

The mammalian assemblage of Mazan (Vaucluse, France) and its position in the Early Oligocene European palaeobiogeography

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Abstract The locality of Mazan (Provence, South-Eastern France) yielded numerous remains of vertebrates, including numerous isolated teeth and a few bone fragments of mammals. A preliminary faunal list was published by Triat et al; the present systematic revision of the mammalian remains and the description of new specimens reveal that the assemblage comprises 18 taxa belonging to 7 orders and 10 families. Among the mammalian remains, the theridomyids and cricetids are the two most abundant groups. This revision confirms the ascription of the locality to the biochronological unit MP21, which corresponds to the very beginning of the Oligocene. As this locality overlies the Late Eocene faunas of Mormoiron, it clearly illustrates the drastic changes induced by the European ‘Grande-Coupure’ in Southeastern France like in the rest of Europe. A palaeobiogeographic analysis based on a comparison with 22

other Early Oligocene localities allows deciphering the European mammalian palaeobiogeography at the beginning of the Oligocene. The mammalian assemblage of Mazan shows significant affinities with other localities from Western Europe (especially French and Spanish localities), while localities from the eastern part of Europe (Anatolian, Bavarian and Bohemian localities) are noticeably different, even though these were not subjected to strong palaeobiogeographic differentiation nor endemism. The locality of Paguera 1 (Majorca)—possibly already insular in the Early Oligocene—shows peculiar affinities with Anatolian and Bavarian localities rather than with those in Western Europe. This, together with the absence of strong endemism, suggests the existence of land connections with the Anatolian region, but also between the Anatolian and the Bavarian regions, permitting faunal exchanges.

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Abbreviations

FSL Faculté des Sciences de Lyon, France
NMB Natural History Museum, Basel, Switzerland
m/M Lower/upper molars
H Crown height
TrW Trigonid width
TaW Talonid width
TaL Talonid length

1 Introduction and geological setting

The locality of Mazan is situated in the Provence (South-eastern France, Fig. 1a), in the southern part of the Mormoiron Basin (Vaucluse), part of a succession of

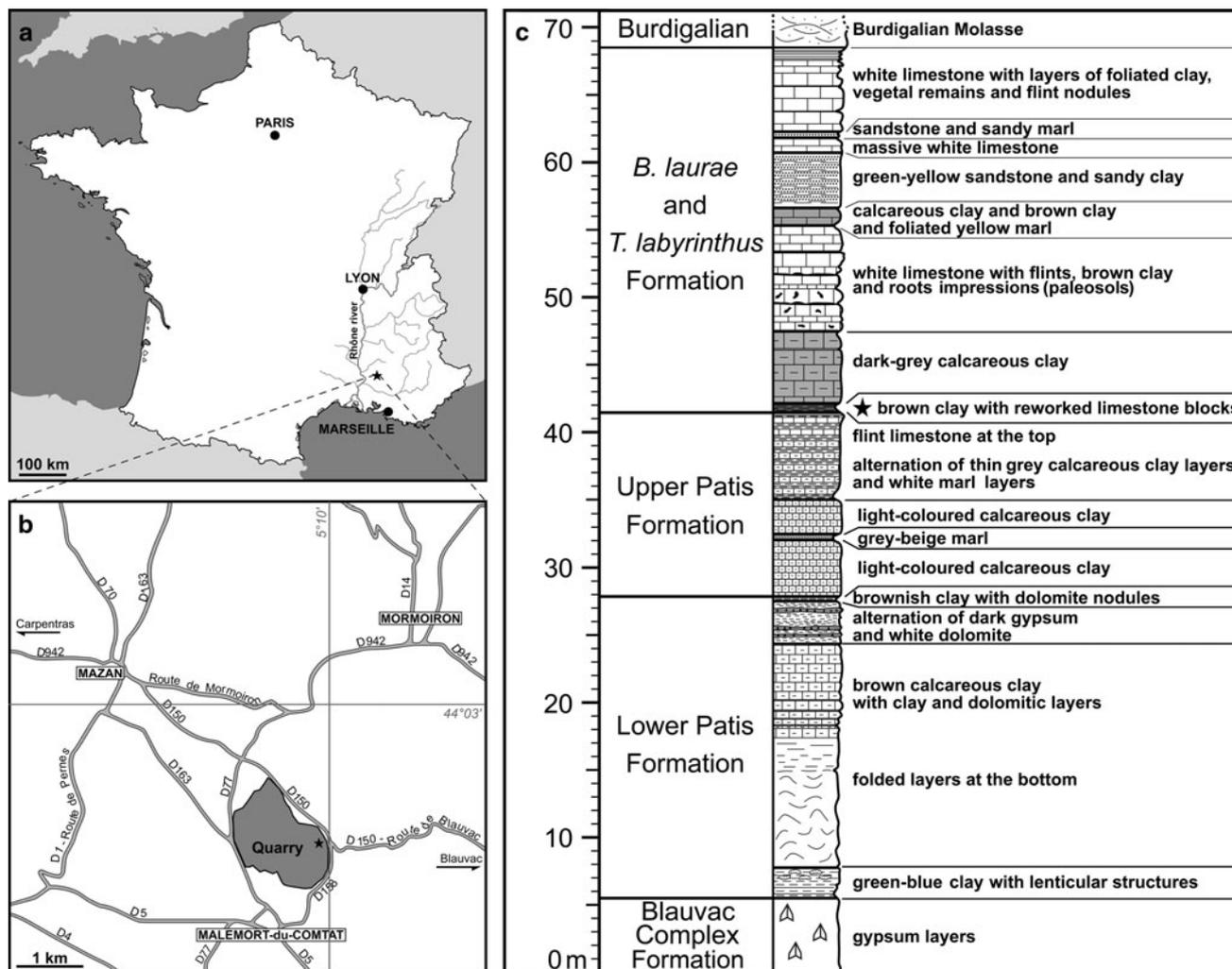


Fig. 1 Sketch map of France with **a** the location of Mazan at national scale, **b** at local scale, and **c** the synthetic log of the Cenozoic sedimentary deposits and geological formations in the Malemort-du-

Comtat quarry, modified after Triat et al. (1971). The layer, which yielded the studied mammalian assemblage is indicated by a star

basins that subsided between the rising Alps and the Rhodanian through. Although the quarry that yielded the fossil remains is partly located in the municipality of Malemort-du-Comtat, the mammal locality is usually called after the nearest town Mazan (Fig. 1b). The Palaeogene deposits in the Malemort-du-Comtat quarry comprise a sequence of 60 meters including four formations and starting with the gypsum beds of the Blauvac Complex Formation (Fig. 1c). A comprehensive section was drawn and studied by Triat et al. (1971; table 1). The basal formation, the so called “Blauvac Complex” Formation, is composed of gypsum and yielded a charophyte flora equivalent to that of the gypsum beds from Mormoiron, France (well-known for its Late Eocene *Palaeotherium* fauna). The charophyte flora is also equivalent to that of the Eocene Montmartre gypsum Formation (Paris Basin, France) and Bembridge Limestone Formation (southern

England). However, some charophyte taxa found in the “Blauvac Complex” Formation are also known in the Lower Hamstead beds (southern England), which are Early Oligocene in age (Feist-Castel 1976). The two formations that follow on top of the “Blauvac Complex” Formation are mainly composed of dolomitic, calcareous clays (Lower Patis Formation) and calcareous clays (Upper Patis Formation), and are both characterised by a complete absence of fossil remains. On top of the section, the so-called “*Brotia laurae* and *Tympanotonos labyrinthus* Formation” is composed of marls and detritic limestones, which yielded numerous charophytes, gastropods and mammalian remains. This formation is named after the freshwater gastropods that are abundant throughout this formation.

It is noteworthy that in their initial publication, Triat et al. (1971) assigned an Early Oligocene age to the lower

part of the section (just above the gypsum, i.e. “Blauvac Complex” Formation), and a ‘Middle’ Oligocene age (today no longer recognised as a valid stage) to the rest of the section above the Lower Patis Formation, due to the fact that the Eocene–Oligocene boundary was not yet precisely known by that time. Based on the present revision of the fossil assemblage, we can now undoubtedly assign an early Early Oligocene age to the “*Brotia laurae* and *Tympanotonos labyrinthus* Formation”, implying therefore that the Eocene–Oligocene boundary lies somewhere within the Lower and Upper Patis Formations.

A preliminary faunal list of the mammals was published by Triat et al. (1971). All remains come from brown–black, clayish paleosol layers (indicated by a star on the Fig. 1c), located at the base of the “*Brotia laurae* and *Tympanotonos labyrinthus* Formation”. Other fossiliferous layers found in the quarry were very poor but apparently of an identical age because of the presence of *Theridomys aquatilis*. In addition to mammal remains, tortoise carapaces, crocodile teeth and squamate vertebrae and maxillary fragments were also found. Here, we present a review and a description of the mammalian remains found at the Mazan locality, and we compare this mammalian assemblage with other Early Oligocene localities in order to reconstruct the evolution of the European palaeobiogeography after the Eocene–Oligocene transition.

2 Materials and methods

2.1 Specimens and terminology

Due to intense quarry activities, the material is often damaged, especially the tiniest specimens are generally broken. All the described 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 98250 to FSL 98831.

The terminology used to describe molars follows Crochet (1980) for marsupials and insectivores, Daxner-Höck and Höck (2009) for Gliridae, Maridet and Ni (2013) for cricetids, Vianey-Liaud and Schmid (2009) for theridomorphs, Remy (2004) and Franzen (2007) for perissodactyls, and Bärmann and Rössner (2011) for artiodactyls.

A clear distinction between the first and second molars was not always possible; in the cases of theridomyids and glirids such teeth are not separated and identified as M1/2 and m1/2.

The measurements generally consist of the maximal length and width of teeth (except when otherwise indicated). As theridomorphs are only weakly hypsodont at the beginning of the Oligocene, we measured the maximal

length and width, as these are easier for comparisons. However, we also measured the length and width of the wear surface according to Vianey-Liaud (1972) for comparison with her data (these measurements are available on request to the authors). All the measurements are given in millimetres.

2.2 Biochronologic framework

The biochronologic framework is based on the European Land Mammal Ages (ELMA, Sen 1997) which is subdivided into a succession of European mammal reference levels for the Palaeogene (MP; Schmidt-Kittler et al. 1987), each of them being correlated with the Palaeogene geological time scale (Luterbacher et al. 2004; Vandenberghe et al. 2012). For the biogeographic analysis, Mazan is compared with 22 other Early Oligocene European localities (Table 1, Electronic Supplementary Material 1). Previous studies have quantified the mammalian faunal turnovers based on regional assemblages (Legendre and Hartenberger 1992; Legendre et al. 2006). Their results showed that, after the Eocene–Oligocene faunal change, the turnovers occurring between the biochronological units MP21 and MP22 were relatively low, but high again between MP22 and MP23. In order to reconstruct the European palaeobiogeography at the beginning of the Oligocene we made a compilation of localities assigned to MP21 and MP22 (between ca. 33.9 and 30.8 Ma, Vandenberghe et al. 2012). The age of each locality generally is according to the original assignation of the authors, except for the localities discussed below.

For Olalla 4A, Freudenthal (1996) initially suggested a MP22 age, due to the association of *Elfomys* (*Issiodoromys*) *medius* and *Sciurumys cayluxi* (these taxa appear in MP22 in the Quercy region). However, the locality also yielded *Blainvillimys langei* and *Pseudoltinomys gaillardi*, which are usually considered as typical of MP21. Consequently the correlation of this locality to MP22 seems questionable, and we thus adopt a more cautious opinion and rather propose an MP21–22 age. Interestingly, if the age of Olalla 4A is indeed older than initially proposed, this could partly explain the noticeable similarities with the mammalian assemblage of Mazan, and especially the occurrence in Mazan of a glirid very similar to *Glamys olallensis* (Freudenthal 1996) from Olalla 4A (see Sect. 3, below).

For the locality Paguera 1 from Majorca, Hugueneu and Adrover (1982) initially proposed a Late Oligocene age based on the glirids (Hugueneu 1997b). However, a revision of the cricetids and comparison to those of Olalla 4A (Freudenthal 1996), allows us to identify *Eucricetodon* cf. *atavoides*, and this rather indicates an Early Oligocene age (MP22–23).

