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The Ruminantia (Mammalia, Cetartiodactyla) from the Oligocene to the Early Miocene of Western Europe: systematics, palaeoecology and palaeobiogeography

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THE RUMINANTIA (MAMMALIA, CETARTIODACTYLA) FROM THE OLIGOCENE TO THE EARLY MIOCENE OF WESTERN EUROPE: SYSTEMATICS, PALAEOECOLOGY AND PALAEOBIOGEOGRAPHY

THÈSE

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Cover pictures

left : *Litocranius walleri* (with the courtesy of Jill Mason)

right : *Hydropotes inermis* (Bastien Mennecart)

To Jean-Pierre

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ABSTRACT

Nowadays, the ruminants are the most ecologically diverse hoofed mammals of the world. All the extent of families (including related species from the Burdigalian) and feeding habits can be deduced from the mandible shape. The Tragulidae possess a small *coronoid* process, a shortened diastema, and a weak *incisura vasorum*. The Eupecora have an elongated diastema (extremely extended within the Giraffidae), the *coronoid* process is elongated. The Cervidae are generally more slender than the Bovidae. A trend from the massive mandible of the grazers, to the mixed feeders, the folivore, and the slender selective browsers can be observed within the Cervidae and the Bovidae. For older taxa, some doubt still exists as to their phylogeny and palaeoecology. The transitional position of the latest Oligocene-Aquitanian ruminants' mandible shape, between the primitive *Gelocus* and the extent of families, suggests a basal radiation of the Eupecora without extant representatives. The mandibles of Early Oligocene and Eocene ruminants have a similar shape, retaining a primitive form close to the common ancestor.

The earliest confirmed record of ruminants in Western Europe are the German and French Gelocidae *sensu stricto* (*Phaneromeryx gelyensis*, “*Gelocus” minor*, and *Rutitherium nouleti* being unique, lost, and cannot been placed in a geological timeframe and the location of their discovery is unknown). The reassessment of the European ruminants leads to new phylogenetic attributions and an unexpected diversity during the Oligocene. *Iberomeryx minor* was often considered as a Lophiomerycidae. However, based on new material and new descriptions, this tiny ruminant is a Tragulidae (the shape of the p4 without mesolingual conid, huge *Dorcatherium* fold on lower molars, general shape of the mandible). The description of new specimens of a small Lophiomerycidae confirms the existence of “*Lophiomeryx*” *gaudryi*. Similar observations can be made for the latest Oligocene Eupecora “*Amphitragulus*” *feningre~~i~~*. A new combination is proposed for the Chattian *Mosaicomeryx quercyi* (Jehenne, 1987). It is the sister taxon of *Prodremotherium elongatum*, which are not considered as Gelocidae anymore. A new genus and species (*Babameryx engesseri* Mennecart, 2012) has been published. This primitive species could be at the base of the Eupecora radiation.

An exhaustive study of the European ruminants in a clear temporal framework allows a new interpretation of their biostratigraphy. The earliest undeniable European ruminants occurred only after the “Grande-Coupure” event (MP20/21), at the same age as the Oi1 glaciation event (ca. 33.5 My; part of Migrations1), whereas the first true ruminants appeared earlier in the Middle and Late Eocene in North America and Asia. Following this extinction/origination event, the earliest European ruminant families Lophiomerycidae and Gelocidae diversified rapidly. Later, at MP23, the new families Bachitheriidae and Tragulidae migrated from Asia (ca. 30.5 My; part of Migrations1). Swamps and forests dominated the European landscape, but at the beginning of MP24, a global change coinciding with the Oi2 glaciation event, occurred. In Switzerland, it was marked by the regression of the UMM (Lower Marine Molasse) and by the Renish Sea, and drastic changes of the sedimentological context that generated a drier climate and a faunal renewal. Within the European ruminant community, we note the disappearance of the Gelocidae and the Tragulidae, and only the larger species of Bachitheriidae and Lophiomerycidae survived (Extinction1).

At MP24/25 (ca. 29.2 My), the Bachitheriidae diversified and the Mosaicomerycidae appeared in Europe (Speciation1). The European mammal evolution was relatively quiet and steady until MP27. The environment was generally wooded and the sedimentation in the Swiss Molasse was typically dominated by fluvial deposits.

Around MP28, large changes occurred in the faunal communities. The diversity of the evolution pattern of the ruminants can be precisely defined for this period, thanks to the record of numerous rich and temporally well-defined localities. First, a specific renewal resulted in ruminants more specialised for open habitats (Extinction2 and Migration2). In Pech Desse, only primitive taxa (*Prodremotherium*, *Bachitherium*, and *Lophiomeryx*) associated with *Amphitragulus* have been found. Then a rapid extinction occurred, during the emergence of new migrants, the High Ruminantia: Eupecora (Extinction3 and Migrations3). In Gaimersheim 1, only *Bachitherium* still survived, when *Dremotherium* and *Babameryx* arrived. In Pech du Fraysse, only Eupecora are present. In Switzerland, this short time interval coincided with sedimentological changes related to a drier environment.

The transition between the Oligocene and the Miocene (ca. 22.9 My) was marked by the Mi1 glaciation event, which coincided with a general fragmentation of the environment. In spite of this, the ruminant community was not strongly affected. However, a general trend highlights size changes; the small species derived into smaller species and the medium size species into larger ones. At the end of MN2, a huge diversity of hornless saber-toothed ruminants belonging to uncertain families is recorded (Speciation2).

Some Swiss Aquitanian localities (Engehalde, Tavannes Sous le Mont, and Wallenried) have been studied in detail. The new excavation of Engehalde provides a partial skeleton of *Dremotherium feignouxi*. Moreover, a comparison with the old collections led to the conclusion that different fauna were probably linked to a small diachronism or a mosaic environment. The first late Aquitanian locality from the Central Jura Molasse provided a very rich and diversified fauna. This area proved that the Aquitanian hiatus within the Jura should be reconsidered. A new discovery in Wallenried allowed the complete diagnosis of *Friburgomeryx wallenriedensis* and a reassessment of the species of *Andegameryx*.

To conclude, comparison with previous studies on the diversity of the European ruminants highlights the inaccurate interpretation of this regional evolution. As opposed to the regional evolution which suggests few migrations, this study highlights an evolutionary pattern marked by several huge Asiatic migrations, strongly related with global and environmental changes (clearly defined in Switzerland) and punctuated by some speciation phases. Europe should be considered more as a Dead End (migration/extinction) than an area with a normal evolutionary diversification (speciation).

RÉSUMÉ

De nos jours, les ruminants représentent le groupe de mammifères ongulés le plus diversifié. Les familles actuelles (en incluant les espèces relatives à partir du Burdigalien), ainsi que le régime alimentaire, peuvent être déduits de la forme de la mandibule. Les Tragulidae possèdent un petit processus coronoïde, un diastème entre les prémolaires et la canine inférieures court, et une faible incisure vasculaire. Les Eupécora, quant à eux, possèdent un diastème allongé (extrêmement dans le cas des Giraffidae), tout comme le processus coronoïde. Les Cervidae sont généralement plus graciles que les Bovidae. Au sein d'une même famille, nous pouvons observer un continuum dans la forme de leur mandibule allant d'animaux mangeurs d'herbe vers les mangeurs de fruits. Pour des taxons plus anciens que le Burdigalien, des doutes subsistent quant à leur phylogénie et leur paléoécologie. La position transitoire de la forme de la mandibule des ruminants de la fin de l'Oligocène et de l'Aquitanien, située entre le primitif *Gelocus* et les familles actuelles, suggère une radiation basale des Eupécora avec des groupes sans représentants actuels. Les ruminants de l'Eocène et de Oligocène inférieur ont une forme de la mandibule relativement similaire, probablement liée à la rétention de la forme ancestrale.

La plus ancienne archive certifiée de ruminants en Europe de l'ouest concerne les Gelocidae *sensu stricto* allemands et français (*Phaneromeryx gelyensus*, « *Gelocus* » *minor*, et *Rutitherium nouleti* étant des fossiles uniques, perdus et dont l'origine stratigraphique et géographique restent floues). La révision des ruminants européens a contribué à la mise à jour de nouvelles attributions phylogéniques et d'une diversité de ces animaux non suspectée durant l'Oligocène. *Iberomeryx minor* était souvent considéré comme étant un Lophiomerycidae. Cependant, sur la base de nouveau matériel et de nouvelles descriptions, ce petit ruminant appartient à la famille toujours existante des Tragulidae (la p4 ne possède pas de conide mésolingual, les molaires ont un très fort pli *Dorcatherium*, la forme généralement compact de la mandibule). La description de nouveaux spécimens d'un très petit Lophiomerycidae confirme l'existence de « *Lophiomeryx* » *gaudryi*. Nous pouvons constater la même chose pour l'Eupécora de la fin de l'Oligocène « *Amphitragulus* » *feningrei*. Une nouvelle combinaison est proposée pour le ruminant du Chattien *Mosaicomeryx quercyi* (précédemment *Gelocus quercyi* Jehenne, 1987). Ce taxon est le groupe frère de *Prodremotherium elongatum* qui, pour le coup, n'appartiennent plus à la famille des Gelocidae. Un nouveau genre et espèce (*Babameryx engesseri* Mennecart, 2012) a été publié. Ce taxon relativement primitif dans sa forme pourrait être à la base de la radiation des Eupécora.

Une étude exhaustive des ruminants européens dans un cadre temporel bien défini permet une nouvelle interprétation de leur répartition biostratigraphique. Les premiers ruminants européens indéniables arrivent après la « Grande-Coupure » (MP20/21), au moment de la glaciation Oi1 (~33.5 Ma ; première vague migratrice de Migrations1), les plus anciens connus provenant de l'Eocène Moyen et Supérieur d'Amérique du Nord et d'Asie. Suite à cet événement d'extinction et de migrations, les premières familles de ruminant européens, les Lophiomerycidae et les Gelocidae, se diversifient rapidement, suivi de nouvelles arrivées plus tardives, les Bachitheriidae et Tragulidae (~30.5 Ma ; dernière vague migratrice de Migrations1). Les marécages et les forêts dominaient les environnements européens. Cependant, au début de MP24, un changement climatique correspondant à la glaciation Oi2 se produit. En Suisse, ce changement se retranscrit par la régression de l'UMM (Molasse Marine Inférieure) et la mer rhénane accompagnées de changements sédimentologiques drastiques générés par un climat plus sec et un renouvellement faunique. Au sein de la communauté de ruminants européens, nous observons la disparition des Gelocidae et des Tragulidae. Seules les espèces les plus larges de Bachitheriidae et de Lophiomerycidae persistent (Extinction1).

Durant MP24/25, les Bachitheriidae se diversifient en de nombreuses espèces et les Mosaicomerycidae apparaissent en Europe (Spéciation1). L'évolution des mammifères européens, jusqu'à MP27, reste constante sans profonds changements.

L'environnement est dominé par des forêts et la sédimentation dans le bassin molassique suisse est dominée par des dépôts fluviatiles.

Autour de MP28, de grands changements apparaissent dans les communautés fauniques. La diversité dans l'évolution de la communauté des ruminants peut être précisément définie grâce à un enregistrement faunique riche. Tout d'abord, nous observons un renouvellement spécifique résultant d'un habitat plus ouvert (Extinction2 et Migration2). A Pech Desse, seuls des taxons primitifs sont retrouvés (*Prodremotherium*, *Bachitherium*, et *Lophiomeryx*), associés à *Amphitragulus*. Il s'en suit une rapide extinction coïncidant avec l'émergence de nouveaux migrants : les Eupécora (Extinction3 and Migrations3). A Gaimersheim1, seul *Bachitherium* persiste, quand *Dremotherium* et *Babameryx* arrivent. A Pech du Fraysse, seuls des Eupécora sont présents. En Suisse, cette période très courte coïncide à des changements climatiques correspondant à des environnements plus arides.

La transition entre l'Oligocène et le Miocène (~22.9 Ma), marquée par la glaciation Mi1, coïncide avec une fragmentation générale de l'environnement. Cependant, la communauté des ruminants n'a pas été profondément changée. Néanmoins, nous pouvons observer une tendance à un changement de la taille, pouvant être lié à ce changement climatique. Les petites espèces deviennent plus petites, tandis que les espèces de taille moyenne deviennent plus grandes. A la fin de MN2, il y a une très grande diversité de ruminants à dents de sabre dont l'attribution familiale reste encore sujette à discussion (Spéciation2).

Quelques localités de l'Aquitanien suisse (Engehalde, Tavannes Sous le Mont, et Wallenried) ont été étudiées en détails. La nouvelle excavation de Engehalde a permis la découverte d'un squelette partiel de *Dremotherium feignouxi*. De plus, une comparaison avec l'ancienne collection permet de conclure que ces deux faunes (nouvel et ancienne fouille) sont différentes, ce qui est probablement liées à un léger diachronisme ou une mosaïque d'environnements. Tavannes Sous le Mont est la première localité aquitanienne de la molasse du Jura central. Cette localité a donné une faune très riche et diversifiée. Ces dépôts prouvent que la lacune aquitanienne du Jura devrait être reconsidérée. De nouvelles découvertes dans la carrière de Wallenried permettent de compléter la diagnose de *Friburgomeryx wallenriedensis* et de réviser l'espèce d'*Andegameryx* présente.

Pour conclure, en comparant nos résultats avec ceux des précédentes études, nous pouvons remarquer que leur conclusion sur une évolution locale des ruminants en Europe, qui implique peu de migrations, n'est pas cohérente. Nous suggérons, à l'opposé, une évolution marquée par d'importantes migrations asiatiques, fortement liées à des changements climatiques et environnementaux (bien définis en Suisse) et ponctuée par des phases de spéciation locale. L'Europe devrait être considérée comme un cul-de-sac géographique où l'évolution des communautés est marquée par des phases de migration et d'extinction plutôt qu'une zone possédant une diversification normale basée sur la spéciation.

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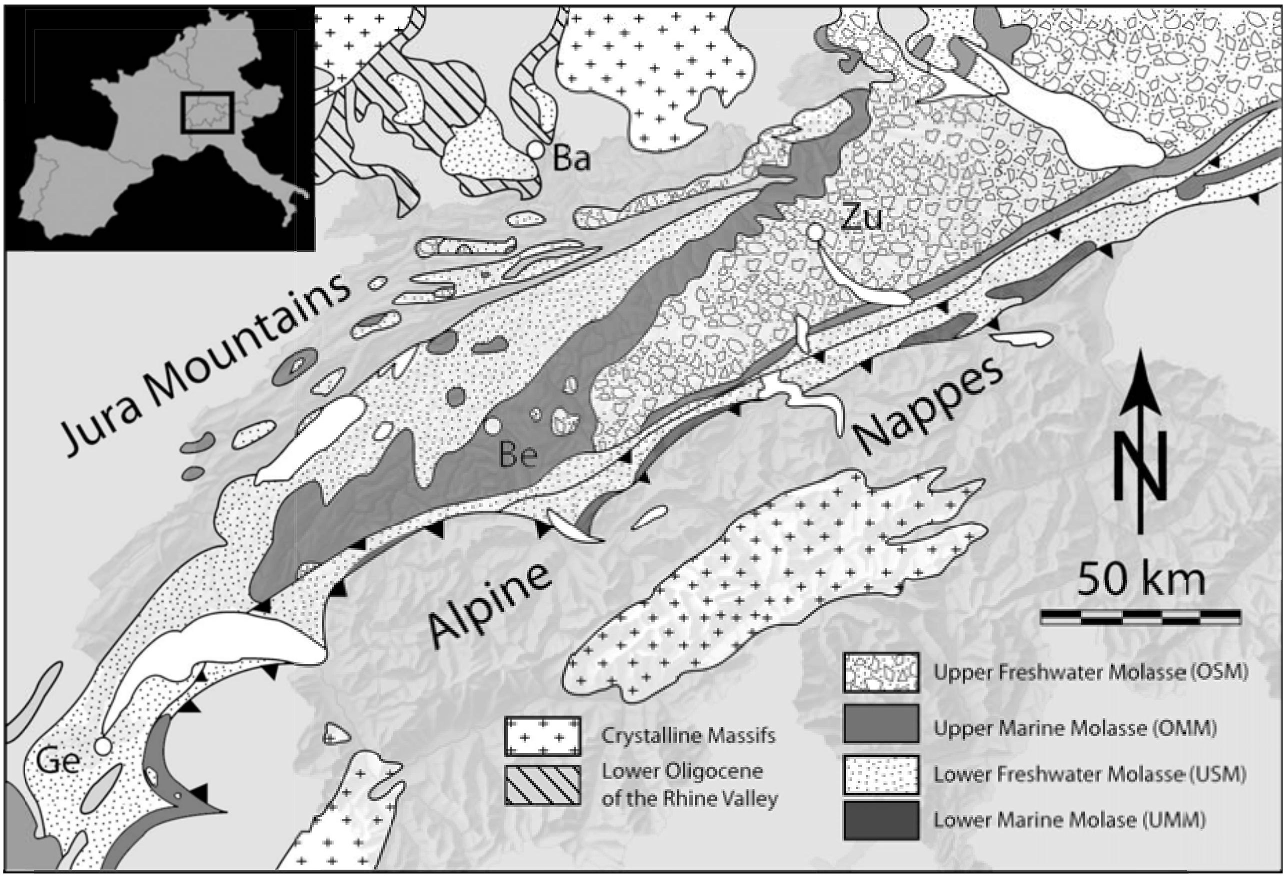
Saviez-vous qu'un castor ne s'éloigne jamais plus de 30 mètres du rivage ? Qu'en Angleterre, dans la ville de York, on est autorisé à tuer un écossais s'il porte un arc avec des flèches ? Ou comment Chuck Norris a réussi à faire mettre son slip rouge par dessus le collant à Superman ? Ou que Vivaldi a composé ses 4 saisons suite à une journée passée dans le Connemara ? Ou même que Valence n'est qu'à 15 minutes de Lyon ? Et que dire de ces paléotripes de 2 jours avec 1500 km de route ? Que du plaisir ! Même si le Benshies a déménagé, cela restera notre repaire de pirates irlandais où la Guinness, associé à d'autres Bibi-nes et Byer, coule à Flo, tout en préparant des projets absurdes pour sauver le monde, attablés autour de notre table ronde. Tant de soirées, de discussions, des films en tout genres (Plan 9 from out of Space, Brain Dead, Star Crash, Meet the Feebles), de chopines (le « h » n'est pas une coquille) qui m'ont aidés à rédiger ce manuscrit.

MERCI POUR TOUS CES BON MOMENTS
ET ESPERANT QU'IL Y EN AURA BEAUCOUP D'AUTRES !!!

I - Introduction



Map of the Swiss Molasse Basin

1 - General introduction

1.1 Aims of the thesis

The ruminants are defined by "the fusion of the cuboid and the navicular in the tarsus, the absence of upper incisors, and incisiform lower canines" (Métais & Vislobokova 2007; Fig. 1), and tetracusp upper molars without metacone. However, in the fossil record, it is very rare to find postcranial elements associated to dental remains and the premaxillary bones are often unpreserved. The first indubitable ruminants occurred in Asia and North America during the Middle Eocene (Métais & Vislobokova 2007). The true European Ruminantia families are divided into two infraorders: the Tragulina and the Pecora. The Tragulina are considered to be the most primitive in having doglegged astragalus trochleas, no posterolingual cristid on p4, a *Dorcatherium* fold (or a similar structure) on lower molars, and relatively bunoselenodont molars (Tab.1). Nowadays, one family of Tragulina still exists: the Tragulidae (3 genera: *Hyemoschus*, *Tragulus*, and *Moschiola*). The Pecora are more derived. They are divided into two parvorders: the Protopecora and the Eupecora. The main differences between these two taxa and the Tragulina families can be observed in the mandible shape, the p1 shape and position (Mennecart et al. 2011, 2012; Fig. 2, Tab. 1), and the p4 shape (Janis & Lister 1985; Erfurt & Métais 2007; Fig. 3, Tab. 1). Currently, all ruminants, except Tragulidae, are Eupecora (nearly 190 genera; Mennecart et al. 2012). The majority of the Eupecora males possess appendages. Considering the soft tissues, the Tragulidae only possess three stomach chambers, whereas the Eupecora have four (Rössner 2007).

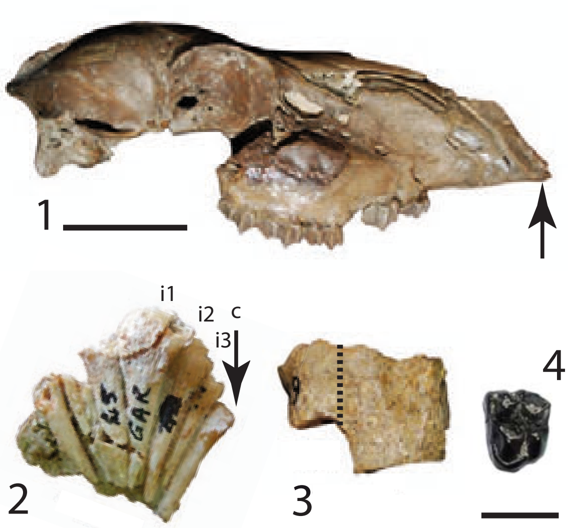


Fig. 1 The Ruminantia characteristics: **1** the absence of upper incisors (skull of *Dremotherium feignouxi*; MNHN SG4304, Holotype); **2** incisiform lower canines (anterior portion of mandible with left i1-c and right i1-3 of *Lophiomeryx chalaniati*: USTL GAR45); **3** fusion of the cuboid and the navicular (cubo-navicular bone of *Lophiomeryx mouchelini*: NMB OV9); **4** four cusps upper molar without metacone (left M1 in occlusial view of *Babameryx engesseri*: NMO K11/15, holotype). **1** Scale bar equals 50 mm. **2**-**4** Scale bar equals 10 mm.

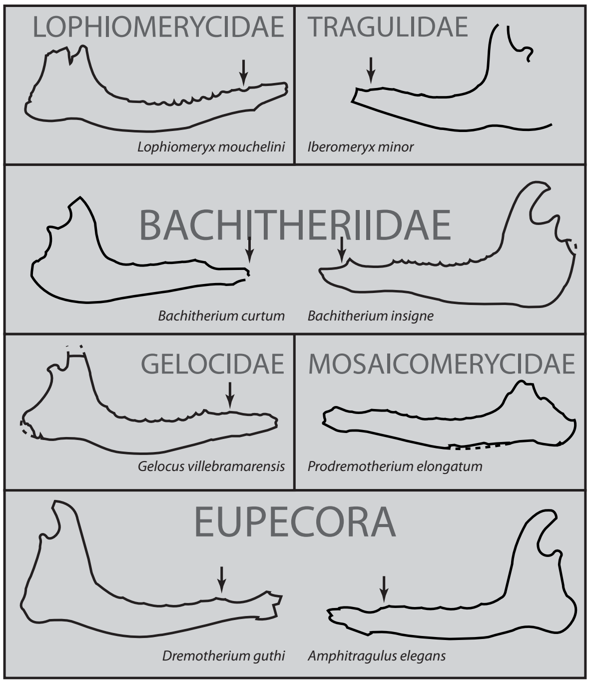


Fig. 2 Shape of the mandible of the Oligocene and Early Miocene European Ruminantia families: Lophiomerycidae (*Lophiomeryx mouchelini*, IPHEP VIL.1973-257), Tragulidae (*Iberomeryx minor*, NMB Sc.118), Bachitheriidae (*Bachitherium curtum*, NMB QB63; *B. insigne*, collection Loggia), Gelocidae (*Gelocus villebramarensis*, IPHEP VIL.1970-121), Mosaicomerycidae (*Prodremotherium elongatum*, MNHN Qu4769), and Eupecora (*Dremotherium guthi*, IPHEP LM.1968.MA; *Amphitragulus elegans*, NMB MA7926). The arrow, when present, indicates the place of the p1.

Order	**Cetartiodactyla**					
Suborder	**Ruminantia**					
Infraorder	**Tragulina**			**Pecora**		
Parvorder				**Protopecora**		**Eupecora**
Family	**Lophiomerycidae**	**Tragulidae**	**Bachitheriidae**	**Gelocidae**	**Mosaicomerycidae**	
	Morphological Characteristics					
Postcranial bones						
astragalus trochleas	dogleged	dogleged	dogleged	aligned	aligned	aligned
astragalus articular facet crest	present	absent	absent	absent	absent	absent
metatarsal bones	unfused	partly fused	fused	fused	fused	fused
Mandible (Fig. 2)						
diastema	short	short	long	short	long	long
mandible ventral profile	regular convex	regular convex	straight	regular convex	regular convex	regular convex
Lower dentition						
p1	leaf-like	blade-like	tusk.like	small conical	absent	variable
p4 shape (Fig. 3)	long & narrow	short & narrow	short & narrow	long & narrow	long & narrow	compact
p4 mesolingual conid	present	absent	absent	present	present	present
p4 posterolingual cristid	absent	absent	absent	present	present	present
molar trigonid	open	open	closed	closed	closed	closed
molar postentocristid	absent	absent	present	small	present	present
molar anterior conid	absent	present	absent	absent	absent	absent
Dorcatherium fold	variable	present	present	absent	absent	absent
tooth crown height	low	low	low	low	low	variable
Appendages	Absent	Absent	Absent	Absent	Absent	variable

Tab. 1 Morphological comparison (postcranial bones, mandible, lower check teeth) between Oligocene and Early Miocene European Ruminantia (Lophiomerycidae, Tragulidae, Bachitheriidae, Gelocidae, Mosaicomerycidae, and Eupecora).

The family Amphimerycidae existed during the Eocene of Europe. This small selenodont taxon has for a long time been considered as primitive European Ruminantia (Matthew 1929; Colbert 1941; Simpson 1945; Geraads et al. 1987; McKenna & Bell 1997; Hooker & Weidmann 2000; Theodor et al. 2005). However, Stehlin (1910), Viret (1961), Webb & Taylor (1980), and Métais et al. (2001) refuted this hypothesis, concluding that they are ruminant-like Artiodactyla, possessing convergences with this suborder such as the fusion of the cuboid and the navicular bones. Moreover, the recent reassessment of the primitive European artiodactyls proposed by Erfurt & Métais (2007) confirmed the endemic origin of this family. The characteristics permitting the distinction between Ruminantia and Amphimerycidae are the following: elongated and compressed lower premolars with aligned cuspids, the presence of a diastema between the lower premolars, p1 adjacent to c, p4 not similar to that of Ruminantia by having an isolated mesolingual conid, and upper molars without a metacone. Erfurt & Métais (2007) concluded, such as Viret (1961), that dental morphology of the Amphimerycidae is more similar to that of the endemic European Paleogene artiodactyls Xiphodontidae and Dacrytheriidae.

A huge diversification of ruminant families occurred in Asia during the Eocene and the Oligocene (Vislobokova 1997; Métais & Vislobokova 2007). This suborder probably originates in this continent. Similar families occurred in Europe only from the Oligocene, and were much less diverse (Fig. 4). The Eupecora appeared last, earliest representatives are known from the Chattian (Fig. 4). The current Eupecora families (Cervidae, Moschidae, Bovidae, Giraffidae, Antilocapridae), characterized mainla by the presence of cranial appendages, have been recorded since the Burdigalian (Fig. 4, Tab. 1). The ruminants are unknown during the Oligocene in Africa (Fig. 4). The occurrence of Eupecora there is related to the Proboscidean Datum event (Burdigalian; Van der Made 1999).

Fig. 3 Morphology of the lower 4th premolar of the Paleogene and Aquitanian European Ruminantia families: Tragulidae (*Iberomeryx minor*, *Dorcatherium crassum*), Lophiomerycidae (*Lophiomeryx mouchelini*, *L. chalaniati*, “*L.”* nov. sp., *“L.” gaudryi*), Bachitheriidae (*Bachitherium curtum*, *B. insigne*, *B. guirountensis*, *B. lavocati*), Gelocidae (*Gelocus communis*, *G. villebramarensis*), Mosaicomerycidae (*Mosaicomeryx quercyi*, *Prodremotherium elongatum*), and Eupecora (*Babameryx engesseri*, “*Amphitragulus*” *feningrei*, *Dremotherium guthi*, *D. feignouxi*, *A. quercyi*, *A. elegans*, *Pomelomeryx gracilis*, *A. primaevus*, *Bedenomeryx milloquensis*, *B. paulhiacensis*).

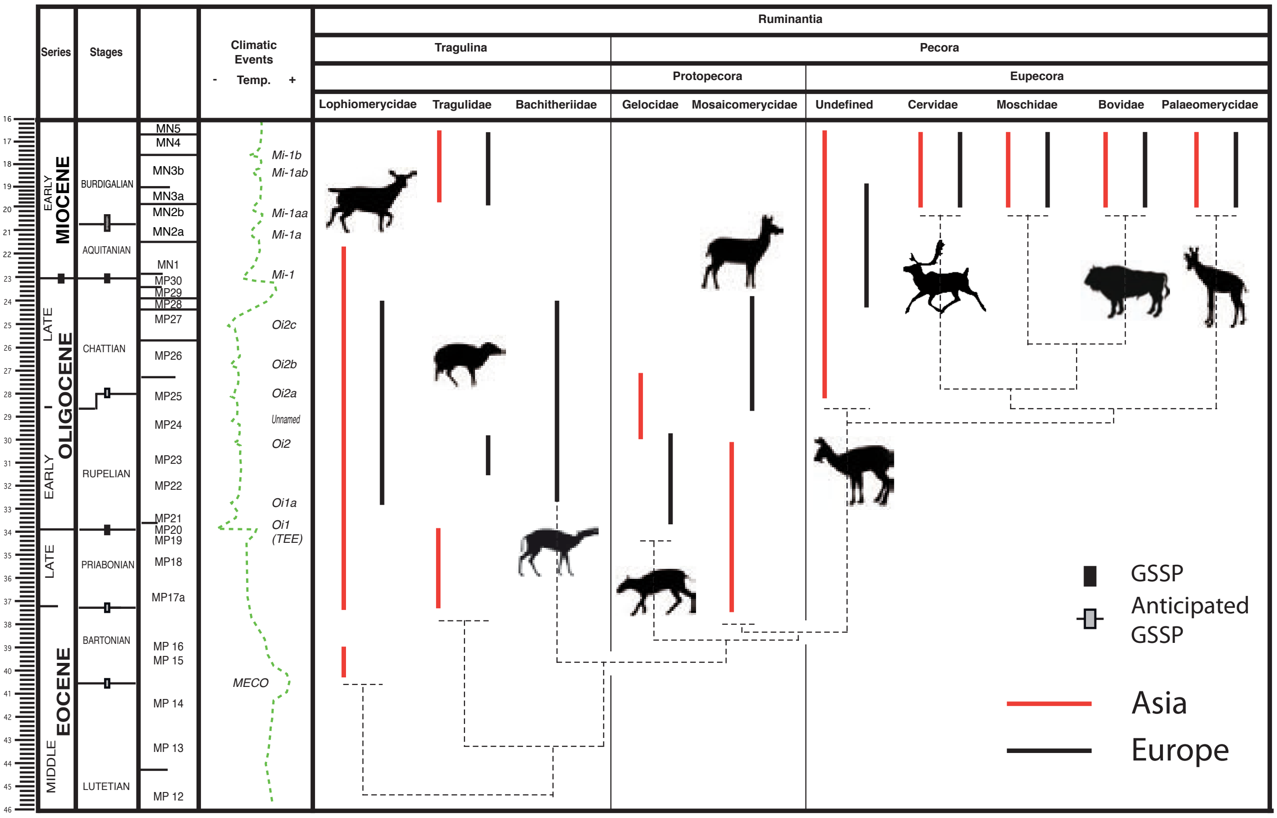


Fig. 4 Biostratigraphy and geographical distribution of Ruminantia families present in Europe and Asia during the Eocene to the Early Miocene (Jehenne 1985, 1987; Gentry 1994; Solounias et al. 1995; Vislobokova 1996, 1997; Blondel 1997; Gentry et al. 1999; Vislobokova, I. & Daxner-Höck, G. 2002; Hassanin& Douzery 2003; Métais & Vislobokova 2007; Mennecart et al. 2011, 2012, accepted; Rössner pers. comm.; Chapter 4, 5, 6, 7, and 9).

Regarding the Swiss mammal localities, except for the Swiss Oligocene Perissodactyls that were partly published (Becker 2003, 2009; Becker et al. 2009, in press; Scherler et al. 2011), the large mammals are still under study. The Swiss Oligocene and Early Miocene ruminants have been hardly studied since the second part of the XXth century. In the historical publications (e.g., Stehlin 1901, 1914), the material was rarely identified to the species level and most of the time the descriptions were poorly developed, often implying the use of erroneous faunal listings (Mayo 1980; Engesser & Mayo 1987; Engesser & Mödden 1997). Only Becker et al. (2004, 2010) and Mennecart et al. (2011, 2012) have recently published reviews of Swiss ruminant remains (*Iberomeryx minor*, *Dremotherium feignouxi*, *Dremotherium guthi*, “*Amphitragulus” quercyi*, “*Amphitragulus*” *feningrei*, *Babameryx engesseri*). Similar observations can be made amongst the other Western European countries. Some German localities yielding Oligocene ruminants were published during the second part of the XXth century (e.g., Heissig 1978, 1987). In France, two PhD theses and related papers giving descriptions of south western France ruminants (Jehenne 1985, 1987, 1988; Sudre & Blondel 1996; Blondel 1996; 1997, 1998) are the most recent works.

Several major recent publications have focused on Asiatic and North American ruminants (e.g., Vislobokova 1996, 1997; Métais et al. 2001, 2009; Vislobokova & Daxner-Höck 2002; Webb 2008). The descriptions are mainly based on comparisons with European species defined during the XIXth century (e.g., Saint Hilaire 1833; Pomel 1846; Filhol 1877, 1881). However, for 25 years, almost no descriptions or revised diagnoses based on European specimens have been proposed. Usually, the authors consider that the European ruminant evolution is local and anagenetic, from one species to another and from one family to another (Jehenne 1985; Jehenne & Brunet 1992; Blondel 1997). Moreover, the palaeobiogeography of the primitive ruminants remains unclear.

In light of new Swiss discoveries (e.g., Beuchille, Poillat, Engehalde, Sous le Mont) and from the revision of the old European collections (e.g., Ronzon, Bumbach, Montclar de Quercy, Saint Henry, Saint André, Rickenbach, Coderet), this study mainly aims to reassess the Western European Ruminantia from the Oligocene and the Early Miocene, to define a new biostratigraphical framework, and to reconsider the palaeobiogeography of the early ruminants. Moreover, ecomorphology analyses based on extant ruminants allow the palaeoecology of some extinct ruminants to be defined. The combination of the results enables a correlation of the evolution of the European ruminant communities with the major biotic and abiotic events, and the identification of new events/crise in the European mammal communities during the Oligocene and Early Miocene.

1.2 Organization of the Dissertation

This thesis dissertation is a compilation of published articles (Chapter 2, 4, 7, 8, and 10) and preformatted articles. In addition to the Introduction and the Conclusion, it is organized in three main parts, chronologically ordered from the Early Oligocene to the Early Miocene.

I Introduction

Chapter 1 (General introduction) introduces general information about the ruminants and their evolution. The aims of the dissertation are explained in detail (systematics, palaeoecology, palaeobiogeography).

Chapter 2 (Mandible shape of ruminants) presents the current and extinct ecological diversity of the ruminants. A geometric morphometrics analysis performed on the mandible shape gives information on the morphomecanics of the jaw, the (palaeo)diet and the phylogeny of the ruminants.

Chapter 3 (Material and methods) defines the materials taken into consideration and the related locations and sedimentary basins. Attention is focused on the Swiss Molasse Basin. This chapter also presents the stratigraphical framework, the anatomical terminologies, and the specific methods such as the geometric morphometrics, the ecomorphology, and the cenogram analysis.

II Early and mid-Oligocene

Chapter 4 (Systematics and palaeodiet of *Iberomeryx minor*) describes the fossils of *Iberomeryx minor* (Tragulidae, Ruminantia) recorded in Switzerland and France. Anatomical and geometric morphometric analyses are performed to define the biostratigraphy, the phylogeny, and the palaeodiet of this primitive ruminant.

Chapter 5 (Early Oligocene European ruminants) reviews the main species of Tragulina and Protopecora (except for the Mosaicomerycidae family) from Western Europe (Czech Republic, France, Germany, Italy, Spain, Switzerland). Biostratigraphic, phylogenetic, and ecologic conclusions are deduced, including faunal turnovers.

Chapter 6 (New genus *Mosaicomeryx*) describes a new family and a new genus of Protopecora. Mosaicomerycidae is a new step in the evolution of the ruminants, and contributes to the basal radiation of the Pecora. Its biostratigraphy and palaeobiogeography are discussed.

III Latest Oligocene

Chapter 7 (Large mammals from Rickenbach) reviews the large mammal fauna from Rickenbach (MP29, type locality, Switzerland). This presents the description of the new species and genus *Babameryx engesseri* (Ruminantia) and a cenogram analysis based on the revised fauna.

Chapter 8 (Late Oligocene changes in mammal communities) is a short contribution describing and synthesizing the various climatic events that occurred during the latest Oligocene in Europe. This study focuses mainly on the Swiss mammal record and the sedimentary changes within the Swiss Molasse Basin.

Chapter 9 (Latest Oligocene ruminants) reviews the oldest Eupecora from Western Europe (France, Germany, Spain, Switzerland). Biostratigraphical and ecological conclusions are deduced, including the ruminant response to the Oligocene-Miocene transition.

IV Early Miocene (Aquitanian)

Chapter 10 (Late Aquitanian mammals from Engehalde) reviews the mammal fauna from Engehalde (MN2b, Switzerland).

Chapter 11 (First evidence of Aquitanian deposits in the south-central Jura Molasse) presents preliminary results on the new mammal locality Tavannes – Sous le Mont (MN2b, Switzerland).

Chapter 12: (Wallenried, new research and fossils) discusses the historical and recent excavations of Wallenried (MN2b, Switzerland). The study and the reassessment of the ruminants from Wallenried concludes on the co-occurence of 3 different species (*Friburgomeryx wallenriedensis*, *Andegameryx andegaviensis*, and Ruminantia 3). The palaeoenvironment of Wallenried could have been an open swampy area.

V Conclusion

Chapter 13 (Conclusion and perspectives) combines the results of the previous chapters. A general biostratigraphic chart of the European Oligocene and Early Miocene ruminants associated with the major faunal and climatic events is proposed. The palaeobiogeography of the Old World ruminants is discussed. Suggestions for future studies are presented.

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2 - MANDIBLE SHAPE OF RUMINANTS: BETWEEN PHYLOGENY AND FEEDING HABITS

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Abstract

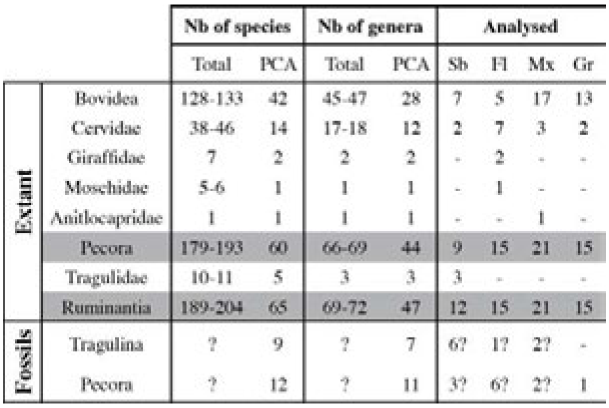
Previous authors have demonstrated that the mandible morphology of ruminants is strongly related to phylogeny and diet. We performed a geometric morphometric analysis defined by the landmark configurations of ruminant mandible specimens, using a Principal Component Analysis (PCA) of the variability in shape. The analysis is based on 21 fossils and 65 extant ruminant species from 65 genera (18 fossil and 47 extant) covering the diversity of the group. As a weak intraspecific variability is assumed, one mandible specimen per species has been used in the analysis. The PCA (PC1: 36.0% and PC2 15.3%) reveals progressive trends in the mandible shape of extant and fossil taxa related to phylogeny and feeding habits. Within extant ruminants, Tragulina can easily be distinguished from the Pecora along the PC1 axis. Tragulina possess elongated premolars, a small *diastema*, an enlarged angular process, a weak *incisura vasorum*, a short coronoid process inclined backwards, a stout condylar process and a subvertical *ramus*. Bovidae have mainly negative PC2 values and can broadly be separated from the Cervidae that mostly plot in the positive side of the axis. However, selective browser Bovidae plot in an overlapped area with Cervidae in the positive side of the PC2 axis. Bovidae often bear an enlarged *corpus mandibulae*, a lengthened molar row, and shortened premolar row and *diastema*. The *ramus* is more backward inclined giving a more efficient lever arm to the masseter muscles, with a less individualized angular process. Within Bovidae, this mandible shape change is observed along the PC2 axis. The enlargement of the *corpus mandibulae* and the elongation of the molar row are related to the increase of the hypsodonty and the grazing habit. Within Cervidae, few similar distinctions between the mandible shape and the diet can be observed. Giraffidae belong to a homogeneous group characterized by an extreme elongation of the *diastema* forming a slender *corpus mandibulae*. Selective browser Bovidae, Moschidae and Antilocapridae plot within the Cervidae/Bovidae overlapped area.

Regarding the fossil specimens, three different categories are observed. The true Cervidae, which bear antlers, are within the extant Cervidae. *Hoplitomeryx* plot close to extant Antilocapridae within the Cervidae/Bovidae overlapped area. The other Miocene species, related to either extinct families or ancestral representatives of extant families, plot between the primitive *Gelocus villebramarensis* and extant Pecora. The mandible shape of primitive Tragulina does not permit the distinction of different feeding habits. However, primitive Tragulina form a separate group that could correspond to the ruminant primitive state mandible shape.

2.1 Introduction

The ruminants are one of the most diverse large mammal groups in the world with about 210 species in approximately 70 genera and 6 families (see Table 1). They occupy numerous ecological niches covering many different types of environment such as deserts, grasslands, savannas, forested areas, and mountains. Their feeding habits vary from selective browsing to pure grazing, classically distinguished on the base of their body mass [10,11]. However, some large forms can feed on leaves while some smaller ruminants can ingest grass (*Giraffa*

Table 1. Comparison between the exhaustive number of extant ruminants (data from literature) and the sampling number used in the PCA. Bovidae, [1, 2, 3]; Cervidae, [1, 2, 4]; Giraffidae, [5, 6]; Moschidae, [2, 7]; Antilocapridae, [8]; Tragulidae, [9]. Nb: number; PCA: this chapter; Sb: selective browser; Fl: folivore; Mx: mixed feeder; Gr, grazer.



		Nb of species		Nb of genera		Analysed			
		Total	PCA	Total	PCA	Sb	Fl	Mx	Gr
Extant	Bovidea	128-133	42	45-47	28	7	5	17	13
	Cervidae	38-46	14	17-18	12	2	7	3	2
	Giraffidae	7	2	2	2	-	2	-	-
	Moschidae	5-6	1	1	1	-	1	-	-
	Anitlocapridae	1	1	1	1	-	-	1	-
	Pecora	179-193	60	66-69	44	9	15	21	15
	Tragulidae	10-11	5	3	3	3	-	-	-
	Ruminantia	189-204	65	69-72	47	12	15	21	15
Fossils	Tragulina	?	9	?	7	6?	1?	2?	-
	Pecora	?	12	?	11	3?	6?	2?	1

cameloparaldis and *Ourebia ourebi*, respectively; see Table 2).

Numerous ecomorphological studies on postcranial bones have recently demonstrated that the ruminants, especially Bovidae, that cover the largest range of ecological variability among the ungulates, are good ecological proxies [89,90,91,92,93].

The mandible is considered to be the biological structure that permits mastication [94]. Many authors argued that the mandible's morphology is directly related to feeding habits [40,95,96,97,98,99,100,101,102]. Additionally, some research has suggested a phylogenetic link in the mandible shape evolution [40,96,98,102].

Based on a Principal Component Analysis of ruminant mandible shapes (Relative Warp Analysis), this chapter basically follows the study of Mennecart et al. [40].

Table 2. Referred specimens of 21 fossil and 65 extant ruminant mandibles used for PCA. The feeding categories and the body mass are provided according to literature, excepted for the species with the mention "this chapter" (*Amphitragulus elegans*, *Germanomeryx fahlbuschi*, *Hispanomeryx duriensis*, *Archaeomeryx optatus*, *Floridameryx floridanus*), where the body mass is calculated using the methods of Legendre [16], Martinez and Sudre [42], and Scott [88]. (f), fossil; (e), extant; (Sb), selective browser; (Fl), folivore; (Mx), mixed feeder; (Gr), grazer. Confident feeding categories of *Gelocus villebramarensis, Germanomeryx fahlbuschi*, *Hispanomeryx duriensis, Hoplitomeryx matthei*, *Archaeomeryx optatus*, *Bachitherium lavocati*, *Dorcatherium naui*, *Floridameryx floridanus*, and *Leptomeryx evansi* are unknown in the literature. However, based on their bunoselenodont or well-selenodont molars, we consider that these taxa were likely to have been either selective browsers (Sb?) or folivores (Fl?) or mixed feeders (Mx?). Composite specimens: *Amphimoschus ponteleviensis* (PIMUZ A/V351, PIMUZ A/V358, PIMUZ A/V360, SMNS 47441); *Bachitherium lavocati* (USTL PDS1330, two unrefered specimens from Gaimersheim stored in the BSP); *Floridameryx floridanus* (UF 13832, UF 19395); *Hispanomeryx matthei* (MNCN-33301, MPZ 2008/177, TOR3B-28).

Ruminantia species	Family	Housing institution	Diet	Body mass (kg)	References
Pecora					
Alces alces (e)	Cervidae	[12]	Fl	500-600	[12, 13]
Ammotragus lervia (e)	Bovidae	[14]	Gr	63-145	[14]
Amphimoschus ponteleviensis (f)	Bovidae?	Composite	Fl	40	[15, 16]
Amphitragulus elegans (f)	Moschidae?	NMB MA7926	Sb	12	[17, this chapter]
Antidorcas marsupialis (e)	Bovidae	[18]	Mx	30-40	[18]
Antilocapra americana (e)	Antilocapridae	[19]	Mx	45-70	[19]
Bison antiquus (f)	Bovidae	ANSP 12976	Gr	500-700	[20, 21]
Bison bison (e)	Bovidae	[20]	Gr	300-900	[20]
Blastocerus dichotomus (e)	Cervidae	[22]	Mx	80-125	[22]
Bos grunniens (e)	Bovidae	[23]	Gr	350-800	[23]
Bos taurus (e)	Bovidae	–	Mx	300	[13, comm. pers. Vernon]
Boselaphus tragocamelus (e)	Bovidae	[24]	Mx	170-270	[24]
Bubalus mindorensis (e)	Bovidae	[25]	Mx	180-300	[25]
Budorcas taxicolor (e)	Bovidae	[26]	Mx	250-350	[26]
Capra cylindricornis (e)	Bovidae	[27]	Mx	55-140	[27]
Capra ibex (e)	Bovidae	[28]	Gr	67-117	[28]
Capra sibirica (e)	Bovidae	[29]	Gr	130	[29]
Capreolus capreolus (e)	Cervidae	MHNF 9017-1979	Fl	25	[30, 31]
Capreolus pygargus (e)	Cervidae	[32]	Fl	32-49	[32]
Capricornis crispus (e)	Bovidae	[33]	Fl	30-45	[33]
Cephalophus maxwellii (e)	Bovidae	[34]	Sb	8-10	[34]
Cephalophus natalensis (e)	Bovidae	NMB 3572	Sb	12-14	[35]
Cephalophus silvicultor (e)	Bovidae	NMB 9279	Sb	43-80	[35]

Cephalophus zebra (e)	Bovidae	NMB 2684	Sb	15-20	[35]
Cervus nippon (e)	Cervidae	[36]	Mx	26-33	[36]
Connochaetes gnou (e)	Bovidae	[37]	Gr	110-160	[37]
Dama dama (e)	Cervidae	[38]	Gr	40-70	[38]
Dicrocerus elegans (f)	Cervidae	[39]	Fl	50	[15, 16, 39]
Dremotherium feignouxi (f)	Moschidae?	NMB MA7925	Fl	15	[7, 40]
Dremotherium guthi (f)	Moschidae?	[41]	Mx	11-16	[41, 42, 43]
Eotragus sansaniensis (f)	Bovidae	[44]	Fl	27	[9, 16, 44]
Gazella gazella (e)	Bovidae	NMB 7035	Mx	15-20	[35]
Gazella dorcas (e)	Bovidae	NMB 11031	Mx	15-23	[13, 35]
Gazella soemmeringi (e)	Bovidae	NMB 8369	Mx	35-46	[35]
Gazella subgutturosa (e)	Bovidae	NMB 2497	Mx	20-43	[45]
Gazella thomsoni (e)	Bovidae	NMB 7571	Mx	17-30	[13, 35]
Gelocus villebramarensis (f)	Gelocidae	[46]	Sb?	14	[40, 46]
Germanomeryx fahlbuschi (f)	Palaeomerycidae	Composite	Fl?	>100	[15, 47, this chapter]
Giraffa camelopardalis (e)	Giraffidae	[48]	Fl	1000-1150	[48, 49]
Hispanomeryx duriensis (f)	Moschidae	Composite	Fl?	5-6	[50, this chapter]
Hoplitomeryx matthei (f)	Hoplitomerycidae	[52]	Sb?	15-20	[51, 52]
Hydropotes inermis (e)	Cervidae	NMB	Fl	8-12	[13, 53]
Madoqua guentheri (e)	Bovidae	[54]	Sb	3-5	[54]
Madoqua kirkii (e)	Bovidae	[55]	Sb	4-5	[55]
Madoqua saltiana (e)	Bovidae	NMB 8064	Fl	3-4	[35]
Mazama nemorivaga (e)	Cervidae	[56]	Sb	8-30	[56, 57]
Moschus moschiferus (e)	Moschidae	NMB 5110	Fl	4-12	[7, 30]
Muntiacus muntjak (e)	Cervidae	NMB 3744	Fl	7-12	[30]
Nemorheadus goral (e)	Bovidae	[58]	Mx	22-35	[58]
Neotragus moschatus (e)	Bovidae	NMB 2122	Fl	4-9	[35]
Odocoileus hemionus (e)	Cervidae	[59]	Fl	70-150	[59]
Odocoileus virginanus (e)	Cervidae	[60]	Fl	45-65	[13, 60]
Okapia johnstoni (e)	Giraffidae	[61]	Fl	200-300	[61]
Oreamno americanus (e)	Bovidae	[62]	Gr	45-135	[62]
Oreotragus oreotragus (e)	Bovidae	NMB 8360	Mx	5-16	[13, 35]
Ourebia ourebi (e)	Bovidae	NMB 8773	Gr	8-21	[35]
Ovis ammon (e)	Bovidae	[63]	Gr	110-182	[63]
Ovis canadensis (e)	Bovidae	[64]	Gr	70-95	[64]
Ovis dalli (e)	Bovidae	[65]	Mx	45-85	[65]
Ozotoceros bezoarticus (e)	Cervidae	[66]	Mx	30-40	[66]
Pantholops hodgsonii (e)	Bovidae	[67]	Mx	26-39	[67]
Procapra gutturosa (e)	Bovidae	[68]	Gr	20-40	[68]
Procervulus dichotomus (f)	Cervidae	[69]	Mx	40	[15, 16, 69]
Przewalskium albirostre (e)	Cervidae	[70]	Gr	180-230	[70]
Pseudois nayaur (e)	Bovidae	[71]	Gr	35-75	[71]
Pudu puda (e)	Cervidae	NMB 2209	Sb	10	[57]
Raphicerus melanotis (e)	Bovidae	NMB 4228	Mx	9-11	[13, 35]
Saiga tatarica (e)	Bovidae	NMB 1908	Gr	35	[30, 72]
Sylvacapra grimmia (e)	Bovidae	NMB 8400	Fl	11-26	[13, 35]
Taurotragus oryx (e)	Bovidae	[73]	Mx	340-600	[73]
Tetracerus quadricornis (e)	Bovidae	[74]	Sb	17-22	[74]
Tragelaphus eurycerus (e)	Bovidae	[75]	Fl	150-220	[75]

Tragulina					
Archaeomeryx optatus (f)	Archaeomerycidae	[76]	Sb?	<5	[76, this chapter]
Bachitherium cf. *curtum* (f)	Bachitheriidae	NMB Qu.B.63	Sb	7-8	[77, 78]
Bachitherium insigne (f)	Bachitheriidae	Coll. Loggia	Fl?	36	[79]
Bachitherium lavocati (f)	Bachitheriidae	Composite	Mx?	7-8	[42, this chapter]
Dorcatherium crassum (f)	Tragulidae	[39]	Sb?	24	[9, 16, 80]
Floridameryx floridanus (f)	Gelocidae?	Composite	Sb?	6-10	[81, this chapter]
Hyemoschus aquaticus (e)	Tragulidae	NMB 8699	Sb	12	[13, 30]
Hypertragulus hesperius (f)	Hypertragulidae	[76]	Mx	<5	[76, 82]
Leptomeryx evansi (f)	Leptomerycidae	[83]	Sb?	3	[83, 84]
Moschiola meminna (e)	Tragulidae	NMB 2588	Sb	5	[9, 13]
Nanotragulus loomsi (f)	Hypertragulidae	[83]	Sb	3	[83, 85]
Tragulus javanicus (e)	Tragulidae	NMB 1891	Sb	1-4	[13, 30]
Tragulus kanchil (e)	Tragulidae	NMB 3002	Sb	4	[86]
Tragulus napu (e)	Tragulidae	NMB 10007	Sb	2	[86]

By analysing a larger sample of 86 fossil and extant ruminant species and a reassessment of 18 anatomical landmarks, this study intends to give a more robust geometric morphometric analysis of the relationship between mandible morphology, phylogeny and feeding habits.

2.2 Material and Methods

2.2.1 Sampling

This analysis is based on mandible specimens of 21 fossil and 65 extant ruminant species from 65 genera (18 fossil and 47 extant), stored pro part in the *Bayerische Staatssammlung für Paläontologie* (Germany), the *Staatliches Museum für Naturkunde Stuttgart* (Germany), the *Université des Sciences et Techniques du Languedoc* (France), the *Paläontologisches Institut und Museum der Universität Zürich* (Switzerland), the *Musée d'histoire naturelle de Fribourg* (Switzerland), and the *Naturhistorisches Museum Basel* (Switzerland), and extracted pro parte from literature (see Table 2).

The juvenile specimens and the specimens from captive individuals have been excluded from the Principal Component Analysis, because they do not always bear all adult characteristics and sometimes display abnormal shape developments, respectively. On the other hand, a low intraspecific variability of the mandible morphology being assumed within wild adult ruminants (personal observation), the sampling included one adult gender-unspecific specimen per species (priority left mandibles). The referred specimens of extant ruminants cover all actual ruminant families and represent two-thirds of the actual generic diversity and one-third of the actual specific diversity (see Table 1). The sampling strategy aims to optimally cover the size range and the feeding categories within all infraorders of extant ruminants (Tragulina and Pecora) (Figure 1 and 2).

The feeding categories are mainly based on those of Janis [13]: Sb, selective browser (fruits and dicotyledonous herbage foliage selector); Fl, folivore (at least 90% of dicotyledonous herbage); Mx, mixed feeder (intermediate feeder with variable diets of dicotyledonous and monocotyledonous plants); Gr, grazer (at least 90% of monocotyledonous grass material).

Regarding the fossil sampling, we focused on primitive Tragulina and Pecora from the Middle Eocene to the Oligocene of Eurasia and North America, and we completed the sampling pool with mandibles of derived taxa from the Neogene of the same area.

Due to badly preserved samples, the analysis of *Floridameryx floridanus*, *Bachitherium lavocati*, *Amphimoschus ponteleviensis,* and *Hispanomeryx matthei* has been based on composite specimens.

The feeding habit attributions of the fossil and extant referred species have been extrapolated from literature (Table 2).

2.2.2 Principal Component Analysis (PCA)

The mandible specimens were photographed in lateral view with a horizontal orientation of the tooth row, using a camera FinePix S6500fc. The software TpsDig version 2.16 [104] was used to digitize 18 anatomical landmarks (representing anatomically, geometrically, and linked homologous points) on each picture, representing the complete mandible shape (including the *ramus* and the angular process).

The selected anatomical landmarks, illustrated in Figure 1, are parameters that were usually included in previous studies on mandible morphology [40,96,97,102,105,106]. In the species without a first lower premolar, the corresponding landmark (anterior part of p1) is superimposed to the next landmark (anterior part of premolar row).

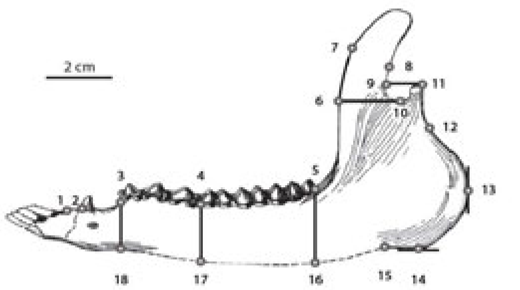


Figure 1. Location of anatomical landmarks used for the PCA on a ruminant mandible (*Leptomeryx evansi*; AMNH 11870). Scale bar: 2 cm. 1, posterior part of c; 2, anterior part of p1; 3, anterior part of premolar row; 4, anterior part of molar row; 5, posterior part of molar row; 6, projection of 10 on the anterior part of the *ramus*; 7, maximum of convexity of the coronoid process; 8, maximum of concavity of the coronoid process; 9, projection of 11 on the posterior part of the coronoid process; 10, mandibular incisure; 11, condylar process; 12, maximum of concavity of the *ramus*; 13, largest part of the angular process; 14, lower part of the angular process; 15, *incisura vasorum*; 16, projection of 5 on the lower part of the *corpus mandibulae*; 17, projection of 4 on the lower part of the *corpus mandibulae*; 18, projection of 3 on the lower part of the *corpus mandibulae*.

The geometric morphometric analysis follows basically the method exposed by several authors [40,107,108,109]. Conventional morphometric methods use linear distance measurements, which are strongly correlated to size.

To eliminate the non-shape variation (size) on the landmark configurations, a General Procrustes Analysis was performed [110]. The coordinates of the mandible landmarks were processed by the least-square method that transforms the landmark configurations, superimposing it (translating, scaling and rotating) on a mean shape (consensus) and resulting in the minimal possible sum of the squares of the distances between the corresponding homologous points [110,111].

Thin-Plate Spline function (TPS) was applied to map the landmark configurations represented as deformation grids, where one mandible is deformed or "warped" into another. Shape differences can then be described in terms of deformation-grid differences depicting the objects [110].

The shape data describing these deformations (partial warps) can be used as shape variables for statistical comparisons of the variation in mandible shape. Principal Component Analysis was applied to the partial warp scores resulting in the Relative Warp Analysis.

In order to achieve equal scaling of each regional shape variation, the distortion parameter of Relative warps (Principal Component axes) was set at $\alpha = 0$.

