is an abundance of rodents, especially theridomyids, which provide new information on the early radiation of the family. The homogeneity of the new assemblage suggests that the Les Alleveys fauna is entirely Bartonian in age and not as previously thought mixed with Priabonian elements. Bartonian faunas rich in a diversity of micromammals are relatively uncommon in Europe outside the Quercy region of France and this is the first such fauna from Mormont and from Switzerland. The rodents are here treated systematically and a new species of *Elfomys*, *E. engesseri* sp. nov. is described. A few teeth of an undescribed species tentatively referred to '*Protadelomys*' provide an archaic element, whereas a single milk premolar of *Patriotheridomys*? suggests a considerable range for the genus prior to the middle Priabonian. The Les Alleveys theridomyids, together with a range of other early family members are analysed cladistically. The analysis confirms both the distinctness of the subfamily Remyinae and that the genus *Estellomys* is a primitive theridomyine; it shows *Paradelomys* to be a primitive member of the Columbomyinae, but finds no dental synapomorphies to support the Issiodoromyinae as represented by *Elfomys* and *Pseudoltinomys*.

RESUME

Aux Alleveys (Mormont, Canton de Vaud, Suisse), une fissure karstique remplie de sédiment sidérolithique fossilifère, échantillonnée en 1986, a livré une faune éocène comprenant 27 taxons du niveau espèce, surtout des micromammifères. Cette fissure appartient au même système fissural karstique que celui qui fut exploité au même endroit, en 1852, par Chavannes et Morlot. Grâce aux techniques de tamisage, qui n'avaient pas été mises en oeuvre en 1852, la nouvelle récolte comprend beaucoup de rongeurs, surtout des théridomyidés, qui apportent des informations inédites sur la radiation précoce de la famille. L'homogénéité de ce nouvel assemblage suggère que la faune des Alleveys est d'âge uniquement bartonien et qu'elle n'est pas mélangée avec des éléments d'âge priabonien, comme cela avait été supposé auparavant. Les faunes bartoniennes comprenant une riche diversité de micromammifères sont relativement peu fréquentes en Europe, en dehors de la région du Quercy (France). Et c'est la première de cet âge trouvée au Mormont ou ailleurs en Suisse. Les rongeurs sont étudiés systématiquement et une nouvelle espèce d'*Elfomys*, *E. engesseri* sp. nov., est décrite. Quelques dents appartenant à une espèce non décrite et attribuées avec doute à '*Protadelomys*' représentent un élément archaïque, alors qu'une unique prémolaire de lait de *Patriotheridomys*? suggère que ce dernier genre possède une extension stratigraphique considérable avant le Priabonien moyen. Les théridomyidés des Alleveys, ainsi que d'autres membres anciens de la famille, font l'objet d'une analyse cladistique qui confirme le caractère nettement différent de la sous-famille des Remyinae et que le genre *Estellomys* est un Theridomyinae primitif; cette analyse montre que *Paradelomys* est un membre primitif des Columbomyinae, mais ne révèle aucune synapomorphie dentaire qui supporte les Issiodoromyinae, tels que représentés par *Elfomys* et *Pseudoltinomys*.

Introduction

The long-abandoned quarry of Les Alleveys was used in the 19th Century to exploit the Urgonian limestones of the Jura. It is situated within the commune of La Sarraz, coordinates 528'260/168'520, at the western extremity of Mormont (Figs. 1a–c). In 1852, S. Chavannes and A. Morlot discovered and collected from a horizontal karstic fissure in the quarry (Chavannes 1852; herein Fig. 1d), which contained fossiliferous Sidérolithique matrix, consisting of red clay alternating with sandy layers with quartz and ferruginous pisoliths. It was from these coarse layers that almost all the fossils were collected. They were deposited in the Musée Géologique de Lausanne (MGL). This fauna, referred to as "Les Alleveys 1852", was revised by Hooker & Weidmann (2000: passim and faunal list in Table 1).

[1] Department of Palaeontology, Natural History Museum, Cromwell Road, London, SW7 5BD, UK.
[2] Sentier du Molard 3, 1805 Jongny, Switzerland.
[*] Corresponding author: Jerry J. Hooker. E-mail: j.hooker@nhm.ac.uk

Fig. 1. a–c) Location maps of the Les Alleveys site (Mormont, Canton de Vaud, Switzerland). d) The fissure of Les Alleveys (1222-6, 1852), copied from a water-colour sketch without a scale made by S. Chavannes (1852: 19); in his text, Chavannes indicated that the fissure was 20–30 feet long (ca. 6–9 m). e) The fissure of Les Alleveys (1222-6, 1986); see Hooker & Weidmann (2000) for details. (d) and (e) are reproduced with permission from Hooker & Weidmann (2000: figs 9,11).

In 1986, in what we judge to be a continuation of the 1852 fissure, close to the original site, one of us (MW) extracted nearly 500 kg of sediment from the fissure (Fig. 1e), emptying it completely. After washing and sieving, this material yielded a total of about 700 teeth and innumerable bone fragments of mammals, rare reptile teeth and numerous teeth of marine fish (pycnodont bony fish and odontaspid sharks), the last reworked from the Cretaceous limestones. Of the mammal teeth, 115 are of identifiable rodents, treated here. It is this fauna, referred to here as "Les Alleveys 1986", the study of whose rodents forms the subject matter of this paper. The specimens are conserved at the MGL and a selection of casts has been deposited in the Department of Palaeontology, Natural History Museum, London (BMNH). The locality of Les Alleveys bears the number 1222-6 in the numbering system of the "Cadastre des mammifères fossiles de la Suisse" deposited at the Naturhistorisches Museum Basel (NMB).

Table 1. Faunal list of mammals from Les Alleveys 1986 (Bartonian, Canton de Vaud, Switzerland). * Indicates taxa also in the 1852 collection.

Order 'Didelphimorphia'
  Family Herpetotheriidae
    *Amphiperatherium fontense**
    Amphiperatherium cf. *minutum*
Order Leptictida?
  Family Pseudorhynchocyonidae
    Pseudorhynchocyonidae undet.
Order Rodentia
  Family Pseudosciuridae
    *Sciuroides siderolithicus**
    Suevosciurus? sp.
  Family Theridomyidae
    '*Protadelomys*'? sp.
    Remys sp.
    Paradelomys sp.
    Elfomys engesseri sp. nov.*
    Pseudoltinomys aff. *crebrum*
    Estellomys ibericus
    Patriotheridomys? sp.
    Theridomyinae indet.
Order Lipotyphla
  Family Amphilemuridae
    Gesneropithex sp.
Order Chiroptera
  Family Hipposideridae
    *Pseudorhinolophus morloti**
  Family Emballonuridae
    Vespertiliavus sp.
  Family Vespertilionidae
    *Stehlinia minor**
  Family Molossidae
    Cuvierimops? sp.
    Archonta – order undifferentiated
  Family Nyctitheriidae
    Nyctitheriidae indet.
Order Primates
  Family Omomyidae
    Pseudoloris parvulus
    *Necrolemur antiquus**?
Order Carnivora or Creodonta
    indet.
Order Artiodactyla
  Family Choeropotamidae
    Tapirulus sp.
  Family Mixtotheriidae
    Mixtotherium lavergnense
  Family Xiphodontidae
    Haplomeryx sp.
    Dichodon sp.*
  Family Amphimerycidae
    Pseudamphimeryx sp.*

Table 2. Statistics of length and width measurements in millimetres of cheek teeth of *Paradelomys* sp. from Les Alleveys 1986. N = number; OR = observed range; SD = standard deviation; V = coefficient of variation.

Tooth	N	OR	Length Mean	SD	V	N	OR	Width Mean	SD	V
P^4	4	1.43–1.55	1.51			4	1.31–1.55	1.45		
$M^{1/2}$	6	1.63–1.81	1.75	0.0810966	4.63	8	1.76–1.98	1.84	0.0769043	4.18
M^3	3	1.63–1.78	1.71			3	1.63–1.73	1.69		
P_4	2	1.44–1.66	1.55			2	1.09–1.28	1.19		
$M_{1/2}$	7	1.67–1.85	1.73	0.0714142	4.13	8	1.42–1.64	1.50	0.0753562	5.02
M_3	1		2.14			2	1.65–1.67	1.66		

Because screenwashing was applied to the 1986 collection of specimens, unlike that of 1852, the number of small teeth and the diversity of small mammal species are much greater. The smaller number of larger species recovered than in 1852 (Hooker & Weidmann 2000: table 2) suggests that a larger quantity of sediment was surveyed by Chavannes and Morlot. The fauna from 1986 numbers 27 species-group taxa (Table 1). The occurrence of *Mixtotherium lavergnense* and *Sciuroides siderolithicus* indicates a Bartonian age (partly equivalent to the Robiacian European Land Mammal Age). The occurrence of *S. siderolithicus* and of *Elfomys engesseri* sp. nov. (see below) otherwise known only from Eclépens-Gare (main fauna) is strong evidence for contemporaneity of these fissures. The presence of both *Leptolophus stehlini* and *Palaeotherium castrense castrense* at Eclépens A (with a fauna nearly identical to that of Eclépens-Gare), representing the overlap part of the range of each, allows these fissures to be dated as middle Bartonian, contemporaneous with French sites high in the Molasse de Saïx (formerly Sables du Castrais) such as Lautrec (Tarn). Lautrec and Eclépens-Gare also uniquely share the occurrence of *Palaeotherium lautricense*. Thus, Les Alleveys, Eclépens A and Eclépens-Gare (main fauna) are older than such sites as Robiac and Paris Basin sites in the Calcaire de Saint-Ouen (Paris, Grisolles) where *P. castrense robiacense* occurs; they are also younger than such sites as Viviers (Tarn) from lower in the upper part of the Molasse de Saïx (Hooker & Weidmann 2000). Figure 2 shows the calibration of the localities to the GPTS via other biostratigraphies.

Charophytes in the Calcaires et Marnes de Langlade at Langlade, situated in the upper part of the Molasse de Saïx, therefore approximately contemporaneous with the Lautrec and Viviers localities, indicate the zone of *Chara friteli* (Riveline 1984: 366–367). The top of the underlying zone, that of *Raskyella peckii*, was originally defined by the last appearance of *R. peckii* (Riveline 1986), until this species was found to range upward to overlap part of the *R. vadaszi* zone (Martín-Closas et al. 1999), which succeeds the *C. friteli* zone. The *C. friteli* zone was originally an interval zone defined at the base by the last appearance of *R. peckii* and at the top by the first appearance of *R. vadaszi* (Riveline 1986). The top of the *R. peckii* zone was redefined by Martín-Closas et al. (1999) as the first appearance of *C. friteli*, by implication making the *C. friteli* zone begin slightly lower down. Nevertheless, they correlated the *C. friteli* zone quite precisely with part of the marine calcareous nannoplankton zone NP17 (Martín-Closas et al. 1999: fig. 8). Near coincidence of the *C. friteli* zone also with planktonic foraminiferal zone P14 of Blow (1979) (Martín-Closas et al. 1999: fig. 8), not P14 of Blow (1969) (Anadón et al. 1983), shifts to a slightly younger position the Bartonian mammal sites discussed by Hooker & Weidmann (2000: fig. 78). Although the *R. vadaszi* Zone is well calibrated to the late Bartonian in France (Martín-Closas et al. 1999), its association with early NP17 and SBZ17 at Pontils (Anadón et al. 1983) suggests diachronism between France and Iberia. This would
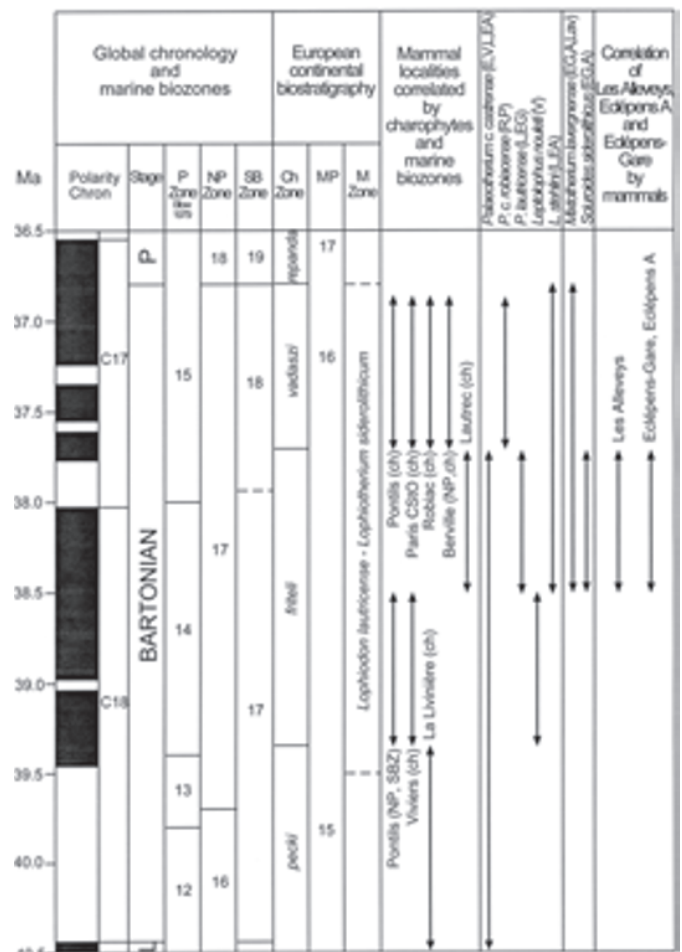

Fig. 2. Correlation chart of selected European Bartonian mammal localities with the GPTS via charophyte and marine biozones. Double arrowed ranges of localities and mammal taxa approximate error bars. Individual localities are correlated by means of particular biozones (labelled). Ranges in the left-hand taxon column are estimated via the relevant locality ranges. Ranges in the right-hand taxon column refer to key Eclépens-Gare/Eclépens A taxa shared with Les Alleveys and correlated by means of other taxa shared with Lautrec, giving the range for the Eclépens-Gare and Eclépens A localities in the last column. Les Alleveys is judged synchronous with these on the basis of the two taxa shared with Eclépens-Gare (see Hooker & Weidmann 2000 for more details). The timescale follows Gradstein et al. (2004), but the start of the Priabonian is equated with the base of NP18, following Hardenbol et al. (1998). Biostratigraphical abbreviations: ch, charophyte zone (Martín-Closas et al. 1999); CStO, Calcaire de St Ouen; MP, Mammalian Paleogene Reference Level (Brunet et al. 1987); M, mammal zone (Hooker 1986); NP, Paleogene calcareous nannoplankton zone; P, planktonic foraminiferal zone (Blow 1979); SBZ, shallow benthic zone (Serra-Kiel et al. 1998). Locality abbreviations: A, Les Alleveys; E, Egerkingen; EA, Eclépens A; EG, Eclépens-Gare; L, Lautrec; Lav, Lavergne; P, Paris, Calcaire de St Ouen; R, Robiac; V, Viviers. Stage abbreviations: L, Lutetian; P, Priabonian.

be congruent with the similarity of some of the Pontils mammals to those of La Livinière (Fig. 2).