Because they are geographically far from the other European localities, Kocayarma and Kavakdere from Turkey (Ünay-Bayraktar 1989) present noticeable differences in their faunal composition. These differences make their age estimation difficult with regard to the European biochronological framework (see Table 1 in Electronic Supplementary Material 1). Although their age remain imprecise, several taxa in common with other European localities included in the analysis indicate to some extent an actual faunal similarity and justify a posteriori to join them into a same biogeographic study.

2.3 Palaeobiogeographic dataset and analysis

A palaeobiogeographic dataset has been composed based on the compilation of 23 Early Oligocene mammalian faunas, including the assemblage of Mazan (Table 1, Electronic Supplementary Material 1). All regional lists have been brought together in order to construct a presence/absence matrix. Thereby, the taxonomy was standardized following the most recent taxonomic revisions, the species belonging to a same phyletic lineage have been grouped as a single taxon, and all undetermined taxa at species level have been excluded from the matrix. The carnivores, primates, and chiropters are only known from less than half of the localities, and therefore could have produced an artificial endemic signal for these localities. Consequently, they have been excluded from the analysis in order to avoid any bias among the localities. The raw faunal lists and the palaeobiogeographic matrix are available online (Electronic Supplementary Material 2).

The palaeobiogeographic analysis is based on the coefficient of taxonomic similarity of Raup and Crick (1979). This similarity coefficient (S) is a probabilistic index corresponding to a confidence level associated with a unilateral randomization test (see Maridet et al. 2007 for a detailed explanation and a probabilistic formulation of this index). As a result, the index between each pair of compared localities also provides a test of significance. A very high Raup and Crick index value ($S > 0.95$) indicates a significant similarity between the taxonomic assemblages of two localities (they non-randomly share too many taxa in common). In contrast, a very low Raup and Crick index value ($S < 0.05$) shows a significant difference in the assemblage of two localities (they non-randomly share too few taxa in common). For each pair of localities, the associated null distribution of the number of shared species was estimated by generating successive random re-samplings from the common pool of species without taking into account the observed probabilities of species occurrence (Harper 1981).

In order to provide a graphic representation of the palaeobiogeographic affinities between all localities considered in

the analysis, and taking into account only significant values, we transformed the Raup and Crick index values matrix into a significant/non-significant value matrix (by coding: significant similarity = 1; significant dissimilarity = -1; insignificant = 0). We then clustered the localities using the neighbour-joining method based on the significant/insignificant values matrix. The palaeobiogeographic analysis and the clustering have been done using the software PAST (Hammer et al. 2001).

3 Systematic palaeontology

Class Mammalia Linnaeus, 1758
 Order Notometatheria Kirsch, Lapointe, and Springer, 1997
 Family Herpetheriidae Trouessart, 1879

Peratherium elegans (Aymard, 1846) (Fig. 2a)

Referred specimens and measurements. Left M3, FSL 98812 (2.13×3.00 mm; Fig. 2a); left indet. m, FSL 98813 (2.46×1.65 mm).

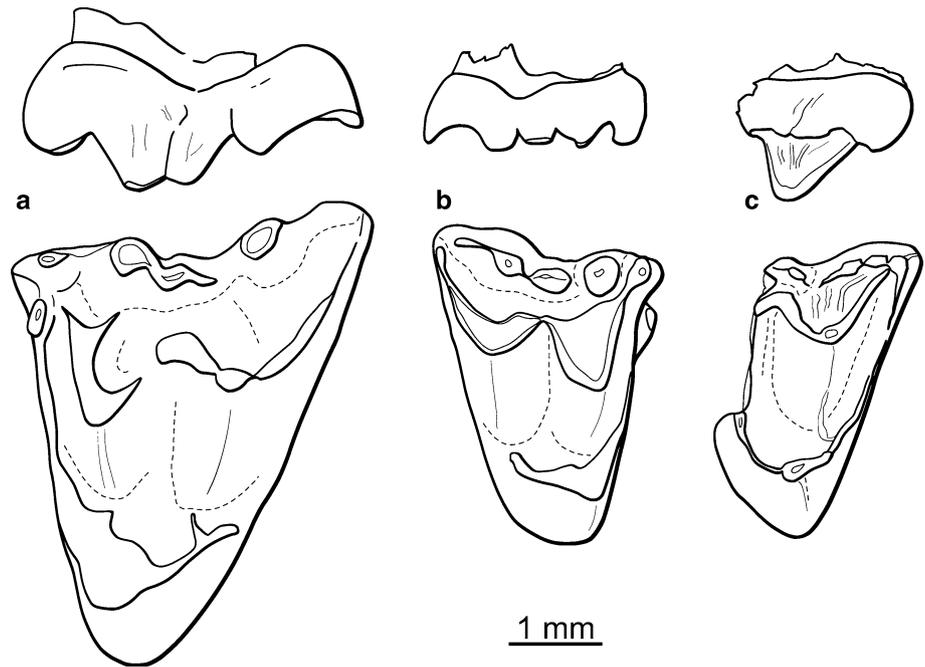
Remarks. The species *Peratherium elegans* is part of a lineage including the Late Eocene *P. cuvieri*, the Early Oligocene *P. elegans* and the Late Oligocene *P. antiquum* (Crochet, 1979). The Mazan specimens, the size of which corresponds to *P. elegans*, show some characteristics of the lineage: a large sized M3 shows a dominant cusp B joined by a crest with cusp C (a characteristic which is also seen in the type locality of Ronzon, Ladevèze et al. 2012); the junction of the cusps B and C on the upper molars differentiates *P. elegans* from the older *P. cuvieri*. Some damaged lower molars show a long posterior cingulid joining the top of the hypoconulid. *P. elegans* is a common species in post-Grande-Coupeure levels: Ronzon, Hamstead, Aubrelong, Ravet, but not at Hoogbutsel (Crochet 1979, 1980; Hooker 2010; Smith 2003).

Amphiperatherium minutum (Aymard, 1846) (Fig. 2b)

Referred specimens and measurements. Right M3, FSL 98814 (1.33×2.00 mm; Fig. 2b); left D4, FSL 98815 (1.30×0.93 mm); left M1, FSL 98816 (1.60×1.68 mm); right M1, FSL 98817 (1.53×1.70 mm); right M2, FSL 98818 (1.63×1.78 mm); left M4, FSL 98819 (0.80×1.56). Left indet. lower molar, FSL 98820 (1.47×1.02 mm); left indet. lower molar, FSL 98821 (1.63×1.00 mm).

Remarks. The smaller-sized teeth correspond with the dimensions of *A. minutum*. Characteristic features of this species are, on the upper molars: isolated cusp B, cusps C and D joined by a crest, paracingulum often only developed on the buccal part. On the lower molars: generally

Fig. 2 **a** *Peratherium elegans*.
Left M3, FSL 98812.
b *Amphiperatherium minutum*.
Right M3, FSL 98814.
c Herpetotheriidae indet. Right
damaged M3, FSL 98822. Each
molar is illustrated in labial
view (*top*) and occlusal view
(*bottom*)



short postero-cingulids disappearing at the base of hypoconulid and m4 with reduced but normal talonid with the hypoconulid joining the hypoconid. This species is frequent in post-Grande-Coupure (MP21) localities: Ronzon, Hoogbutsel, Upper Hamstead, Aubrelong, Ravet (Crochet 1979, 1980; Hooker 2010; Smith 2003) and can be found until the early Late Oligocene (MP25) in localities such as Belgarri or Le Garouillas (Crochet 1995).

Herpetotheriidae indet. (Fig. 2c)

Referred specimen and measurement. Right damaged M3?, FSL 98822 ($>1.87 \times 1.90$ mm).

Description. The tooth lacks the metacone, has a size similar to *A. minutum* but differs from the M3 of this species in having a wide and continuous paracingulum ending labially in a cusp and continuing on labial side with indistinct cusps till cusp C; the centrocrista, strongly dilambodont and joins the base of cusp C; this pattern reminds of the holotype of *P. matronense* Crochet, 1979 from Condé-en-Brie, but it could possibly also represent a variant of *A. minutum*.

Order Erinaceomorpha Gregory, 1910
Family Erinaceidae Fischer de Waldheim, 1817

Tetracus nanus Aymard, 1850

Referred specimens and measurements. Anterior part of left m2, FSL 98825 (L \times TrW: 1.30 \times 1.55 mm); right damaged p4, FSL 98826 ($>1.38 \times 1.40$ mm); left damaged biradiculate p1, FSL 98827 (1.17 \times 0.62 mm).

Remarks. The morphology and size of these fragmentary teeth, directly compared with the casts of *Tetracus nanus* from the Early Oligocene of Quercy, correspond well to *T. nanus* first described at Ronzon (Crochet 1995), particularly in having a slender p4 without basal labial cingulum but with a faint metaconid (Crochet 1995).

Order Soricomorpha Gregory, 1910
Family Nyctitheriidae Simpson, 1928

Nyctitheriidae indet.

1971 – cf. *Saturninia gracilis* Stehlin & Schaub Triat et al., p.241

Referred specimens. All upper and lower teeth fragments are so damaged that they cannot be measured, and they have been grouped under two inventory numbers: upper teeth fragments = FSL 98828; lower teeth fragments = FSL 98829.

Remarks. Some heavily damaged molars with acute cusps and fragmentary denticulate lower incisors indicate the presence of this family but cannot be determined more precisely due to their incompleteness.

Order Chiroptera Blumenbach, 1979
Superfamily Vespertilionoidea Gray, 1821

Vespertilionoidea indet.

Referred specimen and measurement. Right m1/2 talonid, FSL 98830 (TaL = 0.75 mm; TaW = 1.01 mm)

Description. This fragmentary small tooth displays a clearly myotodont morphology with posteristid joining

directly hypoconid and entoconid, and a well marked and independent entoconulid, large labial and posterior cingula but no lingual cingulum.

Remarks. The above described features make it possible to attribute this tooth to Vespertilionoidea. It cannot be attributed to *Quinetia misonnei* (Quinet, 1965) from Hoogbutsel, which is a clearly nyctalodont form, but could possibly be related with *Myotis/Leuconoe salodorensis* Revilliod, 1922 from Oensingen, Switzerland (MP 26), which is approximately of the same size.

Order Rodentia Bowdich, 1821

Family Sciuridae Gray, 1821

Palaeosciurus goti Vianey-Liaud, 1974 (Fig. 3)

1971 – Sciuridé ou Paramyidé indet. Triat et al., p.241

Referred specimen and measurement. Left M3, FSL 98831 (1.70 × 1.75 mm)

Remarks. The tooth is a little smaller than the M3 from the type locality Mas-de-Got (MP 22; 1.85 × 1.88 mm). Its shape, only a little stretched labially, corresponds well to that of the type species; the long anteroloph, protruding more lingually than the elongate protocone, the protoloph with several constrictions, and the absence of metaloph are also in agreement with *P. goti*. As the central basin does not show any granulations, it is certainly different from the teeth of the flying squirrels described by Heissig (1979), even if the M3 of these forms are unknown.

Family Theridomyidae Alston, 1886

Subfamily Issidoromyinae Tullberg, 1899

Pseudoltinomys gaillardii (Stehlin, 1951) (Fig. 4a-j)

Referred specimens. 51 isolated teeth, FSL 98250 to 98300: 2 P4; 3 D4; 13 M1/2; 8 M3; 5 p4; 1 d4; 11 m1/2; 8 m3.

Measurements. See Table 2 in Electronic Supplementary Material 3.