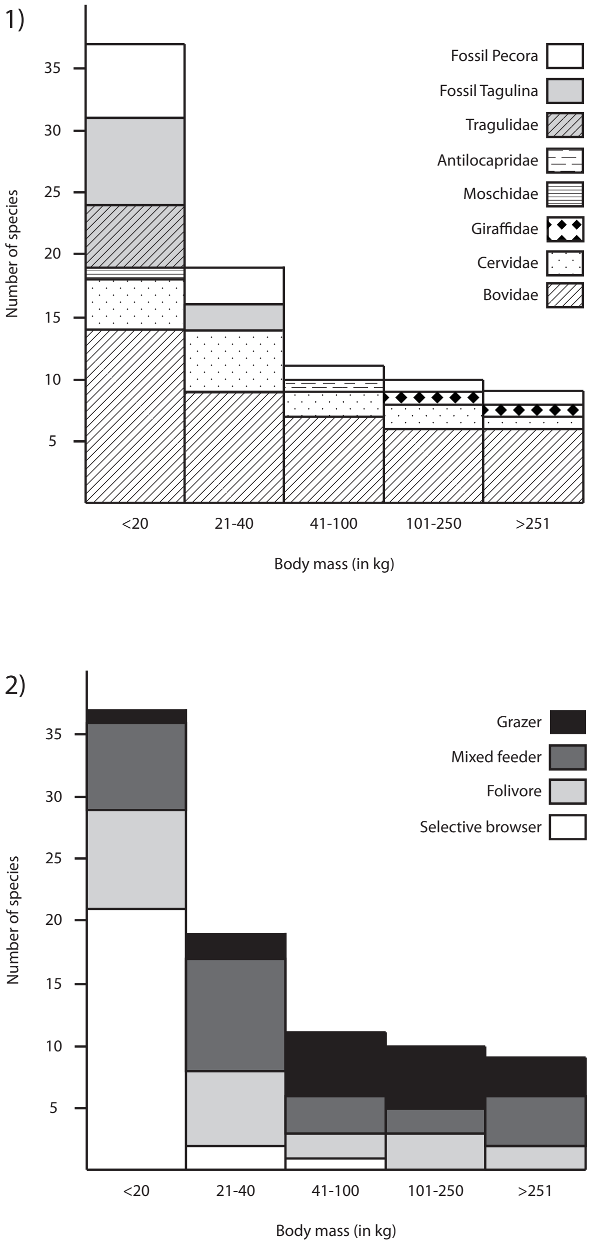


Figure 2. 1) Diagram of body mass distribution of the various species used in the PCA, taxonomically separated by function of their family. 2) Diagram of body mass distribution of the various species used in the PCA, separated by function of their feeding habit. The masses are provided in Table 1. The body mass categories are very similar to those of Jarman [103] and Gagnon and Chew [35].

This procedure is the most suitable for exploratory and taxonomic studies [112]. The superimposing and Relative Warp Analysis were performed using the software TpsRelw version 1.46 [113]. Softwares of the "TPS" series used in this chapter are freeware (http://life.bio.sunysb.edu/morph).

2.2.3 Abbreviations

PCA, Relative Warp Analysis; PC, Principal Component axes; c, canine; p1, lower first premolar. ANSP, *Academy of Natural Sciences Philadelphia* (United States); BSPG, *Bayerische Staatssammlung für Paläontologie* (München, Germany); MHNF, *Musée d'histoire naturelle de Fribourg* (Switzerland); MNCNB, *Museo Nacional de Ciencias Naturales* (Madrid, Spain); NMB, *Naturhistorisches Museum Basel* (Switzerland); MPZ, *Museo Paleontologico de la Universidad de de Zaragoza* (Spain); PIMUZ, *Paläontologisches Institut und Museum der Universität Zürich* (Switzerland); SMNS, *Staatliches Museum für Naturkunde Stuttgart* (Germany); TOR3B, *Toril-3A*; UF, *Florida Museum of Natural History, University of Florida* (Gainesville, United State of America); USTL, *Université des Sciences et Techniques du Languedoc* (Montpellier, France).

2.3 Results

The 18 anatomical landmarks generated 32 axes (PC) for each mandible specimen. The results of the PC's, using shape components, permitted the distinction of different groups of ruminants based on the total difference of the mandible shape. PC1 explained 36.0% and PC2 15.3% of total shape variance (Figure 3).

This means that 51.3% of the total shape variance can be explained without the use of other PC's. On PC1, elongation of the *diastema* is positively associated with the thinning-up of the *corpus mandibulae* on its posterior part and of the *ramus*, and the disappearance of p1 (see shape deformation grids in Figure 3.1).

On PC2, the *diastema* and premolar row elongation, the shallowing-up *corpus mandibulae*, the forward projection of the *ramus*, the salience of the angular process, and the development of the *incisura vasorum* occur in a positive variance (see shape deformation grids in Figure 3.1).

Both PC1 and PC2 are informative from both a phylogenetic (Figure 3.2) and ecologic (Figure 3.3) perspective. These two PC's permit the net discrimination of the extant Ruminantia infraorders, Tragulina and Pecora, by a vertical separation line. The character combination of extant Tragulina (Tragulidae) is a weak *incisura vasorum*, a sub-vertical *ramus*, a short coronoid process inclined backwards, a weakly developed angular process, a stout condylar process, a rather short *diastema* (due to the presence of a p1 in primitive taxa), and a lengthened premolar row. They plot in a small area from -0.042 to -0.023 on PC1 and from 0.004 to 0.013 on PC2, and are exclusively selective browsers (Figure 3, Table 2). On the other hand, the mandible shape of extant Pecora (Bovidae, Cervidae, Giraffidae, Moschidae, and Antilocapridae) is characterized by a strong *incisura vasorum*, a slender *ramus* inclined backwards, a developed coronoid process, a slender condylar process and *corpus mandibulae*, a long *diastema*, and shortened premolar row.

The p1 in fossil ruminants can be either separated from the other premolars, integrated to the premolar row, or absent (see shape deformation grids in Figure 3.1). The extant Pecora mainly plot as positive PC1 values, and negative and positive PC2 values. Bovidae exclusively plot in the negative-values domain of PC2, whereas Cervidae plot preferentially in the positive-values domain (only *Pudu puda* plots in the negative-values domain of both PC1 and PC2, but very close to 0).

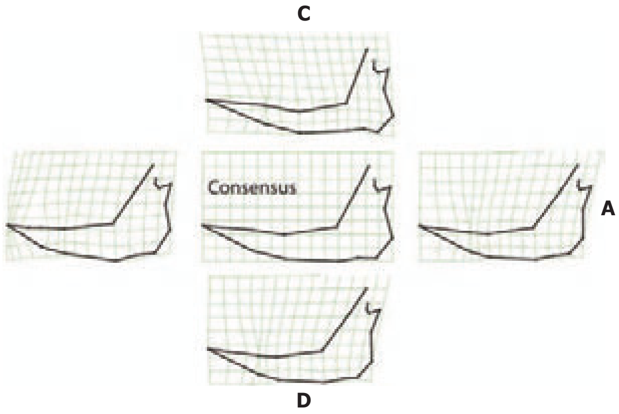
An overlapped area between Cervidae and Bovidae occurred in the lowest positive-values domain of PC2 (from 0 to 0.036). Moschidae and Antilocapridae plot in this overlapped area. Giraffidae plot in the highest positive-values domain of PC2 (> 0.065), and are clearly discriminated from other Pecora (Figure 3.2).

Furthermore, within extant Pecora, the feeding habits are strongly related to variations in the mandible shape (Figure 3.3).

Grazer Bovidae plot exclusively in the negative-values domain, PC2 and selective browser Bovidae mainly plot in the positive-values domain PC2. In positive-values domain PC1 values, a trend from grazers to mixed feeders, folivore and selective browser Bovidae is discriminated by a progressive increase of PC2 values (Figure 3.3 and Figure 4.1 to 4.4). There is a progressive transition

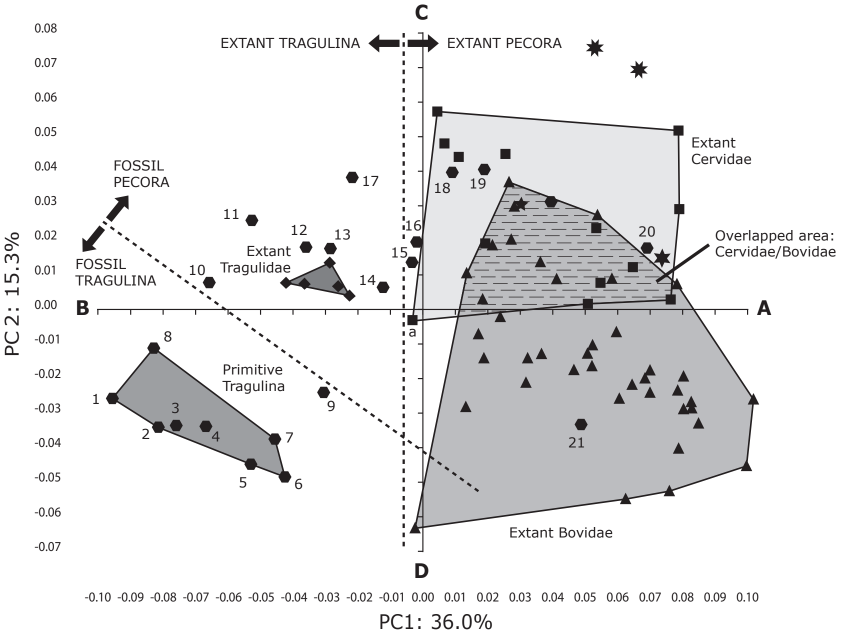
Figure 3 (opposite page). PCA for distortion parameter $\alpha = 0$ of ruminant mandibles obtained from 21 fossil species (*Archaeomeryx optatus*: Shara Murun, Late Eocene; *Hypertragulus hesperius*: John Day, Late Oligocene; *Bachitherium curtum*: Quercy, Oligocene; *Bachitherium* cf. *insigne*: Cereste, Early Oligocene; *Bachitherium lavocati*: Pech Desse and Gaimersheim 1, Late Oligocene; *Leptomeryx evansi*: Cheyenne River, Early Oligocene; *Nanotragulus loomsi*: Muddy Creek, Late Oligocene; *Dorcatherium crassum*: Griesbeckerzell, Middle Miocene; *Gelocus villebramarensis*: Villebramar, Early Oligocene; *Amphimoschus ponteleviensis*: Kapfnach and Languenau1, Early and Middle Miocene; *Amphitragulus elegans*: Montaigu le Blin, Early Miocene; *Dremotherium guthi*: La Milloque, Late Oligocene; *Germanomeryx falhbuschi*: Sandelzhausen, Middle Miocene; *Eotragus sansaniensis*: Sansan, Middle Miocene; *Hispanomeryx duriensis*: Toril-3 and Manchones-1, Middle Miocene; *Dremotherium feignouxi* Montaigu le Blin, Early Miocene; *Procervulus dichotomus*: Rauscheröd, Early Miocene; *Dicrocerus elegans*: Sansan, Middle Miocene; *Bison antiquus*: Holocene) and 65 extant species (see Table 1 and 2). 1) Shape deformation grids representing the mean shape (consensus) and the maximum values of PC1 and PC2. 2) Scatter plots of PC1 versus PC2 with taxonomic characterization. The A-B axis indicates the shape variation of the mandible "warped" from the mean shape (consensus) into the maximum positive (A) and negative (B) deviations in the axis of PC1; the C-D axis the shape variation of the mandible "warped" from the mean shape (consensus) into the maximum positive (C) and negative (D) deviations in the axis of PC2. 3) Same scatter plots as in 2) with diet characterization

1)



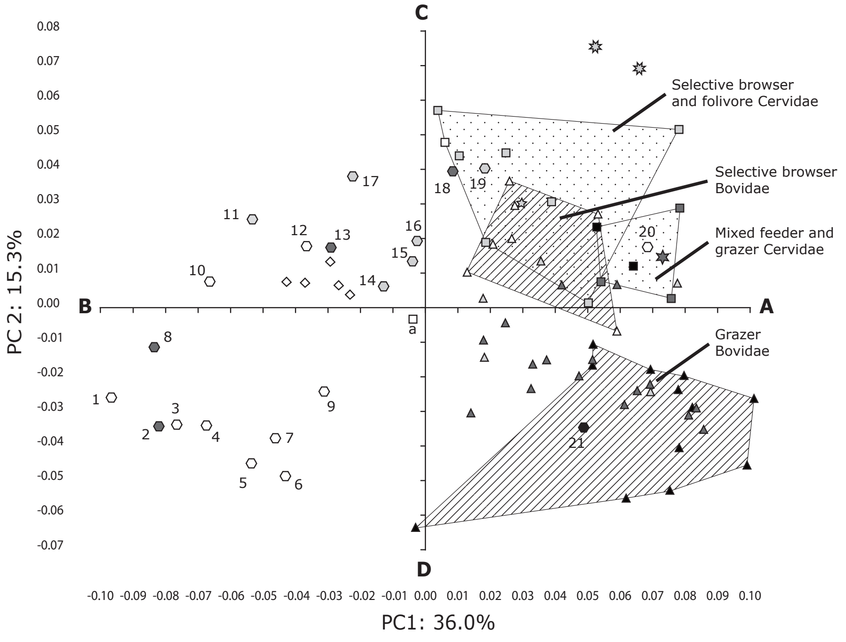
2)

Tragulidae	◆
Cervidae	■
Moschidae	★
Bovidae	▲
Giraffidae	✸
Antilocapridae	✶
Fossils	⬢



1. TRAGULINA, *Archaeomeryx optatus*
2. TRAGULINA, *Hypertragulus hesperius*
3. TRAGULINA, *Bachitherium insigne*
4. TRAGULINA, *Bachitherium curtum*
5. TRAGULINA, *Leptomeryx evansi*
6. TRAGULINA, *Nanotragulus loomsi*
7. TRAGULINA, *Floridameryx floridanus*
8. TRAGULINA, *Bachitherium lavocati*
9. TRAGULINA, *Dorcatherium naui*
10. PECORA, *Gelocus villebramarensis*
11. PECORA, *Amphimoschus pontiliviensis*
12. PECORA, *Amphitragulus elegans*
13. PECORA, *Dremotherium guthi*
14. PECORA, *Germanomeryx fahlbuschi*
15. PECORA, *Eotragus sansaniensis*
16. PECORA, *Hispanomeryx duriensis*
17. PECORA, *Dremotherium feignouxi*
18. PECORA, *Procervulus dichotomus*
19. PECORA, *Dicroceros elegans*
20. PECORA, *Hoplitomeryx matthei*
21. PECORA, *Bison antiquus*

a. PECORA, *Pudu puda*



3)

	Sb	Fl	Mx	Gr
Tragulidae	◇			
Cervidae	□	▨	▩	■
Moschidae		☆		
Bovidae	△	△	▲	▲
Giraffidae		✡		
Antilocapridae			✶	
Fossils	⬡	⬡	⬢	⬢

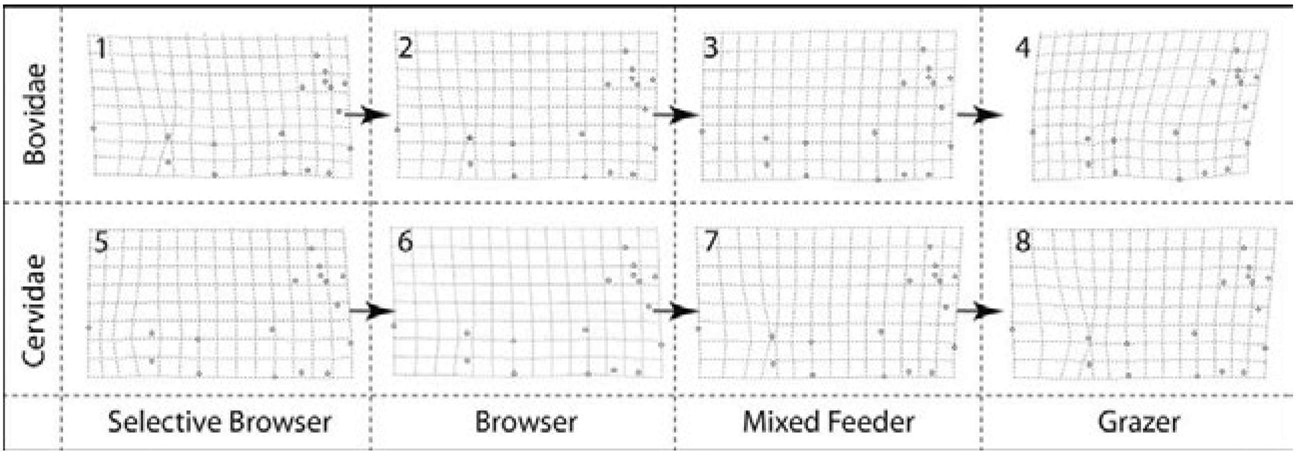


Figure 4. Compilation of shape deformation grids indicating the feeding habit trend within Bovidae (1-4) and Cervidae (5-8). 1, *Cephalophus natalensis*; 2, *Capricornis crispus*; 3, *Gazella subgutturosa*; 4, *Saiga tatarica*; 5, *Pudu puda*; 6, *Muntiacus muntjack*; 7, *Cervus Nippon*; 8, *Przewalskium albirostre.*

from a slender *corpus mandibulae* with an elongated *diastema* and premolar row, a marked *incisura vasorum* and angular process, and subvertical slender *ramus* in the selective browser Bovidae to a stocky *corpus mandibulae* with a short *diastema* and premolar row, a few developed *incisura vasorum* and angular process, and backward enlarged *ramus* in the grazer Bovidae. Within extant Cervidae, the selective browsers and folivores can be differentiated from mixed feeders and grazers (Figure 3.3). Plotted in the highest positive-values domain of PC1 and the lowest positive-values domain of PC2, the mixed feeder and grazer Cervidae is characterized by a less marked angular process, a shorter premolar row, an elongated *diastema*, and a slightly backward inclined *ramus* (Figure 3.3 and Figure 4.12 to 4.15). Moschidae and Antilocapridae, represented by only one species each (*Moschus moschiferus* and *Antilocapra americana*), plot in the same values domain as folivore Cervidae and mixed feeder Cervidae. Only one feeding habit, folivore, characterizes the Giraffidae.

Regarding the fossil taxa, the separation line of fossil Tragulina/Pecora is clear but differs from extant Tragulina/Pecora by an anticlockwise rotation of ca. 45°. The primitive Tragulina form a distinct group plotted exclusively in the quadrant defined by negative values of both PC1 and PC2. The primitive ruminant *Archaeomeryx optatus* has the most negative value of PC1 (-0.097; Figure 3). The three species of Bachitheriidae (*Bachitherium* cf. *curtum*, *B. insigne*, *B. lavocati*) are concentrated in a very low variation of PC1 values (from -0.068 to -0.082; Figure 3). The Miocene Tragulidae *Dorcatherium crassum* plots between the primitive Tragulina and the extant Tragulidae.

The supposed Gelocidae *Floridameryx floridanus* is very close to the primitive Tragulina *Leptomeryx evansi* and *Nanotragulus loomsi* (Figure 3). *Gelocus villebramarensis* has the most negative value of PC1 (-0.066; Figure 3) within Pecora and is somewhat isolated, but with a positive value of PC2 (0.008; Figure 3) that differs from the negative-values domain of primitive Tragulina. Most of the Miocene Pecora species plot between *Gelocus villebramarensis* and extant Cervidae area. Even *Eotragus sansaniensis*, the oldest known true Bovidae [44,114], plots in this transitional zone. However, the Early/Middle Neogene Ruminantia *Dicroceros elegans* and *Procervulus dichotomus* plot within the values domain of extant Cervidae. Only the Pliocene Hoplitomerycidae *Hoplitomeryx matthei* plots in a totally singular location, close to extant Antilocapridae. Contrary to extant taxa, the distinction of feeding habits among the fossil specimens is unclear, except for the grazer *Bison antiquus*, that is a subactual Bovidae plotted logically within extant grazer Bovidae.

2.4 Discussion

2.4.1 Phylogeny

As suggested by Mennecart et al. [40], the results of the PCA confirm that the mandible shape of ruminants can be used to distinguish the main taxonomic groups, especially at the infraorder level (Tragulina *versus* Pecora). However, mandible shapes of primitive Tragulina and Pecora differ from those of their extant relatives (Figure 3.2). Primitive Tragulina form a homogenous group plotted in the quadrant defined by both negative PC1 and PC2 values. They are characterized by a p1 separated from other premolars, a short *diastema*, a thick *corpus mandibulae*, a developed angular process, and a wide vertical *ramus*. The mandible of the primitive Tragulina is close to the basic shape observed in ruminant evolution. *Archaeomeryx optatus*, often considered as the most primitive grade of assigned ruminants [76,85,115,116,117], has the lowest PC1 value. This ruminant possesses the characteristic

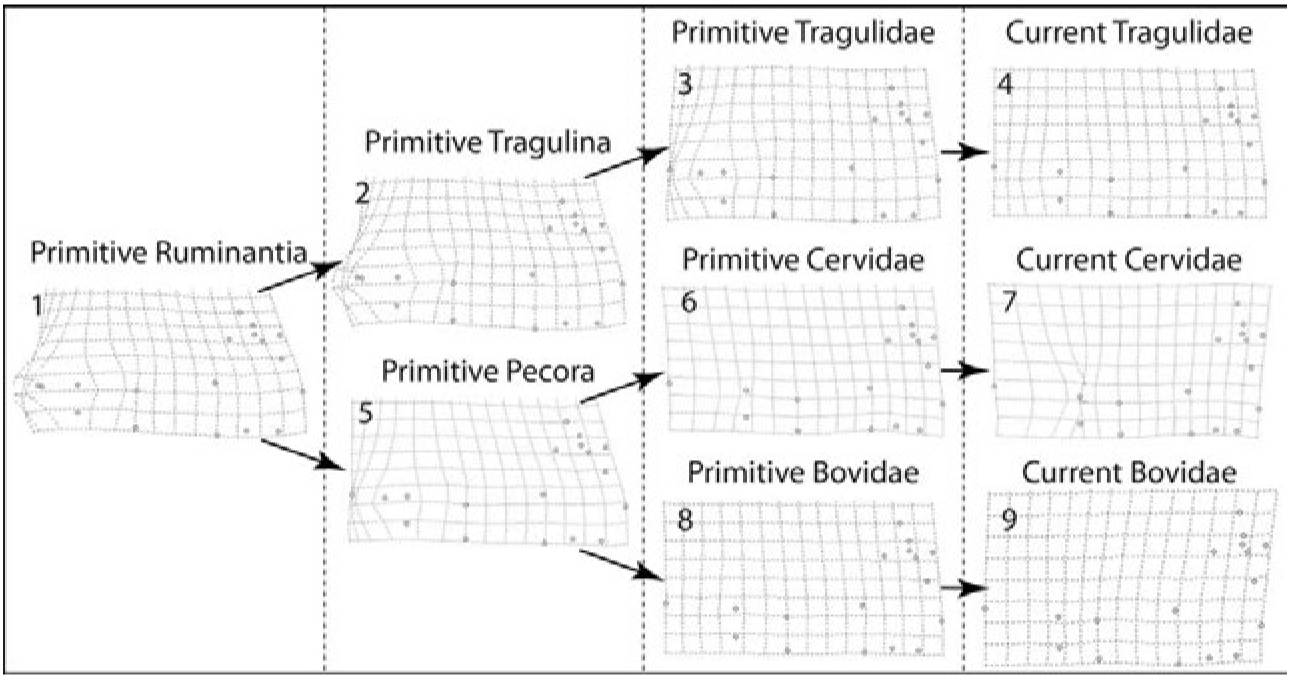


Figure 5. Compilation of shape deformation grids indicating the evolutionary trends in the mandible shape from the primitive grade *Archaeomeryx optatus* (2-4 for Tragulina and 5-9 for Pecora). 1, *Archaeomeryx optatus*; 2, *Hypertragulus hesperius*; 3, *Dorcatherium naui*; 4, *Tragulus napu*; 5, *Gelocus villebramarensis*; 6, *Procervulus dichotomus*; 7, *Alces alces*; 8, *Eotragus sansaniensis*; 9, *Gazella gazella*.

“fused” cubonavicular bone, but upper incisors are persistent, the median metapods are unfused, and the lateral ones are not reduced [115]. *Bachitherium* species are concentrated in a small PC1 range values. Regarding PC2 values, *Bachitherium lavocati* is separated from the very close *B. curtum* and *B. insigne*. This medium size Bachitheriidae is the later known *Bachitherium* (MP28). It has an elongated *diastema*, as of the larger *B. insigne* (Sudre 1986). Because *Brachitherium curtum* and *B. insigne* have a similar biostratigraphic range and have been discovered in some similar localities, Wehrli [119] suggested a synonymy of these two species and a marked sexual dimorphism. However, the *diastema* length and the proportions of the postcranial remains indicate obvious different ecological niches. *Bachitherium curtum* lived in wooded humid area whereas *B. insigne* lived in light forest habitats [78]. According to Sudre [120], the most suitable strategy is to maintain two distinctive species, despite the similarity of the mandible shapes.

The mandible shape of *Dorcatherium crassum* discriminates it from primitive Tragulina, but it also differs from extant Tragulidae by having a p1, a shorter *diastema*, and a stockier *corpus mandibulae*. Extant Tragulidae form a homogenous group composed only of selective browsers, but it is impossible to determine if the consistency of the PC values are controlled by a strong taxonomic or feeding affinity (Figure 3). As a result, a general trend within Tragulina is observed from primitive Ruminantia (*Archaeomeryx optatus*), primitive Tragulina (*Hypertragulus hesperius*), to primitive Tragulidae (*Dorcatherium crassum*), and to extant Tragulidae (*Tragulus napu*) (Figure 5.1 to 5.4). The mandible evolves to a slender shape, a lengthened *diastema*, a loss of p1, a salient mandible process, and a backward inclined *ramus*.

The Late Miocene Pseudoceratinae *Floridameryx floridanus* of North America plots within the primitive Tragulina in the PCA (Figure 3.2). Webb [81] considered this taxon as a primitive Ruminantia by having an upright lower canine and no appendages, belonging to Gelocidae on the basis of basicranial features and premolar structures. However, Métais and Vislobokova [85] argued that Pseudoceratinae, including *Pseudoceras*, are probably not Gelocidae, because the related postcranial and molar features are closer to those of *Moschus* than *Gelocus*. Pseudoceratinae have a combination of primitive and derived features that should be assigned to another family. Moreover, Gelocidae seem to be restricted to the Early Oligocene of Europe [121]. Hooker and Weidmann [122] argued that the unique and lost specimen of *Gelocus*? *minor* does not come from Mormont (Late Eocene), but from another unknown locality, dating from after the Grande-Coupure. “*Gelocus*” *whitworthi* from the African Miocene differs from European *Gelocus* species by having a well-developed metastylid, an elongated and forked postentocristid, and a marked *Palaeomeryx* fold on the lower molars [17,123,124, personal observation]. Early Miocene *Gelocus gajensis* from Asia clearly displays Lophiomerycidae characteristics such as a rounded metaconid, open trigonid and talonid, and a crested third basin on lower molars [125, personal observation].

Gelocus villebramarensis has the most negative PC1 value of the Pecora (Figure 3.2) and is considered as Protopecora or the most primitive Pecora [85,126,127]. It is defined by having a short *diastema* and elongated premolars with a relatively large *corpus mandibulae* in comparison with extant Pecora, and a p1 either isolated or adjacent to premolars (Figure 5.5). Tooth p1 is adjacent to premolars in *Amphitragulus elegans* and *Dremotherium guthi*, and is absent in other Pecora. According to the evolutionary trend (Figure 5), the loss of p1 is associated to a lengthening of the *diastema*. Based on the PCA (Figure 3.2), *Gelocus villebramarensis* seems closer to "tragulid-like" taxa than extant Pecora. However, it clearly differs from primitive Tragulina by having a more elongated *diastema* and a more slender mandible shape.

Regarding the genus *Dremotherium* (Late Chattian to Aquitanian), the premolars become shorter and the *corpus mandibulae* more slender. The two species, *D. guthi* and *D. feignouxi*, have a similar PC1 value and the difference on the PC2 is probably related to their distinctive feeding habits (Figure 3). The Miocene referred specimens form a homogeneous group (Figure 3). Miocene *Procervulus dichotomus* and *Dicrocerus elegans* cannot be distinguished from the extant Cervidae. An evolutionary trend can be observed in the shape variation of the cervid mandibles from the primitive Ruminantia (*Archaeomeryx optatus*), to the primitive Pecora (*Gelocus villebramarensis*), the primitive Cervidae (*Procervulus dichotomus*) and the extant Cervidae (*Alces alces*) (see Figure 5.1, 5.5 to 5.7). The mandible becomes very slender with a more marked *incisura vasorum* and an elongated *diastema*. The premolar row is slightly reduced and the molar row slightly elongated. The mandible process is smaller, but more salient, and the *ramus* is more backward inclined.

Other fossil Pecora, condensed between the primitive *Gelocus villebramarensis* and extant Cervidae, are rather removed from extant relatives, except for the subactual *Bison antiquus*, which has a logical position within grazer Bovidae, and the insular Pliocene *Hoplitomeryx matthei*, which is isolated. The most suitable explanation is that the mandible shapes of the Early Miocene ruminants are still primitive and quite analogous. Furthermore, Palaeomerycidae are extinct and the extant Moschidae diversity is not representative of the past Moschidae.

In the literature, no consensus about the family attribution of *Amphitragulus* and *Dremotherium* has been suggested. These true Eupecora, which appeared during the Late Oligocene [41,79], have been considered as Palaeomerycidae [17,128], Cervidae [129,130], and most often as Moschidae [7,41,80,131]. The attribution to Moschidae is mostly based only on the presence of an elongated saber-like upper canine and the absence of appendages. But these features are observed in all European ruminants until the Burdigalian. *Amphitragulus* and *Dremotherium* probably do not belong to extant family, but to a transitional one, which has been replaced consecutively due to the migration of true Cervidae (*Ligeromeryx praestans* and *Procervulus praelucidus*) related to the *Brachyodus* event during the Burdigalian [69,132,133].

Many authors argued that *Hoplitomeryx* and *Amphimoschus* belong to the family Hoplitomerycidae on the basis of a large, bicuspid third lobe on m3 in which the median valley between both cusps is open posteriorly. Both genera share a large, inflated and smooth surfaced auditory bulla, lack a *Palaeomeryx* fold, and have fairly high crowned molars [17,52,134]. However, in the PCA, these two species do not plot together, *Amphimoschus artenensis* plotting close to *Amphitragulus elegans* and *Hoplitomeryx matthei* within the extant Cervidae area (Figure 3). After Gentry [135] and Gentry et al. [80], *Amphimoschus* seems to be related to Bovidae. On the other hand, *Hoplitomeryx* is an insular mammal having singular characteristics, such as five horns. The resemblance between these two genera is probably due to convergences.

Eotragus sansaniensis is the oldest true Bovidae known [80,195]. Solounias et al. [195] consider it as an ancestor of the extant Boselaphini (*Tetracerus quadricornis* and *Boselaphus tragocamelus*). These three species have quite similar PC2 values with a rather large range of PC1 values that confirm the primitive stage of *Eotragus sansaniensis*. An evolutionary trend can be observed in the shape variation of the bovid mandibles from the primitive Ruminantia (*Archaeomeryx optatus*), to the primitive Pecora (*Gelocus villebramarensis*), the primitive Bovidae (*Eotragus sansaniensis*) and the extant Bovidae (*Gazella gazella*) (see Figure 5.1, 5.5, 5.8 and 5.9). The mandible becomes larger with a weakly marked *incisura vasorum* and an elongated *diastema*. The premolar row is reduced and the molar row slightly elongated. The mandible process is smaller, but more salient, and the *ramus* is more backward inclined.

Phylogenetic relationships between Giraffidae and primitive Palaeomerycidae are still under discussion. The most recent analysis suggests that they are a sister group [6]. Extant Giraffidae plot totally in isolation due to the extreme lengthening of the *diastema* and the high gracility of the mandible shape. The PCA does not identify a phylogenetic or feeding control of the singular and highly homogeneous mandible shape, because extant Giraffidae are exclusively folivore. After the dental micro-wear analysis of Franz-Odendaal and Solounias [138], the giraffid *Sivatherium hendeyi* from Early Pliocene of South Africa was identified as a mixed feeder. Regrettably, neither direct observation nor literature allowed us to consider this taxon in our analysis. However, an illustration of *Sivatherium hendeyi* from Alleyne Nicholson [138, figure 245] shows a very slender mandible with an elongated *diastema* very similar to those of *Giraffa camelopardalis* and *Okapia johnstoni*. Cervidae and Bovidae are highly diversified mammal families, and the specimens of these families are the most abundant in our PCA (Table 1). The related species analysed present a very large range of body mass and feeding habits (Figure 2., Table 1). Cervidae mainly plot in positive-values domain of PC2 and Bovidae in the negative-values domain. The cervids generally have a more slender mandible with an elongated *diastema*, a proportionally larger premolar row, a marked *incisura vasorum*, and a smaller but more salient mandible process (Figure 5). However, a mixed area between these two families is observed. This area groups the most massive Cervidae and the most slender Bovidae.

The extant Moschidae *Moschus moschiferus* and the past *Hispanomeryx duriensis* have similar PC2 values. But, as for *Eotragus sansaniensis*, the respective PC1 values permits us to make the distinction between fossil and extant species.

2.4.2 Feeding Habits

The PCA of this chapter reveals the general trends in the mandible shape variation as related to feeding habits (selective browser, folivore, mixed feeder and grazer) especially of extant ruminants, but less obviously in fossil ruminants. The families represented by a unique representative or with an uncertain feeding habit do not discriminate consistent feeding trends (Antilocapridae, Archaeomerycidae, Gelocidae, Hoplitomerycidae, Hypertragulidae, Leptomerycidae, Moschidae, Palaeomerycidae). Within primitive ruminants, the feeding habit related to mandible shape is not apparent. Particularly, the mandible shape of primitive Tragulina does not permit us to differentiate different feeding behaviours (Figure 3.3). For example, according to a dental micro-wear study of Blondel [77], *Bachitherium curtum* was a selective browser feeding on leaves and fruits, and *Bachitherium insigne*, which was a larger form, could have fed on leaves. However, no obvious distinction in mandible shape is observed (Figure 3.3). *Bachitherium lavocati* show a very faint difference in mandible shape compared with other *Bachitherium* species (especially the ratio between the molars row length and the *diastema* length). This taxon, based on postcranial remains analysis, lived in more open area [78] and could have included more grass in its diet, such as the contemporaneous *Bedenomeryx lamilloquensis* and *Dremotherium guthi* [43].

Within extant Pecora, an unambiguous trend of the feeding habits, from selective browser to grazer, is observed in Bovidae (Figure 3.3 and Figure 4.1 to 4.4), which is assumed to be a good proxy for ecomorphological analyses [90,91,92,93]. The shortening of the *diastema* and of the premolar row (compared to the molar row), associated with a smooth *incisura vasorum* and a faint angular process, leads to a thickening of the *corpus mandibulae* that correlates with the high molar crown, thus with an increase of the hypsodonty index (high crown/molar length ratio) [97]. The strongly hypsodont dentition permits feeding on grass containing abrasive phytoliths, typical of grazer habit [97]. Moreover, the backward tilting of the *ramus*, also observed in grazer Bovidae, permits them to have a better lever arm of the mastication muscles located on the *ramus* (masseter, temporalis). These muscles strongly contribute to mastication [139]. Consequently, the association of a high hypsodonty index, a stock mandible and an efficient lever arm characterize the tough food eater Bovidae. These features are notably well-developed in the subactual grazer *Bison antiquus*. Extant Cervidae do not show such a clear feeding trend as within the Bovidae, but we can differentiate between the group formed by the selective browsers and the folivores, and the group formed by the mixed feeders and the grazers. Even if it is not so marked within the Bovidae, Cervidae with the stockiest mandibles feed on more fibrous vegetables, such as grass. The difference of consistency of results between these two families is probably due to the fact that few Cervidae have been analyzed in comparison to Bovidae (Table 1), and that Bovidae possess a larger biodiversity range than Cervidae. In the PCA, the two analyzed Giraffidae are folivores and are clearly discriminated. The extinct genus *Sivatherium* (not analyzed in this chapter) shows a mandible quite similar to extant Giraffidae by having an extremely elongated *diastema* and a rather slender shape. However, this genus has been considered as a mixed feeder by Franz-Odendaal and Solounias [137] and in the illustration of Alleyne Nicholson [138, Figure 245], the premolar row is reduced, the *corpus mandibulae* is distally massive, and the *ramus* is inclined backwards. These characteristics, similar to those observed within the mixed feeder Bovidae, suggest that Giraffidae also show an analogous trend of the mandible shape variation related to feeding habits.

Regarding the fossil taxa, the correlation of the mandible shapes with the feeding habits is much less apparent, probably due mainly to the feeding specializations being less developed. For example, the referred *Dremotherium* species have quite a similar mandible shape, except a slightly more slender *corpus mandibulae* in *D. feignouxi* (Figure 3). However, according to postcranial and dental micro-wear studies [78,43], *Dremotherium guthi* probably lived in open forests and fed on grass, whereas the postcranial remains of the later and larger *D. feignouxi* reveal an animal living in open areas [140]. Indeed, the latter has an elongated cervical [17,130] as in extant folivore antelopes *Litocranius walleri* and *Ammodorcas clarkei* [17,35,141]. We suggest a similar diet for *D. feignouxi*.

2.5 Conclusion

The ruminant mandible shape is a useful proxy to differentiate the main ruminant taxonomic groups through time. Primitive Tragulina possess a stockier mandible than primitive Pecora, and it is also the case for the extant representatives. In both cases, the more negative PC1 values correspond to more primitive mandible shapes and the evolutionary trend led to a more slender form with a more elongated *diastema* and a lost p1.

First assigned to Gelocidae, *Floridameryx floridanus* seems to belong to Tragulina. However, without taking into account other morphological and morphometrical characteristics, the PCA does not supply sufficient information to discuss family level taxonomy. Within extant Pecora, Giraffidae differ by having an extremely elongated *diastema*. Cervidae are generally more slender than Bovidae, but an overlapped area between these two families groups the most massive Cervidae and the most slender Bovidae together.

Regarding the feeding habits, the well-diversified extant Bovidae show that an unambiguous trend from selective browser to grazer relates to the variation in mandible shape. The terminal state of this trend shows the combination of a high hypsodonty index, an elongated molar row compared to the premolar row, an enlarged *corpus mandibulae*, a stockier mandible, and a more efficient lever arm of the mastication muscles (masseter and temporalis) that permits feeding on tough food such as grass. This trend is also roughly observed within non-Bovidae Pecora, but to a lesser extent. On the other hand, confident feeding category discrimination for fossil taxa cannot be clearly identified. Only the cervid *Dicroceros elegans* and the subactual bovid *Bison antiquus* show mandible shapes in coherence with the feeding habits observed within extant representatives.

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3 - MATERIAL AND METHODS

3.1 Material

All the referred material used for this study is related to European ruminants, with a focus on Swiss localities, and housed in the main European Natural History Museums. This material has been partly published in the 19th and 20th centuries (e.g., Stehlin 1901, 1914; Blondel 1997), but no recent work includes any revisions or updated results, except for the work of Becker et al. (2004) and Mennecart et al. (2011) who revised the species *Iberomeryx minor,* and Becker et al. (2010) and Mennecart et al. (2012) who revised the genera *Dremotherium*, *Andegameryx*, *Amphitragulus* and *Babameryx*. Additionally, the newly collected specimens and data are integrated, mainly those from the excavations along the future route of the Transjurane highway (Canton Bern and Canton Jura, Switzerland). These excavations were partly led by the 'Section d'archéologie et paléontologie' (Porrentruy, Canton Jura, Switzerland) and myself. The listings of the referred specimens are included separately into the different chapters of this manuscript.

3.2 Locality distribution

The major Western European basins, including 281 localities from MP21 to MN4 with ruminant remains, have been considered in this study (Fig. 1, Tab. 1). Specimens from 159 localities were directly observed in various institutes, museums, and privates' collections. Their biostratigraphic correlations were mainly obtained from the literature. Regarding the Swiss localities, 68 were directly considered. These localities are generally well dated by small mammals (Mayo 1980; Engesser & Mayo 1987; Engesser 1990; Engesser & Mödden 1997). The main Swiss localities, in terms of diversity, richness and preservation, are described below and shown in Figure 2:

3.2.1 Oligocene

Welschenrohr (Swiss national grid reference ~607.000/~237.000) corresponds to a sandy level from the Molasse Alsacienne Formation (USM = Untere Süsswasser Molasse = Lower Freshwater Molasse) of the Jura Molasse (Becker 2003). Greppin (1870) attributed an early Chattian age to this locality.

Lovagny14 (French Molasse Basin) corresponds to a bluish calcareous marly level from the USM and has been dated to the European Reference Level MP23 by Engesser & Mödden (1997).

Soulce (586.275/239.975) corresponds to a lacustrine lithographic limestone bed from the Molasse Alsacienne Formation and has been dated to European Reference Level MP23 by Becker (2003) and Mennecart et al. (2011).

Court (~593.706/ ~232.706) corresponds to a dark marly level from the USM (Untere Süsswasser Molasse = Lower Freshwater Molasse) of the Jura Molasse. It is preliminarily dated to the European Reference Level MP23 (pers. obs.).

La Beuchille (593.125/244.580) belongs to the Molasse Alsacienne Formation and is dated to the European Reference Level MP24, slightly older than Heimersheim (O. Maridet, pers. comm.). It has a similar age as the nearby localities Poillat and Pré Chevalier.

Pré Chevalier (594.650/244.600) belongs to the Molasse Alsacienne Formation. It is dated to the European Reference Level MP24, slightly older than Heimersheim (O. Maridet, pers. comm.). It has a similar age as the nearby localities La Beuchille and Poillat.

Poillat (594.795/244.510) belongs to the Molasse Alsacienne Formation. It is dated to the European Reference Level MP24, slightly older than Heimersheim (O. Maridet, pers. comm.). It has

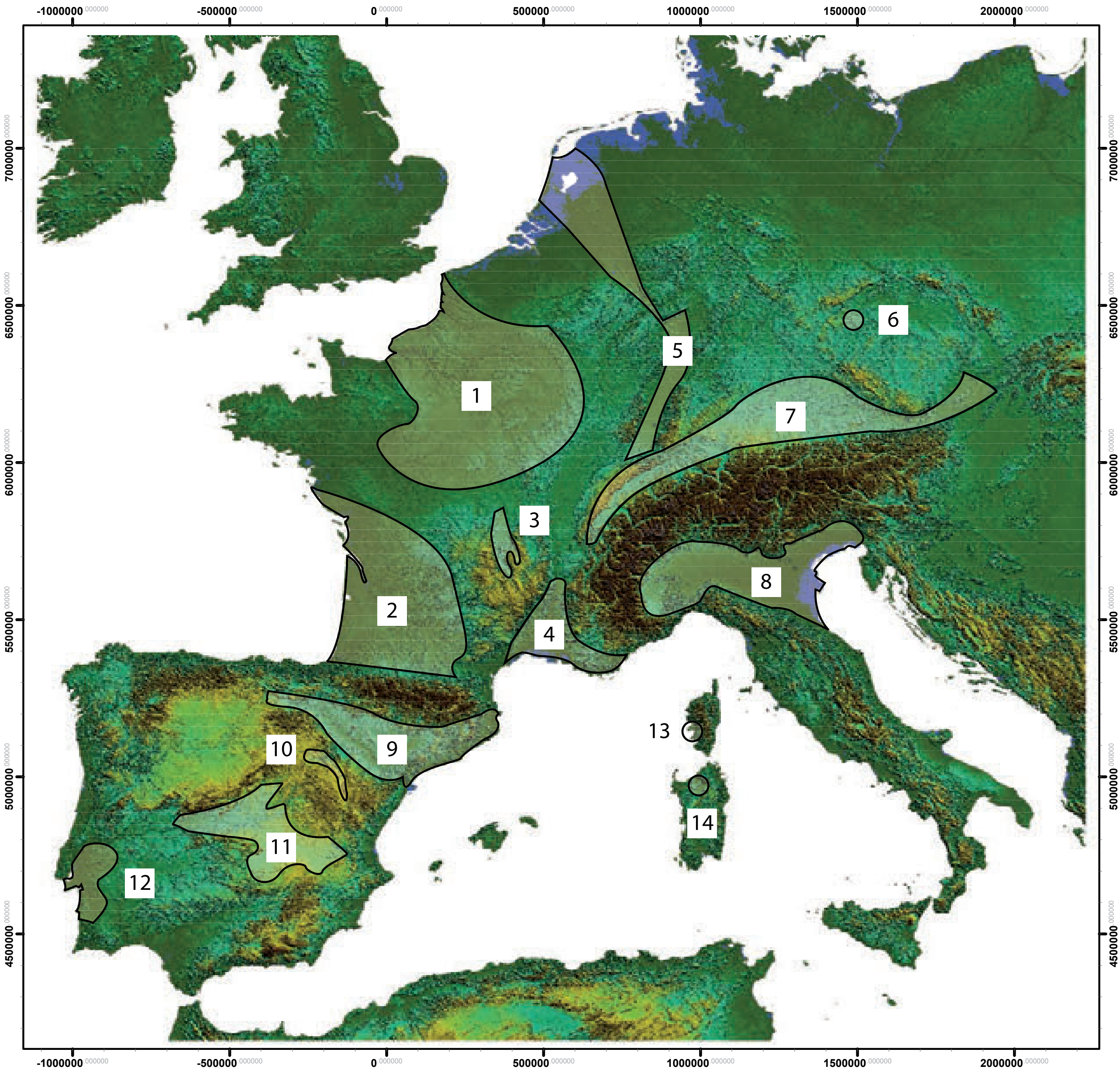

Figure 1 Location of the Western European sedimentological basins containing Oligocene and Early Miocene ruminant localities (modified from Jarvis et al. 2008). **1** Paris Basin, **2** Aquitaine Basin & Quercy, **3** Limagne Graben, **4** Aix Basin, **5** Rhine Graben, **6** Doupoov Hill, **7** Molasse Basin, **8** Pô Basin, **9** Ebro Basin, **10** Calatayud-Montalban Basin, **11** Taj Basin, **12** Tagsu Basin, **13** Vazzio Basin, **14** Oschiri Basin.

a similar age as the nearby localities Poillat and Pré Chevalier.

Grenchen1 and ***Grenchenbergtunnel*** (596.500/228.875) correspond to fossiliferous levels of the Molasse Alsacienne Formation dated to the European Reference Level MP24 (Engesser & Mödden 1997).

Bumbach (636.075/185.500) is located in the Subalpine Molasse, within the Honnegg-Bäuchlen fan. It has been dated by small mammals to the European Reference Level MP25 (Engesser & Mödden 1997).

Moutier Gare (596.650/228.200) belongs to the Molasse Alsacienne Formation. Its age is late Rupelian close to MP24-25 (Berger pers. comm.).

Oensingen Ravellen (620.960/238.180) belongs to the Knauermolasse Formation (synonym of the Aarwangen Molasse and lateral equivalent of the Molasse Alsacienne Formation within the the eastern Jura Molasse and the distal Plateau

Table 1 Oligocene and Early Miocene Western European localities containing ruminants of respective age. The data come from either direct observation in museums or literature (e.g., Pomel 1854; Viret 1929; Richard 1946; Astre 1954; Bergounioux & Crouzel 1968; Ginsburg 1969; Hartenberger et al. 1970; Heissig 1978; Hugueney et al. 1983; Sudre 1986; Brunet & Sudre 1987; Engesser & Mayo 1987; Fejfar 1987; Ginsburg et al. 1987; Heissig 1987; Hugueney et al. 1987; Remy et al. 1987; Sudre & Blondel 1996; Engesser & Mödden 1997; Hugueney 1997; Gentry et al. 1999; Ginsburg 1999; Rössner & Rummel 2001; Merle et al. 2002; Aguilar et al. 2003; Ferrandini et al. 2003; Van der Made 2008; Ménouret & Guérin 2009; Antoine et al. 2011). M, locality known by material in museum; L, locality only known by literature.

1 Paris Basin

France

Artenay	MN4	M
Blois	MN1	M
Chevilly	MN4	M
Chilleurs aux bois	MN3b	M
Chitenay	MN3	M
Espira du Conflent	MN3	L
Etampes	MP24	L
Fertais Alais	Stampian	L
Gas	MP24	L
Itteville	MP24	L
La Brosse	MN3	L
Le Gibet à Etampes	MP24-25	L
Les Beilleaux	MN3	L
Maintenon	MP24	M
Mauvières	MN3	L
Neuville au bois	MN3b	L
Ormoy	upper Stampian	L
Pierrefitte	upper Stampian	L
Pontigné les Buissonneaux	MN3	L
Sambin	MN4-5	M
Selles sur Cher	MN2b	M
Vayres-sur Essonne	MP23?	L

2 Aquitaine Basin & Quercy

France

Aillas	Stampian?	L
Aubrelong 1	MP21	L
Aucamville	upper Stampian	L
Auterive	MN1	M
Bach	Sannoisian	M
Barbothan les thermes	MN2b	M
Beaupuy	Aquitanian	M
Belgarric	MP25	L
Bezian	MN4	L
Bourret	upper Stampian	L
Cadillac	Stampian	L
Cavalé	MP22	L
Caylux	Sannoisian	M
Chidrac	MP28/30	M
Coulou	MP23	L
Dieupentale	MP29/30	M
Domilhiac	upper Stampian	L
Escamps bei Halbenque	MP25	M
Espeyrasse	MP26	L
Gannat	MP30	L
Gibel	MN1	M
Ginestou	midlle Stampian	L
Goyranns	Aquitanian	L
Gratentour	Aquitanian?	M
Grepiac	Aquitanian	M
Hautevigne	upper Stampian	M
Itardie	MP23	M
Ithier près Tournon	middle Stampian	M
La Comberatière	MP29	M
Lacroix Falgarde	Aquitanian	L
La Deveze	MP26	L
La Milloque	MP29	M
La Plante 2	MP22	L
La Plante 3	MP25	L
La Romieu	MN4	M
La Tuque près Ladignac	Early Oligocene	M
Lalbenque près d'Escamps	MP25	M
Larromieu	MP24-27	M
Latou	Stampian	L
Laugnac	MN2b	L
Le Garouillas	MP25	M
Les Bourgadots	middle Stampian	L
L'Estaque	MP26?	M
Mas de Got	MP22	L
Mas de Pauffie	MP26	L
Mege	MP23	L
Moissac vallon de la Madeleine	MN1	M
Monségur	Stampian	L
Montagnac	MN1/2a	M
Montclar de Quercy	MP23	M
Montclar de Quercy	MP25	M
Montgiscard	upper Stampian	L
Montréal du Gers	MN4	M
Mouillac	Eocene-Oligocene	M
Mounayne	MP23	L
Murs	MP23	M
Nassiet près Amou	MP24-25	M
Paulhiac	MN1	M
Pech Crabit	MP23	L

Pech David	Aquitanian	M
Pech Desse	MP28	M
Pech du Fraysse	MP28	M
Pechbonnieu	MN1	M
Phalip	MP25	L
Pompignan	upper Stampian	M
Portal	MP28	L
Portet sur Garonne	Aquitanian	L
Pouvourville	Aquitanian	L
Puylaurens	Sannoisian	L
Rabastens	MP24	M
Raynal	Eocene-Oligocene	M
Real	upper Stampian	M
Renneville		M
Ressens		M
Rigal-Jouet (Caylus)	MP25	L
Roqueprune 2	MP23	L
Ruch-Ravet	MP21	L
Saint Loup Cammas	Aquitanian	M
Saint Martin de Castillon	MP23	L
Sainte-Gemme	Stampian	M
Saint-Ferme	Stampian	L
Saint-Géry	MP24/25	M
Saint-Martin-de-Casselvi	MP23	L
Savenes	MP24-27	M
Tauriac	upper Stampian	L
Thezels	MP30	M
Thil	MN3	M
Tourliac	upper Stampian	L
Tournon	MP23-25	M
Vallon d'Auradou près Pennes	MP24-27	M
Venerque	MP28-30	M
Verdun sur Garonne	upper Stampian	L
Villebramar	MP22	L

3 Limagne Graben

France

Antoingt	MP25	L
Authezat	MP25	L
Benissons-Dieu	MP23/25	L
Boudes	MP25?	L
Chaptuzat	MP25?	L
Châtelguyon	Aquitanien?	L
Coderet	MP30	M
Cournon	MP28	M
Crèchy 1-2	MP30	L
Crèchy-Bas	MP29	L
La Sauvetat	MP25	M
Langy	MN2a	M
Les Chauffours	MP29	M
Mailhat	MP23/28	L
Montaigu le Blin	MN2a	M
Nonette	MP25?	L
Peublanc	MP30	L
Romagnat	MP29	L
Ronzon	MP21	M
Saint Gerand le Puy	MN2a	M
Saint Menoux	MP26	L
Saulcet	MN1	M

4 **Aix Basin**

France

Beaulieu	MN3/4	L
Boujac	MP28	L
Cereste	MP23/24?	M
Les Milles	MP26	L
Marseille	MP26	M
Saint André	MP26	M
Saint Henri	MP26	M
Sarèle	MP28	L

5 Rhine Graben

Germany

Seckbach	MP22-25	L
Weinheim	MP22	L

6 Doupov Hill

Czech Republic

Detan	MP21-23	M

7 Molasse Basin

France

Lovagny	MP23	M
Pyrimont Challonges	MN1	M

Switzerland

Aarwangen	MP27	M
Alstatten	MN2	M
Baden	Oligocene	M
Balm	MP22	M
Balsthal Bännli	MP28	M
Basel St Jacob	MP29	M
Basel-Gellerstrasse	Chattian?	M
Benken	MN3/4	M
Bierkeller Reichenbach	MN1-3a	M
Boningen	MP27	M
Brochen Flüh	MP29	M
Bruttelen	MN3a	M
Buchberg	MN3-4	M
Bumbach	MP25	M

Champvent	MP24-27	M
Chavornay	MP24-27	M
Court	MP23	M
Dornachbrugg (Birs)	MP22	M
Ebnat-Kappel	MP28	M
Engehalde Alte	MN2b	M
Engehalde Neufeld	MN2b	M
Eriz Losenegg	MP27	M
Estavayer (Fribourg)	MN2-3	M
Glovelier	MN4	M
Grenchen1	MP24	M
Küttigen	MP30	M
La Beuchille	MP24	M
La Chaux (Francastel)	MN2a	M
La Chaux de Fond	MN3-4?	M
La Molière (Payerne)	MN3	M
La Rochette	MP29	M
Lausanne	MN2	M
Luzern	MN3?	M
Mammern	MN1-2?	M
Mathod près Yverdon	MP25-27	M
Mörigen	MP30	M
Möriken-Dorf	MP28-30	M
Möriken-Erlenmoos	MP28-30	M
Moutier gare	MP24-25	M
Mümliswil-Hardberg	MP26	M
Mümliswyl Heltersberg	MP26?-27	M
Mümliswyl Nasihofli	MP27	M
Oberbuchsiten	middle Stampian	M
Oensigen Ravellen	MP26	M
Oulens II	MP25-28?	M
Payerne	MN2-3	M
Poillat	MP24	M
Prè Chevallier	MP24	M
Rappenfluh Bei Aarberg	Aquitanian	M
Rickenbach	MP29	M
Rickenbach bei Bern	Aquitanian	M
Riedwald am Etzel		M
Schwendibach	MP26	M
Soulce	MP23	M
Suscevaz	MP25-27?	M
Tavannes (SLM)	MN2b	M
Teufen	MN2b	M
Veltheim	late Stampian- Lower Aquitanian	M
Waldenburg	MN1	M
Wallenried	MN2a	M
Welschenrohr	Eocene or old Chattian	M
Wildensbuch	MN4	M
Wischberg bei Langenthal	MN1	M
Wolwig Kenisbänli	MP27	M
Wolwig Mattenhof	middle Stampian	M
Wynau I	MP27	M
Wynau III	MP27?	M
Wynau V	MP27	M

Germany (within the Molasse Basin and the fissure fillings from the Franconian and Swabian Jura)

Bernloch 1	MP23	L
Burgmagerbein 1	MP27	M
Burgmagerbein 2	MP21/23	M
Burgmagerbein 5	MP21	M
Burgmagerbein 8	MP21/23	M
Eggingen Mittelhart 3	MN4	L
Ehingen 1	MP23	M
Ehingen 14	MP24-27	M
Ehingen 15	MP24-27	M
Ehingen 4	MP21	M
Ehrenstein 7	MP27	M
Erkertshofen 2	MN4	L
Eselsberg	MP21-22	L
Frohnstetten	Rupelian	L
Gaimersheim 1	MP28	M
Grafenmühle 6	MP21-22	L
Günzburg	MN4	L
Haag 2	MP21	L
Herrlingen 1	MP22	M
Hochberg	MP21	M
Langenau 1	MN4b	M
Langenau 2	MN4b	M
Möhren 04	MP21	L
Möhren 07	MP21-22	L
Möhren 09	MP21	L
Möhren 11	MP21-23	L
Möhren 13	MP22	M
Möhren 16	MP21-23	L
Möhren 18	MP21-23	L
Möhren 19	MP21	L
Möhren 20	MP21	L
Möhren 21	MP21-23	L
Möhren 31	MP21-22	L
Oerlinger Thal	MP21	L
Petersbuch 2	MN3-4	L
Ranscheröd	MN4	L
Reisensburg	MN4	L
Ronheim 1	MP23	L
Rothenstein 10/14	MN2	L

Rothenstein 2	MN3-4	L
Rothenstein 2	Burdigalian	L
Schelklingen 1	MP21-23	L
Treuchtlingen 1	MN2	M
Veringenstadt	MP21	L
Wintershof West	MN3	L
Zuezach-Kaisersthul	MN4?	L

Austria

Oberdorf	MN4	L
Seegraben	MN4	L

8 Pô Basin

Italy

Cadibona	MP25-26	M
Chiavon	MP22-24	L
Maccio	Oligocene	L

9 Ebro Basin

Spain

Las Bardenas de Navarra	MN3	L
Els Casots	MN4	L
Tarazona	MN4	L

10 Calatayud-Montalban Basin

Spain

Artesilla	MN4	L
Calaf	MP22-23	L
Carrascosa del Campo	MP25-26	L
Montalban	MP23	M
Navarrete del Rio	MN2	L
Ramblar	Aquitanian	L
Vivo del Rio	MP28	L

11 Taj Basin

Spain

Cetina de Aragon	MN2b	L
Loranca del Campo	MN3a	L
Valquemado	MN2b	L

12 Tagus Basin

Portugal

Lisbon	MN2	L

13 Vazzio Basin

France

Vazzio	MP29-30	L

14 Oschiri Basin

Italy

Oschiri	MN3	L

Molasse; Habicht 1987; Picot 2002; Becker 2003). It has been dated to the European Reference Level MP 26 (Engesser & Mödden 1997; Engesser & Mödden 1997).

Mümliswil Hardberg (619.525/244.900) belongs to the Süsswasserkalk of Mümliswil (equivalent of the Molasse Alsacienne Formation within the Eastern Jura Molasse). It has been dated to the European Reference Level MP 26 (Engesser & Mödden 1997).

Wynau III (628.675/234.560) belongs to the Knauermolasse Formation (synonym of the Aarwangen Molasse and lateral equivalent of the Molasse Alsacienne Formation within the the eastern Jura Molasse and the distal Plateau Molasse; Habicht 1987; Picot 2002; Becker 2003). It has been dated to the European Reference Level MP 27, older than Aawangen but younger than Mümliswil Hardberg (Engesser et al. 1984).

Aarwangen (624.025/232.575) is the type locality of the Aarwanger Molasse (lateral equivalent of the Molasse Alsacienne Formation within the distal Plateau Molasse; Picot 2002; Becker 2003). It has been dated to MP27 by Engesser & Mayo (1987).

Eriz Losenegg (623.250/232.560) belongs to a gray sandstone level of the Loseneggschichten from the Molasse à charbon of the Subalpine Molasse. It has been dated to the European Reference Level MP 27 (Engesser & Mödden 1997).

Wolfwil kennisbännli (628.355/234.650) belongs to the to the Knauermolasse Formation (synonym of the Aarwangen Molasse and lateral equivalent of the Molasse Alsacienne Formation within the the eastern Jura Molasse and the distal Plateau Molasse; Habicht 1987; Picot 2002; Becker 2003). It has been dated to the European Reference Level MP27 (Engesser & Mödden 1997).

Chavorney (534.650/170.700) is still under study by Engesser and colleagues. It belongs to the Plateau Molasse. It is preliminarily dated to the Late Oligocene.

