Published in "Annales de Paléontologie 105(2): 139–153, 2019"
which should be cited to refer to this work.

Aubenas-les-Alpes (S-E France). Part III – Last and final part of the mammalian assemblage with some comments on the palaeoenvironment and palaeobiogeography

Aubenas-les-Alpes (S-E France). Part III – Dernière partie de l'assemblage mammalien avec quelques commentaires sur le paléoenvironnement et la paléobiogéographie

Olivier Maridet[a,b,*], Marguerite Hugueney[c], Loïc Costeur[d]

[a] *Jurassica Museum, Fontenais 21, 2900 Porrentruy, Switzerland*
[b] *Department of Geosciences, Earth Sciences, University of Fribourg, Chemin du Musée 6, Pérolles, 1700 Fribourg, Switzerland*
[c] *22, avenue Condorcet, 69100 Villeurbanne, France*
[d] *Naturhistorisches Museum Basel, Augustinergasse 2, 4001 Basel, Switzerland*

A B S T R A C T

The study of the new material from Aubenas-les-Alpes makes it possible to add to the faunal list taxa hitherto unknown in this locality (*Neurogymnurus cayluxi*, *Issiodoromys minor*, *Eomys minor*, *Pseudocricetodon* cf. *hausi*, *Pseudocricetodon* aff. *philippi*). New specimens of the shrew *Srinitium marteli* increase our knowledge of this rare insectivore. The characteristics of the theridomorph *I. minor* confirm, as does the whole rodent fauna, the correlation with the MP25 level (Late Rupelian). The assemblage of Aubenas-les-Alpes indicates a rather open and dry environment, in accordance with the Early Oligocene climatic context, but some differences compared to other localities of the same age are also noticed. Finally the mammalian assemblage suggests an ongoing biogeographic differentiation at European scale during the Late Rupelian.

Keywords:
Oligocene (MP25)
Notometatheria
Eulipotyphla
Rodentia
Biostratigraphy
Cenogram

R É S U M É

L'étude du nouveau matériel issu d'Aubenas-les-Alpes permet de compléter la liste faunique par des taxa jusqu'alors inconnus dans cette localité (*Neurogymnurus cayluxi*, *Issiodoromys minor*, *Eomys minor*, *Pseudocricetodon* cf. *hausi*, *Pseudocricetodon* aff. *philippi*). Les nouveaux spécimens de la musaraigne *Srinitium marteli* améliorent notre connaissance de ce rare insectivore. Les caractéristiques du théridomorphe I. *minor* confirment, de même que l'ensemble de la faune de rongeurs, la corrélation avec le niveau MP25 (Rupélien supérieur). L'assemblage d'Aubenas-les-Alpes indique un environnement plutôt sec et ouvert, en accord avec le contexte climatique du début de l'Oligocène, mais quelques différences sont également notées par comparaison aux autres localités du même âge. Finalement l'assemblage mammalien suggère la mise en place d'une différentiation biogéographique à l'échelle européenne au cours du Rupélien supérieur.

Mots clés :
Oligocène (MP25)
Notometatheria
Eulipotyphla
Rodentia
Biostratigraphie
Cénogramme

* Corresponding author. Jurassica Museum, Fontenais 21, 2900 Porrentruy, Switzerland.
E-mail addresses: olivier.maridet@jurassica.ch (O. Maridet), marguerite.hugueney@gmail.com (M. Hugueney), loic.costeur@bs.ch (L. Costeur).

1. Introduction

The vertebrate fossil locality of Aubenas-les-Alpes (Alpes-de-Haute-Provence) is located on the northern part of the Cereste-Forcalquier syncline, within the Luberon geological reserve, 15 km North-West to Manosque. The locality was first mentioned by Roman (1912) and Helmer and Vianey-Liaud (1970) were the first to indicate the occurrence of small mammals in the fossil assemblage (see Menouret et al., 2015 for a detailed presentation of the locality and geological framework). Later Vianey-Liaud (1971, 1972a, b) and Vianey-Liaud et al. (1995) gave the following list of rodents: *Theridomys lembronicus*, *Blainvillimys blainvillei*, *Archaeomys gervaisi*, *Eucricetodon* aff. *huberi*, *Pseudocricetodon* aff. *incertus*, *Pseudocricetodon moguntiacus*, *Pseudodryomys/Oligodyromys* sp., *Gliravus garouillensis* (=*?Gliravus* cf. *bruijni,* =*Gliravus priscus*). In addition Crochet (1974, 1980, 1995) reported in the locality the occurrence of *Amphiperatherium exile*, *Srinitium* aff. *marteli*, *Myxomygale vauclusensis*, *Geotrypus antiquus* and *Geotrypus acutidentatus*. As mentioned by Menouret et al. (2015), one of the particularities of the locality is to present an association of small and large mammals which is rare in Southeastern France for that period. Recent samplings have been undertaken in order to improve our knowledge of the mammalian assemblage. The present publication focuses on the recently found specimens and add some species hitherto unknown to the faunal list.

2. Material and methods

Material: The studied material comes from a number of different samples. Part of the material was collected by Ducreux, Hugueney and Truc in the framework of the study of dating, correlations and palaeoenvironments of the Apt, Forcalquier and Manosque basins formations (Ducreux et al., 1985); L.C and O.M. also collected samples in 2010.

The specimens found by M.H., L.C. and O.M. and the figured specimens are deposited in the collections of the University Claude Bernard Lyon 1 (FSL, 'Faculté des Sciences de Lyon'), and are catalogued with the numbers: FSL 219005 to FSL 219049. The specimens found by Menouret (smaller fractions picked up by M.H) are deposited in the collections of the Requien Museum of Avignon (MR 3.003.213, MR 3.003.285 and MR 3.008.838 to MR 3.008.860).

Specimens and terminology: The material of small mammals is mainly composed of isolated teeth, plus a few fragmentary maxillaries or mandibles. The terminology used to describe the molars follows Hutchison (1974) and Crochet (1980) for marsupials and insectivores, Daxner-Höck and Höck (2009) for Gliridae, Maridet and Ni (2013) for Cricetidae, Vianey-Liaud (1972b) for Theridomyidae, and Bärmann and Rössner (2011) for *Lophiomeryx*. A clear distinction between the first and second molars was not always possible; in the cases of theridomyids and glirids both teeth are not separated and described as M1/2 and m1/2. The measurements generally consist of the maximal length L and width W of teeth (except when indicated otherwise), in millimeters. The given measurements are those of the newly collected specimens.

In the geographic repartition lists we group the numerous Quercy localities under the name Quercy and give only the stratigraphic extension; the names of the localities are found in Remy et al. (1987).

Biochronological framework: The biochronological framework is based on the European mammal reference levels for the Palaeogene (MP; Schmidt-Kittler, 1987), each of them being correlated to the Palaeogene geological time scale (Luterbacher et al., 2004, Vandenberghe et al., 2012). For the age of the localities we follow the numerical ages of Escarguel et al. (1997).

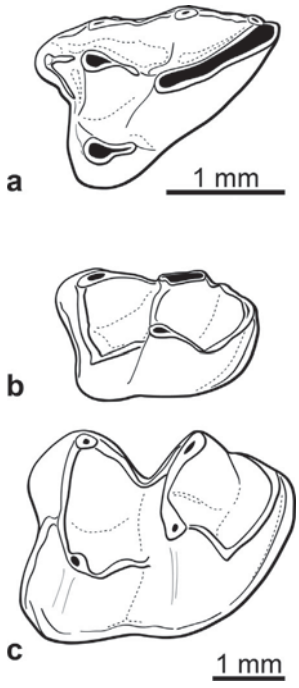

Fig. 1. a, Amphiperatherium exile from Aubenas-les-Alpes: left D3, (FSL 219005). b–c, *Neurogymnurus cayluxi* from Aubenas-les-Alpes: b, right m3 (FSL 219006); c, right m2 (FSL 219007).
a, Amphiperatherium exile d'Aubenas-les-Alpes : D3 gauche, (FSL 219005). b–c, Neurogymnurus cayluxi *d'Aubenas-les-Alpes : b, m3 droite (FSL 219006) ; c, m2 droite (FSL 219007).*

Abbreviations: FSL = Faculté des Sciences de Lyon; MR = Musée Requien, Avignon; NMB = Naturhistorisches Museum Basel; p/P = lower/upper premolars; m/M = lower/upper molars; L = maximal length; W = maximal width; H = crown height; TrW = trigonid width; TaL = talonid length; TaW = talonid width.

Analysis of mammalian communities' structure: Cenograms are rank-ordered body-size distributions of a community of terrestrial potential prey mammals (Legendre, 1986, 1989). Body masses are estimated from lower first molar measurements, see Legendre (1989) for a full description of the method. For the present study, teeth measurements were mostly taken from the material of Aubenas-les-Alpes but when m1s measurements were not available, data have been collected from the literature from other localities of similar age.

3. Systematic Palaeontology

Order NOTOMETATHERIA Kirsch, Lapointe and Springer, 1997
Family HERPETOTHERIIDAE Trouessart, 1879
Genus ***Amphiperatherium*** Filhol, 1879
Amphiperatherium exile (Gervais, 1848-52)
Fig. 1a

Type-locality: Cournon (Puy-de-Dôme, MP28).

Distribution: Quercy (France) from MP19 to MP28; Heimersheim, MP24 (Northern part of the upper Rhine Graben, Germany); Boningen, MP27 (cf., Olten, Suisse); Gaimersheim 1, MP28 (Bavaria, Germany); Herrlingen 8–9, MP 28–29 (Baden-Württemberg, Germany); Rickenbach, MP29 (Solothurn, Suisse); Coderet, MP30 (Allier, France).

Material from Aubenas-les-Alpes and measurements: left D3 (FSL 219005; L = 1.84, W = 1.28).

Remarks: This species was mentioned in Aubenas-les-Alpes by Crochet (1980). The D3 is very similar in size and morphology to a specimen of Late Oligocene of Germany figured by Ziegler (1990)

under this species name.

Order EULIPOTYPHLA Waddell, Okada and Hasewaga, 1999
Family ERINACEIDAE Fischer, 1814
Genus ***Neurogymnurus*** Filhol, 1877
Neurogymnurus cayluxi Filhol, 1877
Fig. 1b–c

Type-locality: Quercy, France, old collections (Oligocene but precise age unknown).

Distribution: Quercy (France) from MP23 to MP28; Montalbán, MP23 (Teruel, Spain); Antoingt MP25 (Puy-de-Dôme, France); Les Matelles, MP25 (Hérault, France); St-Vincent-de-Barbeyragues, MP25 (Hérault, France); Bumbach, MP25 (Schangnau, Switzerland); Oensingen MP26 (Solothurn, Switzerland); Mümliswyl, MP26 (Switzerland); Wolfwil, MP26 (Solothurn, Switzerland); Wynau 1, MP27 (Bern, Switzerland); Boningen, MP27 (Olten, Switzerland).

Material from Aubenas-les-Alpes and measurements: right m2 (FSL 219006; L = 3.28, TrW = 2.48, TaW = 2.59); right m3 (FSL 219007; L = 2.65, W = 1.70).

Description and comparisons: New sampling yielded only two lower teeth: one m2 and one m3. They are morphologically close to those of *Galerix nanus* but their size is much larger. Furthermore the m2 shows a posterior basal cingulum that connects (more or less completely) to the base of the entoconid; the posterior arm of the hypoconid is also connected to the entoconid. The smaller m3 shows a complete talonid; the hypoconid and entoconid are connected and the reduced talonid is completely closed by crests; a faint and independent basal posterocingulum is present. Their morphological features (together with the size) rather correspond to that of *Neurogymnurus cayluxi* a rare insectivore from Quercy.

Remarks: *Neurogymnurus* is known with certainty only from MP24 onwards (MP23 citations are doubtful). The earlier and smaller species is *N. cayluxi*. The later described species, *N. mediterraneus* Viret, 1947 is larger and very poorly known (Marseille-St. André, type-locality, MP26). *Neurogymnurus* has often coexisted with *G. nanus* in the early Oligocene localities (Crochet, 1995). However *G. nanus* last occurrences are known from the MP25 localities L'Escoufle, Rigal-Jouet and Garouillas (Crochet, 1995) whereas *N. cayluxi* persists until MP28 with modifications in size only (Crochet, 1974). *N. cayluxi* was hitherto not reported from Aubenas-les-Alpes.

Family SORICIDAE Fischer, 1814
Subfamily CROCIDOSORICINAE Reumer, 1987
Genus ***Srinitium*** Hugueney, 1976
Srinitium* cf. *marteli Hugueney, 1976
Fig. 2a–c

Type-locality: St-Martin-de-Castillon (Vaucluse, MP24).