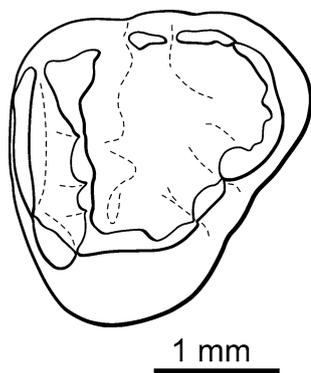


Fig. 3 *Palaeosciurus goti*. Left M3 in occlusal view, FSL 98831

Remarks. The dimensions of these teeth correspond well to those of *P. gaillardii* from Ronzon, Aubrelong 1 and Ravet. They also partly overlap the dimensions of the smallest specimens of *P. major* Vianey-Liaud, 1976, and the dimensions of the largest specimens of *Issidoromys medius* (Vianey-Liaud, 1976) of La Plante 2 (MP 22; Vianey-Liaud, 1974, 1976). As indicated by Hartenberger (1973) the size is also very similar to that of *P. cuvieri* from the Late Eocene but the hypsodonty is larger (H/L index of the lower molars reaches 0.93 at Ronzon, 0.95 at Mazan vs. 0.75 at Montmartre and other Late Eocene localities); moreover some morphological differences are noted: in *P. gaillardii*: lower molar mesolophid is long and generally reaches the lingual border and in the upper molars longitudinal crest is interrupted between sinus and synclinal II; in *P. cuvieri* the mesolophid is shorter and the longitudinal crest of the upper molars is complete. A large D4 displays an ornamented pattern with accessory longitudinal crests between the major anticlines, which is not seen in the other very simple teeth; the metaloph is interrupted before the hypocone and connected to the mesoloph and posteroloph by two short longitudinal crests; oblique crests also exists between the short mesoloph and the mesostyle.

Subfamily Theridomyinae Alston, 1876

Theridomys aquatilis Aymard, 1849 in Gervais (Fig. 5a-l)

1971 – *Isoptychus aquatilis* Triat et al., p.240

1972 – *Theridomys (T.) aquatilis* Vianey-Liaud, p.312, Fig. 6

Referred specimens. 46 isolated teeth, FSL 98301 to 98347: 6 D4; 7 M1/2; 9 M3; 4 p4; 6 d4; 13 m1/2; 1 m3.

Measurements. See Table 3 in Electronic Supplementary Material 3.

Remarks. Because of their morphology (particularly the absence of synclinal I in the lower molars), their size, and low hypsodonty (H max. for m1/2 = 1.86 vs. 1.82 at Ronzon), these teeth correspond well to the species from Ronzon already described by Vianey-Liaud (1972), who also illustrated two lower molars from the Lyon collections of Mazan. We emphasize that the material from Mazan is different from *T. margaritae* Vianey-Liaud (1989) from Hoogbutsel and La Plante 2, the teeth from Hoogbutsel being more hypsodont (H max. for m1/2 = 2.07 despite, in average, a little smaller length). No D4 has ever been recovered from Ronzon so its morphology is unknown. In Mazan, if on one hand the very elongate d4 is easy to recognize, the D4 of *T. aquatilis* is on another hand difficult to distinguish from those of *Blainvillimys langei*. Either, none are preserved, or they are only a little larger than those of *B. langei*. Five large D4s with an undulated labial rim, a relatively long longitudinal crest, and a more or less reduced postero-labial part are tentatively ascribed

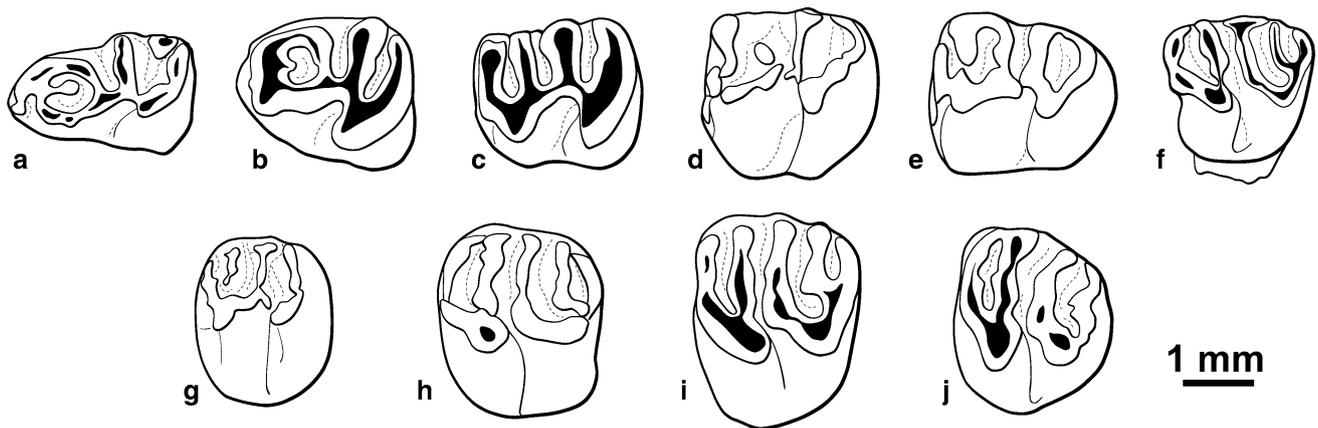


Fig. 4 *Pseudoltinomys gaillardii* (a–j). **a** Left d4, FSL 98250. **b** Left p4, FSL 98251. **c** Left m1, FSL 98252. **d** Left m2, FSL 98253. **e** Left m3, FSL 98254. **f** Left D4, FSL 98255. **g** Right P4, FSL 98256. **h** Left

M1, FSL 98257. **i** Left M2, FSL 98258. **j** Left M3, FSL 98259. All teeth are illustrated in occlusal view

to *T. aquatilis*. We have to notice that *T. aquatilis* seems to be a rare taxon, which, in France, is recognized with certainty only at Ronzon and Mazan (perhaps also at Ste Marthe in Dordogne), but never in the very nearby Quercy localities despite their abundant theridomorph faunas.

Blainvillimys langei Vianey-Liaud, 1972 (Fig. 5m–y)

1971 – *Theridomys* aff. *varians* Triat et al., p.240

1972 – *Theridomys* (*B.*) *langei* Vianey-Liaud, p.332, fig. 19 c–e

Referred specimens. 227 isolated teeth, FSL 98350 to 98578: 11 P4; 20 D4; 63 M1/2; 27 M3; 10 p4; 6 d4; 66 m1/2; 24 m3.

Measurements. See Table 4 in Electronic Supplementary Material 3.

Remarks. Vianey-Liaud (1972) already assigned two teeth of the Mazan collection to this species. The present measurements of the referred specimens correspond well to the dimensions of *B. langei* from Aubrelong 1 (MP 21; Vianey-Liaud, 1972). The maximal height measured on the Mazan m1/2 is 2.12 mm (vs. 2.26 in Aubrelong) and for the M1/2, 2.51 instead of 2.50. The morphological variations observed on the Aubrelong specimens also exist in all the teeth from Mazan: in the m1/2, the protoconid-metaconid crest can be rectilinear (23/66) or displays a more or less marked antero-lingual undulation (28/66); the metaconid rarely shows a tendency to form a synclinid I (5/66); this tendency seems to be a little more frequent in the m3 and even in one lower m3 this minute synclinid is closed. On the m1/2, the lingual opening of the third synclinid forms a relatively large angle (see Vianey-Liaud and Schmid 2009, fig. 3A). On the D4, the morphology is similar at Mazan and Aubrelong and the labial rim of the tooth is rectilinear. On the P4, the syncline IV is absent (6/11) or poorly developed. The morphology of the three molars is similar to that of Aubrelong 1.

Family Cricetidae Fischer von Waldheim, 1817

Genus *Eucricetodon* Thaler, 1966

Eucricetodon sp.1 (Fig. 6a–d)

1988 – *Eucricetodon* sp.1 Freudenthal, p.206, fig. 1. 13–14

Referred specimens and measurements. Right M2, FSL 98579 (1.17 × 1.13 mm, Fig. 6a); left m1, FSL 98580 (1.44 × 0.98 mm, Fig. 6b); right m1, FSL 98581 (1.38 × 0.87 mm, Fig. 6c); right m1, FSL 98582 (1.44 × 0.90 mm, Fig. 6d).

Description. Small cricetid with slender crests and a relatively rounded shape of the M2 and m1. The M2 is strongly worn; the paracone is connected to the anterior part of the protocone; the mesoloph is short and somehow connected to the metalophule; a crest joins the metacone to the posteroloph. In the m1, the ectolophid is longitudinal or oblique, and it is connected directly to the protoconid and is not located in the middle of the tooth but rather labially. In two of the three m1s (Fig. 6b, d) the anteroconid and the anterolophid are limited to a spear at the anterior tip of the tooth and the anterolophids are either barely developed or totally absent, whereas in the third m1 (Fig. 6c) the anterolophid is developed but small and surrounded by two thin anterolophids. The mesolophids are short or absent, and none of the three m1s possesses an ectomesolophid or a protoconid hind arm. In two m1s (Fig. 6b, d) the posterolophid starts very labially.

Remarks. In the present paper we do not consider the genus *Atavocricetodon* Freudenthal, 1996 to be valid (see Maridet et al. 2009 for details), and so ascribing our specimens to the genus *Atavocricetodon* has not been considered.

The specimens from Mazan display noticeable similarities with *Eucricetodon* sp.1 from Hoogbutsel (Freudenthal

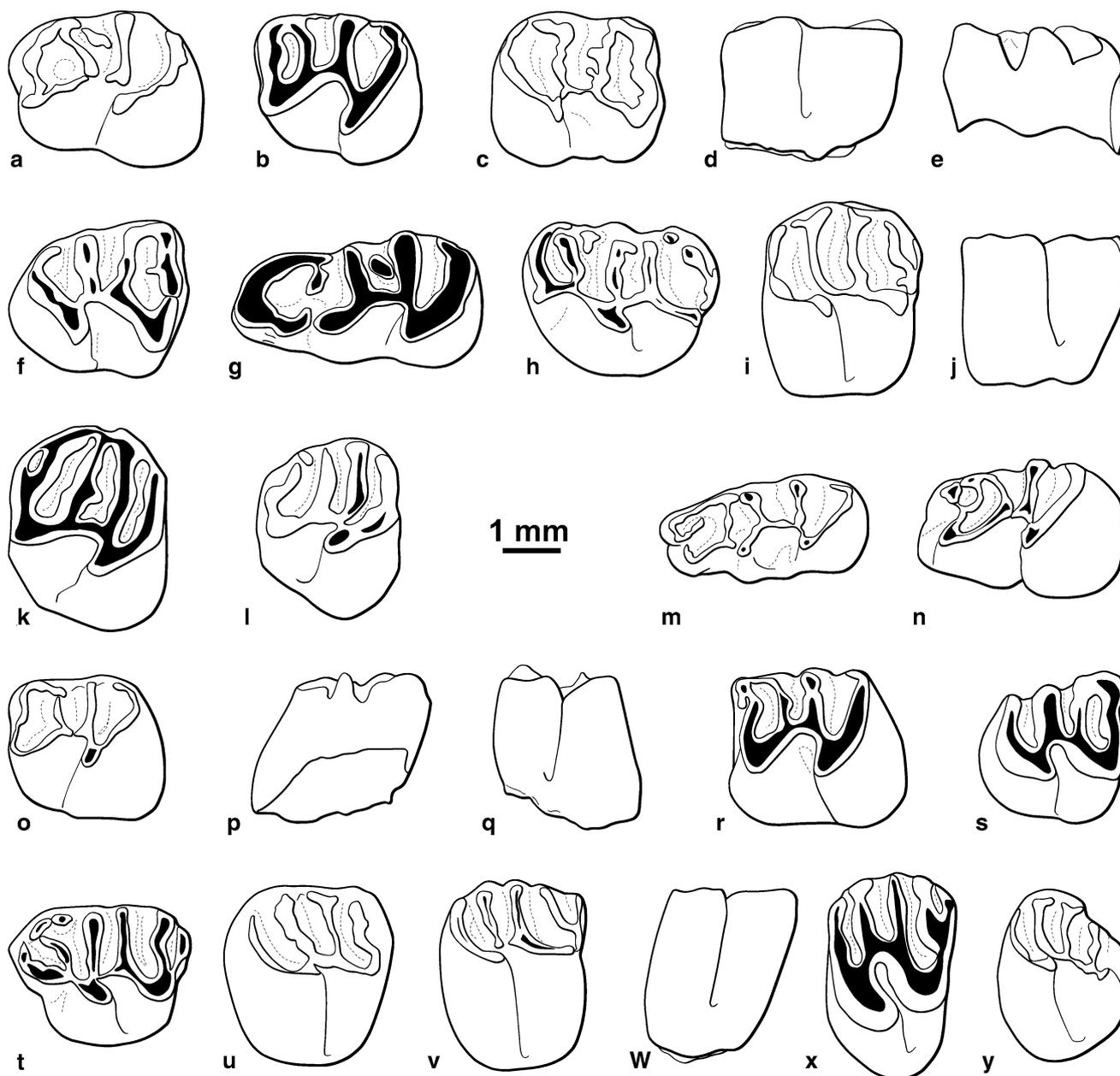


Fig. 5 *Theridomys aquatilis* (a–l). a Left p4, FSL 98301. b Left m1, FSL 98302. c Right m2, FSL 98303. d Right m2, FSL 98303 (labial view). e Right m2, FSL 98303 (lingual view). f Right m3, FSL 98304. g Left d4, FSL 98305. h Left D4, FSL 98306. i Left M1, FSL 98307. j Left M1, FSL 98307 (lingual view). k Right M2, FSL 98308. l Right M3 FSL 98309. *Blainvillimys langei* (m–y). m Left d4, FSL 98350.