The 1852 collection suggested mixed ages for the fauna, nearly all the taxa indicating Bartonian and only one, a semi-hypsodont theridomyine (*Isoptychus*), indicating late Priabon-
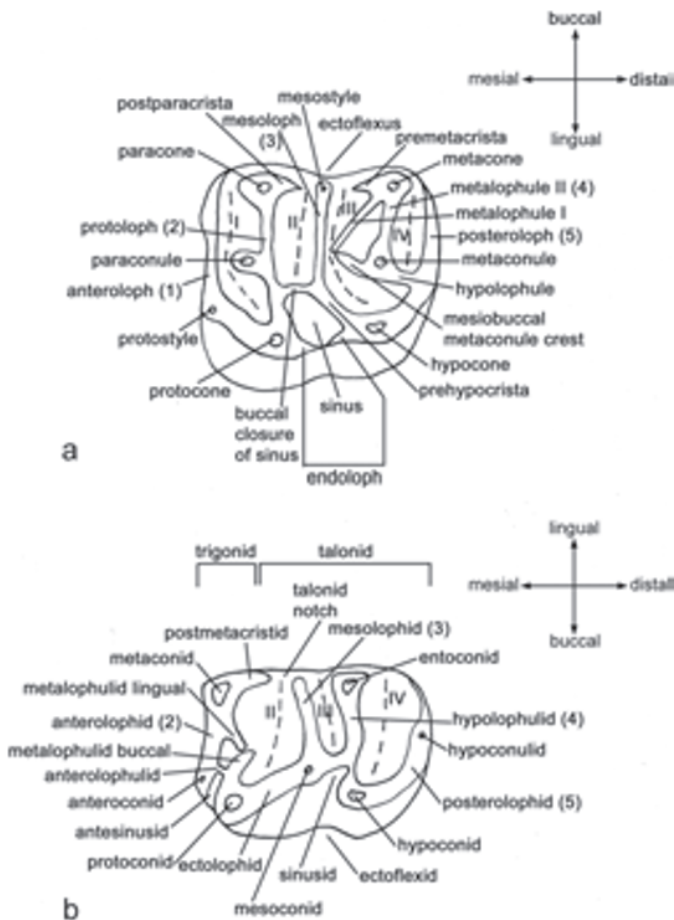
Fig. 3. Dental terminology diagram for primitive Theridomyidae from various sources, mainly Hartenberger (1973), Hooker (1986). a) Left $M^{1/2}$. b) Left $M_{1/2}$. Derived theridomyids have more hypsodont, more lophodont cheek teeth in which transverse crests (anticlines in uppers, anticlinids in lowers) and valleys (synclines in uppers, synclinids in lowers) are numbered in Arabic and Roman numerals respectively. The latter are labelled on the diagrams, the former added in brackets after the relevant crest term, to show homologies. N.B., Anticlinid 1 and synclinid I are not developed in primitive theridomyids. Slightly different terminology applies to pseudosciurids for which see Hooker (1986: text-fig.31).

ian (Headonian ELMA) (Hooker & Weidmann 2000). The 1986 collection in contrast contains only one semihypsodont tooth, a *Patriotheridomys*? DP_4 of primitive aspect, and quite unlike those of the 1852 collection. This suggests that the Les Alleveys fauna is entirely middle Bartonian in age and that the Priabonian element is from a different Mormont fissure and has been mislabelled.

In terms of Paleogene Mammalian Reference Levels (MP), Les Alleveys is slightly older than Robiac, the reference locality for MP16. In practice, all Bartonian (although not all Robiacian) European mammal localities are regularly referred to MP16, but which contravenes the principle of reference levels as points in time, not intervals (Schmidt-Kittler 1987: 16). Relevant MP levels are shown in Figure 2 opposite their reference

localities, but within a standard biostratigraphical and chronostratigraphical scheme.

Ten species-group taxa of theridomyoid rodents are described here. The pseudosciurids are poorly represented, but the theridomyids are relatively abundant and, being at quite an early stage in their history, have the potential to provide us with information on the nature of their radiation and relationships of subfamilies. These relationships are investigated by cladistic analysis. Figure 3 shows the dental terminology used in the theridomyid descriptions.

Institutional abbreviations: BMNH, Department of Palaeontology, Natural History Museum, London (UK); MGL, Musée Géologique de Lausanne (Switzerland).

Systematic palaeontology

Order Rodentia BOWDICH 1821
Superfamily Theridomyoidea ALSTON 1876
Family Pseudosciuridae ZITTEL 1893
Genus *Sciuroides* MAJOR 1873
***Sciuroides siderolithicus* (PICTET & HUMBERT 1869)**
(Figs. 4a–c)

Lectotype. – Right maxilla with M^{1-2} (MGL.39562) from Eclépens-Gare.
Paralectotype. – Right dentary with M_{1-3} (MGL.39560) from Eclépens-Gare.
Referred material. – Right maxilla with DP^4-M^1 (MGL.40095); right dentary with DP_4-M_1 (MGL.40093: LM.2933), both from Eclépens-Gare. Left DP^4 (MGL.47049) from Les Alleveys 1852.
New material. – Two right $M^{1/2}$ (MGL.47496, 47625); right P_4 (MGL.47487); right $M_{1/2}$ (MGL.47482); from Les Alleveys 1986.

Diagnosis. – See Schmidt-Kittler (1971: 30).

Description. – Of the two $M^{1/2}$s, MGL.47625 has a complete simple metalophule I, arising from the hypocone and a metalophule II that is broken lingual of metaconule 2 (Fig. 4a). In contrast, MGL.47496 has a simple metalophule II, which joins a metaconule 1-bearing metalophule I lingually before joining the hypocone. The former condition is like that of the lectotype (Hooker & Weidmann 2000: fig. 18b), the latter condition is recorded for the first time for *S. siderolithicus*. Both morphs occur also in *S. rissonei* HOOKER 1986 (see Hooker 1986: pl. 15, figs 3, 7). MGL.47625 is 2.58 mm long by 2.67 mm wide. MGL.47496 is 2.71 mm long by 2.80 mm wide.

MGL.47487 is the first P_4 to be attributed to this species (Fig. 4b). The tooth is 2.61 mm long and 2.25 mm wide. It is abraded mesially, but the length measurement is only a slight underestimate, by little more than the thickness of the enamel. The tooth outline tapers gently mesially and the mesial margin is blunt, suggesting that before damage there had been two cusps developed. There is a very weak mesoconid and there is
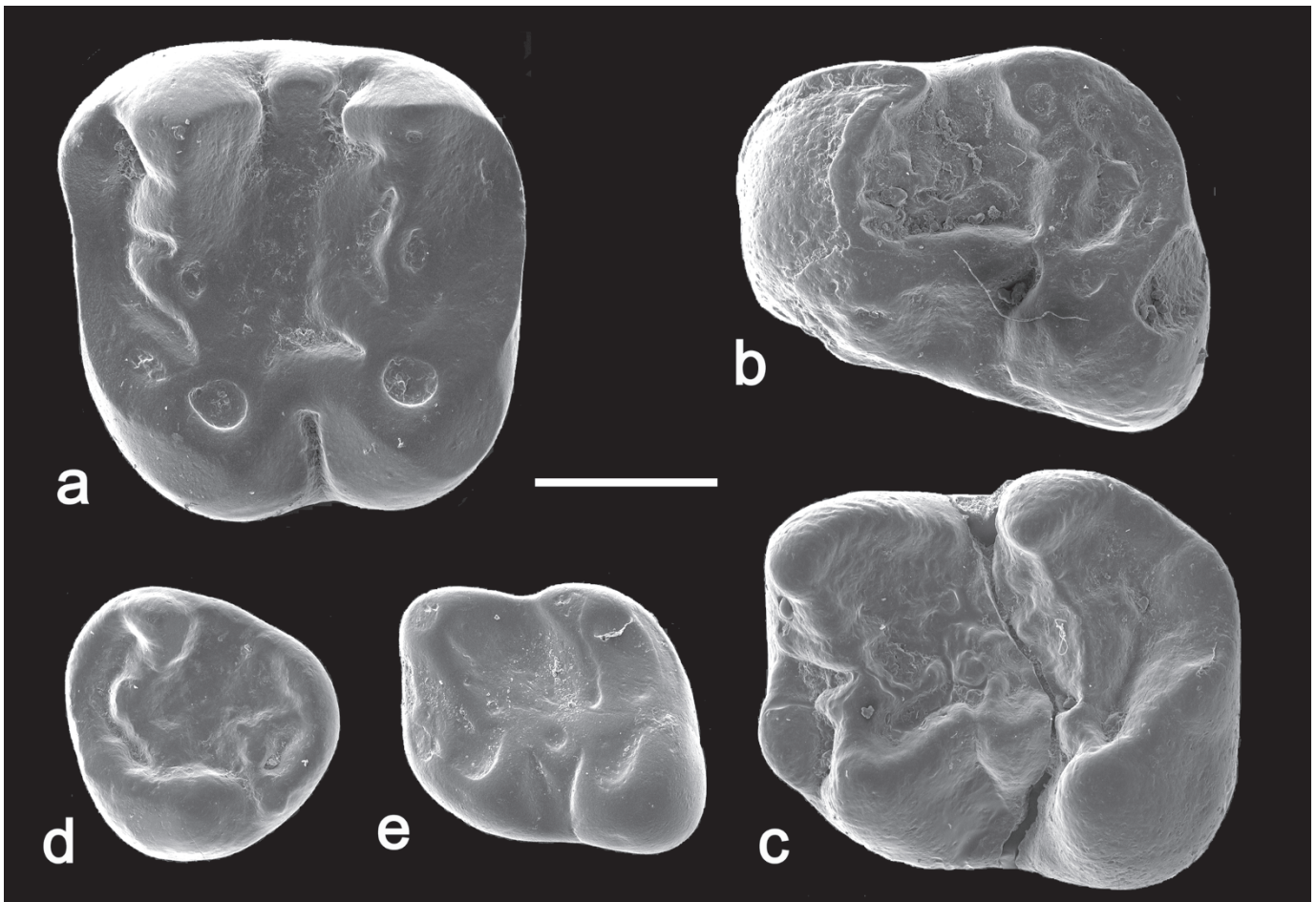
Fig. 4. Scanning electron micrographs of gold-palladium-coated epoxy casts of cheek teeth of Pseudosciuridae from Les Alleveys 1986, in occlusal view. a–c) *Sciuroides siderolithicus*. d, e) *Suevosciurus*? sp. a) Right $M^{1/2}$ (reversed), MGL.47625. b) Right P_4 (reversed), MGL.47487. c) Right $M_{1/2}$ (reversed), MGL.47482. d) Right M^3 (reversed), MGL.47572. e) Right $M_{1/2}$ (reversed), MGL.47469. Scale bar: 1 mm.

enamel wrinkling in the talonid basin. The tooth resembles those described for other species of *Sciuroides*, except that the post-hypolophulid basin lacks enamel wrinkling unlike *S. russelli* (Hartenberger & Louis 1976).

The $M_{1/2}$ is 2.66 mm long by 2.20 mm wide and is unworn (Fig. 4c). The height of the protoconid and hypoconid are 1.31 mm and 1.39 mm respectively. It is very similar in morphology to the paralectotype $M_{1/2}$s (Hooker & Weidmann 2000: fig. 18d). The only clear difference is that the enamel wrinkling in the talonid basin is slightly coarser. This seems not to be enhanced by its unworn state, as the paralectotype shows only light wear and the enamel wrinkling is still visible.

Discussion. – The new specimens increase the number of $M^{1/2}$ known from 3 to 5 (4 individuals) and the number of $M_{1/2}$ from 3 to 4 (3 individuals). The P_4 is the first record of this tooth type for the species. M^3 remains unknown. The measurements increase the size range for the species, which was previously very narrow for $M^{1/2}$ length (Hooker & Weidmann 2000: fig. 19). The range increase for $M^{1/2}$ is at the higher end, so that

there is almost total overlap with *S. rissonei* and still very little with *S. romani* (Hartenberger 1973). It is still distinguishable from *S. rissonei* by its bent lower molar ectolophid and lack of marked enamel wrinkling on the molars. Specimens from Quercy identified as *S. siderolithicus* by Schmidt-Kittler (1971: figs 10a–b, 13) fit *S. romani* for size. *S.* cf. *siderolithicus* from Mazaterón is shown below not to belong to this genus, but rather to *Protadelomys*. *S. siderolithicus* is therefore still unknown outside Mormont. This may reflect an absence of closely contemporaneous localities elsewhere yielding micromammals (Hooker & Weidmann 2000: 124–125, fig. 78), rather than a true restricted geographical range.

Genus *Suevosciurus*? Dehm 1937
Suevosciurus? sp.
(Figs. 4d, e)

Material. – Right M^3 (MGL.47572); right $M_{1/2}$ (MGL.47469); from Les Alleveys 1986.

Description. – The M^3 is 1.51 mm long by 1.57 mm wide (Fig. 4d). The height of its slightly worn protocone is 0.77 mm. It is subrounded to subtriangular in outline, has a complete protoloph with paraconule, an indistinct metalophule II and metacone and an unbroken endoloph confluent with a strong anteroloph, the junction bulging slightly with a protostyle. The tooth is moderately worn, but without penetration to the dentine. The valleys bear no enamel wrinkling. The morphology is typical of *Suevosciurus* or *Treposciurus* SCHMIDT-KITTLER 1970.

The $M_{1/2}$ is 1.70 mm long by 1.54 mm wide at the talonid (Fig. 4e). It is more heavily worn than the M^3 with much dentine exposed on all the cusps and along part of the hypolophulid, although the tooth must have been low crowned in the unworn state. There appears to have been no anterolophulid, but the anteroconid is prominent. The mesoconid is prominent too and largely fills the sinusid. It shows no sign of linking to the hypoconid as in derived species of *Suevosciurus*. There is no enamel wrinkling preserved, although this may have been removed by wear. The morphology is typical of *Suevosciurus* or *Treposciurus*.

Discussion. – M^3 and $M_{1/2}$ of early members of *Treposciurus* and *Suevosciurus* are very similar morphologically (Hooker 1986) and wear and the existence of only two teeth prevents conclusive identification. However, of known Bartonian representatives, *T. preecei* HOOKER 1986 and *S. authodon* HOOKER, 1986, sizes of MGL.47572 and 47469 are closer to the latter. The M^3 just exceeds the maximum dimensions of that tooth in *S. authodon*, which are 1.500 mm for length and 1.525 mm for width. The $M_{1/2}$ equals the maximum length measurement and slightly exceeds the maximum width measurement of that tooth in *S. authodon*, which are 1.700 mm for length and 1.500 mm for width (Hooker 1986: table 19). Together with a record of *S. authodon* from the Bartonian fauna of Dielsdorf, Switzerland (Hooker & Weidmann 2000: 125), these specimens indicate that *Suevosciurus* was not restricted to southern England during the Bartonian as originally suggested (Hooker 1986), although its European distribution at that time seems to have been patchy, being absent from Grisolles, Robiac and Quercy. See Hooker (1986) and Hooker & Weidmann (2000) for reidentification of taxa previously attributed to this genus from these sites.

Family Theridomyidae ALSTON 1876
Genus '*Protadelomys*'? HARTENBERGER 1969
'*Protadelomys*'? sp.
(Figs. 5a–e)

Material. – two right $M_{1/2}$ s (MGL.47599, 47557); right M_3 (MGL.47624); from Les Alleveys 1986.
Doubtfully attributed material. – Left DP^4? (MGL.47490); left M^3 (MGL.47433); from Les Alleveys 1986.

