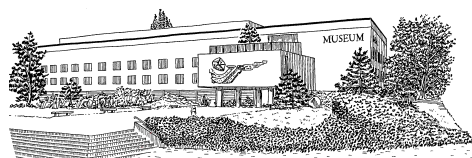


# R E V U E D E PALÉOBIOLOGIE

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## New small mammal fauna of late Middle Eocene age from a fissure filling at La Verrerie de Roches (Jura, NW Switzerland)

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### Abstract

The recent palaeontological investigations along the future motorway A16 (Transjurane) in the vicinity of the historical site of La Verrerie de Roches (Jura, NW Switzerland) led to the discovery, in 2006, of a new Eocene fauna of small mammals trapped in siderolithic deposits of a fissure filling. Its study permits the description and the identification of twenty dental specimens including the following taxa: *Sciuroides* cf. *romani*; *Paradelomys crusafonti* (Thaler, 1966); *Paradelomys ruetimeyeri* (Pictet & Humbert, 1869); *Elfomys* cf. *tobieni*; *Elfomys engesseri* Hooker & Weidmann, 2007; *Adapis* aff. *sudrei*; *Necrolemur* aff. *antiquus*; *Mixtotherium lavergnense* (Sudre, 1977). This mammal assemblage, especially the theridomyoid association, is typical for the Robiacian European Land Mammal Age (ELMA), corresponding to the Bartonian stage (late Middle Eocene) and fits best with the Reference Level MP16 and the *Lophiodon lauricense-Lophiotherium siderolithicum* Mammal Biozone. Despite heavy taphonomical bias, the referred fauna seems to correspond to contemporaneous faunas elsewhere in Europe and suggests a forested, perhaps deciduous, environment.

### Keywords

Systematics, biostratigraphy, ecology, Rodentia, primates.

### Résumé

**Une nouvelle faune de micromammifères de l'Eocène moyen terminal provenant d'un remplissage karstique de La Verrerie de Roches (Jura, NO Suisse).**- Les récentes excavations paléontologiques le long de la future autoroute A16 (Transjurane), à proximité du site historique de La Verrerie de Roches (Jura, NO Suisse), ont conduit à la découverte en 2006 d'une nouvelle faune de micromammifères éocènes piégés dans les dépôts sidérolithiques d'un remplissage karstique. Son étude a permis la description et l'identification de vingt restes dentaires, incluant les espèces suivantes: *Sciuroides* cf. *romani*; *Paradelomys crusafonti* (Thaler, 1966); *Paradelomys ruetimeyeri* (Pictet & Humbert, 1869); *Elfomys* cf. *tobieni*; *Elfomys engesseri* Hooker & Weidmann, 2007; *Adapis* aff. *sudrei*; *Necrolemur* aff. *antiquus*; *Mixtotherium lavergnense* (Sudre, 1977). Cet assemblage de mammifères, et tout particulièrement son association de théridomyoïdes, est typique pour le Robiacien (Bartonian, Eocène moyen terminal). Cette composition faunique correspond au niveau de référence MP16 et à la biozone *Lophiodon lauricense-Lophiotherium siderolithicum*. Malgré un évident biais taphonomique lié aux processus de remplissages karstiques, la faune étudiée est similaire aux faunes contemporaines européennes et indique un environnement forestier probablement caduque.

### Mots-clés

Systématique, biostratigraphie, écologie, Rodentia, primates

## I. INTRODUCTION

The term “sidérolithique”, introduced by Thurmann (1836), has for a long time been wrongly considered as a stratigraphical unit at the scale of Western Europe (Tapsoba, 1967; Autran *et al.*, 1979; Michon, 2001). In fact, it designates the phenomenon of weathering and superficial mechanical erosion of calcareous basements leading to the formation of lateritic palaeosols, which are frequently reworked in depressions or fissures (Aubert, 1975; Hamel, 1998). Within the Jura Mountains, the

siderolithic deposits directly overlap the Mesozoic basement, mainly by filling in fissures of palaeokarsts, and are dated from the Middle to the Late Eocene (e.g., Stehlin, 1903; Fleury, 1909; Liniger, 1925; Picot, 2002). The mammal faunas associated with these deposits biostratigraphically range from MP14 (Egerkingen; Switzerland) to MP19 (Oberbösgen, Entreroches; Switzerland) (Schmidt-Kittler *et al.*, 1987; Biochrom'97, 1997; Hooker & Weidmann, 2000; Picot, 2002).

In the Delémont valley (Canton Jura, NW Switzerland; Fig. 1), the siderolithic is well known and has been

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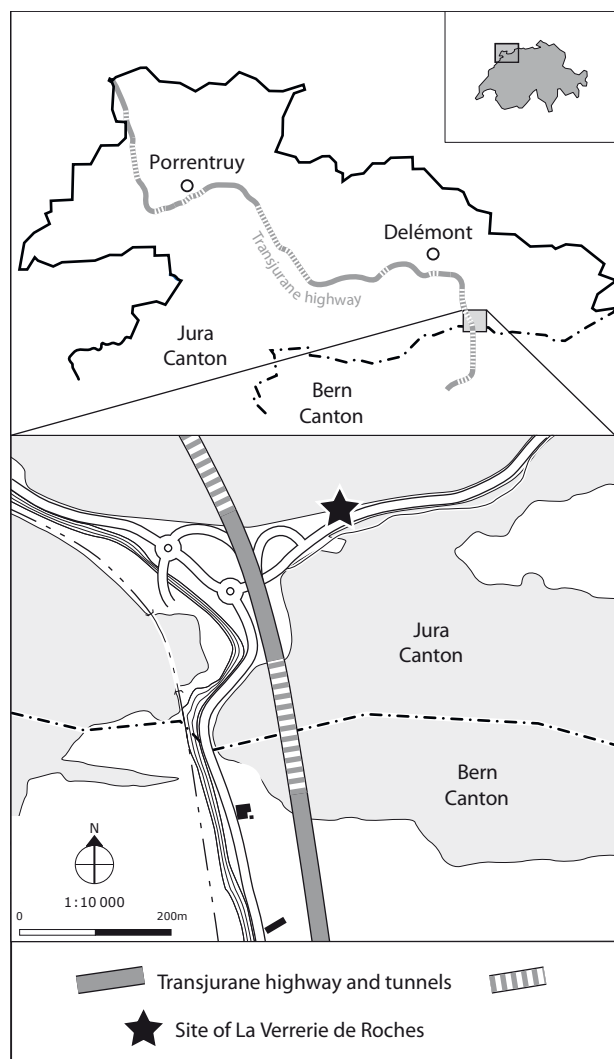


Fig. 1: Geographical location of the fissure filling of La Verrerie de Roches (Jura, NW Switzerland).

Fig. 1: Localisation géographique de la poche de remplissage karstique de La Verrerie de Roches (Jura, NO Suisse).

largely exploited for industry during the 19th century. However, in comparison to the systematic studies of the Swiss localities of Egerkingen and Mormont in the framework of European Eocene mammals (Stehlin, 1903, 1904, 1905a, b, 1906, 1908, 1910, 1912, 1916; Hartenberger, 1969, 1970, 1973; Hooker & Weidmann, 2000, 2007), the fossiliferous locality of La Verrerie de Roches remained poorly recognised and exploited, and few palaeontological investigations were done. The only published reference is that of Stehlin (1916: p. 1509, fig. CCCLXV), who mentioned a fragmentary right hemimandible with m1-m2 attributed to *Primates incertae sedis*.

The recent palaeontological investigations along the future motorway A16 (Transjurane) led to the discovery, in 2006, of a new fauna of small mammals found in a fissure filling of La Verrerie de Roches (Canton Jura, NW

Switzerland; Fig. 1). We report here the description and the identification of this new Eocene fauna. For the first time, the biochronostratigraphical range covered by the fissure fillings of La Verrerie de Roches is established. Additionally, the above-mentioned fauna is included in a short ecological interpretation as an attempt to reconstruct its habitat.