Distribution: L'Escoufle, MP24 (Quercy, France); Itzac-Delazens, MP 24–25 (Tarn, France); ?Pech-du-Fraysse, MP28 (Quercy, France).

Material from Aubenas-les-Alpes and measurements: left mandible fragment broken behind anterior alveolus of m3, with

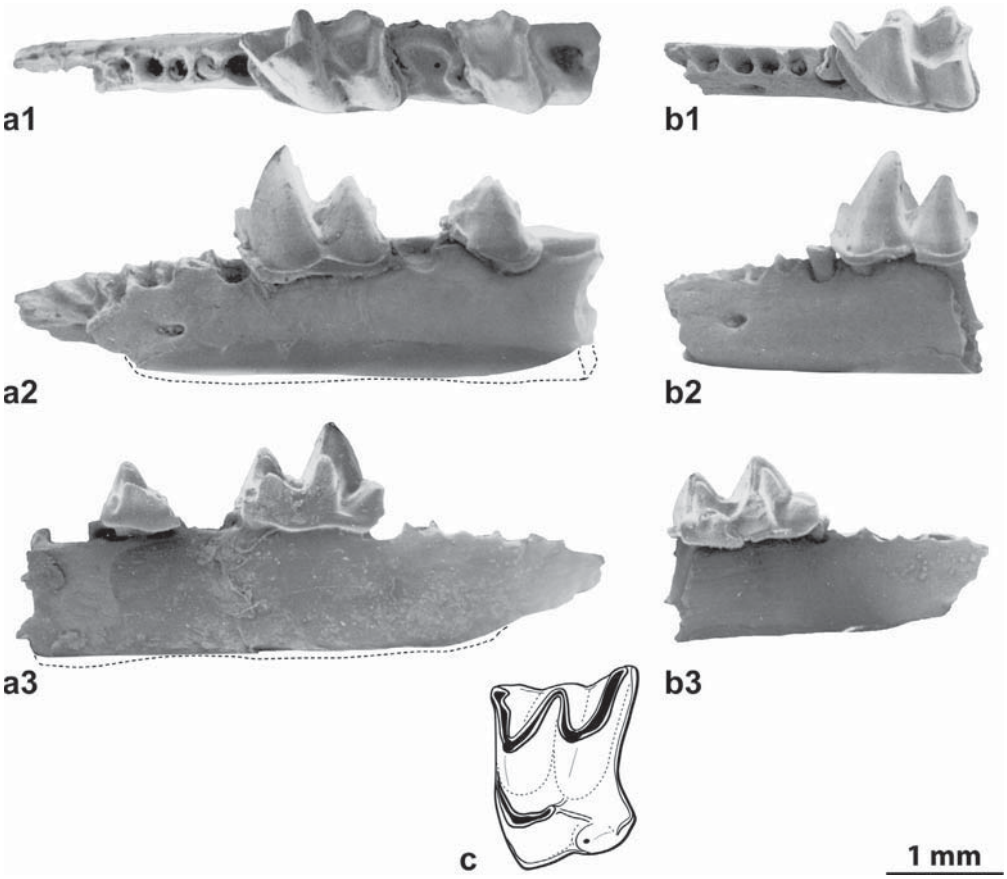

Fig. 2. a–c, *Srinitium* aff. *marteli* from Aubenas-les-Alpes (a, c) and *Srinitium marteli* from St-Martin-de-Castillon (b): a, left mandible with m1 and talonid of m2, (a1, occlusal view; a2, labial view; a3, lingual view; FSL 219008); b, anterior part of left mandible with m1, holotype (b1, occlusal view; b2, labial view; b3, lingual view; FSL 97441); c, left M2 (occlusal view; FSL 219009).
a–c, Srinitium *aff.* marteli *d'Aubenas-les-Alpes (a, c) et* Srinitium marteli *de St-Martin-de-Castillon (b) : a, mandibule gauche avec m1 et talonid de la m2, (a1, vue occlusale ; a2, vue labiale ; a3, vue linguale ; FSL 219008) ; b, partie antérieure de la mandibule gauche avec m1, holotype (b1, vue occlusale ; b2, vue labiale ; b3, vue linguale ; FSL 97441) ; c, M2 gauche (vue occlusale ; FSL 219009).*

alveoli for I, 5 uniradiculate antemolars and biradiculate p4, complete m1 and talonid of m2 (FSL 219008; L left alv. a1–p4 = 1.10; left mandible with m1–m2 (L = 2.63; H int. under m1 = 1.13; m1 (FSL 219009; L = 1.34, TrW = 0.84, TaW = 0.86). Left M2 (FSL 219010; L = 1.21, W = 1.57).

Description and comparisons: The massive mandible shows five alveoli between i and the biradiculate p4 corresponding to five uniradiculate antemolars. The inferior mandibular rim is nearly rectilinear. The large foramen mentale is located partly under the anterior root of p4 and extends under a5. No foramen is visible on the symphysis. As the mandible is dark brown no coloration of the teeth is visible. The m1 shows a large and complete ectocingulid that do not reach the lingual edge anteriorly but is enlarged in a peak under the protoconid (however no disto-labial edge of the protoconid is connected to the ectocingulid) and ends at the base of the hypolophid. A faint lingual cingulid is visible under the trigonid. The hypolophid ends at the level of the entoconid but is well separated from it.

In our collection a left M2 is more or less rectangular, wider than longer. The preprotocrista ends at the base of the paracone and the postprotocrista is divided in two crests, one joining the base of the metacone whereas the other one is directed to a well-cuspulated independent hypocone. A lingual basal cingulum surrounds the protocone base; it is interrupted under the hypocone and continues in a posterior cingulum surrounding the entire posterior rim from the emarginated hypoconal flange, up to the metastyle.

Crochet (1995) reported, without description, two upper molars from Aubenas-les-Alpes referred to this species despite a larger size. In our material only one M2 is nearly complete; it is a little larger than that of *S. marteli* (St-Martin-de-Castillon, MP24), but shows similar characteristics such as the massive tubercles, the divided postprotocrista and the lingual cingulum under the protocone. However the hypocone is better developed as a massive independent tubercle and the hypoconal flange is less extended backwards. The mandible is larger and more massive and the mandibular foramen is a little more posterior. The m1 is similar to that of *S. marteli* but a little larger; it shows a developed peak under the protoconid but without cingulum crest of the protoconid; this peak is nearly absent in *S. marteli* and rather indicates a close phylogenetic relationship between the soricid of Aubenas-les-Alpes and *S. marteli* from St-Martin-de-Castillon. The size enlargement corresponds well to the remarks of Ziegler (2009) concerning the evolution of *Srinitium* aff. *caeruleum* (MP21/22) to *S. caeruleum* (MP28). However in this species the ectocingulid of the lower molars is much more developed with a clear cingulum crest on the protoconid and the hypocone of the upper molars is not developed. More material is needed to enhance the knowledge of the Aubenas-les-Alpes material and its relationships with *S. marteli*, and to decide if, as proposed by Ziegler, *S. marteli* and *S. caeruleum* constitute two geographically vicariant lineages.

Family TALPIDAE Fischer, 1817
Genus ***Percymygale*** Hugueney and Maridet, 2017
Percymygale vauclusensis (Crochet, 1995)

Type -locality: St-Martin-de-Castillon (Vaucluse, South East France, MP24).

Distribution: Quercy (France) from MP24 to MP25; Les Matelles, MP25 (Hérault, France); St-Vincent-de-Barbeyragues, MP25 (Hérault, France) Oberleichtersbach, MP 30 (Bavaria, Germany); Boningen, MP27 (Olten, Suisse).

Material from Aubenas-les-Alpes: fragmented teeth and bones.

Remarks: Some damaged teeth and bones correspond to this small talpid species, created by Crochet (1995) based on the material from St-Martin-de-Castillon (MP24). This material was previously referred to *Myxomygale* cf. *antiqua* by Hugueney (1972) but is now type of the new genus *Percymygale* (Hugueney and Maridet, 2018). Crochet (1995) already noticed the occurrence of some teeth of this species in Aubenas-les-Alpes.

Genus ***Geotrypus*** Pomel, 1848
Geotrypus antiquus (De Blainville, 1840) and *Geotrypus acutidentatus* (De Blainville, 1840)

Remarks: Crochet (1995, p. 64) reports from Aubenas-les-Alpes two species assigned to the genus *Geotrypus*. In our material some teeth fragments, larger than those of *Percymygale* could be assigned to this genus but none is sufficiently well-preserved to be measured and referred with certainty to one of these two species. Additional Eulipotyphla broken specimens are not described: a tooth (MR 3.008.838); a bone (MR 3.008.839).

Order RODENTIA Bowdich, 1821
Family SCIURIDAE Fischer, 1817
Genus ***Heteroxerus*** Stehlin and Schaub, 1951
Heteroxerus* aff. *costatus (Freudenberg, 1941)
Fig. 3a–b

Type-locality: Gaimersheim (Germany, MP28).

Distribution: Garouillas, MP25 (Quercy, France); Rigal-Jouet 1, MP25 (Quercy, France); Belgarric (Quercy, MP25).

Material from Aubenas-les-Alpes and measurements: right partly broken M3 (FSL 219010; L = 1.45?, W = 1.59?); left m1 (FSL 219011; L = 1.55, W = 1.43).

Discussion and comparisons: The broken M3 is short, wider than long. The anteroloph is lower than the trigone and with a faint lingual crest oriented to the trigone. The m1 displays two roots with low crown and well-individualized tubercles (particularly the anteroconid, the mesoconid, the mesostylid and the entoconid); there is also a faint indication of an entolophid.

The Oligocene history of European sciurids is badly known due to scarcity of material, but could be more complex than what is presently known. Three genera are present in the European Early Oligocene *Palaeosciurus*, *Heteroxerus* and "*Sciurus?*" (Oligocene "flying" squirrels excluded); and three species *P. goti* Vianey-Liaud 1974, *H. costatus* (Freudenberg, 1941) and *"Sciurus?" dubius* (Schlosser 1884) which has the same size as *H. costatus*. In addition the "giant" *Comtia bernardi* Vianey-Liaud 2014 (in Vianey-Liaud et al., 2014) and *Sciurus schlosseri* Freudenberg, 1941 that is in fact a theridomorph (Freudenberg, 1941) are excluded from our comparison.

The m1 of Aubenas, with marked and voluminous tubercles, reminds particularly of the lectotype of *"Sciurus" costatus* from Gaimersheim (Germany, MP28; = *Heteroxerus costatus* in Kristkoiz, 1992) but it corresponds to the lowest part of the size range. Its dimensions also correspond to the size of the material from Garouillas (Quercy, MP25) referred to *Heteroxerus* nov. sp. by Vianey-Liaud et al. (1995), but the authors did not compare it with *H. costatus*.

Palaeosciurus dubius shows no trace of entolophid. *Palaeosciurus goti* is excluded because of its larger size and less developed accessory tubercles. Furthermore *P. goti* differs in having poorly-developed anteroconid, mesoconid and mesostylid. It is however noteworthy that the m1 from Aubenas-les-Alpes displays the same size and similarities in morphology with teeth of *Palaeosciurus* aff. *goti* from Herrlingen 8 and 9 (Germany, MP28 and 29) described and figured by Ziegler (1994). Finally, the m1 of Heimersheim referred by Bahlo (1975) to "*Sciurus*" sp. is smaller and without incipient entolophid. One tooth was previously reported from Aubenas-les-Alpes (Vianey-Liaud et al., 1995) as *Heteroxerus* sp. We confirm here the generic attribution and tentatively refer the above mentioned specimen to a form closely related to *Heteroxerus costatus: Heteroxerus* aff. *costatus*.