n Left p4, FSL 98351. o Left m1, FSL 98352. p Left m1, FSL 98352 (lingual view). q Left m1, FSL 98352 (labial view). r Left m2, FSL 98353. s Right m3, FSL 98354. t Left D4, FSL 98355. u Left P4, FSL 98356. v Left M1, FSL 98357. w Left M1, FSL 98357 (lingual view). x Left M2, FSL 98358. y Left M3, FSL 98359. The teeth are illustrated in occlusal view unless otherwise indicated

1988): slender crests, mesoloph(id)s short or absent, posterolophid starting labially on the m1, anteroconid and the anterolophid limited to a spear at the anterior tip of the tooth. Based on these features, it seems likely that the small populations from Hoogbutsel and Mazan belong to a same lineage (Fig. 7 in Electronic Supplementary Material 4). The size of *E. sp.1* from both localities enters within the lower size range of *Eucricetodon nanoides* Freudenthal,

1996 (Fig. 8 in Electronic Supplementary Material 4), but the morphology allows a clear distinction between the two species. *Eucricetodon minusculus* Freudenthal, 1996 is noticeably smaller than *E. sp.1*, but has some morphological similarities such as the weakly-developed anteroconid and the short mesoloph(id)s. It is, however, not possible to unambiguously state whether *E. sp.1* and *E. minusculus* belong to a same lineage or not. Consequently, we use an

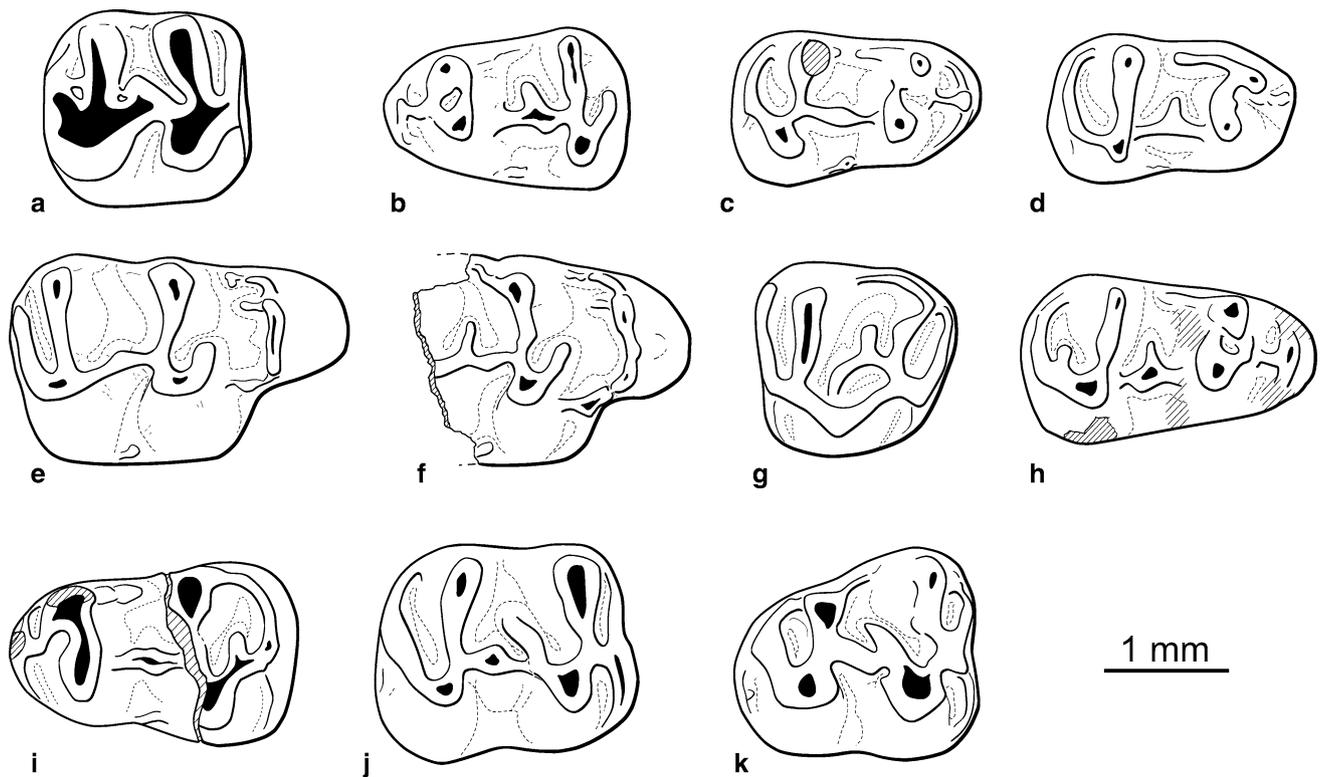


Fig. 6 *Eucricetodon* sp.1 (a–d). a Right M2, FSL 98579. b Left m1, FSL 98580. c Right m1, FSL 98581. d Right m1, FSL 98582. *Eucricetodon* sp.2 (e–k). e Right M1, FSL 98583. f Right M1, FSL

98584. g Left M3, FSL 98585. h Right m1, FSL 98586. i Left m1, FSL 98587. j Right m2, FSL 98588. k Right m3, FSL 98589. All teeth are illustrated in occlusal view

open nomenclature for the specimens from Mazan and Hoogbutsel.

Eucricetodon sp.2 (Fig. 6e–k)

1988 – *Eucricetodon* sp.2 Freudenthal, p.206, fig. 1. 15

Referred specimens and measurements. Right M1, FSL 98583 (1.96 × 1.22 mm, Fig. 6e); fragm. right M1, FSL 98584 (not measurable, Fig. 6f); left M3, FSL 98585 (1.21 × 1.18 mm, Fig. 6g); right m1, FSL 98586 (1.71 × 1.10 mm, Fig. 6h); left m1, FSL 98587 (1.70 × 1.07 mm, Fig. 6i); right m2, FSL 98588 (1.54 × 1.28 mm, Fig. 6j); right m3, FSL 98589 (1.43 × 1.24 mm, Fig. 6k).

Description. Medium-sized cricetid with elongated first molars compared to the two other cricetids of Mazan. M1 is characterized by a large and narrow anterior lobe whereas the anterocone itself is rather elongated following a lingual-labial axis; the protostyle is connected to the anterocone by a thick anteroloph; the mesocone is either weak or absent; the protocone spur is short and ends freely in the anterosinus; a small spur start posteriorly to the anterocone but never reaches the protocone spur so the anterolophule is not complete; the mesoloph is either short or absent. M3 is elongated and possesses well-developed hypocone and metacone; the axioloph joins the metaloph to

the protocone and bears a short mesoloph. The m1 displays an elongated shape; the anteroconid is well-developed but the surrounding anterolophids are short, leaving the anterosinusid and protosinusid open; both teeth possess a short mesolophid, a short hypoconid hind arm and a large mesoconid; in one m1 the metaconid spur joins directly the anteroconid whereas the anterolophulid is absent (Fig. 6i); in the other m1 (Fig. 6h) the protoconid and the metaconid are connected anteriorly and the anterolophulid joins the metalophid to the anteroconid. The m2 and the m3 lack the mesolophids and hypoconid hind arms; the protoconid hind arms are long but end freely in the mesosinusid; the mesoconid is well developed for the m2 only.

Remarks. In Hoogbutsel, Freudenthal (1996) identified one M1 as *E. sp.2*, which is larger than *Eucricetodon atavus*. This tooth is characterized by a large and narrow anterior lobe (whereas the anterocone itself is small), a short mesoloph, lack of the mesocone, and a small spur starting posteriorly to the anterocone but not joining the protocone spur. These features are the same in *E. sp.2* from Mazan and the size is similar, suggesting that both populations likely belong to the same lineage. Likewise, the M1s of *Eucricetodon atavoides* Freudenthal, 1996 and *Eucricetodon hugueneyae* Freudenthal, 1996 display a large and wide anterior lobe, but the

anterocone seems more developed and the mesoloph longer. Interestingly, the m1s of *E. atavoides* and *E. hugueneyae* display an elongated shape, which also reminds the shape of the m1s of *E. sp.2* from Mazan. However, *E. sp.2* differs from these two species in having: in the m1 a short protoconid hind arm merging with the metaconid and an oblique hypolophid; in the M1 shorter protocone spurs; in all molars shorter mesoloph(id)s; in missing the lined surface of the enamel (see Freudenthal 1996, pl. 1-2). Furthermore *E. sp.2* differs specifically from *E. atavoides* in missing the thick cingulum that joins the anteroloph(id)s, labially on lower molars and lingually on upper molars.

These differences indicate that *E. sp.2* could constitute an independent lineage, even though they could also be the result of a morphological evolution within a single lineage considering the age difference of the two localities. However, until now the material is insufficient to state whether *E. sp.2* could belong to one of these lineages or not.

Eucricetodon atavus (Misonne, 1957) (Fig. 7a–u)

1971 – *Eucricetodon* cf. *atavus* Triat et al., p.240

Referred specimens. The material is composed of 80 isolated molars, FSL 98590 to 98669: 5 right M1 (including 1 broken); 10 left M1 (5 broken); 9 right M2 (2 broken); 5 left M2 (1 broken); 3 right M3; 3 left M3; 4 right m1 (1 broken); 9 left m1 (3 broken); 13 right m2 (3 broken); 3 left m2; 8 right m3 (4 broken); 8 left m3 (5 broken).

Measurements. See Table 5 in Electronic Supplementary Material 3 and Figure 8 in Electronic Supplementary Material 4.

Description. Small to medium-sized cricetid with relatively more massive cusp(id)s comparatively to the other cricetids of Mazan. In upper molars the mesoloph varies from absent to average, and it never reaches the labial border. In the M1 the anterior lobe is wide whereas the anterocone is relatively narrow; the lingual anteroloph is usually better developed than the labial one and bears occasionally a protostyle at its extremity (e.g., Fig. 7c); none of the M1s have complete anterolophule, as the protocone spur ends in most specimens freely in the anterosinus (connected to the paracone in one case, Fig. 7b); some M1s possess a spur starting posteriorly from the anterocone, also ending freely in the anterosinus (Fig. 7c–d). The M2 always has long anterolophs, the lingual one being usually shorter than the labial one. In the M3, the axioph and the metaloph can be complete or incomplete; the metacone is weakly developed.

The shape of the m1 is characterized by a posterior part noticeably wider than the anterior part; the anteroconid is small but always well developed; the protoconid hind arm is short, either free or connected to the metaconid; the mesolophid, ectomesolophid and hypoconid hind arm all vary

from absent to moderately developed; the anterolophulid and the metaconid spur are usually well-developed but can be incomplete; one tooth possesses a small additional spur starting labially from the anterolophulid (Fig. 7n). Like in the m1, the m2 displays a noticeable variability of the mesolophid, ectomesolophid and hypoconid hind arm; the protoconid hind arm is longer comparatively to the m1, it ends usually freely in the mesosinus but can also connect to the metaconid; in two teeth the mesolophid and protoconid hind arm are connected to each other by an additional crest (e.g., Fig. 7q). The protoconid hind arm in the m3 is larger than is the m2, from moderate to long; the entoconid is well developed in most specimens.