Description. – $M_{1/2}$: The two teeth are low crowned and simple in structure for a theridomyid. MGL.47599 is 2.23 mm long by 1.52 mm wide mesially and 1.64 mm wide distally (Fig. 5c); its nearly unworn hypoconid is 0.96 mm high. MGL.47557 is 2.12 mm long by 1.78 mm wide mesially and 1.79 mm wide distally (Fig. 5d); its nearly unworn hypoconid is 0.89 mm high. The former is narrower mesially than distally and may be an M_1, whereas the latter has comparable mesial and distal widths and may be an M_2. They have the deeply grooved antesinusid of this family (see Hooker & Weidmann 2000) and distinct simple cresting. The ectolophid is somewhat bent and joins the hypolophulid about one quarter of the distance from the hypoconid to the entoconid. There is a very weak mesoconid that bulges slightly buccally from the ectolophid. In MGL.47557 it also sends a short narrow crest lingually into the talonid basin, like an incipient mesolophid. The talonid basin bears coarsely wrinkled enamel with a tendency to form ridges parallel with the oblique part of the ectolophid. The protoconid is situated not exactly opposite the metaconid, but slightly more distally as in *Paradelomys* (q.v.). The hypolophulid is gently sigmoidal, swelling slightly in the middle. Buccal of its link with the ectolophid, it recurves to join the hypoconid, making a broad concavity at the back of the sinusid. There is a prominent postmetacristid, which ends abruptly distally, leaving a wide talonid notch. There is a weak anteroconid, which is joined to the buccal branch of the metalophulid by an anterolophulid. An extensive fovea is created by joining up of the anterolophulid, lingual branch of the metalophulid and the anterolophid on MGL.47599. The metalophulid is interrupted on MGL.47557. There is a distinct ectoflexid.
M_3: The tooth is 2.67 mm long by 2.10 mm wide mesially and 2.08 mm wide distally and is moderately worn (Fig. 5e). It has a well developed distal lobe, with prominent entoconid and hypolophulid, there is an anterolophulid and some coarse enamel folds in the talonid basin parallel to the ectolophid, as in the $M_{1/2}$s. Also like these tooth types, the anteroconid and mesoconid are weak, the hypolophulid is gently sigmoidal and the protoconid is distally displaced with respect to the metaconid. Unlike these tooth types, however, the postmetacristid is weaker and there is no fovea developed mesially. Instead, the lingual branch of the metalophulid is buccolingually orientated and directly joins the anterolophid and anterolophulid.
M^3: The tooth is 2.64 mm long by 2.79 mm wide (Fig. 5b). It is similar in size to that of *Sciuroides siderolithicus*, but differs in being relatively broader and in lacking an endoloph, presence of which is diagnostic of that genus. The paracone bears a postparacrista. Distal of the protoloph, there is much coarse enamel wrinkling and the sinus is essentially closed at its buccal end. There are foveae formed by mesiobuccally and mesiolingually directed crests linking the protoloph to the anteroloph. The enclosing of foveae mesially on the tooth is comparable to the condition in the $M_{1/2}$s, suggesting conspecificity.
DP^4?: This is an unusual tooth. It is 1.84 mm long by 1.68 mm wide (Fig. 5a). It is very low crowned and bears an almost complete encircling crest. The outline shape is subtriangular with very rounded angles, the buccal margin being nearly
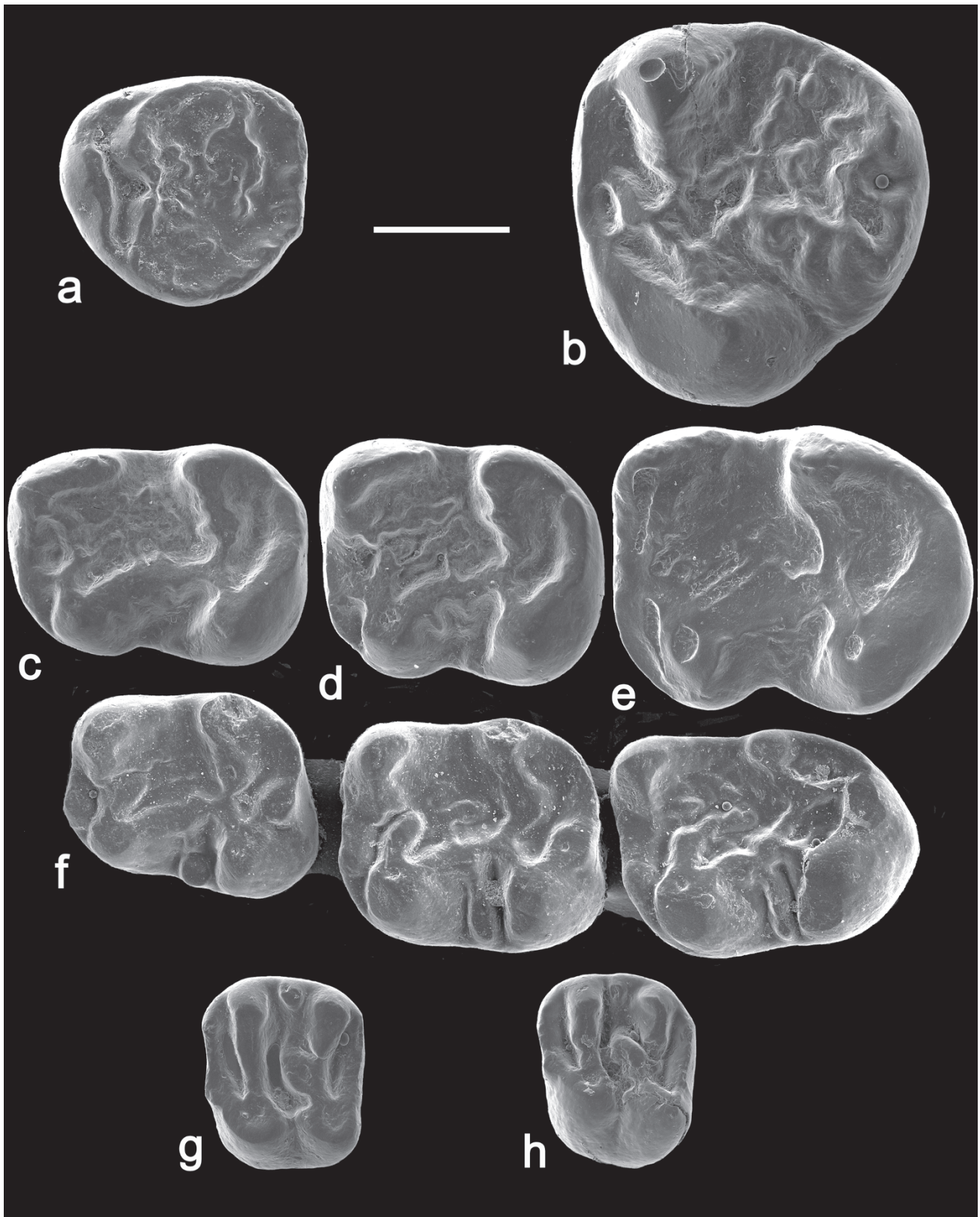
Fig. 5. Scanning electron micrographs of gold-palladium-coated epoxy casts of cheek teeth of Pseudosciuridae from Les Alleveys 1986, in occlusal view. a–c) *Sciuroides siderolithicus*. d, e) *Suevosciurus*? sp. a) Right $M^{1/2}$ (reversed), MGL.47625. b) Right P^4 (reversed), MGL.47487. c) Right $M_{1/2}$ (reversed), MGL.47482. d) Right M^3 (reversed), MGL.47572. e) Right $M_{1/2}$ (reversed), MGL.47469. Scale bar: 1 mm.

straight and the lingual margin broadly convex. Apart from being an upper cheek tooth, its identity as to locus is difficult to establish. It is nearly unworn and bears no interstitial facets. However, one end (mesial or distal) is straight and would presumably have abutted the next tooth in the row. The opposite end is strongly convex, raised above the level of the rest of the marginal cresting and appears to represent the end of a cheek tooth row. There are two irregular transverse crests, which are linked buccally by a mesio-distal crest that forms part of the buccal wall. The transverse crest adjacent to the straight mesial or distal margin bifurcates a short distance away from the buccal margin and the branch further from the centre of the tooth continues further lingually, but without reaching the lingual crested margin. The other transverse crest, however, is complete, joining the buccal and lingual marginal crests. The centre of the basin bears some coarse cresting. It is difficult to recognize any distinct cusps, although one is weakly developed towards the buccal end of the complete transverse crest. On the basis that the strongly convex end represents the end of a cheek tooth row, the tooth must be an M^3, P^4 or DP^4. On a rodent M^3, the portion nearer the M^2 (i.e. mesial) typically has the strongest cusps and crests, which is the reverse of the pattern in MGL.47490. The strongly convex end must therefore be mesial and the tooth therefore a P^4 or DP^4. The very low crown height is suggestive of a DP^4. Moreover, a nearly unworn DP^4 would exist too early in ontogeny to be succeeded by an erupted M^1, which would account for the absence of a distal interstitial facet. The crown pattern of this tooth is not unlike that of '*Protadelomys*' *lugdunensis* HARTENBERGER 1969 (pl.4, fig. 1b), although in this species the outline is transversely elongate. It is therefore tentatively concluded that MGL.47490 is a DP^4 of '*Protadelomys*'? sp.

Discussion. – The dimensions and morphology of the lower molars are similar enough to indicate a single species and the crown pattern on the M^3 is suggestive of belonging here too. It appears to be distinct from any so far described. However, the number of specimens and of tooth types is insufficient to justify naming it as new. The lower molars are primitive in a number of ways: low crown height, presence of a mesoconid, absence of any accessory crests and presence of a distinct ectoflexid. It has particular similarities to '*Protadelomys*' *lugdunensis* in the shape of the hypolophulid and the tendency to form coarse wrinkling parallel to the ectolophid (Hartenberger 1969: pl. 4, fig. 4; Sudre et al. 1990: pl.1, figs 4, 6 [aff.]), which may be indicative of a close relationship (Fig. 5f). Other similarities are simply primitive and the Les Alleveys teeth are larger than those of '*P*'. *lugdunensis*. Distinctive derived features are the strong postmetacristid with wide talonid notch, the fovea enclosed by crests at the mesial end ($M_{1/2}$ and M^3), closed sinus on M^3 and the near continuous strong cresting (all the teeth). Theridomyids of this grade of evolution are typical of Lutetian sites (e.g. Lissieu, Egerkingen) and this taxon is an unusual survivor in the early Bartonian. It is conservatively

dubbed '*Protadelomys*'? sp. here to indicate possible relationships and the paraphyletic nature of the genus *Protadelomys*. Hopefully, additional tooth types will be found in future Mormont fissures to enhance our knowledge of this interesting taxon.

A somewhat similar taxon has been described from the Spanish Bartonian site of Mazaterón under the name *Sciuroides* cf. *siderolithicus* (Pelaez-Campomanes 1996: 1365–1367, fig. 1, pl. 1). This taxon is represented by isolated cheek teeth from all loci, although no $M_{1/2}$s have been figured. The P^4 is relatively broader than that of *Sciuroides*; $M^{1/2}$ differs from that genus in lacking a metalophule I; the DP_4 and P_4 have a hypolophulid that links the entoconid to the hypoconulid (rather than to the hypoconid) as in '*P*'. *lugdunensis*; M_3 has a sigmoidal hypolophulid as in *P. cartieri* HARTENBERGER 1969, '*P*'. *lugdunensis* and '*P*'. sp. from Les Alleveys; and M_3 has a deep antesinusid typical of primitive theridomyids, not pseudosciurids. The DP^4, however, is more like that of *Sciuroides* and very different from that tentatively identified for '*P*'. sp. from Les Alleveys. It cannot be excluded that this DP^4 from Mazaterón belongs to a different taxon from the other teeth, but all the other tooth types appear to be more closely related to species of *Protadelomys* than to any other theridomyoid. Little overlap of well preserved tooth types with '*P*'. sp. from Les Alleveys inhibits a detailed comparison, but relationship appears not to be close.

Subfamily Remyinae HARTENBERGER 1973
Type genus. – *Remys* THALER 1966.
Included genus. – *Pairomys* THALER 1966.

Comment. – The subfamily has most recently been defined thus: milk teeth and premolars of primitive pattern; very small with respect to the molars (e.g. *Remys minimus* from Le Bretou: length P^4/length M^1 = 0.77; length P_4/length M_2 = 0.78); with discrete conules and metaloph attached to the protocone rather than to the hypocone. Lower dentition of simple pattern: sinusid confluent with synclinid III; anticlinids 2–3 and 4–5 forming two more or less compressed, closely spaced Vs; mesolophid absent; hypoconulid present but poorly developed; infraorbital foramen vast, with strong gutter; mandible sciurognathous. (Translated from Vianey-Liaud et al. 1994: 137). This definition is a mix of primitive and derived characters. The cladistic analysis below identified a single unequivocal synapomorphy for the subfamily: M^{1-2} prehypocrista passing through metaconule. For apomorphies paralled elsewhere in the matrix, see Figure 14b.

Genus *Remys* THALER 1966
Type species. – *Remys garimondi* THALER 1966 from Fons 1, France.
Referred species. – *Remys minimus* HARTENBERGER 1973 from Robiac, France.

Diagnosis. – Remyinae brachyodont to feebly hypsodont; differing from *Pairomys* by the presence of the lingual arm of the hypoconid, which may or may not be continuous with the entolophid (translated from Vianey-Liaud et al. 1994).

Remys sp.
(Figs. 5g, h)

Material. – Two right $M^{1/2}$s (MGL.47601, 47472) from Les Alleveys 1986.

Description and discussion. – MGL.47601 is 1.18 mm long by 1.46 mm wide; its unworn hypocone is 1.04 mm high. MGL.47472 is 1.19 mm long by 1.43 mm wide. For size therefore these teeth fit within the *R.* cf. *garimondi* assemblage from the early Priabonian of Malpérié, France, and are larger than any *R. minimus* upper molar (Hartenberger 1973, 1988). Both Les Alleveys teeth have a strong metaconule from which arises a buccally trending weak crest, but which does not reach the mesostyle. The sinus is almost closed off lingually by a notched endoloph. There is a distinct protostyle. Morphologically, therefore, the Les Alleveys 1986 *Remys* specimens resemble *R. minimus*. The $M^{1/2}$ of *R. garimondi* from the early Priabonian of Malpérié (Vianey-Liaud et al. 1994: fig. 9n) lacks the protostyle and is more lophodont with a complete but thin mesoloph joining a smaller metaconule. The Les Alleveys *Remys* therefore may belong to a new species, but the material available is insufficient to define it adequately.

Subfamily Columbomyinae Thaler 1966

Comment. – This subfamily was originally erected to contain the genera *Columbomys* Thaler 1962 and *Sciuromys* Schlosser 1884. Its diagnosis has been given thus: hypsodont dentition; lower molars without mesolophid and presenting a discrete anteroconid (translated from Vianey-Liaud 1979: 143). Cladistic analysis (see below) points to inclusion of the genus *Paradelomys* in the subfamily. Unequivocal synapomorphies defining the subfamily with emended content are: P^4 usually with distinct ectoflexus; protocone on upper cheek teeth situated more mesially than paracone in at least some individuals of an assemblage; lower molar ectolophid bent in at least some individuals; lower molar protoconid situated more distally than metaconid.

Genus *Paradelomys* Thaler 1966

Type species. – *Paradelomys crusafonti* Thaler 1966 from Sossis, Spain.
Included species. – *Paradelomys ruetimeyeri* (Pictet & Humbert 1869) from Entreroches, Switzerland.

Diagnosis. – Low crowned **theridomyid with relatively elongate** *and lophodont* **cheek teeth, upper molars with broad sinus complete buccally** and mesoloph usually weak or intermittent; *no lower molar mesoconid; anterior palatine foramina extending midway between the premaxillary-maxillary suture and P^4* (characters in bold are autapomorphies; those italicized are synapomorphies with other theridomyids except *Protadelomys*; from Hooker & Weidmann 2000: 43). N.B., the elongation character is no longer considered distinctive. The cladistic analysis below shows the genus to be paraphyletic. Moreover, the most primitive unnamed species described below lacks the buccal closure of the sinus in most individuals.

Paradelomys sp.
(Figs. 6, 13a)

Material. – 4 right P^4s (MGL.47486, 47550, 47594, 47608), 9 $M^{1/2}$s (MGL.47399, 47428, 47435, 47497, 47547, 47556, 47562, 47574, 47618), 3 M^3s (MGL.47565, 47571, 47575), 2 P_4s (MGL.47436, 47598), 9 $M_{1/2}$s (MGL.47439, 47483, 47546, 47549, 47559, 47570, 47588, 47592, 47609), 2 left M_3s (MGL.47561, 47604), from Les Alleveys 1986.