## II. MATERIAL AND METHODS

Twenty teeth of small mammals were discovered by screening-washing of the siderolithic deposits of a fissure filling (ca. 350 kg of sediments) from La Verrerie de Roches. The referred material is stored in the collection PAL A16 of the Musée jurassien des Sciences naturelles in Porrentruy, Switzerland.

Dental nomenclatures and measurements follow Hooker & Weidmann (2007) for the Rodentia, Szalay & Delson (1979) and Godinot (2003) for the Primates, and Berthet (2003) for the Cainotherioidea. Biometrical measurements, taken under the binocular, have a precision of 0.01 mm and are indicated as length x width in millimetres. The ecological parameters and their abbreviations are defined by Hooker & Weidmann (2000). The biochronological framework is based on chronological correlations of the European Land Mammal Ages (ELMA) defined by the succession of European mammal reference levels (MP-levels; Brunet *et al.*, 1987; Biochrom'97, 1997), the standard biozones (Hooker, 1986, 1987, 1996), the Swiss Reference Faunas (Berger, 2011), and the Paleogene geological time scale (Luterbacher *et al.*, 2004; Vandenberghe *et al.*, 2012).

**Anatomical abbreviations.** C/c, upper/lower canine; D/d, upper/lower deciduous tooth; I/i, upper/lower incisor; M/m, upper/lower molar; P/p, upper/lower premolar.

**Institutional abbreviations.** MGL, Musée géologique de Lausanne; MJSN, Musée jurassien des Sciences naturelles, Porrentruy; NMB, Naturhistorisches Museum Basel.

## III. SYSTEMATICS

**Class Mammalia Linnaeus, 1758**  
**Supercohort Marsupialia Illiger, 1811**  
**Family Didelphidae Gray, 1821**  
**Subfamily Herpetotheriinae Trouessart, 1879**  
**Herpetotheriinae indet.**  
**Pl. II, fig. B**

**Referred material:** Left P1 (MJSN VRR006-219); fragmentary right M4 (MJSN VRR006-209).

**Description:** Both referred specimens are incomplete. The referred P1 (1.5 x 1.0) is probably two-rooted

with a high crown and a very short distal denticle. The referred M4 is 1.60+ long by 2.65 wide. The buccal wall is relatively long; it has a weak stylocone (stylar cusp B *sensu* Hooker, 1986) and a strong mesostyle (stylar cusp C *sensu* Hooker, 1986), and is strongly dilambdodont.

**Discussion:** The referred specimens probably belong to herpetotheriid marsupial, but their incompleteness does not permit a detailed level of identification. The combination of abovementioned characters could be indicative of a taxon close to *Amphiperatherium fontense* (Crochet, 1980; Hooker & Weidmann, 2000).

**Supercohort Placentalia Owen, 1837**  
**Order Rodentia Bowdich, 1821**  
**Superfamily Theridomyoidea Alston, 1876**  
**Family Pseudosciuridae Zittel, 1893**  
**Genus *Sciuroides* Major, 1873**  
*Sciuroides cf. romani* (Hartenberger, 1973)  
**Pl. I, figs. A1-A3**

**Referred material:** Right DP4 (MJSN VRR006-213); right P4 (MJSN VRR006-212); left M1/2 (MJSN VRR006-208).

**Description:** The referred upper cheek teeth are brachyodont and bunoselenodont, with four main, well-developed cusps and a complete endoloph, but without enamel wrinkles. DP4 (1.94 x 2.16) is sub-triangular, short and broad, with a concave mesiolingual margin, very close protocone and hypocone, a strong paracone, a broken protoloph, and a well-developed anteroloph. The metalophule I, the hypolophule and the prehypocrista are lacking; the metalophule II is strong, but does not join the hypocone. P4 (1.94 x 2.11), whose protoloph is broken, is trapezoidal in occlusal view. The protocone and hypocone are poorly separated and the protoconule and metaconule are distinct. The metalophule II is complete, arising lingually from the hypocone, whereas the metalophule I, arising from the hypocone as well, is broken. M1 is small (2.21 x 2.09) with a weak paraconule extending from the protoloph at around 45% of distance to mesial margin. The metacone is separated from the distal edge by the posteroloph. There is a partial mesoloph, a buccally open sinus, and a prehypocrista that mesially bypasses the metaconule. The hypolophule is missing, but the protocone is located approximately opposite to the paracone. There is a mesiobuccal metaconule crest and a few-developed but complete metalophule I, joining the prehypocrista and the metacone.

**Discussion:** The complete endoloph on upper cheek teeth and the metalophule I linking the hypocone and the metacone on M1/2 are typical features of the genus *Sciuroides* (Hooker & Weidmann, 2000). The M1/2 is very similar to *S. romani* by its unwrinkled enamel and its reduced size reduction (Hartenberger, 1973, 1988; Hooker & Weidmann, 2000). However, its dimensions (Fig. 2) are smaller than the specimens from Le Bretou and Robiac (type-locality of the species) presented by

Hartenberger (1973, 1988). This fact, associated with a shorter and broader DP4 and a poorly developed metalophule I on M1/2 brings this specimen rather close to *S. cf. romani* from Pontils in Spain (Anadón *et al.*, 1983; Hooker & Weidmann, 2000).

**Family Theridomyidae Alston, 1876**  
**Subfamily Columbomyinae Thaler, 1966**  
**Genus *Paradelomys* Thaler, 1966**  
*Paradelomys crusafonti* (Thaler, 1966)  
**Pl. I, fig. D1-D2**

**Referred material:** Left p4 (MJSN VRR006-211); right m1/2 (MJSN VRR006-228).

**Description:** The referred p4 (1.50 x 1.20) is mesially wide and somewhat hypsodont, and bears distinct protoconid and metaconid. The mesoconid is indistinct and the ectolophid joins the hypolophulid, but without mesially overhanging the sinusid. The referred m1/2 (1.57 x 1.38) is low-crowned, transversally elongated, and possesses a long trigonid. It lacks an anterolophulid, mesolophid, mesoconid, and ectoflexid. The antesinusid is long and located distobuccally behind the anteroconid, separating it from the protoconid. The metalophulid is nearly complete, somewhat straight and without distal deflection behind the anteroconid. The protoconid is situated more distally than the metaconid. The postmetacristid is indistinct. The ectolophid is complete, nearly straight and oblique, joining the hypolophulid at about one quarter of the distance from the hypoconid to the entoconid. The hypoconid does not overhang the sinusid mesially. The hypolophid is complete and slightly sinusoidal.

**Discussion:** The presence of two cusps at the mesial end of the referred p4 can be related to intraspecific variability (Jeremy J. Hooker, pers. com.). With the ectolophid attached without overhanging the sinusid on p4 and with the hypoconid situated slightly more distally than the metaconid, the well-developed antesinusid between the anteroconid and the protoconid, and the loss of the mesoconid on m1/2, the referred specimens MJSN VRR006-211 and MJSN VRR006-228 are typical for the genus *Paradelomys* (Hooker & Weidmann, 2000; 2007). In size, they are slightly smaller than the *P. crusafonti* specimens of Robiac (Fig. 2) and Eclépens B (Lp4 MGL 46928 = 1.68; Lm1/2 = 1.73 ± 0.09; Hooker & Weidmann, 2000), but they lie entirely within the ranges of the smaller specimens of *P. crusafonti* described from Le Bretou, Sosis (type locality), and Fons 4 (Fig. 2; Hartenberger, 1973).