Remarks. The morphology of these specimens fits the description of the type population from Hoogbutsel (Misonne 1957) and enters in the morphological variability described by Freudenthal (1988, 1996). Freudenthal (1996) created a species *E. atavoides* because of “the resemblance with *A. atavus*” (Freudenthal 1996, p.4), thus implying a strong affinity between the two species, for instance stronger than with *E. nanoides*. However, based on our observations, *E. atavus* and *E. nanoides* share several interesting features such as the generally wide shape of the anterior lobe in the M1; the posterior part noticeably wider than the anterior part, and the well-developed anteroconid in the m1; and the often short or absent hypoconid branch in the m1; *E. nanoides* is, however, partly smaller. In contrast, the larger *E. atavoides* has the M1 with an anterior lobe narrower and a more elongated shape (Fig. 7 in Electronic Supplementary Material 4); the m1 width also has an elongated outline but with a less marked difference between the anterior and posterior widths and with the hypoconid branch short or absent. Based on these observations, *E. atavus* could be closely related to *E. nanoides* (and possibly also *E. nanus* Peláez-Campomanes, 1995 if we hypothesize an *E. nanoides*-*E. nanus* lineage). Nevertheless, these similarities of *E. atavus* with *E. nanoides* do not exclude an affinity of *E. atavus* with *E. atavoides* too, as suggested by Freudenthal (1996). With regard to this question, the intermediate size of *E. atavus* compared to *E. nanoides* and *E. atavoides* (Fig. 7 in Electronic Supplementary Material 4) makes it a good candidate to be their common ancestor, although more material from other localities will be necessary to confirm this hypothesis.

Family Gliridae Thomas, 1897

Genus *Glamys* Vianey-Liaud, 1989

Glamys aff. *G. olallensis* Freudenthal, 1996 (Fig. 8a–i)

1971 – *Gliravus* taille *priscus* Triat et al., p.241

Referred specimens and measurements. Left DP4, FSL 98670 (0.66 × 0.78 mm); left DP4, FSL 98671 (0.69 × 0.79 mm);

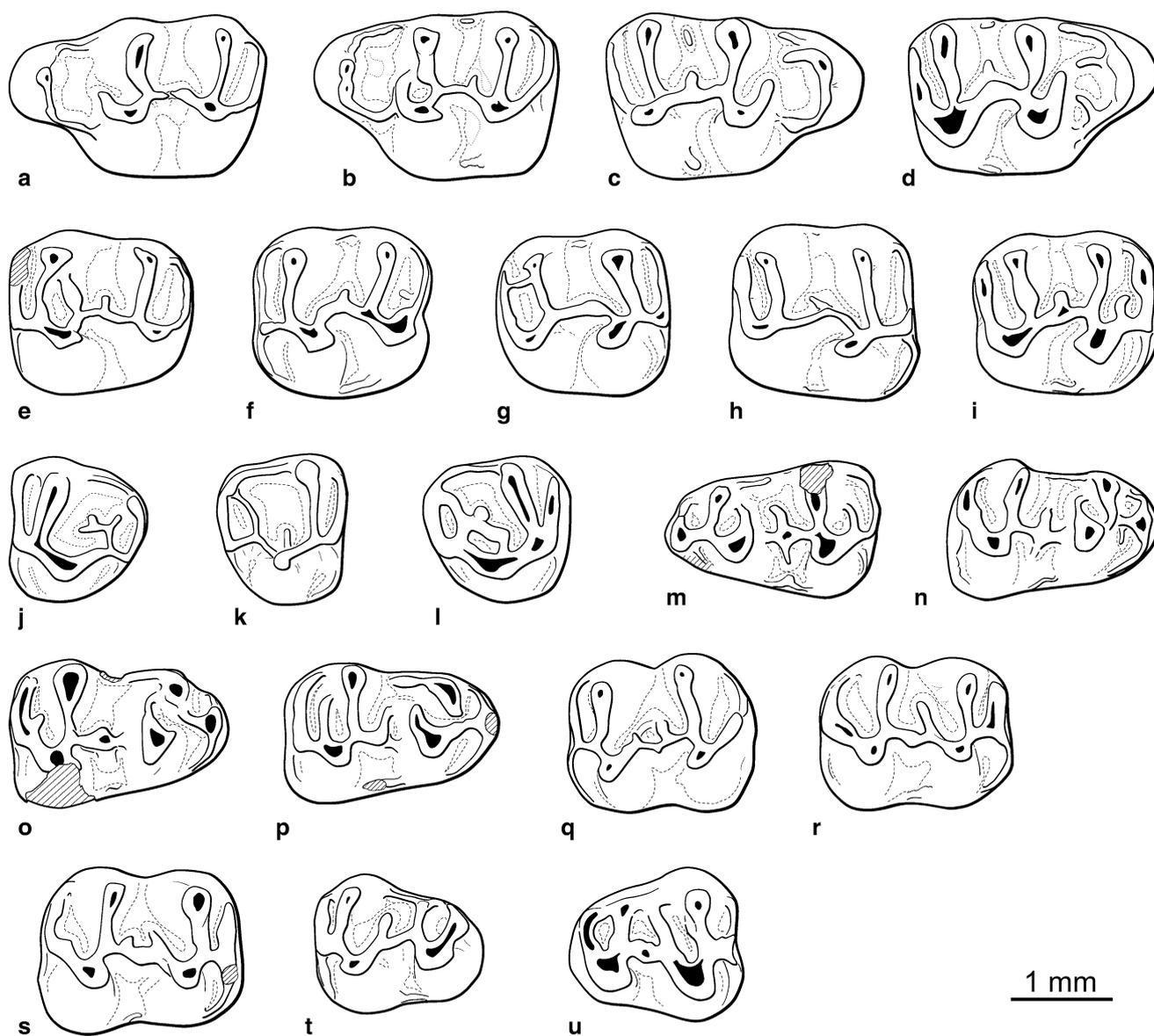


Fig. 7 *Eucricetodon atavus* (a–u). **a** Left M1, FSL 98595. **b** Left M1, FSL 98596. **c** Right M1, FSL 98590. **d** Right M1, FSL 98591. **e** Left M2 FSL 98614. **f** Left M2 FSL 98615. **g** Right M2 FSL 98605. **h** Right M2 FSL 98606. **i** Right M2 FSL 98607. **j** Left M3, FSL 98622. **k** Right M3, FSL 98619. **l** Right M3, FSL 98620. **m** Left m1,

FSL 98629. **n** Right m1, FSL 98625. **o** Right m1, FSL 98626. **p** Right m1, FSL 98627. **q** Left m2, FSL 98651. **r** Right m2, FSL 98638. **s** Right m2, FSL 98639. **t** Left m3, FSL 98662. **u** Right m3, FSL 98654. All teeth are illustrated in occlusal view

right P4, FSL 98672 (0.69 × 0.95 mm); right P4, FSL 98673 (0.72 × 0.92 mm); left P4, FSL 98674 (0.66 × 0.85 mm); right M1/2, FSL 98675 (0.77 × 0.94 mm); right M1/2, FSL 98676 (0.70 × 0.90 mm); right M1/2, FSL 98677 (0.75 × 0.90? mm); left M3, FSL 98678 (0.69 × 0.86 mm); left dp4, FSL 98679 (0.72 × 0.69 mm); left p4, FSL 98680 (0.78 × 0.72 mm); right m1/2, FSL 98681 (0.79 × 0.84 mm); right m1/2, FSL 98682 (0.82 × 0.85 mm); left m1/2, FSL 98683 (0.84 × 0.90 mm); right m3, FSL 98684 (0.85 × 0.85 mm); right m3, FSL 98685 (0.80 × 0.78 mm); right m3, FSL 98686 (0.77 × 0.75 mm); right m3, FSL 98687 (0.75 × 0.79 mm); left m3, FSL 98688 (0.82 × 0.83 mm)

Description. The M1/2 and P4 are characterized by a V-shaped trigone sometimes fused in endoloph; in P4 the anteroloph is well developed; the anterior centroloph is long (but disconnected from the paracone in the M1/2); the posterior centrolophs and extra ridges are always missing in the M1/2 and P4. Likewise, M3 has only one centroloph and a V-shaped endoloph. The lower molars are characterized by a somewhat rounded shape; in the m1/2 and the m3 the metalophid is in most specimens connected to the metaconid whereas the mesolophid shows much more variability, short and isolated in the middle of the tooth or longer and reaching the lingual border; when reaching the

lingual border, the mesolophid is connected to the endolophid in the m1/2 but connected to the entoconid in the m3; the endolophid is generally interrupted; extra ridges and centrolophids are always missing; the m1/2 and the m3 have two roots.

Remarks. Despite a similar length, these specimens differ from the genus *Moissenetia* Huguenev and Adrover, 1995 by a different shape of the m1/2 (much wider than long in *Moissenetia*) and generally in missing the mesolophid merging with the entoconid in the m1/2. However, the presence of a mesolophid directed towards the entoconid in the m3 suggests that the above-described specimens could be somehow related to *Moissenetia*. With regard to the V-shaped endoloph, the total absence of posterior centroloph and the well-developed anteroloph in P4, *Glamys olallensis* Freudenthal, 1996 is the species sharing the most common features with our specimens. Although the morphology of *Glamys priscus* (Stehlin and Schaub, 1951) is also generally similar, our specimens differ in being slightly smaller and with a generally more complex morphology (independent centrolophs, metalophids and mesolophids less frequently isolated and longer). The specimens from Mazan are consequently referable to *Glamys olallensis*, although differing from this species by missing the centrolophid, which can be interpreted as a primitive feature and suggests that the population of Mazan is likely an earlier stage of the lineage from Olalla 4A.

Genus *Butseloglis* Vianey-Liaud, 1993

Butseloglis micio (Misonne, 1957) (Fig. 8j–r)

Referred specimens. The material is composed of 52 isolated molars, FSL 98689 to 98740: 1 DP4; 4 P4; 11 M1/2 (2 partially broken); 7 M3; 1 dp4; 6 p4; 15 m1/2; 7 m3.

Measurements. Table 6 in Electronic Supplementary Material 3.

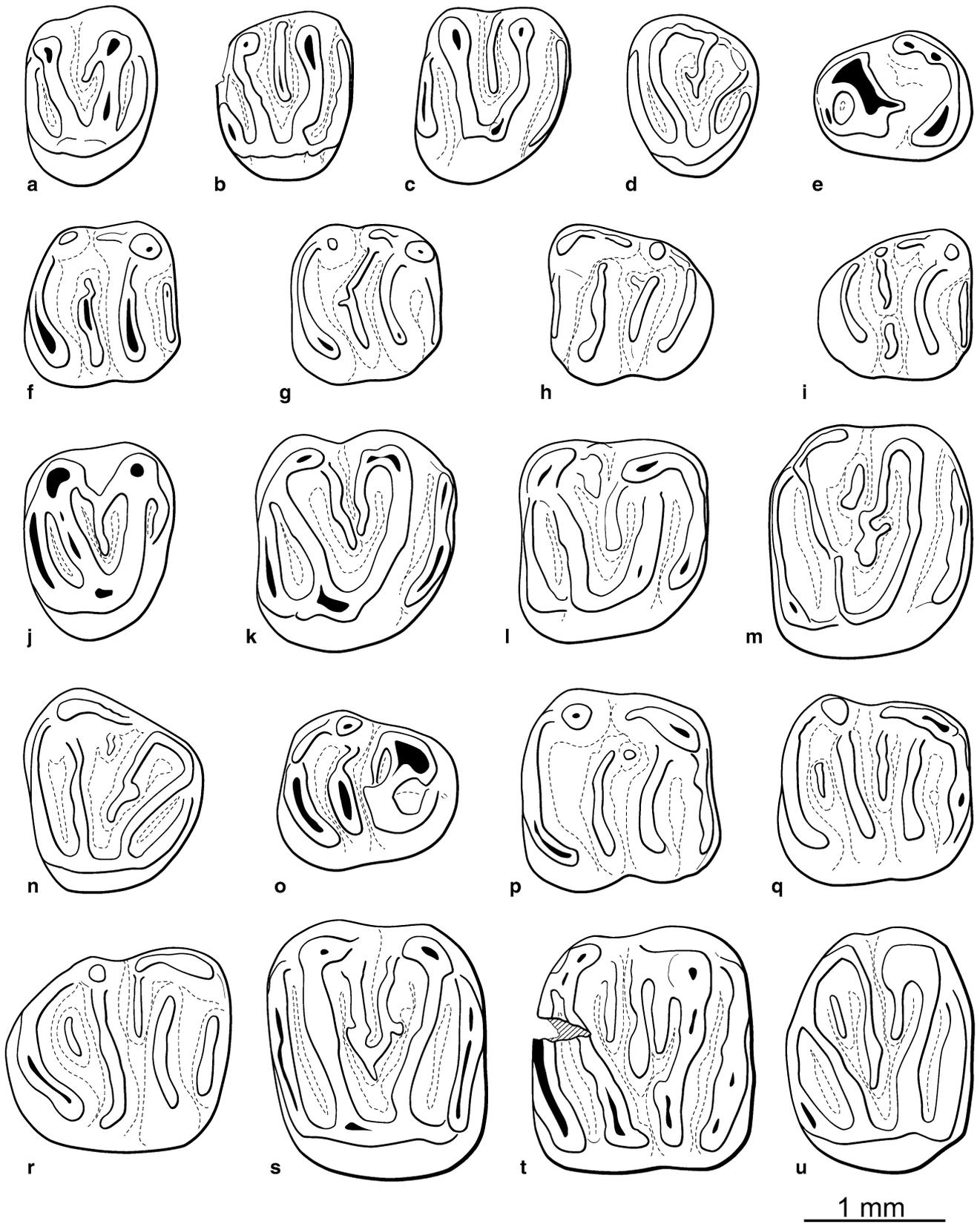
Description. The DP4 displays a sub-triangular shape with short anteroloph and posteroloph; the anterior centroloph is long whereas the posterior one is absent. The P4s always possess an anterior centroloph, whereas the posterior one can be absent; the anteroloph is thick but very short, connected labially to the paracone and lingually to the protoloph; the posterior sinus is also always closed; the P4s have two roots but the labial one is divided. In M1/2, the endoloph is V- or U-shaped; the posteroloph is always connected to the endoloph and the metacone so the posterior sinus is always closed whereas the anterior sinus is often open lingually (in one case also labially, Fig. 8m); both the anterior and posterior centrolophs are always present, the posterior one being sometimes disconnected from the metacone; the centrolophs often display complex undulations in the middle of the tooth and they often join