Description. – P^4: The four teeth are similar in proportion and general cusp pattern to other *Paradelomys* P^4s from Mormont (Fig.6a; Hooker & Weidmann 2000). Two have a shallow ectoflexus. Three are slightly longer than broad, the fourth is equidimensional. All four have an open sinus; in one it is wide lingually but narrower in the other three, where remnants of an endoloph exist. Two have a complete mesoloph, whereas it is weak and interrupted in the other two.
$M^{1/2}$: Of the nine specimens, two are too corroded to judge details of crown pattern. Of the remaining seven, two have a closed sinus (Figs. 6b, c). Two have a metalophule I (Figs. 6c, h), one of which, although very worn and having lost its distobuccal corner, shows both a complete endoloph and a closed sinus (Fig. 6h). All the rest show a sinus that is widely open lingually (Figs. 6e, f). In all, the mesoloph is almost lacking, being mainly represented by a small swelling that joins neither the mesostyle nor the prehypocrista. One specimen has a short mesial crest from the metaconule (Fig. 6b), a little like derived *Elfomys*. The paraconule is large in all but one of the noncorroded specimens. Its size is judged by how far it projects from the centre of the protoloph to the mesial tooth margin. Here it varies from 45–70% of the distance. Two specimens are unworn. Of these, the height of the protocone is 1.27 mm in MGL.47428 and 1.23 mm in MGL.47556. The length of each is 1.79 mm, making the percentage heights 70.9 and 68.7 respectively.
M^3: Of the three specimens, two have a closed (Figs. 6d, j), another an open sinus (Fig. 6g). One with a closed sinus also has a remnant endoloph (Fig. 6d). Two have a complete mesoloph (Figs. 6d, j) while the third has some complex cresting and
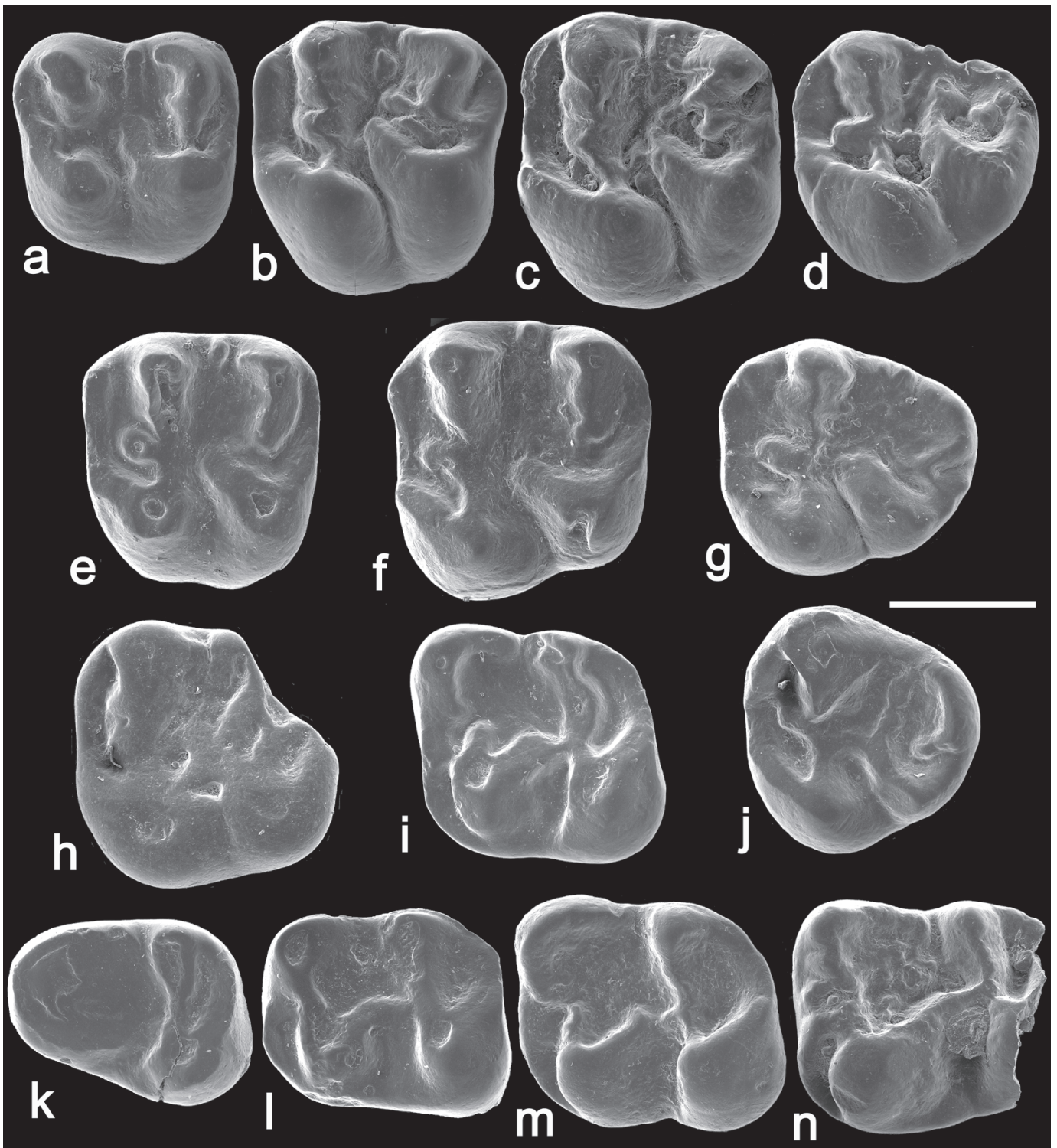
Fig. 6. Scanning electron micrographs of gold-palladium-coated epoxy casts of cheek teeth of *Paradelomys* sp. from Les Alleveys 1986, in occlusal view. a) Right P^4 (reversed), MGL.47550. b) Right $M^{1/2}$ (reversed), MGL.47428. c) Right $M^{1/2}$ (reversed), MGL.47556. d) Left M^3, MGL.47571. e) Right $M^{1/2}$ (reversed), MGL.47547. f) Right $M^{1/2}$ (reversed), MGL.47435. g) Left M^3, MGL.47575. h) Left $M^{1/2}$, MGL.47574. i) Left $M_{1/2}$, MGL.47570. j) Right M^3 (reversed), MGL.47565. k) Right P_4 (reversed), MGL.47598. l) Left $M_{1/2}$, MGL.47546. m) Right $M_{1/2}$ (reversed), MGL.47483. n) Left M_3, MGL.47604. Scale bar: 1 mm.

wrinkling in the distal area of the tooth (Fig. 6g). Like M$^{1-2}$, the paraconule is large, extending from 55–75% of the distance to the mesial margin.

P$_4$: Both teeth are similar to other described Mormont *Paradelomys* P$_4$s (Hooker & Weidmann 2000). One has a single mesial cusp (Fig. 6k), the other, although with a damaged mesial margin, has two mesial cusps. Both have a faint incipient mesolophid arising from the ectolophid, unlike the molars.

M$_{1/2}$: The metalophulid varies considerably from a complete straight crest (probably M$_1$s) (Fig. 6l) to a state where it is broken and respective arms are deflected distally so that the antesinusid is confluent with the talonid basin (probably M$_2$s) (Figs. 6i, m). The anterolophid may be confluent with the lingual arm of the metalophulid. All but two (Fig. 6l) show a lingual bulge on the ectolophid (Figs.6i, m), but nothing that could be classified as a mesolophid. The ectolophid may be straight and oblique (Figs. 6i, m) or bent with its distal part longitudinally orientated (Fig. 6l). The antesinusid is large in all, owing to the slight distal positioning of the protoconid.

M$_3$: One of the two specimens is heavily worn, but shows a bent ectolophid. The other is broken distally, but its distally tapering outline shows it to be a third molar. Its ectolophid is oblique (Fig. 6n). Both lack any sign of a mesolophid. The metalophulid is straight but notched in MGL.47604 (Fig. 6n), which has an anterolophulid as well as a connection from the lingual arm of the metalophulid to the anterolophid, leaving a small fovea between. In MGL.47561 the metalophulid is broken, with its buccal arm projecting distally into the talonid basin.

Discussion. – As usual in the genus *Paradelomys*, morphological variation is high. Size is intermediate between the Grisolles and Robiac assemblages (Table 2; Hooker & Weidmann 2000: fig.30; Hartenberger 1973; Hartenberger & Louis 1976), there being much overlap with both. The mean length is nearer the Grisolles assemblage for the M$^{1/2}$ and nearer the Robiac assemblage for M$_{1/2}$. The single M$^{1/2}$ from Eclépens-Gare (Hooker & Weidmann 2000: figs 29j, 30) integrates well dimensionally and morphologically with the Les Alleveys 1986 assemblage. Although also morphologically variable, the larger Grisolles assemblage is unlike that of Les Alleveys 1986 in having the majority of its upper molars bearing a metalophule I and in having lower molars with a consistently broken and distally deflected metalophulid. It is uncertain to what taxonomic rank these differences relate and, until a detailed study of the morphological variation of all assemblages of *Paradelomys* is undertaken, it would be inappropriate to either name it or attribute it to an existing species. Nevertheless, the Les Alleveys, Grisolles and Robiac assemblages appear to share more similarities (mainly primitive) than any of them do with Priabonian assemblages of *P. crusafonti*, whilst *P. ruetimeyeri* remains very poorly known.

Subfamily Issiodoromyinae TULLBERG 1899

Comment. – This subfamily currently contains three genera: *Issiodoromys* BRAVARD in GERVAIS, 1852, *Pseudoltinomys* and *Elfomys*. It has been diagnosed thus: Theridomyidae with medium to very short palatal vault; bulla large to very large; ascending mandibular ramus inclined to very inclined, then reduced in the very hypsodont forms; teeth brachyodont to very hypsodont; lower molars with two or three roots in the early forms, two roots from the level of San Cugat (Escamps); antesinusid disappearing in the hypsodont forms; sinus reuniting with synclinal II at least on the least worn teeth; flat incisors. (Translated from Vianey-Liaud 1976: 5). Few if any of the skull characters are yet known for the more primitive species of each genus. The dental characters distinguish only the more derived members or are simply primitive and inappropriately introduce a stratigraphic component. Cladistic analysis (see below) found no dental synapomorphies for the subfamily.

Genus *Elfomys* HARTENBERGER 1971

Type species. – *Elfomys parvulus* HARTENBERGER 1971, from Fons 4, Gard, France.*Included species.* – *Elfomys tobieni* (THALER 1966), *E. nanus* (THALER 1969), *E. hartenbergeri* VIANEY-LIAUD & RINGEADE 1993.

Diagnosis. – Issiodoromyinae with microdont tendency, brachyodont and semi-hypsodont (rank of hypsodonty of M$_{1-2}$ at 1.5); lower molars with well defined antesinusid; upper molars with the external extremities of the anticlinids well detached, at least in a part of the population; mandible more gracile with ascending ramus more inclined than in *Pseudoltinomys* but less reduced than in *Issiodoromys*; upper masseteric crest very marked and lower masseteric crest still present. (Translated from Vianey-Liaud 1976: 21).

Comment. – The only unequivocal synapomorphy found in the cladistic analysis below was the presence in at least some individuals of a mesiobuccal metaconule crest. For apomorphies paralleled elsewhere in the matrix, see Figure 15. Primitive members of the genus are known only by teeth.

Elfomys engesseri sp. nov.
(Figs. 7, 8, 13c)

v. 2000 *Elfomys* aff. *tobieni* (THALER) – Hooker & Weidmann: 46–47, fig. 31c–e.

Holotype. – Right M$^{1/2}$ (MGL.47580) from Les Alleveys 1986.
Paratypes. – Right DP^4 (MGL.47500); 3 P^{4}s (MGL.47392, 47405, 47595); 12 M$^{1/2}$s (MGL.47425, 47438, 47491, 47494, 47504, 47554, 47579, 47582, 47584, 47587, 47607, 47617); 2 M^{3}s
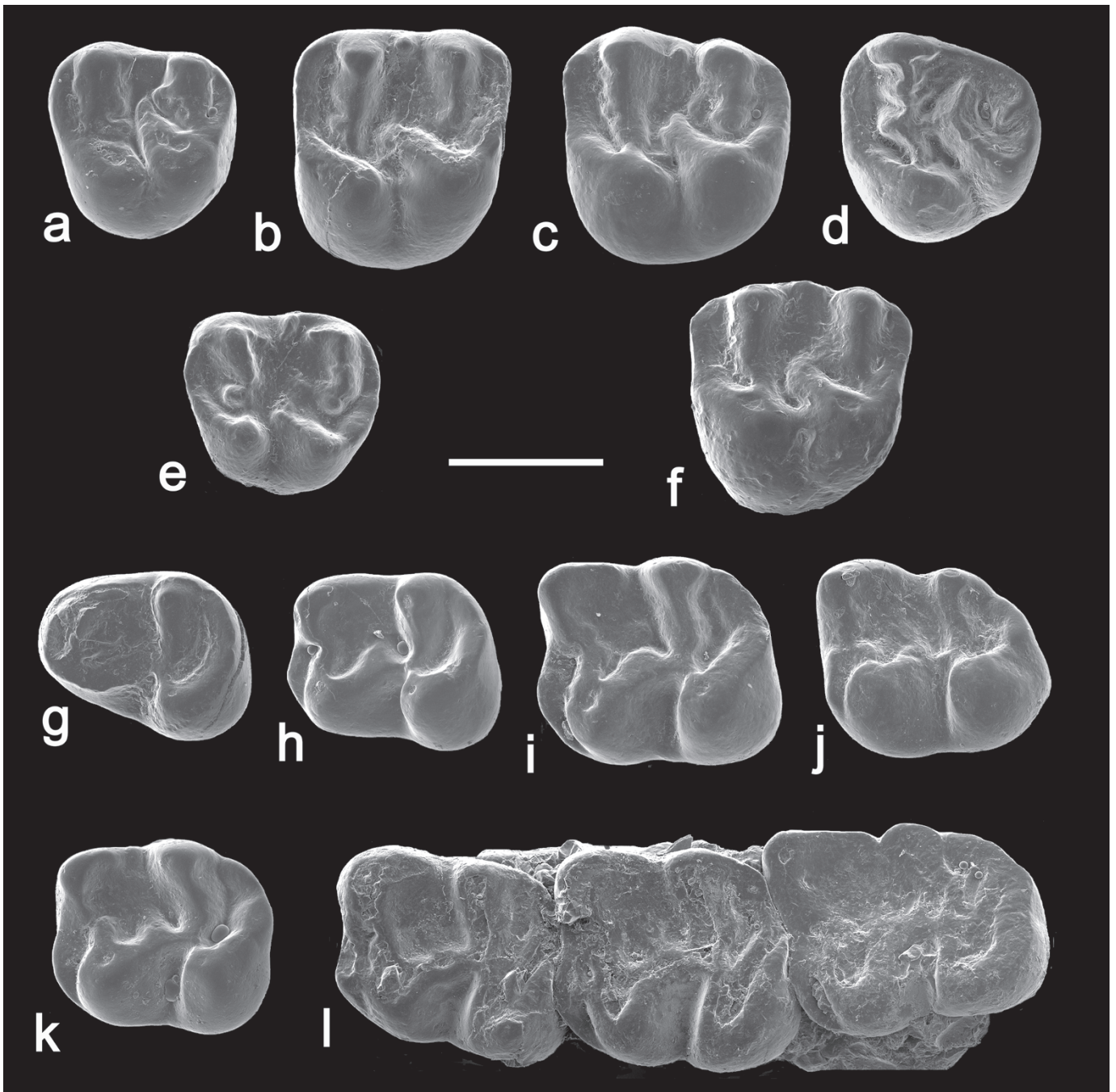
Fig. 7. Scanning electron micrographs of gold-palladium-coated epoxy casts of cheek teeth of *Elfomys engesseri* sp. nov. from Les Alleveys 1986, in occlusal view. a) Left P^4, MGL.47392. b) Right $M^{1/2}$ (reversed) holotype, MGL.47580. c) Left $M^{1/2}$, MGL.47494. d) Right M^3 (reversed), MGL.47466. e) Right DP^4 (reversed), MGL.47500. f) Left $M^{1/2}$, MGL.47617. g) Right P_4 (reversed), MGL.47501. h) Left $M_{1/2}$, MGL.47586. i) Left $M_{1/2}$, MGL.47493. j) Right M_3 (reversed), MGL.47622. k) Left $M_{1/2}$, MGL.47455. l) Left M_{1-3}, MGL.47440. Scale bar: 1 mm.