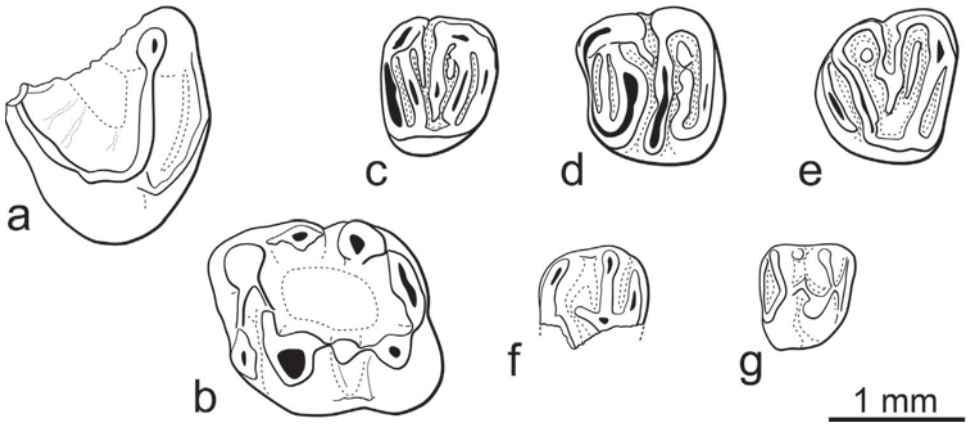

Fig. 3. Sciuridae, Gliridae and Eomyidae from Aubenas-les-Alpes (occlusal views). a–b, *Heteroxerus* aff. *costatus*: a, right M3 (FSL 219010); b, left m1 (FSL 219011). c–e, *Branssatoglis planus*: c, right P4 (FSL 219012); d, left m1 (FSL 219013); e, right M3 (FSL 219014). f–g, *Eomys minor*: f, left M1-2 (FSL 219016); g, right D4 (FSL 219015). *Sciuridae, Gliridae et Eomyidae d'Aubenas-les-Alpes (vues occlusales). a–b,* Heteroxerus *aff.* costatus *: a, M3 droite (FSL 219010) ; b, m1 gauche (FSL 219011). c–e,* Branssatoglis planus *: c, P4 droite (FSL 219012) ; d, m1 gauche (FSL 219013) ; e, M3 droite (FSL 219014). f–g,* Eomys minor *: f, M1-2 gauche (FSL 219016) ; g, D4 droite (FSL 219015).*

Family **Gliridae** Muirhead, 1819
Genus ***Branssatoglis*** Hugueney, 1967
Branssatoglis planus (Bahlo, 1975)
Fig. 3c–e

Type-locality: Heimersheim, MP24 (Northern part of the upper Rhine Graben, Germany).

Distribution: Piste d'Aguaton, MP20? (Teruel, Spain); Quercy (France) from MP 20 to MP22); Hoogbutsel, MP21 (Brabant, Belgium); Montalbán, MP23 (Teruel, Spain); Gröben 3, MP24 (Bavaria, Germany); Gaimersheim 1, MP28 (Bavaria, Germany); plus numerous localities from MP 19 to MP23 in Germany (Heissig, 1987).

Material from Aubenas-les-Alpes and measurements: P4 (FSL 219012; L = 1.04, W = 0.86); M3 (FSL 219013; L = 0.98, W = 1.17); m1 (FSL 219014; L = 1.08, W = 1.14).

Remarks: Vianey-Liaud (1994) figured some teeth with a very complicated dental pattern and referred them to this species as "*B. planus* (evolved grade)". In Vianey-Liaud et al. (1995) these teeth are mentioned as *Oligodyromys* sp. In our collections the specimens show a more simple morphology corresponding better to *B. planus*.

Genus ***Gliravus*** Stehlin et Schaub, 1951
Gliravus garouillensis Vianey-Liaud, 1994

Type-locality: Quercy (old collections).

Distribution: Quercy (France) from MP24 to MP 25; Gandesa, MP26 (Ebro, Spain); Loranca 2, MP30? (Cuenca, Spain).

Remarks: Vianey-Liaud (1994) noticed one tooth of *G. garouillensis* in Aubenas-les-Alpes and figured it as *Glamys priscus* in Vianey-Liaud et al., 1995, p. 263, fig. 3i. This taxon was not found in our recent sampling.

Family **Eomyidae** Winge, 1887
Genus ***Eomys*** Schlosser, 1884
Eomys minor Comte and Vianey-Liaud, 1987
Fig. 3f–g

Type-locality: Belgarric (Quercy, MP25).

Distribution: La Blache MP24/25 (Alpes-de-Haute-Provence, France).

Material from Aubenas-les-Alpes and measurements: right D4 (FSL 219015; L = 0.73, W = 0.79); left M1-2 (FSL 219016; L = 0.86, W = not measurable).

Description and comparisons: Two long transverse crests are present, the protocone is directed obliquely backwards and the longitudinal crest is interrupted and centrally located (Maridet et al., 2010); the mesoloph is absent and the posteroloph short on molars but larger on D4 which displays also a long anteroloph. These teeth could correspond to *Eomys* sp. cited in Vianey-Liaud et al. (1995, p. 259).

Family **Cricetidae** Fischer, 1817
Genus ***Eucricetodon*** Thaler, 1969
Eucricetodon* cf. *huberi (Schaub, 1925)
Fig. 4g

Type-locality: Mümliswyl (Solothurn, Switzerland, MP26).

Distribution: Quercy (France) from MP25 to MP26; Etampes, MP24 (Essonne, France); Itteville, MP24 (Essonne, France); Maintenon, MP24 (Eure-et-Loir, France); Heimersheim, MP24 (Northern part of the upper Rhine Graben, Germany); Vialenc, MP25 (Cantal, France); St-Martin-de-Casselvi, MP25 (Tarn, France); St-Menoux, MP26 (Allier, France); St-Henri, MP26 (Bouches-du-Rhône, France); Oensingen, MP26 (Solothurn, Switzerland).

Material from Aubenas-les-Alpes and measurements: right m1 (FSL 219023; L = 1.52, W = 1.02).

Description and comparisons: m1 with rather massive and rounded cuspids, anteroconid included. The mesoconid is prominent and connected to a short but thick mesolophid. The ectolophid is not located on the axis of the tooth but rather labially. The metaconid ridge is well-developed and long but does not totally close the labial sinusid.

Vianey-Liaud (1971, p. 620, fig. 5) figured three upper molars (2 M1, 1 M2) from Aubenas-les-Alpes as *Eucricetodon huberi*. In 1972a, other teeth were figured and referred to *E. huberi* in the text and the plates (pl. 3, fig. 1–6) but in contradiction referred to *E.* cf. *huberi* in the figures (p. 11–13, fig. 4a–b, e–g). Some measurements are given but their numbering is not in accordance with that of the figures and it is not possible to assign them to a precise tooth. Comte (1985) revised the previous material of Vianey-Liaud and figured some teeth as *E. huberi* (fig. 3a–f) but excluded from this taxon the large previously figured M2 (he referred it to *Pseudocricetodon* aff. *incertus*) and the figured m2 and m3 (referred to *Pseudocricetodon moguntiacus*). *E. huberi* is a very poorly known taxon even in its type-locality since only the holotype of Mümliswyl-Nasihofli is known (MP26); Lm1-m2, m1: L = 1.80, W = 1.20; m2: L = 1.64, W = 1.40) and a M1 (L = 2.16, W = 1.44). The holotype of *E. huberi* – and also the M1 – are medium-sized *Eucricetodon* with massive rounded tubercles and simple pattern; the tooth from Aubenas-les-Alpes figured by Comte seems to correspond well to this pattern. However, considering the scarcity of this taxon and the smaller size compared to the type

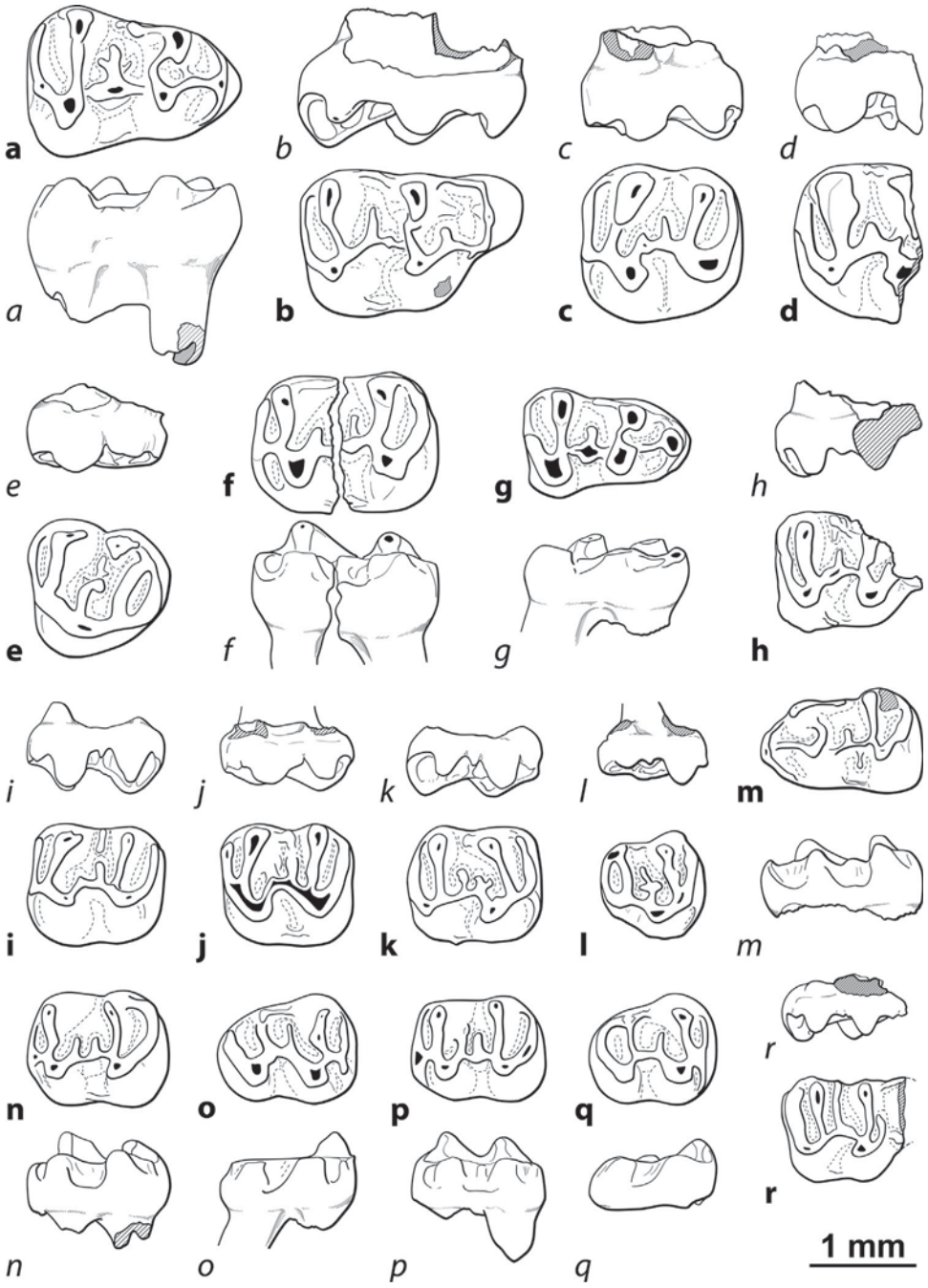

Fig. 4. Cricetidae from Aubenas-les-Alpes (bold characters indicate the occlusal view, italic characters indicate the labial view). a, *Heterocricetodon* cf. *hausi*, right m1 (FSL 219017). b–f, *Pseudocricetodon* aff. *incertus*: b, right M1 (FSL 219018); c, left M2 (FSL 219019); d, damaged right M2 (FSL 219020); e, left M3 (FSL 219021); f, broken left m2 (FSL 219022). g, *Eucricetodon* cf. *huberi*, right m1 (FSL 219023). h–q, *Pseudocricetodon moguntiacus*: h, damaged right M1 (FSL 219024); I, left M2 (FSL 219025); j, left M2 (FSL 219026); k, right M2 (FSL 219027); l, right M3 (FSL 219028); m, left m1 (FSL 219029); n, left m2 (FSL 219030); o, right m3 (FSL 219031); p, left m2 (FSL 219032); q, right m3 (FSL 219033). r, *Pseudocricetodon philippi*, damaged right M1 (FSL 219034).
Cricetidae d'Aubenas-les-Alpes (les caractères gras indiquent la vue occlusale, les caractères en italique indiquent la vue labiale). a, Heterocricetodon *cf.* hausi*, m1 droite (FSL 219017). b–f,* Pseudocricetodon *aff.* incertus *: b, M1 droite (FSL 219018) ; c, M2 gauche (FSL 219019) ; d, M2 droite cassée (FSL 219020) ; e, M3 gauche (FSL 219021) ; f, m2 gauche cassée (FSL 219022). g,* Eucricetodon *cf.* huberi*, m1 droite (FSL 219023). h–q,* Pseudocricetodon moguntiacus *: h, M1 droite cassée (FSL 219024) ; I, M2 gauche (FSL 219025) ; j, M2 gauche (FSL 219026) ; k, M2 droite (FSL 219027) ; l, M3 droite (FSL 219028) ; m, m1 gauche (FSL 219029) ; n, m2 gauche (FSL 219030) ; o, m3 droite (FSL 219031) ; p, m2 gauche (FSL 219032) ; q, m3 droite (FSL 219033). r,* Pseudocricetodon philippi*, M1 droite cassée (FSL 219034).*

specimen, we cannot be sure of the identification at the specific level.