***Paradelomys ruetimeyeri* (Pictet & Humbert, 1869)**  
**Pl. I, fig. E**

**Referred material:** Right m1/2 (MJSN VRR006-210).

**Description:** The referred m1/2 (2.04 x 1.64) is large-sized, low-crowned, transversally elongated, and

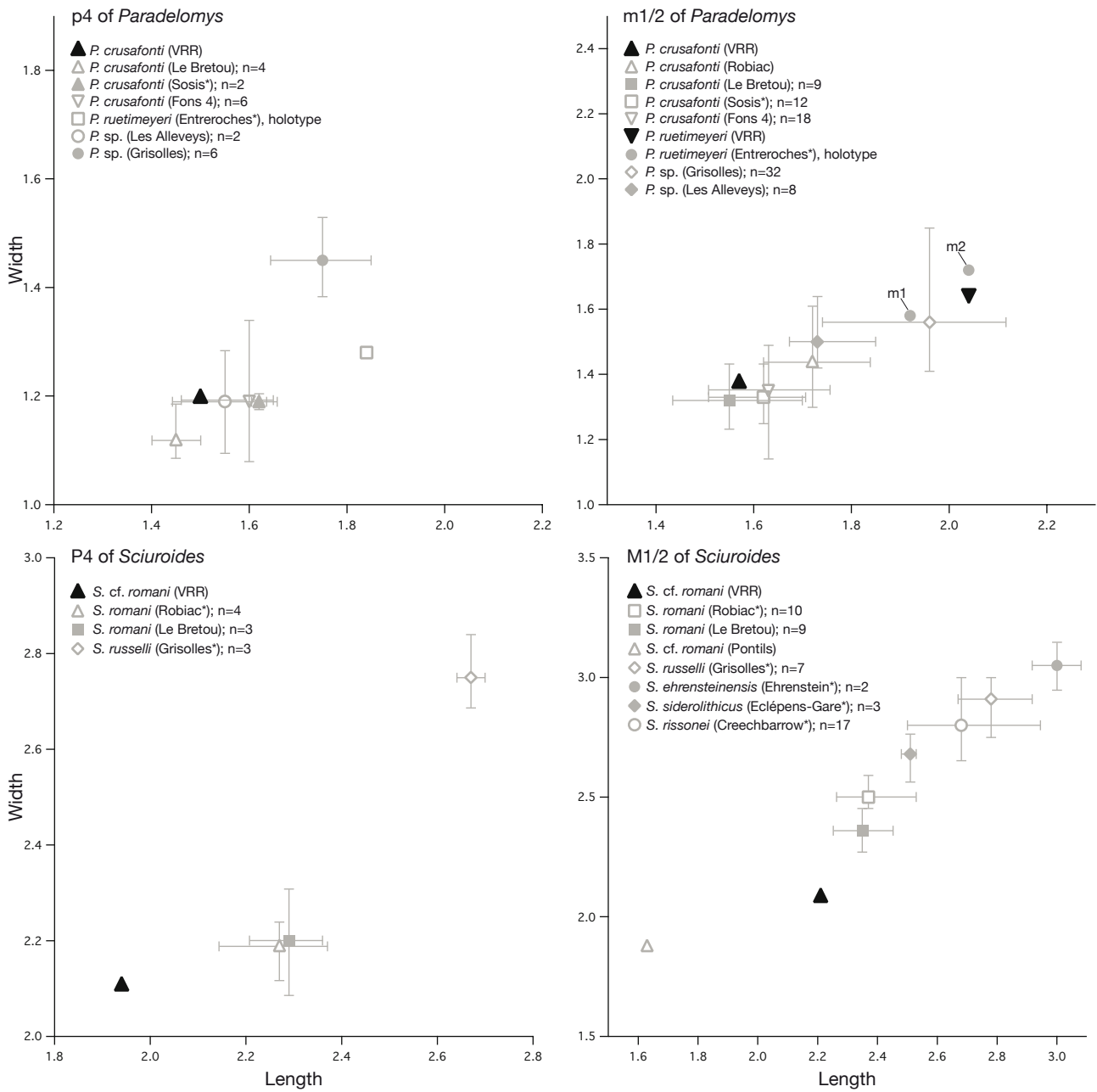


Fig. 2: Biometrical measurements (length x width in mm) of teeth of *Paradelomys* (p4 and m1/2) and *Sciurooides* (P4 and M1/2) from la Verrerie de Roches, with comparison with other species from different localities (measurements taken from the literature: Hartenberger, 1973, 1988; Hartenberger & Louis, 1976; Ginsburg *et al.*, 1982; Anadón *et al.*, 1983; Hooker & Weidmann, 2000, 2007). \* type locality.

Fig. 2: Mesurations biométriques (longueur x largeur en mm) des dents de *Paradelomys* (p4 et m1/2) et *Sciurooides* (P4 and M1/2) de La Verrerie de Roches, et comparaisons avec d'autres espèces provenant de différentes localités (mesures prises de la littérature: Hartenberger, 1973, 1988; Hartenberger & Louis, 1976; Ginsburg *et al.*, 1982; Anadón *et al.*, 1983; Hooker & Weidmann, 2000, 2007). \* localité type.

possesses a long trigonid. The hypolophid is nearly straight, weakly developed and the tooth lacks a mesolophid and mesoconid. The anteroconid, antesisinid, protoconid, and ectoflexid are well developed. The ectolophid is straight and joins the hypolophid at about one quarter of the distance from the hypoconid to the

entoconid. The protoconid and hypoconid are situated slightly more distally than the metaconid and entoconid, respectively, and the hypoconid does not overhang the sinusid mesially. The postmetacristid is indistinct and the talonid notch is wide. The metalophulid is complete and nearly straight without distal deflection and seems to be

connected to the anterolophid by a faint anterolophulid, leaving a sort of fovea between them.

**Discussion:** As for *P. crusafonti* m1/2 MJSN VRR006-228, this referred m1/2 is typical for the genus *Paradelomys* in that its hypoconid is situated slightly more distally than the metaconid, there is a notch between the anteroconid and the protoconid, and the mesoconid is lost (Hooker & Weidmann, 2000, 2007). In size (Fig. 2), it lies entirely outside the ranges of *P. crusafonti*, spans those of *P. sp.* of Grisolles (Hartenberger & Louis, 1976), and fits very well with those of *P. ruetimeyeri* of the type locality Enteroches (holotype: right p4-m2 MGL 40464; Hooker & Weidmann, 2000). For these reasons, we suggest an assignation to *P. ruetimeyeri* for the probably m2 of La Verrerie de Roches. Also, the belonging of the large *P. sp.* of Grisolles to *P. ruetimeyeri* is always questionable. Finally, the highlighted co-occurrence of both species (*P. ruetimeyeri* and *P. crusafonti*) in the assemblage of La Verrerie de Roches could be a further argument or an evolutionary history of two lineages with different sizes as suggested, amongst different hypothesis, by Hooker & Weidmann (2000).

#### Subfamily Issidoromyinae Tullberg, 1899

#### Genus *Elfomys* Hartenberger, 1971

#### *Elfomys cf. tobieni* (Thaler, 1966)

#### Pl. I, figs. C1-C2

**Referred material:** Right p4 (MJSN VRR006-225); left broken m3 (MJSN VRR006-220).

**Description:** The referred p4 (1.14 x 1.07) is short with a protoconid and a metaconid somewhat fused in a half-moon shape. The ectolophid joins the hypolophid at the lingual part of the hypoconid, that slightly overhangs the deep sinusid mesially. The prehypolophulid part of the ectolophid is no longer than half of the total length. On the referred m3 (1.50 x 1.0), which is broken buccally, the trigonid is long and the anterolophulid is thin, connecting the anterolophid and a broken metalophulid that is distally deflected. The protoconid is transversally opposite to the metaconid, the hypolophulid is complete and nearly straight, the hypoconid overhangs slightly the sinusid mesially, and the postmetacristid is indistinct.