(MGL.47466, 47600); 5 P_4s (MGL.47501, 47564, 47585, 47597, 47621); left dentary fragment with M_{1-3} (MGL.47440); 12 $M_{1/2}$s (MGL.47403, 47422, 47432, 47455, 47474, 47493, 47498, 47563, 47567, 47568, 47576, 47586); 3 M_3s (MGL.47470, 47581, 47622); from Les Alleveys 1986.

Referred specimen. – Left $M^{1/2}$ (MGL.47481) from Les Alleveys 1986.

Derivatio nominis. – In honour of Burkart Engesser in recognition of his contributions to small mammal palaeontology and for his help to the authors with their Mormont project.
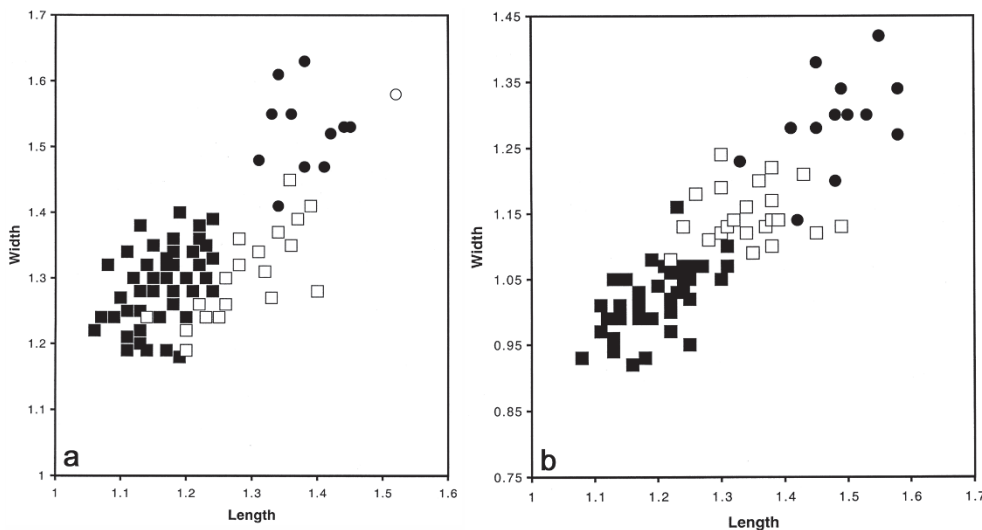
Fig. 8. Scatter diagrams of length versus width in millimetres of species of *Elfomys*. a) M$^{1/2}$. b) M$_{1/2}$. ■ = *E. parvulus* from Fons 4 and Malpérié; □ = *E. tobieni* from Robiac; ○ = *E. engesseri* from Les Alleveys 1986; ● = *E. engesseri* from Eclépens-Gare. Values of *E. parvulus* and *E. tobieni* from Hartenberger (1973: fig.13) and of *E. engesseri* from Eclépens-Gare from Hooker & Weidmann (2000).

Table 3. Statistics of length and width measurements in millimetres of cheek teeth of *Elfomys engesseri* sp. nov. from Les Alleveys 1986. Abbreviations as in Table 2.

Tooth	N	OR	Length Mean	SD	V	N	OR	Width Mean	SD	V
DP^4	1	1.28				1		1.17		
P^4	3	1.19–1.31	1.26			3	1.25–1.38	1.32		
M$^{1/2}$	12	1.31–1.47	1.39	0.0519542	3.74	11	1.41–1.63	1.52	0.0638891	4.20
M^3	2	1.27–1.30	1.29			2		1.30–1.35	1.33	
P$_4$	5	1.22–1.45	1.32	0.0988938	7.49	5	1.05–1.17	1.11	0.04827	4.35
M$_{1/2}$	14	1.33–1.58	1.48	0.068388	4.62	13	1.14–1.42	1.29	0.0736502	5.71
M$_3$	4	1.53–1.81	1.70			4		1.23–1.43	1.33	

Diagnosis. – Large *Elfomys*, mean length of M$_{1/2}$ 1.47 mm. Cheek teeth low crowned. Weak paraconule on all M$^{1/2}$s, extending from the protoloph 35–55% of the distance to the mesial margin. Mesiobuccal metaconule crest present on M$^{1/2}$ of c.15% of individuals. M$^{1/2}$ mesoloph scarcely developed.

Differential diagnosis. – All other species of *Elfomys* have better developed M$^{1/2}$ mesoloph. All except *E. hartenbergeri* (which is larger) are smaller. *E. parvulus, E. hartenbergeri* and *E. nanus* have M$^{1/2}$ with frequently developed mesiobuccal metaconule crest and the paraconule may be missing. *Elfomys hartenbergeri* and *E. nanus* have higher crowned cheek teeth.

Description. – For measurements, see Table 3.

DP^4?: This tooth is longer than wide, low crowned, the cusps appear gracile and the parastylar area bulges mesially (Fig. 7e). The mesostyle is tiny and there is no mesoloph. The protocone and hypocone are well separated. The paraconule does not join the anteroloph. These features when compared with the P^{4}s are suggestive of DP^4.

P^4: Out of 3 specimens, only one has a complete mesoloph. On another, the prehypocrista extends 2/3rds of the distance from the hypocone to the mesostyle, without continuing as a mesoloph (Fig. 7a). The third is intermediate. In all, the mesostyle is oval, elongated mesiodistally. All have a remnant

endoloph, developed either fully lingually or slightly more buccally, leaving a shallow narrow sinus.

M$^{1/2}$: Out of 13 specimens, only three have a negligeable paraconule (Figs. 7c, f). In the rest it is present but small (Fig. 7b), projecting mesially from the protoloph, although in most cases less so than is typically the case for *Paradelomys* (q.v.). The distance range towards the mesial margin is 35–55%. Two have a mesiobuccally directed crest from the metaconule (Fig. 7f), typical of more derived species (e.g. *E. parvulus*, Hartenberger 1973: pl. 6, figs 5, 8). In one of these (MGL.47491) the crest has a distobuccal extension to the metacone, forming a metalophule I. In none of the teeth does the prehypocrista reach more than about half way from the hypocone to the mesostyle, there being no intervening development of mesoloph. All but two specimens have a sinus that opens into the central valley. Of the exceptions, one (MGL.47584) has bridged the sinus because of heavy wear, the other (MGL.47617) retains a complete endoloph (Fig. 7f). Two specimens are nearly unworn. Of these, the height of the protocone is 1.02 mm in MGL.47580 (holotype) and 1.06 mm in MGL.47494. Tooth length is 1.42 mm in the former and 1.44 mm in the latter, giving percentage heights of 71.8 and 73.6 respectively. These are very slight underestimates as the teeth are not completely unworn.

Fig. 9. Scanning electron micrographs of gold-palladium-coated epoxy casts of cheek teeth of *Pseudoltinomys* aff. *crebrum* from Les Alleveys 1986. a) Right P^4 (reversed), MGL.47591. b, c) Right M^3 (reversed in c), MGL.47552. d) Left $M_{1/2}$, MGL.47437. e) Left $M_{1/2}$, MGL.47434. (b) is lingual view, the rest are occlusal views. Scale bar: 1 mm.

M^3: One specimen (MGL.47466) has a partial mesoloph nearly reaching the mesostyle (Fig. 7d). In the other (MGL.47600), the prehypocrista dies out half way to the mesostyle, but sends another crest towards a very weak metacone. In MGL.47466, the paraconule is relatively strong (55%), whereas in MGL.47600 it is weak (35%). The sinus is open in both.

P_4: The teeth are relatively short with no obvious division of the main mesial cusp (Fig. 7g), although most are too worn to be certain of this. The ectolophid joins the hypolophulid just lingual of the hypoconid.

$M_{1/2}$: Out of 10 isolated teeth (two others being too worn to judge), only two have an anterolophulid, isolating a fovea on its lingual side. In addition, both M_1 and M_2 in the dentary fragment, although worn, have an anterolophulid (Fig. 7l). In the rest, the antesinusid penetrates deeply distolingually behind the anteroconid so that the metalophulid is angled distally (Figs. 7h, I, k). The anteroconid is joined by a strong anterolophid to the metaconid. In eight specimens, there is a short mesolophid that is probably not dentine cored (Figs. 7h, k). MGL.47403 has the longest, extending just over a third of the distance from the ectolophid to the lingual margin.

M_3: All specimens taper somewhat distally (Figs. 7j, l). They have weak hypolophulids and relatively small entoconids. There is no mesolophid, although the basin floor is raised slightly in the appropriate position in one (Fig. 7j).

Discussion. – The plots of both $M^{1/2}$ and $M_{1/2}$ lie largely outside those of closely related *E. tobieni*, with a small overlap at the lower end (Fig. 8). There is in fact less overlap than between *E. tobieni* and the even smaller *E. parvulus* (Hartenberger 1973: fig. 13). Table 3 shows low coefficients of variation for these teeth of *E. engesseri* indicative of a single species. The $M^{1/2}$ from Eclépens-Gare matrix block II, attributed to *E.* aff. *tobieni* by Hooker & Weidmann (2000: fig. 31c) is slightly larger than any of those from Les Alleveys 1986 (Fig. 8a), but addition of its measurements to the latter assemblage increases the coefficient of variation only to 4.44 for length and reduces it slightly to 4.13 for width, indicating that it too belongs to *E. engesseri*. Presence, although on average small size, of the $M^{1/2}$ paraconule, absence of a mesoloph and low frequency of the mesiobuccal metaconule crest are all primitive features, making *E. engesseri* overall more primitive than any other named species of *Elfomys*. According to the dating of the Eclépens-Gare, Eclépens A and Les Alleveys faunas by parsimony analysis of shared taxa as middle Bartonian (modified from Hooker & Weidmann 2000), this is also the earliest named species of *Elfomys*, although Sudre et al. (1990: 20) indicated a new undescribed species from the MP14 (late Lutetian) locality of Laprade, Quercy, France.

Genus *Pseudoltinomys* Lavocat 1952

Type species. – *Pseudoltinomys gaillardi* Lavocat 1952.
Included species. – *Pseudoltinomys cuvieri* (Pomel 1853); *P. phosphoricus* Hartenberger 1973; *P. mamertensis* Hartenberger 1973; *P. cosetanus* Hartenberger in Anadón, Feist, Hartenberger, Muller & Villalta-Comella 1983; *P. crebrum* Pelaez-Campomanes 1996.

Diagnosis. – Teeth brachyodont to moderately hypsodont; sinus confluent with the adjacent synclinal, sinusid confluent with the adjacent synclinid, on little to moderately worn teeth; lower molars with two or three roots; antesinusid generally present; mandibular structure close to that of the Theridomyinae, differing from them by the stronger inclination of the ascending ramus and the higher position of the incisive foramen; palatal structure close to that of the Theridomyinae; profile elevated. (Translated from Vianey-Liaud 1976: 5).

Comment. – This diagnosis combines primitive and derived states. The cladistic analysis below found one of the most primitive species, *P. crebrum*, defined only by characters paralleled elsewhere in the matrix, although nevertheless diagnostic at the relevant node. These are: grade 2 hypsodonty (see Appendix 1), loss of M^{1-2} paraconule, M^{1-2} with complete mesoloph, M^{1-2} hypolophule in most individuals, M^3 with small paraconule (see Appendix 1), lower molar ectolophid broken distally at junction with hypolophulid.

Pseudoltinomys aff. *crebrum* Pelaez-Campomanes 1996
(Figs. 9, 13d)

Material. – Right P^4 (MGL.47591); doubtfully left P^4 (MGL.47560); right M^3 (MGL.47552); 2 left $M_{1/2}$s (MGL.47437, 47434), from Les Alleveys 1986.

Description. – P^4: MGL.47591 is 1.60 mm long by 1.62 mm wide (Fig. 9a). Its unworn protocone height is 1.31 mm, making it 81.9% of the length. It is therefore higher crowned than the other theridomyid P^4s in the Les Alleveys 1986 assemblage that are attributed to *Paradelomys*, *Elfomys* and *Estellomys* (Fig. 13d). This together with its strong mesoloph and appropriate size allow it to be attributed to *Pseudoltinomys*. Its morphology in other ways, however, is more primitive than that of P^4 of other *Pseudoltinomys* species where this tooth type is known. Thus, it has a mesiobuccal crest from the metaconule like *Elfomys* and the protoloph is broken, the lingual end of the buccal branch linked by a crest to the anteroloph. The otherwise most primitive species with a known P^4 (*P. mamertensis*) has a complete protoloph with an unbridged syncline I (Hartenberger 1973: pl. 5, figs 1, 15). The doubtfully attributed MGL.47560 is 1.68 mm in both length and width, which may be a slight underestimate as it is rolled. Its outline tapers mesially, the protocone and

hypocone are well separated and the mesoloph is weak and incomplete.

M^3: The lightly worn tooth is 1.73 mm long by 1.90 mm wide (Figs. 9b, c). It has four anticlinals consisting of anteroloph, protoloph, mesoloph confluent with prehypocrista and short metalophule II that does not join the hypocone. There is a small paraconule, projecting 40% of the distance from the protoloph to the mesial margin. The mesoloph is narrower than the prehypocrista or the other lophs. There is a very narrow connection between the end of the prehypocrista and the protoloph, which would have been bridged by heavy wear creating a closed sinus.

$M_{1/2}$: MGL.47437 is 1.94 mm long by 1.60 mm in maximum width (Fig. 9d); MGL.47434 is 2.08 mm long by 1.59 mm in maximum width (Fig. 9e). Both are very similar and, as MGL.47437 is almost unworn, it is possible to gain a good idea of its crown height. The height of the hypoconid of this specimen is 1.15 mm, thus 72% of maximum tooth width and 59% of length. The entoconid is as tall as the metaconid and its lingual and distolingual slope reduces the post-hypolophulid basin to a narrow crescent. There is only the faintest expression of a mesolophid and this only on MGL.47434. In both, the ectolophid is broken at its distal end, making no connection with the hypolophulid. There is a prominent anteroconid and no anterolophulid. The two branches of the metalophulid are angled distally, producing a distal protrusion where they meet. Thus, the antesinusid penetrates deeply behind the anterolophid.

Discussion. – In morphology, there is a close resemblance to *P. crebrum* from Mazaterón and Miñana, Almazán Basin, Spain (Pelaez-Campomanes 1996: 1367–1371, fig. 2, pls. 2–3), recorded for this species. Insufficient tooth types and too few specimens of any from Les Alleveys prevent a comprehensive comparison with the Mazaterón and Miñana assemblages. However, crown height appears very similar. The mesoloph on the Les Alleveys M^3 is better developed than in *P. crebrum* (Pelaez-Campomanes 1996: pl.2, fig. 6). P^4 is less transversely elongate than that of *P. crebrum* (Pelaez-Campomanes 1996: pl. 2, fig. 3) and, unlike the latter, lacks an endoloph; it is nevertheless similar in its complete mesoloph and broken protoloph, although the figured Mazaterón tooth is at an advanced wear stage. The two $M_{1/2}$s from Les Alleveys are very similar to the figured specimens of *P. crebrum* (Pelaez-Campomanes 1996: pl. 3, figs. 4–5, 7), especially in the configuration of the metalophulid and the separation of the ectolophid from the hypolophulid. However, the slightly larger size of the Les Alleveys teeth precludes exact identity with the Spanish species, although the relationship appears very close.