Fig. 8 *Glamys* aff. *G. olallensis* (a–i). **a** Right P4, FSL 98672. **b** Right M1/2, FSL 98676. **c** Right M1/2, FSL 98675. **d** Left M3, FSL 98678. **e** Left p4, FSL 98680. **f** Right m1/2, FSL 98682. **g** Right m1/2, FSL 98681. **h** Left m3, FSL 98688. **i** Right m3, FSL 98686. *Butseloglis micio* (j–r). **j** Right P4, FSL 98690. **k** Right M1/2, FSL 98694. **l** Right M1/2, FSL 98695. **m** Right M1/2, FSL 98696. **n** Left M3, FSL 98705. **o** Right p4, FSL 98713. **p** Right m1/2, FSL 98719. **q** Right m1/2, FSL 98720. **r** Right m3, FSL 98734. *Bransatoglis* cf. *B. planus* (s–u). **s** Left M1/2, FSL 98742. **t** Right M1/2, FSL 98741. **u** Right M3, FSL 98743. All teeth are illustrated in occlusal view

each other; three roots. In M3 the anterior and posterior sinuses are closed; the metaloph can be interrupted; both the anterior and posterior centrolophs are present, the posterior one being always much longer than the anterior one; the centrolophs are sometimes interrupted or can merge together, or with the metaloph, or with the posterior extra ridge leading to complex combination of morphologies in the middle of the tooth; three roots.

The dp4 displays a very simple morphology; the anterolophid, the endolophid and the posterolophid are connected forming a continuous crest around the tooth from the protoconid to the hypoconid; the lingual part shows almost no structure except for short mesolophid on the labial border. In p4 s the mesolophid is usually free, thicker labially than lingually, but merges with the entoconid in one tooth; the anterolophid is sometimes interrupted; the centrolophid is always present, starting lingually from the metaconid and merging sometimes with the metalophid; the metaconid and hypoconid are much larger than the other cuspids; p4s possess one root with two pulp cavities. The m1/2 usually has 3 roots, sometimes 2 roots with a division of the anterior one; the mesolophid is in most specimens free and oriented toward the metaconid (Fig. 8p), but in two cases connected to the entoconid (Fig. 8q); the centrolophid is present in about half of the teeth, and it is usually short and disconnected from the metaconid; the endolophid is almost always missing; the posterior extra ridge is present in less than half of the teeth and usually very short; the very weakly-developed anterior ridge is present in only one tooth. In m3, the metalophid is usually connected to the metaconid whereas the centrolophid is often free; the mesolophid is always connected to the entoconid; the posterior extra ridge is usually very short but frequent whereas the anterior one is rare; the endolophid is missing; m3 has two roots but the anterior one has two pulp cavities and can sometimes be divided.

Remarks. The general shape and size of our specimens fit well with *Butseloglis micio* from Hoogbutsel (Vianey-Liaud 2003) and Olalla 4A (formerly *Gliravus itardiensis* Vianey-Liaud, 1989 in Freudenthal 1996). Furthermore, the morphological variability described above enters within the variability described by Freudenthal (1996). However, it is noteworthy that the extra ridges (in upper and lower



molars) are rare and very weakly developed in Mazan by comparison to Itardies (Vianey-Liaud 1989), Olalla 4A and even Hoogbutsel (Misonne 1957), suggesting that the population from Mazan could constitute a very early stage within the *B. micio* lineage.

Genus *Bransatoglis* Hugueney, 1967

Bransatoglis cf. *B. planus* (Bahlo, 1975) (Fig. 8s–u)

Referred specimens and measurements. Right M1/2, FSL 98741 (1.15 × 1.26 mm); left M1/2, FSL 98742 (1.11 × 1.35 mm); right M3, FSL 98743 (0.96 × 1.28 mm); left m1/2, FSL 98744 (partly broken, 1.04? × 1.10? mm).

Description. The two M1/2s are characterized by a somewhat squared shape and a U-shaped endoloph; the anteroloph and posteroloph are merging with the paracone and the metacone respectively; in contrast they can be free or connected to the entoloph lingually; both the anterior and posterior centrolophs are long even joining each other in one tooth (Fig. 8s); the endoloph is interrupted in one M1/2 (Fig. 8t). The M3 is much wider than long, with two well-developed centrolophs (the posterior one being longer than the anterior one) and a short posterior extra ridge between the centroloph and the metaloph; the anteroloph and the posteroloph are connected to the trigone on both labial and lingual sides. The m1/2 is heavily damaged by shows a centrolophid merging with the metaconid and a well-developed extra ridge between the mesolophid and the posterolophid.

Remarks. Although the size is similar, these specimens differ from those of *B. micio* in having a more squared shape, a slightly lower crown, and well-developed extra ridges in both upper and lower molars. The shape and size of these specimens fits well with *Bransatoglis planus* (Bahlo, 1975) from Gröben 3 as described and illustrated by Uhlig (2001). However, in Gröben 3 the anteroloph and posteroloph are always connected to the endoloph forming a continuous wall on the lingual border of the upper molars, and the lower molars possess several extra ridges, which is not the case in our specimens. Considering the scarcity of this material, we tentatively ascribe these specimens to *Bransatoglis* cf. *B. planus*.

Order Perissodactyla Owen, 1848

Family Palaeotheriidae Bonaparte, 1850

Genus *Plagiolophus* Pomel, 1847

Plagiolophus sp. (Fig. 9a–c)

Referred specimens. Right D2/D3 labial wall, FSL 98745 (Fig. 9a); right upper incisor, FSL 98746 (Fig. 9b); left lower p2, FSL 98747 (Fig. 9c).

Description. The right D2 or D3 labial wall measures 15.4 mm in length and shows large columnar para- and

meso-styles, enlarging at their base and forming a basal ridge along the length of the tooth (Fig. 9a). Both the styles and the ridge are not as large as in *Palaeotherium*. The right upper incisor is typical, in size and morphology, for *Plagiolophus* such as observed on *Plagiolophus* material from Euzet-les-Bains (NMB, pers. obs., Fig. 9b). The left lower p2 has a length of 7.35 mm and a width of 4.3 mm. It has a prominent anteriorly-positioned protoconid, and a small paralophid and protolophid are also visible. An incipient ?metaconid seems to be attached to the posterolabial side of the protoconid. A strong cingulum runs all around the base of the tooth crown. The roots are broken, but the tooth clearly had two roots (Fig. 9c).

Remarks. An ascription to *Plagiolophus* sp. is quite tentative with regards to the few specimens found in Mazan. Nonetheless, based on the size and morphology, our specimens are closer to *Plagiolophus* than any other Early Oligocene genus of perissodactyls. For instance our specimens differ from *Palaeotherium* in being noticeably smaller. Joomun et al. (2010) indicate that *Plagiolophus minor* is the last survivor of the genus in the Oligocene but a specific attribution of the available material is not possible.

Order Cetartiodactyla Montgelard et al., 1997

Family Cainotheriidae Camp and Van der Hoof, 1940

Genus *Plesiomeryx* Gervais, 1873

Plesiomeryx cf. *cadurcensis* Gervais, 1873 (Fig. 9d–e)

1971 – ?*Paroxacron* Triat et al., p.241

Referred specimens and measurements. A complete left M2, FSL 98748 (3.39 × 4.5 mm, Fig. 9d); a partial right upper molar, FSL 98749 (Length = 3.56 mm, Fig. 9e).

Description. The M2 (FSL 98748) is rather subquadrate in shape and has crescent-shaped cusps (Fig. 9d). The protocone is not fully aligned with the metaconule and metacone, being slightly more anteriorly positioned than both others. A weak protostyle is present. A spur arises from a secondary cusp (lingual cone?) on the postprotocrista and runs anteriorly in the posterior fossa. The labial styles are well marked and constitute the typical cainotheriid labial wall morphology (on both FSL 98748 and 98749). The postparacrista joins the mesostyle. An anterior and a slight posterior cinguli are present. The other fragmentary upper molar is poorly preserved but shows a close morphology to the first one (Fig. 9e).

Remarks. The upper molars, especially the M2 with its subquadrate shape and crescent-shaped cusps is typical of cainotheriids (Hürzeler 1936), and more specifically of *Plesiomeryx* rather than *Paroxacron*, especially considering the mesostyle area, the mesostyle being less connected to the postparacrista in *Paroxacron* than in *Plesiomeryx*.