Wynau V (628.840/234.670) belongs to the to the Knauermolasse Formation (synonym of the Aarwangen Molasse and lateral equivalent of the Molasse Alsacienne Formation within the eastern

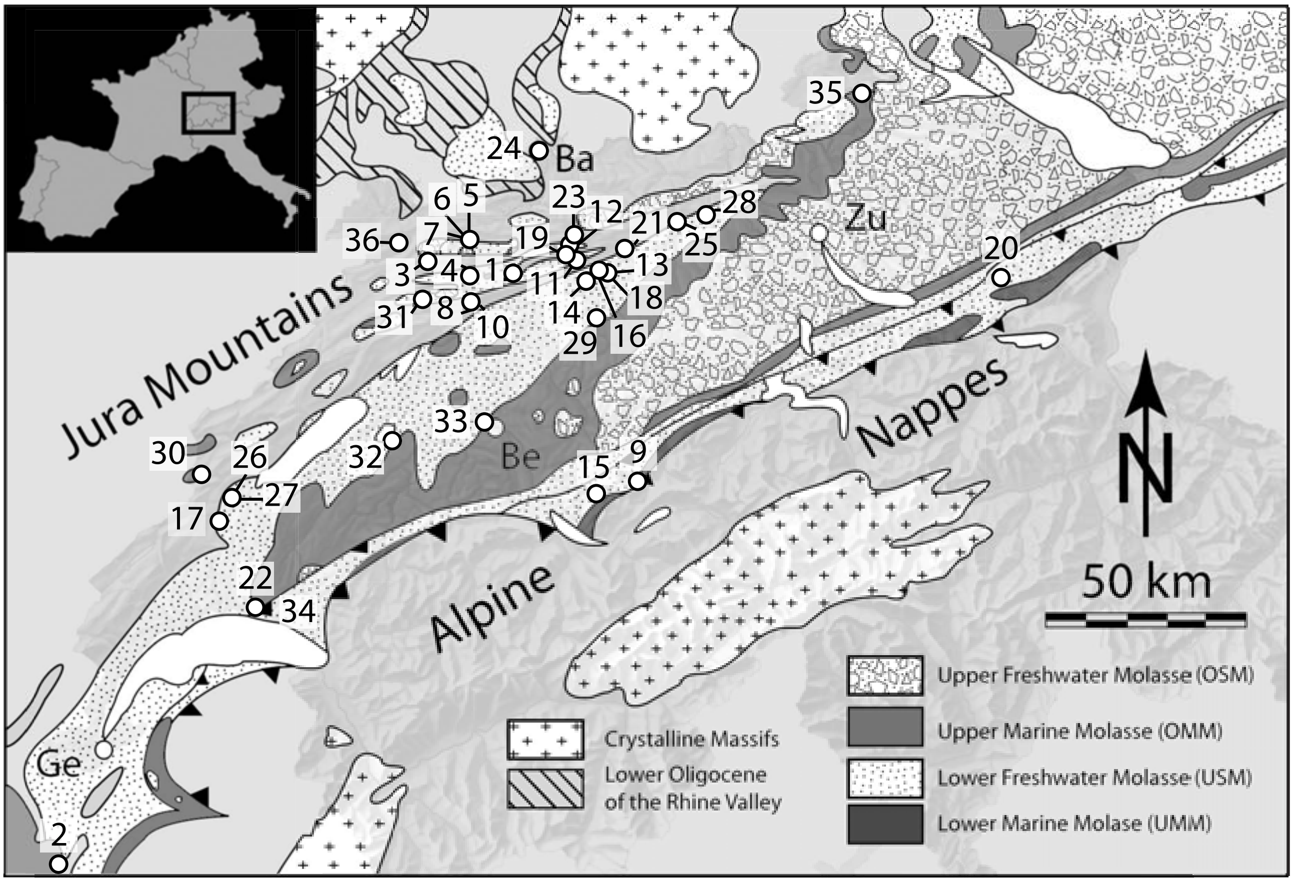

Figure 2 Location of the main Swiss ruminant localities (diversity, abundance or preservation). **Oligocene**: **1** Welschenrohr, **2** Lovagny14, **3** Soulce, **4** Court, **5** La Beuchille, **6** Pré Chevalier, **7** Poillat, **8** Grenchen1 and Grenchenbergtunnel, **9** Bumbach, **10** Moutier gare, **11** Oensingen ravellen, **12** Mümliswil Hardberg, **13** Wynau III, **14** Aarwangen, **15** Eriz Losenegg, **16** Wolfwil kennisbännli, **17** Chavorney, **18** Wynau V, **19** Balstahl Bännli, **20** Ebnatt Kappel, **21** Rickenbach, **22** La Rochette, **23** Brochene Flüh Waldenbuch, **24** Basel St Jakob, **25** Küttigen, **26** Mathod près Yverdon, **27** Suscevaz, **28** Möriken. **Miocene**: **29** Wischberg bei Langenthal, **30** La Chaux, **31** Tavannes Sous le Mont, **32** Wallenried, **33** Engehalde Neufeld, **34** Lausanne, **35** Benken and Wildensbuch, **36** Glovelier.

Jura Molasse and the distal Plateau Molasse; Habicht 1987; Picot 2002; Becker 2003). It is preliminarily dated to the European Reference Level MP27.

Balstahl Bännli (620.490/240.120) belongs to the to the Knauermolasse Formation (synonym of the Aarwangen Molasse and lateral equivalent of the Molasse Alsacienne Formation within the the eastern Jura Molasse and the distal Plateau Molasse; Habicht 1987; Picot 2002; Becker 2003). Following the preliminary analysis of the small mammals (B. Engesser, pers. comm.) and the identification of the ruminants, this locality had been dated to the European Reference Level MP28.

Ebnatt Kappel (727.880/235.040) belongs to the Ebnater Schichten (USM) and has been dated to the European Reference Level MP28 (Engesser & Mödden 1997).

Möriken (656.200/252.075) belongs to the Knauermolasse Formation (synonym of the Aarwangen Molasse and lateral equivalent of the Molasse Alsacienne Formation within the the eastern Jura Molasse and the distal Plateau Molasse; Habicht 1987; Picot 2002; Becker 2003). Due to the presence of *Microbunodon*, it could be dated to the European Reference Level MP28.

Rickenbach (632.200/242.300) belongs to the Knauermolasse Formation (synonym of the Aarwangen Molasse and lateral equivalent of the Molasse Alsacienne Formation within the eastern Jura Molasse and the distal Plateau Molasse; Habicht 1987; Picot 2002; Becker 2003). This is the type locality of the European Reference Level MP29 (Engesser & Mayo 1987) and had been the topic of a recent publication (Mennecart et al. 2012)

La Rochette (541.200/151.720) belongs to the Molasse à charbon of the Subalpine Molasse. Similar to the age of Rickenbach, it has been dated to the European Reference Level MP29 by Engesser et al. (1984) and Berger (1998).

Brochene Flüh (622.000/247.575) belongs to the Calcaires delémontiens Formation. The small mammal levels Brochene Flüh 19/20 and Brochene Flüh 53 have been dated to the European Reference Levels MP29 and MP30, respectively (Engesser & Mödden 1997; Becker et al. 2002).

Basel St Jakob (613.850/265.725) belongs to the Tüllingersüsswasserschichten Formation (synonym of the Calcaires delémontiens Formation; Picot 2002). It has been dated to the European Reference Level MP29, younger than Brochene Fluh 53 but older than Küttigen (Engesser & Mödden 1997).

Küttigen (645.875/250.650) belongs to the Knauermolasse Formation (synonym of the Aarwangen Molasse and lateral equivalent of the Molasse Alsacienne Formation within the eastern Jura Molasse and the distal Plateau Molasse; Habicht 1987; Picot 2002; Becker 2003). It has been dated to the European Reference Level MP30 (Engesser & Mödden 1997).

Mathod près Yverdon (533.130/180.810) is still under study by Engesser and colleagues. It belongs to the USM deposits of the Plateau Molasse and was dated to the Late Oligocene.

Suscevaz (534.000/179.240) is still under study by Engesser and colleagues. It belongs to the USM deposits of the Plateau Molasse and is provisionally dated to the Late Oligocene.

3.2.2 Miocene

Wischberg bei Langenthal (624.650/227.639) belongs to the Obere Bunte Mergel Formation (USM). It had been dated to the European Reference Zone MN1 (Engesser & Mödden 1997).

La Chaux (527.300/187.225) belongs to local lacustrine limestone deposits of the USM of the western Jura Molasse. It had been dated to the European Reference Zone MN2b (Engesser & Mödden 1997).

Tavannes Sous le Mont (583.140/230.150) is the first Aquitanian large mammal locality from the central Jura Molasse. It corresponds to fluvial sandstones and has been dated to the European Reference Zone MN2b (B. Engesser, pers. comm.).

Wallenried (574.45/192.45) belongs to the Molasse grise de Lausanne Formation (USM). It has been dated by small mammals to the European Reference Zone MN2b (Becker et al. 2001).

Engehalde Neufeld (600.160/201.250) belongs to the Obere Bunte Mergel Formation (USM). It has been dated to the European Reference Zone MN2b (Becker et al. 2010).

Lausanne (~538.000/~153.000) belongs to the Molasse grise de Lausanne Formation (USM). The various localities are all dated to the European Reference Zones MN1-2 (Engesser et al. 1993).

Benken (692.200/278.900) and ***Wildensbuch*** (~693.000/~278.000) belong to the 'St. Galler Schichten' and the 'Krokodilen Schichten' of the OMM (Obere Meeresmolasse = Upper Marine Molasse) and have been dated to the European Reference Zones MN3–4 (Bolliger 1992).

Glovelier (580.36/242.08) is a karstic fissure filled by sand deposits with mixed continental and marine remains. It has been dated to the European Reference Zone MN4 (Becker 2003; Kälin & Kempf 2009).

3.3 Stratigraphic correlations

Following the synthesis of Berger (2011), the biochronological framework is based on correlations between the European Land Mammal Ages (ELMA), defined by the succession of European mammal reference zones (MP-levels and MN-zones; Mein 1976, 1989, 1999; Schmidt-Kittler 1987; Steininger 1999), the Swiss Reference Faunas (Bolliger 1997; Engesser & Mödden 1997; Kälin 1997; Kempf et al. 1997; Kälin & Kempf 2009), and the Paleogene and Neogene geological time scale (Lourens et al. 2004; Luterbacher et al. 2004) (Fig. 3).

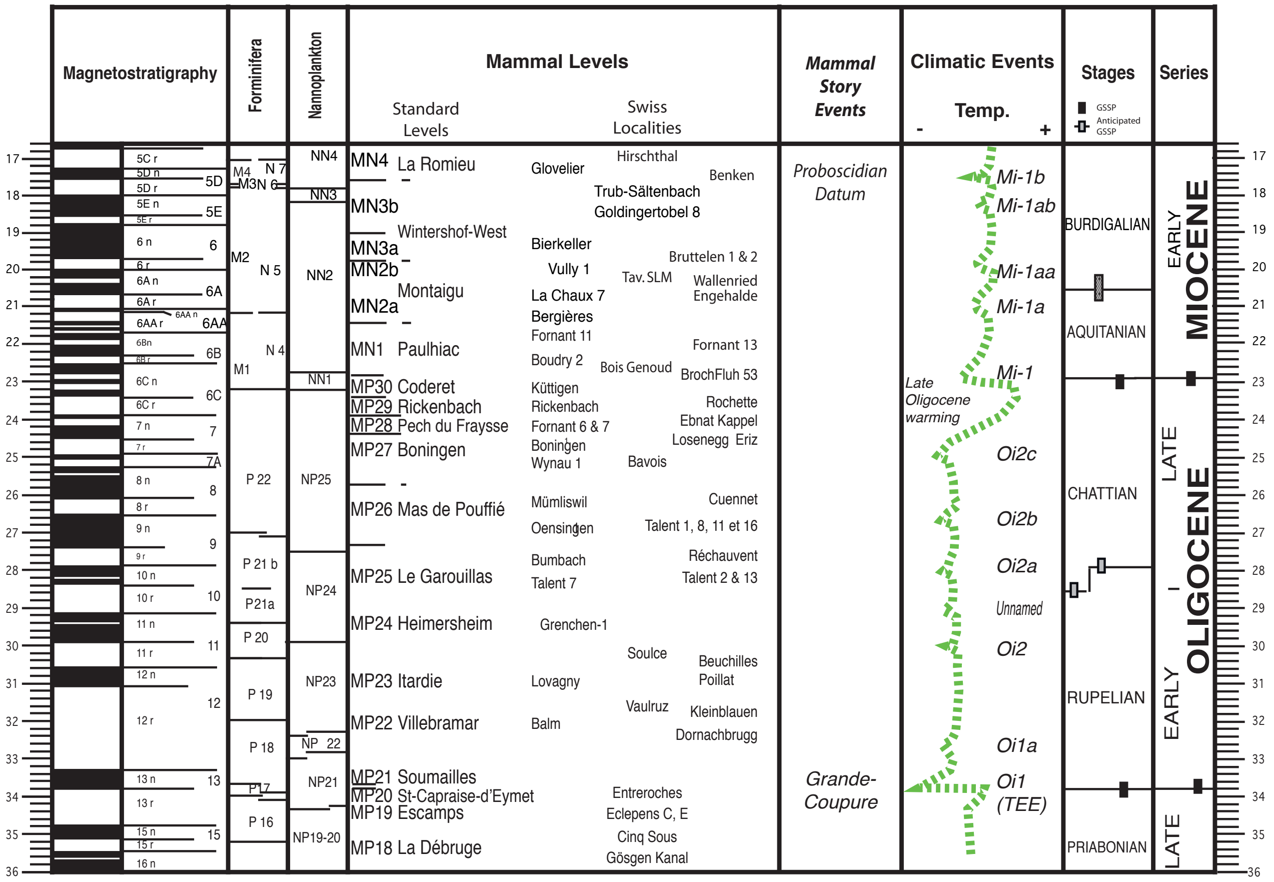

Figure 3 Chronological correlations of the Mammal Levels and Zones with the magneto-bio-chronostratigraphie, the circum-Mediterranean marine chronology, and climatic events (Mein 1999; Zachos et al. 2001; Berger & al. 2005; Kälin & Kempf 2009; Pälike & Hilgen 2008; Berger 2011).

3.4 Systematics

3.4.1 Systematic palaeontology

The identifications are based on anatomical feature descriptions, comparative anatomy and biometrical measurements. Various dental terminologies are used (Fig. 4). An adapted nomenclature from Gentry et al. (1999) has been used in Chapter 4, whereas the dental nomenclature from Janis (1987) has been used in Chapter 6. The other chapters follow the ruminant dental terminology of Bärmann & Rössner (2011). The measurements are given with a precision of 0.1 mm.

3.4.2 Synonymy abbreviations

Conventional abbreviations used in front of the year in the synonymy list follow Matthews (1973): '*' the work validates the species; '.' the authors agree on the identification; 'v' the authors have seen the original material of the reference; '?' the allocation of the reference is subject to some doubt; 'non' the reference actually does not belong to the species under discussion; 'pars' the reference applies only in part to the species under discussion; 'no' means the authors were unable to check the validity of the reference. Years in italics indicate a work without description or illustration.

3.4.3 Anatomical abbreviations.

i, lower incisive; c, lower canine; p, lower premolar; m, lower molar; d, lower decidual premolar; C, upper canine; P, upper premolar; M, upper molar; D, upper decidual premolar; Mc, Metacarpal, Mt, Metatarsal; L, length; W, width.

3.5 Specific methods

Specific methods have been used during this study and are precisely described in the respective chapters.

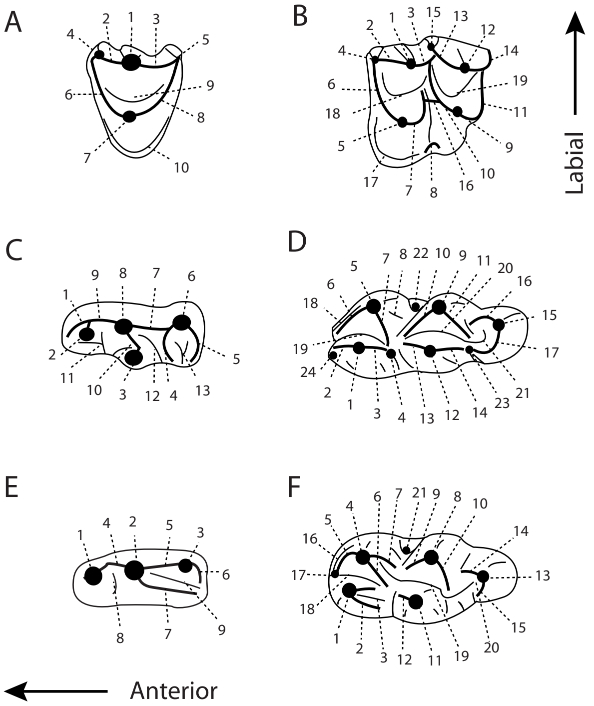

Figure 4 Nomenclatures of the dentition (*Chapter **4**; “Chapter **6**; when not specified, in the other chapters). **A** Upper premolars. 1 anterolabial cone, “paracone, 2 anterolabial crista, “preparacrista, 3 posterolabial crista, “postparacrista, 4 anterior style, “parastyle, 5 posterior style, “metacone, 6 anterolingual crista, “prehypocrista, 7 lingual cone, “hypocone, 8 posterolingual crista, “posthypocrista, 9 fossa, 10 lingual cingulum. **B** Upper molars. 1 paracone, 2 preparacrista, 3 postparacrista, 4 parastyle, 5 protocone, 6 preprotocrista, 7 postprotocrista, 8 entostyle, 9 metaconule, *hypocone, 10 premetaconulecrista, *praehypocrista, 11 postmetaconulecrista, *posthypocrista, 12 metacone, 13 premetacrista, 14 postmetacrista, 15 mesostyle, 16 premetaconulecrista bifurcation, 17 lingual cingulum, 18 anterior fossa, 19 posterior fossa. **C** Lower premolars (Pecora). 1 anterior stylid, “preprotoconulidcristid, 2 anterior conid, “protoconulid, 3 mesolingual conid, *“metaconid, 4 posterolingual conid, *hypoconid, “entocristid, 5 posterior stylid, “hypocristid, 6 posterolabial conid, “hypoconid, 7 posterolabial cristid, “*Palaeomeryx* fold, 8 mesolabial conid, “protoconid, 9 anterolabial cristid, “preprotocristid, 10 transverse cristid, “postprotocristid, 11 anterior valley, 12 posterior valley, “medial valley, 13 back valley, “posterior valley. **D** Lower molars (Pecora). 1 metaconid, 2 premetacristid, 3 postmetacristid, 4 metastylid, 5 protoconid, 6 preprotocristid, 7 internal postprotocristid, “postprotocristid, 8 external postprotocristid, “*Palaeomeryx* fold, 9 hypoconid, 10 prehypocristid, 11 posthypocristid, 12 entoconid, 13 preentocristid, 14 postentocristid, 15 hypoconulid, 16 prehypoconulidcristid, 17 posthypoconulidcristid, 18 anterior cingulid, 19 anterior basin, 20 posterior basin, 21 back basin of m3, 22 ectostylid, 23 entostylid, 24 mesostylid. **E** lower premolars (Tragulidae). 1 anterior conid, *protoconulid, 2 mesolabial conid, *protoconid, 3 posterolabial conid, 4 anterolabial cristid, 5 posterolabial cristid, 6 posterior stylid, 7 labial cristid, 8 anterior valley, 9 posterior valley. **F** Lower molars (Tragulidae). 1 metaconid, 2 postmetacristid, 3 *Dorcatherium* fold, 4 protoconid, 5 preprotocristid, 6 internal postprotocristid, 7 lingual wall, 8 hypoconid, 9 prehypocristid, 10 posthypocristid, 11 entoconid, 12 preentocristid, 13 hypoconulid, 14 prehypoconulidcristid, 15 posthypoconulidcristid, 16 anterior cingulid, 17 anterior conid, 18 anterior fossa, 19 posterior fossa, 20 back fossa of m3, 21 ectostylid.

3.5.1 Geometric morphometrics

Geometric morphometrics (Chapters 2 and 4) is a quantitative study of the shape differences between specimens having a similar structure. In this particular case, I used landmarks on images of mandibles (bone is considered as flat) that provide information on the phylogeny and the diet.

3.5.2 Ecomorphology

Ecomorphology (Chapters 7, 10, and 11) “is primarily concerned with analysis of the adaptiveness of morphological features and all dependent, correlated topics such as the comparisons of adaptations in different organisms, modifications of adaptive features due to competition and other causes, structure of ecological communities, diversity within taxa, etc.” (Bock 1994). Methods related to ecomorphology have been applied, mainly in collaboration with master student Florent Hiard, on postcranial remains (Hiard 2010).

3.5.3 Cenogram

Cenogram (Chapter 7) is an analysis of the terrestrial non-flying herbivores mammals’ bodyweight structure. Estimated body mass is ranked from the heavier to the lighter forming a curve in a graph. The slopes and the size of the strokes between the slopes are compared with cenograms of extant communities, enabling the definition of palaeoenvironments.

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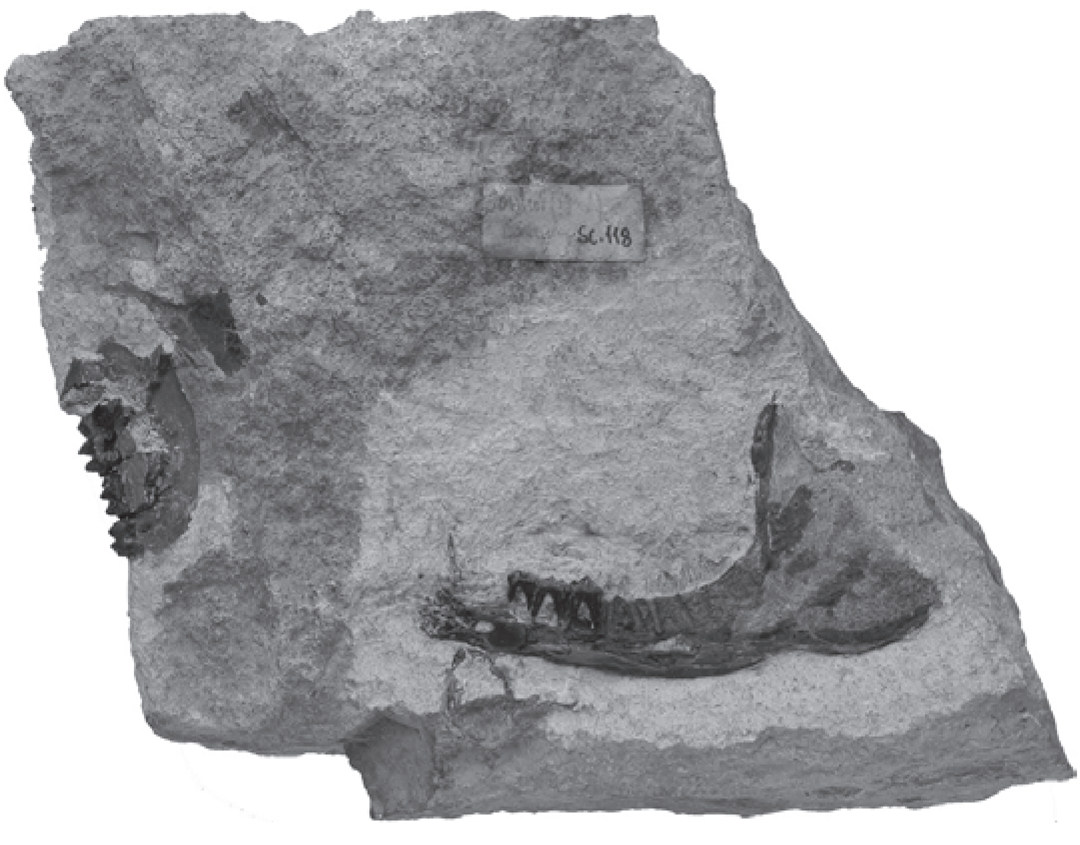
II - EARLY AND MID-OLIGOCENE



NMB Sc 118 *Iberomeryx minor* from Soulce
(Mennecart et al. 2011)

4 - *IBEROMERYX MINOR* (MAMMALIA, CETARTIODACTYLA) FROM THE EARLY OLIGOCENE OF SOULCE (CANTON JURA, NW SWITZERLAND): SYSTEMATICS AND PALAEODIET

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Abstract

The primitive ruminant genus *Iberomeryx* is poorly documented, as it is essentially only known from rare occurrences of dental remains. Therefore, the phylogeny and palaeobiology of *Iberomeryx* remain rather enigmatic. Only two species have been described: the type species *I. parvus* from the Benara locality in Georgia, and the Western European species *I. minor* reported from France, Spain, and Switzerland. *Iberomeryx savagei* from India has recently been placed in the new genus *Nalameryx*. All these localities are dated to the Rupelian and correspond mainly to MP23 (European mammal reference level). Based on the short height of the tooth-crown and the bunoselenodont pattern of the molars, *Iberomeryx* has often been considered as a folivore/frugivore. The *I. minor* remains from Soulce (NW Switzerland) are preserved in Rupelian lacustrine lithographic limestones. One specimen from this locality represents the most complete mandible of the taxon with a partially-presevered ramus. Moreover, the unpreserved portion of the mandible left an imprint in the sediment, permitting the reconstruction of the mandible outline. Based on a new description of these specimens, anatomical comparisons and Relative Warp Analysis (24 landmarks) of 94 mandibles (11 fossil and 83 extant) from 31 ruminant genera (10 fossil and 21 extant) and 40 species (11 fossil and 29 extant), this study attempts a preliminary discussion of the phylogeny and the diet of the species *I. minor*. The results permit to differentiate Pecora and Tragulina on the first principal component axis (first Relative warp) on behalf of the length of the diastema c/cheek teeth, the length of the premolars and the angular process. The mandible shape of *I. minor* is similar to those of the primitive Tragulina, but it differs somewhat from those of the extant Tragulidae, the only extant family in the Tragulina. This difference is essentially due to a stockier mandible and a deeper *incisura vasorum*. However, in consideration of the general pattern of its cheek teeth, *I. minor* as well as possibly *Nalameryx* should be considered to represent the only known primitive Tragulidae from the Oligocene. Moreover, *I. minor* should have been a selective browser (fruit and dicot foliage) but, similarly to small Hypertragulidae and Tragulidae, may also have exceptionally consumed animal matter.

4.1 Introduction

Iberomeryx species are small ruminants from the Early Oligocene of Eurasia. The genus, defined by Gabunia (1964), is essentially known by few dental remains and is still poorly documented. Although it has been placed in the infraorder Tragulina, based on its very primitive characteristics, such as bunodont teeth, and an open trigonid and talonid, its suprageneric phylogeny is still under debate. In the opinion of Cope (1888) *Iberomeryx* belongs to the Xyphodontidae; Stehlin (1914), Carlson (1926), Webb & Taylor (1980), and Sudre (1984) placed it in the Tragulidae; Caroll (1988) in the Moschidae; Gabunia (1964, 1966) and Ghaffar et al. (2006) in the Cervidae; Janis (1987), Métais & Vislobokova (2007), and Métais et al. (2009) in the Lophiomerycidae and Blondel (1997) referred to it as a close relative of *Lophiomeryx*. In addition, for a long time, most of the specimens now attributed to *Iberomeryx* were considered to belong to the genus *Cryptomeryx* (e.g., Schlosser 1886; Gaudant 1979; Sudre 1984). However, Bouvrain et al. (1986) revised the taxonomy of the Oligocene ruminants of the Phosphorites du Quercy (SW France) and reassessed *Cryptomeryx* as a synonym for *Iberomeryx*. Among the *Iberomeryx* species described in the literature, only two are considered as valid: the type species *I. parvus* from the Benara locality in Georgia (Gabunia 1964, 1966) and the Western European species *I. minor* from the localities Itardies, Mounayne, Roqueprune 2, and Lovagny in France (Remy et al. 1987; Blondel 1997; Engesser & Mödden 1997), Montalban in Spain (Blondel 1997), and Beuchille, Pré Chevalier, and Soulce in Switzerland (Gaudant 1979; Engesser & Mödden 1997; Becker et al. 2004; this study). These *Iberomeryx* localities are Rupelian in age and correspond, when dated by small mammals, to MP23 (European mammal reference level; Remy et al. 1987; Schmidt-Kittler 1987; Engesser & Mödden 1997; Schmidt-Kittler et al. 1997; Lucas & Emry 1999; Becker et al. 2004). However, Sudre & Blondel (1996) attributed upper molar remains from La Plante 2 in France (MP22) to *I.* cf. *minor* and Antoine et al. (2008) suggested the presence of *I.* cf. *parvus* from the Kizilirmak Formation in Turkey (Late Oligocene). These occurrences could be the earliest and the latest records of the genus *Iberomeryx*, respectively. According to Sudre & Blondel (1996), *Iberomeryx matsoui*, reported from the German localities Burgmagerbein 8 (MP21; Heissig 1987), Herrlingen 1 (MP22; Heissig 1978; Schmidt-Kittler et al. 1997), and Ehingen 1 (MP23; Heissig 1987) is a synonym for the small Gelocidae *Pseudogelocus scotti*. The Late Oligocene Asian species, *I. savagei*, first described as *Cryptomeryx savagei* (Nanda & Sahni 1990), discovered in the Kargil Formation in India (Blondel 1997; Nanda & Sahni 1998; Guo et al. 2000; Barry et al. 2005), has recently been included in the new genus *Nalameryx* (Métais et al. 2009). Other European specimens display uncertain affinities with the genus *Iberomeryx*. Stehlin (1910: 988, fig. 183) assigned small-sized ruminant remains from the old collections of the Phosphorites du Quercy (SW France) to ? *Cryptomeryx decedens*. The species *Cryptomeryx major* published by Schlosser (1886) was never figured and the referred material has apparently been lost. From some localities, dated as being younger than MP23, primitive ruminants have been recorded, which were, without confidence, attributed to *Iberomeryx*: La Ferté Alais (MP24; Blondel 1997), Garouillas (MP25; Sudre 1995), and Mümliswil-Hardberg (MP 26; Engesser & Mödden 1997). These doubtful specimens are in need of revision, as the dental structure of primitive ruminants is very similar and can easily be confused. According to Geraads et al. (1987) and Martinez & Sudre (1995), only the combination of the astragalus shape, the diastema length, the mandible robustness, the p4 structure, and the lower molar shape permit to differentiate between them. In fact, their reassessment could ascribe them to small Gelocidae or *Bachitherium vireti* from the Early Oligocene.

Regarding the diet of *Iberomeryx minor*, Sudre (1984) and Becker et al. (2004) proposed a folivore/frugivore trophic mode based on the bunoselenodont structure of cheek teeth. However, *I. minor* molars and premolars are more bunodont and sharper than those of the extant Tragulina that add significant amounts of animal matter to their diet (Dubost 1984; Sudre 1984; Rössner 2007).

The specimens of *I. minor* from Soulce (Rupelian, NW Switzerland) are preserved in a lacustrine lithographic bed. Notably, the locality yielded the most complete mandible of this taxon with a partially-preserved ramus and an imprint of the missing portion of the mandible. Based on a re-description of these specimens, anatomical comparisons and Relative Warp Analysis (24 landmarks) of fossil and extant ruminant mandibles (94 specimens),

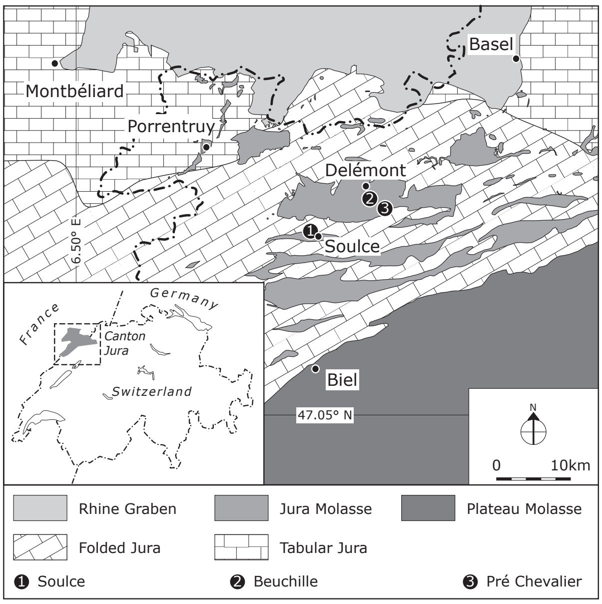


Fig. 1: Geographical and geological setting of the mammal localities of Soulce, Beuchille and Pré Chevalier (Early Oligocene, north-central Jura Molasse, NW Switzerland).

this study discusses the phylogeny and the diet of the species *I. minor*.

4.2 Geological setting and taphonomy

The *Iberomeryx* specimens were found one kilometre northwest of Soulce (Canton Jura, NW Switzerland; 47°18'39.24"N/7°15'26.28"E). They were discovered by Fleury (1910) in Early Oligocene deposits (Fig. 1). In the Early Oligocene of the north-central Jura Molasse, sedimentation was controlled by multiple incursions of the Rhenish Sea, and three successive transgressive–regressive cycles are known from the Oligocene deposits of the Rhine Graben (Picot 2002; Berger et al. 2005a, b; Picot et al. 2008). In the Porrentruy region (Ajoie district), the first two cycles are recorded, whereas only the second cycle, known as the global Rupelian transgression, generated a contemporaneous incursion in the whole north-central Jura area at the top of NP22 and base of NP23 (ca. MP22; ~32 Ma). A possible ephemeral connection with the Perialpine sea, via a discreet canyon called the *Rauraque* depression, has been postulated by some authors (e.g., Martini 1990; Berger 1996; Berger et al. 2005a, b). The regression of this second incursion is clearly diachronic, occurring from NP23 to NP24 (ca. top MP22–MP23; ~31 Ma) in a northward and possible westward direction. During this regressive time interval, a deltaic system was established at the southern border of the Rhenish Sea and this marine facies began to prograde northwards (Pirkenseer 2007). The Soulce locality was located within the distal western part of this deltaic environment (Fig. 2).

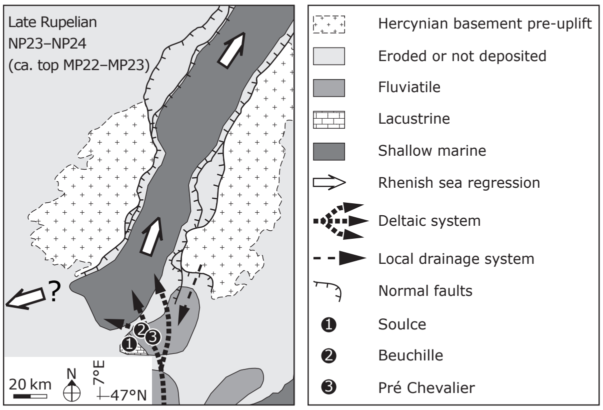


Fig. 2: Palaeogeographical map of the southern Rhine Graben and the north-central Jura Molasse during the Late Rupelian, highlighting the regression of the second incursion of the Rhenish sea (modified after Berger et al. 2005b; Pirkenseer 2007; Picot et al. 2008).

According to the description of the outcrop (Fleury 1910; Rollier 1910) and in agreement with the geological map (Pfirter et al. 1996; Pfirter 1997) and the recent works on lithostratigraphy (Picot 2002; Berger et al. 2005a), the base of the short section is defined by Paleogene siderolitic fissure-fills and deposits (*Bolustone*, Ziegler 1956; *Bohnerzkonglomerate*, Greppin 1855) within and overlaying Mesozoic bedrock. The base of the overlying continental interval is formed by approximately four meters of marly, calcareous and sandy deposits of the *Molasse alsacienne sensu stricto* (*sensu* Picot 2002). The *Iberomeryx* specimens were preserved in a 95 cm thick lacustrine lithographic limestone bed, extraordinarily rich in plant-, mollusk-, and vertebrate remains. Because of the many articulated fish skeletons (*Esox*, *Umbra*, *Leuciscus*).and two articulated amphibian specimens (*Palaeobatrachus* cf. *diluvianus*), this bed can be described as a conservation Lagerstätte.

Mammals are only represented by a few isolated and disarticulated remains of Palaeochoeridae, Anthracotheriidae, and the referred *Iberomeryx* of this study (Gaudant 1979). The disparate preservation of the articulated skeletons and the isolated remains is a consequence of the particular taphonomic processes involved. By analogy to the model of Messel proposed by Franzen (1985), it is assumed that the lake-dwelling fish and amphibian population died directly within a more or less stagnant freshwater lake. After a short time floating (depending of water depth and temperature), the cadavers would have sunk to the bottom of the lake to be preserved in the form of articulated skeletons. According to Behrensmeyer & Hook (1992), the remains of *Iberomeryx* are proposed to be the result of occasional flood events, that were responsible for the transport and sorting of terrestrial vertebrate elements and their deposition within a small lake, where they were well preserved in the bottom sediment. The remains of *Iberomeryx,* although disarticulated, are unworn, excluding a long *post mortem* transport.

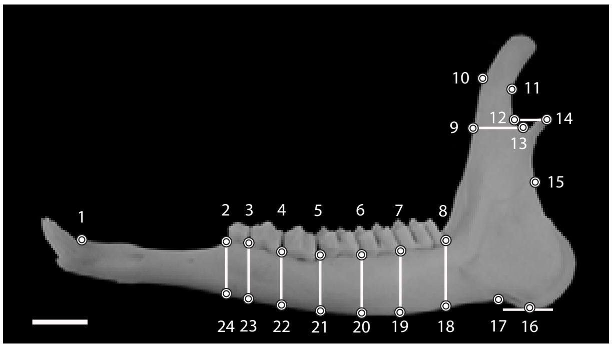


Fig. 3: Location of anatomical landmarks used for the Relative Warp Analysis on a ruminant mandible (*Capreolus capreolus*; MHNF 9017-1979). Scale bar: 2 cm. **1,** posterior part of c; **2,** anterior part of p2; **3,** anterior part of p3; **4,** anterior part of p4; **5,** anterior part of m1; **6,** anterior part of m2; **7,** anterior part of m3; **8,** posterior part of m3; **9,** projection of **13** on the anterior part of the ramus; **10,** maximum of convexity of the coronoid process; **11,** maximum of concavity of the coronoid process; **12,** projection of **14** on the posterior part of the coronoid process; **13,** mandibular incisure; **14,** condylar process; **15,** maximum of concavity of the ramus; **16,** lower part of the angular process; **17,** *incisura vasorum*; **18,** projection of **8** on the lower part of the *corpus mandibulae*; **19,** projection of **7** on the lower part of the *corpus mandibulae*; **20,** projection of **6** on the lower part of the *corpus mandibulae*; **21,** projection of 5 on the lower part of the *corpus mandibulae*; **22,** projection of **4** on the lower part of the *corpus mandibulae*; **23,** projection of **3** on the lower part of the *corpus mandibulae*; **24,** projection of **2** on the lower part of the *corpus mandibulae*.

4.3 Material, methods and abbreviations

4.3.1 Systematic palaeontology

The referred and morphometric comparison material include the dental remains of *Iberomeryx minor* from the Soulce, Beuchille and Pré Chevalier localities (Canton Jura, NW Switzerland) and in part the Phosphorites du Quercy localities (old collections and Itardies, SW France; Sudre 1984) from the collection of the *Musée jurassien des sciences naturelles* (Switzerland), the *Naturhistorisches Museum Basel* (Switzerland), and the *Université des Sciences et Techniques du Languedoc* (Montpellier, France). The identifications are based on anatomical feature descriptions, comparative anatomy and biometrical measurements, following the ruminant dental terminology of Gentry et al. (1999). All measurements are given with a precision of 0.1 mm. The biochronological framework is based on the European Land Mammal Ages (ELMA) defined by the succession of European mammal reference levels (MP; Schmidt-Kittler 1987) and the Paleogene geological time scale (Luterbacher et al. 2004).

4.3.2 Relative Warp Analysis (RWA)

This analysis is based on 11 fossil and 83 extant ruminant mandibles (where available left mandibles) from 31 genera (10 fossil and 21 extant) and 40 species (11 fossil and 29 extant), stored pro parte in the *Musée d'histoire naturelle de Fribourg* (Switzerland) and the *Naturhistorisches Museum Basel* (Switzerland), and extracted pro parte from the literature (see Table 1). The number of studied specimens per species varies between one (notably for all extinct species) to twelve (Tab. 1). The selected material exclusively consists of gender-unspecific, adult specimens. We noted that juvenile specimens do not always bear all adult characteristics and that certain specimens held in captivity at zoos display a strange mandible development. They were, therefore, not included in the analysis. The extant ruminants included in the analysis essentially belong to the three genera of the Tragulina monofamily (Tragulidae) and the two most diversified families of Pecora (Bovidae and Cervidae), completed by some specimens of the Moschidae monogenus (*Moschus*). Our sampling aims to optimally cover the size range and the feeding categories in each infraorder of extant ruminants (Tragulina and Pecora). The feeding categories are mainly based on those of Janis (1986): (Sb), selective browser (fruits and dicotyledonous herbage foliage selector); (Fl), folivore (at least 90% of dicotyledonous herbage); (Mx), mixed feeder (intermediate feeder with variable diets

Tab. 1: Referred specimens of 11 fossil and 83 extant ruminant mandibles used for RWA. The feeding categories and the body mass are provided according to the literature, excepted for *Gelocus villebramarensis* for which body mass is calculated with the method of Legendre (1989). (**f**)**,** fossil; (**e**)**,** extant; (**Sb**), selective browser; (**Fl**), folivore; (**Mx**), mixed feeder; (**Gr**), grazer. Confident feeding categories of *Gelocus villebramarensis, Dorcatherium naui*, and *Leptomeryx evansi* are unknown in the literature. However, based on their bunoselenodont molars, we consider that these three taxa likely were selective browsers (**Sb ?**).

Ruminantia species	**Family**	**Housing institution**	**n**	**Diet**	**Body mass**	**References**
Pecora						
Alces alces (e)	Cervidae	CI R-584-20	1	Fl	500-600 kg	Franzmann (1981); Janis (1986)
Bison antiquus (f)	Bovidae	ANSP 12976	1	Gr	500-700 kg	Meagher (1986); Rivals et al. (2007)
Bos taurus (e)	Bovidae	–	2	Mx	300 kg	Janis (1986); pers. comm. Anne-Sophie Vernon
Capreolus capreolus (e)	Cervidae	MHNF	4	Fl	25 kg	Gordon & Illius (1988); Fortelius & Solounias (2000)
Cephalophus natalensis (e)	Bovidae	NMB	1	Sb	12-14 kg	Gagnon & Chew (2000)
Cephalophus silvicultor (e)	Bovidae	NMB	3	Sb	43-80 kg	Gagnon & Chew (2000)
Cephalophus zebra (e)	Bovidae	NMB	2	Sb	15-20 kg	Gagnon & Chew (2000)
Dicrocerus elegans (f)	Cervidae	–	1	Fl	50 kg	Heizmann et al. 1996; Kaiser & Rössner (2007); Costeur & Legendre (2008)
Dremotherium feignouxi (f)	Moschidae	NMB MA	1	Fl	15 kg	Prothero 2007; pers. comm. Florent Hiard
Dremotherium guthi (f)	Moschidae	IPHEP LM.1968 MA.1	1	Fl	11-16 kg	Jehenne 1987; Martinez & Sudre (1995); Prothero (2007)
Gazella gazella (e)	Bovidae	NMB	4	Mx	15-20 kg	Gagnon & Chew (2000)
Gazella dorcas (e)	Bovidae	NMB	4	Mx	15-23 kg	Janis (1986); Gagnon & Chew (2000)
Gazella soemmeringi (e)	Bovidae	NMB	1	Mx	35-46 kg	Gagnon & Chew (2000)
Gazella subgutturosa (e)	Bovidae	NMB	2	Mx	20-43 kg	Kingswood & Blank (1996)
Gazella thomsoni (e)	Bovidae	NMB	1	Mx	17-30 kg	Janis (1986); Gagnon & Chew (2000)
Gelocus villebramarensis (f)	Gelocidae	IPHEP Vil.1970-121	1	Sb ?	7 kg	Brunet & Jehenne (1976); this study
Hydropotes inermis (e)	Cervidae	NMB	7	Mx	8-12 kg	Janis (1986); Gordon & Illius (1988)
Madoqua saltiana (e)	Bovidae	NMB	1	Fl	3-4 kg	Gagnon & Chew (2000)
Mazama nemorivaga (e)	Cervidae	–	1	Sb	8-30 kg	Matthew (1908); Eisenberg (2000)
Moschus moschiferus (e)	Moschidae	NMB	5	Fl	4-12 kg	Gordon & Illius (1988); Prothero (2007)
Muntiacus muntjak (e)	Cervidae	NMB	6	Fl	7-12 kg	Gordon & Illius (1988)
Neotragus moschatus (e)	Bovidae	NMB	1	Fl	4-9 kg	Gagnon & Chew (2000)
Odocoileus virginamus (e)	Cervidae	NMB	3	Fl	45-65 kg	Janis (1986); Smith (1991)
Oreotragus oreotragus (e)	Bovidae	NMB	3	Mx	5-16 kg	Janis (1986); Gagnon & Chew (2000)
Ourebia ourebi (e)	Bovidae	NMB	3	Gr	8-21 kg	Gagnon & Chew (2000)
Procervulus dichotomus (f)	Cervidae	BSP 1979 XV 555	1	Mx	20 kg	Rössner (1995); Kaiser & Rössner (2007); Costeur & Legendre (2008)
Pudu puda (e)	Cervidae	NMB	1	Sb	10 kg	Eisenberg (2000)
Raphicerus melanotis (e)	Bovidae	NMB	1	Mx	9-11 kg	Janis (1986); Gagnon & Chew (2000)
Saiga tatarica (e)	Bovidae	NMB	2	Gr	35 kg	Gordon & Illius (1988); Sokolov (1974)
Sylvacapra grimmia (e)	Bovidae	NMB	2	Fl	11-26 kg	Janis (1986); Gagnon & Chew (2000)
Tragulina						
Bachitherium cf. *curtum* (f)	Bachitheriidae	NMB Qu.B.63	1	Sb	7-8 kg	Blondel (1996, 1998)
Dorcatherium naui (f)	Tragulidae	–	1	Sb ?	32 kg	Gentry et al. (1999); Rössner (2007); Costeur & Legendre (2008)
Hyemoschus aquaticus (e)	Tragulidae	NMB	2	Sb	12 kg	Janis (1986); Gordon & Illius (1988)
Iberomeryx minor (f)	Tragulidae	NMB Sc.118	1	Sb	3-4 kg	Martinez & Sudre (1995); this study
Leptomeryx evansi (f)	Leptomerycidae	AMNH 11870	1	Sb ?	3 kg	Frick (1937); Zanazzi & Kohn (2008)
Moschiola meminna (e)	Tragulidae	NMB	4	Sb	5 kg	Janis (1986); Rössner (2007)
Nanotragulus loomsi (f)	Hypertragulidae	AMNH 31525	1	Sb	3 kg	Frick (1937); Métais & Vislobokova (2007)
Tragulus javanicus (e)	Tragulidae	NMB	12	Sb	1-4 kg	Janis (1986); Gordon & Illius (1988)
Tragulus kanchil (e)	Tragulidae	NMB	3	Sb	4 kg	Meijaard & Sheil (2007)
Tragulus napu (e)	Tragulidae	NMB	1	Sb	2 kg	Meijaard & Sheil (2007)

of dicotyledonous and monocotyledonous plants) and (Gr), grazer (at least 90% of monocotyledonous grass material). Regarding the fossil sampling, we focused on the *Iberomeryx minor* specimen of Soulce and other primitive Tragulina and Pecora from the Early Oligocene of Western Europe and North America, and we completed the sampling pool with mandibles of derived taxa from the Neogene.

The mandible specimens were photographed in lateral view with a horizontal orientation of the tooth row, using a camera FinePix S6500fc. The software TpsDig version 1.31, a program for digitizing landmarks and outlines for geometric morphometric analyses developed by Rohlf at the Department of Ecology and Evolution (State University of New York), was used to digitize 24 anatomical landmarks (representing anatomically, geometrically, and linked homologous points) on each digital image representative of the overall mandibular form (including the ramus). The chosen anatomical landmarks, illustrated in Figure 3, are parameters, which were usually also included in previous studies on mandibular morphology (e.g., Joeckel 1990; Spencer 1995; Perez-Barberia & Gordon 1999; MacFadden 2000; Raia et al. 2010).

Regarding the geometric morphometric analysis, the method follows that proposed by Querino et al. (2002) and Raia et al. (2010). Traditional morphometric methods use linear distance measurements, which strongly correlate with size. To eliminate the non-shape variation (size) on the landmark configurations, a General Procrustes Analysis was performed (Adams et al. 2004). The coordinates of the mandible landmarks were processed by the least-square method that transforms a landmark configuration, superimposing them (translating, scaling and rotating) on a mean shape (consensus), so that the smallest possible sum of the squares of the distances between the corresponding homologous points results (Monteiro & Reis 1999; Adams et al. 2004). The configurations of the mandible landmarks were combined to analyze only the differences with the consensus.

Thin-Plate Spline function (TPS) was applied to map the landmark configurations represented as deformation grids, where one mandible is deformed or "warped" into another. Shape differences can then be described in terms of deformation-grid differences depicting the objects (Adams et al. 2004). The shape data describing these deformations (partial warps) can be used as shape variables for statistical comparisons of the variation in shape of the mandibles (Tab. 1). Principal Component Analysis was applied to the partial warp scores resulting in Relative Warp Analysis. In order to achieve equal scaling of each regional shape variation, the distortion parameter of Relative warps (principal component axes) was set at $\alpha = 0$. This procedure is the most suitable for exploratory and taxonomic studies (Rohlf 1993). The superimposing and Relative Warp Analysis were performed using the software TpsRelw version 1.46, a program to perform a Relative Warp Analysis developed by Rohlf at the Department of Ecology and Evolution (State University of New York). All software of the "TPS" series used in this work is freeware (http://life.bio.sunysb.edu/morph).

4.3.3 Abbreviations

Conventional abbreviations used in front of the year in the synonymy list follow Matthews (1973): * the work validates the species; . the authors agree on the identification; v the authors have seen the original material of the reference; ? the allocation of the reference is subject to some doubt; *non* the reference actually does not belong to the species under discussion; *pars* the reference applies only in part to the species under discussion; no sign the authors were unable to check the validity of the reference. Years in italics indicate a work without description or illustration.

i, lower incisive; **c**, lower canine; **p**, lower premolar; **m**, lower molar; **dext.**, right; **sin.**, left. **Sb**, selective browser; **Fl**, folivore; **Mx**, mixed feeder; **Gr**, grazer. **RWA,** Relative Warp Analysis; **Rw,** Relative warp.

AMNH, American Museum of Natural History (New York, United States); **ANSP,** Academy of Natural Sciences Philadelphia (United States); **BSPG,** *Bayerische Staatssammlung für Paläontologie und Geologie* (München, Germany); **CI,** Chichester Inc. (New York, United States); **IPHEP,** *Institut International de Paléoprimatologie, Paléontologie Humaine: Évolution et Paléoenvironnements, Université de Poitiers* (France); **MHNF**, *Musée d'histoire naturelle de Fribourg* (Switzerland); **MJSN**, *Musée jurassien des sciences naturelles* (Switzerland); **MNHN**, *Musée national d'Histoire naturelle* (Paris, France); **NMB**, *Naturhistorisches Museum Basel* (Switzerland); **USTL**, *Université des Sciences et Techniques du Languedoc* (Montpellier, France).

4.4 Systematic palaeontology

Order **Cetartiodactyla** Montgelard, Catzeflis & Douzery 1997
Suborder **Ruminantia** SCOPOLI 1777
Infraorder **Tragulina** FLOWER 1883
Family **Tragulidae** MILNE-EDWARDS 1864
Genus ***Iberomeryx*** GABUNIA 1964

Type species– Iberomeryx parvus Gabunia 1964, from Benara (Georgia), Early Oligocene (MP23; Lucas & Emry 1999).

Other species referred to the genus– Iberomeryx minor (Filhol 1882), Early Oligocene of Western Europe.

Iberomeryx minor (Filhol 1882)

Synonymy (updated from Sudre 1984)

non	1877	*Lophiomeryx gaudryi* Filhol: 447, figs. 279–280.
*	*1882*	*Bachitherium minor* – Filhol: 138.
pars	1886	*Cryptomeryx gaudryi* – Schlosser: pl. II, figs. 13–14.
v	*1910*	*Cryptomeryx gaudryi* – Fleury: 277.
v	*1914*	*Cryptomeryx gaudryi* – Stehlin: 184.
	1926	*Cryptomeryx gaudryi* – Carlson: 69.
	1962	*Cryptomeryx* – Friant: 114.
	1966	cf. *Cryptomeryx gaudryi* – Palmowski and Wachendorf: 241, pl. 15, fig. 7.
	1967	*Cryptomeryx* – Friant: 96.
	1973	*Bachitherium* ? sp. – Bonis et al.: tab. 2(4).
?	*1978*	*Cryptomeryx* cf. *gaudryi* – Heissig: 271, tab. 4.
v	1979	*Cryptomeryx gaudryi* – Gaudant: 889, figs. 17–20.
	1980	*Cryptomeryx* – Webb and Taylor: 124.
v	1984	*Cryptomeryx gaudryi* – Sudre: 6, figs 1–9.
*	1986	*Iberomeryx minor* – Bouvrain et al.: 102, fig. 2.
.	1987	*Iberomeryx minor* – Geraads et al.: 44, figs. 16, 27, 36.
?	*1987*	*Iberomeryx matsoui* – Heissig: 108, fig. 6.
v	*1996*	*Iberomeryx minus* – Sudre & Blondel: 178, tab. 1.
v	*1997*	*Iberomeryx minus* – Blondel: 584, tabs. 8–9.
v.	2004	*Iberomeryx minor* – Becker et al.: 184, fig. 5.
	2007	*Iberomeryx minus* – Métais and Vislobokova: 195.

Holotype– fragmentary mandible with tooth row p3–m3 dext. (MNHN QU4234; Bouvrain et al. 1986: 103, fig. 2). Filhol (1882) first described this type as a tooth row p2–m3 dext., but p2 has been lost.

Type locality – Unknown (from the old collections of the Phosphorites du Quercy, SW France).

Stratigraphical range– Early Oligocene, mainly MP23 sites in Western Europe: Soulce**,** Beuchille and Pré Chevalier in Switzerland; Itardie, Mounayne, Roqueprune 2 and Lovagny in France; and Montalban in Spain (Gaudant 1979; Sudre 1984; Remy et al. 1987; Blondel 1997; Becker et al. 2004).

Referred material (Fig. 4)– NMB Sc.118 (Gaudant 1979: 889), tooth row with m1–m3 dext. and nearly complete mandible with p2–p4 sin. from the Soulce locality (NW Switzerland).

Compared material (Fig. 5)– MJSN BEU001–409 (old number BEU-700-J1; Becker et al. 2004: 184, fig. 5), fragmentary tooth row with m1–m3 dext. from the Beuchille locality (NW Switzerland); MJSN BEU001–410 (new material), fragmentary mandible with p4 dext. from the Beuchille locality (NW Switzerland); MJSN BEU001–411 (new material), fragmentary mandible with m1–m2 dext. from the Beuchille locality (NW Switzerland); MJSN PRC004–159 (new material), fragmentary mandible with p4–m3 dext. From the Pré Chevalier locality (NW Switzerland); NMB Q.B.32 (Sudre 1984: 11, fig. 5), fragmentary mandible with p3–m3 sin. from the older collection of the Phosphorites du Quercy (SW France).

Emended diagnosis– Small-sized ruminant with upper molars possessing the following combination of characters: well-marked parastyle and mesostyle in colonnette shape; strong paracone fold; metacone fold absent; metastyle absent; unaligned external walls of metacone and protocone; strong postprotocrista stopping up against the anterior side of the praehypocrista; continuous lingual cingulum, stronger under the protocone. Lower dental formula is primitive (3–1–4–3) with unmolarized premolars. Tooth c is adjacent to i3. Tooth p1 is one-rooted, reduced and separated from c and p2 by a short diastema. Premolars have a well-developed protoconulid. Teeth p2–p3 display a distally bifurcated hypoconid, forming a posterior fossette. Tooth p3 is the largest premolar. Tooth p4 displays no metaconid and a large posterior fossette nearly closed by unfused lingual and labial cristids. Regarding the lower molars, the trigonid and talonid are lingually open with a trigonid more tapered than the talonid. The anterior fossette is open, due to a forward orientation of the praeprotocristid and an anterior protoconulid. The postprotocristid is oblique, without *Palaeomeryx* fold. Postprotocristid, postmetacristid and praeentocristid are fused and Y-shaped. Protoconid and metaconid display a weak *Tragulus* fold and a well-developed *Dorcatherium* fold, respectively. The mandible displays an angular convex ventral profile, a marked *incisura vasorum*, a strong mandibular angular process, a vertical ramus, and a stout condylar process. It differs from *I. parvus* by larger trigonids on the lower molars and a smaller protoconulid and a larger posterior fossette on p4.

4.4.1 Description

The referred specimens from Soulce (NMB Sc.118; Fig. 4) are composed of a part of a tooth row sin. bearing m1-3 (Figs. 4a1, 4b1–b2) and a nearly complete mandible dext. bearing p2-4 as well as its counterpart with an imprint of m1-3 (Figs. 4a2, 4c1–c2). Both tooth rows have a

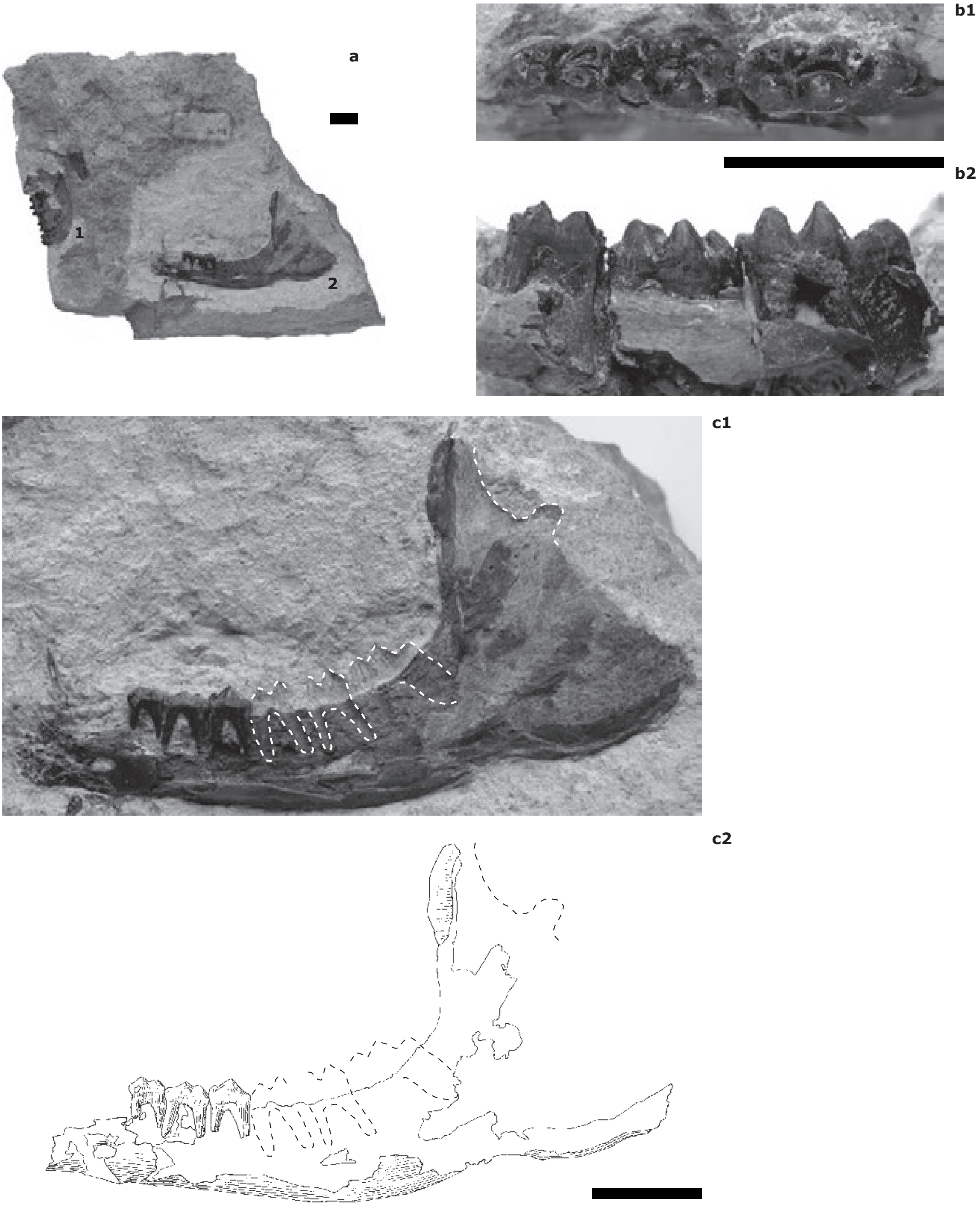


Fig. 4: *Iberomeryx minor* specimens (NMB Sc.118) from the lacustrine lithographic limestone bed of Soulce (Early Oligocene, north-central Jura Molasse, NW Switzerland). Scale bars: 1cm. Tooth row with m1–m3 dext., lingual view photograph (**a1**, **b2**), occlusal view photograph (**b1**); nearly complete mandible with p2–p4 sin., labial view photograph (**a2**, **c1**), labial view drawing (**c2**).