**Discussion:** The above-mentioned characters, in particular the combination of a prehypolophulid no longer than half of the total length of p4 and a broken, distally deflected metalophulid on m3, fit well with the genus *Elfomys* (Hooker & Weidmann, 2007). However, the dimensions of the referred specimens (Fig. 3) lie largely outside the plots of *E. parvulus* (Hartenberger, 1973; Vianey-Liaud & Ringeade, 1993) and barely reach the lower end of those of *E. engesseri* from Les Alleveys 1986 (Hooker & Weidmann, 2007). On the other hand, they narrowly overlap the upper-value domain of those of *E. tobieni* from Robiac, the type locality of this species (Hartenberger, 1973). Owing to the meagre sampling of La Verrerie de Roches, to the slightly larger width of

the p4 (MJSN VRR006-225) in comparison with the described specimens of *E. tobieni* (Hartenberger, 1973), and to the incomplete state of the m3 (MJSN VRR006-220), the referred specimens are assigned to *E. cf. tobieni*.

#### *Elfomys engesseri* Hooker & Weidmann, 2007

#### Pl. I, figs. B1-B5

**Referred material:** Left DP4 (MJSN VRR006-217); left P4 (MJSN VRR006-215); two right M1/2s (MJSN VRR006-226, MJSN VRR006-227); left p4 (MJSN VRR006-222).

**Description:** The referred dental specimens are low crowned. DP4 (1.24 x 1.23) is longer than wide and lacks its mesoloph. The protocone and the metacone are separated and the anteroloph does not seem to join a paraconule. P4 (1.28 x 1.39) possesses a strong endoloph, a protocone and a hypocone weakly separated, and an indistinct ectoflexus. It is further characterised by a partly buccally closed sinus, a weak hypolophule that joins the posteroloph, and by the absence of a metalophule I. The referred M1/2s (1.49 x 1.55; 1.36 x 1.46) lack a postmetacrista. The premetacrista and the metalophule I are present and the endoloph is incomplete. The paraconule is rather small (*sensu* Hooker & Weidmann, 2007), its size being judged by its degree of projection from the centre of the protoloph to the mesial tooth margin (<50 %). The metacone is separated from the distal edge by a posteroloph, the sinus is buccally open, and the mesoloph, almost absent, is only represented by a weak buccal extension of the prehypocrista, the latter bypassing mesially the metaconule in MJSN VRR006-226. The posteroloph is present, the mesiobuccal metaconule crest is absent or incomplete, the protocone is approximately opposite to the paracone, and the hypolophule can be present or absent. On p4 (1.30 x 1.06), only one mesial cusp constitutes the mesial border of the tooth and forms a half-moon with a distally-oriented secondary lophid. The mesoconid is distinct and the ectolophid joins lingually the hypolophulid without really overhanging the sinusid mesially.

**Discussion:** According to Hartenberger (1973) and Hooker & Weidmann (2007), the brachyodont, small-sized cheek teeth, the absence of an ectoflexus, a protocone and hypocone poorly separated on P4, the small-sized paraconule, the incomplete or absent mesiobuccal metaconule crest, the buccally open sinus, the possible lack of a hypolophule linking metalophule II with posteroloph on M1/2, and M1/2 less than 1.5 mm long, support evidence for attribution to a species of *Elfomys* more primitive than *E. parvulus* and *E. tobieni* (Astibia *et al.*, 2000; Hooker & Weidmann, 2007). The referred specimens are clearly larger than the size range of those of both *E. parvulus* and *E. tobieni* (Hartenberger, 1973), but fit very well with the dimension plots of those of *E. engesseri* from Les Alleveys 1986 (type locality) and Eclépens-Gare (Hooker & Weidmann, 2007; Figs. 3

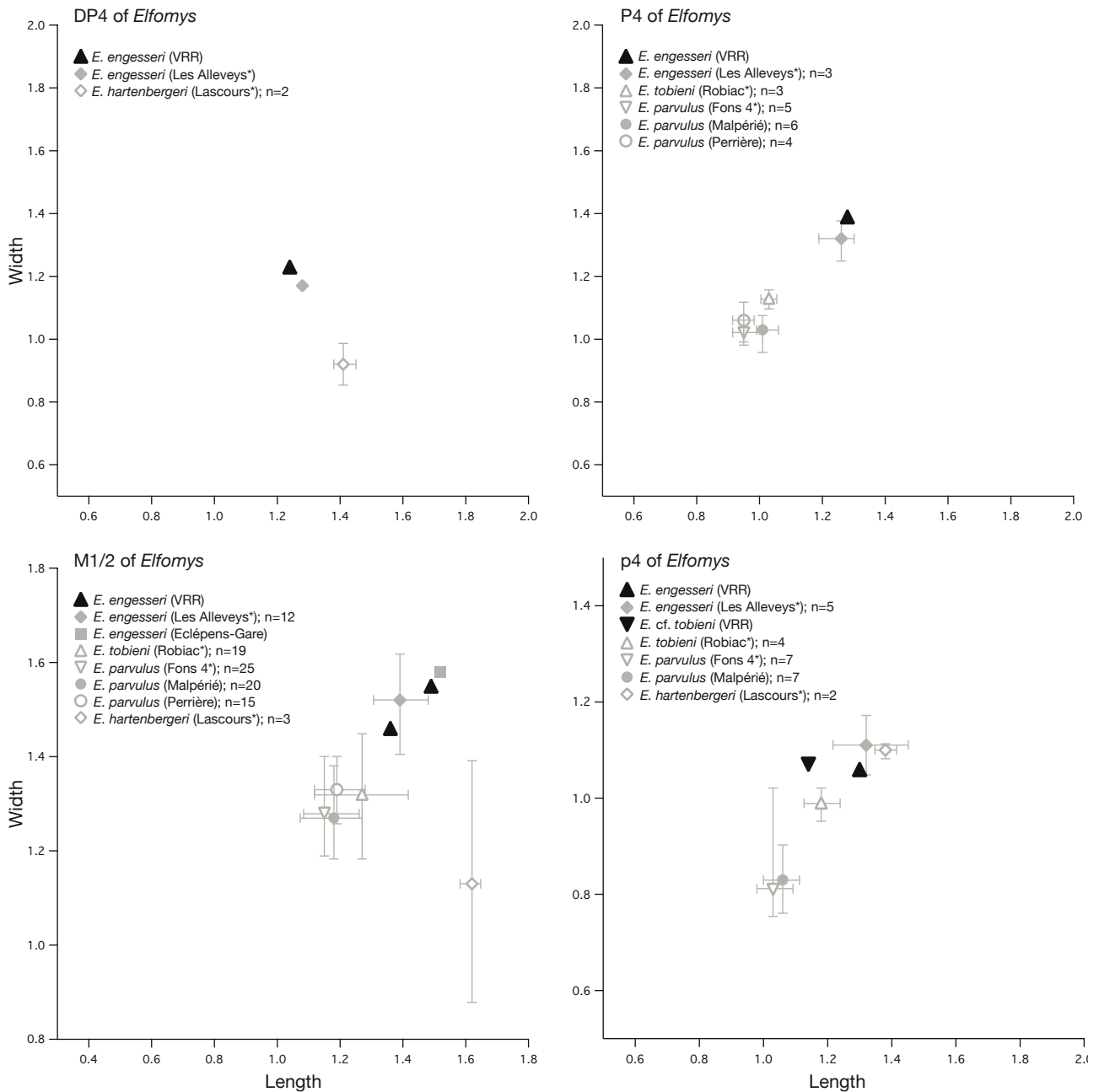


Fig. 3: Biometrical measurements (length x width in mm) of teeth of *Elfomys engesseri* (DP4, P4, M1/2, and p4) from la Verrerie de Roches, with comparison with other species of *Elfomys* from different localities (measurements taken from the literature: Hartenberger, 1973; Vianey-Liaud & Ringeade, 1993; Hooker & Weidmann, 2007). \* type locality.