The Les Alleveys teeth are also morphologically similar to those of the Le Bretou assemblage of *P. mamertensis*, especially in the well developed mesoloph of M^3 and in crown height. The P^4 is, however, less lophodont. There is also less development of the $M_{1/2}$ mesolophid than in *P. mamertensis* and this character is more like the state in *P. cosetanus*. However, both these species are considerably smaller than the Les Alleveys 1986 taxon.
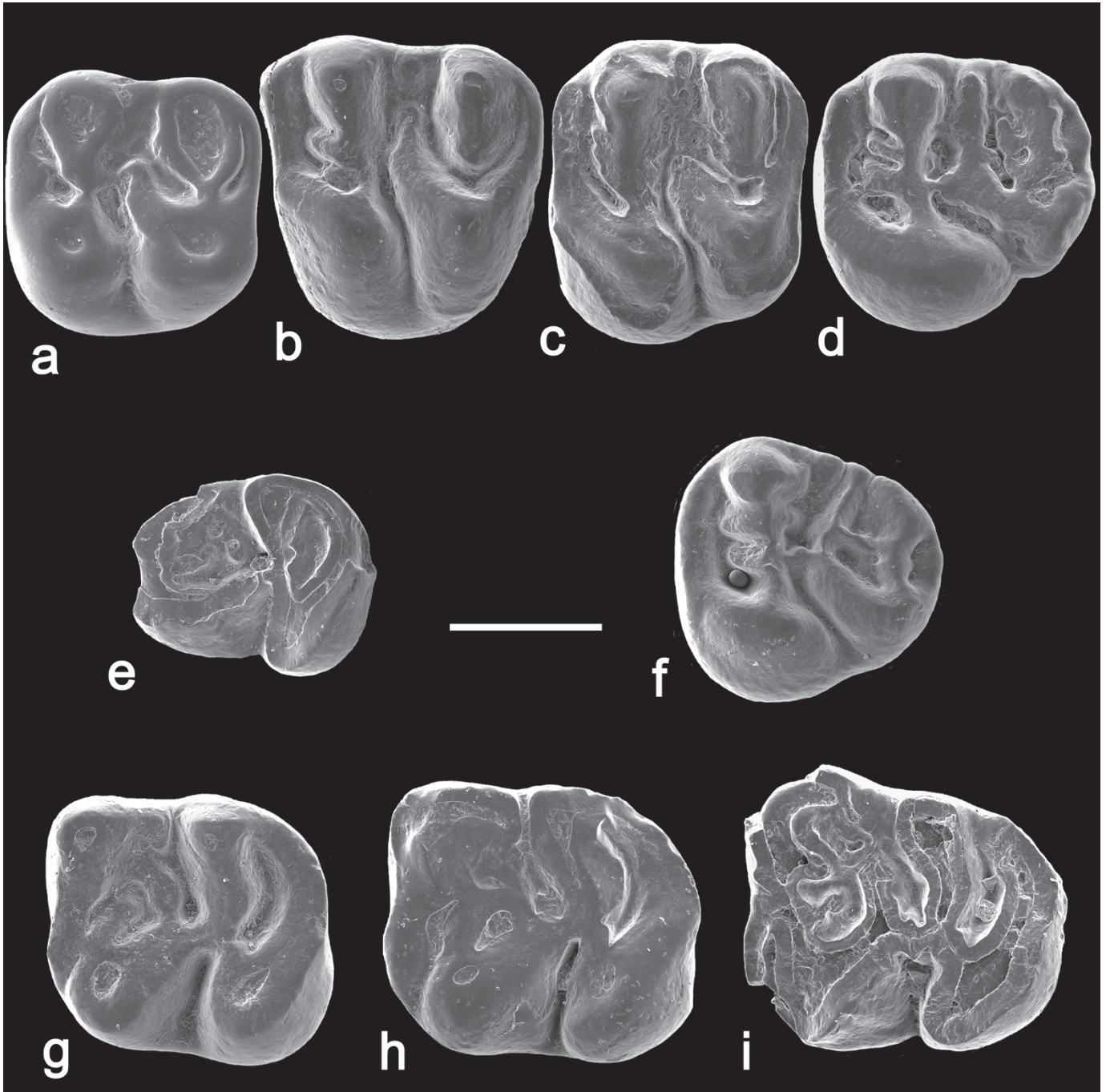
Fig. 10. Scanning electron micrographs of gold-palladium-coated epoxy casts of cheek teeth of *Estellomys ibericus* from Les Alleveys 1986, in occlusal view. a) Left P^4, MGL.47619. b) Right $M^{1/2}$ (reversed), MGL.47569. c) Right $M^{1/2}$ (reversed), MGL.47473. d) Left M^3, MGL.47614. e) Right P_4 (reversed), MGL.47499. f) Left M^3, MGL.47499. g) Left $M_{1/2}$, MGL.47620. h) Left $M_{1/2}$, MGL.47545. i) Left M_3, MGL.47404. Scale bar: 1 mm.

Subfamily Theridomyinae ALSTON 1876

Type genus. – *Theridomys* JOURDAN 1837.
Included genera. – *Archaeomys* LAIZER & PARIEU 1839; *Blainvillimys* STEHLIN & SCHAUB 1951; *Estellomys* HARTEN-

BERGER 1971; *Isoptychus* POMEL 1853; *Patriotheridomys* VIANEY-LIAUD 1975; *Protechimys* SCHLOSSER 1884; *Thalerimys* TOBIEN 1972; *Toeniodus* POMEL 1853.

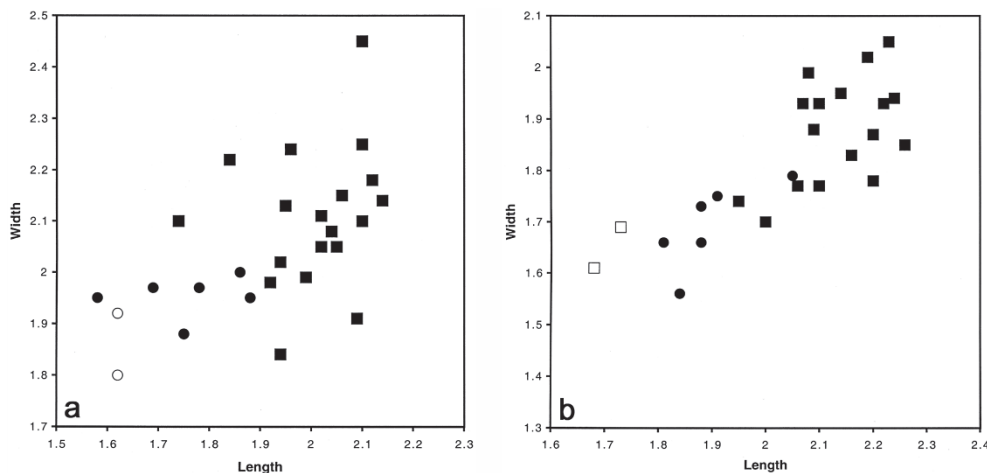*Diagnosis.* – Upper and lower cheek dentition with five crests,

Fig. 11. Scatter diagrams of length versus width in millimetres of species of *Estellomys*. a) M$^{1/2}$. b) M$_{1/2}$. ■ = *E. cansouni* from Fons 4; □ = *E. ibericus* types from Sossis; ● = *E. ibericus* from Les Alleveys 1986; ○ = *E. ibericus* from Mormont (undifferentiated). Values of *E. cansouni* and *E. ibericus* types from Hartenberger (1973: fig.5).

Table 4. Statistics of length and width measurements in millimetres of cheek teeth of *Estellomys ibericus* from Les Alleveys 1986. Abbreviations as in Table 2.

Tooth	N	OR	Length Mean	SD	V	N	OR	Width Mean	SD	V
P^4	3	1.58–1.69	1.65			3	1.56–1.83	1.70		
M$^{1/2}$	7	1.58–1.88	1.74	0.1124616	6.46	6	1.88–2.00	1.95	0.0403319	2.07
M^3	4	1.64–1.92	1.79			4	1.67–1.97	1.80		
P$_4$	1		1.63			1		1.31		
M$_{1/2}$	6	1.81–2.05	1.90	0.0836062	4.40	7	1.56–1.79	1.70	0.0783156	4.61
M$_3$	1		2.13			1		1.84		

internal sinus 'proverse'; teeth semihypsodont to hypsodont; anterior palatine foramina vast. (Translated from Vianey-Liaud 1979: 147).

Comment. – More recently, Vianey-Liaud (1998) has discussed the subfamily definition and stressed such characters as obliquity of the sinus and sinusid, the elongation of the milk premolars and well developed mesolophid. With inclusion of *Estellomys* (Vianey-Liaud et al. 1994), supported by the cladistic analysis below, however, the DP4 elongation character is no longer diagnostic. The other two are described here (Appendix 1, characters 27, 28(2)) as unequivocal synapomorphies thus: lower molar hypoconid overhanging sinusid mesially; lower molar mesolophid weak and long.

Genus *Estellomys* HARTENBERGER 1971

Type species. – *Estellomys cansouni* HARTENBERGER 1971.
Included species. – *Estellomys ibericus* (THALER 1966).

Original diagnosis. – Theridomyidae close to *Sciuroides* but with distinct tendency towards hypsodonty (translated from Hartenberger 1973: 18).

Comment. – As a very primitive theridomyine, the cladistic analysis below found only two homoplastic characters defin-

ing the genus: M^3 with well developed metaloph, plus reversal of loss of the M$^{1-2}$ hypolophule.

Estellomys ibericus (THALER 1966)
(Figs. 10, 11, 13b)

vp 1857   *Theridomys siderolithicus* – Pictet: pl.6, fig.12.
*   1966   *Adelomys ibericus* – Thaler: 46–48, fig.9.
.   1973   *Estellomys ibericus* (THALER) – Hartenberger: 19–21, fig. 4G.
v.   2000   *Estellomys* aff. *cansouni* Hartenberger – Hooker & Weidmann: 48, figs 31g–j, 32.

Types. – Two right M$_{1/2}$s, Sabadell Museum, holotype, UM.1918, paratype, UM.1887, from the early Priabonian of Sossis, Spain.
Material. – 3 P^{4}s (MGL.47558, 47619, 47623), 7 M$^{1/2}$s (MGL. 47473, 47569, 47578, 47589, 47590, 47593, 47616), 4 M^{3}s (MGL.47499, 47551, 47555, 47614), right P$_4$ (MGL.47418), 7 M$_{1/2}$s (MGL.47431, 47462, 47545, 47553, 47577, 47613, 47620), M$_3$ (MGL.47404); from Les Alleveys 1986.

Emended diagnosis. – Small species of *Estellomys*, mean length of M$^{1/2}$ 1.74 mm (see Table 4).

Description. – P^4: All three specimens are worn and show substantial tip wear. All four main cusps are of essentially equal size and are equally spaced, the tooth outline being sub-

quadrate. All show a prehypocrista that does not reach the mesostyle, which is isolated. Vestiges of an endoloph are present on the adjacent walls of protocone and hypocone of MGL.47619 (Fig. 10a) and in the heavily worn MGL.47558, these two cusps are joined. There is no clearly developed paraconule, but wear inhibits observation. The general pattern is like *E. cansouni* Hartenberger 1971 (Hartenberger 1973: fig. 4A), but differs in lacking the complete mesoloph of the latter species.

$M^{1/2}$: All but one (Figs. 10b, 13b) of the seven specimens have either heavy dietary wear or are broken or corroded. Nevertheless, all show outlines that are broader than long. The protocone extends markedly more lingually than the hypocone in two specimens (Fig. 10c), which seems not to be purely positional (i.e. likely M^2), but a feature of the genus (Hartenberger 1973: fig. 4B, pl. 3, figs 7–8; Hooker & Weidmann 2000: fig. 31h). Two specimens (MGL.47590, 47578) show a complete mesoloph, the rest showing variable incompleteness, thus comparable with *E. cansouni* (Hartenberger 1973: figs 4B–C, pl. 3, figs 7–8). The paraconule is weak in most, its projection from the protoloph to the mesial margin ranging from 30–55% of the distance. In one (Fig. 10c), the metalophule II has a narrow connection to the posteroloph (hypolophule). Another (MGL.47590) has a short mesiobuccal projection from metalophule II like derived species of *Elfomys*. An endoloph is lacking on all specimens, although very deep wear has merged the exposed dentine of the protocone and hypocone on MGL.47578. MGL.47569 is nearly unworn lingually; the protocone is 1.37 mm high and tooth length is 1.88 mm; height is therefore 73% of length.

M^3: The four specimens show consistency of outline but great morphological variation in cresting and development of minor cusps. The teeth are longer than wide with a massive lingually projecting protocone and distinct emargination of the lingual margin. All have an essentially complete mesoloph, but in two it bypasses the mesostyle distally (Fig. 10f). The sinus varies from completely open to completely closed (Figs. 10d, f). Two specimens have a doubled paraconule, which contrasts with that of M^{1-2} by being larger, its distance range to the mesial margin being 55–65%. All have a distinct metalophule II, two with an additional posteroloph (Figs. 10d, f), one of which (MGL.47499) has a mesiodistal crest joining the mesoloph to the metalophule II (Fig. 10f).

P_4: The single tooth (Fig. 10e) is worn and corroded but is similar in cusp pattern to that of *E. cansouni* (Hartenberger 1973: pl. 3, fig. 9), with distinct protoconid and metaconid. It differs in having the ectolophid attaching more lingually to the hypolophulid and in being relatively shorter. $M_{1/2}$: The tooth outline is relatively broad, matching the situation in the uppers (Figs. 10g, h). The hypoconid encroaches mesially on the sinusid, making it narrow and oblique, a feature of the genus and of the subfamily Theridomyinae. There is much variation in development of the various crests. Of the six sufficiently complete specimens, five have an anterolophulid, this crest being absent in MGL.47545 (Fig. 10h). There is

variation in development of a mesolophid from a mere lingual bulge on the ectolophid (MGL.47553) to a crest crossing more than half way to the lingual margin (Fig. 10g). There may be other crests in the talonid basin too, especially on those with the weaker mesolophid. These other crests include a remnant of the buccal branch of the metalophulid (Figs. 10g, h) and longitudinal crests that emanate from the trigonid (metaconid or lingual branch of the metalophulid) and may join the mesolophid (Fig. 10h). The postmetacristid is usually well developed (Figs. 10g, h) and may form a metastylid (Fig. 10g). The buccal branch of the metalophulid and the anterolophid are consistently present, but the lingual branch of the metalophulid is often absent (Fig. 10g). Similar variation is present in *E. cansouni* (Hartenberger 1973: figs 4D,E,G, pl. 3, figs 10–13).

M_3: The single tooth is worn and somewhat corroded, but has a moderate length, dentine-cored mesolophid and there are two short crests projecting distally from the lingual arm of the metalophulid (Fig. 10i). Like most of the $M_{1/2}$s, the hypoconid is projected mesially, overhanging the sinusid distally.

Discussion. – Although numbers are relatively low, length and width dimensions of both $M^{1/2}$ and $M_{1/2}$ have coefficients of variation appropriately low to represent a single species (Table 4). The dimensions are significantly smaller than those of *E. cansouni* from Fons 4 (Fig. 11; Hartenberger 1973: table 4, fig. 5). In the case of the lowers, they are close to the only previously known specimens, the two type $M_{1/2}$s, of *E. ibericus* (Fig. 11b; Thaler 1966: fig. 9; Hartenberger 1973: figs 4G, 5B). In fact, both teeth from Sossis are relatively broader than any from Les Alleveys 1986, although the differences are slight. The M_{1-2} of one individual of *Estellomys* from the early Priabonian of Eclépens B are relatively broader again, but are also smaller than *E. cansouni*, to which they were attributed with an 'aff.' qualification, whilst recognising an approach to *E. ibericus* in dimensions (Hooker & Weidmann 2000). Adding the measurements of the Sossis *E. ibericus* specimens to those from Les Alleveys 1986 shifts the means to 1.85 mm for length and 1.69 mm for width, increases the coefficient of variation for length slightly to 6.14 and reduces it for width to 4.47. This is good evidence that the Les Alleveys 1986 assemblage indeed belongs to *E. ibericus*. Adding also the measurements of M_{1-2} from Eclépens B shifts the means to 1.81 mm for length and 1.69 mm for width, further increases the coefficient of variation for length to 7.57 and reduces it for width to 4.37. This suggests that the Eclépens B *Estellomys* lower molars belong to *E. ibericus*.