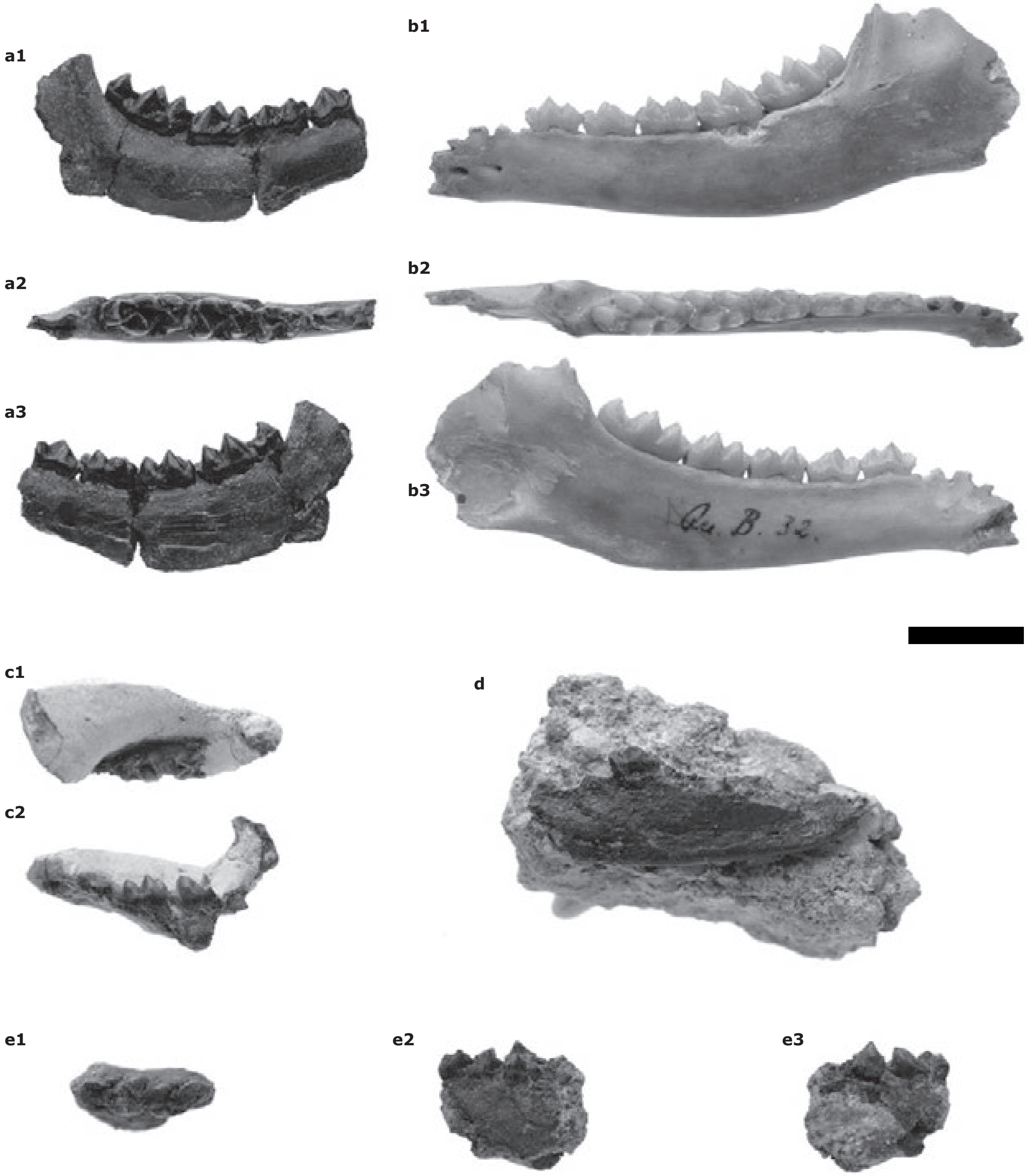


Fig. 5: Compared material. *Iberomeryx minor* specimens from the localities Pré Chevalier and Beuchille (Early Oligocene, north-central Jura Molasse, NW Switzerland) and from the Phosphorites du Quercy (old collections, SW France). Scale bar for all figures: 1 cm. **a,** Pré Chevalier (MJSN PRC004–159), fragmentary mandible with p4–m3 dext., labial view (**1**), occlusal view (**2**), lingual view (**3**); **b,** Phosphorites du Quercy (NMB Q.B.32), fragmentary mandible with p3–m3 sin., labial view (**1**), occlusal view (**2**), lingual view (**3**); **c,** Beuchille (MJSN BEU001–409), fragmentary tooth row with m1–m3 dext., occlusal view (**1**), lingual view (**2**); **d,** Beuchille (MJSN BEU001–410), fragmentary mandible with p4 dext., lingual view; **e,** Beuchille (MJSN BEU001–411), fragmentary mandible with m1–m2 dext., occlusal view (**1**), labial view (**2**), lingual view (**3**).

Tab. 2: Dental length (in mm) of lower cheek teeth of *Iberomeryx minor* from Soulce, Beuchille, and Pré Chevalier (Early Oligocene, north-central Jura Molasse, NW Switzerland) and from Itardies and the old collections of the Phosphorites du Quercy (Oligocene, SW France), and of compared Paleogene Tragulina. *, data from literature; **n,** specimen number; **(),** measured from the tooth imprint in the sediment of the referred mandible specimen (NMB Sc.118) from Soulce.

Localities	**Inventory number**	**References**	**p2**	**p3**	**p4**	**m1**	**m2**	**m3**
Iberomeryx minor								
Soulce	NMB Sc.118 sin.	figured by Gaudant (1979)	3.7	4.3	3.9	(4.4)	(5.4)	(7.9)
	NMB Sc.118 dext.	figured by Gaudant (1979)				4.4	5.8	8.2
Beuchille	MJSN BEU001–411						4.9	
	MJSN BEU001–410				4.7			
	MJSN BEU001–409	figured by Becker et al. (2004)					4.9	
Pré Chevalier	MJSN PRC004–159				4.0	5.1	5.3	8.1
Itardie	USTL ITD28	Sudre (1984)						8.1*
	USTL ITD29	Sudre (1984)						8.5*
Quercy (old collections)	–	figured by Schlosser (1886); Sudre (1984)			4.4*	4.8*	5.0*	7.5*
	NMB Q.B.29				4.0	4.4	5.0	7.8
	NMB Q.B.32	figured by Sudre (1984)		5.4	4.7	5.2	5.4	8.6
	NMB Q.B.197	partially figured by Sudre (1984)	3.8	4.6	4.2	4.6		
	NMB Q.W.540						6.1	8.2
	NMB Qu.B.30						5.5	7.8
	NMB Qu.B.31						5.4	7.6
		n	2	3	7	7	11	11
		Mean	3.8	4.8	4.3	4.7	5.3	8.0
		Standard deviation	0.1	0.6	0.3	0.3	0.4	0.3
Archaeotragulus krabiensis								
Krabi (Thailand)		Métais et al. (2001)	5.5 (n=1)*	7.2 (n=1)*	7.0 (n=1)*	7.0 (n=2)*	7.3 (n=2)*	10.5 (n=1)*
Nalameryx savagei								
Bugti Hills (Pakistan)		Métais et al. (2009)				5.7 (n=?)*	6.2 (n=?)*	
Kargil (India)		Nanda & Sani (1990)			4.3 (n=2)*	5.0 (n=3)*	5.7 (n=2)*	8.3 (n=1)*
Lophiomeryx mouchelini								
Villebramar (France)		Brunet & Sudre (1987)	9.8 (n=2)*	11.8 (n=5)*	11.2 (n=5)*	10.2 (n=5)*	11.2 (n=6)*	17.2 (n=5)*
Krabimeryx primitivus								
Krabi (Thailand)		Métais et al. (2001)			6.3 (n=2)*	9.1 (n=1)*	8.6 (n=3)*	13.0 (n=3)*
Zhailimeryx jingweni								
Tuqiaogou (China)		Guo et al. (2000)			6.7 (n=1)*	6.6 (n=2)*	7.0 (n=2)*	

similarly advanced degree of wear and could belong to the same individual. All measurements are summarized in Table 2.

Tooth p1 is one-rooted, the other premolars are two-rooted, weakly differentiated and only display a very slight molarization on p3-4. The protoconulid of p2-3 is completely worn. On p3-4 and the molars, the anterior labial cingulid is well developed (slightly damaged on m1-3 due to the preparation of the specimen). Teeth p2-3 have the same occlusal pattern: elongated outline (p3 is of the same dimension as m1) with the presence of a hypoconid (absent on p4) and a closed basin backward of the latter. On p4, the metaconid is absent and the protoconulid is slightly oblique and separated from the protoconid by a deep groove.

Lower molar cuspids are bunoselenodont, high, and quite tapered (Fig. 4b2). The protoconid is spherical and displays a shallow and broad groove forming a weak *Tragulus* fold; the *Paleomeryx* fold is absent. The metaconid displays a deep incisure on its posterior part, characteristic of the *Dorcatherium* fold, forming an open buckle on the lingual side of the crown. The exostylid is always present between the protoconid and the hypoconid. The entoconid is well rounded on its posterior part, without postentocristid, giving a spherical aspect to the proximal half of the lower molars. The anterior part of the entoconid is tapered, with a relatively striking praeentocristid that joins the postmetacristid and forms a keel as described by Sudre (1984). This keel is lingually slightly concave, but does not form a real *Zhailimeryx* fold. The postmetacristid, postprotocristid and praeentocristid are converging and Y-shaped. The anterior valley is open forwards; the praehypocristid and the posthypocristid are angular with a right dihedron; the talonid is broader than the trigonid. Tooth m1 is trapezoid and m2 is rectangular. Following the same pattern as p4, the anterior part of the trigonid on m1 is elongated in front of the metaconid by a strong protoconulid. The latter is decreasingly well developed on m2-3. The entoconulid on m1-2 is weakly developed and separated from the entoconid by a groove. A posterior cingulid surrounds the base of the hypoconulid on m3 (Fig. 4b1).

The mandible outline is stout. Its anterior part is fragmented, but nevertheless displays a double *foramen*

Tab. 3: Morphological comparison (mandible, lower cheek teeth, astragalus, metatarsal) between extant Tragulina (Tragulidae), primitive Tragulina (*Archaeotragulus*, *Iberomeryx*, *Nalameryx*, *Nanotragulus*, *Leptomeryx*, *Lophiomeryx*, *Krabimeryx*, *Zhailimeryx*, *Bachitherium*), Miocene Tragulina (*Dorcatherium*)*,* primitive Pecora*,* (*Gelocus*, *Prodremotherium*), and Miocene Pecora (*Dremotherium*, *Procervulus*).

	TRAGULINA											**PECORA**			
	Tragulidae					**Hyper-traguli-dae**	**Lepto-meryci-dae**	**Lophiomerycidae**			**Bachi-teriidae**	**Gelocidae**		**Moschi-dae**	**Cervi-dae**
	Extant Tragulidae	***Archaeotragulus***	***Dorcatherium***	***Iberomeryx***	***Nalameryx***	***Nanotragulus***	***Leptomeryx***	***Lophiomeryx***	***Krabimeryx***	***Zhailimeryx***	***Bachitherium***	***Gelocus***	***Prodremothe-rium***	***Dremotherium***	***Procervulus***
body size	medium	small	medium	small				medium	small		small to medium	small	medium		
mandible ventral profile	angular convex	?	angular convex		?	straight		regular convex	?	angular convex	straight	regular convex	?	regular convex	
incisura vasorum	weak	?	marked		?	marked	weak	marked	?		weak	marked	?	strong	
ramus inclination	vertical	?	vertical		?	subvertical	vertical	subvertical	?		backwards		?	backwards	
condylar process	stout	?	stout					?			stout		?	stout	slender
diastema c/cheek teeth	short	?	short		?	short		long	?	short	long				
p1	absent	?	present						?	present			absent		
p1 shape	–	?	leaf-like	?	leaf-like	tusk-like	small conical	leaf-like	?	leaf-like	tusk-like	small conical	–		
diastema p1/p2	–	?	absent	present	?	present			?	present			–		
lower premolar	short narrow	elongate narrow	short and narrow				short wide	elongate narrow	?	short and wide		elongate and wide			
p2-3 posterior basin	closed (blade-like)	?	closed			open	closed	open	?	open	closed	open			
p3 longer than p4	yes				?	no	equal	yes	?		equal	no			
p4 smaller than m1	equal		yes			equal	yes	no		equal		no			
p4 entoconid	absent						present	absent					present		
p4 metaconid	absent					present					absent	present			
p4 posterior valley	nearly closed fossette					wide ling. open	narrow post. open	wide and lingaully open			nearly closed fossette	wide ling. open	narrow and lingually open		
p3-m3 ant. cingulid	marked	strong	marked	strong		strong	weak	strong					weak		
m occlusal morphology	bunoselenodont					selenodont		bunoselenodont			selenodont				
m Y-shape config.	present					absent			present		absent				
m trigonid shape	open					closed		open			closed				
m talonid shape	open					closed		open			closed				
m *Palaeomeryx* fold	absent						variable	absent				variable	absent	présent	
m *Dorcatherium* fold	present					absent	variable	absent	present		absent				
m *Tragulus* fold	present					absent	?	absent	?	absent					
m praeprotocristid	anteriorly oriented					lingually oriented		anteriorly oriented				lingually oriented			
m protoconulid	present					absent			present		absent				
m postentocristid	absent					present		absent			present	variable	present		
m praemetacristid	present	absent	present	absent		present		absent			present				
m metacone-paracone	angular	?	angular			aligned	angular	aligned	angular	aligned	angular	aligned			
trochlea astragal angle	present	?	present				absent	present	?		present	absent			
astragal articular facet	no crest	?	no crest		crest	?		crest	?		no crest				
metatarsal bone	partly fused	?	partly fused		?	unfused	partly fused	unfused	?		fused				

mentale located under the short diastema p1/2. The *corpus mandibulae* presents an angular convex ventral profile. The *incisura vasorum* is rounded, well marked, and located under the anterior border of the ramus. The latter is almost vertical. The angular, coronoid and condylar processes are only partially preserved, nonetheless some observations can be noted: the angular process is high, large and smoothly rounded (relatively large and with constant radius); the coronoid process is marked; the condylar process, the outline of which can be reconstructed due to the association of the preserved fossil (head) and imprint (neck), is very stout (Figs. 4c1-c2).

4.4.2 Taxonomical affinities

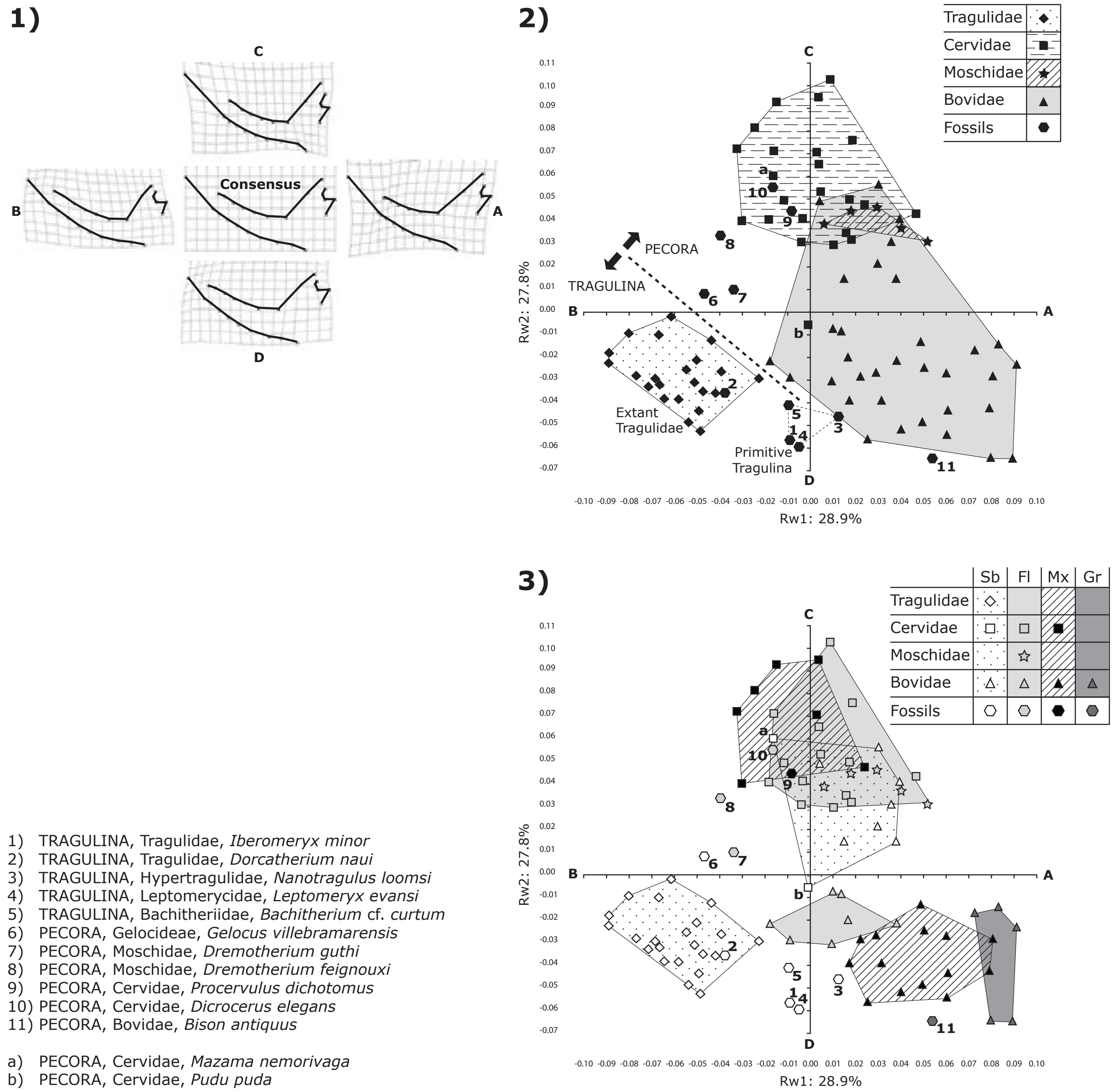
Table 3 summarizes the morphological comparisons between primitive and Miocene ruminants (Tragulina and Pecora) and extant tragulids. The specimens from Soulce (NMB Sc.118; Fig. 4) were first mentioned by Stehlin (in Fleury 1910) and first described by Gaudant (1979) as *Cryptomeryx gaudryi*. They correspond to a very small-sized ruminant, smaller than the European *Lophiomeryx* and *Prodremotherium* species. The diastema between p1/p2 observed on the nearly complete mandible (Figs. 4a2, 4c1–c2) is proportionally shorter than those of the Western European *Bachitherium*, North American *Leptomeryx*, and Eurasiatic *Lophiomeryx*. The *incisura vasorum* of the mandible is similar to those of *I. minor* (Figs. 5b1, 5b3) from the Phosphorites du Quercy (SW France) and stronger than those of *Bachitherium* and *Leptomeryx.* Moreover p2–3 differ from *Bachitherium* by the presence of a hypoconid and p4 differs from the Hypertragulidae (*Nanotragulus*), Leptomerycidae (*Leptomeryx*), Lophiomerycidae (*Lophiomeryx*, *Krabimeryx*, *Zhailimeryx*), Gelocidae (*Gelocus*, *Prodremotherium*), and modern Pecora (*Dremotherium*, *Procervulus*) by the absence of a metaconid (Geraads et al. 1987; Guo et al. 2000; Métais et al. 2001). The lower molars of *Lophiomeryx* as well as of the Hypertragulidae (*Nanotragulus*), Leptomerycidae (*Leptomeryx*), Bachitheriidae (*Bachitherium*), and Pecora (*Gelocus*, *Prodremotherium*, *Dremotherium*, *Procervulus*) also differ by the absence of the typical Y-configuration and, contrary to Blondel (1997), also by the absence of a *Dorcatherium* fold (variable in *Leptomeryx*). The specimens from Soulce (Fig. 4) exhibit the same dental pattern (e.g., hypoconid on p2–3, metaconid absent on p4 as well as protoconulid present, open trigonid and talonid, a strong *Dorcatherium* fold, and Y-configuration on lower molars) as *Archaeotragulus, Iberomeryx* (Fig. 5), *Nalameryx*, *Dorcatherium,* and extant Tragulidae. According to the description of Métais et al. (2001), *Archaeotragulus* teeth bear many characters that differ from the Soulce specimens (e.g., larger size, p4 of the same dimension as m1, lower molar praehypocristid less-lingually oriented; see Tabs. 2, 3). *Dorcatherium* shows teeth more bunodont and larger in size (Sudre 1984). Most modern Tragulidae (e.g., *Tragulus*, *Moscholia*) have derived lower premolars with a transformation of the posterior basin to a cristid, that gives the teeth a blade shape. The morphometric data (Tab. 2) is very similar to that of *Iberomeryx minor* from the Phosphorites du Quercy (SW France) and from the Jura Molasse (NW Switzerland), but also to that of the small species of the genus *Nalameryx* (*N. savagei*) from Kargil (India) and the Bugi Hills (Pakistan). However, the lower molars of *N. savagei* differ because of the presence of a more developed *Tragulus* fold and an oblique less-lingually oriented cristid (Métais et al. 2009).

In this study the emended diagnosis of *I. minor* is based on dental and mandible morphology, such as a well-developed *Dorcatherium* fold, a large posterior fossette closed by unfused lingual and labial cristids on p4 and a marked *incisura vasorum*. Therefore, the referred specimens from Soulce (Fig. 4) as well as those from Beuchille (Figs. 5c1–c2, 5d, 5e1–e3) and Pré Chevalier (Figs. 5a1–a3) can be confidently assigned to *I. minor.*

4.5 Relative Warp Analysis

The 24 anatomic landmarks generated 44 axes (Rw's) for each ruminant mandible. The results of the Rw's, using shape components, permitted the distinction of different groups of ruminants based on the total difference of the mandible shape. Rw1 explained 28.9% and Rw2 27.8% respectively. This means that 56.6% of shape variance (Fig. 6), can be explained without the use of other Rw's. On Rw1, elongation of the premolars is positively associated with the enlargment of the condylar process and the forward projection of the ramus (see shape deformation grids in Fig. 6.1). On Rw2 the diastema c/cheek teeth elongation, the shallowing-up *corpus mandibulae* and the development of the *incisura vasorum* occur in a positive variance (see shape deformation grids in Fig. 6.1).

Both Rw1 and Rw2 are informative from both a phylogenetic (Fig. 6.2) and ecologic (Fig. 6.3) perspective. Theses two Rw's permit the discrimination of the Ruminantia infraorders, Tragulina and Pecora. The group characters of extant Tragulina (see shape deformation grids in Fig. 6.1) are a weak *incisura vasorum*, a vertical ramus, a short coronoid process inclined backwards, a stout condylar process, a rather short diastema c/cheek teeth, and enlarged premolars (p3 being the largest). The extant Tragulina plot in the negative-values domain of both Rw1 and Rw2 (Fig. 6.2). Contrarily, the Pecora (Cervidae, Moschidae, Bovidae) mainly plot as positive Rw1 values , and negative and positive Rw2 values. The Bovidae values are preferentially but not exclusively located in the negative domain while the Cervidae values plot preferentially in the positive domain and Moschidae are located in the mixed area between Cervidae and Bovidae (Fig. 6.2). The Pecora mandible shape is



1) TRAGULINA, Tragulidae, *Iberomeryx minor*
2) TRAGULINA, Tragulidae, *Dorcatherium naui*
3) TRAGULINA, Hypertragulidae, *Nanotragulus loomsi*
4) TRAGULINA, Leptomerycidae, *Leptomeryx evansi*
5) TRAGULINA, Bachitheriidae, *Bachitherium* cf. *curtum*
6) PECORA, Gelocideae, *Gelocus villebramarensis*
7) PECORA, Moschidae, *Dremotherium guthi*
8) PECORA, Moschidae, *Dremotherium feignouxi*
9) PECORA, Cervidae, *Procervulus dichotomus*
10) PECORA, Cervidae, *Dicrocerus elegans*
11) PECORA, Bovidae, *Bison antiquus*

a) PECORA, Cervidae, *Mazama nemorivaga*
b) PECORA, Cervidae, *Pudu puda*

Fig. 6: RWA for distortion parameter $\alpha = 0$ of ruminant mandibles obtained from 11 fossil specimens (*Bison antiquus*, *Dicrocerus elegans*, *Dremotherium feignouxi*, *Dremotherium guthi*, *Gelocus villebramarensis*, *Procervulus dichotomus*, *Brachitherium* cf. *curtum*, *Dorcatherium naui*, *Iberomeryx minor*, *Leptomeryx evansi*, *Nanotragulus loomsi*; see Tab. 2) and 83 extant specimens (see Tab. 2). **1)** Shape deformation grids representing the mean shape (consensus) and the maximum values of the two first Relative warps (Rw's). **2)** Scatter plots of the first versus the second Rw with taxonomic characterization. The A axis indicates the shape variation of the mandible "warped" from the mean shape (consensus) into the maximum positive deviations in the axis of Rw1; the B axis the shape variation of the mandible "warped" from the mean shape (consensus) into the maximum negative deviations in the axis of Rw1; the C axis the shape variation of the mandible "warped" from the mean shape (consensus) into the maximum positive deviations in the axis of Rw2; and the D axis the shape variation of the mandible "warped" from the mean shape (consensus) into the maximum negative deviations in the axis of Rw2. **3)** Indication of the diet. A, B, C, and D axes as in **2)**.

characterized by a strong *incisura vasorum*, a ramus inclined backwards, a developed coronoid process, a slender condylar process, a long diastema c/cheek teeth, and shortened premolars (see shape deformation grids in Fig. 6.1). However, there is also some feeding-habit dependant variation of the mandible shape (Fig. 6.3).

Grazers plot exclusively in the quadrant defined by positive Rw1 values and negative Rw2 values. In the lower half of the graph, defined by negative Rw2 values and positive Rw1 values, a trend from grazers over mixed feeder to folivore Bovidae is discriminated with decreasing Rw1 values. Selective browser Tragulidae are characterized by negative values of both Rw1 and Rw2. On the other hand, Cervidae with different feeding adaptations, Moschidae and selective browser Bovidae mainly have positive Rw2 values (Fig. 6.3).

Extinct taxa present two types of cases. Middle Miocene to Pleistocene Ruminantia plot together with their extant relative family (e.g., *Dorcatherium naui* within extant Tragulidae; Figs. 6.2–3), whereas peculiar shapes occur among more primitive extinct groups (e.g., primitive Tragulina; Figs. 6.2–3).

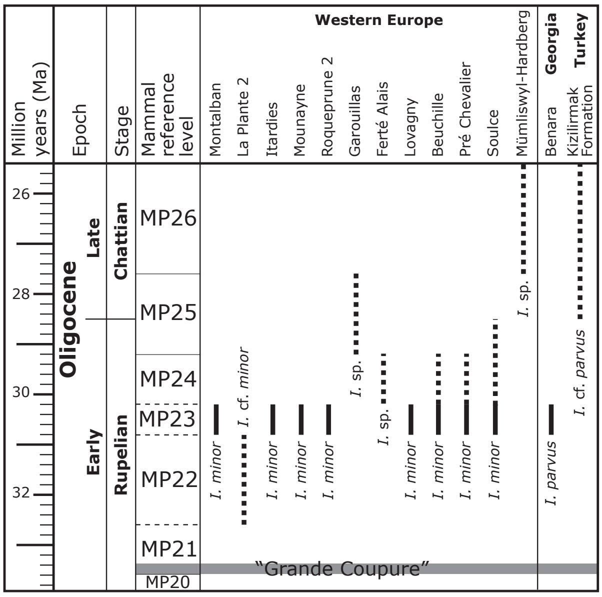


Fig. 7: Synthesis of the Oligocene occurrences of Eurasian *Iberomeryx*. The chronostratigraphy and Mammal reference levels are based on Luterbacher et al. (2004). The time interval (ca. 33.6–33.4 Ma) of the "Grande-Coupure" event (Stehlin 1910) is based on the high-resolution stratigraphy in the Belgian Basin after Hooker et al. (2004, 2009). The biochronostratigraphical ranges are revised in accordance with Remy et al. (1987), Sudre & Blondel (1996), Blondel (1997), Lucas & Emery (1999), Vianey-Liaud & Michaud (2003), Becker et al. (2004), and Antoine et al. (2008).

4.6 Discussion

4.6.1 Biostratigraphy

Figure 7 illustrates a biostratigraphic synthesis of the Oligocene Eurasian *Iberomeryx*. According to Sudre & Blondel (1996) and Blondel (1997), the earliest record of *Iberomeryx* can be dated to the European Mammal reference level MP22 thanks to a few specimens assigned to *I.* cf. *minor* from La Plante 2. On another hand, the latest record could be the specimens of *I.* cf. *parvus* provisionally identified by Antoine et al. (2008) from the Late Oligocene Kizilirmak Formation in Turkey. All other well-dated localities yielding *I. minor* can be assigned to the level MP23 (Montalban, Itardies, Monayne, Roqueprune 2). Lucas & Emery (1999) state that the age of the Benara locality, which is the type locality of *I. parvus*, also corresponds to the level MP23. The Swiss *I. minor* localities remain poorly dated. At the Beuchille locality, the upper 15 m of the section is dated by *Blainvillimys avus* and corresponds to MP24 (Vianey-Liaud & Michaud 2003; Becker et al. 2004). However, *I. minor* remains were discovered at the base of the section, just above a level yielding *Pseudocricetodon* cf. *montalbanensis* (MP23 after Brunet & Vianet-Liaud 1987 and Aguilar et al. 1997). Based on lithostratigraphy, the Pré Chevalier locality can be correlated with Beuchille and is probably of the same age. The *Iberomeryx minor* specimens from Soulce were recovered from the *Calcaires inférieurs* Formation. This lacustrine formation is laterally equivalent to other formations of the Swiss Jura Molasse (e.g., *Calcaires de Moutier*), and seems to be restricted to the Rupelian. Gaudant (1979) assigned an Oligocene age younger than MP21 to the bone bed of Soulce without confidence, because of the absence of *Iberomeryx* in Ronzon (MP21, France). Considering these biostratigraphic data, an age older than MP22 and even older than MP23 for *I. minor* seems very unlikely. To date, except for the *I.* cf. *minor* specimens of La Plante 2, no findings argument against its first occurrence within the European Mammal reference level MP23. Nonetheless, a slightly older or younger age can, at present, not be excluded with confidence.

4.6.2 Phylogenetic implications

Primitive Pecora and Tragulina mandible shapes differ slightly from those of their respective extant relatives (Fig. 6). The results of the RWA do not permit the separation of *Iberomeryx minor* from other Oligocene Tragulina Hypertragulidae (*Nanotragulus loomsi*), Leptomerycidae (*Leptomeryx evansi*), and Bachitheriidae (*Bachitherium curtum*) on behalf of the characteristics of its mandible shape. The primitive Tragulina form a homogenous group plotting between extant Tragulina and Bovidae and characterized by a mandible shaped similarly to that of a Suoid (short diastema c/cheek teeth, enlarged vertical ramus, *corpus mandibularis* and angular process, and p1 separated from other premolars). The mandible of the primitive Tragulina represents the rather basic shape throughout Tragulina evolution. *Gelocus villebramarensis* from the Early Oligocene has a shorter diastema and more elongated premolars with a relatively larger *corpus mandibularis* relative to extant Pecora, and can possess a p1 either isolated or adjacent to the premolars. Tooth p1 is not separated from the other premolars in *Dremotherium* and is absent in other Pecora. This evolutionary trend in p1 is associated with an elongation of the diastema c/cheek teeth. Even if *Gelocus* resembles "tragulid-like" taxa more than extant Pecora, it clearly has a more elongated diastema c/cheek teeth and a more slender general mandible shape than Oligocene Tragulina. In the genus *Dremotherium* (Late Chattian to Aquitanian), premolars become shorter and the *corpus mandibularis* becomes more slender. Finally, Miocene *Procervulus dichotomus* and *Dicrocerus elegans* cannot be distinguished from the extant Cervidae.

Our results support that phylogeny contributes to shape variation in ruminant mandibles. However, a confident assignment of *I. minor* to a Tragulina family is only possible if the overall set of its morphological and morphometrical characteristics is taken into account. Janis (1987), Métais & Vislobokova (2007), and Métais et al. (2009) considered *Iberomeryx* to belong to the Lophiomerycidae, and Blondel (1997) to be close to *Lophiomeryx*. Like *Lophiomeryx*, *Iberomeryx* has an open trigonid and an open talonid on the lower cheek teeth and an angle between the trochleas of the astragalus (Brunet & Sudre 1987). These dental features are also present in the primitive taxa *Krabimeryx, Archaeotragulus* (Métais et al. 2001), and *Zhailimeryx* (Guo et al. 2000). Additionally, the extant Tragulidae, *Bachitherium* or the Anoplotherioidea (a sister group of the Ruminantia) do not possess aligned trochleas. The aligned trochleas are a characteristic feature of the derived Ruminantia such as the Pecora (Martinez & Sudre 1995). Moreover, *Iberomeryx* differs from *Lophiomeryx* because of the astragalus articular facet with the cubo-navicular bone that does not bear a crest (Brunet & Sudre 1987; Martinez & Sudre 1995). The metatarsal bones of *Lophiomeryx* are not fused (Geraads et al. 1987; Blondel 1997) and, on the upper molars, the metacone and paracone are aligned contrary to *Bachitherium* (Ferrandini et al. 2000) and the Tragulidae. The pattern of the lower cheek teeth of *Iberomeryx* and *Lophiomeryx* is totally different, although the trigonid and talonid are open in these two taxa. The open trigonid in *Iberomeryx* is accounted for by the presence of a small protoconulid in front of the protoconid, whereas it is due to the anterior orientation of the praeprotocristid in *Lophiomeryx.* The lower molars of *Iberomeryx* bear a Y-shape on the cristids and a deep *Dorcatherium* fold on a well-individualised metaconid. These characteristic features are known from Miocene Tragulidae. The *Dorcatherium* fold is absent in *Lophiomeryx* and the metaconid, which is simple, thin, and conical, is located in the axis of the postprotocristid (Brunet & Sudre 1987, Janis 1987). Even if *Iberomeryx* shares many primitive features with *Lophiomeryx*, there are evident differences in the features (e.g., *Dorcatherium* fold, *Tragulus* fold, general premolar shape) that relate it rather to the Tragulidae than to the Lophiomerycidae as suggested by Stehlin (1914), Carlson (1926), Webb & Taylor (1980), and Sudre (1984).

Rössner (2007) and Sánchez et al. (2010) only considered *Archaeotragulus* from the Eocene, *Afrotragulus*, *Dorcatherium*, *Dorcabune*, *Siamotragulus*, *Yunannotherium* from the Neogene and the three extant genera (*Tragulus*, *Hyemoschus*, *Moscholia*) to be representatives of the Tragulidae. The Paleogene fossil record of tragulids is extremely poor and Oligocene tragulid evolution lacks fossil evidence (Gentry and al. 1999, Métais and al. 2009). Without more data, even the affiliation of *Archaeotragulus* to the Tragulidae remains debatable (Métais et al. 2009). *Nalameryx savagei* shows morphological and morphometrical features very similar to those of *Archaeotragulus* and *Iberomeryx*. The two species of *Nalameryx* (*N. savagei*, *N. sulaimani*) have been placed in the Lophiomerycidae due to an open trigonid on the lower molars, the absence of a praemetacristid and an antero-lingual orientation of the praeprotocristid (Métais et al. 2009). They share these characteristic features with the Tragulidae. *Nalameryx* genus could thus also be considered as a representative of the Tragulidae from the Oligocene.

4.6.3 Palaeodiet

The RWA of this study reveals progressive trends in the shape of the mandible of extant and some fossil ruminants related to their feeding habits (selective browser, folivore, mixed feeder and grazer). The only evident anomaly in the RWA concerns the position of the small, South American Cervidae *Mazama nemorivaga* among the mixed feeder (-folivore) cervids (Fig. 6.3). This species is known to feed on fruits and leaves. Its recent ancestor was a larger leaf eater ruminant (Eisenberg 2000), which later became a small sized frugivore/folivore. This might explain the position of *M. nemorivaga* near the folivore cervids, contrariwise to the position of *Pudu puda*, which is also a small, South American, extant frugivore/folivore Cervidae. Dwarfism and fruit feeding seem to have appeared independently and at different times in these two taxa (Eisenberg 2000).

Since the Middle Miocene, the feeding-habit related mandible shapes have been similar to those of extant ruminants. In the primitive ruminants, this relation is not evident. The mandible shapes of primitive Tragulina do not permit to differentiate between different feeding adaptations (Fig. 6.3). However, the primitive Tragulina analysed in this study form a distinctive group. *Leptomeryx evansi* was a C3-browser *sensu lato* (Wall & Collins 1998; Zanazzi & Khon 2008), comparable to extant *Pudu puda* and the genus *Tragulus*, which both are selective browsers (Wall & Collins 1998; see Tab. 1). The small Hypertragulidae *Nanotragulus loomsi* fed on soft food such as fruits or leaves, and possibly insects (Métais & Vislobokova 2007). According to a microwear study of Blondel (1996), *Bachitherium curtum* was a selective browser feeding on leaves and fruits. In addition, *Iberomeryx minor* possessed a large coronoid process, which indicates that the temporalis muscle and therefore the orthal retraction phase of the chewing cycle (food acquisition phase of mastication) were important similar as in *Leptomeryx evansi* and browsers *sensu lato* (Wall & Collins 1998). The angular process has nearly the same shape within primitive and extant Tragulina (quiet wide masseteric fossa). Cheek teeth are brachyodont, but with sharper and higher bunoselenodont cusps than in extant Tragulidae, which are nearly of same size.

Within mammalian herbivores, the total metabolic requirement increases with weight but with a decreasing rate. Large forms require more total energy, but small forms require more energy with respect to their weight (Kleiber 1975). Regarding the same metabolism and the same diet, the retention time is shorter for small animals. Fruits contain proportionally less cell wall (hemicellulose, cellulose and lignin) than leaves and grass (Demment & Soest 1985). Thus, a heavier animal can develop a diet including lower-quality food (more cell wall, less energy). Hope (1977) interpreted the negative correlation between fermentation rate and increasing body mass as a decrease in the proportion of dicotyledons with respect to monocotyledons in the diet. Such a categorisation of diets in function of the body mass can also be observed in ruminants (Bodmer 1990). Small-sized Tragulidae can eat fruits and significant amounts of animal matter such as insects, crabs, carrion and fish (Sudre 1984; Métais & Vislobokova 2007; Rössner 2007). That is why *Iberomeryx minor* should be selective browser, and could also eat some insects, similar to extant Tragulidae.

4.7 Conclusions

Both phylogeny and feeding adaptation contribute to the variation in the shape of ruminant mandibles. However, without taking into account other morphological and morphometrical characteristics, notably the dental structure, our RWA does not supply sufficient information to discuss taxonomy higher than at family level. Furthermore confident feeding category discrimination, more advanced than grazer versus browser, cannot be achieved. Only the combined fundamental study of comparative anatomy and RWA permit our taxonomic and ecologic deductions on the species *Iberomeryx minor*. The latter is a primitive ruminant characteristic for the Rupelian and probably restricted to the European mammal reference level MP23. *Iberomeryx minor* as well as possibly *Nalameryx* should be considered as the only Tragulidae from the Oligocene and thus the missing link between the enigmatic Eocene Asiatic “tragulid-like” *Archaeotragulus* and the classical Neogene and extant tragulids (*Afrotragulus*, *Dorcatherium*, *Dorcabune*, *Siamotragulus*, *Yunannotherium*, *Tragulus*, *Hyemoschus*, *Moscholia*). Moreover, *Iberomeryx minor* should be considered as a selective browser, similar to extant Tragulidae, which also fed on animal matter.

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5 - EARLY OLIGOCENE EUROPEAN RUMINANTIA (MAMMALIA): COMMUNITIES AND EVOLUTION

In preparation for *Paleontographica*

5.1 Introduction

The ruminants are the most ecologically and geographically diverse group of living ungulates since the Neogene (Janis & Scott 1987; Mennecart et al. accepted). They first appeared during the Eocene in North America and Asia (Guo et al. 2000; Métais et al. 2001; Métais & Vislobokova 2007), whereas many authors signalled occurrences of the Gelocidae *Phaneromeryx gelyensis* (Saint-Gély-du-Fesc, France), *Rutitherium nouleti* (Caylux, France), and "*Gelocus*" *minor* (Mormont, Switzerland) in Late Eocene deposits of Western Europe (Gervais 1848; Filhol 1876, 1877; Pavlov 1900; Stehlin 1910; Ginsburg & Hugueney 1987; Jehenne 1987; Sudre & Blondel 1996; Blondel 1997; Guo et al. 2000; Blondel 2001; Métais & Vislobokova 2007). Unfortunately, no direct observations of remains of *Phaneromeryx gelyensis* and "*Gelocus*" *minor* have been made due to the loss of the specimens. Moreover, the illustrations and descriptions of the mandible of *Phaneromeryx* published by Gervais (1848-52, fig.24, pl.14) and Jehenne (1985, fig.4) underline selenodont lower cheek teeth with elongated and narrow premolars bearing a small postmetacristid, and derived molars bearing an entostylid and a postentocristid, and without an external postprotocristid. These characteristics clearly differ from the primitive Gelocidae appearing to be more similar to the derived Mosaicomerycidae (chapter 6). Also, the age of these supposed Eocene localities is uncertain.

The lignite from Coulondres, near Saint-Gély-du-Fesc, is clearly attributed to the Eocene (De Rouville 1894; Roman 1897, 1903), but other younger coal deposits have also been discovered in the area of Saint-Gély-du-Fesc (Hardenberg et al. 1970). Moreover, a precise stratigraphical context of the only referred specimen of *Phaneromeryx* is lacking (Sudre 1978; Jehenne 1985; Métais & Vislobokova 2007) and, after other taxa were discovered in the coal deposits of Saint-Gély-du-Fesc such as *Plagiolophus* or *Palaeotherium*, an Oligocene age cannot be excluded (Remy 2000; Hooker et al. 2009).

The Caylux locality, where *Rutitherium* remains have been described, is a karstic region with many phosphorus bearing fissure-fillings that were exploited during the second half of the XIXth century. The first discovery by J.-A. Poumarède of these phosphorus deposits dates from 1860 (Gèze 1994). In an area of 2 km around the town of Caylux, nearly 10 phosphorus fillings have been exploited. Some of these fillings can be separated by hundreds of meters and contain distinct faunas of different ages, such as Pech Crabit (MP23) and Mass de Pouffié (MP26). In the case of Caylux fossils, the exact provenance of the specimens remains unknown, leading to a combination of Eocene and Oligocene fissure fillings. Bouvrain et al. (1986) reassessed *Rutitherium nouleti*. The holotype, figured by Filhol (1877, figs. 281-282), possesses an elongated and narrow p4. The lower molars lack an external postprotocristid, the cuspids are quite bunodont, and the postentocritstid seems missing. They concluded that the holotype is in fact a *Gelocus communis*. Other specimens described by Sudre (1984) have been ascribed to the latest Oligocene ruminant *Amphitragulus quercyi* (compact p4, small entostylid and postentocristid on lower molars). Recently, Hooker & Weidmann (2000) published a review of the Mormont Entreroche fauna (Switzerland). Unfortunately, the only referred specimen of "*Gelocus*" *minor* has been lost. Hooker & Weidmann (2000) suggested that the absence of both Oligocene karstic fillings and additional findings of "*Gelocus*" *minor* remains at Mormont could indicate an origin from another locality, such as the quarry of Eclepens just one kilometre away from the karstic system of Mormont. The Oligocene marly deposits of this quarry were quite rich with mammalian fauna (Rhinocerotidae, Cainotheriidae) dated from MP28 (Berger, pers. comm.). Moreover, some authors attempted to assign this species to the genus *Iberomeryx* (Sudre & Blondel 1996; Blondel 1997).

Due to the lack of further findings, European ruminants are considered to be characteristic of post-Grande-Coupure Asiatic migrants (Blondel 1997; Mennecart et al. accepted). Six valid genera, divided into five families, are known in the Early and mid-Oligocene of Western Europe: *Iberomeryx* Gabunia 1964, *Lophiomeryx* Pomel 1853, *Bachitherium* Filhol 1977, *Paragelocus*/*Pseudogelocus* Schlosser 1902, *Gelocus* Aymard 1855, *Mosaicomeryx* Mennecart et al. in prep. (Saint-Hilaire 1833; Pomel 1846; Filhol 1877, 1881, 1882; Gabunia 1964; Geraads et al. 1987; Janis 1987; Jehenne 1987; Sudre & Blondel 1996; Blondel 1997; Métais & Vislobokova 2007; Mennecart et al. 2011, chapter 6). Few recent publications studied these poorly known taxa and their familial attribution, their ecology and their biostratigraphy remain highly uncertain (Blondel 1997; Métais & Vislobokova 2007; Antoine et al. 2011). The reassessment of the old collections and the integration of new data on Early Oligocene ruminants allow their biostratigraphic ranges and dispersal area to be improved. Moreover, the evolution of this mammal group highlights changes and crises among Western European communities, probably linked to climatic events. Even if the Mosaicomerycidae, with the new genus *Mosaicomeryx* and *Prodremotherium*, are a family from this period, they are treated in detail in chapter 6.

5.2 Material and methods

The study is based on 120 Western European localities dating from MP21 to MP27 (France: 60; Germany: 36; Switzerland: 20; Italy: 3; Czech Republic: 1; see Table 1). The referred specimens come from 50 Western European localities (Table 1). Moreover, 70 Western European localities from the literature have been used for comparison (Table 1).

Institutional Abbreviations. BMNH, British Museum Natural History (London, England); BSPG, Bayerische Staatssammlung für Paläontologie und Geologie (München, Germany); IPHEP, Institut International de Paléoprimatologie, Paléontologie Humaine: Évolution et Paléoenvironnements, Université de Poitiers (France); MGA, Musée de Géologie-Lubéron-Apt (France); MHNF, Musée d'histoire naturelle de Fribourg (Switzerland); MHNT, Muséeum d'histoire naturelle de Toulouse (France); MJSN, Musée jurassien des sciences naturelles (Switzerland); MNHN, Musée national d'Histoire naturelle (Paris, France); NMB, Naturhistorisches Museum Basel (Switzerland); NMBE, Naturhistorisches Museum der Burgergemeinde Bern (Switzerland); UCBL, Université Claude Bernard (Lyon, France); USTL, Université des Sciences et Techniques du Languedoc (Montpellier, France).

5.3 Systematic palaeontology

Infraorder **TRAGULINA** Flower, 1883
Family **LOPHIOMERYCIDAE** Janis, 1987
Genus ***Lophiomeryx*** Pomel, 1853

Type species. *Lophiomeryx chalaniati* Pomel, 1853 from La Sauvetat (Allier, France), MP25.

Further included species. *L. gaudryi* Filhol, 1877, *L. minor* Lydekker, 1885, *L. angarae* Matthew & Granger, 1925, *L. gobiae* Matthew & Granger, 1925, *L. turgaicus* Flerov, 1938, *L. benaraensis* Gabunia, 1964, *L. gracilis* Miao, 1982, *L. shinaoensis* Miao, 1982, *L. mouchelini* Brunet & Sudre, 1987, *L. kargilensis* Nanda & Shani, 1990.

Diagnosis (adapted from Brunet & Sudre 1987 and Métais & Vislobokova 2007). Ruminant, which displays a relatively primitive dental formula: 0/3 – 1/1 – 3/4(3) – 3/3. The *corpus mandibulae* presents a concave ventral profile just behind the mandible symphysis, then it becomes regularly convex until the beginning of the ramus, where there is a rounded *incisura vasorum*. The angular process is posteriorly elongated. The symphysis is long, narrow, and highly concave. On the anterior part of the mandible there are two *foramen mentale*.

C is reduced. P2-3 are elongated with a lingual shelf variously developed. P4 is narrow and possesses a strongly

Table 1. Geographical and biostratigraphical distribution of the Western European Ruminantia localities during the Early and mid-Oligocene.

Species (*type species)	**Locality (* type locality, - direct observations)**	**Country**	**Mammal Zone (* Standard level)**	**References**
«*Lophiomeryx*» nov. sp.	Montalban -	Spain	MP23	Brunet & Sudre 1987, BiochroM'97 1997
«*Lophiomeryx*» *minor* Lyddeker, 1885	*Caylux	France	Rupelian	Lyddeker 1885, Brunet & Sudre 1987, Blondel 1997
«*Lophiomeryx*» *gaudryi* Filhol, 1877	*Raynal	France	Rupelian	Filhol 1877, Schlosser 1886, Bouvrain et al. 1986, Brunet & Sudre 1987
	Möhren 13 -	Germany	MP22	BiochroM'97 1997
	Quercy -	France	Rupelian	
Lophiomeryx mouchelini Brunet & Sudre, 1987	*Villebramar	France	*MP22	Brunet 1970, Brunet & Sudre 1987, Sudre 1995, BiochroM'97 1997,
	Calaf	Spain	MP21	Brunet & Sudre 1987, BiochroM'97 1997
	Detan -	Cz. Republic	MP21-23	Fejfar 1987, Sudre 1995, Ménouret & Guérin 2009
	Herrlingen 1 -	Germany	MP22	BiochroM'97 1997
	Larromieu -	France	Rupelian	
	Lovagny -	France	MP23	Brunet & Sudre 1987, BiochroM'97 1997, Engesser & Mödden 1997
	Mas de Gaston	France	MP23	Remy et al. 1987, Blondel 1997
	Mas de Got	France	MP22	Remy et al. 1987, Blondel 1997
	Möhren 9 -	Germany	MP21-22	Heissig1978, Brunet & Sudre 1987
	Möhren 13 -	Germany	MP22	Heissig1978, Heissig 1987, Brunet & Sudre 1987
	Moissac-IV	France	MP24	Antoine et al. 2011
	Mounayne	France	MP23	Brunet & Sudre 1987, Remy et al. 1987, BiochroM'97 1997, Blondel 1997
	Murs -	France	MP23	Remy 2000
	Pech Crabit	France	MP23	Brunet & Sudre 1987, Remy et al. 1987, BiochroM'97 1997, Blondel 1997
	La Plante 2	France	MP22	Bonis et al. 1973, Brunet & Sudre 1987, Remy et al. 1987, BiochroM'97 1997, Blondel 1997
	Poillat -	Swiss	MP24	Mennecart et al. 2011
	Roqueprune 2	France	MP23	Blondel 1997
	Saint Gemme -	France	Rupelian	Richard 1946
	Saint Martin de Castillon	France	MP24	Pomel 1853, Brunet & Sudre 1987, BiochroM'97 1997,
	Welschenrohr -	Swiss	Rupelian	Greppin 1870, Rütimeyer 1883, Stehlin 1914
**Lophiomeryx chalaniati* Pomel, 1853	*La Sauvetat -	France	MP25	Pomel 1853, Filhol 1877, Hugueney 1997, Brunet & Sudre 1987
	Antoing	France	MP25	Brunet & Sudre 1987, Brunet & Sudre 1987, Sudre 1995, Hugueney 1997
	Belgarric	France	MP25	Brunet & Sudre 1987, Remy et al. 1987, Sudre 1995, BiochroM'97 1997, Blondel 1997
	Bénissons Dieu	France	MP23-25	Brunet & Sudre 1987, Sudre 1995, Hugueney 1997
	Carascosa del Campo	Spain	MP26	Brunet & Sudre 1987, Lacomba & Morales 1987, Sudre 1995, BiochroM'97 1997
	Cournon	France	MP28	Pomel 1853, Brunet & Sudre 1987, Sudre 1995, BiochroM'97 1997, Hugueney 1997
	La Devèze	France	MP25	Blondel 1997
	Le Garouillas -	France	*MP25	Brunet & Sudre 1987, Remy et al. 1987, Sudre 1995, BiochroM'97 1997, Blondel 1997, Blondel 1998
	Malhat	France	MP23-28	Brunet & Sudre 1987, Sudre 1995, Hugueney 1997
	Moissac-III -	France	MP26	Antoine et al. 2011
	Moissac-IV	France	MP24	Antoine et al. 2011
	Mümliswyl Hardberg -	Swiss	MP26	Mayo 1983, Brunet & Sudre 1987, Sudre 1995, Engesser & Mödden 1997
	Nonette	France	MP25?	Hugueney 1997

Lophiomeryx chalaniati (continued)	Pech Desse -	France	MP28	Brunet & Sudre 1987, Remy et al. 1987, Sudre 1995, BiochroM'97 1997, Blondel 1997
	Rabastens -	France	MP24	Richard 1931, Brunet & Sudre 1987, Sudre 1995
	Rigal-Jouet	France	MP25	Brunet & Sudre 1987, Remy et al. 1987, BiochroM'97 1997, Blondel 1997
	Saint Martin de Casselvi	France	???	Bergounioux & Crouzel 1968, Brunet & Sudre 1987, Sudre 1995
	Seckbach	Germany	MP22-24	Brunet & Sudre 1987, Sudre 1995
	Tournon	France	late Rupelian	Filhol 1877
	Vallon d'Auradou	France	Chattian	
Iberomeryx minor (Filhol, 1882)	*Quercy -	France	Oligocene	Filhol 1882, Schlosser 1886, Sudre 1984, Bouvrain et al. 1986, Sudre & Blondel 1996, Mennecart et al. 2011
	La Beuchille -	Swiss	MP24	Becker et al. 2004, Mennecart et al. 2011
	Court -	Swiss	Rupelian	
	Ehingen 4 -	Germany	MP23	Heissig 1987
	Itardie -	France	*MP23	Sudre 1984, Remy et al. 1987, Sudre & Blondel 1996, BiochroM'97 1997, Blondel 1997, Mennecart et al. 2011
	Lovagny -	France	MP23	BiochroM'97 1997, Engesser & Mödden 1997, Mennecart et al. 2011
	Montalban -	Spain	MP23	Sudre & Blondel 1996, BiochroM'97 1997, Mennecart et al. 2011
	Mounayne	France	MP23	Remy et al. 1987, Sudre & Blondel 1996, BiochroM'97 1997, Blondel 1997, Mennecart et al. 2011
	Pech Crabit	France	MP23	Blondel 1997
	Pré Chevalier -	Swiss	MP24	Mennecart et al. 2011
	Roqueprune 2	France	MP23	Sudre 1984, Remy et al. 1987, Sudre & Blondel 1996, BiochroM'97 1997, Mennecart et al. 2011
	Soulce -	Swiss	MP23	Fleury 1910, Stehlin 1914, Gaudant 1979, Sudre 1984, Sudre & Blondel 1996, Mennecart et al. 2011
**Bachitherium curtum* (Filhol, 1877)	*Lamandine-Haute -	France	Oligocene	Filhol 1877, Filhol 1882, Sudre 1986
	Bernloch 1 -	Germany	MP23	Heissig 1978, Heissig 1987, Sudre 1995, BiochroM'97 1997
	Burgmagerbein 1 -	Germany	MP27	
	Burgmagerbein 2 -	Germany	MP23	Heissig 1978, Heissig 1987
	Burgmagerbein 8	Germany	MP21-23	Heissig 1987, Sudre 1995
	Cadillac	France	Stampian	Richard 1946
	Chavorney -	Swiss	Chattian	
	Coulou	France	MP23	Remy et al. 1987
	Detan -	Czech Republic	MP21-23	Ménouret & Guérin 2009
	Ehningen 1 -	Germany	MP23	Heissig 1978, Heissig 1987
	Ehningen 14 -	Germany	???	
	Ehingen 15 -	Germany	???	
	Eriz Losenegg -	Swiss	MP27	Engesser & Mödden 1997
	Le Garouillas -	France	*MP25	Sudre 1995, BiochroM'97 1997,
	Gas	France	MP24	Sudre 1995, BiochroM'97 1997
	Grenchen 1 -	Swiss	MP24	Stehlin 1914, Engesser & Mödden 1987, BiochroM'97 1997, Engesser & Mödden 1997
	Herrlingen 1 -	Germany	MP22	Heissig 1987, Sudre 1995, BiochroM'97 1997
	Itardie	France	*MP23	Bonis et al. 1973, Sudre 1986, Remy et al. 1987, Sudre 1995, BiochroM'97 1997, Blondel 1997, Blondel 1998
	Ithier (Tournon)	France	Rupelian	Richard 1946
	Itteville	France	MP24	Sudre 1995, BiochroM'97 1997
	Maintenon	France	MP24	Sudre 1995, Merle et al. 2002
	Marseille	France	MP26	Repelin 1916
	Mege	France	MP23	Remy et al. 1987
	Les Milles -	France	MP26	Repelin 1916, Sudre 1995, Ménouret & Guérin 2009