Fig. 3: Mensurations biométriques (longueur x largeur en mm) des dents d'*Elfomys engesseri* (DP4, P4, M1/2, and p4) de la Verrerie de Roches, et comparaisons avec d'autres espèces provenant de différentes localités (mesures prises de la littérature : Hartenberger, 1973 ; Vianey-Liaud & Ringeade, 1993 ; Hooker & Weidmann, 2007). \* localité type.

and 4). Moreover, the morphological characters, such as the incomplete endoloph and the absence of mesoloph are similar to those of *E. engesseri*.

**Order Primates Linnaeus, 1758**  
**Suborder Strepshirini Saint-Hilaire, 1812**  
**Superfamily Lemuroidea Gray, 1821**  
**Family Adapidae Trouessart, 1879**

**Subfamily Adapinae Trouessart, 1879**  
**Genus *Adapis* Cuvier, 1821**  
***Adapis* aff. *sudrei* (Gingerich, 1977)**  
**Pl. II, fig. D**

**Referred material:** Left p4 (MJSN VRR006-207).  
**Description:** The referred p4 (2.54+ x 1.68+) is molariform, with a protocristid lingually intersecting

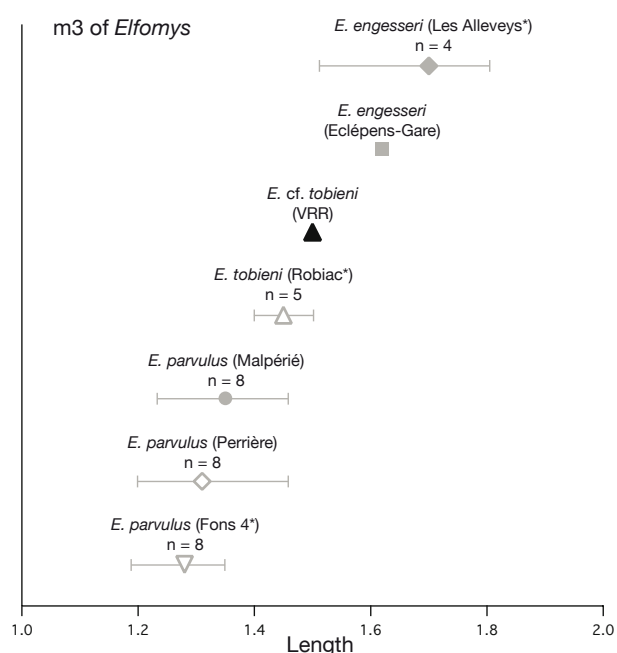


Fig. 4: Length (in mm) of the m3 of *Elfomys cf. tobieni* from La Verrerie de Roches, in comparison with the m3 of other *Elfomys* species from different localities (measurements taken from the literature: Hartenberger, 1973; Hooker & Weidmann, 2000, 2007). \* type locality.

Fig. 4: Longueur (en mm) de la m3 d'*Elfomys cf. tobieni* de La Verrerie de Roches, en comparaison avec les m3 d'autres espèces d'*Elfomys* provenant de différentes localités (mesures prises de la littérature: Hartenberger, 1973; Hooker & Weidmann, 2000, 2007). \* localité type.

the straight cristid obliqua and a paraconid located in a midline position of the paracristid. The trigonid, in which torsion is strong, is shorter and narrower than the talonid. The paraconid is not cusped, but is formed where the paracristid thickens slightly at its mesiolingual part. The protoconid and the hypoconid are higher than the metaconid. There is a well-developed cingulid that starts at the middle of the mesial face, surrounds the entire buccal border, and ends at the level of the hypoconid. There is no cingulid on the lingual border, and the tooth bears two roots in its mesial and distal parts.

**Discussion:** The referred p4 presents the typical morphology of *Adapis*, such as advanced molarisation and the lingual position of the intersection between the cristid obliqua and the protocristid. However, the dimensions are clearly smaller than those of all known *Adapis* species, even those of the small-sized *A. sudrei*, which is, on the other hand, very close in morphology (Gingerich, 1977). Additionally, the historic specimen m1/2 NMB VR15 from La Verrerie de Roches attributed to Primate *incertae sedis* by Stehlin (1916: p. 1509, fig. CCCLXV) is very close in dimensions and morphology. Therefore, although the record is very scarce, the

referred material reveals that they correspond to the same taxon belonging to the genus *Adapis*. Because of the close morphological similarity to *A. sudrei*, but given the significant difference in size, both specimens are cautiously attributed to *A. aff. sudrei*.

**Infraorder Tarsiiformes Gregory, 1915**  
**Superfamily Tarsioidea Gray, 1825**  
**Family Omomyidae Trouessart, 1879**  
**Subfamily Microchoerinae Lydekker, 1887**  
**Genus *Necrolemur* Filhol, 1873**  
***Necrolemur aff. antiquus* Filhol, 1873**  
**Pl. II, fig. A**

**Referred material:** Right i1 (MJSN VRR006-218).

**Description:** The crown of the referred i1 (2.66 x 1.22; H = 1.42) is lanceolate and mediolaterally narrow, and is apically slightly bent. The main cusp forms lingually a gentle fold from the base to the apex of the crown, nearly parallel to the anterior cingulum. There is no buccal cingulum. In the triangle formed by the apical confluence of the buccal and lingual cingula lies a distal interstitial facet indicating contact with i2. The mesial interstitial facet is marked by striations, attributed to fur grooming (Rose *et al.*, 1981). By comparing the orientation of these striations in *Vectipithecus smithorum* and *Microchoerus* (Hooker & Harrison, 2008), the referred i1 is seen to be significantly procumbent, angled at about 30 degrees to the horizontal as in *Vectipithecus smithorum*.

**Discussion:** The combination of the abovementioned features is typical for the genus *Necrolemur*. The dimensions are rather small, plotting slightly out of the range of *Necrolemur antiquus*. However, it is attested that the *Necrolemur antiquus* lineage shows a slight increase of size during the interval MP17-20 (Godinot, 2003). For this reason, the referred specimen is tentatively attributed to *Necrolemur aff. antiquus*.

**Order Carnivora Bowdich, 1821**  
**Carnivora indet.**  
**Pl. II, figs. C1-C2**

**Referred material:** Left p2 (MJSN VRR006-205); right p2 (MJSN VRR006-206).

**Description:** Both referred p2s (4.0+ x 2.3; 4.3+ x 1.95+) are reduced, high, and rather slender, with an indistinct mesial denticle and a low, short and sharp distal one. In occlusal view, a longitudinal crest is mesially well developed and distally only marked on the lower part of the crown. The paracone is medially slightly bended with a tip located in the mesial half of the tooth. The cingulum is complete along the cervix, but weaker lingually and buccally.

**Discussion:** The two referred p2s differ from endemic European Paleogene artiodactyls by more simple morphology and less elongated distal part (Erfurt & Métais, 2007; Theodor *et al.*, 2007), from *Simamphicyon*



*helveticus* (Pictet & Humbert, 1869) by a higher crown and from *Quercygale helvetica* (Rütimeyer, 1862) and *Q. angustidens* (Filhol, 1872) by a shorter distal denticle (de Beaumont, 1965; 1966). They are quite similar to *Cynodictis* (de Bonis, 1978: 307, figs. 11 and 12; Hooker & Weidmann, 2000: 76, fig. 48) in morphology and, regarding their approximate dimensions, they should be close to *Cynodictis exilis* Filhol, 1876. However, owing to the meagre record of specimens in La Verrerie de Roches, a generic attribution cannot be supported and an ascription to Carnivora indet. is more cautious.