Two $M^{1/2}$s from Eclépens B were also attributed to *E.* aff. *cansouni* by Hooker & Weidmann (2000). Their length and width dimensions plot within the lower end of Hartenberger's (1973: fig. 5A) scatter for *E. cansouni*, but which is within the zone of overlap with *E. ibericus* from Les Alleveys 1986. Adding the Eclépens B measurements to those of the Les Alleveys 1986 assemblage shifts the means to 1.75 mm for
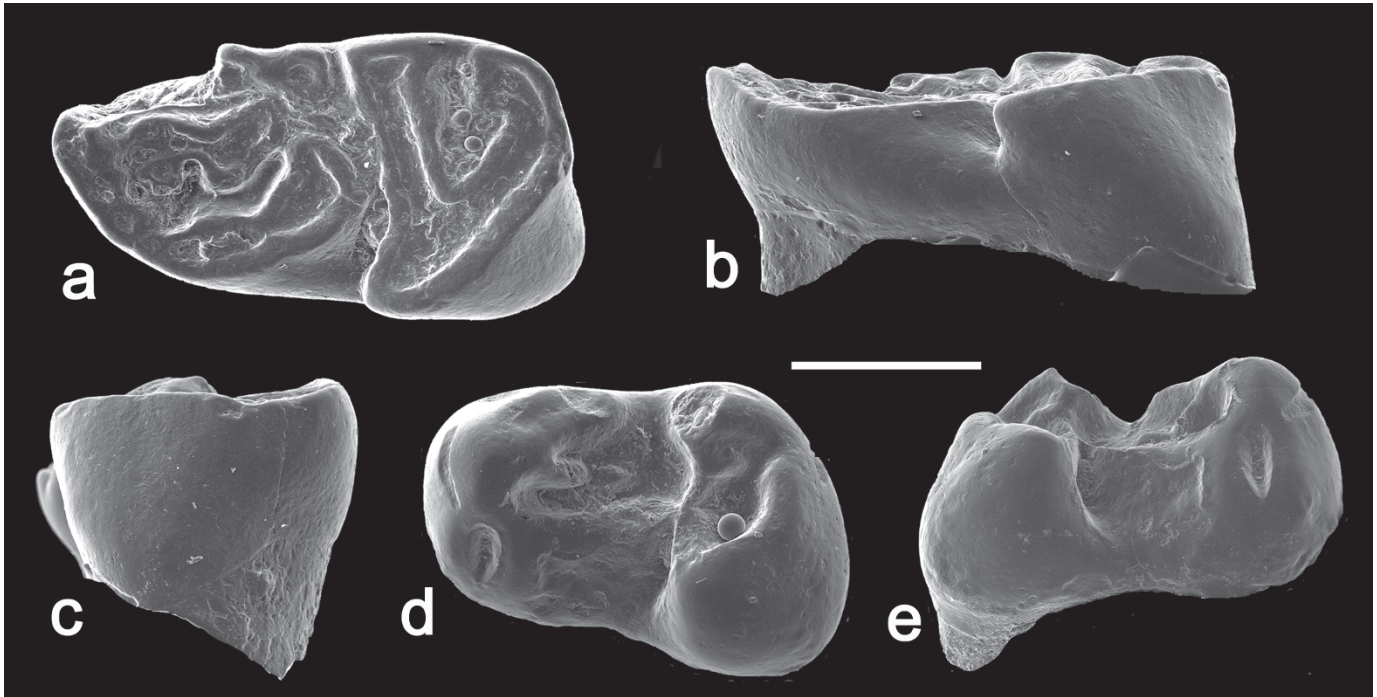
Fig. 12. Scanning electron micrographs of gold-palladium-coated epoxy casts of cheek teeth of Theridomyinae from Les Alleveys 1986. a–c) *Patriotheridomys*? sp., left DP$_4$, MGL.47402. d, e) Theridomyinae indet., right P$_4$ (reversed in d), MGL.47419. Views are: occlusal (a, d), buccal (b, e) and distal (c). Scale bar: 1 mm.

length and to 1.99 mm for width, reduces the coefficient of variation for length to 5.69 and increases it for width to 3.41. A maxilla with M$^{1-2}$ from Mormont undifferentiated was also attributed to *E.* aff. *cansouni* by Hooker & Weidmann (2000: figs 31g, 32). Its tooth measurements are shown in Figure 11a. Adding the length and width dimensions to those of Les Alleveys 1986 and Eclépens B shifts the means to 1.73 mm for length and to 1.96 mm for width and increases the coefficient of variation for length to 5.90 and for width to 4.40. Nevertheless, the coefficients of variation for all three localities combined are well within the limits acceptable for a single species and are therefore referred here to *E. ibericus*.

As Fons 4, Eclépens B and Sossis are all penecontemporaneous sites in the early Priabonian, Hartenberger's (1973) idea that *E. ibericus* is ancestral to *E. cansouni* is an unlikely scenario. The Les Alleveys 1986 occurrence of *E. ibericus* extends the known range of the species and of the genus *Estellomys* down into the Bartonian.

Genus *Patriotheridomys*? Vianey-Liaud 1975
Patriotheridomys? sp.
(Figs. 12a–c)

Material. – Left DP$_4$ (MGL.47402) from Les Alleveys 1986.

Description. – The tooth is quite worn and there is some breakage mesiolingually. Length is 2.79 mm, width 1.64 mm. It is elongate and pointed mesially. The width is therefore 59% of the length. The ectolophid is strongly convex buccally, ending distolingually in a cuspate swelling and giving rise to a protoconid at the convexity (Fig. 12a). The sinusid is open, the ectolophid making no contact with the hypolophulid. There is an oblique valley paralleling the distal branch of the ectolophid, which does not open mesiobuccally at an antesinusid. There is an irregular median longitudinal crest lingual of this valley. There is a series of confluent cuspules making up the sharply convex mesial end, but no division into distinct identifiable cusps. There are two cuspules on the lingual edge distal of the broken area and mesial of the entoconid. The buccal and lingual walls of the distal region of the tooth enclosing synclinid IV diverge occlusally, indicating considerable crown height in the unworn state (Fig. 12c). Wear more mesially is lighter and crown height here appears to have been lower (Fig. 12b). The posterolophid recurves mesially on the lingual side to form a hook.

Discussion. – The only theridomyids with such an elongate DP$_4$ are theridomyines and the issiodoromyines *Pseudoltinomys* and *Issiodoromys*. Affinity with *Pseudoltinomys* can be excluded because of its simpler pattern of ridges mesial of the hypolophulid (e.g. Vianey-Liaud 1975: fig.13). The elongation is nevertheless much less marked than in most theridomyines or *Issiodoromys*, being matched only by similar aged, but smaller and lower crowned '*Theridomys*' *varleti* Hartenberger & Louis, 1976 from Grisolles (Vianey-Liaud & Ringeade
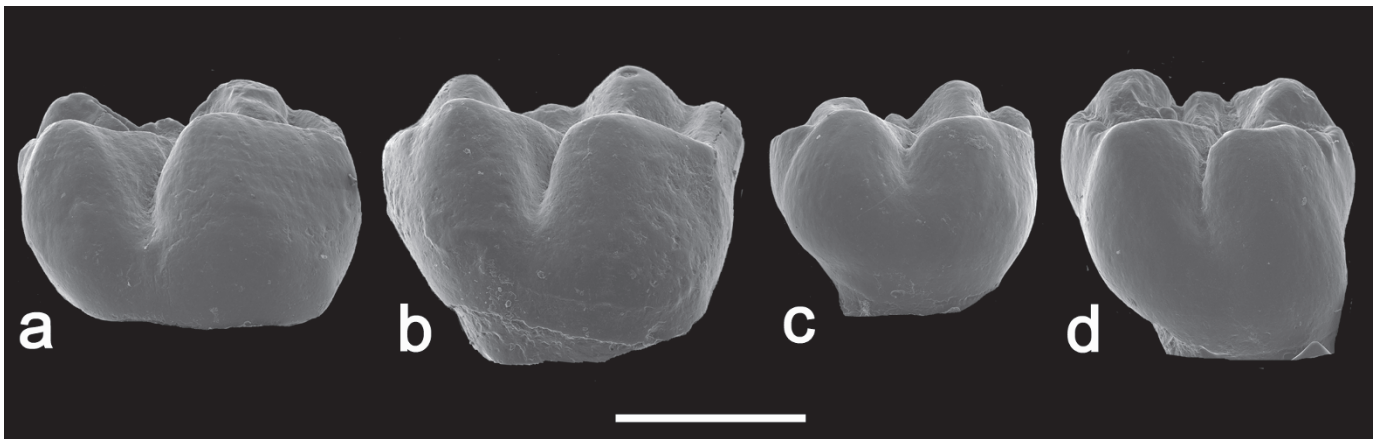
Fig. 13. Scanning electron micrographs of gold-palladium-coated epoxy casts of upper cheek teeth of Theridomyidae from Les Alleveys 1986, in lingual view. a) *Paradelomys* sp., right $M^{1/2}$, MGL.47556. b) *Estellomys ibericus*, right $M^{1/2}$, MGL.47569. c) *Elfomys engesseri*, left $M^{1/2}$ (reversed), MGL.47494. d) *Pseudoltinomys* aff. *crebrum*, right P^4, MGL.47591. Scale bar: 1 mm.

1993: fig.34). The greatest similarity of pattern, outline shape and hypsodonty is with *Patriotheridomys*. Here the connection between the ectolophid and hypolophulid is often broken in *P. altus* VIANEY-LIAUD 1975 (e.g. Vianey-Liaud & Ringeade: 1993, fig. 1d,h). The hook-like lingual end of the posterolophid is also typical of *P. altus* (e.g. Vianey-Liaud & Ringeade 1993: fig. 1c, f, h, i). The absence of an antesinusid is as noted by Vianey-Liaud & Ringeade (1993) a primitive feature and is the state present in *P. sudrei* VIANEY-LIAUD & RINGEADE 1993. MGL.47402 is, however, more primitive than either *P. altus* or *P. sudrei* in its relative shortness. Using mean measurements from Vianey-Liaud (1975) and Vianey-Liaud & Ringeade (1993), width is 50% of the length in *P. sudrei* and 41% of length in *P. altus*. Although only a single tooth, identity with the genus *Patriotheridomys* is tentatively made, suggesting a long range backward in time from the middle of the Priabonian to the early Bartonian.

Theridomyinae gen. et sp. indet.
(Figs. 12d, e)

Material. – Right P_4 (MGL.47419) from Les Alleveys 1986.

Description. – The tooth is 2.25 mm long by 1.61 mm wide. It is elongate with the ectolophid joining the hypolophulid at around its midpoint (Fig. 12d). The mesial end of the tooth is rolled, although the bluntness appears real as the enamel has not been removed. There is an antesinusid and a crest extends distally from the mesial end half way along the talonid basin. The posterolophid does not reach the entoconid. Crown height is relatively low (Fig. 12e).

Discussion. – The tooth has a longer pre-hypolophulid portion than is typical for other theridomyid subfamilies, including the issiodoromyine *Pseudoltinomys*, and for *Estellomys*. It is too small to belong to the *Patriotheridomys*? sp. represented by a DP_4. It is overall quite similar to the P_4 of '*Theridomys*' *varleti* (Hartenberger & Louis 1976: pl.1, fig.3), although the median talonid crest is shorter and it lacks the enamel wrinkling of that species. It is also slightly larger than the largest '*T*'. *varleti* P_4. It is clearly different from the much larger and more hypsodont and lophodont *Isoptychus* species previously recorded from the 1852 collection (Hooker & Weidmann 2000: fig.35) and judged here to have been mislabelled as to locality. It is concluded to belong to a theridomyine, but which is too incomplete to identify or name.

Interrelationships of the subfamilies of the Theridomyidae

The Les Alleveys 1986 theridomyid assemblage includes some of the most primitive members of three of the five recognised subfamilies, namely: Theridomyinae (*Estellomys ibericus*, *Patriotheridomys*? sp., Theridomyinae indet.), Issiodoromyinae (*Elfomys engesseri* sp. nov., *Pseudoltinomys* aff. *crebrum*) and Remyinae (*Remys* sp.). In addition, the genus *Paradelomys*, represented here by an undetermined species, has not been allocated to a subfamily since it was shown not to belong to the family Pseudosciuridae (Hartenberger & Louis 1976; Hooker 1986; Hooker & Weidmann 2000). Later and more derived species and genera have evolved many convergent features of hypsodonty and lophodonty, making a clear understanding of their interrelationships difficult to achieve. Character states of early more primitive forms, which are likely to represent an early stage in the radiation of the group are judged more likely to provide a better idea of these relationships. A cladistic analysis is conducted here of the more primitive members of subfamilies Remyinae, Issiodoromyinae, Theridomyinae and Columbomyinae, including the representative taxa at Les Alleveys. Oligocene *Sciuromys* is included here as, despite its
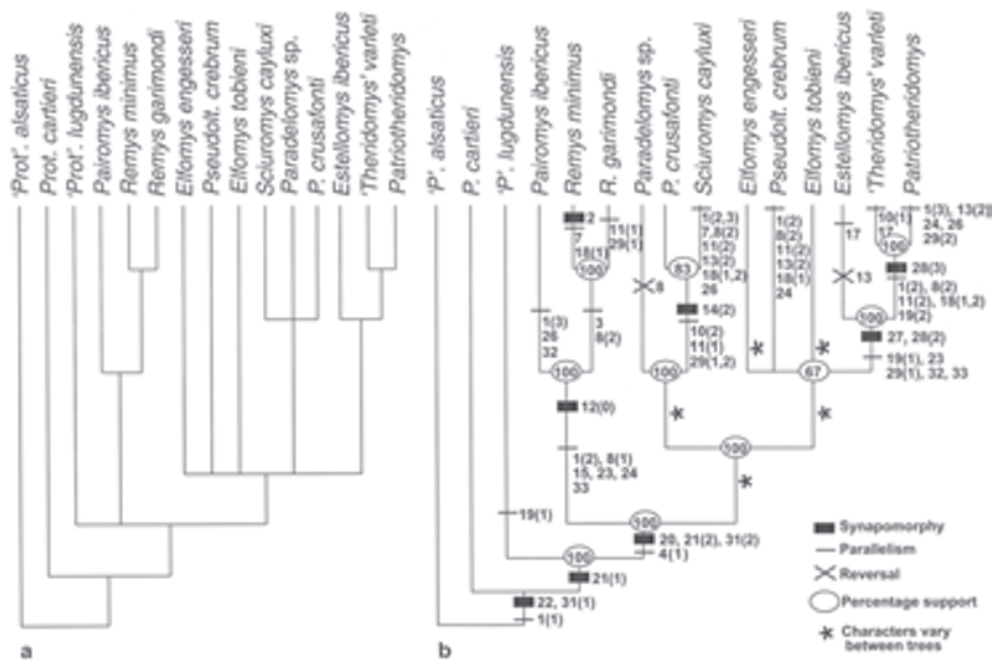
Fig. 14. Consensus trees of the six maximum parsimony trees generated by PAUP, from the data matrix in Appendix 2. a) Strict consensus; b) majority rule consensus, with characters under the Deltran optimization, common to all trees. Branches with character distributions that vary between trees are indicated by asterisks and those characters relevant to trees 2 and 4/5 are shown in Figure 15. *Prot.* = *Protadelomys*; *Pseudolt.* = *Pseudoltinomys*.

young age, it is the most primitive currently accepted columbomyine and remains relatively conservative compared to genera in other subfamilies. The data matrix of fifteen taxa and 33 characters is shown in Appendix 2 and the character descriptions and codings are in Appendix 1. All multistate characters were treated as ordered. *Protadelomys alsaticus* HARTENBERGER, 1969 was employed as outgroup, treated as paraphyletic with respect to the ingroup, which was assumed to be monophyletic. The matrix was analysed by PAUP 4.0b10 (Swofford 2002) using the Branch and Bound algorithm.

Results of the cladistic analysis

PAUP found six maximum parsimony trees (MPT) of 93 steps. The consistency index excluding uninformative characters (CI) is 0.5275 and the retention index is 0.7095. The strict consensus tree (Fig. 14a) groups *Pairomys ibericus* VIANEY-LIAUD, SCHMIDT-KITTLER & PELAÉZ-CAMPOMANES 1994, *Remys minimus* and *Remys garimondi* as a Remyinae clade, which is sister group to a clade comprising all the other taxa except species of *Protadelomys*. This large clade of 'other taxa' contains a Theridomyinae clade, with *Estellomys ibericus* as sister to '*Theridomys*' *varleti* and *Patriotheridomys*, a Columbomyinae clade, consisting of an unresolved trichotomy of species of *Paradelomys* plus *Sciuromys cayluxi* SCHLOSSER 1884, and three unresolved branches consisting of *Pseudoltinomys crebrum* plus species of *Elfomys*. Successively more basal to the two major clades are '*Protadelomys*' *lugdunensis*, *P. cartieri* and the outgroup '*P*'. *alsaticus*.