Genus ***Pseudocricetodon*** Thaler, 1969
Pseudocricetodon* aff. *incertus (Schlosser, 1884)
Fig. 4b–e
Type-locality: Mouillac (Quercy, old collections).

Distribution: Quercy (France) from MP25 to MP 28; St-Menoux, MP26 (Allier, France); St-Henri, MP26 (Bouches-du-Rhône, France); Boujac, MP26 (Gard, France); St-Privat-des-Vieux, MP 26 (Gard, France); Gandesa, MP26 (Ebro, Spain); Oensingen, MP26 (Solothurn, Switzerland); Mirambueno 4C, MP26 (Teruel, Spain); Boningen, MP27 (Olten, Suisse); Ehrenstein 7, MP27 (Baden-Württemberg, Germany); Gaimersheim, MP28 (Bavaria, Germany); Rickenbach, MP29 (Solothurn, Suisse).

Material from Aubenas-les-Alpes and measurements: right M1 (FSL 219018; L = 2.04, W = 1.42); left M2 (FSL 219019; L = 1.46, W = 1.49); right frag. M2 (FSL 219020; L = not measurable, W = 1.52); left M3 (FSL 219021; L = 1.27, W = 1.28); left m2 (FSL 219022a; L = 1.61, W = 1.31); right frag. m2 (FSL 219022b; L = not measurable, W = 1.37).

Description and comparisons: The upper molars are characterized by relatively gracile cusps and crests, with the development of some accessory crests (for instance crests starting from the paracone and anterocone of the M1). In addition, the M1 displays a small crescent-like anterocone, a small mesocone located slightly anteriorly to the mesoloph and an incomplete anterior protolophule. The M2 and M3 have an incomplete or absent posterior protolophule and a short mesoloph (with accessory spurs for the M3). The only m2 found recently is characterized by well-developed anterolophids, a short protoconid posterior arm and a short and thin mesolophid. In the locality, *Pseudocricetodon* aff. *incertus* differs from *Heterocricetodon* cf. *hausi* (see below) in being slightly smaller and with a slightly lower crown.

Remarks: Among our material from Aubenas, of which size is similar to *Eucricetodon dubius*, most of the teeth show the development of accessory crests which are reminiscent of *Pseudocricetodon incertus*. These teeth correspond to the M2 from Aubenas-les-Alpes described and figured by Comte (1985, fig. 14 j) and compared to *P. incertus* from Boujac. They were referred by him to *P.* aff. *incertus*. Vianey-Liaud et al. (2014), studying again the material from Boujac, referred some large teeth to the Spanish form *Pseudocricetodon landroveri* (Daams et al., 1989). So far, even with the few new specimens presented above, this population remains insufficient to identify it at species level with certainty.

Pseudocricetodon moguntiacus (Bahlo, 1975)
Fig. 4h–q

Type-locality: Heimersheim, MP24 (Northern part of the upper Rhine Graben, Germany).

Distribution: Quercy (France) from MP23 to MP28; St-Martin-de-Castillon, MP24 (Vaucluse, France); Dürrenberg, MP24? (cf., Jura, Switzerland); St-Martin-de-Casselvi, MP25 (Tarn, France); Bernloch 1B, MP23 (Baden-Württemberg, Germany); Burgmagerbein 2, MP25 (Bavaria, Germany); Ehingen 5, MP25 (Baden-Württemberg, Germany); St-Jean-de-Cuculles, MP26 (Hérault, France); St-Mathieu-de-Treviers, MP26 (Hérault, France); ?St-Victor-la-Coste, MP29 (Gard, France).

Material from Aubenas-les-Alpes and measurements: right broken M1 (FSL 219024a; L = not measurable, W = 1.15); left broken M1 (FSL 219024b; not measurable); right M2 (FSL 219025; L = 1.24, W = 1.15); left M2 (FSL 219026; L = 1.20, W = 1.12); left M2 (FSL 219027; L = 1.18, W = 1.11); right M3 (FSL 219028; L = 0.97, W = 1.03); left m1 (FSL 219029; L = 1.52, W = 1.02); left m2 (FSL 219030; L = 1.26, W = 1.08); left m2 (FSL 219031; L = 1.16, W = 1.01); right m3 (FSL 219032; L = 1.25, W = 1.02); right m3 (FSL 219033; L = 1.13, W = 1.05).

Description and comparisons: All molars are characterised by low crown and very gracile cusp(id)s. The M1 is partly broken but shows a well-developed mesocone, a short mesoloph and a spur starting from the mesostyle, but not joining each other's. Other upper molars are characterised by an average size or long mesoloph and a well-developed but generally incomplete posterior protoloph, and well-developed mesostyle closing the labial sinus. The m1 shows a well-developed anterolophid but a relatively small anteroconid; the mesolophid is short; the ectomesolophid is also present but thinner and slighty more posteriorly located than the mesolophid; a weakly-developed labial posterolophid is present. Other lower molars display an average size mesoloph and a well-developed protoconid hind arm for m2.

Vianey-Liaud (1971) reports *Pseudocricetodon montalbanensis* Thaler, 1972 in Aubenas, and in 1972a (27, fig. 10 a–g + pl. 1 fig. 7 et pl. 3, fig. 1–10) figured some teeth as *P.* aff./cf. *montalbanensis* pointing out to their larger size. Comte (1985) referred the previously known material and new findings to the more recently described *Pseudocricetodon moguntiacus*. The population of *P. moguntiacus* from Heimersheim is not homogeneous: some teeth of *Eucricetodon* are present, and even if these teeth are removed, Freudenthal et al. (1994) notice that two species of *Pseudocricetodon* of slightly different size could be present (see Bahlo, 1975, fig. 21), the smallest being of the same size as *P. montalbanensis* Thaler, 1969 from Montalbán, (Spain, MP23) and apparently not very different in morphology. The size of the holotype of *P. moguntiacus* (M2: L = 1.08, W = 1.00) is similar to the size of *P. montalbanensis*; as *P. moguntiacus* and *P. montalbanensis* are morphologically very close, and as no precise study comparing both of them exists, the small species of Heimersheim could be *P. montalbanensis,* and *P. moguntiacus* could be a junior synonym. But a larger species does exist in Heimersheim and many teeth are referred to it (Comte, 1985; Vianey-Liaud et al., 1995). In our samples from Aubenas-les-Alpes all the teeth correspond to this larger species except two teeth (m2, FSL 219030 and m3, FSL 219033; Fig. 4p–q), of which size is intermediate between *P. monguntiacus* and *Pseudocricetodon philippi*, and corresponding to the maximal sizes of *P. montalbanensis.* At the time, the synonymy of *P. montalbanensis* and *P. moguntiacus* is not proved and we refer the larger sized form of the Heimersheim population to *P. moguntiacus*. Our material from Aubenas-les-Alpes is very poor but we notice also large size variations within *Pseudocricetodon* which suggests the co-occurrence of two species (as already noticed by Freudenthal et al., 1994) in addition to *P. philippi*. It is also noteworthy that the smaller m3 (FSL 219033) is proportionally shorter which is so far the only morphological difference observed.

Pseudocricetodon philippi Hugueney, 1971
Fig. 4r

Type-locality: St-Martin-de-Castillon, MP24 (Vaucluse, France).

Distribution: Quercy (France) from MP 23 to MP 28; Balm, MP22 (Solothurn, Switzerland); Les Chapelins, MP23 (Vaucluse, France); Terrenoire, MP24 (Alpes-de-Haute-Provence, France); Dürrenberg, MP24? (Jura, Switzerland); Heimersheim, MP24 (Northern part of the upper Rhine Graben, Germany); Gabsheim, MP24 (Rhineland-Palatinate, Germany); St-Henri, MP26 (Bouches-du-Rhône, France); Mirambueno 4C, MP26 (Ebro, Spain).

Material from Aubenas-les-Alpes and measurements: damaged right M1 (FSL 219034; L = not measurable, W = 1.15).

Description and comparisons: The tooth is very small with gracile cusps, and a very low crown. The anterocone is broken off but its broad base indicates that it was wide. A long mesoloph reaches the labial border and a short protocone anterior arm forms a loop connecting to the protoloph. The morphology and size both lie in the variability of this species as described in St-Martin-de-Castillon. It is smaller than *P. simplex* Freudenthal et al., 1994 and differs morphologically from the forms of Turkish Thrace previously referred to this genus but now referred to the genus *Lignitella* Ünay-Bayraktar, 1989 (Freudenthal et al., 1994).

Genus ***Heterocricetodon*** Schaub, 1925
Heterocricetodon* cf. *hausi Engesser, 1987
Fig. 4a

Type-locality: Bumbach 1 (Switzerland, MP25).

Distribution: St-Martin-de-Casselvi, MP25 (Tarn, France); Mirambueno 4B, MP25 (Teruel, Spain); Réchauvent-Cristallin, MP25 (Vaud, Switzerland); Puycelci, MP26 (Quercy, France); Mümliswyl-Hardberg, MP26 (Solothurn, Switzerland).

Material from Aubenas-les-Alpes and measurements: right m1 (FSL 219017; L = 1.94, W = 1.42).

Description and comparisons: This right m1 is clearly larger and with a higher crown than all the other cricetid m1s found in our samples. It displays a very elongated shape, lingually placed protoconid and hypoconid, straight hypolophid and multicrested mesolophid and is reminiscent of *H. hausi*. It is however a little smaller than the unique m1 from the type-locality. It is noteworthy that in the Mümliswyl Basel collection, a large M3 (NMB Mu 10; L = 1.35, W = 1.33) was also referred to *H. hausi* by Engesser (1987). A large M3, with a similar morphology, was found in Aubenas-les-Alpes but rather referred to *Pseudocricetodon* aff. *incertus* due to its slightly smaller size (L = 1.27, W = 1.28) and its lower crown (compared to the m1). The scarcity of the material from Aubenas-les-Alpes does not allow further comparisons so far. The question remains open whether the M3 from Aubenas-les-Alpes should be in fact referred to *Heterocricetodon* cf. *hausi* or in contrast if the M3 described by Engesser (1987) could be referred to the population of *Pseudocricetodon incertus* described by Vianey-Liaud et al. (2014). Some additional cricetid specimens more or less broken have not been precisely referred to (MR 3.008.840–3.008.841).

Family THERIDOMYIDAE Alston, 1876
Subfamily ISSIODOROMYINAE Tullberg, 1899
Genus *Issiodoromys* Bravard *in* Gervais, 1848
Issiodoromys minor (Schlosser, 1884)
Fig. 5a–b

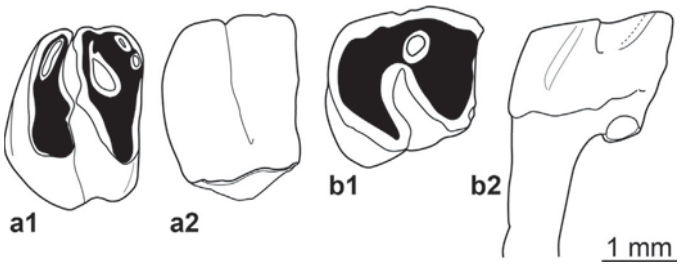

Fig. 5. *Issiodoromys minor* from Aubenas-les-Alpes: a, left M1-2 (a1, occlusal view; a2, lingual view; FSL 219035); b, right m1-2 (b1, occlusal view; b2, lingual view; FSL 219036).
Issiodoromys minor *d'Aubenas-les-Alpes : a, M1-2 gauches (a1, vue occlusale ; a2, vue linguale ; FSL 219035) ; b, m1-2 droites (b1, vue occlusale ; b2, vue linguale ; FSL 219036).*

Type-locality: Mouillac (Quercy, old collections).

Distribution: Quercy (France) from MP24 to MP25; Dürrenberg, MP24? (Jura, Switzerland); Itzac-Delazens, MP 24-25 (aff., Tarn, France); St-Martin-de-Casselvi, MP25 (Tarn, France); Aurillac, MP25 (Cantal, France); La Sauvetat, MP25 (Puy-de-Dôme, France); Can Quaranta MP25 (Campins, Spain); Mirambueno 3B, 15, 4B, MP25 (Teruel, Spain); Carrascosa, MP25 (Cuenca, Spain).

Material from Aubenas-les-Alpes and measurements: right m1 (FSL 219035; L = 2.12, W = 1.77, H = 1.47); left M1-2 (FSL 219036; L = 1.65, W = 1.70, H = 2.25).