**Order Cetartiodactyla Montgelard *et al.*, 1997**

**Suborder Tylopoda Illiger, 1811**

**Superfamily Cainotherioidea**

**Camp & van der Hoff, 1940**

**Family Mixtotheriidae Pearson, 1927**

**Genus *Mixtotherium* Filhol, 1880**

***Mixtotherium lavergnense* (Sudre, 1977)**

**Pl. II, fig. E**

**Referred material:** Right M1 (MJSN VRR006-204).

**Description:** The small-sized and low-crowned M1 (2.9 x 3.8) has a short premetaconule crista that does not join the paracone, a large protocone distant from the paraconule, and a moderate W-shaped ridge (dilambdodonty) of the ectoloph. The notch between the paraconule and the protocone is shallow and the styles are crested.

**Discussion:** According to the cladistic analysis of Hooker & Weidmann (2000), *Oxacron? courtoisii* differs from the referred specimen in its high-crowned teeth, recurved premetaconule crista, weak dilambdodonty, and non-crested styles. On the other hand, the referred specimen presents a combination of characters typical of the genus *Mixtotherium*, such as a moderate dilambdodonty, crested styles, and a short premetaconule crista. By its size and its large protocone distant from the paraconule, it is distinct from *M. gresslyi* and *M. infans*. These features, however, can be observed on the holotype of *Mixtotherium lavergnense* from Lavergne (Hooker & Weidmann, 2000).

#### IV. DISCUSSION

##### The age of the fauna from La Verrerie de Roches

The mammal assemblage of La Verrerie de Roches is clearly affected by taphonomic processes linked to the fissure filling, most expressly by post-mortem fluvial transport sorting near or within the entrance of the cave system. However, the dental remains are well preserved and show no evidence of post-mortem abrasion, especially on the tooth surfaces. Moreover, the stratigraphic range homogeneity of the faunal composition excludes important faunal mixing and long-time averaging, and allows us to tentatively give a biostratigraphic age to the locality (Fig. 5).

The mammal assemblage of La Verrerie de Roches is typical for the Robiacian European Land Mammal Age (ELMA), corresponding approximately to the Bartonian Stage (late Middle Eocene). The faunal association can be correlated with the European mammalian biostratigraphy, in terms of Reference Level (Brunet *et al.*, 1987) and standard biozones (Hooker, 1986, 1987, 1996).

The age of the fauna is restricted to MP15-16 by the occurrence of the issidoromyid *Elfomys* cf. *tobieni* (Fig. 5). Indeed, the species *Elfomys tobieni* appears in Europe for the first time in the assemblage of La Livinière 2 (Reference Level MP15; Hooker, 1986). This primitive theridomyid has not been found so far in the older reference locality of Egerkingen (MP14, Switzerland). The younger reference locality of Robiac (MP16, France), is the type locality of *Elfomys tobieni*, where abundant remains have been found (Hartenberger, 1973). It is considered as the last occurrence of the species (Hooker, 1987; Vianey-Liaud & Ringead, 1993).

The record of *Sciuroides* cf. *romani*, *Elfomys engesseri*, and *Mixtotherium lavergnense*, three taxa only recorded so far in localities dated to MP16, reinforces this minimum age. The M1/2 MJSN VRR006-208 is small-sized for *S. romani* and could correspond to a form close to *S. cf. romani* from Pontils in Spain (Anadón *et al.*, 1983; Hooker & Weidmann, 2000). The referred specimens of *E. engesseri* from La Verrerie de Roches lie within the range of this species, only found in the fissure fillings of Les Alleveys and Eclépens-Gare (Mormont, Switzerland; Hooker & Weidmann, 2007). Additionally, the occurrence of *Mixtotherium lavergnense* is restricted to Robiacian localities, such as the fissure fillings of Eclépens-Gare and Lavergne (Quercy, France) (Biochrom'97, 1997; Hooker & Weidmann, 2000).

Regarding *Paradelomys ruetimeyeri*, its stratigraphic range is not well known, in contrast to *P. crusafonti*. According to the second alternative for the evolutionary history of Hooker & Weidmann (2000: 44), the occurrence of *P. ruetimeyeri* in La Verrerie de Roches could be referred to the *Paradelomys* assemblage of Grisolles (MP16, France) and to *P. ruetimeyeri* of Entreroches (MP19, Mormont, Switzerland), whereas *P. crusafonti* spans the stratigraphic range MP16-17 (Hooker & Weidmann, 2000).

In summary, the small mammals from La Verrerie de Roches fit best with the Reference Level MP16 (Fig. 5) and to the *Lophiodon lautricense-Lophiotherium siderolithicum* Mammal Biozone. It is characterised by key taxa, especially the theridomyoid association, very similar to those of Les Alleveys from the fissure fillings of Mormont (Switzerland) and of the reference locality of Robiac (France).

##### Ecological diversity of the fauna from La Verrerie de Roches

The fauna of La Verrerie de Roches is inconsistent in size by being restricted to the smallest animals (Tab. 1).

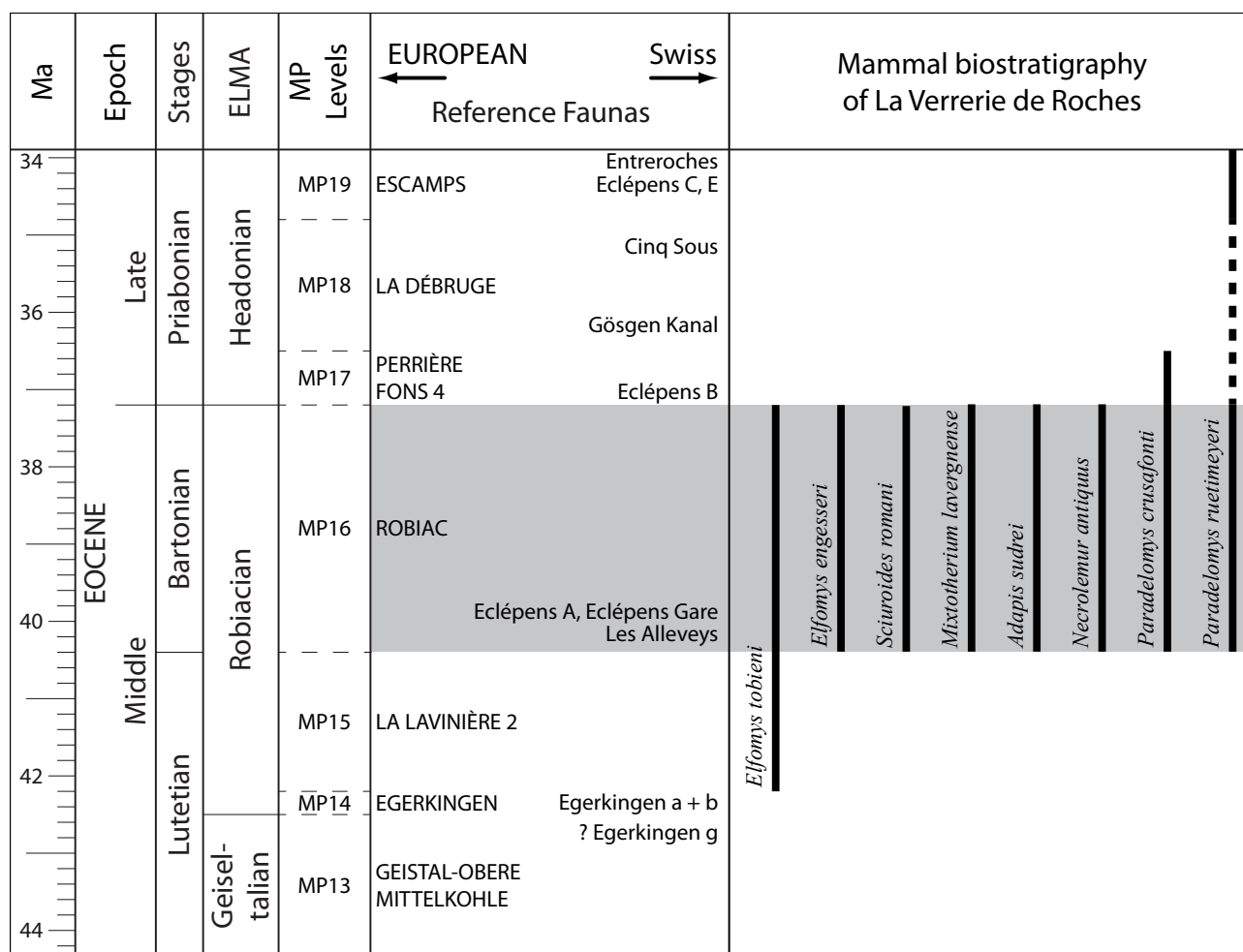


Fig. 5: Stratigraphy of the Late Eocene with the biostratigraphic distributions of the small mammal species studied. Dashed lines correspond to the supposed boundaries delimiting the ranges of the localities referred to a given European mammalian reference level (according to Hartenberger, 1973; Hartenberger & Louis, 1976; Biochrom'97, 1997; Vianey-Liaud & Ringade, 1993; Hooker & Weidmann, 2000, 2007).