Bachitherium curtum (continued)	Möhren 13 -	Germany	MP22	Heissig 1978, Heissig 1987, Sudre 1995, BiochroM'97 1997
	Monclar-de-Quercy -	France	MP25	Astre 1954, Muratet et al. 1992
	Moutier gare -	Swiss	MP26	Stehlin 1914
	Mounayne	France	MP23	Remy et al. 1987, Sudre 1995, BiochroM'97 1997, Blondel 1997
	Nassiet près Amou	France	MP24-25	Viret 1938
	Ormoy	France	MP24	Sudre 1995, BiochroM'97 1997, Merle et al. 2002
	Pech Crabit	France	MP23	Remy et al. 1987, Sudre 1995, BiochroM'97 1997, Blondel 1997
	Pierrefitte	France	MP24	Sudre 1995, Merle et al. 2002
	Rigal-Jouet	France	MP25	Remy et al. 1987, Sudre 1995, BiochroM'97 1997, Blondel 1997
	Ronheim 1 -	Germany	MP22	Heissig 1978, Heissig 1987, Sudre 1995, BiochroM'97 1997
	Roqueprune 2	France	MP23	Bonis et al. 1973, Remy et al. 1987, Sudre 1995, BiochroM'97 1997, Blondel 1997
	Saint André -	France	MP26	Ménouret & Guérin 2009
	Saint Ferme	France	Stampian	Richard 1946
	Saint Henri -	France	MP26	Ménouret & Guérin 2009
	Treuchtlingen 1 -	Germany	???	
	La Tuque -	France	???	
	Vayres su Essonne	France	MP23	Merle et al. 2002
	Weinheim	Germany	MP22	Wehrli 1832, Sudre 1996, BiochroM'97 1997
	Wolfwil kennisbännli -	Swiss	MP27	Engesser & Mödden 1997
Bachitherium insigne (Filhol, 1877)	*Quercy -	France	Oligocene	Filhol 1877, Filhol 1882
	Aarwangen -	Swiss	MP27	Stehlin 1914, Sudre 1986, Engesser & Mayo 1987
	Baden -	Swiss	???	
	Bénissons Dieu	France	MP23-25	Sudre 1986, Hugueney 1997
	Cadibona -	Italy	MP25-26	Kotsakis 1984, Kotsakis 1986, Sudre 1986, Azzaroli 1990
	Céreste -	France	MP23-24	Bouvrain & Geraads 1985, Sudre 1986, Geraads et al. 1987, Sudre 1995, Geraads et al. 1987, Blondel 1998
	La Devèze	France	MP25	Remy et al. 1987
	Le Garouillas -	France	*MP25	Sudre 1986, Remy et al. 1987, BiochroM'97 1997
	Le Gibet à Etampes	France	MP24	Ginsburg 1969, Sudre 1995
	Mas de Pouffié	France	MP26	Remy et al. 1987
	Oensingen Ravellen -	Swiss	MP26	Stehlin 1914, Sudre 1986, Sudre 1995, Engesser & Mödden 1987, BiochroM'97 1997
	Phalip	France	MP25	Remy et al. 1987
	Rigal-Jouet	France	MP25	Remy et al. 1987, BiochroM'97 1997, Blondel 1997
	Saint Henri -	France	MP26	Sudre 1986, BiochroM'97 1997
	Saint Menoux	France	MP26	Sudre 1986, Sudre 1995, BiochroM'97 1997, Hugueney 1997
	Weinheim	Germany	MP22	Wehrli 1832, Sudre 1996, BiochroM'97 1997
	Wynau III -	Swiss	MP27	BiochroM'97 1997
	Wynau V -	Swiss	MP27	BiochroM'97 1997
Bachitherium vireti Sudre, 1986	*Nassiet -	France	MP23	Sudre 1986
	La Bourgadot	France	MP23	Sudre 1986
	Itardies	France	*MP23	Sudre 1986
Bachitherium guirounetensis Sudre, 1995	*Le Garouillas -	France	*MP25	Sudre 1995, BiochroM'97 1997, Blondel 1997
Bachitherium lavocati Sudre, 1986	*Pech Desse -	France	MP28	Sudre 1986, Blondel 1997
	Gaimersheim 1 -	Germany	MP28	

Bachitherium sp.	Le Garouillas	France	*MP25	Sudre 1986, BiochroM'97 1997, Blondel 1997
	Chiavon	Italy	Rupelian	Kotsakis 1984, Kotsakis 1986, Azzaroli 1990, Hably et al. 2007
	Maccio	Italy	???	Kotsakis 1984, Kotsakis 1986, Azzaroli 1990
	Mas de Pouffie	France	MP26	Blondel 1997
	Saint Menoux	France	MP26	Sudre 1995, BiochroM'97 1997
**Gelocus communis* (Aymard, 1846)	*Quercy -	France	Oligocene	Aymard 1846, Filhol 1877, Jehenne 1985
	Aubrelong 1	France	MP21	Lange 1970, Bonis et al. 1973, Jehenne 1985, Remy et al. 1987, Sudre & Blondel 1996, BiochroM'97 1997, Blondel 1997
	Detan -	Czech Republic	MP21-23	Sudre & Blondel 1996, Ménouret & Guérin 2009
	Ehingen 14 -	Germany	Rupelian	
	Ehingen 15 -	Germany	Rupelian	
	Haag 2 -	Germany	MP21	Heissig 1978, Heissig 1987, Sudre & Blondel 1996
	Möhren 4 -	Germany	MP21	Heissig 1987, Sudre & Blondel 1996
	Pech Crabit	France	MP23	Bonis et al. 1973, Jehenne 1985, BiochroM'97 1997
	Poillat -	Swiss	MP24	Mennecart et al. 2012
	Ravet	France	MP21	Bonis et al. 1973, Remy et al. 1987, Sudre & Blondel 1996, BiochroM'97 1997, Blondel 1997
	Ronzon -	France	MP21	Filhol 1882, Lange 1970, Jehenne 1985, Geraads et al. 1987, Sudre & Blondel 1996, BiochroM'97 1997, Hugueney 1997, Blondel 1998
	Ruch	France	MP21	Jehenne 1985, Sudre & Blondel 1996, BiochroM'97 1997
Gelocus laubei Schlosser, 1901	*Lignites de Bohème (Lukawitz?)	Germany	MP21-22	Schlosser 1901, Jehenne 1985, Sudre & Blondel 1996
	Eselsberg	Germany	Rupelian	Jehenne 1985
	Grafenmühle 6	Germany	MP21-22	Sudre & Blondel 1996
	Möhren 4	Germany	MP21-22	Heissig 1978, Heissig 1987, Sudre & Blondel 1996, BiochroM'97 1997
	Möhren 7	Germany	MP21-22	Heissig 1978, Heissig 1987, Sudre & Blondel 1996, BiochroM'97 1997
	Möhren 13	Germany	MP21-22	Heissig 1978, Heissig 1987, Sudre & Blondel 1996, BiochroM'97 1997
	Möhren 16	Germany	MP21-22	Heissig 1978, Heissig 1987, Sudre & Blondel 1996, BiochroM'97 1997
	Möhren 19		MP21	Heissig 1978, Heissig 1987, Sudre & Blondel 1996, BiochroM'97 1997
	Möhren 20	Germany	MP21-22	Heissig 1978, Jehenne 1985, Heissig 1987, Sudre & Blondel 1996, BiochroM'97 1997
Gelocus villebramarensis Brunet & Sudre, 1976	*Villebramar	France	*MP22	Brunet 1970, Brunet & Sudre 1976, BiochroM'97 1997
	Cavalé	France	MP22	Vianey-Liaud & Schmidt 2009
	Möhren 13	Germany	MP22	Heissig 1978, Jehenne 1985, BiochroM'97 1997
	Ronheim 1	Germany	MP22	Heissig 1978, Jehenne 1985, BiochroM'97 1997
**Pseudogelocus scotti* (Schlosser, 1902)	*Hochberg	Germany	MP21	Schlosser 1902, Jehenne 1985, Sudre & Blondel 1996
	*Oerlinger Thal	Germany	MP21	Schlosser 1882, Schlosser 1902, Jehenne 1985
	Bernloch 1	Germany	MP23	Heissig 1978, Heissig 1987, Sudre & Blondel 1996, BiochroM'97 1997
	Burgmagerbein 2	Germany	MP23	Heissig 1987, Sudre & Blondel 1996
	Burgmagerbein 3	Germany	MP22	Heissig 1978
	Burgmagerbein 5	Germany	MP21	Heissig 1978
	Burgmagerbein 8	Germany	MP21-23	Heissig 1987, Sudre & Blondel 1996
	Ehingen 1	Germany	MP23	Heissig 1978, Heissig 1987, Sudre & Blondel 1996
	Frohnsetten	Germany	Rupelian	Jehenne 1985

Pseudogelocus scotti (continued)	Grafenmühle 6	Germany	MP21-23	Heissig 1987, Sudre & Blondel 1996
	Grafenmühle 10	Germany	MP21-23	Heissig 1987, Sudre & Blondel 1996
	Haag 2	Germany	MP21	Heissig 1978, Heissig 1987, Sudre & Blondel 1996
	Herrlingen 1	Germany	MP22	Jehenne 1985, Heissig 1987, Sudre & Blondel 1996
	La Plante 2	France	MP22	Sudre & Blondel 1996, BiochroM'97 1997, Blondel 1997
	Mas de Got	France	MP22	Sudre & Blondel 1996, BiochroM'97 1997, Blondel 1997
	Möhren 4	Germany	MP21-22	Heissig 1978, Jehenne 1985, Heissig 1987, Jehenne 1985, Sudre & Blondel 1996, BiochroM'97 1997
	Möhren 7	Germany	MP21-22	Heissig 1978, Jehenne 1985, Heissig 1987, Sudre & Blondel 1996, BiochroM'97 1997
	Möhren 9	Germany	MP21-22	Heissig 1978
	Möhren 11	Germany	MP21-22	Heissig 1978, Jehenne 1985
	Möhren 13	Germany	MP22	Heissig 1978, Jehenne 1985, Heissig 1987, Jehenne 1985, Sudre & Blondel 1996, BiochroM'97 1997
	Möhren 16	Germany	MP21-22	Heissig 1978, Heissig 1987, Sudre & Blondel 1996, BiochroM'97 1997
	Möhren 18	Germany	MP21	Heissig 1978
	Möhren 19	Germany	MP21-22	Heissig 1978, Jehenne 1985, Heissig 1987, Sudre & Blondel 1996, BiochroM'97 1997
	Möhren 20	Germany	MP21-22	Heissig 1978, Heissig 1987, Sudre & Blondel 1996, BiochroM'97 1997
	Möhren 31	Germany	MP21-22	Heissig 1978, Jehenne 1985, Heissig 1987, Sudre & Blondel 1996, BiochroM'97 1997
	Ronheim 1	Germany	MP22	Heissig 1978, Jehenne 1985, Heissig 1987, Sudre & Blondel 1996, BiochroM'97 1997
	Schelklingen 1	Germany	MP23	Jehenne 1985, Heissig 1987, Sudre & Blondel 1996, BiochroM'97 1997

concave labial wall and salient styles. The upper molars are tetraselenodont and brachyodont. They grow high wards to the back. The M3 metaconule is variously developed. The paracone possesses a labial rib. The labial wall of the metacone is strongly concave. The parastyle and mesostyle are salient, in small column shape. A faint metastyle is present on M3. There is a strong cingulum around the anterior fossa.

c is incisiform and located adjacent to the incisors. p1 is always reduced and leaf-like, separated from c and p2 by diastemata. p2-3 are elongated and narrow. p4 has a well-developed mesolingual conid and an elongated posterior heel, lingually opened. The lower molars possess a trigonid open mesio-lingually and a talonid open postero-lingually. The metaconid can possess a groove, which could be the *Dorcatherium* fold. The third lobe of the m3 is transversely compressed.

Mc3-4 and Mt3-4 are unfused. Mt2 and Mt5 are strongly reduced, but still present.

Etymology. *Lophio-* is Greek for crest and *-meryx* is Greek for ruminant.

"*Lophiomeryx*" nov. sp.

Fig. 1

1987 non	*Lophiomeryx mouchelini* Brunet & Sudre: 229.

Occurrence. Early Oligocene, MP23, from Spain (Montalban).

Referred material. Montalban (Spain): NMB Mab.2, fragmentary right M1-2; NMB Mab.3, fragmentary left m3; NMB Mab.5, left M1; NMB Mab.6, fragmentary right p3; NMB Mab.7, fragmentary right p4; NMB Mab.8, fragmentary left p4; NMB Mab.9, left m1; NMB Mab.10, fragmentary left m3; NMB Mab.11, fragmentary left M1.

Description

The relatively fragmentary material contains only isolated elements. This species is a little bit smaller than *Lophiomeryx mouchelini*, however, differences can be observed on the bunoselenodont teeth shape. All measurements are summarized in Table 2.

Locality	Inventory number	p3		p4		m1		m2		m3	
«*Lophiomeryx*» nov. sp.											
Montalban	NMB Mab.3										6.6
	NMB Mab.6		3.5								
	NMB Mab.7			3.8							
	NMB Mab.8			4.0							
	NMB Mab.9					9.5	5.2				
	NMB Mab.10										6.1

Locality	Inventory number	M1	
Montalban	NMB Mab.2		8.8
	NMB Mab.5	7.9	9.2
	NMB Mab.11		8.2

Table 2. Dental measurements (in mm) of the "*Lophiomeryx"* nov. sp., in each row, the first set of data is the length and the second is the width.

Lower dentition. The premolars are quite elongated. Contrary to p4, p3 does not possess a mesolingual conid. The anterior part of the tooth finishes abruptly, quite straight, forming a rectangular tooth with an oblique anterior conid. The mesolabial conid is high and central. The mesolingual conid is located on the lingual part of the tooth, at the level of the mesolabial conid. It forms a well-developed cuspid. The transverse cristid goes from the top of the mesolingual conid to the base of the mesolabial conid to reach a posterolingual cristid. There is an oblique cristid in the medial valley, which begins between the posterolabial cristid and the transverse cristid. It can reach the lingual part of p4. It could be the posterolingual conid. The posterolabial conid is curved and distally finishes the tooth. The lower molars are typical of *Lophiomeryx* in having a rounded metaconid, without premetacristid, no postentocristid, and widely opened trigonid and talonid. The preprotocristid is elongated and curved and reaches the lingual part of the tooth. There are no external postprotocristid. The posterior part of the metaconid has a small cristid, which could be assimilated to the *Dorcatherium* fold. The third lobe on m3 is composed only of the hypoconulid and a unique prehypoconulidcristid, which reaches the base of the posthypocristid, forming a blade. The lingual part of this lobe can have a small cingulid.

Upper dentition. The upper molars possess a reduced and narrow metaconule and an oblique metacone. The cristae are straight and do not fuse together. The large protocone is surrounded by a strong cingulum. The metaconule is slightly reduced. The paracone and metacone are globular. The paracone rib is very developed forming a groove on its anterior part. The metacone is also present and developed. The parastyle is big, forming a small column. The mesostyle is smaller.

Taxonomical attribution

This species possesses typical features of Lophiomerycidae (e.g., presence of a mesolingual conid on p4, open trigonid and talonid, absence of postentocristid, globular metaconid). However, the presence of a posterolingual conid on p4, an overdeveloped paracone rib forming an anterior groove and an oblique metacone on the upper molars clearly differ from the known European species of *Lophiomeryx* (Brunet & Sudre 1987). However, big metacone and paracone ribs, paracone and metacone not in the same axis, and reduced metaconule can be observed on *Lophiomeryx kargilensis* from Asia (Nanda & Shani 1990; Métais et al. 2009). Without further specimens, precise taxonomy identification cannot be done, but an attribution to a new species of *Lophiomeryx* is suspected.

"*Lophiomeryx*" *minor* Lyddeker, 1885

1885*	*Lophiomeryx minor* Lyddeker: 314, fig. 39.
1997	*Lophiomeryx minor* Blondel: Tab. 8.

Holotype. Fragment of right maxilla with P3-M3 (BMNH BM1809, Lyddeker 1885, fig. 39).

Figure 1 (opposite page). "*Lophiomeryx*" nov. sp.: from *Montalban* **1**, right fragmentary p3 (NMB Mab.6), lingual (**a**) and occlusal views (**b**); **2**, right fragmentary p4 (NMB Mab.7), lingual (**a**), labial (**b**), and occlusal views (**c**); **3**, left fragmentary p4 (NMB Mab.8), lingual (**a**), labial (**b**), and occlusal views (**c**); **4**, left m1 (NMB Mab.9), lingual (**a**), labial (**b**), and occlusal views (**c**); **5**, left M1 (NMB Mab.5), occlusal view; **6**, left fragmentary M1 (NMB Mab.11), occlusal view; **7**, left fragmentary m3 (NMB Mab.3), lingual (**a**), labial (**b**), and occlusal views (**c**); **8**, left fragmentary m3 (NMB Mab.10), lingual (**a**), labial (**b**), and occlusal views (**c**). "*Lophiomeryx*" *gaudryi*: from the old collections of the *Phosphorites du Quercy* **9**, right mandible with p4-m2 (BSP unnumbered), lingual (**a**), labial (**b**), and occlusal views (**c**); from *Möhren 13* **10**, left fragmentary m3 (BSP 517), lingual (**a**), labial (**b**), and occlusal views (**c**). Scale bar equals 10 mm.


1a
2a
3a
4a
1b
2b
3b
4b
5
2c
3c
4c
6
7a
7b
7c
8a
8b
8c
9a
9b
9c
10a
10b
10c

Species Etymology. Latin word for the smallest.

Type Locality and horizon. Caylux (Tarn et Garonne, France), undated old collections of the Phosphorites du Quercy.

Occurrence. Early Oligocene from France (Caylux).

Referred Material. No additional material.

Diagnose (after Lyddeker 1885 and Brunet & Sudre 1987). *Lophiomeryx* species smaller than *L. chalaniati*, but bigger than *L. gaudryi*. P3-4 are relatively transversally developed with a strong paracone rib. P3 has a convex labial wall. M2-3 possess a reduced metaconule, giving a triangular shape to the teeth. The protocone is backward. The paracone rib is more salient than the metastyle. The lingual cingulum is reduced.

“*Lophiomeryx*” *gaudryi* Filhol, 1877

Fig.1

1877*	*Lophiomeryx gaudryi* Filhol: 447, figs. 279–280.
1882 v non	*Bachitherium minor* Filhol: 138.
1886 v par	*Cryptomeryx gaudryi* Schlosser: pl. II, figs. 13–14, pl. V, fig. 7, 16, and 24 (non pl. VI, fig. 6 and 9).
1910 v non	*Cryptomeryx gaudryi* Fleury: 277.
1914 v non	*Cryptomeryx gaudryi* Stehlin: 184.
1926 non	*Cryptomeryx gaudryi* Carlson: 69.
1962 non	*Cryptomeryx* Friant: 114.
1966 non	cf. *Cryptomeryx gaudryi* Palmowski & Wachendorf: 241, pl. 15, fig. 7.
1967 non	*Cryptomeryx* Friant: 96.
1973 non	*Bachitherium* ? sp Bonis et al.: tab. 2(4).
1978 v non	*Cryptomeryx* cf. *gaudryi* Heissig: 271, tab. 4.
1979 v non	*Cryptomeryx gaudryi* Gaudant: 889, figs. 17–20.
1980 non	*Cryptomeryx* Webb & Taylor: 124.
1984 v non	*Cryptomeryx gaudryi* Sudre: 6, figs 1–9.

Neotype. The holotype (Filhol 1877: 447, figs. 279 & 280 from Raynal, France) is currently lost (Brunet & Sudre 1987, pers. comm. Argot). We propose this neotype: a left mandible with p4-m2 from Quercy (unnumbered specimen from the BSPG collection).

Species Etymology. The species name was given in honour of the palaeomammalogist Albert Gaudryi.

Type Locality and horizon. Raynal (Lot-et-Garonne, France), undated old collections of the Phosphorites du Quercy.

Occurrence. Early Oligocene from France (Raynal) and Germany (Möhren 13, MP22).

Referred Material. Old collections of the Phosphorites du Quercy (France): BSPG unnumbered, right mandible with p4-m2. ; Möhren 13 (Germany): BSPG 517, fragmentary left m3.

Neodiagnose. Tiny ruminant possessing a p4 with mesolingual conid. The trigonid is widely opened contrary to the talonid. The molars possess a small postentocristid and a *Dorcatherium* fold.

Description

This ruminant is quite similar in size to *Iberomeryx minor* (see Table 3). The lower cheek teeth are bunoselenodont.

Lower dentition. The premolars are relatively massive and laterally compressed with a small mesolingual conid linked to the high mesolabial conid by a straight transverse cristid. The anterior conid is globular and slightly oblique. On the back of this tooth, posterior cristid and posterior stylid are separated, forming backwards an opened back valley. The lower molars possess a widely opened trigonid due to a preprotocristid anteriorly oriented. There are no anterior conid. A very weak to absent *Dorcatherium* fold seems to occur on the rounded metaconid without premetacristid. The entoconid is slightly laterally compressed and possesses a small postentocristid partly closing the large talonid. The ectostylid is very small and forms a small column. The third lobe on m3 is only composed of the hypoconulid and a unique prehypoconulidcristid forming a blade, which reaches the base of posthypocristid and postentocristid. The lingual part of this lobe has a cingulid.

Taxonomical attribution

The referred specimens clearly differ in size (Table 3) and shape (fig. 1) from other ruminants. Such as observed by

Table 3. Dental measurements (in mm) of the "*Lophiomeryx" gaudryi*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	Reference	p4		m1		m2		m3	
«Lophiomeryx» gaudryi										
Quercy	BSPG unnumbered		4.0	2.5	5.1	2.7	5.2	3.6		
Möhren 9	BSPG 1517									4.1
Quercy	lost	Filhol 1877	4.0	2.0	4.5	2.5	5.0	3.0	7.0	3.0

Brunet & Sudre (1987), the shape of the p4 is different from the small Early Oligocene Tragulidae *Iberomeryx* in having a mesolingual conid. In the latter, a buckle always forms the third lobe on m3 (Sudre 1984; Mennecart et al. 2011). Also, the presence of a postentocristid on lower molars clearly differs from the European *Lophiomeryx* (Geraads et al. 1987). In this genus, the posthypocristid usually stops on the edge of the tooth, forming a small column on its lingual wall. In this case, the talonid is closed like in *Gelocus* (Geraads et al. 1987). However, the trigonid is widely opened, contrary to the latter. That is why the genus and familial attribution of the species "*Lophiomeryx*" *minor* should be reconsidered.

Lophiomeryx mouchelini Brunet & Sudre, 1987
Fig.2

1870 v	*Amphitragulus* Grepin: 175.
1883	*Amphitragulus elegans* Rütimeyer: 99.
1914 v	*Lophiomeryx chalaniati* Stehlin: 184.
1970	*Lophiomeryx chalaniati* Brunet: 3.
1973	*Lophiomeryx* sp. de Bonis et al.: 109, tab. 2(4).
1978 v	*Lophiomeryx* aff. *angarae* Heissig: 258, fig. 4.
1987 v	*Lophiomeryx* sp. Heissig: fig. 6.
1987*	*Lophiomeryx mouchelini* Brunet & Sudre: 228, fig. 1-3.
1987	*Lophiomeryx* cf. *pomeli* Fejfar: 260, fig. 1-5.
1987 v	*Lophiomeryx* sp. Remy et al.: 185, tab. 3c.
1997 v	*Lophiomeryx chalaniati* Engesser & Mödden: 480.
1997	*Lophiomeryx mouchelini* Blondel: tab. 8.
1997	*Lophiomeryx* cf. *mouchelini* Vislobokova: 220.

Holotype. Left mandible with p1-m3 (IPHEP VIL1973-257, Brunet & Sudre 1987: 227, fig. 1).

Paratype. Right mandible with root of p1 and p2-m3 (IPHEP VIL1974-181, Brunet & Sudre 1987: 227, fig. 2).

Species Etymology. The species name was given in honour of Guy Mouchelin, who participated in the excavations and prepared the fossils of Villebramar (France).

Type locality and horizon. Villebramar (Lot-et-Garonne, France), MP22.

Occurrence. Early Oligocene, from MP21 to early MP24, of Spain (Calaf), France (La Plante 2, Larromieu, Lovagny, Mas de Gaston, Mas de Got, Moissac IV, Mounayne, Murs, Pech Crabit, Roqueprune 2, Saint-Gemme, Saint Martin de Castillon), Switzerland (Poillat, Welschenrohr), Germany (Herrlingen 1, Möhren 9, Mohren 13), and Czech Republic (Detan).

Referred Material. Larromieu (France): MHNT. AL.2011.0.6, left m2-3. Lovagny (France): NMB Lvy10, right m2-3. Murs (France): NMB OV5, right p4; NMB OV6, right fragmentary mandible with p4-m3; NMB OV9, right cubo-navicular; NMB OV10, phalanx I; NMB OV11, phalanx II; NMB OV12, phalanx III; NMB OV75, left astragalus; NMB OV98, left mandible with d3, m1-2; NMB OV99, fragmentary right m3; NMB OV100, right p4; NMB OV101, right p3; NMB OV102, left m1; NMB OV103, left m2. Saint-Gemme (France): NMB MG45, right fragmentary mandible with partial m1-2 and m3 without hypoconulid. Poillat (Switzerland): MJSN POI007-177+178, left *corpus mandibulae* with the roots of p4, fragmentary m1, and m2-3; MJSN POI007-190, fragmentary left maxillary with M1-2; MJSN POI007-261, right fragment of mandible with fragmentary m2 and erupting m3; MJSN POI007-939, left toothless mandible; MJSN POI007-941, fragmentary left maxillary with M1-2. Welschenrohr (Switzerland): NMB UM28, one side prepared left mandible with alveoli of p1-3 and preserved p4-m3. Möhren 9 (Germany): BSPG 1970 XXIII, left broken M. Möhren 13 (Germany): BSPG 1081, cast of right m; BSPG 1084, cast of left M; BSPG 1513, right m3; BSPG 1514, left p3.

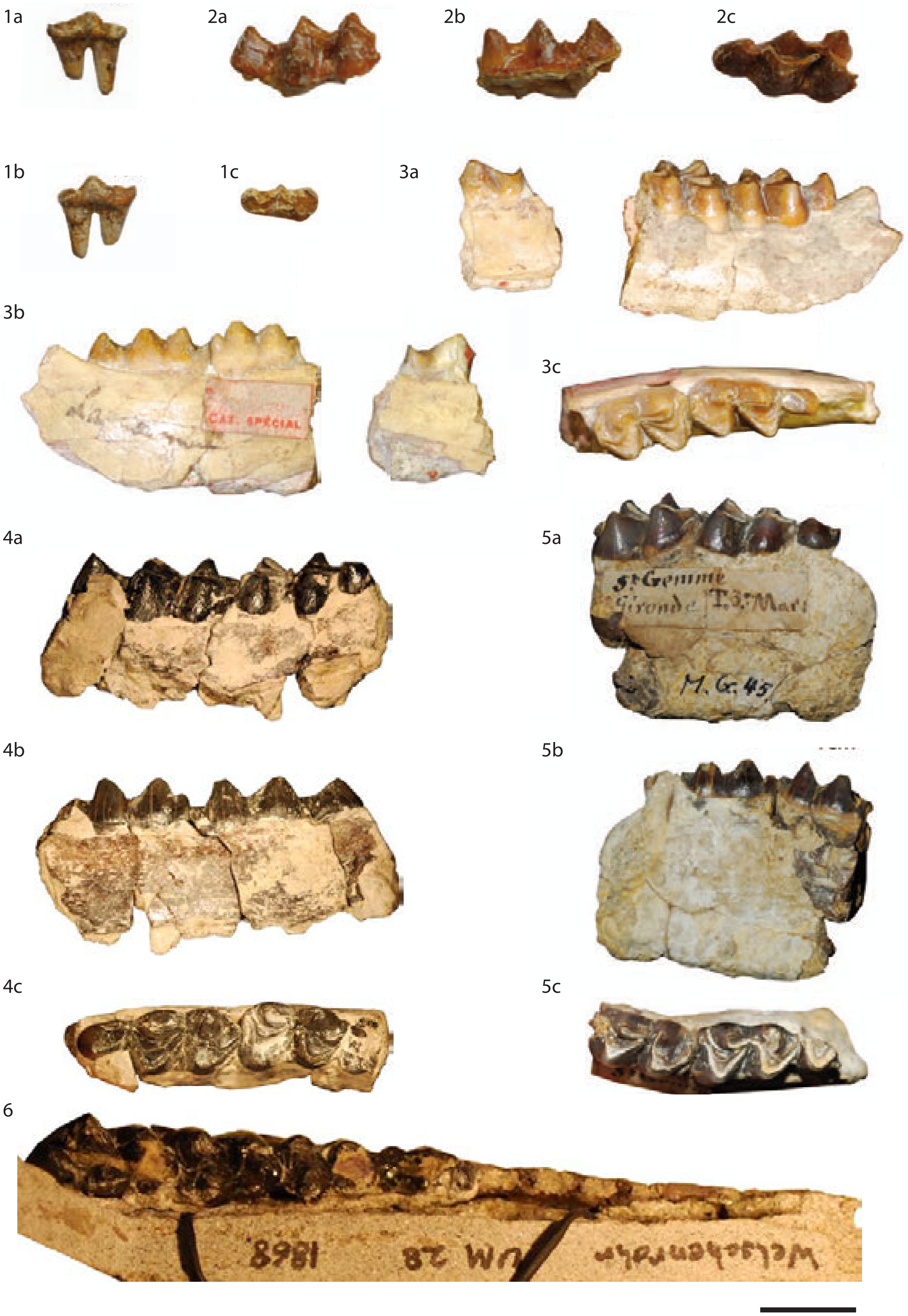


Figure 2. *Lophiomeryx mouchelini*: from Möhren 9 **1** right m3 (BSP 1513), lingual (**a**), labial (**b**), and occlusal views (**c**); **2** left p3 (BSP 1514), lingual (**a**), labial (**b**), and occlusal views (**c**); from *Larromieu* **3** left m2-3 (MHNT.AL.2011.0.6), lingual (**a**), labial (**b**), and occlusal views (**c**); Lovagny **4** right m2-3 (NMB Lvy10), lingual (**a**), labial (**b**), and occlusal views (**c**); from Saint-Gemme **5** right fragmentary mandible with partial m1-2 and m3 without hypoconulid (NMB MG45), lingual (**a**), labial (**b**), and occlusal views (**c**); from *Welschenrohr* **6** one side prepared left mandible with alveoli of p1-3 and preserved p4-m3 (NMB UM28), lingual view. Scale bar equals 10 mm.

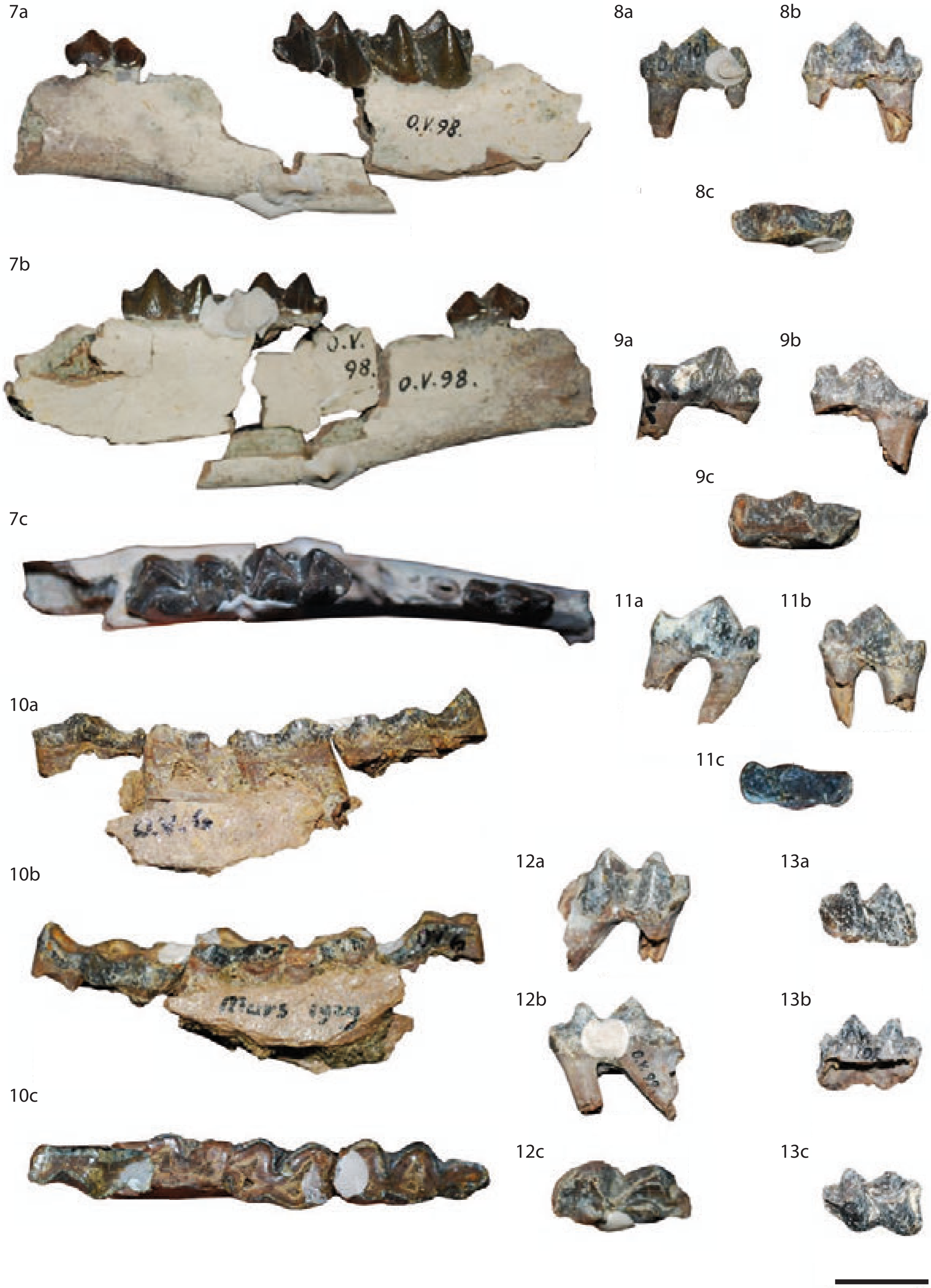


Figure2 (continued). from *Murs* **7** left mandible with d3, m1-2 (NMB OV98), lingual (**a**), labial (**b**), and occlusal views (**c**); **8** right p3 (NMB OV101), lingual (**a**), labial (**b**), and occlusal views (**c**); **9** right p4 (NMB OV5), lingual (**a**), labial (**b**), and occlusal views (**c**); **10** right fragmentary mandible with p4-m3 (NMB OV6), lingual (**a**), labial (**b**), and occlusal views (**c**); **11** right p4 (NMB OV100), lingual (**a**), labial (**b**), and occlusal views (**c**); **12** fragmentary right m3 (NMB OV99), lingual (**a**), labial (**b**), and occlusal views (**c**); **13** left m1 (NMB OV102), lingual (**a**), labial (**b**), and occlusal views (**c**). Scale bar equals 10 mm.

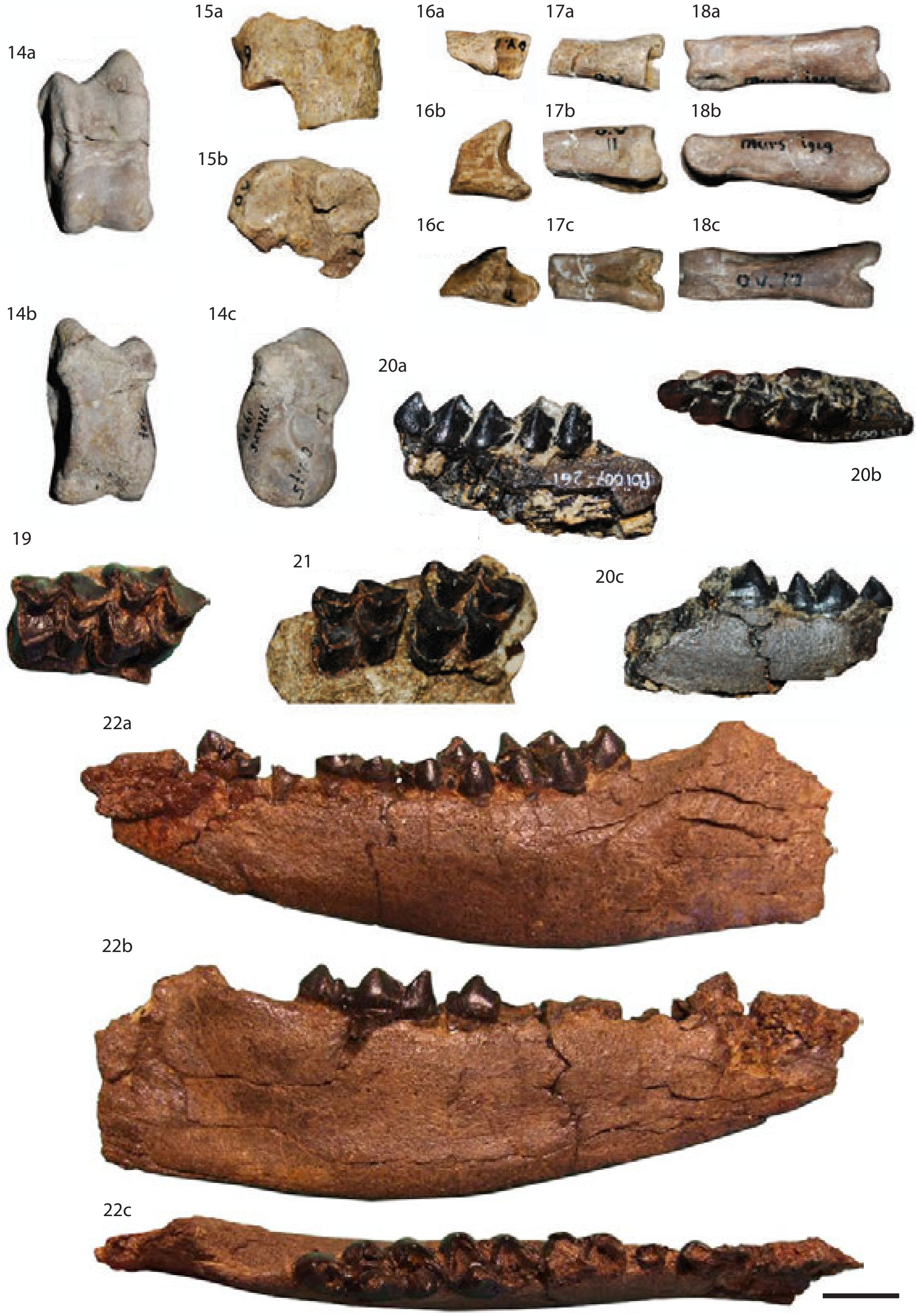


Figure2 (continued). from *Murs* **14** left astragalus (NMB OV75); **15** right cubo-navicular (NMB OV9); **16** phalanx I (NMB OV10); **17** phalanx II (NMB OV11); **18** phalanx III (NMB OV12); from *Poillat* **19** fragmentary left maxillary with M1-2 (MJSN POI007-190), occlusal view; **20** right fragment of mandible with fragmentary m2 and erupting m3 (MJSN POI007-261), lingual (**a**), labial (**b**), and occlusal views (**c**); **21**fragmentary left maxillary with M1-2 (MJSN POI007-941), occlusal view; **22** left *corpus mandibulae* with the roots of p4, fragmentary m1, and m2-3 (MJSN POI007-177+178), lingual (**a**), labial (**b**), and occlusal views (**c**). Scale bar equals 10 mm.

Diagnosis (adapted from Brunet & Sudre 1987). This species is statistically smaller than *L. chalaniati*. The *corpus mandibulae* is low, less high than that of *L. chalaniati*. p1 is strong and separated from c and p2 by diastemata. p2 is elongated, with a strong anterior conid. p3 possesses a mesolabial conid with lingual cristids. The anterolabial cristid forms a lingually well-marked anterior hook. p4 is stockier than that of *L. chalaniati*. Their anterior and posterior valleys are strong. The mesolingual conid is well developed and globular and the talonid is well formed. The anterior and posterior fossae are well formed, shorter and larger than those of *L. chalaniati*, giving a slightly stockier outline to the tooth.

Description

All measurements are summarized in Table 4.

Mandibles. Only 3 fragmentary mandibles of *Lophiomeryx mouchelini* have been discovered in Switzerland. The ventral profile of the *corpus mandibulae* is slightly concave below the cheek teeth. Then, just after the m3, there is an *incisura vasorum* and a relatively flat angular process. The ramus is generally badly preserved. It begins just behind the m3 on NMB UM28. Two *foramen mentale* are located on the anterior part of the mandible.

Adult Lower Dentition. The referred specimens possess variable stages of tooth wear. The specimen MJSN POI007-261 presents an erupting m3, whereas the specimen MJSN POI007-177 has totally worn crowns.

On the labial part of p4, we can observe a bulge probably linked to posterolabial conid. The anterior conid is lingually oriented, implying a reduction in size of the anterior valley. The mesolingual conid is at the level of the mesolabial conid. It is well formed and quite big. The posterior valley is weak, delimited on its posterior part by a very small transverse posterolingual conid reaching the lingual part of the tooth. The posterolabial stylid forms the posterior part of p4. The back valley is lingually well-opened. There is a weak anterior cingulid.

The lower molars possess a lingually opened trigonid and talonid. Their fossae have a flat labial surface. The anterior anterior conid is lacking. The trigonid is open, the preprotocristid being anteriorly oriented and not in contact with the premetacristid. The protoconid is high and labially oblique. The posthypocristid reaches the lingual part of the tooth without contact with the postentocristid, the talonid being open. The hypoconid is smaller than the protoconid. Its prehypocristid is anteriorly oriented. The postentocristid can be present on some specimens (MJSN POI007-261). It is located on the highest part of the entoconid. On the specimens NMB UM28, MJSN POI007-177, and NMB Lvy10, it cannot be observed due to strong dental wear. The prehypocristid is not in contact with the internal postprotocristid, and reaches the preentocristid at its base. The orientation of the internal postprotocristid and the posthypocristid differ as a function of the dental wear. They are oblique on unworn teeth to perpendicular on highly worn teeth. The internal postprotocristid reaches a small, high, and conical metaconid. It does not possess the metacristid. The postmetacristid is more or less present as a function of the dental wear. On the top of the posterior part of the metoconid, a small and shallow groove can be observed on unworn teeth. The external postprotocristid is always missing. The entoconid is devoid of a real postentocristid, and remains well separated from the entoconulid. Laterally, the labial face of this cusp is relatively compressed and flat. On m2-3, the anterior cingulid is well developed. On m3, the hypoconulid is monotuberculated and the height of the entoconulid is highly variable. The latter can produce a cingulid (NMB Lvy10), a cristid joining the postentocristid (MJSN POI007-261), or a conulid more or less separated from the hypoconulid (MJSN POI007-177 and NMB UM28).

Adult Upper Dentition. The upper molars are rather square-shaped and larger from M1 to M3. The cusps are very selenodont. The fossae have flat lingual surfaces. The protocone is widely open and larger than the metaconule. The preprotocrista is straight and lingually oriented. It reaches the parastyle. The postprotocrista is oblique and joins the premetaconulecrista at its middle part, at a slightly lower height . The premetaconulecrista is elongated, thin, straight, and oblique. It finishes at the level of the mesostyle, located side by side to the labial wall. The postmetaconulecrista joins the postmetacrista. The paracone and the metacone are not aligned. The weak paracone rib is stronger than that of the metacone, whereas both possess relatively short and straight cristae. The mesostyle and the parastyle are strong, salient and off-centred from the axis of the labial part of the para-

Table 4. Dental measurements (in mm) of the *Lophiomeryx mouchelini*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	Reference	p1		p2		p3		p4		m1		m2		m3	
Lophiomeryx mouchelini																
Lovagny	NMB Lvy10												11.7	7.5	17.5	7.5
Murs	NMB OV5								11.5	4.7						
	NMB OV6								12.3	5.1	8.2	6.0	10.9	7.6	17.0	7.6
	NMB OV98										10.3	5.6	11.7	6.3		
	NMB OV99															6.6
	NMB OV100								11.9	4.8						
	NMB OV101						12.3	4.7								
	NMB OV102										11.0	5.3				
	NMB OV103												12.0			
Saint-Gemme	NMB MG45												11.8	6.4		6.4
Möhren 13	BSPG 1081												10.3	6.5		
	BSPG 1513														17.5	7.2
	BSPG 1514						9.1	4.2								
Poillat	MJSN POI007-177+178										10.1		11.3	8.1	17.7	7.3
	MJSN POI007-261													8.4	15.9	7.5
Welschenrohr	NMB UM28				9.6		11.6		10.8		10.4		11.6		16.1	
Villebramar	mean value	Brunet& Sudre 1987	5.1	2.9	9.8	3.6	11.8	4.2	11.2	4.9	10.2	6.0	11.2	7.2	17.2	6.7

Locality	Inventory number	d3	
Murs	NMB OV98	9.2	3.2

Locality	Inventory number	M1		M2	
Möhren 13				10.8	13.5
Poillat		11.6	10.9	13.5	12.9
		11.8		13.0	13.0

cone and the metacone. Thus, the labial cusps show a lightly W-shaped external wall. The metastyle is absent. The anterior cingulum is very powerful. It is well marked all around the protocone. There is a weaker posterior cingulum, which stops at the end of the metaconule.

Taxonomical attribution

These specimens share characteristics with the genus *Lophiomeryx*: the corpus mandibularis is low; the lower premolars are laterally compressed and p4 possesses a well-developed metaconid, a reduced anterior valley, and is stockier than that of *L. chalaniati*; the lower molars possess an open trigonid and talonid, due to the anterior orientation of the preprotocristid and the weakly developed to absent postentocristid, the anterior conid is lacking, and the transverse postprotocristd reaches a small, high, and conical metaconid; the upper molars are very simple with a well-developed lingual cingulum, the labial ribs are weakly developed, and the cristae are straight (Brunet & Sudre 1987; Geraads et al. 1987). Regarding the size, the referred specimens (Tab. 4) are smaller than the type species (Tab. 5).

Lophiomeryx chalaniati Pomel, 1853
Fig.3

1853*	*Lophiomeryx chalaniati* Pomel: 98.
1885	*Lophiomeryx chalaniati* Lydekker: 160, figs. 17-18.
1914 v non	*Lophiomeryx chalaniati* Stehlin: 184.
1931 v pars	*Dremotherium nanum* Richard: 321, pl. XVII, fig. 2.
1965?	*Lophiomeryx* sp. Chiang-Siang: 395, fig.
1970	*Lophiomeryx chalaniati* Brunet: 350, tab. 9.

1973 non	*Lophiomeryx* sp. de Bonis et al.: 109, tab. 2(4).
1983 v	*Lophiomeryx chalaniati* Mayo: 906.
1984 v	*Lophiomeryx chalaniati* Sudre: fig.13.
1987	*Lophiomeryx chalaniati* Brunet & Sudre: 225, figs. 4-17.
1987 v	*Lophiomeryx chalaniati* Engesser & Mayo: 73.
1987 v non	*Lophiomeryx* sp. Remy et al.: 185, tab. 3c.
1987 v	*Lophiomeryx chalaniati* Remy et al.: 188, tab. 4c.
1987	*Lophiomeryx* Janis: 200.
1987	*Lophiomeryx* Lacomba & Morales: 297.
1987	*Lophiomeryx chalaniati* Geraads et al.: 46, figs. 2, 9, 15, 26, and 35.
1995 v	*Lophiomeryx chalaniati* Sudre: 228, fig.11-21.
1995 v	*Lophiomeryx chalaniati* Martinez & Sudre: fig D.
1997	*Lophiomeryx* cf. *chalaniati* Vislobokova: 220.
1997	*Lophiomeryx chalaniati* Hugueney: 420.
1997	*Lophiomeryx chalaniati* Hugueney: 421.
1997	*Lophiomeryx* sp. Hugueney: 421.
1997	*Lophiomeryx chalaniati* Hugueney: 426.
1997 v	*Lophiomeryx chalaniati* Engesser & Mödden: 484.
1997 v	*Lophiomeryx chalaniati* Blondel: 574.
1998 v	*Lophiomeryx chalaniati* Blondel: 527.

Holotype. Left mandible with d3-m3 (BMNH BM 34960, Lyddeker 1885: 161, fig. 17; Brunet et Sudre 1987: p. 283, fig. 16).

Species etymology. The species name was given in honour of Edouard R. de Chalaniat, a palaeontologist who studied the marl and limestone deposits in Auvergne, Haute-Loire, and Bourbonnais (France).

Type locality and horizon. La Sauvetat (Puy-de-Dôme, France), MP25.

Occurrence. Mid-Oligocene, from MP24 to early MP28, of Spain (Carrascosa del Campo), France (Antoing, Belgarric, Benissons-Dieu, Cournon, La Devèze, Le Garouillas, Malhat, Moissac III, Moissac IV, Nonette, Pech Desse, Rabastens, Rigal-Jouet, Saint-Martin-de-Casselvi, Tournon, Vallon d'Auradou), Switzerland (Mümliswyl-Heitersberg), and Germany (Seckbach).

Referred material. La Sauvetat (France): MNHN Lim328, left *corpus mandibulae* with m2-3. Le Garouillas (France): USTL GAR20, left *corpus mandibulae* with d3-m2; USTL GAR24, left M3; USTL GAR24, right M; USTL GAR25, right M3; USTL GAR26, left M; USTL GAR28, left M; USTL GAR29, left M; USTL GAR41, right maxillary with P2; USTL GAR45, left i1-c and roots of right i1-3; USTL GAR132, right M3; USTL GAR149, left M1; USTL GAR152, left M2; USTL GAR153, right M3; USTL GAR154, left M3; USTL GAR154, astragalus; USTL GAR159, astragalus; USTL GAR163, astragalus; USTL GAR188, proximal phalanx; USTL GAR189, medial phalanx; USTL GAR190, distal phalanx; USTL GAR2055, calcaneum; USTL GAR2056, cubo-navicular bone. Pech Desse (France): USTL PDS1360, right *corpus mandibulae* with m2-3. Old collections of the Phosphorites du Quercy (France): NMB QuA541, right mandible with i2 and p2-m3. Rabastens (France): MHNT.PAL.2010.0.33, left M1; MHNT.PAL.2010.0.106, right mandible with m2-3. Savenès (France): MHNT.PAL.2011.0.51, left M1. Vallée d'Auradou (France): NMB OG96, right mandible with p3-m3. Mümliswyl-Heitersberg (Switzerland): NMB Mü54, right *corpus mandibulae* with p3-m2; NMB Mü71, right *corpus mandibulae* with d4; NMB UM2292, left d3; NMB UM2293, right *corpus mandibulae* with p2-3; NMB UM2294, right broken mandible with broken p4-m3; NMB UM2296, right i3; NMB UM2297, left i1; NMB UM2298, right i2; NMB UM2320, right astragalus; NMB UM2853, left cubonavicular bone; NMB UM2856, distal part of unfused metapodial bones.

Diagnosis (adapted from Brunet & Sudre 1987). This species is statistically larger than *L. mouchelini*. p1 is shorter, p2 possesses a small to absent anterior conid, the posterior valley is weakly developed on p3-4, and the mesolingual conid is stronger on p4. The molars are quite large with higher crowns. The hypoconulid is linked to the posthypocristid on m3. The *corpus mandibulae* is higher than that of *L. chalaniati*.

Description

All measurements are summarized in Table 5.

Mandibles. The ventral profile of the *corpus mandibulae* is slightly concave below the cheek teeth. It becomes larger under the molars. The diastema between c and p1 is short and highly concave in upper view. The rest of the mandible is slightly convex.

Lower decidual dentition. Only one mandibular specimen has a d3 (NMB UM2292). This tooth is unworn, however the anterior part with the anterior conid is lacking. This tooth is narrow and elongated. The mesolabial conid and the posterolabial stylid are high and longitudinally oriented, with the mesolabial conid higher than the posterolabial stylid. These cuspids are as wide as the tooth and tetrahedral, with a triangular shape in lateral views. The transverse cristid and the anterolabial cristid are labially oriented. The posterolingual conid is weak and lingually oriented. The posterolabial cristid is short, implying a distinct gap between the mesolabial conid and the posterolabial conid. The posterior stylid is slightly curved, joining the posterolabial edge of the tooth and partially closing its posterior part. The posterolingual conid is oblique and lingual. Thus, the posterior stylid and the posterior cristid form a posterolingually-opened triangle on the posterior face of the posterolabial conid. On this opening, there is a neocristid. The latter is curved and reaches the apex of the posterolabial conid. On its postero-lingual extremity, it forms a postero-lingual angle with a spur on its top. The d4 (NMB Mü71) is relatively unworn with broken hypoconid and entoconid. The trigonid is anteriorly opened. The short preprotocristid is anteriorly oriented. The protoconid is strong and globular. The internal postprotocristid joins the weak postmetacristid and preentocristid in a Y-shape. The metaconid is conical, without premetacristid. Between the hypoconid and the protoconid, there is a small ectostylid. The talonid is widely posteriorly opened, due to the absence of the postentocristid. The posthypocristid is transverse. The posterior cingulid is strong. The prehypocristid joins the postprotocristid at a low level, in the axis of the tooth, with a slightly oblique orientation. The anterolabial conid is quite small. It is pyramidal with a base clearly formed by grooves separating this conid from the trigonid and the anterolingual conid. The anterolabial conid is oblique on the anterolingual part of the tooth and forms a kind of blade. On its anterior part, there is an anterior cristid forming the anterior point of the tooth. On the posterior base of the anterolingual conid, there is a spur. The anterior fossa is well surrounded by a relatively strong cingulid.

Adult lower dentition. The anterior lower teeth of *Lophiomeryx chalaniati* are very rare in the fossil record. Only Brunet & Sudre (1987) described a lower anterior dentition of *Lophiomeryx chalaniati* from Le Garouillas (USTL GAR45). The referred lower incisors from Mümliswyl-Heitersberg and the mandible from Quercy (NMB QuA54) complete this lack of data. They are poorly worn, which explains why they are bigger than those on the mandible NMB QuA541. i1 and i2 are bigger and wider than the i3. i1 is highly concave on its posterior part, that is not the case of the i2. Both teeth possess a highly convex anterior part of the crown. The i3 is slightly curved.

The lower premolars are narrow and elongated. From p2 to p4, the complexity of the dental pattern and the size are more important. The p1 is separated from p2 by a small diastema. The mesolabial conid is high, slightly anterior, with a triangular profile forming a leaf like shape. On the p2, the protoconid is as wide as the tooth. On p3-4, it becomes more and more labial. The anterior conid is more and more strong from p2 to p4. This cuspid is joined by the anterior cristid on its base. This cristid is short, straight, and anterior and forms the labial wall of the tooth. On the p2, the mesolabial conid wears a very weak posterolingual transverse cristid. This latter is very well developed on p3, with, on its base, a small mesolingual conid and a large posterior valley. This valley is narrower on the p4, because the mesolingual conid is well developed and the posterolingual conid is more anterior. On p4, the mesolingual conid is lingual, located on the anterior part of the transverse cristid and the posterior part of the mesolabial conid. The mesolingual conid is slightly smaller than the mesolabial conid. The posterolabial cristid is shorter from p2 to p4. The back valley is wider from p2 to p4. On p3, the posterolabial cristid joins the laterally compressed and oblique posterolingual conid. This latter joins the lingual part of the tooth. On p4, this conid is absent and only a weak posterior cristid can be observed. The posterolabial conid forms the posterolabial angle of the tooth. On p3, this cristid ends on the middle of the posterior part of the tooth, whereas on p4, it ends in the posterolingual part of the tooth. The lingual part of the posterolingual wall of p4 is slightly bulged due to the presence of the posterolabial conid.

The trigonid and the talonid of the lower molars are widely open. There is no anterior conid. The opening of the trigonid is due to the oblique orientation of the preprotocristid, the absence of the premetacristid, and

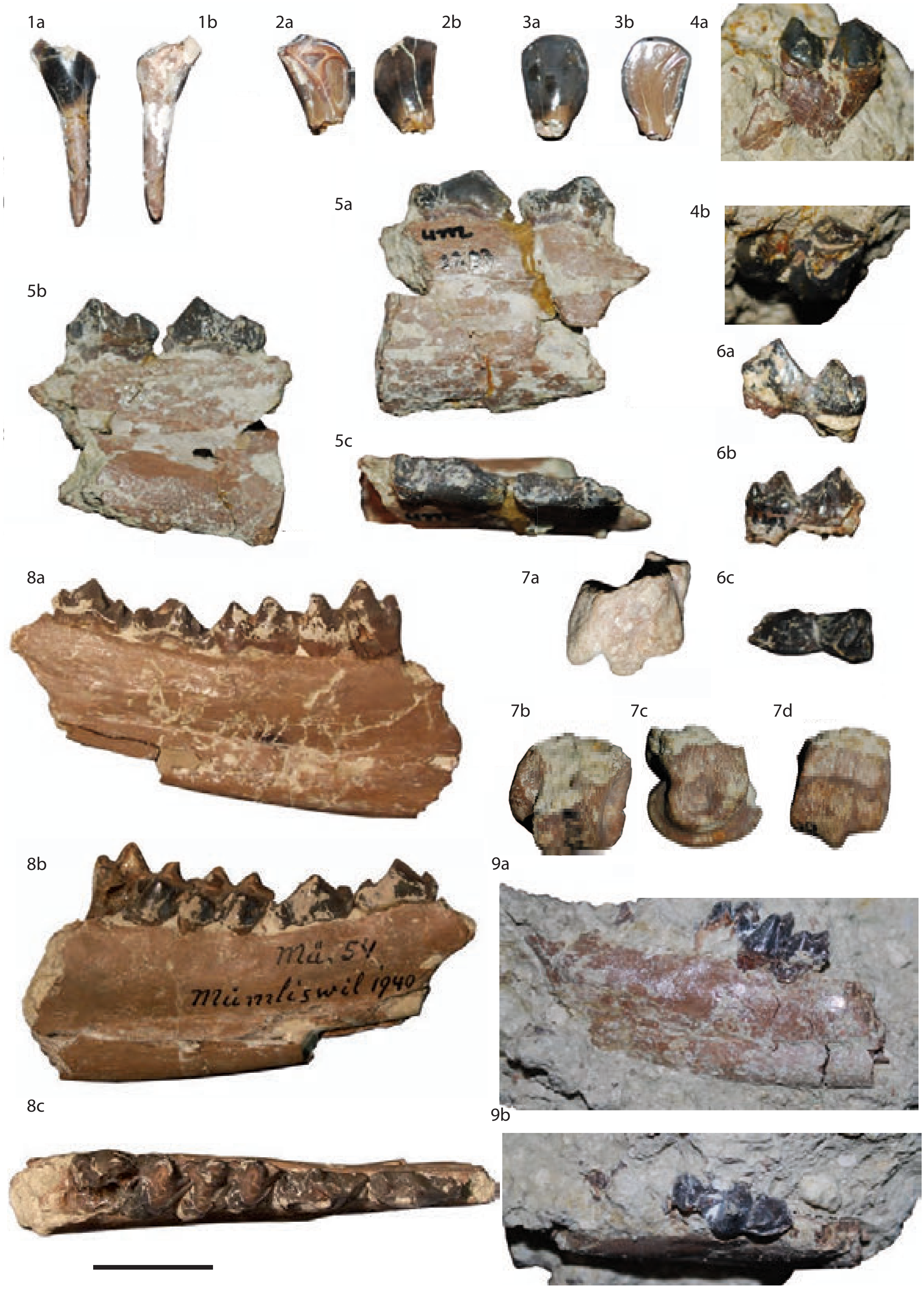


Figure 3. *Lophiomeryx chalaniati*: from *Mümliswyl-Heitersberg* **1** right i3 (NMB UM2296); **2** left i1 (NMB UM2297); **3** right i2 (NMB UM2298); **4** right m3; **5** right *corpus mandibulae* with p2-3 (NMB UM2293), lingual (**a**), labial (**b**), and occlusal views (**c**); **6** left d3 (NMB UM2292), lingual (**a**), labial (**b**), and occlusal views (**c**); **7** distal part of unfused metapodial bones (NMB UM2856); **8** right *corpus mandibulae* with p3-m2 (NMB Mü54), lingual (**a**), labial (**b**), and occlusal views (**c**); **9** right *corpus mandibulae* with d4 (NMB Mü71), lingual (**a**), labial (**b**), and occlusal views (**c**). Scale bar equals 10 mm.