Remarks: The worn right m1 shows only one anterior root a little constricted in the middle, as it is generally the case in

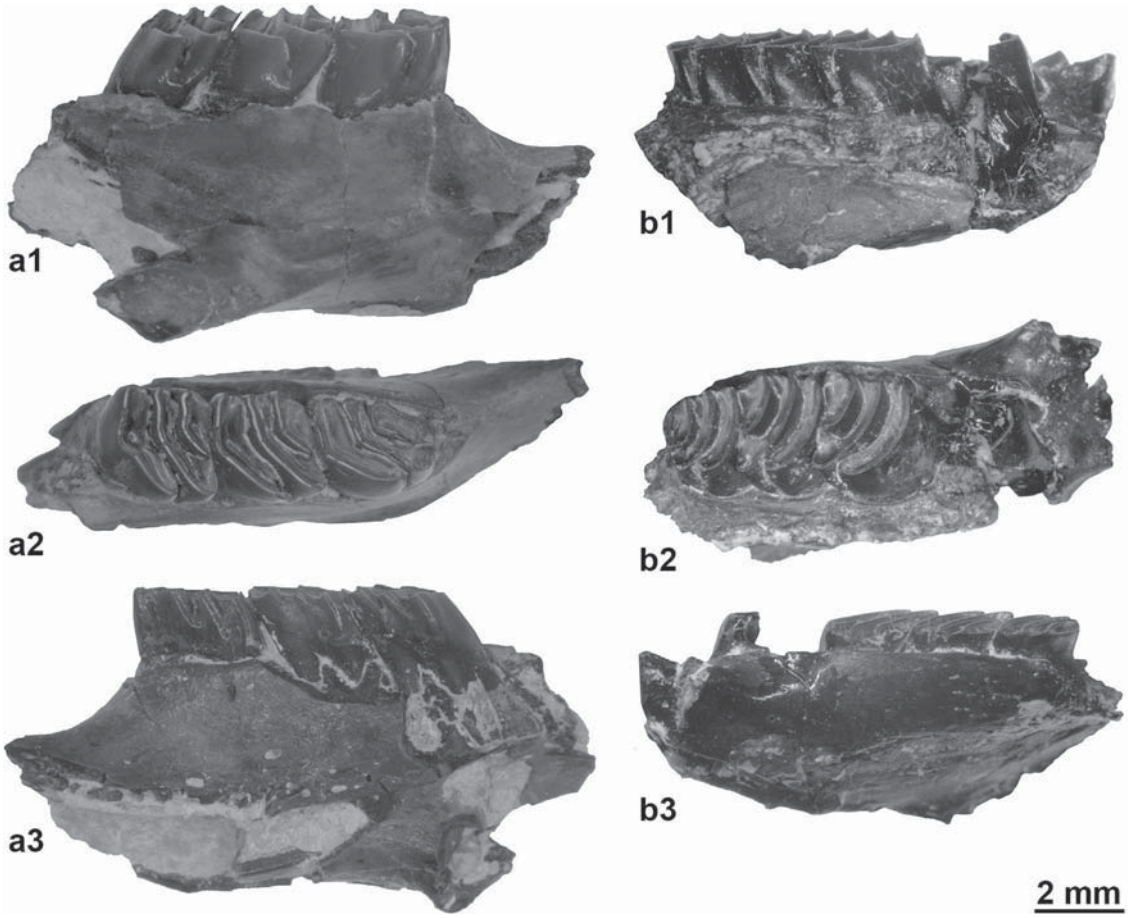

Fig. 6. *Protechimys gervaisi* from Aubenas-les-Alpes: a, right mandible with p4-m2 (a1, labial view; a2, occlusal view; a3, lingual view; FSL 219037). b, right maxillary with damaged P4 and M1-3 (b1, lingual view; b2, occlusal view; b3, labial view; FSL 219038).
Protechimys gervaisi *d'Aubenas-les-Alpes : a, mandibule droite avec p4-m2 (a1, vue labiale ; a2, vue occlusale ; a3, vue linguale ; FSL 219037). b, maxillaire droit avec P4 cassée et M1-3 (b1, vue linguale ; b2, vue occlusale ; b3, vue labiale ; FSL 219038).*

Table 1
Measurements of the new collected teeth of *Protechimys gervaisi* from Aubenas-les-Alpes.
Mesures de la nouvelle collection de dents de Protechimys gervaisi *issue d'Aubenas-les-Alpes.*

		L			W		
	N	min	max	mean	min	max	mean
P4	2	1.89	2.27	2.08	2.18	2.43	2.30
M1-2	10	1.28	2.05	1.74	2.08	2.65	2.39
M3	3	1.67	1.74	1.71	1.86	2.40	2.06
p4	4	2.26	2.55	2.44	1.39	2.7	2.13
m1-2	10	1.82	2.48	2.13	1.55	2.63	2.27
m3	4	1.65	1.84	1.77	1.60	2.35	1.90

Garouillas (Vianey-Liaud et al., 1995), a very small anterior synclinid can be seen antero-labially; the size of the tooth is a little larger than in Lebratières 14 and similar to those of Garouillas or Rigal-Jouet. Too worn to surely distinguish the levels 2 or 3 of *I. minor*, this tooth is larger than those of level 1 defined by Vianey-Liaud (1998) for this species.

M 1-2 is similar to the teeth of Rigal-Jouet and in the middle of the size distribution of Garouillas. Even worn, it shows the sinus fused with first syncline, a characteristic of *Issiodoromys*; the low hypsodonty level and the presence of five labial anticlines indicates a relatively plesiomorph pattern corresponding to MP25 level. *Issiodoromys* was not previously reported from Aubenas-les-Alpes.

Subfamily THERIDOMYINAE Alston, 1876
Genus ***Theridomys*** Jourdan, 1837
Theridomys lembronicus Bravard *in* Gervais, 1848-1852.

Type-locality: Saint-Germain-Lembron (Puy-de-Dôme, France, MP25).

Distribution: Dürrenberg, MP24? (cf., Jura, Switzerland); Antoingt, MP25 (Puy-de-Dôme, France); La Sauvetat, MP25 (Puy-de-Dôme, France); Perrier MP 25 (Puy-de-Dôme); St-Vincent-de-Barbeyragues, MP25 (Hérault, France); Les Matelles, MP25 (Hérault, France); Cournon, MP 28 (Puy-de-Dôme, France).

Material from Aubenas-les-Alpes and measurements: isolated teeth MR 3.008.842- 3.008.846 and FSL 219040-219041: left P4 (L = 3.22, W = 4.82); left P4 (L = 3.27, W = 3.74); right P4 (L = 3.04, W = 3.38); left M1-2 (L = 2.85, W = 3.28); left M1-2 (L = 2.66, W = 3.10); right M3 (L = 2.45, W = 2.25); left p4 (L = 4.97, W = 2.99); right p4 (L = 3.90, W = 2.98); left m1-2 (L = 2.90, W = 2.99); right m1-2 (L = 2.45, W = 3.02).

Remarks: Teeth of this species from Aubenas-les-Alpes were already described and illustrated by Vianey-Liaud (1972b, p. 320–322, Fig. 10a–e). This species is also described from Cournon (Vianey-Liaud, 1972b, fig. 12 h–j), perhaps from a level older than the typical level of this locality which is correlated to MP 28. Our material is not abundant and shows no difference. It is noteworthy that this species was never recorded in the Quercy karstic faunal assemblages.

Genus ***Protechimys*** Schlosser, 1884
Protechimys gervaisi (Thaler, 1966)
Fig. 6a–b
Synonymy
1993 - *Protechimys blainvillei* (Gervais, 1848–1852) Mödden, p. 27–30.
1997 - *Protechimys blainvillei* (Gervais, 1848–1852) Mödden and Vianey-Liaud, p. 361–374.

Type-locality: Antoingt (Puy-de-Dôme, France, MP25).

Distribution: Quercy (France) from MP24 to MP 25; Itzac-Delazens, MP 24–25 (aff., Tarn, France); Rousselou, MP25 (Hérault, France); St-Martin-de-Casselvi, MP25 (Tarn, France); Oensingen, MP26 (Solothurn, Switzerland).

Material from Aubenas-les-Alpes and measurements: right maxilla with M1-3 (FSL 219037; L M1-3 = 5.50.); right mandible with p4-m2 (FSL 219038; L p4-m2 = 5.03); isolated teeth (MR 3.008.847- 3.008.850 and FSL 219042-219045). For measurements see Table 1.

Nomenclature: Gervais (1848–1852) described and illustrated a new species *Theridomys blainvillei* created for two fossils from the locality Antoingt in the Bravard's collection: a maxillary (pl. 47, fig. 17,17a) and a mandible (pl. 47, fig. 18, 18a). No holotype was specified so the two specimens were syntypes.

Stehlin and Schaub (1951: 35) assign this species to the genus *Blainvillimys* which was newly created by Bravard in an unpublished manuscript mentioned by Gervais (1848–1852) in his text. However, as Stehlin and Schaub (1951) thought that the mandible and maxillary were different taxa, they specified that it was only "*pro parte*" and choose–on their own right–the mandible fig. 18, 18a as "typus" (presently lectotype) of *B. blainvillei* (1951: 362). With this designation the mandible becomes "the sole name-bearing type of that nominal taxon; no later designation of a lectotype has any validity" (International Code of Zoological Nomenclature, 1999, art. 74.1.1). Moreover this designation "permanently deprives all other specimens that were formerly syntypes of that nominal taxon of the status of syntype.; they become. . . paralectotype. . . and have no name-bearing function" (ICZN, art. 73.2.2). As paralectotype, the maxillary which is not conspecific with the mandible cannot bear the species-name *blainvillei*. Lavocat (1952: 77) agreed with the designation of the mandible as "type" of *B. blainvillei* Gervais, 1848–1852 and with the fact that the maxillary represents a different taxon. He assigned the maxillary to the teniodont genus *Archaeomys* de Laizer and de Parieu, 1832 and created a new combination *A. blainvillei* (Gervais, 1848–1852) for which he designated this maxillary as "type" (= lectotype). But as explained above this designation is invalid.

Thaler (1966) noticed that "if the two specimens are not conspecific, only one can bear the species name "*blainvillei* Gervais", which is in accordance with the Nomenclatural Code. He created the new species *Archaeomys gervaisi*; its "type" being the maxillary previously illustrated by Gervais as *Theridomys blainvillei*, pl. 47, fig. 17. Since this date, *A. gervaisi* Thaler, 1966 was used in many publications for a teniodont species of theridomorph whereas *Blainvillimys blainvillei* is also commonly used as a non-teniodont theridomoph from the MP25 level.

Later, Mödden (1993) brought back the invalid *Archaeomys blainvillei* (Gervais, 1848–1852), considering *A. gervaisi* a junior synonym of *Archaeomys blainvillei*. However, he seemed to be right when he referred this species to the genus *Protechimys*.

The material from Aubenas-les-Alpes clearly demonstrates that *Blainvillimys blainvillei* and *Protechimys gervaisi* pertain to different genera (Fig. 6 vs. 7). The characteristics of *Protechimys gervaisi* are studied in detail in Mödden and Vianey-Liaud (1997). The same characteristics are observed in the material from Aubenas-les-Alpes: a strong angle of the transverse ridges in the lower molars, a synclinid II with deep lingual opening, a synclinid IV rapidly

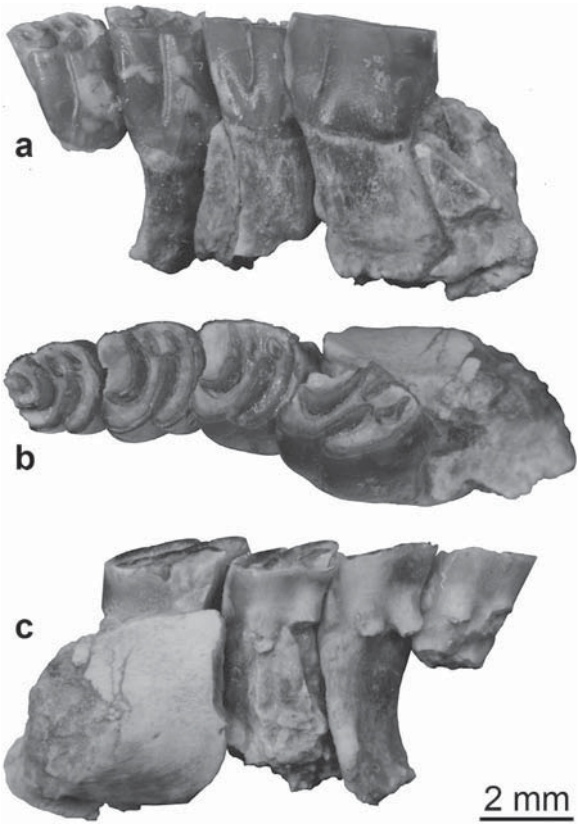

Fig. 7. *Blainvillimys blainvillei* from Aubenas-les-Alpes: right maxillary with P4-M3 (a, lingual view; b, occlusal view; c, labial view; FSL 219039).
Blainvillimys blainvillei *d'Aubenas-les-Alpes : maxillaire droit avec P4-M3 (a, vue linguale ; b, vue occlusale ; c, vue labiale ; FSL 219039).*

disappearing, the pattern of upper molars rapidly reduced to three ridges. Additionally a maxillary and a mandible of this taxon found in the same layers give an idea of the corresponding morphologies of upper and lower tooth rows. All the material fits well with the morphology previously described in Mödden and Vianey-Liaud (1997) and we consequently refer it to *Protechimys gervaisi* (Thaler, 1966).