Fig. 5: Stratigraphie de l'Eocène supérieur et répartitions biostratigraphiques des micromammifères étudiés. Les traits tillés correspondent aux limites supposées séparant les intervalles stratigraphiques des localités référées à un niveau européen à mammifères de référence (d'après Hartenberger, 1973; Hartenberger & Louis, 1976; Biochrom'97, 1997; Vianey-Liaud & Ringade, 1993; Hooker & Weidmann, 2000, 2007).

Table 1: Faunal list of La Verrerie de Roches (Jura, NW Switzerland) with their associated ecological parameters, which comprise size class (AB = <1 kg; C = 1-10 kg) / locomotion class (Ar = arboreal; Sc = scansorial; ST = semi-terrestrial; T = terrestrial) / dietary class (Car = carnivore; F = frugivore; HB = herbivore browser; I = insectivore), according to Hooker & Weidmann (2000).

Tableau 1: Liste faunique de La Verrerie de Roches (Jura, NO Suisse) avec leurs paramètres écologiques associés, qui comprennent taille (AB = <1 kg; C = 1-10 kg) / locomotion (Ar = arboricole; Sc = fouisseur; ST = semi-terrestre; T = terrestre) / régime alimentaire (Car = carnivore; F = frugivore; HB = herbivore folivore; I = insectivore), selon Hooker & Weidmann (2000).

Species	Ecological parameters
<i>Herpetotheriinae</i> indet.	AB / ST / I-F
<i>Sciuroides cf. romani</i>	AB / Sc / F
<i>Paradelomys crusafonti</i>	AB / ST / F
<i>Paradelomys ruetimeyeri</i>	AB / ST / F
<i>Elfomys cf. tobieni</i>	AB / ST / F
<i>Elfomys engesseri</i>	AB / ST / F
<i>Adapis aff. sudrei</i>	C / Ar / HB
<i>Necrolemur aff. antiquus</i>	AB / Ar / F
Carnivora indet.	C / ? / Car
<i>Mixtotherium lavergnense</i>	AB / T / HB

According to Andrews *et al.* (1979) and Legendre (1989), no modern fauna presents such a skewed size range. The restriction of the size of animals in the Verrerie de Roches assemblage is likely due to a major taphonomic sorting. However, its composition remains coherent: the relatively high proportion of size class AB (<1 kg) in comparison with the proportion of size class C (1-10 kg), and the dominance of the locomotion class ST (semi-terrestrial), are indicative of lowland, semi-deciduous forests when compared to ecological histograms from modern localities (Andrews *et al.*, 1979). The number of frugivores and the relative abundances between arboreal, tree dwellers versus scansorial animals fit well with a forested environment. The domination of the frugivores suggests also a low seasonality related to abundance of fruits throughout the year.

The diversity and the ecology of the fauna, in terms of composition, locomotion and diet, presents some similarities to contemporaneous faunas from Europe (Hooker & Weidmann, 2000). However, there are fewer terrestrial animals and herbivorous browsers in La Verrerie de Roches, which is most likely due to the taphonomic processes: the larger animals were not recorded here.

To sum up, although the fauna from La Verrerie de Roches seems to be heavily taphonomically biased, its correspondence to contemporaneous European faunas suggests that it represented a forested environment. The absence of evidence of an opening of the habitat, in contrast to what is documented in southern England between the Bartonian and the late Priabonian (Collinson & Hooker, 1987; Hooker, 1992), is most likely due to taphonomic sorting.

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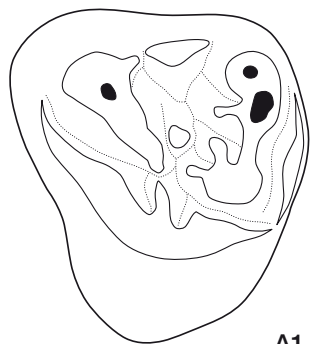
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## Plate I

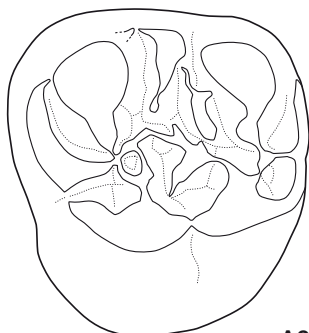
Teeth of Rodentia in occlusal views. *Sciuroides cf. romani*: **A1**, right DP4 (reversed; MJSN VRR006-213); **A2**, right P4 (reversed; MJSN VRR006-212); **A3**, left M1/2 (MJSN VRR006-208). *Elfomys engesseri*: **B1**, left DP4 (MJSN VRR006-217); **B2**, left P4 (MJSN VRR006-215); **B3**, right M1/2 (reversed; MJSN VRR006-227); **B4**, right M1/2 (reversed; MJSN VRR006-226); **B5**, left p4 (MJSN VRR006-222). *Elfomys cf. tobieni*: **C1**, right p4 (reversed; MJSN VRR006-225); **C2**, left m3 (MJSN VRR006-220). *Paradelomys crusafonti*: **D1**, left p4 (MJSN VRR006-211); **D2**, right m1/2 (reversed; MJSN VRR006-228). *Paradelomys ruetimeyeri*: **E**, right m1/2 (reversed; MJSN VRR006-210).

## Planche I

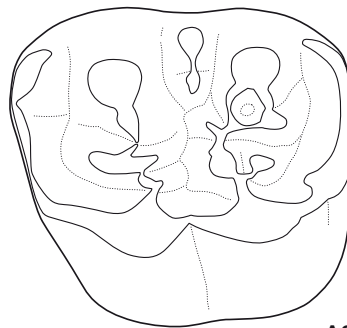
Dents de Rodentia en vues occlusales. *Sciuroides cf. romani*: **A1**, DP4 droite (inversée; MJSN VRR006-213); **A2**, P4 droite (inversée; MJSN VRR006-212); **A3**, M1/2 gauche (MJSN VRR006-208). *Elfomys engesseri*: **B1**, DP4 gauche (MJSN VRR006-217); **B2**, P4 gauche (MJSN VRR006-215); **B3**, M1/2 droite (inversée; MJSN VRR006-227); **B4**, M1/2 droite (inversée; MJSN VRR006-226); **B5**, p4 gauche (MJSN VRR006-222). *Elfomys cf. tobieni*: **C1**, p4 droite (inversée; MJSN VRR006-225); **C2**, m3 gauche (MJSN VRR006-220). *Paradelomys crusafonti*: **D1**, p4 gauche (MJSN VRR006-211); **D2**, m1/2 droite (inversée; MJSN VRR006-228). *Paradelomys ruetimeyeri*: **E**, m1/2 droite (inversée; MJSN VRR006-210).