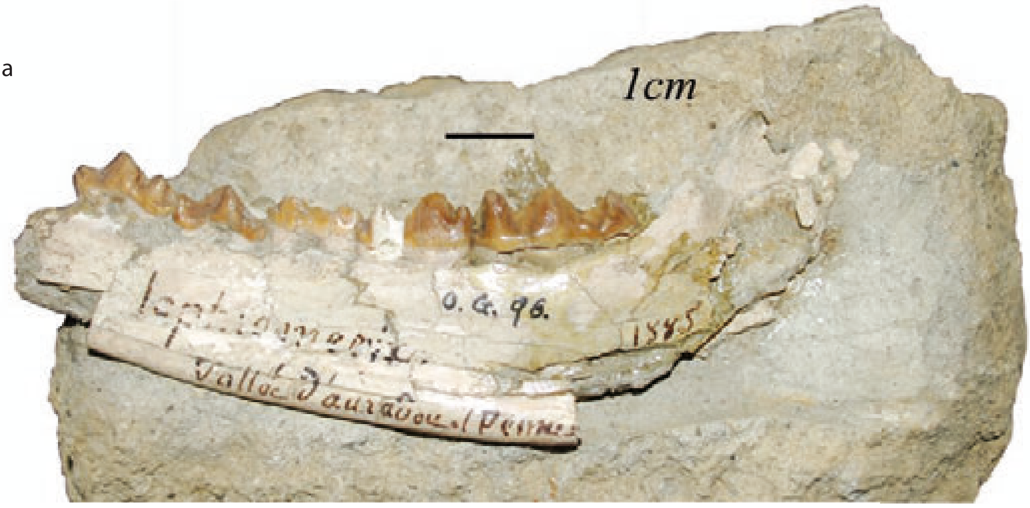
10

11a

12

11b

13a



13b

Figure 3 (continued). from *Savenès* **10** left M1 (MHNT.PAL.2011.0.51), occlusal view; from *Rabastens* **11** right mandible with m2-3 (MHNT. PAL.2010.0.106), lingual (**a**), labial (**b**), and occlusal views (**c**); **12** left M1 (MHNT.PAL.2010.0.33), occlusal view; from *Vallée d'Auradou* **13** right mandible with p3-m3 (NMB OG96), lingual (**a**), labial (**b**), and occlusal views (**c**) . Scale bar equals 10 mm.

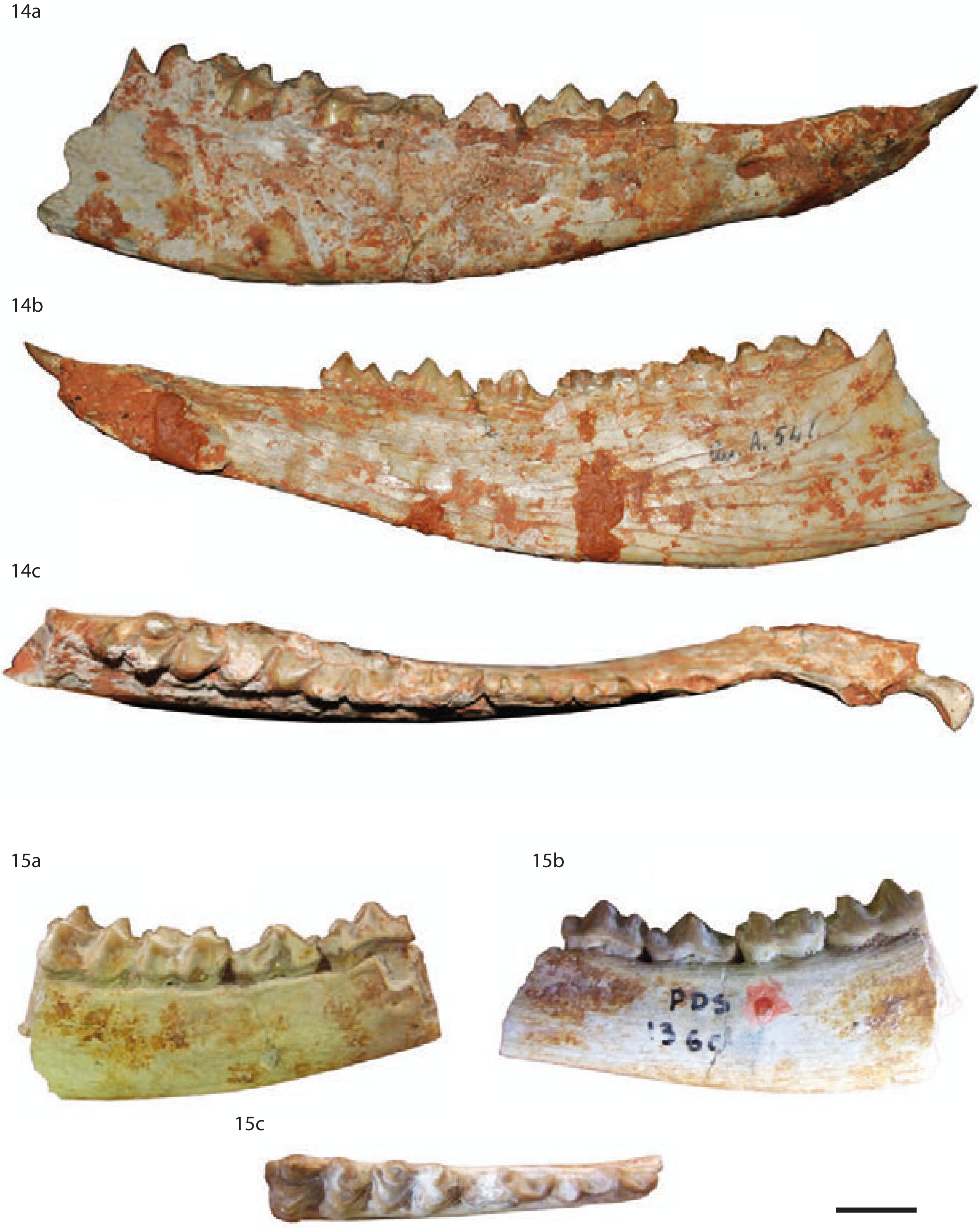


Figure 3 (continued). from *Old collections of the Phosphorites du Quercy* **14** right mandible with i2 and p2-m3 (NMB QuA541), lingual (**a**), labial (**b**), and occlusal views (**c**); from *Pech Desse* **15** right *corpus mandibulae* with m2-3 (USTL PDS1360), lingual (**a**), labial (**b**), and occlusal views (**c**). Scale bar equals 10 mm.

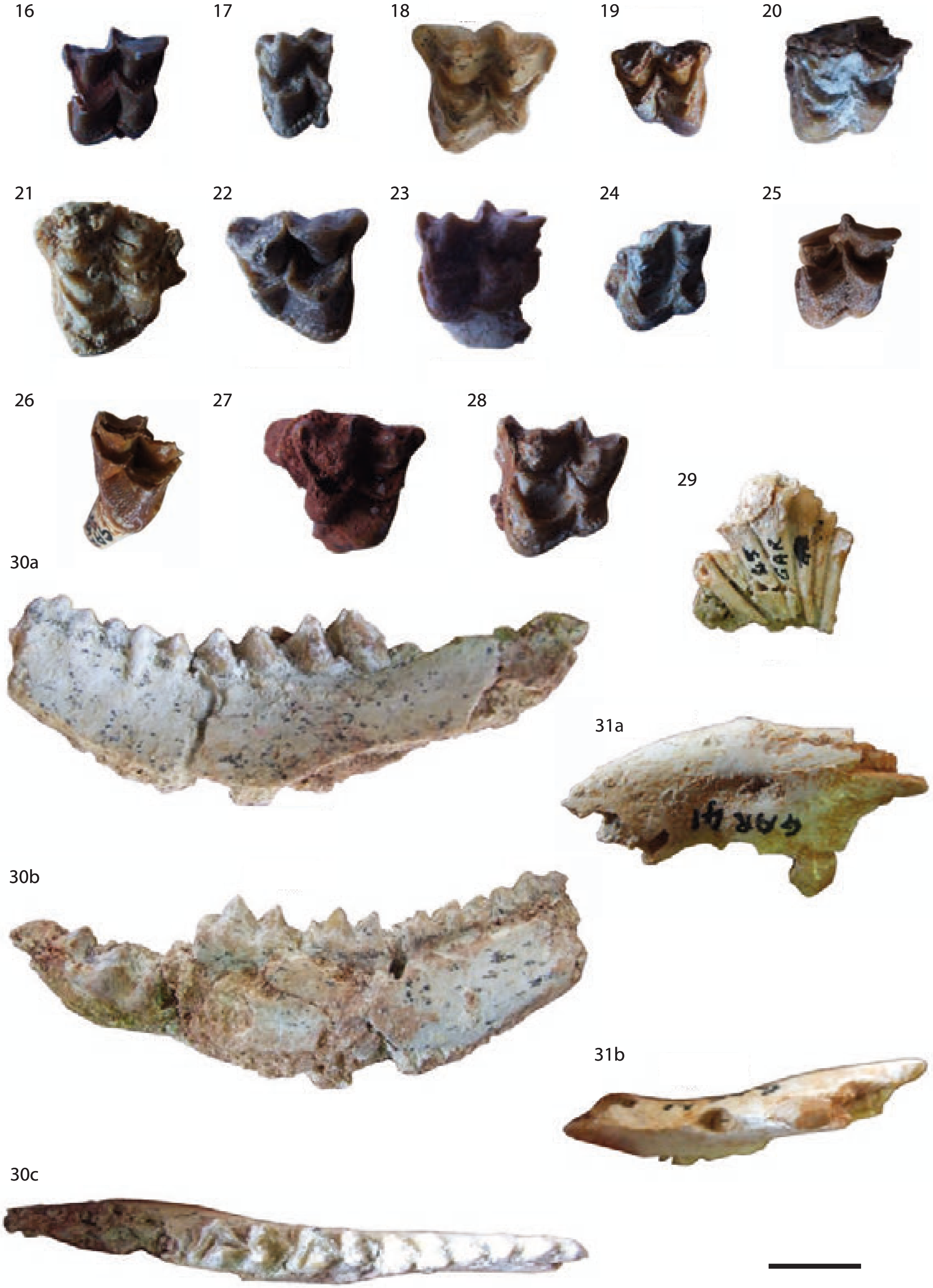


Figure 3 (continued). from *Le Garouillas* **16** left M (USTL GARb), occlusal view; **17** left M (USTL GARa), occlusal view; **18** left M3 (USTL GAR154), occlusal view; **19** (USTL GAR153) right M3, occlusal view; **20** left M2 (USTL GAR152), occlusal view; **21** left M1 (USTL GAR149), occlusal view; **22** right M3 (USTL GAR132), occlusal view; **23** left M (USTL GAR28), occlusal view; **24** left M (USTL GAR26), occlusal view; **25** left M (USTL GAR29), occlusal view; **26** right M3 (USTL GAR25), occlusal view; **27** right M (USTL GAR24), occlusal view; **28** left M3 (USTL GAR24), occlusal view; **29** left i1-c and roots of right i1-3 (USTL GAR45); **30** left *corpus mandibulae* with d3-m2(USTL GAR20), lingual (**a**), labial (**b**), and occlusal views (**c**). Scale bar equals 10 mm.

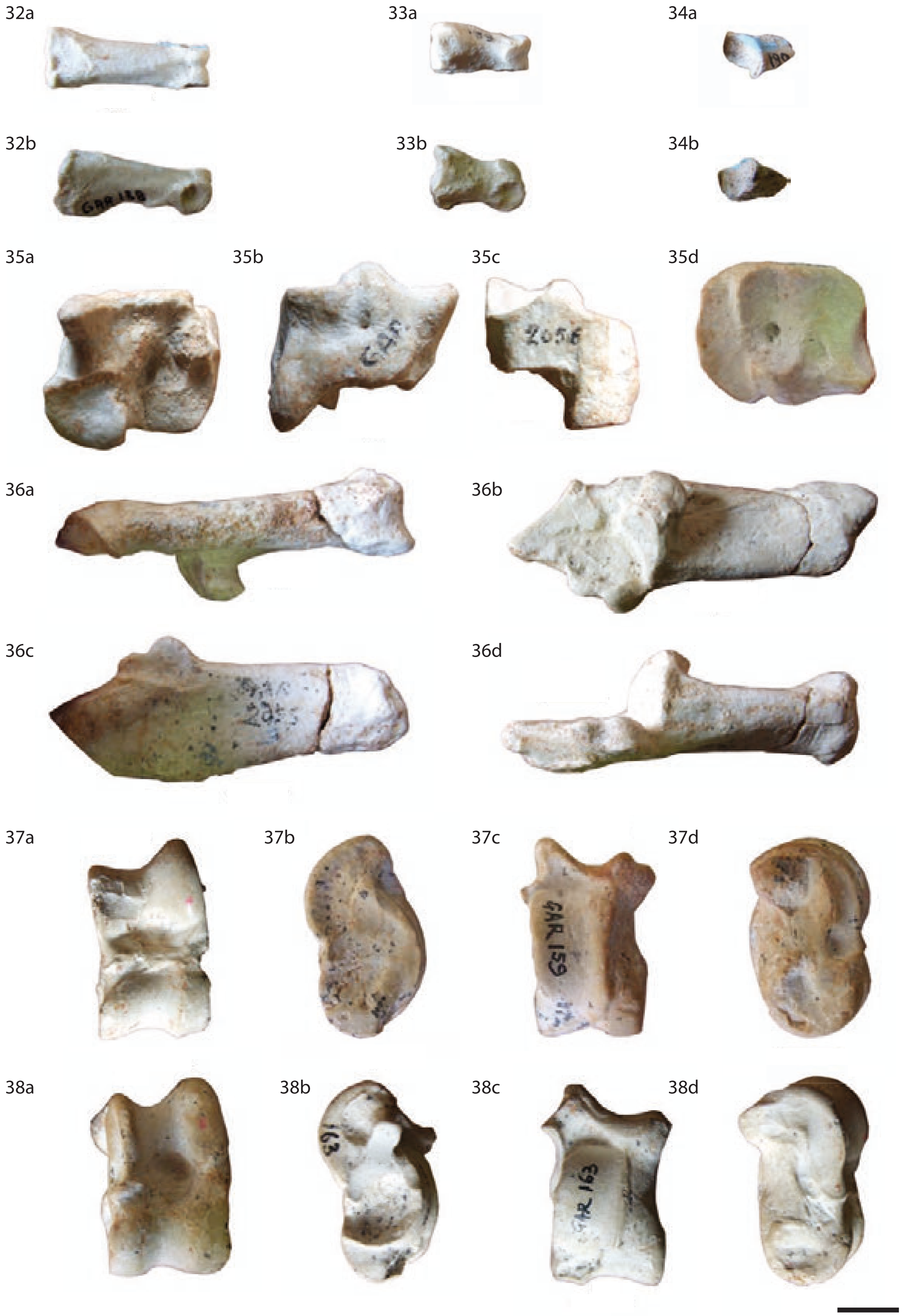


Figure 3 (continued). from *Le Garouillas* **31** right maxillary with P2 (USTL GAR41), occlusal view; **32** proximal phalanx (USTL GAR188); **33** medial phalanx (USTL GAR189); **34** distal phalanx (USTL GAR190); **35** cubo-navicular bone (USTL GAR2056); **36** calcaneum (USTL GAR2055); **37** astragalus (USTL GAR159); **38** astragalus (USTL GAR2055). Scale bar equals 10 mm.

Table 5. Dental measurements (in mm) of the *Lophiomeryx chalaniati*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	Reference	p1		p2		p3		p4		m1		m2		m3	
Lophiomeryx chalaniati																
La Sauvetat	MNHN Lim328												13.2	8.6	19.8	8.4
Larromieu	MHNT.AL.2011.0.6												11.7	7.9	14.7	6.9
Pech Desse	USTL PDS1360						11.3	4.1	11.6	4.9	11.1	6.6	12.6	8.0		
Old collections of Quercy	NMB QuA541				9.6	3.2	11.1	4.2	10.0	5.4	10.1	7.3	12.8	8.2	17.5	7.9
Rabastens	MHNT.PAL.2010.0.106												12.6	7.1	17.0	7.3
Vallée d'Auradou	NMB OG96						12.5	3.8	10.5		10.2		13.1		17.0	
Mümliswyl Heitersberg	NMB Mü54						11.5	4.6	11.8	5.1	11.5	7.8	13.6			
	NMB UM2293															
Le Garouillas	mean value	Brunet & Sudre 1987	5.1	2.4	10.4	3.5	12.4	4.3	12.2	5.4	12.3	7.3	13.5	8.2	18.1	7.7
Old collections of Quercy	mean value	Filhol 1877					10.0	4.0	11.0	5.0	12.5	7.5	14.0	8.5	20.0	9.0

Locality	Inventory number	Reference	d3		d4	
Mümliswyl Heitersberg	NMB Mü71				16.0	
	NMB UM2292		10.8	4.6		
Le Garouillas	mean value	Brunet & Sudre 1987			14.6	5.5

Locality	Inventory number	Reference	P1		P2		P3		P4		M1		M2		M3	
Le Garouillas	USTL GAR24														15.2	14.2
	USTL GAR25														15.6	14.8
	USTL GAR26										12.6	14.7				
	USTL GAR28										11.7	10.6				
	USTL GAR29															14.5
	USTL GAR132												16.0	15.5		
	USTL GAR149										14.6	15.9				
	USTL GAR152												15.6	16.8		
	USTL GAR153														14.4	14.7
Rabastens	MHNT.PAL.2010.0.33										12.0	14.1				
Savenès	MHNT.PAL.2011.0.51										11.5	13.2				
Le Garouillas	mean value	Brunet & Sudre 1987	12.6	5.6	12.4	7.7	10.0	10.1	11.0	12.6	14.6	14.8	13.9	14.5		
Old collections of Quercy	mean value	Filhol 1877									12.0	14.0	16.0	16.0	13.0	16.0

the metaconid, which is relatively posterior. It is at the level of the protoconid. The ectostylid is weak between the protoconid and the hypoconid. The protoconid is well developed and seems to be smaller than the hypoconid. The internal postprotocristid is transverse. It joins the metaconid at its base and fuses with the very weak, short, and straight postmetacristid as well as the preentocristid, which is short and anteriorly oriented. The protoconid does not bear an external postprotocristid. The metaconid is globular and conical. It can bear a posterior groove resembling the *Dorcatherium* fold. The prehypocristid does not join the other cristids and stops in the middle of the tooth. The talonid is lingually open due to the oblique orientation of the posthypocristid and the absence of the postentocristid. The entoconid is laterally compressed with an anterior rounded part. The posthypocristid finishes by an entoconulid more developed on the m2 than the m1. The back fossa of m3 is widely lingually opened. The hypoconulid is high and salient. Its prehypoconulidcristid has a nearly anterior orientation and joins the posthypocristid, stopping before it joins the lingual edge of the tooth. The anterior and posterior cingulids are present.

Taxonomical attribution

The referred specimens share characteristics with the genus *Lophiomeryx*. The lower premolars are highly laterally compressed. The p2 and p3 are in blade-shape. The p4 has a well-developed mesolingual conid. The lower molars have an open trigonid and talonid, due to the anterior orientation of the preprotocristid and the weakly developed to absent postentocristid. There is no anterior conid. The transverse postprotocristd reaches a small, high, and conical metaconid (Brunet & Sudre 1987; Geraads 1987). The corpus mandibularis is high. The p4 is more elongated than in *L. mouchelini*. Regarding the size (Tab. 5), *L. chalaniati* is larger than *L. mouchelini* (Brunet & Sudre 1987).

Family **TRAGULIDAE** Milne-Edwards, 1864
Genus ***Iberomeryx*** Gabunia, 1964

Type species. *Iberomeryx parvus* Gabunia, 1964, from Benara (Georgia), Early Oligocene (MP23; Lucas & Emry 1999).

Further included species. *Iberomeryx minor* (Filhol, 1882).

Amended diagnosis (from Mennecart et al. 2011). Small-sized ruminant with upper molars possessing the following combination of characters: well-marked parastyle and mesostyle in colonnette shape; strong paracone fold; metacone fold absent; metastyle absent; unaligned external walls of metacone and protocone; strong postprotocrista stopping up against the anterior side of the premetaconulecrista; continuous lingual cingulum, stronger under the protocone. Lower dental formula is primitive (3–1–4–3) with unmolarized premolars. Tooth c is adjacent to i3. Tooth p1 is one-rooted, reduced and separated from c and p2 by a short diastema. Premolars have a well-developed anterior conid. Teeth p2–p3 display a distally bifurcated mesolabial conid, forming a posterior valley. Tooth p3 is the largest premolar. Tooth p4 displays no mesolingual conid and a large posterior valley nearly closed by unfused lingual and labial cristids. Regarding the lower molars, the trigonid and talonid are lingually open with a trigonid more tapered than the talonid. The anterior fossa is open, due to a forward orientation of the preprotocristid and an anterior conid. The postprotocristid is oblique, without external postprotocristid. Internal postprotocristid, postmetacristid and preentocristid are fused and Y-shaped. Protoconid and metaconid display a weak *Tragulus* fold and a well-developed *Dorcatherium* fold, respectively. The mandible displays an angular convex ventral profile, a marked incisura vasorum, a strong mandibular angular process, a vertical ramus, and a stout condylar process.

Etymology. *Ibero–* is the Latin name for the ancient Georgian kingdom of Kartli and *–meryx* is the Greek word for ruminant.

Iberomeryx minor (Filhol, 1882)
Fig.4

1877 non	*Lophiomeryx gaudryi* Filhol: 447, figs. 279–280.
1882*	*Bachitherium minor* Filhol: 138.
1886 v par	*Cryptomeryx gaudryi* Schlosser: pl. II, figs. 13–14, pl. V, fig. 7, 16, and 24 (non pl. VI, fig. 6 and 9).
1910 v	*Cryptomeryx gaudryi* Fleury: 277.
1914 v	*Cryptomeryx gaudryi* Stehlin: 184.
1926	*Cryptomeryx gaudryi* Carlson: 69.
1962	*Cryptomeryx* Friant: 114.
1966	cf. *Cryptomeryx gaudryi* Palmowski & Wachendorf: 241, pl. 15, fig. 7.
1967	*Cryptomeryx* Friant: 96.
1973	*Bachitherium* ? sp Bonis et al.: tab. 2(4).
1978 v	*Cryptomeryx* cf. *gaudryi* Heissig: 271, tab. 4.
1979 v	*Cryptomeryx gaudryi* Gaudant: 889, figs. 17–20.
1980	*Cryptomeryx* Webb & Taylor: 124.
1984 v	*Cryptomeryx gaudryi* Sudre: 6, figs 1–9.
1986*	*Iberomeryx minor* Bouvrain et al.: 102, fig. 2.
1987.	*Iberomeryx minor* Geraads et al.: 44, figs. 16, 27, 36.
1987 v non	*Iberomeryx matsoui* Heissig: 108, fig. 6.
1995 v	*Iberomeryx minus* Martinez & Sudre: fig. C.
1996 v	*Iberomeryx minus* Sudre & Blondel: 178, tab. 1.
1997 v	*Iberomerx minus* Blondel: 584, tabs. 8–9.
2004 v	*Iberomeryx minor* Becker et al.: 184, fig. 5.
2007	*Iberomeryx minus* Métais & Vislobokova: 195.
2011 v	*Iberomeryx minor* Mennecart et al.: S115, figs. 4-5.

Holotype. Fragmentary right mandible with tooth row p3-m3 (QU4234, coll. MNHN-Paris, Bouvrain et al. 1986: 103, fig. 2). Filhol (1882) first described this type as a right tooth row p2-m3, but p2 has been lost.

Species etymology. Latin word for the smallest.

Type locality and horizon. Undated old collections of the Phosphorites du Quercy (France).

Occurrence. Early Oligocene, MP23 to early MP24, from Spain (Montalban), France (Itardie, Lovagny, Mounayne, Pech Crabit, Roqueprune 2), Switzerland (Court, La Beuchille, Pré Chevalier, Soulce), and Germany (Ehingen 4).

Referred material. Montalban (Spain): NMB Mab4 Montalban, left M1. Itardie (France): USTL ITD 28, right m3; USTL ITD 907, left M1-2; USTL ITD 908, left p3; USTL ITD 910, left maxillary with D4-M3; USTL ITD 912, left P2-3. Lovagny (France): NMB Lvy9, left P4-M3. Old collections of the Phosphorites du Quercy (France): BSPG 1879 XV 126, right *corpus mandibulae* with d3-m1; BSPG 1879 XV 127, complete left *corpus mandibulae* with p4-m3; BSPG 1879 XV 954, right *corpus mandibulae* with p4-m2; BSPG without number a, right *corpus mandibulae* with m1; BSPG without number b, left *corpus mandibulae* with m1-3; NMB Q.B.32 (Sudre 1984: 11, fig. 5), fragmentary left mandible with p3–m3; MNHN Qu4234 (Holotype), complete right *corpus mandibulae* with p3-m3. Court (Switzerland): unnumbered, left m3. La Beuchille (Switzerland): MJSN BEU001-409 (old number BEU-700-J1; Becker et al. 2004: 184, fig. 5), right fragmentary tooth row with m1-m3; MJSN BEU001-410, right fragmentary mandible with p4; MJSN BEU001-411, right fragmentary mandible with m1–m2. Pré Chevalier (Switzerland): MJSN PRC004-159, right fragmentary mandible with p4-m3. Soulce (Switzerland): NMB Sc.118 (Gaudant 1979: 889), right tooth row with m1-m3 and nearly complete left mandible with p2–p4. Ehningen 4 (Germany): BSPG 1953 I 589, right fragmentary m3.

Amended diagnosis (from Mennecart et al. 2011). It differs from *Iberomeryx parvus* by having larger trigonids on the lower molars and a smaller anterior conid and a larger posterior valley on p4.

Description

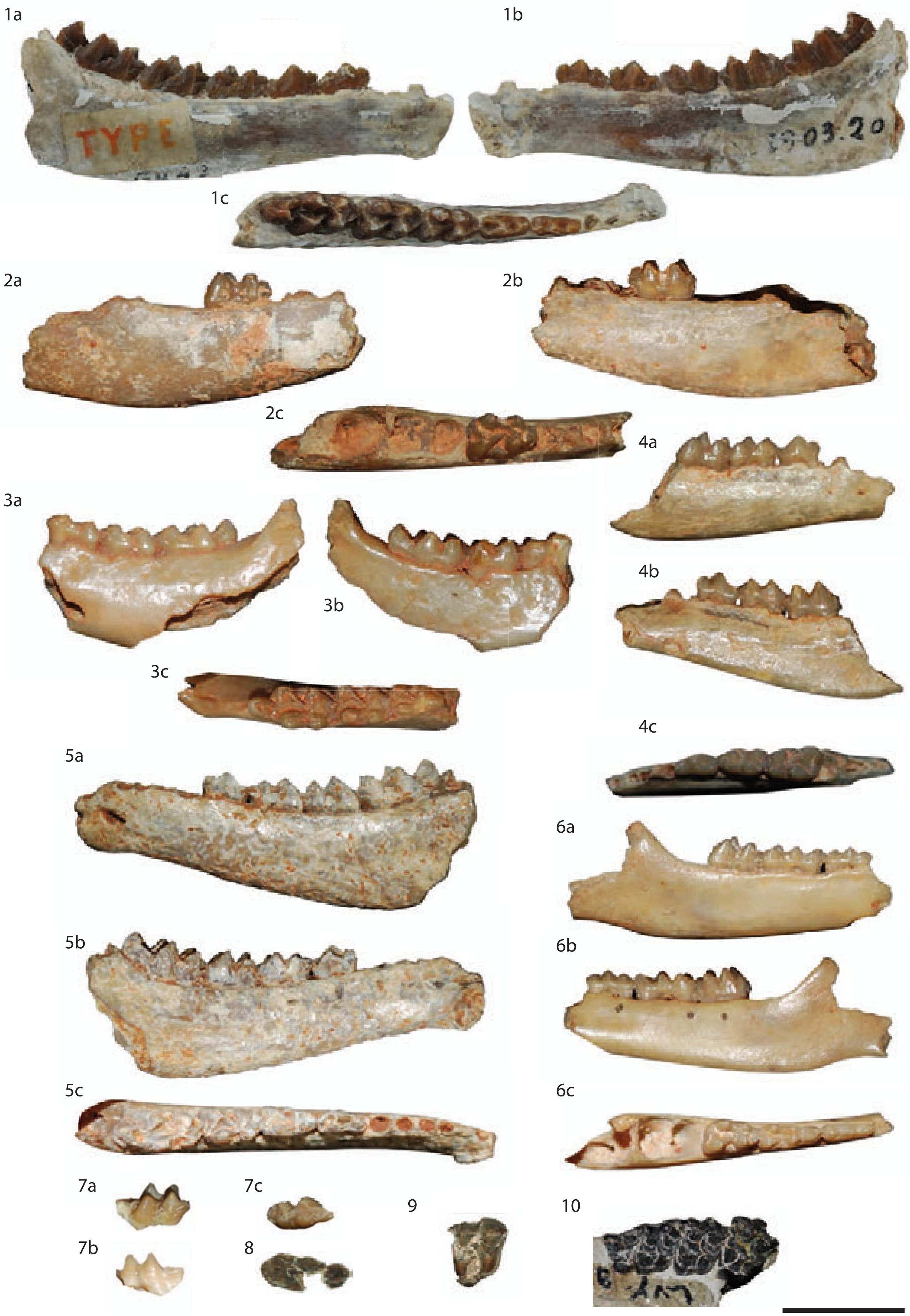
All measurements are summarized in Table 6.

Lower adult dentition. The lower cheek teeth of *Iberomeryx minor* are the object of a recent publication (Mennecart et al. 2011; Chapter 4). p4 is traguline-like in having a large posterior valley due to the absence of the mesolingual conid and the transverse cristid forming the lingual wall. The lower molars possess a well-developed *Dorcatherium* fold, forming a large buckle on the metaconid. The preprotocristid finishes with an anterior conid, common with the other Tragulids.

Upper adult dentition. The badly preserved triangular P4 is as long as wide. The anterolingual conid is aligned with the anterolabial cone. The anterior style is slightly globular with the anterolingual crista ending at its base. The labial wall is relatively flat.

The bunoselenodont molars are larger from M1 to M3. These teeth are relatively triangular in shape due to a reduced and laterally compressed metaconule. The metaconulecrista is slightly curved, the premetaconulecrista ends between the paracone and the metacone, and the postmetaconulecrista ends at the base of the postmetaconulecrista. The enlarged protocone possesses straight cristae. The preprotocrista joins a weak and slightly globular parastyle. The paracone and the metacone have a tetrahedral morphology with aligned cristae. These cusps are not aligned. The paracone rib, without anterior fold, is weakly developed, but much larger than that of

Figure 4 (opposite page). *Iberomeryx minor*: from old collections of the *Phosphorites du Quercy* **1** complete right *corpus mandibulae* with p3-m3 (MNHN Qu4234), lingual (**a**), labial (**b**), and occlusal views (**c**); **2** right *corpus mandibulae* with m1 (BSPG without number a), lingual (**a**), labial (**b**), and occlusal views (**c**); **3** left *corpus mandibulae* with m1-3 (BSPG without number b), lingual (**a**), labial (**b**), and occlusal views (**c**); **4** right *corpus mandibulae* with p4-m2 (BSPG 1879 XV 954), lingual (**a**), labial (**b**), and occlusal views (**c**); **5** complete left *corpus mandibulae* with p4-m3 (BSPG 1879 XV 127), lingual (**a**), labial (**b**), and occlusal views (**c**); **6** right *corpus mandibulae* with d3-m1 (BSPG 1879 XV 126), lingual (**a**), labial (**b**), and occlusal views (**c**); *Ehningen 4* **7** right fragmentary m3 (BSPG 1953 I 589), lingual (**a**), labial (**b**), and occlusal views (**c**); *Court* **8** left m3(unnumbered), occlusal view; *Montalban* **9** left M1 (NMB Mab4), occlusal view; *Lovagny* **10** left P4-M3 (NMB Lvy9), occlusal view. Scale bar equals 10 mm.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8

Table 6. Dental measurements (in mm) of the *Iberomeryx minor*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	Reference	p3		p4		m1		m2		m3	
Iberomeryx minor												
Old collections of Quercy	BSPG 1879 XV 126						4.6	3.9				
	BSPG 1879 XV 127				3.9	1.9	4.2	2.9	4.3	3.1	6.9	3.6
	BSPG 1879 XV 954				4.1	2.3	5.0	3.0	5.5	3.6		
	BSPG without number a						4.9	3.0				
	BSPG without number b							2.7	4.9	3.5	7.3	3.8
	NMB Q.B.32	Sudre 1984	5.0	1.6	4.1	1.9	4.3	3.1	4.5	3.5	8.0	3.5
Ehningen 4	BSPG 1953 I 589										7.7	3.4
Court	unnumbered										8.1	3.3
La Beuchille	MJSN BEU001 409								4.9			
	MJSN BEU001 410				4.2							
	MJSN BEU001 411								4.9	3.3		
Pré Chevalier	MJSN PRC004 159				4.0	1.8	5.1	3.2	5.3	3.4	8.1	3.5
Soulce	NMB Sc.118		4.4		4.4							
	NMB Sc.118						4.5	2.9	5.8	3.4	7.8	3.8
Itardie	USTL ITD 28	Sudre 1984									8.1	3.5
	USTL ITD 908	Sudre 1984	6.6	3.0								
	USTL ITD 29	Sudre 1984									8.5	4.4

Locality	Inventory number	Reference	d3		d4	
Old collections of Quercy	BSPG 1879 XV 126		4.3	1.5	5.0	2.2

Locality	Inventory number	Reference	P2		P3		P4		M1		M2		M3	
Lovagny	NMB Lvy9						4.0	4.2	4.9	6.2	5.8	7.0	6.0	7.9
Montalban	NMB Mab4								5.0	5.6				
Itardie	USTL ITD 907	Sudre 1984							4.5	5.2				
	USTL ITD 910	Sudre 1984							4.7	5.4	5.5	6.2	5.7	6.7
	USTL ITD 912	Sudre 1984	4.3	2.0	4.2	3.0								
	USTL ITD 27	Sudre 1984									5.1	5.1		
	USTL ITD 911	Sudre 1984							5.2	6.1	6.0	6.1	6.1	6.8
Roqueprune	ROQ 2-331	Sudre 1984									6.0	6.9		
	ROQ 2-333	Sudre 1984							4.8	5.0	5.9	6.0	6.2	6.3
	ROQ 2-334	Sudre 1984								5.9		7.0		
	ROQ 2-1160	Sudre 1984							5.5	6.0				

Locality	Inventory number	Reference	D4	
Itardie	USTL ITD 910	Sudre 1984	4.4	4.2

the metacone. The mesostyle forms a blade ending the premetacrista. There are neither metastyle nor ectostyle. A strong cingulum on M1 surrounds the half lingual part of the tooth. This one is smaller on M2 and M3, which finishes on the base of the metaconule.

Taxonomical attribution

These small ruminants were quite common during the Rupelian in Europe: *Pseudogelocus scotti* (Gelocidae), *Bachitherium viretti* (Bachitheriidae), "*Lophiomeryx*" *gaudryi* (Lophiomerycidae), and *Iberomeryx minor* (Tragulidae). Sometimes, identification is difficult (Sudre &

Blondel 1996). The shape of the p4 of *Iberomeryx* is relatively similar to those of *Bachitherium* (Mennecart et al. 2011). However, *Iberomeryx minor* clearly differs from these previous species by having a huge *Dorcatherium* fold and an anterior conid on lower molars. Moreover, its upper teeth possess relatively straight cristae and the paracone rib does not possess an anterior fold (Geraads et al. 1987).

Specimens of *Iberomeryx minor* have been mainly described in localities dating from MP23 to early MP24. However, some *Iberomeryx* sp. specimens have been identified in younger localities such as Le Garouillas (MP25, France) based on rare specimens (USTL GAR439, M3; USTL GAR2308, M3; USTL GAR230, M1; USTL GAR2313, m1) and Mümliswil-Hardberg (MP26, Switzerland) based on a p4 (NMB UM2309) and a partial astragalus (NMB UM2322) (Sudre 1995; Mayo 1983; Engesser & Mayo 1987; Engesser & Mödden 1997). The upper molar from Le Garouillas (Sudre 1995, fig. 24) has been compared with *I. matsoui* from Mas de Got (Quercy, France) and *I. decedens*. However, after the reassessment of the specimen from Mas de Got, it belongs to *Pseudogelocus* cf. *scotti* (Sudre & Blondel 1996). *Iberomeryx decedens* is based on a lost partial skull that probably does not belong to *Iberomeryx* (Sudre 1984). The figured specimen from Le Garouillas (USTL GAR2309) does not display the cingulum surrounding the protocone, the cristae are curved, and the metaconule is enlarged with a metaconule fold. This tooth clearly differs from the upper molars just described, and could belong to a small Tragulina such as a Bachitheriidae. It could also be the case that the premolar and the astragalus from Mümliswil-Hardberg possess Tragulina characteristics: p4 does not possess a mesolingual conid, it has two elongated parallel cristids forming the edges of the enlarged back valley; the astragalus does not possess parallel trochleas and the edges have not similar high. A small and broken lower molar (NMBE unnumbered) has also been discovered in Bumbach (MP25, Switzerland). This specimen clearly does not belong to the genus *Iberomeryx* due to the presence of a postentocristid and a relatively compressed entoconid. Regarding the small size of these specimens from Le Garouillas, Bumbach and Mümliswil-Hardberg and the biostratigraphy of these localities, they appear to belong to the same undefined species.

Family **BACHITHERIIDAE** Janis, 1987
Genus ***Bachitherium*** Filhol, 1882

Type species. *Bachitherium curtum* (Filhol, 1877) from the undated old collections of the Phosphorites du Quercy (?Lamandine-Haute) (France), Oligocene.

Included species. *Bachitherium insigne* (Filhol, 1877), *B. lavocati* Sudre, 1986, *B. vireti* Sudre, 1986, *B. guirounetensis* Sudre, 1995.

Diagnosis (adapted from Geraads et al. 1987 and Métais & Vislobokova 2007). The muzzle is elongated with small orbits placed relatively posteriorly (the anterior border of the orbit is situated above the M2). The postorbital bar is partly formed by the jugal, sagittal crests. The auditory bullae is small, the lacrimal fossa is absent. The paraoccipital apophysis is strong and the posterolateral exposure of the mastoid is limited, the ethmoidal fissure is moderately developed, contrary to the postglenoid process, which is well developed. The angular region of the mandible is extended posteriorly and upwards, and the coronoid process is much higher than the articular joint, suggesting strong abductor muscles. The dental formula is 0/3, 1/1, 3/4, 3/3. The upper canine is tusk-like, slightly curved posteriorly, and occludes against anterior side of caniniform p1. The P1 is lost. There is a very long diastema between the C and the P2. The lower incisors and incisiform canine are small. There is a small diastema between c and p1, and a long diastema between p1 and p2. This complex of anterior teeth, very distant from the cheek teeth, is the main autapomorphy of this genus. The lower premolars are highly laterally compressed. They do not possess a mesolingual conid and the posterior part of the teeth possess a huge antero-posterior groove. The Radius and ulna are separated, the tibia and the fibula are partially fused. The distal extremity is reduced to malleolar bone. The Mc III and IV are unfused, The Mt III and IV are fused proximally. The lateral metatarsals are absent. The astragalus possesses nonparallel trochleae and a crural index similar to that of the extant genus *Moschus*.

Etymology. *Bach–* the old collections of the Phosphorites du Quercy and *–therium* Greek word for wild beast or animal.

Bachitherium curtum (Filhol, 1877)
Fig.5

1877 v*	*Gelocus curtus* n. sp. Filhol: 456, figs 257 and 340.
1882 v	*Bachitherium medium* Filhol: 124.
1885	*Bachitherium curtum* Lydekker: 155.
1914 v	*Bachitherium curtum* Stehlin: 185.
1914 v	*Amphitragulus* spec. II Stehlin: 185.
1914 v	Ruminans indet. (sehr klein) Stehlin: 185.
1916	*Bachitherium* sp. Repelin: 101.
1938	*Bachitherium* cf. curtum Viret: 501.
1954 v	*Dremotherium nanum* Astre: 320.
1970	*Bachitherium curtum* Brunet: tab. 9.
1978 v	*Bachitherium curtum* Heissig: 259, fig. 4.
1984 v	*Bachitherium curtum* Sudre: fig.12.
1985 v	*Bachitherium* Bouvrain & Geraads: 75.
1986	*Bachitherium curtum* Sudre: 753.
1986	*Bachitherium* sp. Kotsakis: 30.
1987	*Bachitherium curtum* Geraads et al.: figs. 6, 11, 22, 23, 31,
1987	*Bachitherium* Janis: 200.
1987 v	*Bachitherium* sp. Engesser & Mayo: 71.
1987 v	*Bachitherium* cf. *curtum* Engesser & Mayo: 74.
1987	*Bachitherium curtum* Remy et al.: 185, tab. 3c.
1987	*Bachitherium* cf. *curtum* Remy et al.: 188, tab. 4c.
1987	*Bachitherium* cf. *curtum* Fejfar: 260, fig. 6.
1987 v	*Bachitherium curtum* Heissig: fig. 6.
1992 v	*Bachitherium curtum* Muratet et al.: 1115.
1995	*Bachitherium curtum* Sudre: 237,
1995 v	*Bachitherium curtum* Martinez & Sudre: fig E.
1997	*Bachitherium curtum* Blondel: 583.
1997	*Bachitherium* sp. Hugueney: 426.
1997 v	*Bachitherium* sp. Engesser & Mödden: 480.
1998	*Bachitherium curtum* Blondel: 528.
2000	*Bachitherium curtum* Ferrandini et al.: 278.
2002	*Bachitherium curtum* Merle et al.: 112, fig.3.

Holotype. Right mandible with p1 and p3-m3 (MNHN Qu3917, Filhol 1877, pl. 20, fig. 340).

Species etymology. Latin word for shortened.

Type locality and horizon. Undated old collections of the Phosphorites du Quercy (?Lamandine-Haute) (France).

Occurrence. Oligocene, MP22 to early MP27, from France (Cadillac, Coulon, Gas, Itardie, Ithier, Itteville, La Tuque, Le Garouillas, Les Milles, Maintenon, Marseille, Mege, Monclar-de-Quercy, Mounayme, Nassiet près Amou, Ormoy, Pech Crabit, Pierrefitte, Rigal-Jouet, Roqueprune 2, Saint André, Saint-Ferme, Saint Henri, Vayres-sur Essonne), Switzerland (Aarwangen, Chavorney, Eriz Losenegg, Grenchen 1, Grenchenbergtunnel, Moutier Gare, Wolfwil Kennisbännli), Germany (Bernloch 1, Burgmagerbein 1, Burgmagerbein 2, Burgmagerbein 8, Herrlingen1, Möhren 13, Ronheim 1, Treuchtlingen 1, Weinheim), and Czech Republic (Detan).

Referred material. Ithier (France): NMB Eyt9, right mandible with p2-4. La Tuque (France): NMB OG12, right M; NMB OG17, right mandible with p2-m3. Marseille (France): UCLB 9326, broken skull. old collections of the Phosphorites du Quercy (France): MNHN Qu3902, right *corpus mandibulae* with p2-m3; MNHN Qu3917 (holotype), complete left *corpus mandibulae* with p1-m3; NMB QB60, left mandible with p3-m3 (p4 is lacking); NMG QuB63, left mandible with p2-m3. Saint André (France): NMB Mar187, right P2; NMB Mar202, right *corpus mandibulae* with d4; NMB Mar202, right maxillary with D2-4; NMB Mar230, left D4 and M1; NMB Mar253, left *corpus mandibulae* with p2-m2; NMB Mar253, left *corpus mandibulae* with p2-4; NMB Mar269, left maxillary with M1-3; NMB Mar308, right *corpus mandibulae* with p2-m1; NMB Mar392a, maxillary with D3-M1; NMB Mar392, left d4, m3, and M1; NMB Mar394, left M2; NMB Mar396, right P4; NMB Mar397, right p3; NMB Mar440, complete left *corpus mandibulae* with p1-m2; NMB Mar440, complete right *corpus mandibulae* with p2-m2; NMB Mar459, right P2, P3, and M1; NMB Mar459, left maxillary with P3-M1; NMB Mar459, left M3; NMB Mar459, right M3; NMB Mar459, right M2; NMB Mar498, left m1; NMB Mar499, right *corpus mandibulae* with p4-m2; NMB Mar587, left P2, P3, and P4; NMB Mar587, right P3 and P4; NMB Mar587, right M1, M2, and M3; NMB Mar587, left M1 and M3; NMB Mar615, right *corpus mandibulae* with p3-m3; NMB Mar615, left *corpus mandibulae* with p4-m3; NMB Mar616a, right maxillary with P3-M3; NMB Mar616b, complete right *corpus mandibulae* with p1-m2; NMB Mar616c, left *corpus mandibulae* with p4-m3; UCLB 8945, UCBL 8947, and, UCBL 8950, complete left *corpus mandibulae* with p1-m3. Saint Henri (France): UCLB 8774, right p2-m3; UCLB 8775, right maxillary with P3-M2; UCLB 8777, p1; UCLB 8779, left *corpus mandibulae* with m1-m3. Monclar-de-Quercy (France): MHNT.PAL.0.57.1, left mandible with m1-3; MHNT.PAL.0.57.2, right mandible with m1-3. Chavorney (Switzerland): NMB Vd14, right M2; NMB Vd15, left m2. Eriz losenegg (Switzerland): NMB Erz1, left d3-4 m1; NMB Erz2, right M1-2; NMB UM6270, left, P3. Grenchen 1 (Switzerland): NMB UM424 right m1; NMB unnumbered distal phalanx. Grenchenbergtunnel (Switzerland): NMBE unnumbered, left mandible with broken p3-m2; NMBE unnumbered, right mandible with m2-3; NMBE unnumbered, right calcaneus; NMBE unnumbered, left calcaneus; NMBE unnumbered, distal part of metapod; NMBE unnumbered, left astragalus. Wolfwil Kennisbännli (Switzerland): NMB Wow1, right M1. Burgemagerbein (Germany): BSPG 1934VII8, left M1; BSPG 1954XII340, left p4; BSPG 1954XII341, left m; BSPG 1954XII342, right M; 1954XII342, left P4; BSPG 1954XII343, left M; BSPG 1954XII344, right d4; BSPG 1954XII346, right P3. Burgmagerbein 1 (Germany): BSPG 1954XVI641, left M; BSPG 1954XVI642, right M; BSPG 1954XVI643, right M; BSPG 1954XVI644, left m3; BSPG 1954XVI645, left p4; BSPG 1954XVI646, left p2; BSPG 1954XVI647, right d2. Herrlingen 1 (Germany): BSPG 1965XIV 1369, right m3; BSPG 1965XIV 1370, left m3; BSPG 1965XIV 1371, right m1; BSPG 1965XIV 1374, left p4; BSPG 1965XIV 1375, left M.

Diagnosis (adapted from Sudre 1995). This is a medium sized Bachitheriidae. The tooth row p2-m3 is 45 mm to 47 mm long, the diastema p1-p2 is 20 mm to 22 mm long, and the metacarpian bones are 70 mm long and the metatarsian bones are 98 mm long.

Description

All measurements are summarized in Table 7.

Mandibles. The specimens from Quercy and Marseille (MNHN Qu3917, NMB QB60, NMB QB62, NMB QB63, UCBL 8945) are well-preserved. The elongated diastema is highly constricted just after the p2. The lower part of the *corpus mandibularis* is straight until the back of the m3. The *incisura vasorum* is not marked and the mandible angular is well-rounded. There is a notch between the end of the angular process and the ramus, which is perpendicular to the *corpus mandibularis*.

Lower decidual dentition. The d3 is very elongated and narrow. However, the studied specimen is incomplete, its anterior part is lacking. The mesolabial conid is high and central. It is as wide as the tooth with two relatively long posterior parallel crests. They are half a tooth long. The posterior valley is anteroposteriorly oriented. The posterolabial conid forms a small column on the posterolabial edge of the tooth. The d4 possesses a flat lingual wall, without metastylid or entostylid. The anterior and posterior cingulid are weakly marked. The ectostylids are present. The posthypocristid is oblique and joins the postentocristid. The lingual cusps are laterally compressed. They possess small and straight cristids. The hypoconid and the protoconid are of the same size. The prehypocristid is oblique and leans on the external postprotocristid. This latter is oblique and joins the postmetacristid. The preprotocristid is oblique and short. It ends at the base of the anterior fossa. The anterolabial conid and the anterolingual conid are labially oblique. There is an anterior cristid on the anterolabial conid. The anterolabial conid forms the posterolingual angle of the anterior fossa.

Adult lower dentition. p1 is conical, tusk-like, and slightly curved. p2 is simple and highly compressed, separated from p1 by a huge and straight diastema. p3 is smaller than p4, but both are relatively elongated and have a similar morphology. The mesolabial conid is high and triangular, as wide as the tooth, and slightly anterior. An anterior cingulid is present. The transverse cristid and the mesolingual conid are absent. The anterolingual cristid is anteriorly oriented on the labial part, until arriving to a groove. The anterior conid is elongated, oblique, and well-marked. The mesolabial conid is divided in two cristids on its posterior part, forming an anteriorly oriented deep posterior valley. This latter characterisitic may be obstructed by a single or double neocristid on p3 as well as on p4 (NMBE ss°). The hypoconid forms a posterolabial angle of the tooth. It is larger on p4 than on p3. On p3, the valley is posteriorly opened, whereas it is closed on p4.

The molars are very selenodont. They become larger from m1 to m3. The anterior conid is absent. The ectostylids are weak. The anterior and posterior cingulids are well marked. The lingual cuspids are relatively well aligned, with a small to absent metastylid and entoconulid. The trigonid and the talonid are relatively small. The preprotocristid is oblique and slightly curved. It joins the well-developed premetacristid. The protoconid is as wide

Figure 5. *Bachiotherium curtum* (this page and opposite): from *Saint André* **1** left *corpus mandibulae* with p1-m3 (NMB Mar440), labial (**a**), lingual (**b**), and occlusal views (**c**); **2** complete left *corpus mandibulae* with p1-m3 (UCLB 8945, CBL 8947, and, UCBL 8950), lingual (**a**), labial (**b**), and occlusal views (**c**); **3** left *corpus mandibulae* with m1-m3 (UCLB 8779), lingual (**a**), labial (**b**), and occlusal views (**c**); **4** right p2-m3 (UCLB 8774), lingual (**a**), labial (**b**), and occlusal views (**c**); **5** right maxillary with P3-M2 (UCLB 8775), occlusal view; **6** p1 (UCLB 8777), lingual (**a**), and occlusal views (b); from *Marseille* **7** right *corpus mandibulae* with p2-m3 (p4 is lacking) (UCLB 8780), lingual (**a**), labial (**b**), and occlusal views (**c**). Scale bar equals 10 mm.

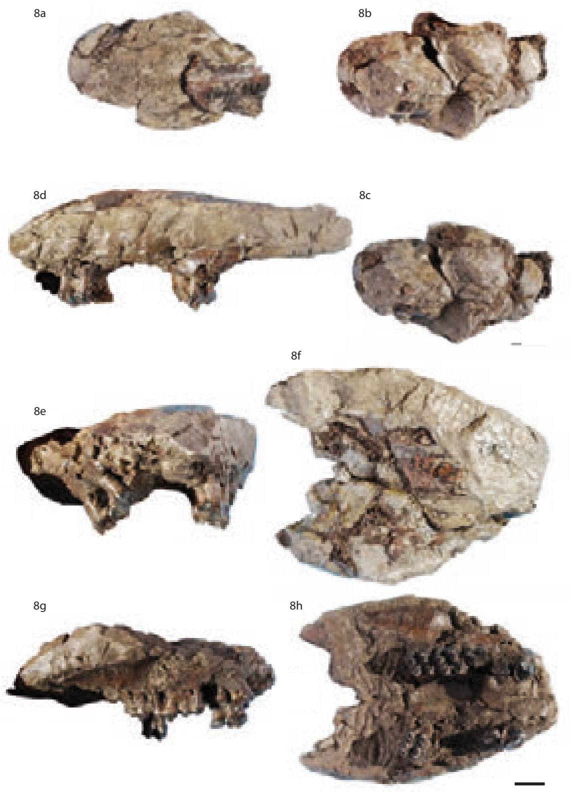


Figure 5 (continued). from *Marseille* **8** broken skull; UCLB 9329, left p2-m3 (UCLB 9326), lingual (**a**), labial (**b**), and occlusal views (**c**). Scale bar equals 10 mm.

as the hypoconid. The external postprotocristid is weakly marked to absent. The internal postprotocristid, the postmetacristid, and the preentocristid are located side by side to the entoconid and the metaconid. The prehypocristid joins the postentocristid. The entoconid and the metaconid are slightly laterally compressed. The high metaconid has a well-marked *Dorcatherium* fold, forming a buckle and a bulge on the lingual face of the metaconid. This fold is more and more marked from m1 to m3. The entoconid has a deep groove on its posterolabial part, forming a bulge on the labial part of the entoconid. The labial cristids are well marked. The postentocristid continues with a small oblique cristid after joining the posthypocristid. There is a spur on the posthypocristid forming a conid joining the postentocristid. The quite rounded back fossa of m3 of *Bachitherium curtum* is complex and obstructed by neocristids.

Adult upper dentition. P3 (NMB UM6270) is half-moon shape. It is slightly laterally compressed. The central anterolingual cone belongs to the lingual wall. It forms only a small bulge on its labial part. It can be distinguished from the posterolingual crista. The fossa is not obstructed by neocritae. The anterior style is globular, salient, and posterior. The anterolabial cone is slightly anterior and high. The anterolabial cone rib is bulged. The anterolabial crista is straight and aligned. The anterolabial cone is slightly anterior. P4 (NMB UM6434) is a worn tooth. The anterolabial cone rib is marked. The posterolabial cone is relatively strong, forming a strong lingual cingulum the anterior style and the anterolabial cone rib. The paracone is anteriorly bulged. Only a small anterior cingulum is present.

The upper molars do not possess cingulum. The fossae are not obstructed by neocrista. The upper molars become larger from M1 to M3. The preprotocrista joins the base of the straight preporocrista. The protocone and the metaconule are similar in size. The postprotocrista ends before the short and curved premetaconulecrista. The metaconule is oblique. The straight postmetaconulecrista joins the base of the postmetacrista. The metacone and the paracone are not aligned. Their cristae are short and straight. The metacone is large, salient, and globular, forming a small column. The metacone rib is weak. The paracone is very globular, with a strong paracone rib. On its anterolabial part, there is a deep groove. The parastyle is well developed at the level of the fusion of the preprotocrista and the preparacrista. There is no ectostyle. The mesotyle is well developed. It can form an isolated spur on M3.

Taxonomical attribution

Bachitherium species may be distinguished from the other genera by the outline of their mandible (Janis 1987; Mennecart et al. 2011, accepted). The elongated diastema is highly constricted just after the p2 and the lower part of this bone is straight. Moreover, the typical traguline-shaped lower premolar (no metaconid, two elongated parallel cristids forming the edges of the enlarged back valley) is only known in Europe within the Bachitheriidae and the Tragulidae (*Iberomeryx* and *Dorcatherium*; Mennecart et al. 2011). The lower molars are highly derived, possessing no cingulum and relatively selenodont cusps. The upper molars do not possess aligned paracone and metacone. In addition, the paracone rib has a huge anterior groove (Sudre 1986; Geraads et al. 1987; Ferrandini et al. 2000). *Bachitherium curtum* possesses

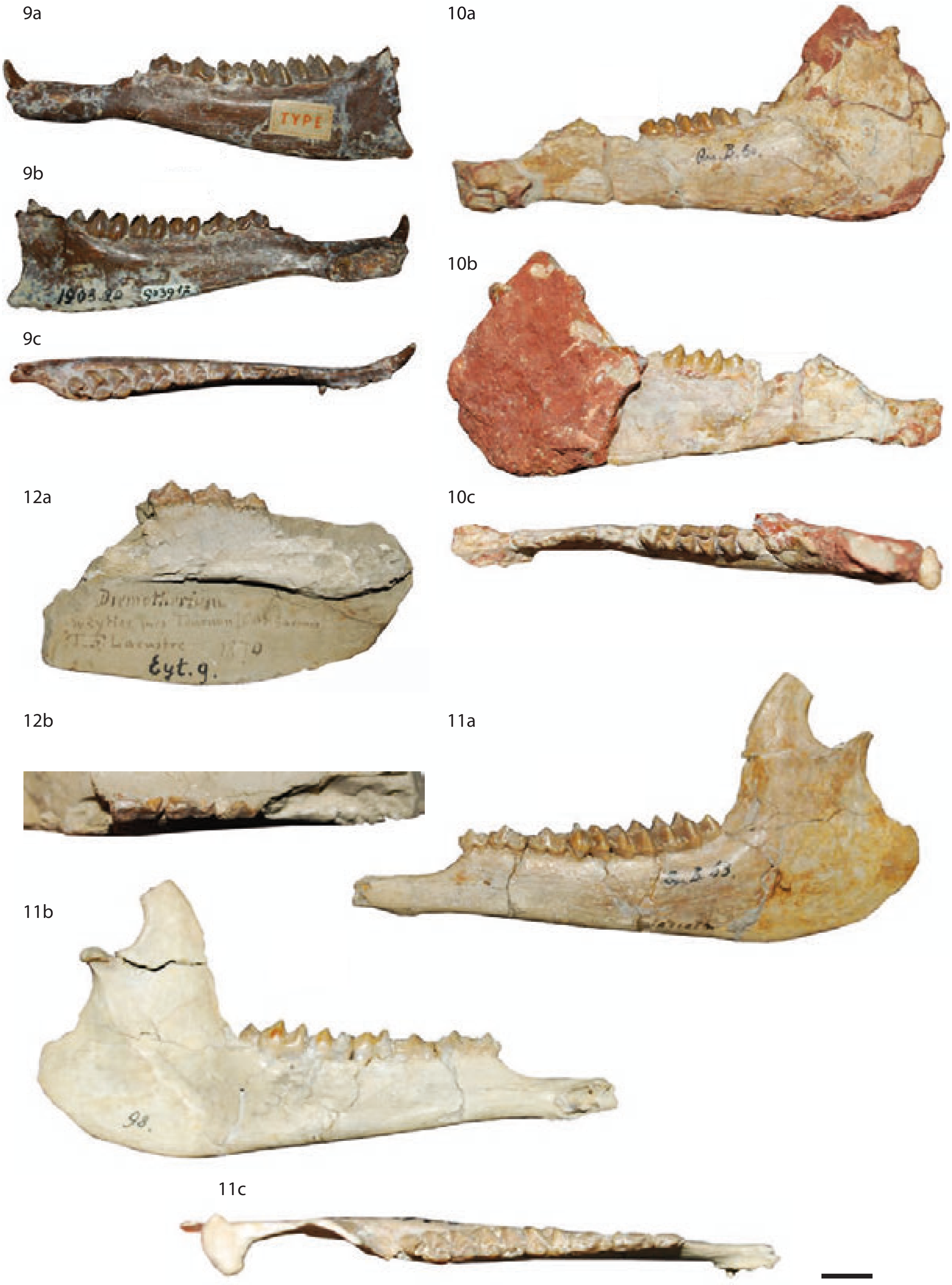


Figure 5 (continued). from old collections of the *Phosphorites du Quercy* **9** complete left *corpus mandibulae* with p1-m3 (MNHN Qu3917), lingual (**a**), labial (**b**), and occlusal views (**c**); **10** left mandible with p3-m3 (p4 is lacking) (NMB QB60), lingual (**a**), labial (**b**), and occlusal views (**c**); **11** left mandible with p2-m3 (NMB QB63), lingual (**a**), labial (**b**), and occlusal views (**c**); from *Ithier* **12** right mandible with p2-4 (NMB Eyt9), lingual (**a**), labial (**b**), and occlusal views (**c**). Scale bar equals 10 mm.