Genus ***Blainvillimys*** Bravard *in* Gervais, 1848–1852
Blainvillimys blainvillei (Gervais, 1848–1852)
Fig. 7

Type-locality: Antoingt (Puy-de-Dôme, MP25).

Distribution: Quercy (France) from MP24 to MP 25; Terrenoire, MP 25 (Alpes-de-Haute-Provence); St-Geniez, MP25 (Alpes-de-Haute-Provence, France); St-Vincent-de-Barbeyragues, MP25 (Hérault, France); Les Matelles, MP 25 (Hérault); St-Martin-de-Briatexte, MP25 (Tarn, France); La Sauvetat, MP25 (Puy-de-Dôme, France); Aurillac, MP25 (Cantal, France); Campins, MP25 (Campins, Spain); Mümliswyl-Heitersberg, MP25 (Solothurn).

Material from Aubenas-les-Alpes and measurements: right maxilla with P4-M3 (FSL 219039; L P4-M3 = 9.15); isolated teeth (MR 3.008.851-3.008.860 and FSL 219046- 219049). For teeth measurements see Table 2.

Remarks: Teeth of this species from Aubenas-les-Alpes were already described and illustrated in Vianey-Liaud (1972b, 2015) and in Vianey-Liaud et al. (1995); our material is not very abundant and shows no different characteristic; we only add its measurements.

Order CETARTIODACTYLA Montgelard *et al.*, 1997
Family LOPHIOMERYCIDAE Janis, 1987
Genus ***Lophiomeryx*** Pomel, 1853
Lophiomeryx chalaniati Pomel, 1853
Fig. 8a–b

Type-locality: La Sauvetat (Puy-de-Dôme, MP25).

Distribution: La Bénissons-Dieu, MP23-25 (Loire, France); Moissac-IV, MP 24 (Tarn-et-Garonne, France); Rabastens, MP24 (Tarn-et-Garonne, France); La Sauvetat, MP25 (Puy-de-Dôme, France); Le Garouillas, MP25 (Lot, Quercy, France); Antoingt, MP25 (Puy-de-Dôme, Auvergne, France); Mas de Gaston, MP25 (Lot, Quercy, France); Nonette, MP25 (France); Rigal-Jouet, MP25 (Tarn-et-Garonne, Quercy, France); Belgarric, MP25 (Lot, Quercy, France); Saint-Martin-de-Casselvi, MP25 (Tarn, France); Carrascosa del Campo, MP25 (Cuenca, Spain); Moissac III, MP26 (Tarn-et-Garonne, France); Saint-Privat-des-Vieux, MP 26 (Alès Basin, France); La Devèze, MP 26 (Quercy, France); Pech Desse, MP 28 (Lot, Quercy, France); Mailhat, MP 28 (Auvergne, France) ; Cournon, MP28 (Puy-Dôme, France); Tournon, Late Rupelian (Ardèche, France); Vallon d'Auradou, Chattien (Lot-et-Garonne, France) Mümliswyl-Heitersberg, MP25 (Solothurn, Suisse); Seckbach, MP24 (Mainz basin, Germany).

Material: fragment of right mandible with m/1 and broken p/4 and m/2 (MR 3.003.213); left navicular-cuboid (MR 3.003.285).

Description and comparisons: On the mandible (Fig. 8a), the m/1 is a typical *Lophiomeryx* lower molar with lingually open anterior and posterior fossa. A visible metaconid is posteriorly positioned and almost fused with a small incipient metastylid. A small parastylid is isolated anteriorly and is joined by the preprotocristid. The entoconid is well developed and has an attached preentoconidcristid, the postentoconidcristid is lacking so that the strong and bulky entostylid is isolated posteriorly. Strong anterior and posterior cingulids are present and a small ectostylid attached to the hypoconid flank is also present. The enamel is slightly wrinkled. The p/4 and m/2 are broken and only their roots are visible. The size of the m/1 (12.75 × 7.10 mm) is in accordance with *Lophiomeryx chalaniati* from the old Quercy collections or from Le Garouillas (Brunet and Sudre, 1987; Mennecart, 2012).

A left fused navicular-cuboid was found together with the mandible fragment. The cuboid part of the bone is thick and disto-

Table 2
Measurements of the new collected teeth of *Blainvillimys blainvillei* from Aubenas-les-Alpes.
Mesures de la nouvelle collection de dents de Blainvillimys blainvillei *issue d'Aubenas-les-Alpes.*

		L			W		
	N	min	max	mean	min	max	mean
D4	2	3.08	3.10	3.09	1.85	1.97	1.91
P4	6	2.32	2.67	2.18	1.93	2.26	2.09
M1-2	16	1.72	2.32	2.06	1.69	2.83	2.18
M3	3	1.68	2.00	1.89	1.60	2.04	1.88
p4	3	2.84	3.00	2.91	1.64	1.86	1.73
m1-2	10	1.98	2.51	2.29	1.38	2.90	2.20
m3	4	1.91	2.14	2.03	1.45	2.00	1.77

Fig. 8. *Lophiomeryx chalaniati* from Aubenas-les-Alpes: a, left navicular-cuboid (proximal view; MR 3.003.285); b, fragment of right mandible with m1 and broken p4 and m2 (b1, occlusal view; b2, labial view; b3, lingual view; MR 3.003.213).
Lophiomeryx chalaniati *d'Aubenas-les-Alpes : a, cuboïde-naviculaire gauche (vue proximale ; MR 3.003.285) ; b, fragment de mandibule droite avec m1, et p4 et m2 cassées (b1, vue occlusale ; b2, vue labiale ; b3, vue linguale ; MR 3.003.213).*

proximally elongated. The navicular part is thinner but broader as is usual in artiodactyls. The facet for the calcaneum is quite large. The elevation of the median tendon is high, and higher than the lateral one. This bone of *Lophiomeryx chalaniati* was described by Brunet and Sudre (1987). The specimen found in Aubenas-les-Alpes (MR 3.003.285) corresponds to this description in large parts. The only noticeable difference would be the elevation of the median tendon which is even higher here than on the specimen (GAR 167) from Le Garouillas (Brunet and Sudre, 1987). Size itself excludes a number of smaller taxa such as *Bachitherium*, or *Gelocus*. Despite the small difference mentioned above, and taking into account that the morphological variability of *Lophiomeryx chalaniati* is poorly known, the specimen is tentatively referred to this species.

4. Conclusions

Considering intensive screen-washing and picking the small rodent teeth remain relatively rare. However, recent sampling allowed identifying four taxa previously unknown in this locality: *Neurogymnurus cayluxi*, *Eomys minor*, *Pseudocricetodon philippi* and *Heterocricetodon* cf. *hausi* (see Table 3). Altogether, thanks to the recent discoveries (including recent publications of Menouret et al., 2015 and Pickford, 2016) the mammalian assemblage of Aubenas-les-Alpes comprises now 26 species distributed into 22 genera, 14 families and 6 orders (Table 3; Fig. 9).

Stratigraphic framework: Two sedimentary episodes are known in the Oligocene of the rhodanian and subalpine regions. The

Table 3
Mammalian faunal list of Aubenas-les-Alpes (MP25, Late Rupelian). Small mammals (Didelphimorphia, Eulipotyphla and Rodentia) and *Lophiomeryx chalaniati* are described in the present study: N = previously unknown; * = previously known but not found in recent samples. Carnivora and Perissodactyla are taken from Menouret et al. (2015), and Cetartiodactyla (except *Lophiomeryx chalaniati*) are taken from Pickford (2016).
Liste faunique des mammifères d'Aubenas-les-Alpes (MP25, Rupélien supérieur). Les petits mammifères (Didelphimorphia, Eulipotyphla et Rodentia) et Lophiomeryx chalaniati *sont décrits dans la présente étude : N = nouveau ; * = déjà connu mais non retrouvé dans les échantillonnages récents. Les Carnivora et Perissodactyla sont tirés de Menouret et al. (2015), et les Cetartiodactyla (sauf* Lophiomeryx chalaniati*) sont tirés de Pickford (2016).*

Notometatheria		
Herpetotheriidae		
Amphiperatherium exile	(Gervais, 1848–52)	
Eulipotyphla		
Erinaceidae		
Neurogymnurus cayluxi	Filhol, 1877	N
Soricidae		
Srinitium aff. *marteli*	Hugueney, 1976	
Talpidae		
Percymygale vauclusensis	(Crochet, 1995)	
Geotrypus antiquus	(De Blainville, 1840)	*
Geotrypus acutidentatus	(De Blainville, 1840)	*
Rodentia		
Sciuridae		
Heteroxerus aff. *costatus*	(Freudenberg, 1941)	
Gliridae		
Branssatoglis planus	(Bahlo, 1975)	
Gliravus garouillensis	Vianey-Liaud, 1994	* (= *Glamys priscus*)
Eomyidae		
Eomys minor	Comte and Vianey-Liaud, 1987	N

Table 3 (*Continued*)

Cricetidae		
Eucricetodon cf. *huberi*	(Schaub, 1925)	
Pseudocricetodon aff. *incertus*	(Schlosser, 1884)	
Pseudocricetodon moguntiacus	(Bahlo, 1975)	
Pseudocricetodon philippi	Hugueney, 1971	N
Heterocricetodon cf. *hausi*	Engesser, 1987	N
Theridomyidae		
Issiodoromys minor	Filhol, 1876	
Theridomys lembronicus	Bravard *in* Gervais, 1848–52	
Protechimys gervaisi	(Thaler, 1966)	
Blainvillimys blainvillei	(Gervais, 1848–1852)	
Carnivora		
Amphicyonidae		
Nimravus intermedius	(Filhol, 1872)	
Perissodactyla		
Rhinocerotidae		
Ronzotherium romani	Kretzoi, 1940	
Molassitherium albigense	(Roman, 1912)	
Amynodontidae		
Cadurcotherium cayluxi	Gervais, 1873	
Cetartiodactyla		
Anthracotheriidae		
Anthracotherium magnum	Cuvier, 1822	
Elomeryx crispus	(Gervais, 1849)	
Lophiomerycidae		
Lophiomeryx chalaniati	Pomel, 1853	

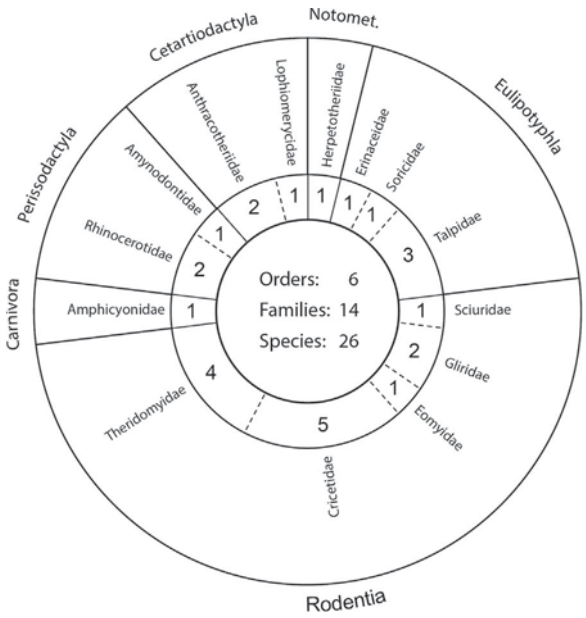

Fig. 9. Pie diagram of the Aubenas-les-Alpes mammalian fauna. Notomet. Notometatheria.
Diagramme en secteurs de la faune mammalienne d'Aubenas-les-Alpes. Notomet. Notometatheria.

fossiliferous layers of Aubenas-les-Alpes belong to the second and main detritic phase of the Apt-Forcalquier basin, called "Marnes de Viens" (Hugueney and Truc, 1976). These deposits are synchronous with the deposits of the Aix-en-Provence and Marseille basins (Répelin, 1916; Hugueney and Truc, 1976), respectively called "Argile des Milles" and "Formation de St-Henri et de St-André". In the 80s, new discoveries of mammals from different Oligocene localities of Provence allowed to precise the biostratigraphic position of Aubenas-les-Alpes, i.e. slightly younger than St-Martin de Castillon, slightly older than Les Milles, and close to Antoingt, Sigonce and Terrenoire (Hugueney and Truc, 1976; Ducreux et al., 1985). Now, the co-occurrence of many taxa, especially with *Blainvillimys blainvillei* also found in Le Garouillas, the reference locality for the MP 25 level (late Rupelian), confirms the age previously proposed for Aubenas-les-Alpes.