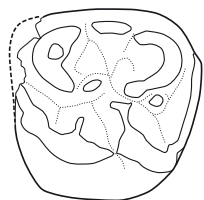
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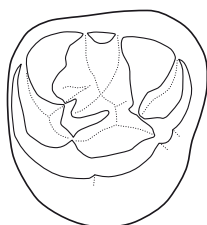
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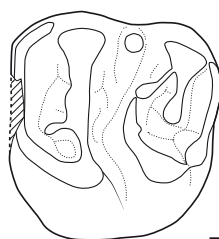
A3



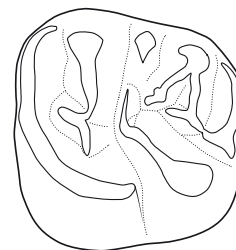
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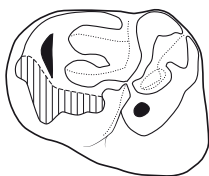
B2



B3



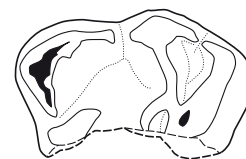
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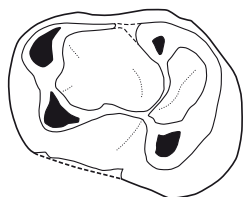
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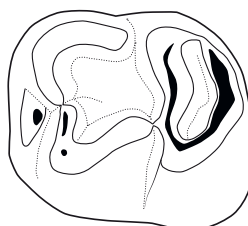
C1



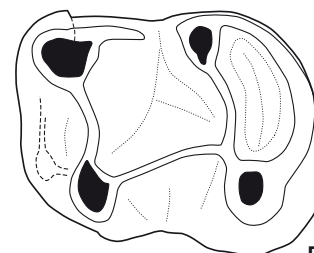
C2



D1



D2



E

1 mm



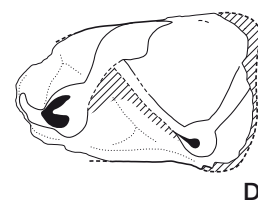
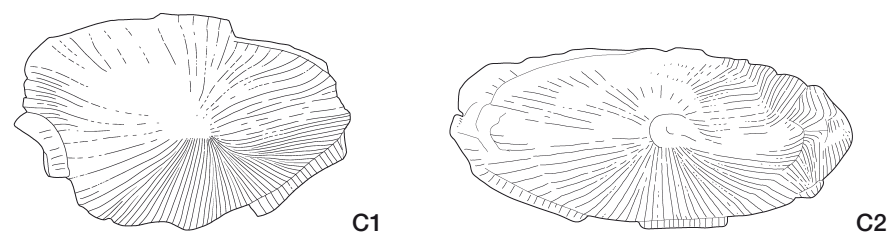
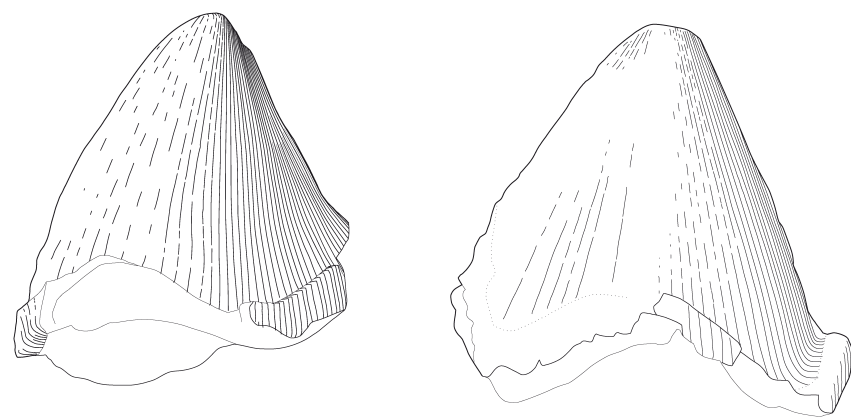
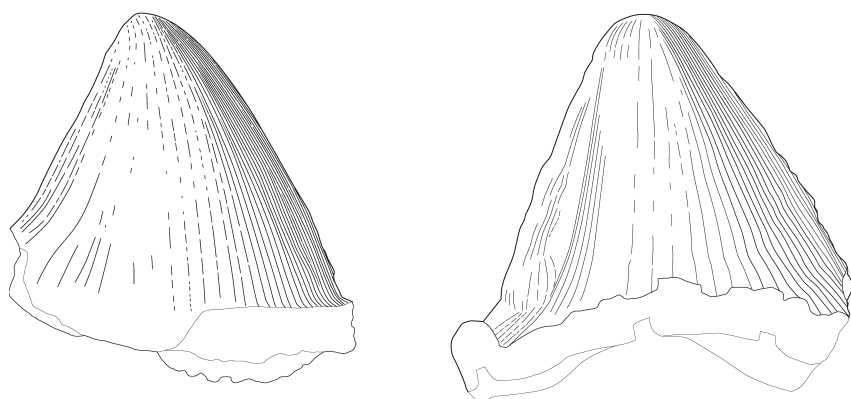
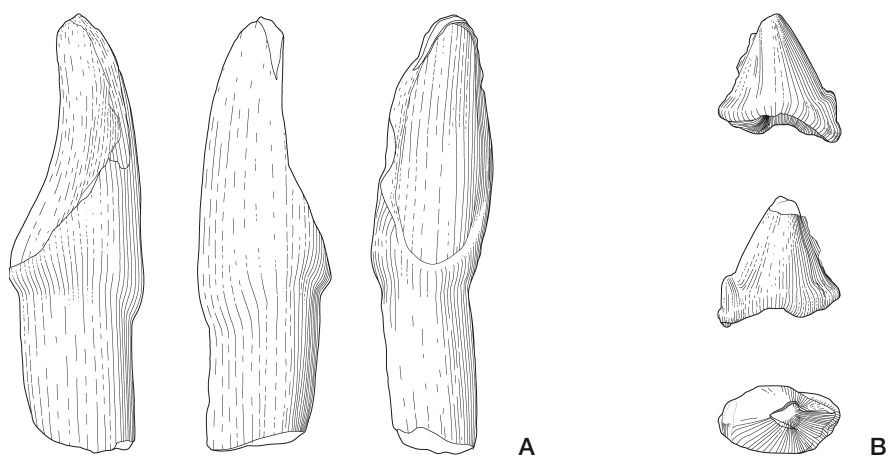
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## Plate II

Teeth of small mammals (excluding Rodentia). *Necrolemur* aff. *antiquus*: **A**, right i1 (reversed; MJSN VRR006-218) in mesial, distal and lingual views. Herpetotheriinae indet.: **B**, left P1 (MJSN VRR006-219) in lingual, labial and occlusal views. Carnivora indet.: **C1**, left p2 (MJSN VRR006-205) and **C2**, right p2 (reversed; MJSN VRR006-206) in lingual, labial and occlusal views. *Adapis* aff. *sudrei*: **D**, left p4 (MJSN VRR006-207) in occlusal view. *Mixotherium lavergnense*: **E**, right M1 (reversed; MJSN VRR006-204) in occlusal view.

## Planche II

Dents de micromammifères (excluant les Rodentia). *Necrolemur* aff. *antiquus*: **A**, i1 droite (inversée; MJSN VRR006-218) en vues mésiale, distale et linguale. Herpetotheriinae indet.: **B**, P1 gauche (MJSN VRR006-219) en vues linguale, labiale et occlusale. Carnivora indet.: **C1**, p2 gauche (MJSN VRR006-205) et **C2**, p2 droite (inversée; MJSN VRR006-206) en vues linguale, labiale et occlusale. *Adapis* aff. *sudrei*: **D**, p4 gauche (MJSN VRR006-207) en vue occlusale. *Mixotherium lavergnense*: **D**, M1 droite (inversée; MJSN VRR006-204) en vue occlusale.



1 mm

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