Table 7. Dental measurements (in mm) of the *Bachitherium curtum*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	Reference	p1		p2		p3		p4		m1		m2		m3	
Bachitherium curtum																
Ithier	NMB Eyt9				6.2	2.7	7.0	3.3	7.1	3.9						
La Tuque	NMB OG17						6.4		7.8							
Montclar-de-Quercy	MHNT.PAL.0.57.1										6.8	4.5	7.1	5.1		5.1
	MHNT.PAL.0.57.2												7.2			
Old collections of Quercy	MNHN Qu3902				5.5	2.4	6.3	3.0	6.8	4.2	6.5	5.1	7.8	5.8	12.8	6.0
	MNHN Qu3917	Holotype	3.4	2.6			6.3	2.5	6.8	3.5	5.7	4.5	6.7	5.4	11.5	5.6
	NMB QB60										6.8	4.5	7.2	5.1		
	NMB QuB63								6.7	3.7	6.7	5.0	7.1	5.5	11.3	5.7
Saint André	NMB Mar253				6.3	2.6	7.5	3.4	7.3	4.6	7.6	5.2	8.6	5.5		
	NMB Mar253				5.9	2.8	7.0	3.5	7.5	3.9						
	NMB Mar308				5.8	2.5	6.6	3.0	7.4	4.0	7.2	5.0				
	NMB Mar392															6.4
	NMB Mar397						7.9	4.0								
	NMB Mar440		4.8	3.8	6.4	2.8	7.4	3.8	8.1	4.7	8.6	5.7	8.7	6.4		
	NMB Mar497								8.6	5.0	7.6	5.8	8.7	6.5		6.6
	NMB Mar498										7.7	5.5				
	NMB Mar499								8.3	5.0	7.5	6.5	8.7			
	NMB Mar615						6.9	3.1	7.5	4.2	7.5	5.3	8.7	5.9	11.6	5.5
	NMB Mar615								7.2	4.3	7.8	5.5	8.5	6.2	12.5	5.9
	NMB Mar616b		3.9	3.4	6.0	2.6	7.1	3.4	8.4	4.0	8.0	6.2	8.7			
	NMB Mar616c									4.0	7.5	5.2	8.7	5.9	11.4	5.5
	UCLB 8945										7.5	5.5	9.2	6.5	13.5	6.3
Saint Henri	UCLB 8777		4.6													
	UCLB 8779										8.2	5.3	8.4	7.5	12.8	6.6
Burgemagerbein	BSPG 1954XII340								7.9	3.6						
	BSPG 1954XII341												8.1	5.4		
Grenchen 1	NMB UM424										8.4	5.5				
Burgemagerbein 1	BSPG 1954XVI644															6.7
	BSPG 1954XVI645								8.2	4.2						
	BSPG 1954XVI646					2.7										
	BSPG 1954XVI647					2.4										
Herrlingen 1	BSPG 1965XIV 1369															4.3
	BSPG 1965XIV 1370														11.7	5.3
	BSPG 1965XIV 1371										6.7	4.4				
	BSPG 1965XIV 1374							6.9	3.2							
Mounayne	USTL MOV128	Sudre 1995											8.2	5.7		
	USTL MOV132	Sudre 1995					7.8	3.8	7.2	3.3						
Pech Crabit	USTL PCT265	Sudre 1995									7.2	5.0				
	USTL PCT267	Sudre 1995									7.4	5.2				
	USTL PCT269	Sudre 1995											7.9	5.9		
	USTL PCT275	Sudre 1995											7.6	4.8		
	USTL PCT277	Sudre 1995							7.4	3.9						
	USTL PCT249	Sudre 1995									6.8	5.1				
	USTL PCT266	Sudre 1995									6.7	4.4				
	USTL PCT268	Sudre 1995											7.4	5.6		

Table 7. Dental measurements (in mm) of the *Bachitherium curtum*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	Reference	p1		p2		p3		p4		m1		m2		m3	
Pech Crabit	USTL PCT270	Sudre 1995											7.7	5.3		
	USTL PCT272	Sudre 1995									6.4	4.6				
	USTL PCT274	Sudre 1995											7.2	4.8		
	USTL PCT276	Sudre 1995							7.2	3.4						
Rigal Jouet	USTL RJ	Sudre 1995			7.7	2.8	6.1	3.4	7.0	3.8	7.6	4.8	7.4	5.0	10.8	5.0
	USTL RJ	Sudre 1995							7.8	3.8	7.2	5.3	7.4	5.0	11.8	4.9
	USTL RJ	Sudre 1995									6.6	4.5	7.7	5.6	9.0	4.0
	USTL RJ	Sudre 1995									7.2	5.0	7.6	5.5		
	USTL RJ	Sudre 1995									7.1	5.2	7.3	5.0		
	USTL RJ	Sudre 1995									6.6	5.5				
Itardie	mean value	Sudre 1995			6.9	2.7	6.7	3.0	7.3	3.4	6.9	4.8	7.7	5.3	11.7	5.7
Quercy	mean value	Filhol 1877					7.2	2.5	7.0	4.0	6.0	5.0	7.5	6.0	12.0	6.0
	mean value	Filhol 1882			5.0	2.0	7.2	2.5	7.2	4.0	6.0	5.0	7.5	6.0	12.0	5.5

Locality	Inventory number	d2		d3		d4	
Saint André	NMB Mar202					9.5	4.3
	NMB Mar203			8.0	2.9		
	NMB Mar392					9.2	4.2
	UCLB 8945	5.6	2.5	7.0	3.2	9.1	4.6

Locality	Inventory number	P2		P3		P4		M1		M2		M3	
La Tuque	NMB OG12							8.6	9.1				
Saint André	NMB Mar187	7.5	4.6										
	NMB Mar203							8.6	11.2				
	NMB Mar269							8.5	9.8	9.8	10.4	9.8	10.6
	NMB Mar392a							7.7	9.8				
	NMB Mar392							7.4	9.4				
	NMB Mar394									9.2	12.4		
	NMB Mar396					5.8	8.3						
	NMB Mar459	8.1	5.5	8.0	6.5			7.9	10.0				
	NMB Mar459			8.2	6.8	6.4	8.5	7.9	10.2				
	NMB Mar459											8.8	11.6
	NMB Mar459											9.0	11.5
	NMB Mar459									9.0	11.5		
	NMB Mar587	6.8	4.3	7.3	6.0	6.0	7.5						
	NMB Mar587			7.3	5.9	5.6	7.4						
	NMB Mar587							7.5	8.8	8.7	9.5	8.7	9.5
	NMB Mar587							7.6	9.4			8.4	9.8
	NMB Mar616a			7.0	5.4	6.3	7.7		9.4	9.1	9.5	9.1	10.5
Saint Henri	UCLB 8775	7.2		8.2	6.4	6.0	7.0	8.0	8.1	8.3	9.2		
Burgemagerbein	BSPG 1934VII8							6.9	9.0				
	BSPG 1954XII342							8.2	10.3				
	BSPG 1954XII343									9.1	10.7		
	BSPG 1954XII346			8.1	5.1								
Aarwangen	NMB UM6434					5.5	7.8						
Eriz losenegg	NMB UM6270			8.6	5.6								

Table 7. Dental measurements (in mm) of the *Bachitherium curtum*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	Reference	p1		p2		p3		p4		m1		m2	
Burgemagerbein 1	BSPG 1954XVI641								7.9	10.4				
	BSPG 1954XVI642								7.2					
	BSPG 1954XVI643								7.2					
Herrlingen 1	BSPG 1965XIV 1375								7.1	9.5				
Mounayne	USTL MOV132				7.8	3.8	7.2	3.3						
	USTL MOV129										8.2	9.5		
	USTL MOV127								7.7	8.7				
Roqueprune	USTL ROQ336										8.3	9.1		
	USTL ROQ337						5.5	6.6						
	USTL ROQ338										7.0	8.4		
	USTL ROQ339								7.2	8.5	8.2	9.0		
Pech Crabit	USTL PCT240								7.5	7.5				
	USTL PCT241								7.5	7.5				
	USTL PCT242										8.6	8.4		
	USTL PCT243								7.2	7.5				
	USTL PCT244										7.6	8.5		
	USTL PCT245										7.7	8.1		
	USTL PCT246										7.1	8.3		
	USTL PCT247												8.4	9.0
	USTL PCT248								6.7	8.0				
Wolfwil kennisbännli	NMB Wpw1										6.9	9.0		
Rigal Jouet	USTL RJ				6.8	3.6	5.7	6.8	6.9	7.8	8.4	8.9	7.6	9.1
	USTL RJ				6.9	4.8	5.4	6.3	7.2	8.0	7.5	8.5	7.5	9.0
	USTL RJ										7.5	8.7		
	USTL RJ										7.7	8.6		
Itardie	mean value	Sudre 1995	7.0	3.8	7.4	5.2	5.6	7.2	7.1	7.6	7.9	9.1	8.4	8.9
Quercy	mean value	Filhol 1877			7.0	5.0	5.0	7.0	6.7	8.0	8.0	10.0	8.5	10.0
	mean value	Filhol 1882			7.0	5.0	5.0	7.0	6.7	8.0	8.0	10.0	8.5	10.0

Locality	Inventory number	D2		D3		D4	
Saint André	NMB Mar202	7.9	4.0	8.3	6.2	6.7	7.3
	NMB Mar203					8.0	7.9
	NMB Mar392a			7.5	5.9	9.0	7.8

smaller teeth, diastema, and postcranial bones than the large species *Bachitherium insigne* (see Tables 7 and 8, Sudre 1986).

Bachitherium insigne (Filhol, 1877)

Fig.6

1877 v*	*Gelocus insignis* n. sp. Filhol: 463.
1882 v	*Bachitherium insigne* n. gen. Filhol: 122, pl. XI fig. 1-4.
1885	*Bachitherium insigne* Lydekker: 157.
1914	*Bachitherium insigne* Stehlin: 185.
1969	*Bachitherium insigne* Ginsburg: 1267.
1970	*Bachitherium insigne* Brunet: tab. 9.
1973 non	*Bachitherium medium* de Bonis et al.: tab. 2(4).
1983 v non	*Bachitherium insigne* Mayo: 906.
1985 v	*Bachitherium* Bouvrain & Geraads: 75.
1986	*Bachitherium insigne* Sudre: 753.
1986	*Bachitherium* sp. Kotsakis: 30.
1987 v	*Bachitherium* cf. *insigne* Geraads et al.: 43, fig. 1 and 41.
1987 v	*Bachitherium insigne* Engesser & Mayo: 72.

1987 v non	*Bachitherium insigne* Engesser & Mayo: 73.
1987	*Bachitherium* cf. *insigne* Remy et al.: 188, tab. 4c.
1987	*Bachitherium* cf. *insigne* Janis: 200, fig. 9B.
1995	*Bachitherium insigne* Sudre: 242.
1997	*Bachitherium insigne* Blondel: 583.
1997	*Bachitherium* sp. Hugueney: 426.
1997 v non	*Bachitherium insigne* Engesser & Modden: 484.
1998	*Bachitherium* cf. *insigne* Blondel: 528.

Holotype. Right mandible with p1-p3 (MNHN Qu3918, originally mandible with p1-m3, Filhol 1877: 463).

Species etymology. Latin word for distinguished.

Type locality and horizon. Undated old collections of the Phosphorites du Quercy (France).

Occurrence. Oligocene, from MP22 to early MP27, from France (Benissons-Dieu, Cereste, La Devèze, Le Garouillas, Le Gibet à Etampes, Mas de Pouffié, Phalip, Rigal-Jouet, Saint-Henry, Saint-Menoux), Switzerland (Aarwangen, Baden, Oensingen-Ravellen, Wynau III, and Wynau V), Germany (Weinheim), and Italy (Cadibona).

Referred material. Céreste (France): MGA, unnumbered; old collections of the Phosphorites du Quercy (France): MNHN Qu3845, left m3; MNHN Qu3889, right *corpus mandibulae* with p2-4; MNHN Qu3900, parietal bones; MNHN Qu3903, right maxillary with P4-M3; MNHN Qu3914, left *corpus mandibulae* with p2-m1; MNHN Qu3915, left *corpus mandibulae* with m1-m3; MNHN Qu3918 (holotype), right *corpus mandibulae* with p1-p3; MNHN Qu3929, right maxillary with P2-M3; MNHN Qu3963, maxillary bones and premaxillary with left canine; MNHN Qu3997, left *corpus mandibulae* with p3-m1; MNHN Qu3999, left *corpus mandibulae* with p3-m1; MNHN Qu4000, right *corpus mandibulae* with p3-m2; MNHN Qu4258, complete left *corpus mandibulae* with p2-m3; MNHN Qu4566, right *corpus mandibulae* with p2-4; MNHN Qu4575, right *corpus mandibulae* with p4-m1; MNHN Qu4660, right maxillary with P2-M2; MNHN Qu16542, right maxillary with M1-3; MNHN Qu16548, right *corpus mandibulae* with p3-4; MNHN Qu16551, right maxillary with P3-M3. Marseille (France): UCLB 8780, right *corpus mandibulae* with p2-m3 (p4 is lacking); UCBL 9329 left mandible with p2-m3. Saint André (France): NMB Mar203, right d4 and left m1; NMB Mar441, right *corpus mandibulae* with m1-m2; NMB Mar267, right P3; NMB Mar268, left M1 and M2; NMB Mar497, left *corpus mandibulae* with p4-m3; NMB Mar585, right *corpus mandibulae* with p3-m2; NMB Mar585, left *corpus mandibulae* with p2-m3. Cadibona (Italy): NMB IO14, cast of right mandible wtith p4-m3. Aarwangen (Switzerland): NMB Aw29, left astragalus; NMB Aw68, right p4; NMB UM6434, left P4. NMB Aw62, p4; NMB Aw66, left M1; NMB Aw67, left M2; NMB Aw69, left P4; NMB AW71, left P3. Moutier Gare (Switzerland): NMB UM68, right astragalus; NMB UM125, right m1. Baden (Switzerland): NMB UM5032, right p2. Oensingen-Ravellen (Switzerland): NMB UM49, fragmentary right M; NMB UM50 partial right ramus with broken m3; NMB UM2235, left m3; NMB UM3001, right d4; PIMUZ A/V0132, right mandible with d4-m1. From the Wynau III (Switzerland): NMB Wy153, right mandible with the tooth row p3-m3. Wynau V locality (Switzerland): NMB Wy396, right M.Treuchtlingen 1 (Germany): BSPG 1962XI293, right P4; BSPG 1962XI294, right P3; BSPG 1962XI296, right M; BSPG 1962XI297, right M; BSPG 1962XI299, right p4; BSPG 1962XI300, right p4; BSPG 1962XI302, left p2; BSPG 1962XI305, left m; BSPG 1962XI305, left m.

Diagnosis (adapted from Sudre 1995). Large-sized Bachitheriidae with upper molars a little bit more advanced than for *Bachitherium curtum*: presence of a small posterior cingulum, posterior valley with neocrista, and strong entostyle. The lower molars are more massive than *Bachitherium curtum*. The *Dorcatherium* fold is deeper. p2-m3 is about 63 mm of length. The diastema p1-p2 is from 35 mm to 39 mm long. The metacarpian bones are 109 mm long and the metatarsian bones are 142 mm long.

Description

All measurements are summarized in Table 8.

Mandibles. The ventral part of the mandible is straight. The *incisura vasorum* is smooth. The angular process is enlarged but not rounded. It possesses a huge notch on its upper part, which seems to be unique among the ruminants. The ramus is very large and the coronoid process is small and slightly backward tilted. There is a huge diastema between p1 and p2.

Adult lower dentition. p1 is tusk-like with anterior wear. The other lower premolars are very simple, based on the model of the extant Tragulidae. They are elongated and more complex from p2 to p4. The structure of p2 is similar to p3 as in Tragulidae such as *Iberomeryx* or *Dorcatherium*, and the p3 is similar to the p4 of this animal. The p3 and the p4 are relatively similar, with a more advanced structure in p4. p2 is laterally compressed and blade-like in shape. The mesolabial conid is small, but it is the highest cuspid of the tooth. The posterolabial cristid and the anterolabial cristid are aligned on the centre of the tooth. The mesolabial conid is as wide as the tooth. There is a very small anterior conid. It forms a bulge on the anterior part of the tooth. The posterolabial conid is a bulge on the two faces of the tooth. The mesolabial conid of the p4 is slightly anterior. It is as wide as the tooth and it is the highest conid. It may have a small rib (NMB Wy153, NMB QuB64). On this conid, there are three cristids. The anterolabial cristid is straight and anteriorly oriented. It joins the base of the well-individualised and triangular lingual anterior conid. Such as in *Iberomeryx*, there are two parallel posterior cristids, separating from the mesolabial conid. They form a deep valley, nearly closed. The lingual wall finishes in the posteroligual angle. The posterlabial conid makes the labial wall and stops on the posterior part of the tooth without joining the lingual wall, such as in *Iberomeryx*. The posterior valley may be obstructed with a neocristid or one or two hemineocristids (NMB Wy153, NMB QuB106, NMB QuB35). The presence of these neocristids can vary the function of the tooth within the same tooth row (NMB QuB64). The premolars have a small anterior cingulid.

The lower molars are trapezoid due to quite a large talonid, wider than the trigonid. The m1 has a rounded anterior part. The enamel can be slightly pitted. The trigonid can be partially open due to the semi-fusion of the premeta-cristid and the slightly curved preprotocristid. The anterior conid is absent. The protoconid and the hypoconid are very selenodont. The internal postprotocristid joins the preentocristid and can continue on the postmetacristid. The postprotocristid is oblique. The protoconid possesses an external postprotocristid, which can be well marked (NMB QuB64, NMB QuB35). The ectostylid is less and less developed from m1 to m3. The prehypocristid is oblique. It stops between the internal postprotocristid and the preentocristid without any fusion. The posthypocristid is slightly oblique and fused with the postentocristid. The metaconid and the entoconid are not aligned. That is why there is a small gap between the preentocristid and the postmetacristid. These lingual cuspids are bulged. On the posterior labial part of the entoconid, there is a deep groove, which emphasizes the bulge of this cuspid. The metaconid possesses a well-developed *Dorcatherium* fold forming a real buckle. This groove is more and more marked from m1 to m3. The entoconulid is a small spur. The back fossa of the m3 is lingually opened on the observed specimens. The hypoconulid is strong and crescent-moon shaped. Its posthypocristulid does not join the posthypocristid. The anterior and posterior cingulids are well marked, with the anterior one becoming increasingly bigger from m1 to m3.

Adult upper dentition. The upper molars increase in size from M1 to M3. They possess a weak posterior cingulum. The posterior fossa is obstructed by neocrista, which come from the metaconule and go to the posthypocrista, crossing the basin. The straight preprotocrista joins the base of the preparacrista. The protocone and the metaconule are the same size. The short and curved postprotocrista stops before joining the premetaconulecrista. The metaconule is oblique. The straight postmetaconulecrista reaches the base of the postmetacrista. The metacone and the paracone are not aligned. Their cristae are short and straight. The lingual cusps are bulged. The metacone has a big, globular, and salient mesostyle, which forms a small column. The metacone rib is weak. The paracone is very bulbous and possesses a strong paracone rib. On its anterior part, it possesses a well-developed and quite deep groove. The parastyle is well developed at the level of the fusion between the preprotocrista and the preparacrista. The entostyle is strong.

Taxonomical attribution

Differences between *B. curtum* and *B. insigne* are mainly based on size differences and postcranial adaptations (Sudre 1986). The size of *B. insigne* (Tab.8) is clearly bigger than *B. curtum* (Tab.7).

1a

1b

1c

2a

3a

2b

3b

2c

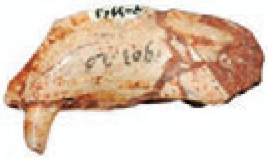
4a

3c

5

4b

4c



6

7b

7a

7c

Table 8. Dental measurements (in mm) of the *Bachitherium insigne*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	Reference	p1		p2		p3		p4		m1		m2		m3	
Bachitherium insigne																
Old collections of Quercy	MNHN Qu3845														14.8	
	MNHN Qu3889				6.1	2.7	7.3	3.5	7.8	4.0						
	MNHN Qu3914				6.8	3.3	7.9	4.0	8.8	5.0	9.4	6.5				
	MNHN Qu3915										9.2	6.0	9.4	7.0	13.4	
	MNHN Qu3918	Holotype	5.3	3.8	6.4	3.0	7.7	3.6								
	MNHN Qu3997						7.9	3.7	8.9	4.7						
	MNHN Qu3999						8.5	3.9	10.0	4.7	9.4	6.3				
	MNHN Qu4000						9.0	4.8	9.5	5.8	10.8	6.7	11.1	7.7		
	MNHN Qu4258				7.0	3.2	8.9	4.4	9.4	5.1		6.8	10.4	7.4	15.8	
	MNHN Qu4566				7.2	3.0	8.5	3.8	9.5	5.0						
	MNHN Qu4575								8.5	4.4	9.0	6.1				
	MNHN Qu16548						7.9	3.4	8.3	4.8						
Saint André	NMB Mar585						7.7	3.6	8.8		8.4		9.9			
	NMB Mar585				5.9		7.8		9.0		7.9		9.2			
	NMB Mar203										8.1	5.5				
	NMB Mar440				5.8	2.6	7.0	3.3	8.0	3.9	7.7	5.5	8.3	6.0		
	NMB Mar441												8.9	6.6	14.1	6.6
Saint Henri	UCLB 8774				6.5	3.2	7.4	4.1	8.5	4.4	7.5	5.6	9.3	6.3	15.5	6.5
Marseille	UCLB 8780				6.3	2.8	8.7	3.7					8.7	6.4	14.7	6.0
	UCLB 9329					2.8	7.6	4.0	8.2	5.0	9.0	6.2	9.0	6.9	14.0	7.1
Aarwangen	NMB Aw62								8.8	4.9						
Oensingen «ravellen»	NMB UM2235														14.4	6.8
	PIMUZ A/V0132										8.5	5.7				
Moutier gare	NMB UM125										8.8	6.1				
Wynau III	NMB Wy153						8.2	3.8	9.0	4.9	9.8	6.5	10.6	7.0	14.5	6.7
Eriz Losenegg	NMB Erz1										8.8	6.0				
Treuchtlingen1	BSPG 1962XI299								8.1	4.0						
	BSPG 1962XI300								8.0	4.0						
	BSPG 1962XI302				6.3	2.7										
	BSPG 1962XI305										7.5	5.6				
	BSPG 1962XI305										8.3	5.6				
Cadibona	NMB IO14								8.7	4.8	7.7	6.0	9.1	7.0	16.1	8.8
Le Garouillas	GAR3										9.0	6.1	10.0	6.5	15.5	7.1
	GAR4										8.7	6.4	10.3	6.5	17.0	7.0
	GAR36				6.8	3.1	8.1	3.5								
	GAR39										8.6	6.4				

Figure 6 (opposite page). *Bachitherium insigne*: from old collections of the *Phosphorites du Quercy* **1** right *corpus mandibulae* with p1-p3 **(**MNHN Qu3918 holotype), lingual (**a**), labial (**b**), and occlusal views (**c**); **2** right *corpus mandibulae* with p3-m2 **(**MNHN Qu4000), lingual (**a**), labial (**b**), and occlusal views (**c**); **3** complete left *corpus mandibulae* with p2-m3 **(**MNHN Qu4258), lingual (**a**), labial (**b**), and occlusal views (**c**); **4** maxillary bones and premaxillary with left canine **(**MNHN Qu3963), upper (**a**), lower (**b**), and lateral views (**c**); **5** right maxillary with P2-M3 **(**MNHN Qu3929), occlusal view; **6** right maxillary with P3-M3 **(**MNHN Qu16551), occlusal view; from the *Wynau III* **7** right mandible with the tooth row p3-m3 **(**NMB Wy153), lingual (**a**), labial (**b**), and occlusal views (**c**); Scale bar equals 10 mm.

Table 8 (continued). Dental measurements (in mm) of the *Bachitherium insigne*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	p1		p2		p3		p4		m1		m2		m3	
Le Garouillas	GAR441			7.0	3.1	9.0	4.0	8.5	4.2	9.2	6.4				
	GAR444			7.0	3.0	9.9	3.1	10.0	4.5	9.0	6.5	10.0	6.0	16.0	6.9
	GAR445							8.5	4.1	9.2	5.6	10.0	6.9	13.5	6.7
	GAR446							9.1	4.0						
	GAR449									8.6	6.4				
	GAR451			7.0	3.2	8.0	3.9								
	GAR2053							8.5	4.9	8.4	6.3	8.8	6.3	14.4	6.6

Locality	Inventory number	Reference	p1		p2		p3		p4		m1		m2		m3	
Quercy	mean value	Filhol 1877			6.5	3.0	8.0	4.0								
	mean value	Filhol 1882			7.0	4.0	8.8	4.5	9.0	6.0	10.0	7.0	11.0	8.0	16.0	8.0

Locality	Inventory number	d4	
Oenisingen	PIMUZ A/V0132	11.8	5.2
	NMB UM3001	12.1	5.4

Locality	Inventory number	Reference	P2		P3		P4		M1		M2		M3	
Old collections of Quercy	MNHN Qu3903						7.2	10.1	9.8	12.8	10.7	13.3	11.1	12.9
	MNHN Qu3929		8.0	5.4	8.2	6.6	7.2	8.6	10.1	11.0	10.8	12.0	11.1	12.0
	MNHN Qu4660						7.2	8.8	9.5	10.5	10.4	11.3		
	MNHN Qu16542								9.0	10.0	9.4	10.1	9.2	10.6
	MNHN Qu16551				8.5	6.1	7.3	8.4	9.0	10.4	10.7	11.0	10.8	11.6
Aarwangen	NMB Aw66								9.2	11.7				
	NMB Aw67										10.7	14.0		
	NMB Aw69						6.9	8.2						
	NMB AW71				8.8	6.1								
Oensingen	NMB UM49										10.5	11.1		
Le Garouillas	GAR1		9.5	4.5	10.5	6.5	7.1	9.5	9.5	10.2	10.3	11.8	11.0	12.5
	GAR2				10.0	7.0	7.0	9.0	9.1	10.2	10.8	11.3	11.0	12.0
	GAR442								10.7	11.8	10.5	11.5		
	GAR443								9.0	9.6				
Marseille	UCLB 9326				7.9	6.4	7.2	8.1	9.4	9.1	9.2			
	UCLB 9326				8.3							8.8	9.3	
Saint André	NMB Mar267				7.6	6.6								
	NMB Mar268								9.4	10.7	9.2	11.6		
Treuchtlingen 1	BSPG 1962XI293						6.5	8.0						
	BSPG 1962XI294				8.3	5.8								
	BSPG 1962XI296										9.3	10.7		
	BSPG 1962XI297										9.4	11.4		
Quercy	mean value	Filhol 1882	8.0		9.0	6.0	7.0	8.5	9.0	10.0	10.5	11.0	11.0	12.0

Bachitherium vireti Sudre, 1986

1938	*Bachitherium* cfr. *curtum* Viret: 501.
1986*v	*Bachitherium vireti* n. sp. Sudre: 753.
1987	*Bachitherium vireti* Remy et al.: 185: tab. 3c.
1995	*Bachitherium vireti* Martinez & Sudre: 198, fig. 4F.
1997	*Bachitherium vireti* Blondel: tab. 8.

Holotype. Left mandible with p1-m1 (UCBL FSL9672, Sudre 1986, fig. 4).

Species etymology. The species name was given in honour of the French palaeontologist Jean Viret.

Type locality and horizon. Nassiet (Landes, France), MP23.

Occurrence. Early Oligocene, MP23, from France (Itardies, La Bourgadot).

Referred material. No additional material.

Diagnosis (adapted after Sudre 1986). Small size ruminant differs from the other species of *Bachitherium* by a very short diastema between p1 and p2 (10 to 15 mm) and small tooth size (p2-m3: 39.5 to 41 mm, p2-p4: 17 to 18 mm, m1-m3: 23 to 24.5 mm; P2-M3: 35 mm, P2-P4: 15 to 18 mm, M1-M3: 24 mm).

Bachitherium guirounetensis Sudre, 1995

1986	*Bachitherium insigne* Sudre: 753.
1987	*Bachitherium* cf. *insigne* Remy et al.: 188, tab. 4c.
1995*v	*Bachitherium guirounetensis* n. sp. Sudre: 243, figs. 25, 26, 28, 32, 37, 40.
1997v	*Bachitherium guirounetensis* Blondel: 587, tab. 8.

Holotype. Fragment of left mandible with p1 (alveoli) and p2-m1 (USTL GAR 441, Sudre 1995, fig. 25b).

Species etymology. The etymology of this species was not defined in the original paper.

Type locality and horizon. Le Garouillas (Tarn et Garonne, France), MP25.

Occurrence. Only locality known

Referred material. No additional material.

Diagnosis (adapted after Sudre 1995). Relatively large *Bachitherium* (p2 to m3 about 62 mm) having elongated metatarsian bones (nearly 129 mm) and a shortened diastema (close to 28 mm).

Bachitherium lavocati Sudre, 1986

1986*v	*Bachitherium lavocati* n. sp. Sudre: 753, fig. 5.
1987	*Bachitherium lavocati* Remy et al.: 188, tab. 4c.
1995	*Bachitherium lavocati* Martnez & Sudre: 198, fig. 4G.
1997	*Bachitherium lavocati* Blondel: 575, fig. 1.2.
1998	*Bachitherium lavocati* Blondel: 527.

Holotype. Left mandible with p1 (root) and p2-m3 (USTL PDS 1330, Sudre 1986, fig.5).

Species etymology. The species name was given as a tribute to Mr. Lavocat who was the first to study in detail the lower dentition of *Bachitherium*.

Type locality and horizon. Pech Desse (Lot, France), MP28.

Occurrence. Late Oligocene, MP28, Germany (Gaimersheim 1).

Referred material. No additional material.

Diagnosis (adapted from Sudre 1986). Similar in size to the medium *Bachitherium curtum* (p2-m3: 51 to 53 mm, p2-p4: 15 to 18 mm, m1-m3: 25 to 26 mm; P2-M3: 48 mm, P2-P4: 20.4 to 22.6 mm, M1-M3: 22 to 25.9), it differs from the previously cited species by having a highly elongated diastema (32 to 34 mm).

Infraorder **PECORA** sensu Webb and Taylor, 1980
Parvorder **PROTOPECORA** sensu Métais et al., 2001
Family **GELOCIDAE** Schlosser, 1886
Genus ***Gelocus*** Aymard, 1855

Type species. *Gelocus communis* Aymard 1846 from Ronzon (South Western France), MP21.

Further included species. *G. laubei* Schlosser, 1901, *G. villebramarensis* Brunet and Jehenne, 1976.

Diagnosis (adapted from Métais & Vislobokova 2007). The skull has a reduced rostrum with orbits closed by a postorbital bar and the anterior border of the orbit located at the level of M1. The molars are brachyodont. The upper molars have a large external style, a median labial rib supporting the paracone, and a parastyle and a metastyle low but well developed. The internal selenes on upper molars are large. The protocone is surrounded by a strong cingulum and has a reduced postprotocrista that is not oriented towards the central portion of the molar (close to the upper molars of the ancestral *Archaeomeryx*). P1 is lost, the upper incisors are absent, and C is elongated (close to that of *Hyemoschus*). The lower molars have conical lingual cuspids and crescentic labial cuspids. A rudiment of paraconid can be observed at the extremity of the preprotocristid. There is a slight labial fold in the enamel on the posterior side of the metaconid in addition to the postmetacristid, which extends towards the centre of the tooth to join the preentocristid. The talonid of p4 has three transverse crests but has a small metaconid. The Mc III and IV are unfused, but the Mt III and IV are fused. The lateral digits are reduced and thin, but complete, splints. The astragalus has parallel trochleae.

Etymology. The etymology of this genus was not defined in the original paper

Gelocus communis (Aymard, 1846)
Fig.7

1846	*Anthracotherium minutum* Blainville: 132.
1846 v	*Amphitragulus communis* n. sp. Aymard: 247.
1848*	*Amphitragulus communis* Gervais: 88, pl. XXXIV, fig. 10-11.
1853	*Amphitragulus communis* Pomel: 101.
1855	*Gelocus communis* n. gen. Aymard: 233.
1856	*Gelocus communis* Aymard: 255.
1859	*Gelocus communis* Gervais: 154, pl. 34, fig.10-11.
1877 v non	*Gelocus communis* Filhol: fig 257.
1877	*Gelocus aymardi* Kowalewsky: 145, pl. 21-22.
1882	*Gelocus communis* Filhol: 240, fig. 151-191.
1883	*Gelocus* Rütimeyer: 64.
1885	*Gelocus communis* Lydekker: 159.
1894	*Gelocus communis* Zittel: 386, fig 315-316.
1896	*Gelocus communis* Röse & Bartels: 90, fig 18-19.
1904	*Gelocus* Lull: 7.
1951	*Gelocus communis* Lavocat: 135, pl.23. fig. 3.
1970	*Gelocus communis* Brunet: 2537.
1970	*Gelocus commune* Lange: 152.
1973	*Gelocus communis* de Bonis et al.: 109, tab. 2(4).
1977	*Gelocus communis* Brunet, Jehenne, & Ringeade: 111.
1978 v	*Gelocus* aff. *communis* Heissig: 249, fig. 4.
1985	*Gelocus communis* Jehenne: 25, fig. 5-7.
1987	*Gelocus communis* Remy et al.: 185, tab. 3c.
1987 v	*Gelocus communis* Heissig: fig. 6.
1987 v	*Pseudogelocus laubei* Fejfar: 260, fig. 7-15.
1987	*Gelocus* Janis: 200, fig. 5.
1987	*Gelocus communis* Geraads et al.: 46, figs. 5, 20, 30, and 42.
1996	*Gelocus communis* Sudre & Blondel: tab. 1.
1997	*Gelocus communis* Hugueney: 426.
1997	*Gelocus communis* Escarguel, Marandat, & Legendre: 445.
1997	*Gelocus communis* Blondel: 585, tab. 8 and 9.
1998	*Gelocus communis* Blondel: 527.

Holotype. Fragmentary right maxillary with M1-M3 (MNHN Qu4191, Gervais 1848: pl. XXXIV, fig. 10).

Species etymology. Latin word for common.

Type locality and horizon. Undated old collections of the Phosphorites du Quercy (France).

Occurrence. Early Oligocene, from MP21 to early MP24, from France (Aubrelong 1, Pech Crabit, Ravet, Ronzon, Ruch), Switzerland (Poillat), Germany (Haag, Ehingen 14, Ehingen 15, Möhren 4), and Czech Republic (Detan).

Referred material. Old collections of the Phosphorites du Quercy (France): BSPG 1879XV159, right mandible with m1 and left mandible with m2-3; MNHN Qu3881, left complete *corpus mandibulae* with p4-m3; MNHN Qu4191 (Holotype), right complete *cor-*

pus mandibulae with p2-m3; MNHN Qu4774, left complete *corpus mandibulae* with p2-m3. Ronzon (France): MHNT.PAL.2011.0.7, right mandible with p4-m3; MHNT.PAL.2011.0.10, left mandible with m2-3; MNHN RZN319, left partial skull with P2-M2; MNHN RZN320, right fragmentary mandible with m1-3; MNHN RZN323, right fragmentary mandible with m2-3; MNHN RZN324, right fragmentary mandible with p4-m3; MNHN RZN325, right m3; MNHN RZN326, left m3; MNHN RZN327, left fragmentary mandible with d4-m2; MNHN RZN335, left fragmentary mandible with m1-3; MNHN RZN336, right fragmentary mandible with p2-4; MNHN RZN346, left fragmentary mandible with p3-m3; MNHN RZN348, right fragmentary mandible with p3-m3; MNHN RZN352, left fragmentary mandible with p2-4; MNHN RZN356, right fragmentary mandible with p3-m3; MNHN RZN356, left fragmentary mandible with m1-3; MNHN RZN357, right fragmentary mandible with p4-m3; MNHN RZN358, right fragmentary mandible with m1-m2; MNHN RZN359, left fragmentary mandible with m2-3; MNHN RZN360, right fragmentary mandible with m1-2; MNHN RZN361, right fragmentary mandible with m1-2; MNHN RZN362, right p3-4; MNHN RZN363, left fragmentary mandible with m1-2; MNHN RZN369, right fragmentary mandible with p1-m3; MNHN RZN534, right maxillary with P3-M3; MNHN RZN536, right fragmentary mandible with p4-m3; MNHN RZN537, right fragmentary mandible with p4-m3; NMB Ro14, left fragmentary mandible with p4-m3; NMB Ro17, left fragmentary mandible with m1-m3; NMB Ro51a, left fragmentary mandible with m1-m3; NMB Ro70, right fragmentary mandible with m1-m3; NMB Ro143, right fragmentary mandible with p4-m3. Poillat (Switzerland): MJSN POI007-237, left fragmentary mandible with m2-m3. Ehingen 14 (Germany): BSPG 1966XXXVI11, two right M's. Ehingen 15 (Germany): BSPG 1971 XXII6, right m. Treuchtlingen 1 (Germany): BSPG 1962XI301, right p3; BSPG 1962XI305, right m3.

Diagnosis (adapted from Jehenne 1985). Small sized *Gelocus* having 3 upper premolars and 4 lower premolars. The upper premolars are elongated and poorly molarised. The metaconid is posterior to the protoconid. The upper molars are more wide than long with quite conical cusps. The postprotocrista and the preprotocrista are perpendicular. The fossae are slightly tilted. The base of the protocone is surrounded by a cingulum. The lower premolars are quite elongated and not well molarised. The lower molar cusps are conical above the metaconid and the entoconid with few-developed cristid. The metastylid is weak and always present.

Description

All measurements are summarized in Table 9.

Mandibles. The *corpus mandibularis* is slender and highly concave. The diastema is very short. The *incisura vasorum* is very well-marked just after the m3. The ramus is quite high and perpendicular to the tooth row.

Adult lower dentition. This small sized ruminant has bunoselenodont molars. The crowns of the specimen MJSN POI007-237 are worn, however, we can observe that the trigonid and the talonid are narrow and the fosae are closed and slightly tilted. The highly curved preprotocristid forms a rounded anterior part of the tooth. It joins a very small premetacristid. The protoconid and the hypoconid are much more proclivous on m2 than on m3. These cuspids are sharped and salient. The internal postprotocristid has a transverse orientation. It joins the base of a weakly developed postmetacristid. The protoconid possesses a very weak external postprotocristid. The posthypocristid reaches the base of the junction of the preentocristid, the internal postprotocristid, and the postmetacristid. The posthypocristid is more oblique on m3 than on m2 and joins the base of the postentocristid. The lingual cuspids are slightly laterally compressed, with a relatively bulbous labial part. These cuspids are not aligned. The metacristid and the preentocristid are small and straight. The postmetacristid splits in two at the posterior base of the metaconid. The labial crest joins the preentocristid, whereas the lingual one ends before reaching the base of the cuspid forming a weak metastylid. The postentocristid is well developed in comparison to the other labial cristids. It is highly curved and joins the posthypocristid to form the postero-lingual edge of the tooth. At this edge, the entoconulid forms a small spur, slightly placed within the back fossa of m3. This spur ends the posterior cingulid. The anterior cingulid is well marked below the preprotocristid. The hypoconulid is quite large in the laterally compressed back fossa.

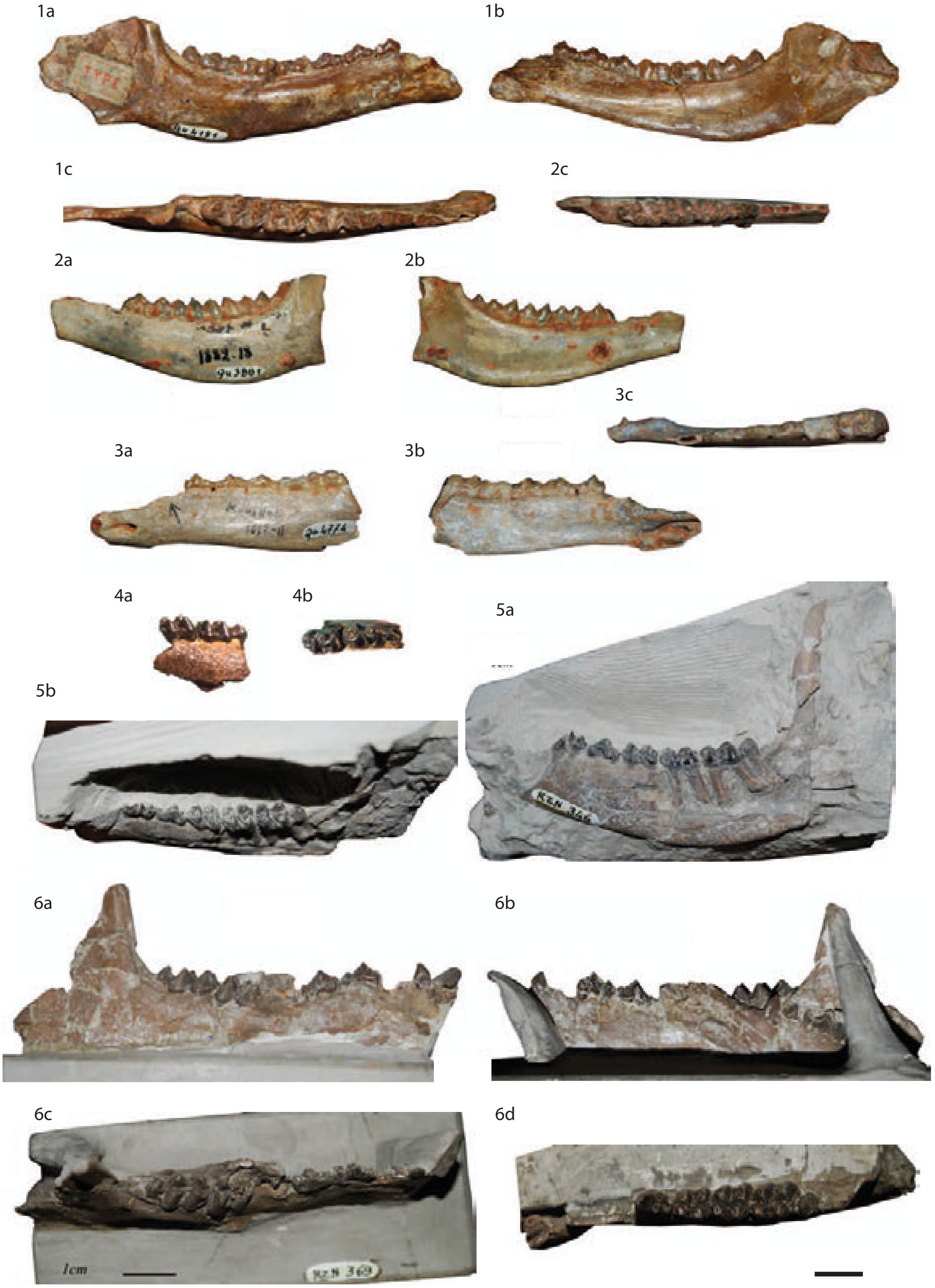


Figure 7. *Gelocus communis*: from old collections of the *Phosphorites du Quercy* **1** right complete *corpus mandibulae* with p2-m3 (MNHN Qu4191; *Holotype*), lingual (**a**), labial (**b**), and occlusal views (**c**); **2** left complete *corpus mandibulae* with p4-m3 (MNHN Qu3881), lingual (**a**), labial (**b**), and occlusal views (**c**); **3** left complete *corpus mandibulae* with p2-m3 (MNHN Qu4774), lingual (**a**), labial (**b**), and occlusal views (**c**); from *Poillat* **4** left fragmentary mandible with m2-m3 (MJSN POI007-237), labial (**a**) and occlusal views (**b**); from *Ronzon* **5** left fragmentary mandible with p3-m3 (MNHN RZN346), labial (**a**) and occlusal views (**b**); **6** right mandible with p1-m3 and left fragmentary mandible with p4-m3 (MNHN RZN369), lingual (**a**), labial (**b**), and occlusal views (**c** & **d**). Scale bar equals 10 mm.

Table 9. Dental measurements (in mm) of the *Gelocus communis*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	Reference	p1		p2		p3		p4		m1		m2		m3	
Gelocus communis																
Old collections of Quercy	BSPG 1879XV159										7.4	4.8	7.7	5.1	11.8	5.7
	MNHN Qu3881									3.2	6.1	5.1	6.6	5.5	10.5	5.2
	MNHN Qu4191	Holotype			5.4	2	6.2	2.9	6.9	3.2	6.8	5.8	7.6	6.1	12.2	6.3
	MNHN Qu4774				6	2.1	7	2.5	7.2	3.3	6	4.7	6.5	5.6		
Ronzon	MHNT.PAL.2011.0.7								7.1		7.6		7.6		12.3	
	MHNT.PAL.2011.0.10														12.1	
	MNHN RZN320										7.7	4.9	8.2	5.8	11.8	5.8
	MNHN RZN323												8.5	5.5		5.5
	MNHN RZN324								6.9	3.3	7	5	7.2	4.8	11.8	5.4
	MNHN RZN325														13.1	5.5
	MNHN RZN326														12.8	6
	MNHN RZN327										7.2	4.3				
	MNHN RZN335										7.6	5	8.3	6.2	12.7	6.2
	MNHN RZN336				6.8	2.4	7.7	3	8.5	3.5						
	MNHN RZN348								6.6	2.8	6.6	4.5	6.6	4.8	11.2	4.8
	MNHN RZN352				6.2		7.4		8							
	MNHN RZN356						7.5		7.5		7.3		8.3		12	
	MNHN RZN356											5	7.7	5.9		5.9
	MNHN RZN357								6.6		7.5		8.4		11.8	
	MNHN RZN359												8.3		1.5	
	MNHN RZN360										7.7	5.5	8.6	5.9		
	MNHN RZN361										7.5	5.1	8.2			
	MNHN RZN363										7.2					
	MNHN RZN369		3.7	1.6			7.6	2.9	6.6	3.8			7.8		11.2	5.5
	MNHN RZN536								6.9	3.4	6.6	4.9	7.1	5.8	12.1	6.2
	MNHN RZN537								6.8	3.5	7.1	4.8	7.3	5.5	12.6	5.4
	NMB Ro14								7.4	3.7	7.7				12.9	6.4
	NMB Ro17										7.3	4.7	8.8	5.7		
	NMB Ro51a										6.7	4.7	7.4	5.5		5.8
	NMB Ro70										6.9	4.6	8.4	5.3		5.5
	NMB Ro143								6.5		7.5		8.5			
	NMB Ro15				5.8	2.2	7.0	3.0	7.0	3.4	7.3	4.7				
	NMB Ro144				5.5	2.1	6.0	2.8	7.0	3.2						
Ehingen 15	BSPG 1971 XXII6											4.7				
Poillat	MJSN POI007-237												7.7	5	11.6	4.9
Ronzon	mean value	Filhol 1881	3.0	3.0	5.8	3.8	6.8	3.8	7.0	4.5	5.8	5.4	7.3	6.0	11.0	6.1
	mean value	Jehenne 1985			6.2	2.3	7.1	3.0	7.1	3.3	7.3	4.6	7.7	5.4	11.5	5.6

Locality	Inventory number	d4	
Ronzon	MNHN RZN327	7.5	3.8

Locality	Inventory number	Reference	P2		P3		P4		M1		M2		M3	
Ronzon	MNHN RZN319		7.5		8.1			6.7	6.7	9.2	7.8	9.8		
	MNHN RZN534					5.4		6	7.2	9.7	8.9	10.1	9	10
	BSPG 1966XXXVI11								6.8	7.8				
	BSPG 1966XXXVI11								6.5	7.9				
Ronzon	mean value	Filhol 1881	5.7	2.0	7.0	4.0	5.5	6.0	6.2	7.7	7.4	9.5	7.0	9.0
	mean value	Jehenne 1985	7.4	3.3	8.1	5.5	6.0	7.1	7.4	8.7	8.3	9.7	9.1	10.3

Taxonomical attribution

The lower molars are very bunodont with conical lingual cuspids. The fossae are small. There is no true *Dorcatherium* fold. The small remnant *Dorcatherium* fold observed by Janis (1987) is a splitting in two of the postmetacristid. The presence of a postentocristid may vary within the same population. In the Ronzon specimens NMB Ro70, NMB Ro17 and NMB Ro51, the postentocristid is lacking, whereas it is present on NMB Ro14. The metastylid is poorly developed. It is probably due to the wearing of the crowns. However, *Gelocus communis* was only known in MP21: Ronzon, Ruch-Ravet, Aubrelong, Möhren4, Haag (Sudre & Blondel 1996). The size of specimens MJSN POI007-237 is similar to those given by Jehenne (1985) for the specimens from the collections of Quercy (Tab.9). These collections are not dated and could be younger than the specimens from Ronzon.

Gelocus laubei Schlosser, 1901

1901*	*Gelocus laubei* n. sp. Schlosser: 22, pl.1 figs. 8 & 12.
1905	*Gelocus laubei* Bayer: 86.
1913	*Gelocus laubei* Kafka: 5.
1978	*Gelocus laubei* Heissig: 272, fig. 4.
1985	*Gelocus laubei* Jehenne: 63.
1987 v	*Pseudogelocus laubei* Fejfar: 260, fig. 7-15.
1987	*Gelocus laubei* Heissig: fig. 6.
1996	*Gelocus laubei* Sudre & Blondel: 173.
2005 v	*Pseudogelocus laubei* Fejfar & Kaiser: 5, figs. 1-5.

Lectotype. Right mandible with p1, p2 and m1 (alveoli), p3-4 and m2-3 (Schlosser 1901, pl.1 fig. 8 & 12; specimen lost after Jehenne 1995).

Species etymology. The etymology of this species had not been defined in the original paper.

Type locality and horizon. Bohemian lignite of Plzen (Czech Republic), MP21-22.

Occurrence. Earliest Oligocene, from MP21 to MP22, from Germany (Eselsberg, Grafenmühle 6, Möhren 4, Möhren 7, Möhren 13, Möhren 16, Möhren 19, Möhren 20) and Czech Republic (Plzen).

Referred material. No additional material.

Diagnosis (after Jehenne 1995**).** Smaller than the type species, but larger than *G. minor*. On the p4, the mesolingual conid is less developed than that on the p4 of *G. communis*. On the lower molars, the lingual conids are les conical and more laterally compressed.

Gelocus villebramarensis Brunet & Jehenne, 1976

1970	*Gelocus communis* Brunet: 2537.
1975	*Gelocus* nov. sp. Brunet: 505.
1976*	*Gelocus villebramarensis* nov. sp. Brunet & Jehenne: 1659, figs. 1-4.
1978	*Gelocus villebramarensis* Heissig: 272, fig. 4.
1985	*Gelocus villebramarensis* Jehenne: 40, fig. 8.
1987	*Gelocus villebramarensis* Heissig: fig. 6.
2009	*Gelocus* cf. *villebramarensis* Vianey-Liaud & Schmidt: 913.

Holotype. Right mandible with p3-m3 (FS Vil. 1970-235, Brunet & Jehenne 1976, fig.2).

Paratype. Right mandible with p3-m3 (FS Vil. 1970-125, Brunet & Jehenne 1976, fig.3); right maxillary with P3-M2 (FS Vil. 1970-256, Brunet & Jehenne 1976, fig.4).

Species etymology. From the Villebramar locality.

Type locality and horizon. Villebramar (Lot et Garonne, France), MP22.

Occurrence. Early Oligocene, MP22, from France (Cavalé, Villebramar) and Germany (Möhren 13, Ronheim 1).

Referred material. No additional material.

Diagnosis (after Brunet & Sudre 1976). Larger and more advanced ruminant than *Gelocus communis*. The lower premolars are more molarized and the mesolingual conid of the p4 possesses rough cristids. The lingual cristids of the lower molars are more elongated. The cingulum on upper molars is reduced.

Genus ***Pseudogelocus*** Schlosser, 1902

Type species. *Pseudogelocus scotti* Schlosser 1902 from Hochberg and Veringenstadt (Bavaria, Germany), MP21.

Further included species. *P. mongolicus* Vislobokova & Daxner-Höck, 2002.

Diagnosis (adapted from Métais & Vislobokova 2007). The fourth lower premolar has a strong anterior conid, an isolated and well-developed mesolingual, and a talonid with distinct posterolabial conid and posterior cristid extending lingually, such as in the Pecora.

Etymology. *Pseudo*– means so-called and –*Gelocus* is a primitive ruminant.

Pseudogelocus scotti (Schlosser, 1902)

1902* pars.	*Paragelocus scotti* n. g., n. sp. Schlosser: 65, pl. IV figs. 2, 5-6.
1910	*Gelocus scotti* Stehlin: 1089.
1978	pars *Pseudogelocus scotti* Heissig: 271, fig. 4.
1984	*Cryptomeryx matsoui* Sudre: 13, fig. 10.
1985	*Gelocus scotti* Jehenne: 57, fig. 10.
1987	*Pseudogelocus scotti* Heissig: fig. 6.
1987	*Iberomeryx matsoui* Remy et al.: tab 3c.
1996	*Pseudogelocus* cf. *scotti* Sudre & Blondel: 174, figs. 1-2.
2002	*Paragelocus* aff. *scotti* Vislobokova & Daxner-Höch: figs. 12-15.

Holotype. Right p4 (Jehenne 1985, fig. 10).

Species etymology. The species name was given as a tribute to the palaeobotanist Dukinfield Henry Scott.

Type locality and horizon. Hochberg and Veringenstadt (Bavaria, Germany), MP21.

Occurrence. Early Oligocene, from MP21 to MP23, from France (Mas de Got, La Plante2) and Germany (Bernloch 1, Burgagerbein 2, Burgmagerbein 3, Burgmagerbein 5, Burgmagerbein 8, Ehingen 1, Frohnsetten, Grafenmühle 6, Grafenmühle 10, Haag 2, Herrlingen 1, Möhren 4, Möhren 7, Möhren 9, Möhren 11, Möhren 13, Möhren 16, Möhren 18, Möhren 19, Möhren 20, Möhren 31, Ronheim1, Schelkingen 1).

Referred material. No additional material.

Diagnosis (after Jehenne 1985). This species is smaller than the type species but larger than *Gelocus minor*. The mesolingual conid of the p4 is higher, more separated from the mesolabial conid, and more posterior than that of *G. communis*. The upper molars possess a well-individualized protocone and strong styles.

5.4 Discussion

5.4.1 Lophiomerycidae

The place of the Lophiomerycidae within the Ruminantia has often been discussed (Lydekker 1885; Schlosser 1886; Cope 1887, 1889; Viret 1961; Romer 1966; Janis 1987; Blondel 1997). This family is characterised by a combination of primitive and evolved characteristics, which are difficult to interpret in terms of phylogeny. Representatives of this family possess unfused metapodial bones, a huge angle between the trochleas of the astragalus, a well-marked cubo-navicular boundary on the astragalus, and open talonid and trigonid on lower molars (Martinez & Sudre 1995; Geraads et al. 1987; Brunet & Sudre 1987; Blondel). These characteristics also seem to be shared with the primitive Artiodactyla. On the other hand, the lack of true *Dorcatherium* fold and the presence of a premolar metaconid differ from Tragulidae (Mennecart et al. 2011). Moreover, the shape of the lower molars is quite peculiar within the Ruminantia. The molar metaconid is globular and conical, and is in the axis of the internal postprotocristid. The trigonid and the talonid do not possess a depression in their fossa forming a flat surface. The presence of a metaconid on the p4 could have been a convergence with the Gelocidae, which seems to be the most suitable taxon for the origin of the Pecora. The molars of the Gelocidae are more evolved than the Lophiomerycidae, with more selenodont cusps and closed trigonid and talonid already present in the gelocid Protopecora (Janis 1987). That is why the Lophiomerycidae could be considered as the most primitive ruminant family in Europe.

The Lophiomerycidae are known from the late Middle Eocene with *Zhailimeryx jingweni* from China (Guo et al. 2000). This family is a characteristic post-Grand-Coupure migrant in Europe, where it appeared in MP22 with *Lophiomeryx* (Brunet & Sudre 1987). The presence of the latter during the Eocene of China, with *L. shinaoensis* and *L. gracilis*, is still under discussion (Brunet & Sudre 1987; Vislobokova 1997; Métais et al. 2001; Métais & Vislobokova 2007), and the attribution of these species to the genus *Lophiomeryx* remains doubtful (Métais et al. 2009). The same doubts exist for the species *L. gobiae* (Vislobokova 1997) and *L. angarae* from the Early Oligocene of Mongolia. The latter possesses an opened trigonid and talonid, as is also the case for the Tragulidae (Mennecart et al. 2011). Following our results, the distinction of Tragulidae/Lophiomericydae within the Tragulina can be based on lower molars with the presence of an anterior conid in Tragulidae and the absence of a premetacristid in Lophiomericydae. Other dental features permit the discrimination of Tragulidae and Lophiomerycidae, such as a well-developped *Dorcatherium* fold on lower molars and the absence of mesolingual conid on p4 in Tragulidae (Mennecart et al. 2011). From these characteristics, *L. shinaoensis*, *L. gracilis*, and *L. angarae* are closer to Tragulidae than to Lophiomerycidae. Regarding *L. gobiae*, Vislobokova (1997) proposed to assign it to the Hypertragulidae. Also, the confusion between Tragulidae and Lophiomerycidae has already been discussed by Mennecart et al. (2011) in the study of *Iberomeryx minor*.

Moreover, even if the Mongolian and Chinese taxa belong to another genus, *Lophiomeryx* remains a ubiquitous genus well known throughout Eurasia that inhabited Western Europe (Spain, France, Switzerland), Central Europe (Germany, Czech Republic), Asia Minor (Georgia), and Central Asia (Kazakhstan, India). The species of this genus were the biggest ruminants in Europe during the Oligocene. First described in Switzerland, *Lophiomeryx mouchelini* is the oldest known ruminant in Switzerland with *Iberomeryx minor* and *Gelocus communis*. These species were hitherto considered to be restricted to the MP22-23 biozones (Brunet & Sudre 1987). However, the new discoveries of *Lophiomeryx mouchelini*, *Ibero-meryx minor*, *and Gelocus communis* remains in the Swiss Jura Molasse localities of Poillat, Pré Chevalier and Beuchille, permit the extension of the biostratigraphic range of these species to early MP24 (older than the standard level Heimersheim, pers. comm. O. Maridet). Only upper molar fragments and a talonid associated to a third lobe of m3 has been observed in the NMB for the *Lophiomeryx* of Montalban (Spain). However, these specimens are slightly smaller, narrower, and with a lower crown than those of the previous species *Lophiomeryx mouchelini* and those described by Brunet & Sudre (1987). The back fossa of the m3 is narrow and the entoconid is laterally compressed, with a weak postentocristid on its upper part. The p4 can possess an additional posterolabial cristid, an overdeveloped paracone rib forming an anterior groove, and an oblique mesolabial conid that clearly differ from European *Lophiomeryx*. However, the big metacone and paracone ribs, the paracone and metacone not aligned, and reduced metaconule can be observed in specimens of *Lophiomeryx kargilensis* from Asia (Nanda & Shani 1990). Also, the specimens from Montalban are clearly bigger than those of *Lophiomeryx gaudryi* (Tab.2). The presence of this new species associated with "*L.*" *gaudryi* and *L. mouchelini* shows an unexpectedly huge diversity of the Lophiomerycidae in Europe during the Rupelian. The last occurrence of *Lophiomeryx* corresponds to *Lophiomeryx chalaniati* from Cournon (MP28) and coincides with the arrival of the Eupecora (Migrations3).

5.4.2 Tragulidae

The Tragulidae is the only Rupelian family, which still exists today with three different genera: *Tragulus* and *Moscholia* in Asia, and *Hyemoschus* in Africa (Rössner 2007). The dichotomy between the Tragulidae and the Pecora, dated by the molecular clock, occurred during the Middle Eocene (Hassanin & Douzery 2003). The Palaeogene Tragulidae fossil record is very poor (Gentry et al. 1999; Métais et al. 2009; Mennecart et al. 2011). Only *Archaeotragulus krabiensis* (Métais et al. 2001) and *Iberomeryx* species (Mennecart et al. 2011) have been defined. The shape of the p4 (without mesolingual conid with two elongated parallel cristids forming the edges of the enlarged back valley) associated with a big *Dorcatherium* fold on quite bunodont molars, is also observed in Neogene fossils and extant Tragulidae. During the Neogene, this family is well-diversified with at least 5 genera (*Afrotragulus*, *Dorcatherium*, *Dorcabune*, *Siamotragulus*, *Yunannotherium*; Rössner 2007; Sanchez et al. 2010). The presence of an anterior conid seems also to be common in *Archaeotragulus*, *Iberomeryx*, and *Dorcath-*

erium and could be a primitive state among the tragulids (Mennecart et al. 2011).