Palaeoenvironmental context: As such, Aubenas-les-Alpes yielded an assemblage which species diversity of both large and small mammals is equivalent to several other MP25 localities such as Mümliswyl, Oensingen 11, Bumbach 1, Rigal-Jouet, Belgarric, Terrenoire (see online Appendix 1). In this context, Le Garouillas is an exception with its higher taxonomic richness and a total of 37 species. Consequently, the mammalian community of Aubenas-les-Alpes is diversified enough to undertake an analysis of its species body mass structure (see Material and methods; Table 4; Appendix 1). The cenogram (Fig. 10) presents a shape characterized by a large size gap from 1 to 10 kg and a larger number of species among small mammal (producing a noticeable slope difference between small and large mammals). This configuration is similar to the cenograms of other Early Oligocene localities such as Rigal Jouet, St-Menoux and Burgmagerbein 2 which are interpreted as open, dry and rather cold environments (Legendre, 1989). This interpretation is coherent with the climatic change known in Europe at the Eocene/Oligocene boundary (−34 Ma) due to orbital parameters modification and inducing a significant drop of temperatures and landscape opening at the beginning of the Oligocene (e.g. Elderfield, 2000; Legendre, 1989; Wolfe, 1978; Zachos et al., 2001). However, among the theridomorphs, *Issiodoromys minor* is less abundant than the other taxa, which could indicate a more closed and humid environment. Indeed *Issiodoromys* is usually considered to live in more open and dryer environments than *Theridomys, Protechimys* and *Blainvillimys* (Vianey-Liaud, 1972b). The cricetid material is also poor and only constituted of isolated teeth which make each specimen difficult to identify with certainty. The genera *Paracricetodon* and *Melissiodon*, which are frequent in most of the contemporaneous Oligocene localities (Remy et al., 1987), have not been found at Aubenas-les-Alpes. Consequently, these peculiarities of the small mammalian assemblage may be due either to a particular environment which could have induced ecological exclusions compared to other contemporaneous Oligocene localities, or these differences could be the result of sampling bias as rodent teeth remain relatively rare in the fossiliferous layers of Aubenas-les-Alpes.

Geographic distribution of species: From a biogeographical point of view, the European fossil record of this period of time is not

Table 4
Estimation of body mass based on the material of Aubenas-les-Alpes when available, or the same taxon from another locality, close geographically and biochronologically when possible. Measurements of m1s are given in millimeters, and equations for estimating the body size are corrected after Legendre (1989) (see online Appendix 1).
Estimation du poids corporel sur la base du matériel d'Aubenas-les-Alpes quand disponible, ou du même taxon d'une autre localité, la plus proche possible géographiquement et biochronologiquement. Les mesures des m1 sont données en millimètres, et les équations d'estimation de la taille sont corrigées à partir de Legendre (1989) (voir Appendix 1).

Taxa	Measurements m1(mm)	Body mass (g)	Origin of data	References
Amphiperatherium exile	L = 2.08, W = 1.26	22.0	Herrlingen 8	Ziegler, 1998
Neurogymnurus cayluxi	L = 3.90, W = 2.00	164.6	Quercy, old collections	this study
Srinitium aff. *marteli*	L = 1.34, W = 0.86	4.8	Aubenas-les-Alpes	this study
Percymygale vauclusensis	L = 1.60, W = 1.07	10.0	St-Martin-de-Castillon	Hugueney and Maridet, 2018
Geotrypus antiquus	L = 2.46, W = 1.49	40.9	Enspel	Schwermann and Martin, 2012
Geotrypus acutidentatus	L = 2.09, W = 1.26	22.2	Quercy, old collections	this study
?*Heteroxerus* aff. *costatus*	L = 1.55, W = 1.43	32.6	Aubenas-les-Alpes	this study
Branssatoglis planus	L = 1.08, W = 1.14	11.6	Aubenas-les-Alpes	this study
Gliravus garouillensis	L = 0.99, W = 0.84	5.8	Garouillas	Vianey-Liaud, 1994
Eomys minor	L = 0.90, W = 0.85	5.0	La Blache	Maridet et al., 2010
Eucricetodon cf. *huberi*	L = 1.52, W = 1.02	17.4	Aubenas-les-Alpes	this study
Pseudocricetodon aff. *incertus*	L = 1.62, W = 1.09	21.9	St-Privat-des-Vieux	Vianey-Liaud et al., 2014
Pseudocricetodon moguntiacus	L = 1.52, W = 1.02	17.4	Aubenas-les-Alpes	this study
Pseudocricetodon philippi	L = 0.95, W = 0.65	3.5	St-Martin-de-Castillon	Freudenthal et al., 1994
Heterocricetodon cf. *hausi*	L = 1.94, W = 1.42	47.7	Aubenas-les-Alpes	this study
Issiodoromys minor	L = 2.12, W = 1.77	82.1	Aubenas-les-Alpes	this study
Theridomys lembronicus	L = 2.54, W = 2.31	179.9	Aubenas-les-Alpes	this study
Protechimys gervaisi	L = 2.07, W = 2.26	120.9	Aubenas-les-Alpes	this study
Blainvillimys blainvillei	L = 2.34, W = 2.06	127.4	Aubenas-les-Alpes	this study
Ronzotherium romani	L = 44.5, W = 30.0	1991477.9	Saint-Henri	Menouret and Guérin, 2009
Molassitherium albigense	L = 29.8, W = 19.0	522734.6	Saint-Henri	Menouret and Guérin, 2009
Cadurcotherium cayluxi	L = 33.0, W = 21.0	716373.3	Aubenas-les-Alpes	Menouret et al., 2015
Anthracotherium magnum	L = 37.0, W = 28.0	1526084.6	Rickenbach	Ménnecart et al., 2012
Elomeryx crispus	L = 18.0, W = 13.5	163211.5	Hempstead beds	this study
Lophiomeryx chalaniati	L = 12.8, W = 7.1	35832.3	Aubenas-les-Alpes	this study

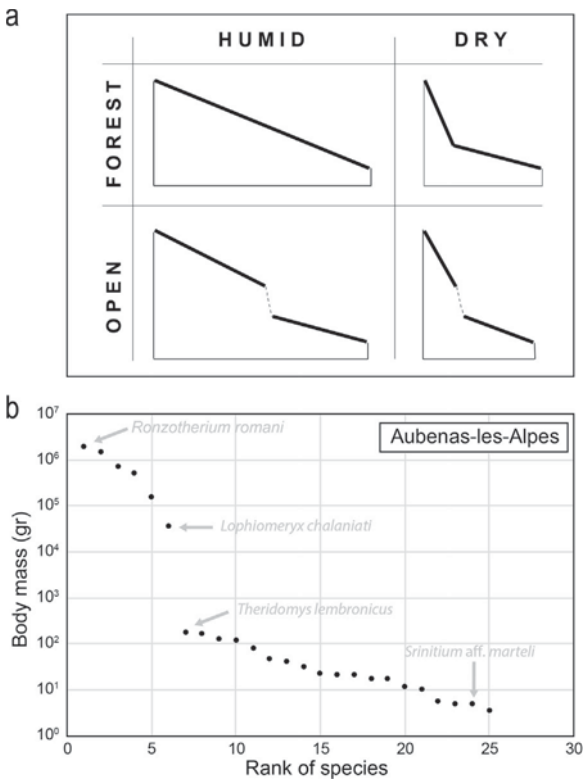

Fig. 10. a, cenograms (graphic interpretation of the rank-ordered body-size distributions of communities of terrestrial potential prey mammals; modified after Legendre, 1989); b, cenogram of the Aubenas-les-Alpes mammalian assemblage.
a, cénogrammes (interprétation graphique de la distribution des poids des proies potentielles au sein des communautés de mammifères terrestres ; modifié à partir de Legendre, 1989) ; b, cénogramme de l'assemblage mammalien d'Aubenas-les-Alpes.

rich enough to undertake a quantified analysis as for Mazan in the beginning of the Oligocene (Maridet et al., 2013), however some observations can be made. Four types of species compose the mammalian assemblage of Aubenas-les-Alpes. Some species are rare in Europe and present a relatively limited geographical distribution such as *Geotrypus acutidentatus*, *Srinitium marteli*, *Eomys minor*, *Heteroxerus costatus* and *Cadurcotherium cayluxi* (only know from the French record), *Theridomys lembronicus* and *Protechimys gervaisi* and *Molassitherium albigense* (only in French and Swiss record) or *Elomeryx crispus* (only in French and Czech records, although that might also be the result of a sampling bias). In contrast, among the species found in Aubenas-les Alpes, only a few are common in the European fossil record and known from southern (Iberian basins) to northern Europe (German basins) such as *Pseudocricetodon incertus*, *Pseudocricetodon philippi* and *Bransatoglis planus*. The third category of species are those presenting a relatively large distribution but excluded from southern Europe (Iberian basins) records such as *Amphiperatherium exile*, *Percymygale vauclusensis*, *Geotrypus acutidentatus*, *Geotrypus antiquus*, *Pseudocricetodon moguntiacus*, *Nimravus intermedius* and *Ronzotherium romani*. Finally some species present also a large distribution but are excluded from the northernmost regions (especially German sedimentary basins) such as *Neurogymnurus cayluxi*, *Heterocricetodon hausi*, *Issiodoromys minor*, *Blainvillimys blainvillei*, *Anthracotherium magnum* and to a lesser extent *Lophiomeryx chalaniati* only known from only one German locality. These observations suggest an intermediate position of Aubenas-les-Alpes in the European biogeography, but also an ongoing biogeographical differentiation between northern and southern regions, in contrast with the relatively homogeneous condition found at the beginning of the Oligocene (Maridet et al., 2013).

Disclosure of interest

The authors declare that they have no competing interest.

Acknowledgements

We want to thank Bernard Menouret for providing part of the specimens described in the frame of this publication. We also thank Damien Becker for sharing personal information and for numerous discussions that contributed to improve this study. O.M. and L.C.

researches on Palaeogene mammals are supported by a grant of the Swiss National Science Foundation (Nº 200021-162359). We thank Christine Balme for her help in organizing field work in the Geological Reserve of the Luberon and for her constant interest in our research. Finally, we also thank two referees Paloma López-Guerrero and Reinhard Zeigler for helpful comments on previous versions of this publication.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version

References

Bahlo, E., 1975. Die Nagetierfauna von Heimersheim bei Alzey (Rheinhessen, Westdeutschland). Abhandlungen des Hessischen Landesamtes für Bodenforschung 71, 1–182.

Bärmann, E.V., Rössner, G.E., 2011. Dental nomenclature in Ruminantia: Towards a standard terminological framework. Mammalian Biology –. Zeitschrift für Säugetierkunde 76, 762–768, http://dx.doi.org/10.1016/j.mambio.2011.07.002.

Becker, D., Antoine, P.O., Maridet, O., 2013. A new genus of Rhinocerotidae (Mammalia, Perissodactyla) from the Oligocene of Europe. Journal of Systematic Palaeontology 11, 947–972.

Brunet, M., Sudre, J., 1987. Évolution et systématique du genre Lophiomeryx Pomel, 1853 (Mammalia, Artiodactyla). Münchner Geowissenchaftliche Abhandlungen A10, 225–242.

Comte, B., 1985. Éléments nouveaux sur l'évolution des genres *Eucricetodon* et *Pseudocricetodon* (Eucricetodontinae, Rodentia, Mammalia) de l'Oligocène d'Europe occidentale. Palaeovertebrata 15 (1), 1–169.

Crochet, J.-Y., 1974. Les Insectivores des Phosphorites du Quercy. Palaeovertebrata 6 (1973), 109–159.

Crochet, J.-Y., 1980. Les Marsupiaux du Tertiaire d'Europe. Fondation Singer-Polignac, Paris, pp. 1–279 (Thèse).