The majority rule consensus tree (Fig. 14b) further resolves the Columbomyinae clade, with *Paradelomys* sp. as sister

taxon to *P. crusafonti* plus *Sciuromys cayluxi*, which is distinct from a clade consisting of Theridomyinae plus *Pseudoltinomys* and species of *Elfomys*.

Of the six MPTs, only tree 1 differs from the majority rule consensus in its resolution of the Columbomyinae. *Sciuromys* as sister to a *Paradelomys* clade, is supported by such reversals as redevelopment of upper molar postparacristae and premetacristae (character 3) and loss of lower molar mesolophid (character 28). It would also mean a long ghost range for *Sciuromys* extending from the Early Oligocene back to the middle Bartonian.

Trees 1, 3 and 6 show *Elfomys* as paraphyletic, with *E. engesseri* and *E. tobieni* branching successively below *Pseudoltinomys* and the Theridomyinae. This means that character 16, the mesiobuccal metaconule crest that uniquely defines *Elfomys* is shown as independently acquired, under the Deltran optimization, or as only primitively present and lost in more derived genera, under the Acctran optimization. It also means that *E. engesseri* and *E. tobieni*, which succeed eachother in time (respectively middle and late Bartonian), the latter showing acquisition of derived characters, should precede *Pseudoltinomys crebrum*, which is in fact contemporaneous with *E. engesseri*. Whereas this is not impossible, the topology produces unnecessary ghost ranges. Moreover, the successive nodes at the branching of *E. tobieni* and *P. crebrum* in tree 3 and the node supporting the sister relationship of Columbomyinae and Theridomyinae in trees 1 and 6 are weak. Therefore, trees 1, 3 and 6 are abandoned.

Tree 2 and trees 4 and 5 differ only in the relationships of *Elfomys* species to *Pseudoltinomys* and of these to the Theridomyinae (Fig. 15). The tree 4 topology includes a clade
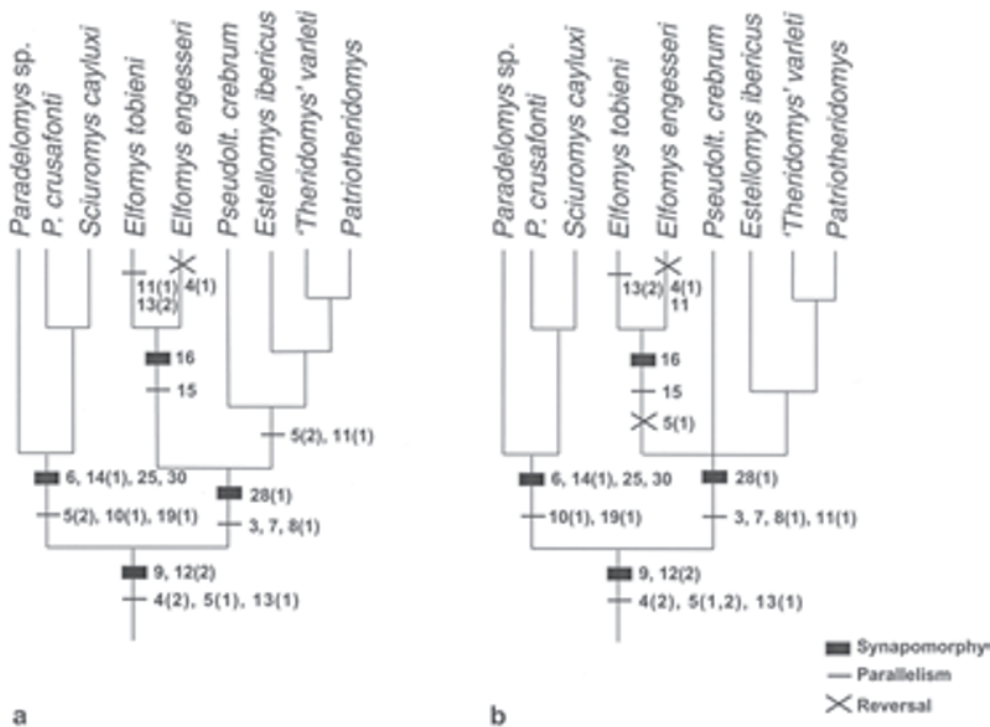
Fig. 15. Parts of maximum parsimony trees 2 (a) and 4/5 (b) with characters, involving the clade comprising Columbomyinae, Issiodoromyinae and Theridomyinae, generated by PAUP from the data matrix in Appendix 2. Characters omitted from branches can be found in Figure 14b. *Pseudolt. = Pseudoltinomys.*

consisting of *Pseudoltinomys* and the species of *Elfomys*. However, this clade is unsupported by any characters and the tree is thus identical to tree 5, where the clade is collapsed into its component branches. In both trees 2 and 4/5, *Elfomys* is monophyletic. The only difference is that in tree 4/5, *Pseudoltinomys* forms an unresolved trichotomy with *Elfomys* and the Theridomyinae, whereas in tree 2 it is sister to the Theridomyinae. This is reflected in small differences in character distributions. These are shown in Figure 15 for the Deltran optimization.

In tree 4/5, *Elfomys* is defined partly by reversal of character 5 from state 2 to state 1, indicating relative shortening of P^4. In the same tree, *E. engesseri* is defined in the Deltran optimization by reversal of characters 4 and 11, which involve partial redevelopment of the upper molar endoloph and reduction of the mesoloph, which are shown as having more derived states at more basal nodes. In Acctran, an extra reversal involves reduction in the incidence of the hypolophule on M^{1-2}, a minor character. Tree 2 is preferred as in Deltran it avoids reversal of characters 5(2) and 11(1), whose derived states have shifted crownwards to define *Pseudoltinomys* plus Theridomyinae. Counterintuitively, tree 2 retains the reversal of the upper molar endoloph loss (4(1)) as defining *Elfomys engesseri*.

In none of the MPTs is there support for the Issiodoromyinae as represented by *Elfomys* and *Pseudoltinomys* and dental characters that have previously been used to support the subfamily (Vianey-Liaud 1976) involve only derived members or are primitive. Nevertheless, the skull characters used to define derived members of the subfamily (Vianey-Liaud 1976) suggest that it is monophyletic, although these cannot be tested in primitive members as little more than dental remains are known prior to the late Priabonian.

There is good support for a Columbomyinae that includes species of a paraphyletic genus *Paradelomys* as early members. The previous generic content, *Sciuromys* and *Columbomys*, gave the subfamily a range in time starting no earlier than the Grande Coupure (early Oligocene) (Vianey-Liaud 1979). *Sciuromys* can be seen to be acquiring such derived states as increased hypsodonty, loss of upper molar paraconule, acquisition of complete upper molar mesoloph and P^4 protoloph in parallel with other theridomyid subfamilies, but superimposed on an otherwise rather primitive plan. The Columbomyinae with inclusion of *Paradelomys* is defined uniquely by: lower molars with distally shifted protoconid and frequently bent ectolophid and P^4 commonly characterised by a distinct ectoflexus, plus several other characters paralleled elsewhere in the family Theridomyidae. The marked morphological distance between *P. crusafonti* and *Sciuromys cayluxi* suggests either rapid evolution between MP19 and 21 or an earlier range extension of the latter in a part of Europe yet to be sampled.

The Theridomyinae includes as a monophyletic group the genus *Estellomys*, once placed in the subfamily Oltinomyinae (Hartenberger 1973). The present study confirms the more recent transfer of the genus to the Theridomyinae (Vianey-Liaud et al. 1994: 122). In trees 2 and 4/5 the clade is defined unequivocally by the mesial overhanging of the sinusid by the hypoconid (character 27) and by the weak but extensive

mesolophid development (character 28(2)) on lower molars as well as by several characters paralleled elsewhere on the cladogram. The presence on M³ of *Estellomys ibericus* of a well developed metaloph (17) is shared with most theridomyine genera, although not with *Patriotheridomys* (Vianey-Liaud & Ringeade 1993). This character may have been independently acquired by *Estellomys* and close relatives of *Theridomys* (under the Deltran optimization) or more likely shared by the theridomyine stem and secondarily reduced in *Patriotheridomys* (under the Acctran optimization).

The relatively remote relationships of the Remyinae reflects their phenetically rather different morphology (Vianey-Liaud et al. 1994) and in particular their M¹⁻² prehypocrista plus mesoloph development, which incorporates the metaconule (12(0)) instead of bypassing it mesially (12(2)) as in other derived theridomyid subfamilies. Characters 2, 7 and 18(1), shown to delimit *Remys minimus*, are likely to be present in *R. garimondi* also, but the tooth types involved are unknown in the latter species.

The problem of Oltinomyinae relationships

The only theridomyid subfamily not represented at Les Alleveys is the Oltinomyinae HARTENBERGER 1971, whose record begins much later around the middle of the Priabonian (MP18). Long considered related to the Remyinae, a comprehensive study has placed them instead close to the Theridomyinae (Vianey-Liaud et al. 1994). The older and perhaps more primitive oltinomyine genus, *Ectropomys* BOSMA & SCHMIDT-KITTLER 1972, does share a number of derived characters with the Remyinae, as well as retaining such primitive states as a partial upper molar endoloph. States shared with the Remyinae are the relatively buccolingually narrow P⁴ (character 2) and the relatively distobuccal position of its M¹⁻² prehypocrista plus mesoloph and shortness of metalophule II, implying incorporation of the now missing metaconule in the prehypocrista (character 12(0)). At the same time, however, it shares more derived characters with other theridomyid subfamilies, including those of lophodonty and hypsodonty.

Ectropomys was therefore coded and added to the matrix and a trial analysis performed with PAUP 4.0b10. The result was five MPTs. The strict consensus of these shows *Ectropomys* as an additional branch in the poorly resolved clade with unresolved Theridomyinae, Columbomyinae, *Pseudoltinomys* and *Elfomys* spp. In the majority rule consensus it plotted as sister group to the Theridomyinae, supporting Vianey-Liaud et al.'s (1994) conclusions. However, its position here in four out of the five MPTs involves such unlikely reversals as partial redevelopment of the upper molar endoloph (character 4(1)) and re-routing of the upper molar prehypocrista and mesoloph (12(2) to 12(0)). It also reverses the order of nodes in the Columbomyinae. If the homology of the coding of character 12 is correct for *Ectropomys*, it suggests that its position close to theridomyines may be resulting

from a long ghost range, likely to have extended down well into the Bartonian, which is emphasizing its probably convergently evolved theridomyine-like characters. Alternatively, if the coding of character 12 is incorrect, *Ectropomys* and the Oltinomyinae may indeed be sister taxon to the Theridomyinae. The finding of pre-MP18 representatives of the Oltinomyinae is potentially the most reliable way of resolving this issue.

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Appendix 1.

Description and coding of characters forming the data matrix (Appendix 2) and used in the cladistic analysis. All multistate characters were treated as ordered. Coding for hypsodonty parameters for Les Alleveys taxa was derived from the text and for others from specimens plus published material (Vianey-Liaud & Ringeade 1993; Vianey-Liaud et al. 1994).

Character 1: Cheek teeth brachyodont, height of $M^{1/2}$ protocone about 50% of tooth length (0); hypsodonty grade 1, height of $M^{1/2}$ protocone about 70% of tooth length (1) (Figs. 11a–c); hypsodonty grade 2, height of $M^{1/2}$ protocone about 80% of tooth length (2) (Fig. 11d); hypsodonty grade 3, greater than 100% (3).

Character 2: P4 of similar width to M1 (0); narrower (1).

Character 3: Crests on upper cheek tooth paracone and metacone (0); no crests (1).

Character 4: Upper cheek tooth endoloph complete (0); incomplete (1); missing (2).

Character 5: P^4 shorter than long, protocone and hypocone poorly separated (0); equidimensional, protocone and hypocone poorly separated (1); equidimensional, protocone and hypocone well separated (2).

Character 6: P^4 without distinct ectoflexus (0); distinct ectoflexus usually present (1).

Character 7: P^4 with protoloph absent or present in only a few individuals (0); consistently with protoloph (1).

Character 8: M^{1-2} paraconule large: mean extending from protoloph c.60% of distance to mesial margin (0); small: mean extending from protoloph c.45% of distance to mesial margin (1); lacking (2).

Character 9: M^{1-2} metacone close to distal edge (0); separated from distal edge by posteroloph (1).

Character 10: M^{1-2} sinus open buccally (0); closed in some (1); closed in all (2).

Character 11: M^{1-2} without mesoloph (0); with partial mesoloph (1); with complete mesoloph (2).

Character 12: M^{1-2} prehypocrista passing through metaconule (0); no prehypocrista (1); prehypocrista bypassing metaconule mesially (2).

Character 13: M^{1-2} hypolophule linking metalophule II with posteroloph missing (0); present in a few individuals (1); present in most (2).

Character 14: Protocone approximately opposite paracone on P^4-M^3 (0); protocone more mesially situated in a few individuals, widening sinus (1); more mesially situated in most individuals, widening sinus (2).

Character 15: upper molars more than 1.5 mm long (0); less than 1.5 mm long (1).

Character 16: M^{1-2} without mesiobuccal metaconule crest (0); some individuals with crest (1).

Character 17: M^3 with metaloph poorly developed (0); well developed (1).

Character 18: M^3 with paraconule large (0); small (1); missing (2). Parameters as for character 8.

Character 19: P4 prehypolophulid part no longer than half the total tooth length (0); slightly longer (1); much longer (2).

Character 20: Lower molar ectoflexid present (0); absent (1).

Character 21: Lower molar mesoconid large (0); small (1); absent (2).

Character 22: Lower molar antesinusid absent (0); present (1).

Character 23: Lower molar trigonid long (0); short, compressing antesinusid (1).

Character 24: Lower molar ectolophid unbroken (0); broken distally at junction with hypolophulid (1).

Character 25: Lower molar ectolophid straight (0); bent in some (1).

Character 26: Lower molar ectolophid slightly oblique (0); very oblique (1).

Character 27: Lower molar hypoconid not mesially overhanging sinusid (0); overhanging (1).

Character 28: Lower molar mesolophid absent (0); weak and short (1); weak and long (2); well developed but incomplete (3).

Character 29: Lower molar metalophulid broken, distally deflected (0); complete, straight, but distally deflected branch present (1); complete, straight, distally deflected branch absent (2).

Character 30: Lower molar protoconid opposite metaconid (0); more distally situated (1).

Character 31: Lower molar hypolophulid undeveloped (0); complete sinusoidal (1); complete, straight (2).

Character 32: Lower molars without distinct postmetacristid (0); with distinct postmetacristid (1).

Character 33: Molars not relatively transversely elongate (0); transversely elongate (1).

Appendix 2.

Data matrix of dental characters of theridomyids used in the cladistic analysis. Characters are described in Appendix 1.

	1111111111222222222223333
	1234567890123456789012345678901234567890123
'Protadelomys' alsaticus	00000000000100000000000000000000
P. cartieri	10000000000100000000100000000100
'P'. lugdunensis	1000???0000100000?101100000000100
Pairomys ibericus	30010001000001000012111010000211
Remys minimus	21110012000001001012111000000201
R. garimondi	2?11???20010001???012111000010201
Paradelomys sp.	10022100110211000011210010000 1200
P. crusafonti	10022100121212000011210010002 1200
Sciuromys cayluxi	30022112122222000211210011002 1200
Elfomys engesseri	10111011100210110001210000010 0200
E. tobieni	10121011101220110001210000010 0200
Pseudoltinomys crebrum	20122012102220000101210100010 0200
Estellomys ibericus	10122011101200001011211000121 0211
Patriotheridomys	30122012102220000221211101132 0211
'Theridomys' varleti	20122??21122?00012212110001310 211