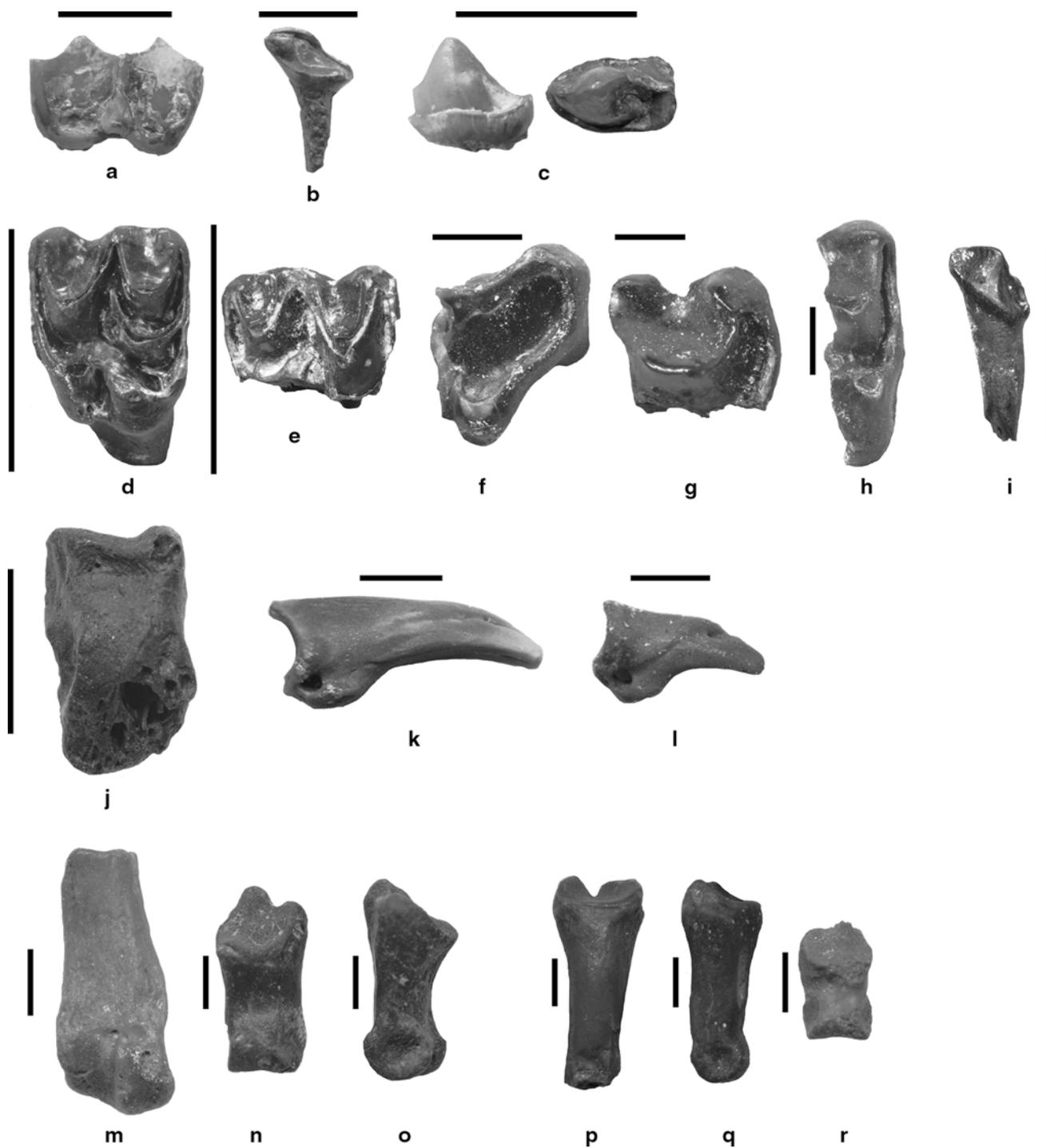


Fig. 9 *Plagiolophus* sp. (a–c). **a** Right D2/D3 labial wall, FSL 98745. **b** Right upper incisor, FSL 98746 (lingual view). **c** Left lower p2, FSL 98747 (left labial view; right occlusal view). *Plesiomeryx* cf. *cadurcensis* (d–e). **d**. Left M2, FSL 98748 (occlusal view). **e** Right upper molar, FSL 98749 (occlusal view). **f** *Plesiomeryx* sp., left partial P3, FSL 98751 (occlusal view). *Cainotheriidae* indet. (**g–r**). **g** Left upper molar, FSL 98753 (fragment, metacone and associated styles, occlusal view). **h** Right upper molar, FSL 98754 (fragment, occlusal view). **i** Right lower premolar, FSL 98758 (lingual view).

j Left partial astragalus, FSL 98811 (plantar view). **k, l** Distal third phalanges, FSL 98796 and 98797 (lateral views). **m** Partial metacarpal, FSL 98808 (plantar view). **n–o** Second phalanges of digits III/IV, FSL 98794 and 98795 (plantar and lateral views, respectively). **p–q** First phalanges of digits II/V, FSL 98767 and 98768 (ventral and lateral views, respectively). **r** Second phalanx of digit II/V, FSL 98791 (plantar view). *Scale bar* in a–c 10 mm; in d–e and i–j 5 mm; and in f–h and k–r 1 mm

Plesiomeryx has slightly more quadratic teeth than *Paroxacron* and is easy to separate from the latter because of a diastema separating the upper canine from the premolar row, a situation that does not occur on *Paroxacron* (Hürzeler 1936). Berger (1959) described a second species of *Plesiomeryx*, *P. hürzeleri*. His diagnosis of the species, especially his description of the upper molars, fits all the characters of the M2 described above and in general to that of *Plesiomeryx cadurcensis* such as exemplified by Blondel (2005). *Plesiomeryx cadurcensis* differs from *P. hürzeleri* by a smaller size (Berger 1959; Erfurt and Métais 2007) although specimens of the Quercy Phosphorites in the collection of the Natural History Museum of Basel reach the size range given by Berger (1959) for *P. hürzeleri* (pers. obs.). It should be noted that the very close morphology of both species calls for a revision of the old Quercy material for taxonomic certainty. The teeth described here fall within the size range and morphology of *P. cadurcensis* (see also Blondel, 2005), and thus we ascribe them to *P. cf. cadurcensis*. More material is needed for a definitive ascription to *P. cadurcensis*.

Plesiomeryx sp. (Fig. 9f)

Referred specimens. A partial left P2, FSL 98750; a partial left P3, FSL 98751 (Fig. 9f); a partial left P4, FSL 98752.

Description. The heavily-worn left P2 is merely a smaller version of the P3 described hereafter. A weak lingual cone, a very slight posterolabial cone and an incipient posterolabial stylid are visible. The left P3 is only partially preserved (posterior part) and heavily worn, the lingual cone is prominent and slightly posteriorly oriented. Incipient posterolabial cone and posterolabial style are present (Fig. 9f). The right P4 is also partial and worn, only the anterior part being preserved. A well-marked anterior cingulum is present. The lingual cone is visible and slightly posteriorly oriented, the well-marked anterolabial cone and anterolabial style are linked by the anterolabial crista.

Remarks. These partial premolars are typical of *Plesiomeryx* and look more advanced than those of *Paroxacron*, especially the P2 (more prominent lingual cone) and P3 (see also Erfurt and Métais 2007). They resemble teeth from the Quercy Phosphorites described by Blondel (2005) and ascribed to *P. cadurcensis*. Tentative measurements of widths made on these fragmentary P3 and P4 would agree with this specific attribution (P3: 2.7? mm; P4: 3.4? mm). However, because of their fragmentary nature, we prefer to ascribe them to *Plesiomeryx* sp.

Cainotheriidae indet. (Fig. 9g–r)

Referred specimens. Left upper molar, FSL 98753 (very fragmentary); right upper molar, FSL 98754 (fragment);

left upper molar, FSL 98755 (fragment); right lower third molar, FSL 98756 (fragment); right lower molar, FSL 98757 (fragment); 1 upper canine, FSL 98759 and 1 right lower first premolar, FSL 98758; 7 lower incisors, FSL 98760 to 98766; 19 phalanges I, digits II or V FSL 98767 to 98785 (fragments); 5 phalanges I, digits III or IV, FSL 98786 to 98790 (fragments); 3 phalanges II, digits II or V, FSL 98791 to 98793 (fragments); 2 phalanges II, digits III or IV, FSL 98794 and 98795 (fragments); 11 phalanges III, FSL 98796 to 98806; 1 proximal end of a right ulna, FSL 98807; 2 distal ends of a metacarpals, FSL 98808 and 98809; 1 navicular, FSL 98810; 1 left partial astragalus, FSL 98811.

Description of the teeth. Fig. 9g–i. The fragmentary left upper molar (FSL 98753, Fig. 9g) is composed of a metacone and its associated mesostyle and metastyle; this metacone is quite large and the styles are well marked. The fragment of right upper molar shows a paracone and its weakly developed parastyle linked to the protoconule. No anterior cingulid is visible (Fig. 9h). The fragment of left upper molar is represented by the labial side of a tooth with its cones and styles; it's heavily eroded and the styles have been rounded. The fragment of a right lower third molar is much eroded but still the back fossa with its entoconulid is recognizable; the hypoconid and strong entostylid (although very much eroded here) is also visible. The peculiar shape of the posterior part of the tooth is typical of cainotheriids. The fragment of right lower molar is composed of an anterior lobe bearing nicely-preserved metaconid and protoconid; an anterior cingulid is visible. We figure here the lower first premolar with its oblique root relative to its crown (FSL 98758, Fig. 9i).

Description of the post-cranial material. Fig. 9j–r. Most of the post-cranial elements are very fragmentary and not identifiable at the genus or species levels; we will thus not describe them in detail and only focus on the best-preserved specimens. The astragalus (Fig. 9j), although slightly eroded, is relatively well preserved, and shows a ridge medially bordering the sustentacular facet like in *Caenomeryx* Hürzeler, 1936 and other cainotheriids (Hürzeler 1936; Martinez and Sudre 1995). Its size is also coherent with cainotheriid astragali from the Quercy Phosphorites (pers. obs. on material in the NMB). The well-preserved third phalanges are morphologically close to those of *Cainotherium* described by Hürzeler (1936). They are of different sizes reflecting their different positions on the various digits (e.g., Fig. 9k–l). They all show the *foramen nutricium* and a distal foramen near the tip. A closer comparison to the very large collection of *Cainotherium*'s third phalanges from the locality of Saulcet (France) in the collections of the NMB, attests of to their cainotheriid affinities. The metacarpal and numerous

phalanges were compared to the material of *Cainotherium* from Saulcet (collection NMB) and to the seminal work of Hürzeler (1936); they all are of cainotheriid animals being morphologically close to *Cainotherium* for instance; we figure some examples here in Fig. 9m–r.

Remarks. All these fragments are typical for Early Oligocene small cainotheriids, although, due to their fragmentary nature, they are very difficult to determine at the genus and species levels. FSL 98753 is quite big (about 2.5 mm in width) for a possible attribution to *Paroxacron* Hürzeler, 1936 or *Plesiomeryx* Gervais, 1873 (although *Plesiomeryx huerzeleri* Berger, 1959 might reach such sizes) but still seems a little too small for *Caenomeryx* (pers. obs.; see also Blondel 2005). Canines and incisors are difficult to identify and the latter's positions in the tooth row are also not easy to find based on isolated remains. Two small upper canines and seven fragmentary lower incisors were identified along with about ten other fragmentary or deciduous incisors. The post-cranial material of Early Oligocene Cainotheridae has never been described in details before (except for *Caenomeryx* in Martinez and Sudre, 1995), and no skeleton in connexion has been found neither for *Oxacron* Filhol, 1884, *Paroxacron*, *Plesiomeryx* nor *Caenomeryx*. Thus, this fragmentary material will not be ascribed to one of these genera here.

4 Discussion

4.1 The mammalian assemblage of Mazan

Even if the fauna of Mazan is not very rich when compared to some other Early Oligocene localities such as for instance Aubrelong 1, Hamstead, Hoogbutsel or Möhren 19, its mammalian assemblage still comprises 18 taxa belonging to 7 orders and 10 families (Table 1). The association of the theridomorphs *Pseudoltinomys gaillardi*, *Theridomys aquatilis* and *Blainvillimys langei* is typical of the MP21 mammalian level, possibly one of the earliest Oligocene localities in France. This level was hitherto not well known and, as it overlies the Upper Eocene faunas of Mormoiron, it illustrates once more the drastic changes induced by the European 'Grande-Coupure' at a regional scale. The mammalian assemblage is dominated by theridomyids and cricetids (small mammals), and by cainotheriid remains (large mammals). As far as cricetids are concerned, the locality of Mazan probably illustrates an ongoing size and morphology differentiation (Fig. 7 in Electronic Supplementary Material 4), which will eventually lead to the high diversity of cricetids later on during the Oligocene in Europe. For cainotheriids, although most remains cannot be identified at generic level as yet, the numerous post-cranial remains suggest further studies in

Table 1 Faunal list of the mammalian assemblage of Mazan yielded by the brown-black clayish paleosol layers at the base of the "Brotia laurae and *Tympanotonos labyrinthus* Formation" in the Malemort-du-Comtat quarry, Mormoiron basin (Triat et al. 1971)

Notometatheria	
Herpetotheriidae	
<i>Peratherium elegans</i>	(Aymard, 1846)
<i>Amphiperatherium minutum</i>	(Aymard, 1846)
Herpetotheriidae indet.	
Erinaceomorpha	
Erinaceidae	
<i>Tetracus nanus</i>	Aymard, 1850
Soricomorpha	
Nyctitheriidae	
Nyctitheriidae indet.	
Chiroptera	
Vespertilionidea	
Vespertilionidea indet.	
Rodentia	
Sciuridae	
<i>Palaeosciurus goti</i>	Vianey-Liaud, 1974
Theridomyidae	
<i>Pseudoltinomys gaillardi</i>	(Stehlin, 1951)
<i>Theridomys aquatilis</i>	Aymard, 1849 (in Gervais)
<i>Blainvillimys langei</i>	Vianey-Liaud, 1972
Cricetidae	
<i>Eucricetodon</i> sp.1	
<i>Eucricetodon</i> sp.2	
<i>Eucricetodon atavus</i>	(Misonne, 1957)
Gliridae	
<i>Glamys</i> aff. <i>G. olallensis</i>	Freudenthal, 1996
<i>Butseloglis micio</i>	(Misonne, 1957)
<i>Bransatoglis</i> cf. <i>B. planus</i>	(Bahlo, 1975)
Perissodactyla	
Palaeotheriidae	
<i>Plagiolophus</i> sp.	
Cetartiodactyla	
Cainotheriidae	
<i>Plesiomeryx</i> cf. <i>P. cadurcensis</i>	Gervais, 1873
<i>Plesiomeryx</i> sp.	
Cainotheriidae indet.	

order to better understand the post-cranial anatomy of Early Oligocene cainotheriids, which could in turn prove useful for systematic and palaeoenvironmental analyses.