Crochet, J.-Y., 1995. Le Garouillas et les sites contemporains (Oligocène, MP25) des Phosphorites du Quercy (Lot, Tarn-et-Garonne, France) et leurs faunes de vertébrés. 4. Marsupiaux et Insectivores. Palaeontographica A 236, 39–75.

Daams, R., Freudenthal, M., Lacomba, J.I., Alvarez, M.A., 1989. Upper Oligocene micro-mammals from Pareja, Loranca Basin, prov. of Guadalajara, Spain. Scripta Geologica 89, 27–56.

Daxner-Höck, G., Höck, E., 2009. New data on Eomyidae and Gliridae (Rodentia, Mammalia) from the Late Miocene of Austria. Annalen des Naturhistorischen Museums in Wien 111A, 375–444.

Ducreux, J.L., Hugueney, M., Truc, G., 1985. La formation des Calcaires et Lignites de Sigonce (Oligocène moyen, Bassin de Forcalquier, Alpes-de-Haute-Provence) : datation à l'aide des Mammifères ; reconstitution des milieux de dépôts. Geobios 18 (1), 109–114.

Elderfield, H., 2000. A world in transition. . .. Nature 407, 851–852.

Engesser, B., 1987. New Eomyidae, Dipodidae, and Cricetidae (Rodentia, Mammalia) of the Lower Freshwater Molasse of Switzerland and Savoy. Eclogae geologicae Helvetiae 80 (3), 943–994.

Escarguel, G., Marandat, B., Legendre, S., 1997. Sur l'âge numérique des faunes de mammifères du Paléogène d'Europe occidentale. In: Aguilar, J.P., Legendre, S., Michaux, J. (Eds.), Actes du Congrès BiochroM' 97, 211. Mémoires et Travaux EPHE Institut de Montpellier, pp. 443–460.

Freudenberg, H., 1941. Die oberoligocänen Nager from Gaimersheim bei Ingolstadt und ihre Verwandten. Palaeontographica 92A, 99–164.

Freudenthal, M., Hugueney, M., Moissenet, E., 1994. The genus *Pseudocricetodon* (Cricetidae, Mammalia) in the Upper Oligocene of the Province of Teruel (Spain). Scripta geologica 104, 57–114.

Gervais, P., 1848-1852. Zoologie et Paléontologie françaises. A. Bertrand, Paris.

Helmer, D., Vianey-Liaud, M., 1970. Nouveaux gisements de rongeurs dans l'Oligocène moyen de Provence. Comptes Rendus sommaires de la Société géologique de France, Paris 2, 45–46.

Hugueney, M., 1972. Les Talpidés de Coderet-Bransat (Allier) et l'évolution de cette famille au cours de l'Oligocène supérieur et du Miocène inférieur d'Europe. Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon 50, 1–81.

Hugueney, M., Maridet, O., 2018. Evolution of Oligo-Miocene talpids (Mammalia, Talpidae) in Europe: focus on the genera Myxomygale and Percymygale n. gen. Historical Biology 30, 267–275, http://dx.doi.org/10.1080/08912963.2017.1282447.

Hugueney, M., Truc, G., 1976. Corrélations stratigraphiques et paléogéographie des formations marines et continentales à la limite Oligocène-Miocène dans le SE de la France. Geobios 9, 363–365, http://dx.doi.org/10.1016/S0016-6995(76)80042-3.

Hutchison, J.H., 1974. Notes on type specimens of European Miocene Talpidae and a tentative classification of Old World Tertiary Talpidae (Insectivora, Mammalia). Geobios 7 (3), 211–256.

International Commission of Zoological Nomenclature, 1999. International Code of Zoological Nomenclature, Fourth Edition. The International Trust for Zoological Nomenclature, London, UK, 306 pp.

Kristkoiz, A., 1992. Zahnmorphologische und schädelanatomische Untersuchungen an Nagetieren aus dem Oberoligozän von Gaimersheim (Süddeutschland). Abhandlungen Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, N.F. 167, 1–137.

Lavocat, R., 1952. Révision de la faune des Mammifères oligocènes d'Auvergne et du Velay. Science et Avenir, Paris, pp. 1–153.

Legendre, S., 1986. Analysis of Mammalian communities from the late Eocene and Oligocene of southern France. Palaeovertebrata 16, 191–212.

Legendre, S., 1989. Les communautés de mammifères du Paléogène (Eocène supérieur et Oligocène) d'Europe occidentale: structures, milieux et évolution. Münchner Geowissenschaftliche Abhandlungen 16, 110.

Luterbacher, J., Dietrich, D., Xoplaki, E., Grojean, M., Wanner, H., 2004. European seasonal and annual temperature variability, trends, and extremes since 1500. Science 303, 1499–1503, http://dx.doi.org/10.1126/science.1093877.

Maridet, O., Hugueney, M., Heissig, K., 2010. New data about the diversity of Early Oligocene eomyids (Mammalia, Rodentia) in Western Europe. Geodiversitas 32 (2), 221–254.

Maridet, O., Hugueney, M., Costeur, L., 2013. The mammalian assemblage of Mazan (Vaucluse, France) and its position in the Early Oligocene European palaeobiogeography. Swiss Journal of Geosciences 106, 231–252, http://dx.doi.org/10.1007/s00015-013-0145-5.

Maridet, O., Ni, X., 2013. A new cricetid rodent from the early Oligocene of Yunnan, China, and its evolutionary implications for early Eurasian cricetids. Journal of Vertebrate Paleontology 33, 185–194, http://dx.doi.org/10.1080/02724634.2012.710283.

Mennecart, B., 2012. The Ruminantia (Mammalia, Cetartiodactyla) from the Oligocene to the Early Miocene of Western Europe: systematics palaeoecology and palaeobiogeography. Geofocus 32, 1–278.

Menouret, B., Guérin, C., 2009. *Diaceratherium massiliae* nov. sp. des argiles oligocènes de Saint-André et Saint-Henri à Marseille et de Les Milles près d'Aix-en-Provence (SE de la France), premier grand Rhinocerotidae brachypode européen. Geobios 42, 293–327.

Menouret, B., Châteauneuf, J.-J., Nury, D., Peigné, S., 2015. Aubenas-les-Alpes, a forgotten Oligocene mammalian site in Provence (S-E France). Part I - Carnivora, Perissodactyla and Microflora. Annales de Paléontologie 101, 241–250.

Mödden, C., 1993. Revision der Archaeomyinae (Rodentia, Mammalia) des europäischen Oligozän. Schweizerische Paläontologische Abhandlungen 115, 1–83.

Mödden, C., Vianey-Liaud, M., 1997. The upper Oligocene tribe Archaeomyini (Theridomyidae, Rodentia, Mammalia): systematics and biostratigraphy. In: Aguilar, J.P., Legendre, S., Michaux, J. (Eds.), Actes du Congrès BiochroM' 97, 211. Mémoires et Travaux EPHE Institut de Montpellier, pp. 361–374.

Pickford, M., 2016. Anthracotheres from the Oligocene of Aubenas-les-Alpes, France. Annales de Paléontologie 102, 243–260.

Remy, J.A., Crochet, J.Y., Sigé, B., Sudre, J., de Bonis, L., Vianey-Liaud, M., Godinot, M., Hartenberger, J.L., Lange-Badré, B., Comte, B., 1987. Biochronologie des phosphorites du Quercy : Mise à jour des listes fauniques et nouveaux gisements de mammifères fossiles. In: Schmidt-Kittler, N. (Ed.), International Symposium on Mammalian Biostratigraphy and Palaeoecology of the European Oligocene, Mainz, A10. Münchner Geowissenschaftliche Abhandlungen, pp. 169–188.

Répelin, J., 1916. Sur l'âge des dépôts oligocènes des bassins d'Aix et de Marseille et en particulier des argiles des Milles et des lignites de Saint-Zacharie. Comptes rendus sommaires des Séances de l'Académie des Sciences 163, 100–102.

Roman, F., 1912. Les Rhinocérotidés de l'Oligocène d'Europe. Archives du Muséum d'Histoire naturelle de Lyon 11, 1–92.

Schmidt-Kittler, N., 1987. International Symposium on Mammalian Biostratigraphy and Paleoecology of the European Paleogene. Münchner Geowissenschaftliche Abhandlungen A10, 1–312.

Schwermann, A.H., Martin, T., 2012. A partial skeleton of *Geotrypus antiquus* (Talpidae, Mammalia) from the Late Oligocene of the Enspel fossillagerstätte in Germany. Paläontologische Zeitschrift 86, 409–439, http://dx.doi.org/10.1007/s12542-012-0129-1.

Stehlin, H.G., Schaub, S., 1951. Die Trigonodontie der simplicidentaten Nager. Abhandlungen Schweizerische palaeontologische Gesellschaft 67, 1–385.

Thaler, L., 1966. Les Rongeurs fossiles du Bas-Languedoc dans leurs rapports avec l'histoire des faunes et de la stratigraphie du Tertiaire d'Europe. Mémoires du Muséum national d'Histoire naturelle, nouvelle série/C - Sciences de la Terre 17, 1–296.

Vandenberghe, N., Hilgen, E.J., Speijer, R.P., 2012. The Palaeogene period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M., Ogg, G. (Eds.), The Geologic Time Scale, Chap. 28. Elsevier B.V, pp. 855–921, http://dx.doi.org/10.1016/B978-0-444-59425-9.00028-7.

Vianey-Liaud, M., 1971. Données nouvelles sur l'évolution des genres *Eucricetodon* et *Pseudocricetodon* à l'Oligocène en Europe occidentale. Comptes Rendus de l'Académie des Sciences Paris D 273, 619–622.

Vianey-Liaud, M., 1972a. Contribution à l'étude des Cricétidés oligocènes d'Europe occidentale. Palaeovertebrata 5 (1), 1–46.

Vianey-Liaud, M., 1972b. L'évolution du genre *Theridomys* à l'Oligocène moyen. Intérêt biostratigraphique. Bulletin du Museum d'Histoire naturelle, Sciences de la Terre, 3e série 98 (18), 296–370.

Vianey-Liaud, M., 1994. La radiation des Gliridés (Rodentia) à l'Eocène supérieur en Europe occidentale et sa descendance oligocène. Münchner Geowissenschaftliche Abhandlungen A26, 117–160.

Vianey-Liaud, M., 1998. La radiation des Theridomyinae (Rodentia) à l'Oligocène inférieur : modalités et implications biochronologiques. Geologica et Palaeontologica 32, 253–285.
Vianey-Liaud, M., 2015. Parallelism in the evolution of dental pattern and systematic implications: the case of *Protechimys major* Schlosser, 1884 (Theridomorpha, Rodentia, Mammalia) and its associated rodents. Comptes Rendus Palevol 14, 451–470.
Vianey-Liaud, M., Comte, B., Lévêque, F., 1995. Le Garouillas et les sites contemporains (Oligocène, MP25) des Phosphorites du Quercy (Lot, Tarn-et-Garonne, France) et leurs faunes de vertébrés. 13. Rongeurs. Palaeontographica A 236, 257–326.
Vianey-Liaud, M., Comte, B., Marandat, B., Peigné, S., Rage, J.-C., Sudre, J., 2014. A new early Late Oligocene (MP26) continental vertebrate fauna from Saint-Privat-des-Vieux (Alès Basin, Gard, Southern France). Geodiversitas 36 (4), 565–622.
Viret, J., 1947. Nouvelles observations sur le genre *Necrogymnurus* Filhol (Erinaceidae). Eclogae geologicae Helvetiae 40/2, 336–343.
Wolfe, J.A., 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. American Scientist 66, 694–703.
Zachos, J.C., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate, 65 Ma to present. Science 292, 686–693.
Ziegler, R., 1990. Didelphidae, Erinaceidae, Metacodontidae and Dimylidae (Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands. Sttuttgarter Beiträge zur Naturkunde B (Geologie und Paläontologie) 158, 1–99.
Ziegler, R., 1998. Wirbeltiere aus dem Unter-Miozän des Lignit-Tagebaues Oberdorf (Weststeirisches Becken, österreich): 5. Marsupialia, Insectivora und Chiroptera (Mammalia). Annalen des Naturhistorischen Museums in Wien 99A, 43–97.
Ziegler, R., 1994. Rodentia (Mammalia) aus der oberoligozänen Spaltenfüllungen Herrligen 8 und Herrlingen 9 bei Ulm (Baden-Württemberg). Stuttgarter Beiträge zur Naturkunde B (Geologie und Paläontologie) 196, 1–81.
Ziegler, R., 2009. Soricids (Soricidae, Mammalia) from Early Oligocene fissure fillings in South Germany–and a phylogenetic analysis of the Heterosoricinae. Palaeodiversity 2, 321–342.