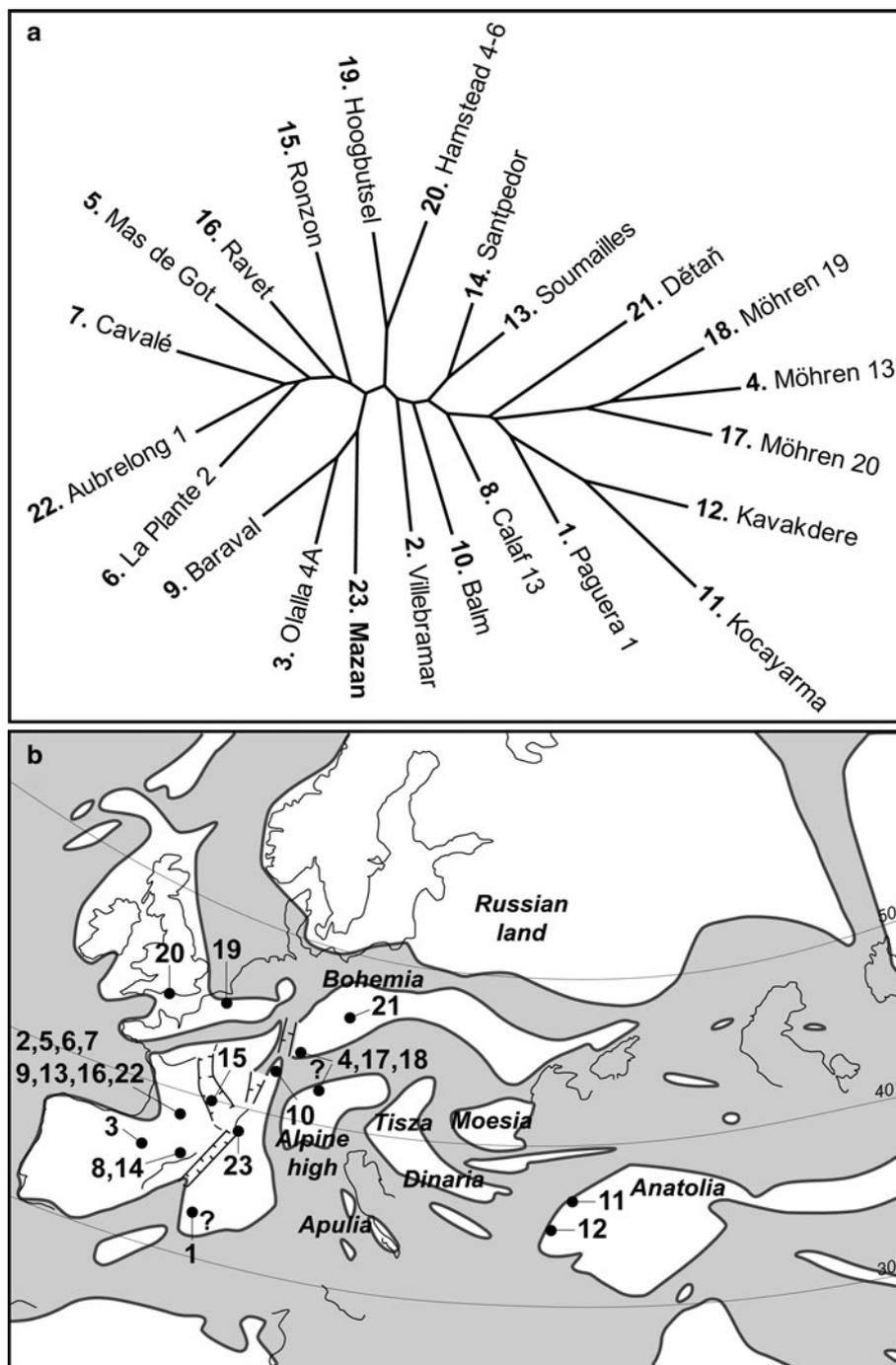
4.2 Mazan and the Early Oligocene palaeobiogeography

The biogeographic analysis based on the comparison with other Early Oligocene European mammalian localities (Table 1 in Electronic Supplementary Material 1, Fig. 12)

Fig. 10 European mammalian palaeobiogeography during the Early Oligocene (MP21–22).

a The mammalian localities are clustered based on significant similarities and dissimilarities of the Raup and Crick index, the tree is built using the neighbour-joining method (see Sect. 2).

b The approximate position of the localities at the Early Oligocene is indicated on the palaeogeographic map by dots and numbers; the list of the localities and the reference numbers are given in the Table 1 (Electronic Supplementary Material 1). The European palaeogeographic map is re-drawn after Popov et al. (2004)



first reveals a general East–West palaeobiogeographic pattern without strong endemism or strong palaeobiogeographic differentiation, although some groups of localities are noticeably separated from others. Second, the localities are not grouped based on their age (MP21 vs. 22) therefore demonstrating that the age difference of the analysed localities did not induce any bias in the palaeobiogeographic results.

The Raup and Crick index values matrix (Electronic Supplementary Material 2) indicates that Mazan is

significantly similar to several other Western European localities, mainly with the localities of Quercy and Central France, but also with Hamstead and Olalla 4A. The tree (Fig. 10a) indicates a possibly even stronger faunal similarity with the localities Baraval (Quercy, S-W France) and Olalla 4A (Teruel, N-E Spain). Mazan is at the same time significantly dissimilar to Dětán, Czech Republic (MP21), supporting the general East–West pattern deciphered by the tree. Interestingly, Dětán presents no significant similarity with any of the other 22 localities, thus indicating a

relatively isolated situation (it is however noteworthy that some taxa identified in Dětán usually occur later in the Oligocene European fossil record, such as *Eomys* cf. *E. zitteli*, *Quercysorex* and *Elomeryx crispus*). The localities of Southern Bavaria (Möhren 13, 19 and 20), geographically the closest from Dětán, are neither significantly similar nor significantly dissimilar to Dětán. Although the positions of the Möhren localities and Dětán were likely relatively close (i.e., on the Bohemian High: Popov et al. 2004), the significant similarity of the Möhren localities with each other but not with Dětán suggest that at that time they could have been geographically separated from Dětán (Alpine High Continental land?: Popov et al. 2004). The locality of Balm is also geographically close to the Bavarian localities but rather clusters with French and Spanish localities. Balm is indeed significantly dissimilar to the three Möhren localities (Electronic Supplementary Material 2), suggesting that it was likely located on another continental block, together with the French and Spanish localities (Fig. 10b).

The two localities in northwestern Turkey, Kavakdere and Kocayarma, are only highly significantly similar to each other but significantly dissimilar with several western and northern localities (Electronic Supplementary Material 2), thus indicating a noticeable East–West palaeobiogeographic differentiation in accordance with the graphic representation (Fig. 10a).

Hamstead 4–6 and Hoogbutsel are grouped on a single branch, which seems in accordance with their presence on the same continental land mass at that time (Fig. 10b). Hamstead 4–6 and Hoogbutsel are indeed significantly similar to each other. It is to be noted that this represents the only significant similarity for Hoogbutsel, whereas Hamstead 4–6 is also significantly similar to Mazan, Aubrelong 1 and Ronzon possibly indicating frequent faunal exchanges between these two continental land mass. Among French localities, a cluster composed of Cavalé, La Plante 2, Mas de Got, Ravet and Ronzon is supported by several significantly similar values. Although the values are not always significantly similar with the other French localities, possibly indicating local particularities, there is no significant dissimilarity among them (Electronic Supplementary Material 2). It indicates a relatively homogeneous palaeobiogeographic context at this scale. Among Spanish localities, Paguera 1 is clearly different from other Spanish localities and clustered with Eastern localities (Fig. 10a). Paguera 1 has indeed no significant similarity with any of the 22 other localities, but is in contrast significantly dissimilar to Aubrelong 1, Cavalé and La Plante 2 (Electronic Supplementary Material 2). The palaeogeographic position of Majorca during the Early Oligocene is still unclear, and it is not possible to assert that Paguera 1 was located on the same continental land mass as the other Spanish and French localities. Thus, insularity of Majorca can not entirely be

ruled out. Interestingly, the possible occurrence of the Asian family Ctenodactylidae in Paguera 1 (Huguency and Adrover, 1985), and the fact that the genus *Moissenetia* (first discovered in Paguera 1) has been identified in the Early Oligocene of Bavaria (Berger, 2008) support this faunal affinity with Eastern Europe rather than with Western Europe. These affinities of Paguera 1 with Anatolian and Bavarian localities provide an interesting insight on possible migration ways at the beginning of the Early Oligocene, which could have connected (at least temporarily) the Anatolian region to the Southwestern European land mass on the one hand (through Dinaric and Apulian lands: Popov et al. 2004), and to the Alpine and Bohemian land masses on the other hand (through Moesian and Tisza lands: Popov et al. 2004). These migration routes for the post-“Grande Coupure” mammal dispersal through the Venetian–Balkan area have already been proposed based on large mammals (Becker 2009) as a reasonable alternative to the north Alpine belt route suggested by Uhlir (1999). More generally, the absence of strong regional endemism or strong palaeobiogeographic differentiation in Europe at the beginning of the Oligocene (Fig. 10a) indicates the likely frequent formation of land connections allowing faunal exchanges between the different continental blocks. Other fossil vertebrates such as the crocodylian *Diplocynodon* present a large geographical distribution (Western Europe, Eastern Europe and Anatolia) at the beginning of the Oligocene, thus also supporting the frequent occurrences of emerged land masses connecting the Anatolian region to Europe through the Venetian–Balkan area (Kotsakis et al. 2004).

5 Conclusions

The systematic revision of the mammalian remains and the description of new specimens reveal that the Mazan assemblage comprises 18 mammalian taxa belonging to 7 orders and 10 families, whereas the theridomyids and cricetids are the two most abundant groups. This revision confirms the ascription of the locality to the biochronological unit MP21, which corresponds to the earliest Oligocene and indicates an unambiguous assignment of the “*Brotia laurae* and *Tympanotonos labyrinthus* Formation” to the Early Oligocene. Furthermore, the comparison of Mazan assemblage with other European localities also provide a re-assessment of the age of the Olalla 4A (MP21–22) and Paguera 1 (MP22–23). Among large mammals, numerous post-cranial remains of cainotheriids emphasize that the post-cranial anatomy of Early Oligocene cainotheriids remains poorly known. Further studies of these elements will lead to a better understanding of their evolutionary history and will in turn prove useful for palaeoenvironmental analyses too.

As, the Mazan locality overlies the Upper Eocene faunas of Mormoiron, its mammalian assemblage illustrates once more the drastic changes induced by the European 'Grande-Coupure' at a regional scale.

From a palaeobiogeographic point of view Mazan shows significant affinities with other localities from Western Europe (especially French and Spanish localities), while localities from the eastern part of Europe (Anatolian, Bavarian and Bohemian localities) are noticeably different. The locality of Paguera 1 (Majorca)—possibly already insular in the Early Oligocene—shows peculiar affinities with Anatolian and Bavarian localities rather than with Western European ones. However no strong endemism can be found in the Early Oligocene biogeography, which suggests the existence of frequent land connections across Europe and especially with the Anatolian region, but also between the Anatolian and the Bavarian regions, permitting faunal exchanges.

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