The tragulid fossil record is very scarce between the Eocene and the Early Miocene (Rössner 2007; Sanchez et al. 2010). The extant Tragulidae live in closed canopy rainforests. They are little diversified, very rare, solitary, and selective browsers. *Archaeotragulus* was discovered in Kari (Thailand) in lignite deposits, and *Iberomeryx* in La Beuchille (Switzerland) in association with a wood-bearing bed indicating the presence of forests (Métais et al. 2001; Becker et al. 2004). Analysis, based on the mandible morphology, indicates that the Tragulidae seems to be exclusively adapted to selective browsing of fruits, leaves, mushrooms, and small animals (Dubost 1984, Rössner 2007, Mennecart et al. 2011). Based on these results, we can suppose that the primitive Tragulidae had a similar ecology to the extant ones. The time-gap without Tragulidae during the Chattian and the Early Miocene in Europe is probably linked to more hostile environmental conditions with no tropical forests.

5.4.3 Bachitheriidae

Many authors thought that *Bachitherium* was very close to *Gelocus* and placed it within the Gelocidae (Filhol 1877; Cope 1887; de Bonis et al. 1973). Lavocat (1946) considered that this taxon was Hypertragulidae due to the presence of tusk-like p1's. Webb & Taylor (1980), based on a large mastoid fissure and an enlarged i1, classified it within the Leptomerycidae. However, the i1 is reduced, and the upper premolar inner crescent is well formed. That is why Bouvrain & Geraads (1985) considered that *Bachitherium* is clearly more derived than Leptomerycidae, but more primitive than the genus *Prodremotherium*. The phylogeny proposed by Geraads et al. (1987) confirms the previous idea that *Bachitherium* is a Protopecora, more derived than *Gelocus*, but more primitive than *Prodremotherium*. The anterolingual cone on P2-3 is well developed, there is a lingual padding on D3. The upper molars are high and the postprotocrista is labially oriented. The diastemata are elongated and the metacarpial bones have a tendency to fuse. Janis (1987) suggested that *Bachitherium* should be separated from the Gelocidae to form a new family, the Bachitheriidae, more primitive than the Lophiomerycidae. Blondel (1997) followed Janis (1987) on the base of the tusk-like p1, the huge diastema between p1-2, the metatarsian bones fused and elongated without bony bridge, and the metacarpian bones slender, short, and unfused. Bachitheriidae was considered as the sister group of Gelocidae, clearly belonging to the Tragulina (Blondel 1997, 2001; Métais & Vislobokova 2007). However, the analysis of Métais & Vislobokova (2007) did not consider the primitive Tragulidae and used some characteristics that were incorrectly applied. Indeed, Martinez & Sudre (1995) confirmed that the shape of the astragalus is clearly different. The trochleas are not in line, without cubo-navicular boundary, such as on extant Tragulidae. The p4 does not possess a mesolingual conid, contrary to the Hypertragulidae, the Leptomerycidae, the Lophiomerycidae and the Pecora (Mennecart et al. 2011). This shape is similar to those of *Iberomeryx* and *Dorcatherium*, two extinct Tragulidae. The species of *Bachitherium* possess a huge variability concerning the external postprotocristid. Amongst the small species, it is small to absent. On the bigger ones, it is present. This fold seems to be linked to the hypsodonty and is not a good phylogenic characteristic. The metartasian bones III and IV are partially fused, and the metacarpian bones III and IV are unfused (Geraads et al. 1987). However, the fusion of these bones seems to be a general trend within the ruminant evolution, because, not all actual Tragulidae possess these fusions and this evolution can be followed within the Pecora evolution (Lull 1904). Moreover, a similar evolution can be followed among the suborder Tylopoda. The presence of a postentocristid seems to be an evolved characteristic. Indeed, within the Pecora evolution we can observe that the primitive *Gelocus* can either possess it or not. The evolved one always has it. The Bachitheriidae are more evolved than the Lophiomerycidae, but are more primitive than the Protopecora. They share many characteristics with the actual and fossil Tragulidae, but they are more evolved.

Bachitherium seems to have been the most diversified European ruminant between MP23 and MP28. The peak of diversity is during MP25 with at least 4 species (Sudre 1995). But this could be biased by the exceptional preservation and the Lagerstätten effect of the Le Garouillas locality. The small species *B. vireti* and *B. curtum* are the oldest representatives and could appear during MP22 or MP23 (Werhli 1932; Heissig 1978, 1987; Sudre 1996). The youngest species is *Bachitherium lavocati* from Pech Desse (MP28). Van der Made (2008) described a new species of *Bachitherium B. sardus* in the Burdigalian of Oschiri (Saridinia). However, this species is only based on postcranial remains, and the association of characteristics does not allow a strict attribution to the genus *Bachitherium*. Moreover, the particular shape of postcranial remains of this taxon could be due to an insular effect such as in *Myotragus* (Spoor 1988).

The Early Oligocene *Iberomeryx minor* was first placed by Filhol (1882) within *Bachitherium* due to the tragulid-shape p4. But the complexity of the lower molars, that possess an anterior conid, permits it to be assigned to the Georgian *Iberomeryx* genera. The species *Andegameryx serum* (Obergfell 1957) from the Early Miocene was also first assigned to *Bachitherium*. However this species is clearly a Pecora in the light of new discoveries (Ginsburg 1999). It does possess neither *Dorcatherium* fold on lower molars nor a tragulid-shape p4.

The differences between the species *B. curtum* and *B. insigne* have never been clearly defined (Sudre 1986). These species are of the same age (Sudre 1995) and Wehrli (1932) considered that the size difference corresponds to a sexual dimorphism. But the diastema length (Sudre 1986), the proportions of the postcranial remains (Sudre 1995; Blondel 1998), and differences in the general shape of the mandible correspond to huge interspecific ecological differences. Due to the proportions of its limbs, the small *Bachitherium curtum* lived in humid wooded to semi-aquatic habitats, such as the actual small Tragulidae and Cephalophini (Blondel 1998). Regarding the dental microwear analysis and the mandible morphology, this Tragulina was a selective browser, eating fruits and leaves (Blondel 1996; Mennecart et al. 2011, 2012). The bigger *Bachitherium curtum* lived in sparse forests (Blondel 1998). It possesses another mandible morphology, which could indicate a feeding habit based mainly of leaves.

5.4.4 Gelocidae

Classically, the Gelocidae are considered to be at the base of the radiation of the Pecora or Protopecora "faute de mieux" (Janis 1987; Janis & Scott 1987; Métais & Vislobokova 2007). This "basket" family contains numerous taxa recorded from the Eocene to the Miocene in Europe, Africa, Asia, and North America. After Janis (1987), Janis & Scott (1987), Webb (2000), and Métais & Vislobokova (2007), this family includes the following genera: *Gelocus*, *Paragelocus*, *Pseudogelocus*, *Prodremotherium, Pseudomeryx*, *Floridameryx*, *Pseudoceras*, *Notomeryx*, *Gobiomeryx*, *Eumeryx*, and *Rutitherium*. Following Janis (1987) and Janis & Scott (1987), the above mentioned genera are unified according to symplesiomorphic characteristics such as a small size, brachiodont teeth, a small p1 separated from the p2 by a small diastema, a small metaconid on the premolars without postmetacristid, an incomplete postentocristid, presence of a cingulum/cingulid on molars, and a small metaconule on M3 (Janis 1987; Janis & Scott 1987). However, considering the "Introduction" chapter and the chapter on the Mosaicomerycidae, the real diversity of the Gelocidae should be restricted to the genera *Pseudogelocus* and *Gelocus*. In addition, only Rupelian European taxa can be seriously attributed to the *Gelocus* genus, excluding *G. whitworthi* (Kenya) and *G. gajensi* (Pakistan). The family Gelocidae should no longer be considered as a primitive evolutionary grade among the ruminants, but more as a very primitive family at the base of the Pecora (Protopecora) or even more primitive.

5.4.5 Biostratigraphy and migration/extinction events

The ruminants first appeared during the Late Eocene. Some exchanges occurred between Asia and North America where similar families have been discovered (e.g., Hypertragulidae, Leptomerycidae; Métais & Vislobokova 2007). However, no ruminant remains are recorded from this period in Europe. The first European ruminant occured just after the Eocene/Oligocene boundary. This boundary, marked by the Oi1 glaciation (Zachos et al. 2001; Berger et al. 2011), is characterized by a huge faunal turnover named the "Grande-Coupure" (Stehlin 1910) or "great cut" (Prothero 1994; Agusti & Anton 2002). We consider that the Asiatic mammal migration following this event occurred between MP21 and MP23. Regarding the ruminants, the Migrations1 (fig.8) can be divided into 3 small phases with the first appearances of the ruminants in Europe: the Gelocidae (MP21; Ronzon; BichroM'97 1997), the Lophiomerycidae and the Bachitheriidae (MP22; respectively Villebramar and Weinheim; Sudre 1996), and the Tragulidae (MP23; Itardie; Mennecart et al. 2011) (Tab.1 and fig.8). The Bachitheriidae have only been mentioned in Germany during MP22 (Herrlingen 1, Möhren 13, Ronheim

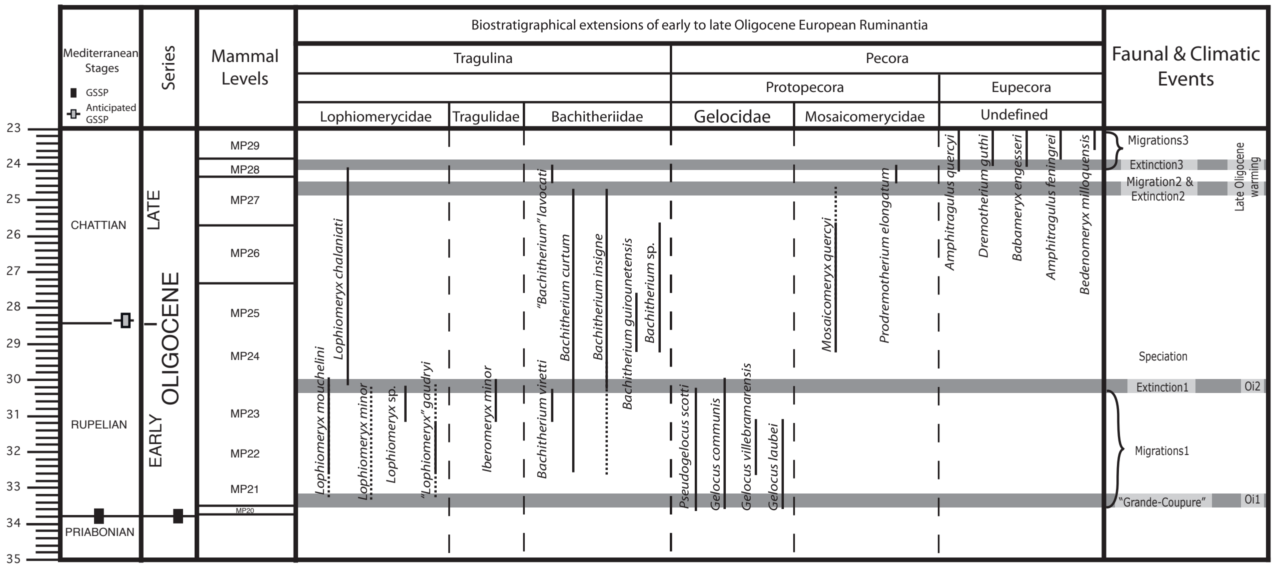


Figure 8. Synthesis of the early to late Oligocene European ruminants. The chronostratigraphy are based on Berger (2011) and the Mammal references levels on Escarguel et al. (1997) and Legendre & Lévêque 1997. The time interval (ca. 33.6–33.4 Ma) of the ‘‘Grande-Coupure’’ event (Stehlin 1910) is based on the high-resolution stratigraphy in the Belgian Basin after Hooker et al. (2004, 2009). The biochronostratigraphical ranges are revised in accordance with the Table 1, Mennecart et al. 2012 and chapter 4 and 6. Climatic events follow Berger 2011 and Faunal events are the ones used in the text.

1, Weinheim; Werhli 1932; Heissig 1978, 1987; Sudre 1996) and the reassessment of the specimens from the Ehingen localities suggests an attribution to Gelocidae and not to Bachitheriidae. However, the reassessment of the fossils from Herrlingen 1 confirms the presence of *Bachitherium* during this period. Contrary to previous authors (Jehenne 1985,1987; Janis 1987; Janis & Scott 1987; Blondel 1997; Métais & Vislobokova 2007), the Gelocidae fossils described here are strictly restricted to the European Rupelian deposits. Regarding the Lophiomerycidae, we described an unsuspected huge diversity with 4 different species, due to the rehabilitation of the “*L.*” *gaudryi*, a newly described species of *Lophiomeryx* and the short co-occurrence of *L. mouchelini* and *L. chalaniati* (tab. 1 and fig. 8). The Paleogene European Tragulidae were just present during a short time period comprised between MP23 and the base of MP24.

A huge extinction event occurred at the base of MP24. This Extinction1 (fig. 8) can be correlated with the Oi2 glaciation (ca. 30.3 Ma; Zachos 2001; Peckar et al. 2006; Berger 2011). In Europe this climatic event is characterized by the regression of the UMM and Rhenan sea (Berger et al. 2005a, 2005b; Berger 2011) and an aridification and opening of the environment (Vianey-Liaud 1991). Only two genera (*Bachitherium* and *Lophiomeryx*) survived this event and only *Bachitherium curtum* crossed the MP23/24 boundary (tab. 1 and fig. 8). The other taxa (*Gelocus* and *Iberomeryx*), essentially selective browsers adapted to swampy environments (Blondel 1998), were probably too specialized and stressed by the disappearance of their preferred food. This major crisis can also be observed within the Rhinocerotoidea (Becker 2009) and the Anthracotheriidae (Scherler 2011). However, Becker (2009) did not notice this major event and remained focused on the “Grande-Coupure”. Scherler (2011) named this event the “mid-Rupelian Faunal Turnover (RFT)”.

The phase of Speciation1 directly follows this latter event with larger species than during the early Rupelian (fig.8). The recorded ruminants are probably adapted to more open environments (Blondel 1998) and less specialized. This speciation phase is characterized by the appearance of *Lophiomeryx chalaniati* in MP24 (MoissacIV; Antoine et al. 2011) and within the Bachitheriidae by the co-occurance of 4 species in MP25 (*B. curtum*, *B. insigne*, *B. guirountensis*, *B.* sp. in Le Garouillas; Brunet & Sudre 1987). The first representative of the Mosaicomerycidae family (*Mosaicomeryx*) arrived during this period (fig. 8). A huge turnover occurred during the transition MP27-MP28. *Bachitherium curtum* and *B. insigne* left space to “*B.*” *lavocati* and *Mosaicomeryx quercyi* to *Prodremotherium elongatum* (Migration2). We can observe changes in the structure of the mammal communities (Legendre 1989; Vianey-Liaud 1992) and within the locomotion types of the ruminants adapted from a forested environment to a more open one (Hiard 2010). This event is directly followed by the last occurrence of Lophiomerycidae, Mosaicomerycidae (Pech Desse, France) and Bachitheriidae (Gaimersheim 1, Germany) in MP28 (Extinction3) and the first migration of the Eupecora (Tab. 1 and fig. 8). The Extinction2 and Extinction3 and the Migration2 and Migrations3 could be linked to the Late Oligocene warming (Zachos 2001; Peckar et al. 2006), which took place during the top of MP27 to the base of MP30 (Berger 2011; fig.8). These recorded extinctions and migrations do not seem to correspond to the "Terminal Oligocene Crisis" (Becker et al. 2009), which only began at MP29 and is characterized by a global cooling due to the Mi1 glaciations.

5.5 Conclusions

The ruminants first appeared in Europe after the Grande-Coupure. The reassessment of the Rupelian and early Chattian ruminants of Europe highlights the huge diversity of this group during this time interval. The biochronology and the biodiversity of the Rupelian ruminant families has been improved. Gelocidae are strictly Rupelian, Lophiomerycidae are well-diversified during this period and Tragulidae occurred just during a short time period corresponding to MP23 and to early MP24. A huge Extinction (Extinction1) arrived at the base of MP24. This event is characterized in detail for the first time in this work. A second and third faunal turnover occurred during the transition between MP27-MP28 (Extinction2) and in MP28 (Extinction3).

The general evolution of the European ruminant communities is due to global changes during the Oligocene. Two different cases can be defined: i) Extinction phase linked directly to climate changes without migration (in this case the event is followed by anagenetic evolution and reduction of the diversity such as during Extinction 1) and ii) Extinction phase linked to climate changes and migrations implying an increase in the biodiversity sometime after the "Grande-Coupure".

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6 - *MOSAICOMERYX QUERCYI*, NEW COMB. RUMINANT FROM THE OLIGOCENE OF EUROPE, AND THE SIGNIFICANCE OF "GELOCIDS"

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Abstract

The description of new material and the reassessment of the specimens previously assigned to *Gelocus quercyi* led us to propose a new genus for this species. Moreover, the description of a juvenile skull and other specimens of *Prodremotherium elongatum* and comparison with *Dremotherium* provide evidence that these two genera are not closely related as previously thought. A phylogenetic analysis based on 35 dental, cranial and postcranial features highlights the misidentification of *Gelocus quercyi* and leads to propose new clades, *Mosaicomerycidae* nov. and *Mosaicomeryx* gen. nov., with *Mosaicomeryx quercyi* new comb. and *Prodremotherium elongatum* as sister group. *Mosaicomericidae* nov. is considered as the sister group of the Eupecora and presents a modular evolution within a new step in the global ruminant evolution. It includes also the Asiatic genera *Notomeryx* and *Gobiomeryx.* Based on the well-dated European localities, the occurrence of *Mosaicomeryx quercyi* comb. nov. corresponds to MP25-26 and this of *Prodremotherium elongatum* to MP28. This time interval covers two major Oligocene faunal and climate changes: the Ectinction1 (MP24), associated to the glaciation Oi2, and the Extinction3/Migrations3 (MP28), associated to the Late Oligocene warming.

6.1 Introduction

Ruminants display a fascinating spectrum of adaptations allowing them to successfully inhabit nearly every terrestrial biome. Yet, the evolutionary history of ruminants remains unresolved. The fossil record documents 45 million years of diversification including several key radiations, each marking important steps in ruminant cladogenesis. Almost 25 million years of this history occurred before the first fossil record of the living ruminant families. Most of the extant ruminant groups (also known as Eupecora, most of them bearing cranial appendages) diversified during the Mid-Miocene (Gentry et al. 1999, Hassanin & Douzery 2003). The basal radiation of Ruminantia occurred probably early in the Eocene, but Eocene ruminants remain poorly documented, especially in Asia where they probably originated, except for few key taxa such as *Archaeomeryx* (e.g., Webb & Taylor, 1980). During the Early Oligocene, ruminants are documented by several forms closely related to tragulids while the Late Oligocene is marked by the first appearance of several forms of "pre-pecora", often included in the "basket" family Gelocidae. The type genus of the Gelocidae, *Gelocus*, appears from the earliest Oligocene (MP21, European mammal reference level) with *G. communis* and *G. laubei*, and their last occurrence does not extend up to MP28 (Late Oligocene) with *Prodremotherium elongatum* whose affinity with 'Gelocidae' is debated (e.g., Janis, 1987). The genus *Prodremotherium* is also reported from the Early Oligocene of Kazakstan (*P. flerowi* Trofimov, 1957) and Mongolia (*P.* sp, Vislobokova & Daxner-Höck, 2002), and from the Late Oligocene of Georgia (*P. trepidum*, Gabunia, 1964), but the generic assignment of these Asiatic forms remains doubtful.

Prodremotherium elongatum, the suprageneric assignment of which remains doubtful, is classically considered to belong to Gelocidae (Jehenne 1977, 1987, Janis 1987, Sudre & Blondel 1996, Blondel 1997, Métais & Vislobokova 2007, Mennecart et al. 2011) and as resulting from a regional evolution of mid-Oligocene European forms (Depéret 1908). However, many authors (Janis 1987, Janis & Scott 1987) recognised that this attribution to Gelocidae can be discussed, but they maintained it within this latter "as a useful piece of descriptive nomenclature". Other authors considered that *Prodremotherium* was a basal Eupecora, close to Bovoidea (Jehenne 1977, Jehenne 1985, Janis & Scott 1987, Jehenne & Brunet 1992), or close to Cervoidea (Webb & Taylor 1980, Janis & Scott 1987). It had also been placed within Prodremotheriidae (Guo et al. 1999, Guo et al. 2000, Métais et al. 2000). Even the family name is matter of confusion, because it literally means "before the Dremotheriidae" while direct links between these two families is still under discussion. Moreover, *P. elongatum* is only known in the badly dated old collections of the Phosphorites du Quercy (Filhol 1877, Jehenne 1977, 1985, 1987, Remy et al. 1987, Jehenne & Brunet 1992) and in one well-dated locality: Pech Desse (MP28; Blondel 1997).

"Gelocus" quercyi is exclusively known by a few upper teeth from the old collection of the Phosphorites du Quercy (Jehenne 1985, 1987, Blondel 1997). This taxon is assigned to this genus due to some primitive characteristics (bunoselenodont crowns, large cingulum, elongated premolars). Comparison with the previously described specimens of *Gelocus* reveals wide morphological discrepancies and suggests that "*G.*" *quercyi* probably belongs to another genus.

The reassessment of the European fossil material referred to both *P. elongatum* and "*G." quercyi* leads us to propose new phylogenetic relationships within the Eurasiatic Pecora.

6.2 Material and methods

6.2.1 Systematic palaeontology

The taxonomic revision and phylogenetical implications proposed here are the results of the study of the dental and postcranial remains of *Gelocus quercyi* and *Prodremotherium elongatum* from the collections of the Bumbach locality (Canton Bern, Central Switzerland), from the Saint Henri and "Marseille" localities (SE France), and in part from the Phosphorites du Quercy localities (old collections and Pech Desse, SW France; Jehenne 1985,1987, Blondel 1987), stored at the collection of the Muséum National d'Histoire Naturelle, Paris (France), the Naturhistorisches Museum Basel (Switzerland), the Naturhistorisches Museum Bern (Switzerland), the Université Claude Bernard Lyon (France), and the Université des Sciences et Techniques du Languedoc (Montpellier, France). The identifications are based on anatomical feature descriptions, comparative anatomy and biometrical measurements, following the ruminant dental terminology detailed in the Figure 1. All measurements are given with a precision of 0.1 mm. The biochronological framework used in this work is based on Berger (2011).

6.2.2 Abbreviations

The abbreviations used in this work follow Matthews (1973): *, the work validates the species; ., the authors agree on the identification; v, the authors have seen the original material of the reference; ?, the allocation of the reference is subject to some doubt; non, the reference actually does not belong to the species under discussion; pars, the reference applies only in part to the species under discussion; no sign, the authors were unable to check the validity of the reference. Years in italics indicate a work without description or illustration.

i, lower incisive; c, lower canine; p, lower premolar; m, lower molar; C, upper canine; P, upper premolar; M, upper molar; Mc, Metacarpal bones; Mt, Metatarsal bones; dext., right; sin., left.

6.2.3 Institutional Abbreviations

MNHN, Muséum National d'Histoire Naturelle, Paris (France); USTL, Université des Sciences et Techniques du Languedoc (Montpellier, France); UCBL, Université

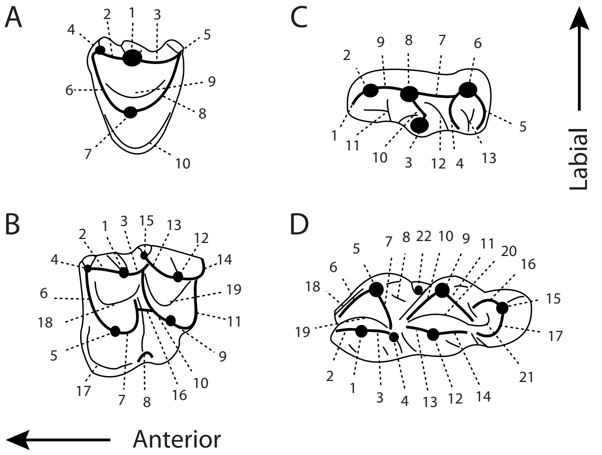

Figure 1: Nomenclature of the dentition. **A**, Upper premolars. 1, paracone; 2, preparacrista; 3, postparacrista; 4, parastyle; 5, metacone; 6, preprotocrista; 7, hypocone; 8, posthypocrista; 9, fossa; 10, cingulum. **B**, Upper molars. 1, paracone; 2, preparacrista; 3, postparacrista; 4, parastyle; 5, protocone; 6, preprotocrista; 7, postprotocrista; 8, entostyle; 9, metaconule; 10, premetaconulecrista; 11, postmetaconulecrista; 12, metacone; 13, premetacrista; 14, postmetacrista; 15, mesostyle; 16, premetaconulecrista bifurcation; 17, cingulum; 18, anterior fossa; 19, posterior fossa. **C**, Lower premolars. 1, preprotoconulidcristid; 2, protoconulid; 3, metaconid; 4, entocristid; 5, hypocristid; 6, hypoconid; 7, *Palaeomeryx* fold; 8, protoconid; 9, preprotocristid; 10, postprotocristid; 11, anterior valley; 12, medial valley; 13, posterior valley. **D**, Lower molars. 1, metaconid; 2, premetacristid; 3, postmetacristid; 4, metastylid; 5, protoconid; 6, preprotocristid; 7, postprotocristid; 8, *Palaeomeryx* fold; 9, hypoconid; 10, prehypocristid; 11, posthypocristid; 12 entoconid; 13, preentocristid; 14, postentocristid; 15 hypoconulid; 16, prehypoconulidcristid; 17, posthypoconulidcristid; 18, anterior cingulid; 19, anterior basin; 20, posterior basin; 21, back basin of m3; 22, ectostylid. Modified from Janis & Scott (1987) and Gentry et al. (1999).

Claude Bernard Lyon; NMB, Naturhistorisches Museum Basel (Switzerland); MNBe, Naturhistorisches Museum Bern (Switzerland).

6.3 Systematic Palaeontology

Order **CETARTIODACTYLA** Montgelard, Catzeflis & Douzery, 1997
Suborder **RUMINANTIA** Scopoli, 1777
Infraorder **PECORA** *sensu* Webb and Taylor, 1980
Family **MOSAICOMERYCIDAE** nov.

Type genus. *Prodremotherium* Filhol, 1877.

Further included genus. *Mosaicomeryx*, nov.

Diagnosis. The P1 is lost. The P2 and P3 are elongated. The upper molars possess a small entostyle. The p1 is absent, with an elongated diastema between c and p2. The p4 has a strong metaconid and four crests lingually oriented. There are neither *Palaeomeryx* nor *Dorcatherium* folds on lower molars but a distinct metastylid. The ectostylid is always present. The metacarpal and metatarsal bones III and IV are proximally fused.

Etymology. «Mosaic» due to the mixing of advanced and primitive characteristics, «meryx» is Greek for ruminant.

Genus ***Mosaicomeryx*** nov.

Type species. *Mosaicomeryx quercyi* (*Gelocus quercyi* of Jehenne 1987).

Diagnose. The P1 is lost. The P2 and P3 are elongated, with a well-formed lingual cingulum on P4. The upper molars are selenodont, with a paracone and a metaconule few conical and cristae elongated and curved. They possess a deep cingulum surrounding the protocone and a small entostyle on the metaconule. The upper molars are quite elongated and the metaconule of the M3 is well developed giving a square shape to these teeth. The p1 is absent; the p4 has a strong metaconid and four crests lingually oriented. There are neither *Palaeomeryx* nor *Dorcatherium* folds on lower molars but a distinct metastylid and an anterior cingulid. The entoconid is transversally compressed and crested anteriorly and posteriorly. The preprotocristid closes trigonid lingually. The ectostylid is always present. The metatarsal bones III and IV are proximally fused, with a metatarsal gulley closed.

Etymology. same as the family.

Mosaicomeryx quercyi (Jehenne, 1987)
(Figs. 2A-E)

1861 v pars	*Palaeomeryx* Fischer-Ooster: 222.
1902	*Dremotherium feignouxi* Giraud: 167.
1914 v pars	Ruminantia inc. sed. Stehlin: 185.
1916	*Prodremotherium* cf. *elongatum* Repelin: 102.
1983 v	*Bachitherium insigne* Mayo: 906.
1985 v* pars	*Gelocus quercyi* n. sp. Jehenne: 49, figs. 9a-e.

1987 v	*Prodremotherium elongatum* Engesser & Mayo: 71.
1987 v	*Bachitherium insigne* Engesser & Mayo: 73.
1987 v* pars	*Gelocus quercyi* n. sp. Jehenne: 132, fig. 1.
1997	*Dremotherium* sp. Huguene y: Tab. 4.
1997 v	*Prodremotherium elongatum* Engesser & Mödden: 483.
1997 v	*Bachitherium insigne* Engesser & Mödden: 484.

Holotype. Maxillary with the tooth row P2-M3 sen. (Qu4151, coll. MNHN-Paris, Jehenne 1985, Fig. 9a, Jehenne 1987, Fig. 1).

Species etymology. From the Quercy localities.

Type locality and horizon. Undated old collections from Quercy (Lot, France).

Additional localities and biochronologic range of *Mosaicomeryx quercyi*. Saint André, "Marseille" (Saint Henri), Saint Géry, in France; Bumbach, Mümliswil Hartberg in Switzerland from MP25 to 26 (Engesser & Mödden 1997).

Referred material. NMB UM459a fragmentary mandible with the tooth row p2-m3 (broken) dext., from the Bumbach locality (Switzerland); NMB UM459b fragmentary mandible with the tooth row p4–m3 (broken) sen., from the Bumbach locality (Switzerland); NMBe 5017072 P3 dext., from the Bumbach locality (Switzerland); NMBe 5017073 P4 sen., from the Bumbach locality (Switzerland); NMB UM2292 distal part of a metapodial bone, from the Mümliswil locality (Switzerland); NMB2317 fragmentary part of a toothless mandible, from the Mümliswil locality (Switzerland); NMB Mar667 fragmentary mandible with p3 and fragmentary p4 sen., m1 sen., fragmentary diastema, M2 sen., M3 sen., from the Saint André locality (France); NMB Mar640 fragmentary mandible with the tooth row m2-3 dext., from the Saint André locality (France); USTL 9326 isolated m1, m2, m3 sen., and m3 sen., from the "Marseille" locality (France); NMHN Qu4151 maxillary with the tooth row P2-M3 sen. (Holotype; Jehenne 1985: Fig. 9a; Jehenne 1987: Fig. 1) from the older collection of the Phosphorites du Quercy (SW France); NMHN Qu4145 maxillary with the tooth row M1-M3 sen., from the older collection of the Phosphorites du Quercy (SW France), NMHN Qu4146 maxillary with the tooth row M2-M3 dext., from the older collection of the Phosphorites du Quercy (SW France); NMHN Qu4147 maxillary with the tooth row M1-M3 dext. (Jehenne 1985: Fig. 9c) from the older collection of the Phosphorites du Quercy (SW France); NMHN Qu4149 maxillary with the tooth row P4-M3 sen., from the older collection of the Phosphorites du Quercy (SW France); NMHN Qu4150 maxillary with the tooth row M2-M3 sen., from the older collection of the Phosphorites du Quercy (SW France); NMHN Qu4152 maxillary with the tooth row M1-M2 sen. (Jehenne 1985: Fig. 9e) from the older collection of the Phosphorites du Quercy (SW France); NMHN Qu4153 maxillary with the tooth row P4-M3 sen. (Jehenne 1985: Fig. 9b) from the older collection of the Phosphorites du Quercy (SW France); NMHN Qu4154 maxillary with the tooth row M1-M3 dext., from the older collection of the Phosphorites du Quercy (SW France); NMHN Qu4155 maxillary with the tooth row P4-M3 sen. (Jehenne 1985: Fig. 9d) from the older collection of the Phosphorites du Quercy (SW France); NMB QuA644 maxillary with the tooth row M2-M3 from the older collection of the Phosphorites du Quercy (SW France); NMB QuA711 maxillary with the tooth row M1-M3 from the older collection of the Phosphorites du Quercy (SW France); NMB QJ80a maxillary with the tooth row P4-M3 from the older collection of the Phosphorites du Quercy (SW France), NMB OT3 Metatarsal bones dext., from the Saint Géry locality (SW France).

Diagnosis. Same as the genus.

Description

The two mandibles from Bumbach seem to belong to the same individual due to the same stage of molar wear (Figs. 2C & 2D). These fossils also possess a well-developed antero-labial cingulid. This one is smaller to absent on the other specimens observed. The measurements of all specimens are summarized in Table 1.

Mandible. Only one specimen possesses a partially preserved *corpus mandibulae* (Fig. 2C). This one is slight, with a small enlargement at the level of the molar row. The ventral profile is straight below the tooth row p2-m2. The lingual groove is deep. At the level of the p2, there is a *foramen mentale* at the half high of the mandible.

Lower adult dentition. It does not seem that *Mosaicomeryx quercyi* had a p1. The anterior part of the p2 does not possess a contact surface with an anterior tooth (Fig. 2C). The three lower premolars possess the same pattern with a rising complexity from p2 to p4. These teeth are relatively elongated. The p2 is much smaller than the p3 and the p4, which are nearly the same size. On the p2, the large protoconid lies in the mesial half of the tooth (Fig. 2C2). Its postero-lingual part possesses a small postprotocristid anteriorly oriented. The preprotocristid is anteriorly oriented and forms the labial wall of the tooth. It finishes with the protoconulid bulge. The *Palaeomeryx* fold makes the labial wall and joins the hypoconid, which is relatively salient, but much less high than the protoconid. It may be fused with the entoconid when this one is present. It forms the postero-lingual edge of the tooth. The posthypocristid stops the postero-jugal and the posterior part of the tooth. The posterior valley is shallow and labially opened. On the p3, the protoconid is central and located on the labial face of the tooth. It possesses a posterior oblique postprotocristid, which joins the lingual edge of the p3, forming a groove between it and the protoconid. The p3 from Saint André (Fig. 2F) differs from the one from Bumbach (Fig. 2C2) by the total absence of entocristid and a bulge on the postprotocristid, which could be a small metaconid. The protoconulid is more developed and transverse and the hypoconid is more globular on the p3 than on the p2. On the p4, the protoconulid is even stronger. From the postprotocristid, a lingual and strong metaconid can be observed. There is a groove between this latter and the protoconid. The hypoconid is absent. It has been replaced by the bifurcated postprotocristid. The hypocristid makes the postero-labial angle of the tooth and the labial part of the p4 (Figs. 2C & D). The entocristid is transverse. It joins the hypocristid, making a posterior basin. The protoconulid is bigger and less oblique. The anterior basin is wider from the p2 to the p4. The medial basin is more and narrower from the p2 to the p4 (Fig. 2C).

The lower molars and the metaconid rib are bigger from m1 to m3 (Figs. 2A, C, & D). The trigonid is closed. The talonid is a little bit lingually opened, due to the posthypocristid, which does not fuse with a very weak postentocristid. The posthypocristid finishes with a well-marked entoconulid. There is no anterior protoconulid. The preprotocristid is oblique, straight until joining the premetacristid on the most anterior part of the tooth. However, it continues a little bit after on the lingual part, giving a cingulid and an antero-lingual stylid. The protoconid is strong and does not wear a *Palaeomeryx* fold. The postprotocristid joins the posterior base of the metaconid, and fuses with the postmetacristid and the preentocristid. The metacristids and the preentocristid are rectilinear. The protoconid and the hypoconid are similar in size. The postprotocristid is from transverse on the m1 to more and more oblique posteriorly on the m2 and the m3. The prehypocristid is oblique. It has a variable ending. It stops at the level of the fusion of the three other cristids to the distal part of the postprotocristid. The posthypocristid is transverse with a weak thickening at the beginning of the cingulid. The metaconid and the entoconid are compressed. The metaconid is gently oblique. It bears a strong metastylid on its posterior part. This latter makes a small column more and more moved away from the postmetacristid from the m1 to the m3. The metastylid is elongated, forming a well-developed blade, an antero- lingual cingulid. No Swiss fossil has a preserved back basin. The anterior cingulid is more and more blurred from the M/1 to the M/3. The posterior cingulid is oblique and joins the posthypocristid on its labial part. The molars of *Mosaicomeryx* are a little bit more bunodont than those of *Bachitherium*. On their back fossa of m3, the hypoconulid, which is highly variable in size and shape, often forms a compressed and oblique buckle. Its posthypocristulid and prehypocristulid are nearly parallel. The posthypoconulidcristid joins the posthypocristid, which is backward on m3. The posthypoconulidcristid reaches the isolated entoconulid, which makes the transition with a well straight postentocristid. The entoconulid possesses a lingal rib with two tiny cristids.

Adult upper dentition. The NMBe 5017072 specimen is a broken P3. Only the labial part is preserved. The paracone and the parastyle are weak. Considering the size, this tooth could belong to *Mosaicomeryx quercyi*. The P4 is triangular due to a preprotocrista and a posthypocrista straight (Fig. 2E). The hypocone is well selenodont. The preprotocrista reaches the parastyle and the posthypocrista joins the base of the metacone. The parastyle and the metacone are salient and form the labial edges of the tooth. The well-selenodont paracone

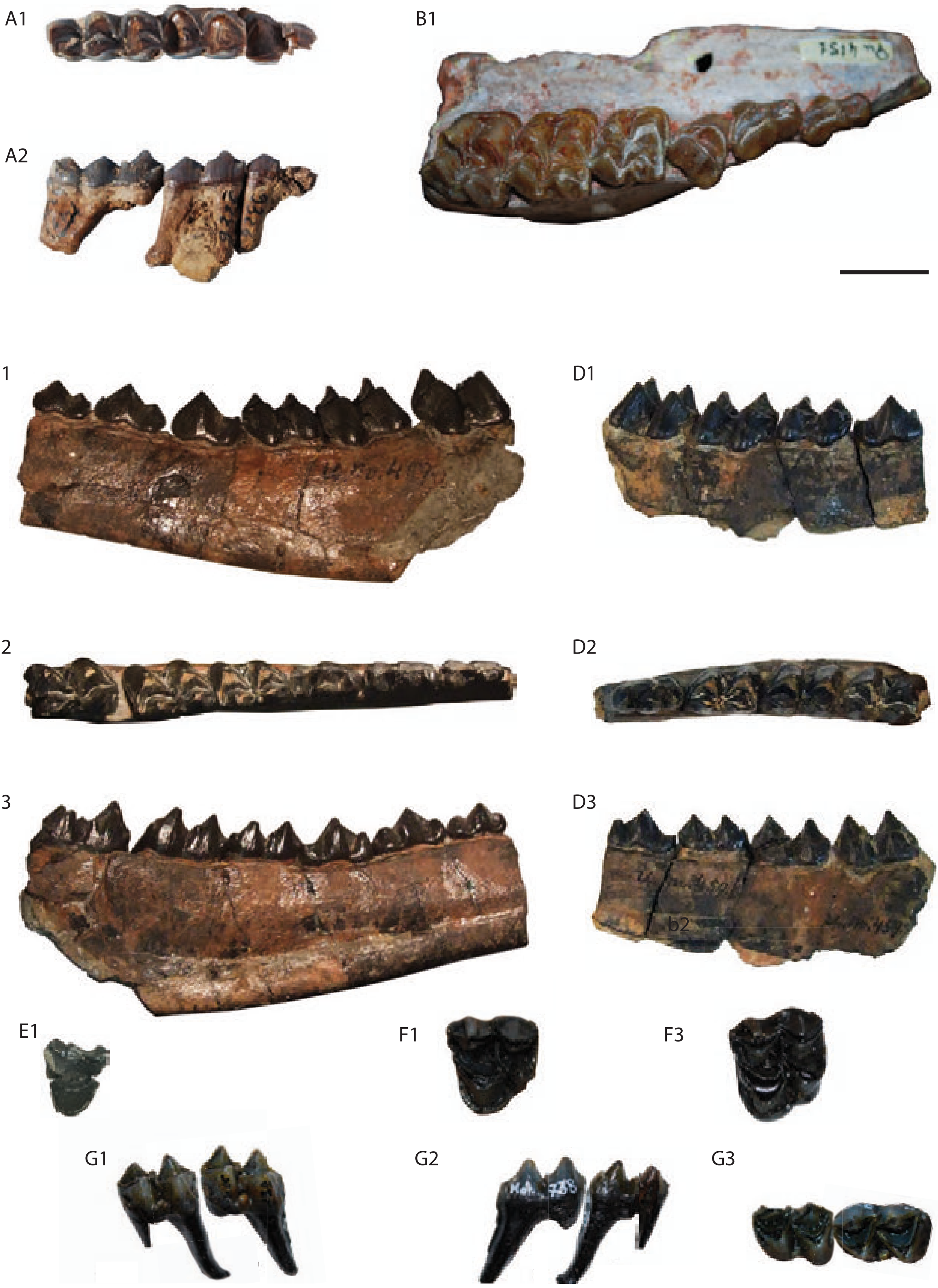
A1
A2
B1
C1
D1
C2
D2
C3
D3
b2
E1
F1
F3
G1
G2
G3

Figure 2 (opposite page): *Mosaicomeryx quercyi* from the old collections from the Phosphorites du Quercy (undated, SW France), Bumbach (mid-Oligocene, Central Switzerland), “Marseille”, and Saint André (mid-Oligocene, SE France). *Scale bar* for all figure 1cm. **A**, “Marseille” (USTL 9326) isolated m1, m2, m3 sen., and m3 sen., occlusal view (1), lingual view (2); **B**, Phosphorites du Quercy (NMHN Qu4151) maxillary with the tooth row P2-M3 sen., occlusal view; **C**, Bumbach (NMB UM459a) fragmentary mandible with the tooth row p2-m3 dext., labial view (1), occlusal view (2), lingual view (3); **D**, Bumbach (NMB UM459b) fragmentary mandible with the tooth row p4–m3 sen., labial view (1), occlusal view (2), lingual view (3); **E**, (NMBe 5017073) P4 sen., occlusal view; **F**, Saint André (NMB Mar667) fragmentary mandible with p3 and fragmentary p4 sen., m1 sen., fragmentary diastema, M2 sen., M3 sen., labial view (1), occlusal view (2), lingual view (3); **G**, Saint André (NMB Mar640) fragmentary mandible with the tooth row m2-3 dext., labial view (1), occlusal view (2), lingual view (3).

Table 1: Dental measurements of *Mosaicomeryx quercyi* from from the Phosphorites du Quercy (undated, SW France), Bumbach (mid-Oligocene, Central Switzerland), “Marseille”, and Saint André (mid-Oligocene, SE France). All measurements are in mm. the first value is the length and the second value is the width.

Localities	**Inventory number**	**P2**	**P3**	**P4**	**M1**	**M2**	**M3**
Quercy	NMHN Qu4151 (Holotype)	9.1/5.1	9.5/ 6.3	6.7/ 8.0	8.2/ 9.6	9.2/ 10.0	10.2/ 11.2
	NMHN Qu4145				10.3/ 11.5	10.9/ 11.4	11.0/ 11.5
	NMHN Qu4146					9.9/ 11.8	10.2/ 11.4
	NMHN Qu4147				8.4/ 10.4	9.5/ 11.0	10.0/ 10.9
	NMHN Qu4149			6.9/ 9.2	9.3/ 10.1	10.2/ 11.3	10.6/ 11.2
	NMHN Qu4150					9.4/ 11.1	9.5/ 10.4
	NMHN Qu4152				9.2/ 10.8	10.5/ 11.8	
	NMHN Qu4153				8.9/	9.9/ 11.2	10.2/ 10.7
	NMHN Qu4154			7.2/ 9.0	9.9/ 10.6	10.9/ 11.3	10.7/ 10.6
	NMHN Qu4155			7.4/ 8.3	9.6/ 10.6	9.9/ 11.1	10.9/ 10.6
	NMB QuA711					9.2/ 10.4	9.2/ 10.0
	NMB QuA644				9.8/ 10.2	10.3/ 10.2	10.1/ 10.5
	NMB QJ80a			6.2/ 8.4	8.4/ 9.8	10.2/ 10.4	10.2/ 10.5
Saint André	NMB Mar667					10.4/ 12.4	
	NMB Mar667						10.5/ 11.6
Bumbach	NMBe 5017073			7.7/8.9			
	n	1/1	1/1	6/6	10/9	14/14	13/13
	Mean	9.1/5.1	9.5/6.3	7.0/8.6	9.2/10.4	10.0/11.1	10.3/10.9
	Standard deviation	-	-	0.53/0.47	0.71/0.57	0.56/0.67	0.51/0.49
		p2	**p3**	**p4**	**m1**	**m2**	**m3**
Bumbach	NMB UM459a	7.7/ 3.5	9.3/ 4.5	9.4/ 4.5	9.0/ 5.9	10.0/ 6.9	/ 6.9
	NMB UM459b			8.9/ 4.5	9.2/ 6.2	10.3/ 6.9	/ 7.0
Saint André	NMB Mar738				9.2/		
	NMB Mar738					10.4/ 6.3	
	NMB Mar667					10.4/ 6.5	
	NMB Mar667			9.0/ 3.9			
	NMB Mar640					10.8/ 6.8	14.6/ 7.2
Marseille	USTL 9326				/ 6.7	12.2/ 7.2	16.3/ 7.2
							16.2/ 7.1
	n	1/1	1/1	3/3	3/3	6/6	3/5
	Mean	7.7/3.5	9.3/4.5	9.1/4.3	9.1/6.3	10.7/6.8	15.7/7.1
	Standard deviation	-	-	0.26/0.35	0.12/0.40	0.79/0.32	0.95/0.13

possesses a big labial rib with a small anterior groove. The P4 has a big lingual cingulum.

The upper molars from the specimens of Saint André (Fig. 2F) possess a huge cingulum around the protocone stopping at the base of the metaconule, such as on the holotype (Fig. 2B). These molars are square. The protocone is large and selenodont. The anterior and posterior basin does not possess neocrista. The preprotocrista joins a strong and slightly curved parastyle. The paracone possesses a strong rib without anterior groove. The paracone and the metacone are selenodont and are not in the same axis. The preprotocrista joins the top of the parastyle. The postprotocrista reaches the premetaconulecrista before its end. The premetacrista finishes by a globular mesostyle. The metacone rib is weak to absent and less and less marked from M1 to M3 when it is present. The postmetacrista joins a well-marked mesostyle, finishing a posterolabial "cingulum" of the metacone on the bigger specimens. The straight posthypocrista joins the base of the metastyle. The metaconule is oblique and becomes very small on M3. Finishing the big cingulum, the metaconule, at its base, possesses a smaller and smaller entostyle from M1 to M3. The prehypocrista is curved and finishes between the metacone and the paracone. The postprotocrista can finish at the level of the prehypocrista or fuse with it and then come back to the paracone to stop within the basin. The posprotocrista never bifurcates.

Metatarsal bones III and IV. The NMB OT3 specimen is complete. These relatively stocky bones possess an unfused distal epiphyse. The condyles are slightly flattened dorsally. The articular facet is weakly developed. The enlarged gulley is distally closed forming a bony bridge.

Discussion. Jehenne (1985, 1987) considered "*Gelocus*" *quercyi* as a large and derived species of *Gelocus*. This species shares with *Gelocus* a lingual cingulum on upper molars. However, this characteristic is symplesiomorphic and can also be observed on the genus *Lophiomeryx* and *Iberomeryx* (Mennecart et al. 2011). The upper molars of *Mosaicomeryx* differ from those of *Gelocus* in being more selenodont, (they are clearly more bunodont on *Gelocus*): the postprotocrista is elongated, curved, and labially oriented whereas this crest is short, straight, and perpendicular to the premetaconulecrista in *Gelocus*. The metaconule is U-shaped and well developed in *Mosaicomeryx* (giving a quadrangular shape to the M3), and not V-shaped as in *Gelocus*. The crowns are generally higher, and the labial cusps are fully-selenodont, not tetrahedral as in *Gelocus communis*. The P4 possesses straight cristae and not concave as in *Gelocus communis* and *Gelocus villebramarensis*. The lingual cusps of the upper premolars of *Mosaicomeryx* are much more salient than those of *Gelocus*. The dental materials previously referred to "*Gelocus*" *quercyi* clearly differs from that of *Gelocus* (*G. communis*, *G. villebramarensis*), and justify the creation of a new generic entity for this species. However, Jehenne (1985, 1987) could have considered the small specimen MNHN Qu4148 as a variability of the population of *"Gelocus" quercyi*. This specimen is clearly reminiscent to *Gelocus* in having bunoselenodont crowns, short and straight postprotocrista, which is perpendicular to the premetaconulecrista, and a reduced metaconule. This specimen has been listed as *Prodremotherium elongatum* in various articles (Engesser & Mayo 1987, Engesser & Mödden 1997). Both genera possess high-evolved molars with extremely simple lower premolars. However, the premolars of *M. quercyi* are clearly shorter than those of *P. elongatum*. The upper molars of *Prodremotherium* are more selenodont than those of *Mosaicomeryx*, but the latter are more selenodont than those of the Eocene Asiatic genus *Notomeryx*. Like in *Notomeryx*, the molars of *Mosaicomeryx* possess a well-developed metastylid, lack a p1, and lack a *Palaeomeryx* fold. Even if the P3 hypocone is less developed on *Mosaicomeryx quercyi* than on *Prodremotherium elongatum*, but more than on *Gelocus communis,* it has a similar shape due to a posterior paracone and relatively laterally compressed salient hypocone. Moreover, *Mosaicomeryx* has a very strong lingual cingulum on its upper molars, which is absent in *Prodremotherium*. *Mosaicomeryx* has smaller premolars and entostyle than *Prodremotherium*. The mesostyle is less globular on *Mosaicomeryx quercyi* than it is on *Prodremotherium elongatum*.

Mosaicomeryx possesses a clear mixture of primitive (huge cingulum, bunoselenodont crown, elongated and simple lower premolars) and derived dental features (elongated and curved cristae, flat metacone rib, strong metastylid). This ruminant, with a strong cingulum on upper molars, does not possess a p1. The lower premolars are simple, without additional cristids (such as the anterior cristid or the anterolingual cristid) and relatively elongated. The molars are selenodont with a well-developed metastylid. Its postcranial remains show metatarsal bones only proximally fused, with a closed metatarsal gulley. All these morphological features allow a generic distinction between the former "*Gelocus*" *quercyi* and other species referred to the genus *Gelocus*. *Mosaicomeryx* shows a transitional stage between the primitive Gelocidae (represented by *Gelocus*) and the Late Oligocene Eupecora (*Dremotherium* or *Amphitragulus*).

Genus ***Prodremotherium*** Filhol, 1877

Type species. *Prodremotherium elongatum* Filhol, 1877 from undated old collections from Quercy (Lot, France)

Further included species. *P. flerowi* Trofimov, 1957; *P. trepidum* Gabunia, 1964.

Diagnosis (after Métais & Vislobokova 2007). The P1 is lost. The P2 and P3 are elongated, with a very weak or no cingulum. There is a long diastema. The upper molars possess a small entostyle. The p1 is absent, with a strong diastema between c and p2. The p4 has a strong metaconid and four crests lingually oriented. There are nether *Palaeomeryx* nor *Dorcatherium* folds on lower molars but a distinct metastylid. The entoconid is transversally compressed and crested anteriorly and posteriorly. The preprotocristid closes trigonid lingually. The ectostylid is always present. The metacarpal bones III and IV are proximally fused. The metacarpal bones II and V are reduced and not functional. The metatarsal bones III and IV are proximally fused, with a metatarsal gulley closed. The astragalus has a transversally extended sustentacular facet and parallel trochleae.

Etymology. «Pro» is the Latin for before, and «dremotherium» is a Ruminantia genus well known in the latest Oligocene/Early Miocene deposits of Europe.

Prodremotherium elongatum Filhol, 1877
(Figs. 3A-C)

1877 v*pars	*Prodremotherium elongatum* n. gen., n. sp. Filhol: 448, pl. 11, 258, 259, 263-268.
1883	*Prodremotherium elongatum* Rütimeyer: 68, pl. VII, figs. 20-21 and pl. VIII, Figs. 30-38.
1896	*Prodremotherium elongatum* Röse & Bartels: 96, figs. 20-21.
1929 v non	*Prodremotherium* sp. Viret: 229, pl. XXXI, figs. 15a, b.
1970	*Prodremotherium* indet. Hartenberger et al.: Tab.3.
1973 v non	*Prodremotherium elongatum* Bonis et al.: 109, Tab. 2(4).
1977 v	*Prodremotherium elongatum* Jehenne: 233, 1 pl.
1985 v	*Prodremotherium elongatum* Jehenne: 75, figs. 12-19.
1987	*Prodremotherium elongatum* Janis: 200, fig. 4.
1987	*Prodremotherium elongatum* Janis & Scott: fig. 11
1987 v pars	*Prodremotherium elongatum* Remy et al.: 188, Tab. 4c.
1995 v	*Prodremotherium elongatum* Martinez & Sudre: fig. H.
1997 v	*Prodremotherium elongatum* Blondel: 576, figs. 2-3.
1997	*Prodremotherium* sp. Hugueney: 426
1998 v	*Prodremotherium elongatum* Blondel: 527.

Holotype. Mandible with the tooth row p2-m3 dext. (Qu4769, coll. MNHN-Paris, Filhol 1877, pl. 11, Figs. 265 and 266).
Paratype. Maxillary with the tooth row P3-M3 dext. (Qu4646, coll. MNHN-Paris, Filhol 1877, pl. 11, Figs. 267 and 268).

Species etymology. Latin for elongated.

Type locality and horizon. undated old collections from Quercy (Lot, France).

Additional localities and biochronologic range of *Prodremotherium elongatum*. Sarèle, Boujac, Cournon, Pech Desse, MP28 (Hartenberger et al. 1970, Remy et al. 1987, Blondel 1997, Hugueney 1997).

Referred material. MNHN Qu4769 mandible with the tooth row p2-m3 dext. (figured by Filhol 1877, pl. 11, Figs. 265 and 266, Jehenne 1985, Fig. 17a), MNHN Qu4640, partial skull of a juvenile with D2-M3 sen. and

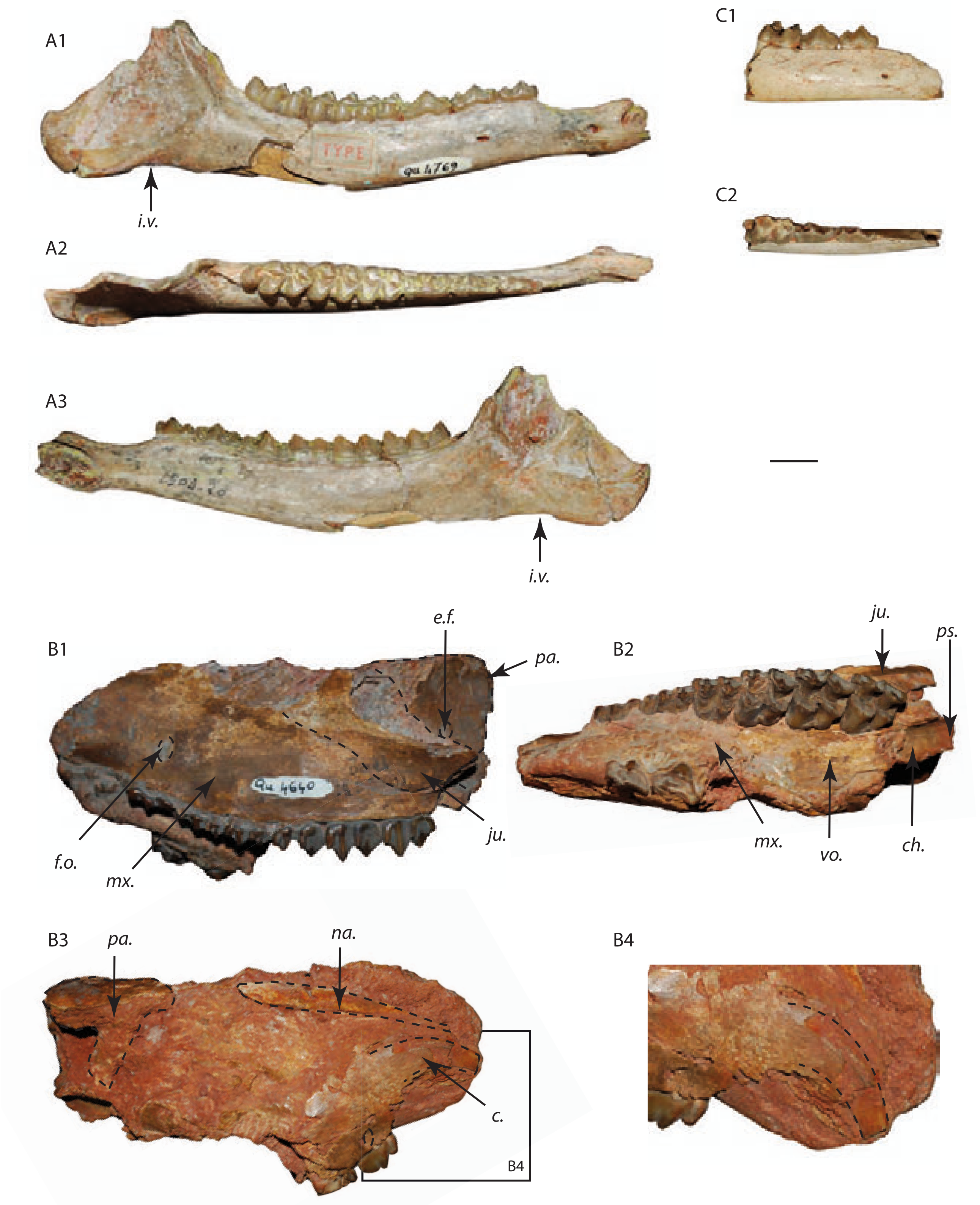

Figure 3: *Prodremotherium elongatum* from the old collections from the Phosphorites du Quercy (undated, SW France). *Scale bar* for all figure 1cm. **A**, Phosphorites du Quercy (MNHN Qu4769) mandible with the tooth row p2-m3 dext., labial view (1), occlusal view (2), lingual view (3); **B**, Phosphorites du Quercy (MNHN Qu4640) partial skull of a juvenile with D2-M3 sen. and C-P3 dext., left view (1), occlusal view (2), right view (3), magnification of the upper canine (4); **C**, Phosphorites du Quercy (MNHN Qu4415) fragmentary mandible with the tooth row p3-m1 dext., labial view (1), occlusal view (2). *c.*, canine; *ch.*, choanes; *e.f.*, *ethomoidal foramena*; *f.o.*, *foramena ovalis*; *i.v.*, *incisura vasorum*; *ju.*, jugal bone; *mx.*, maxillary bone; *na.*, nasal bone; *pa.*, parietal bone; *ps.*, presphenoid; *vo.*, vomer.

C-P3 dext., MNHN Qu4596 partial skull with P3-M3 dext. (figured by Jehenne 1977, Jehenne 1985, Figs. 12-14).

Diagnosis (adapted from Jehenne 1985). This medium size ruminant possesses 3 upper and lower premolars. They are elongated. The upper molars are quite elongated giving a square shape to these teeth. They are well selenodont, with a paracone and a metaconule few conical and cristae elongated and curved. The skull is hornless. The cranium is narrow and elongated. The anterior part of the orbit is located behind the anterior part of the M2. The upper canines are traguloid-like. They are highly curved and laterally compressed.

Description

Mandible. The type specimen of *Prodremotherium elongatum* is an incompletely preserved mandible. The mandibular bone is straight below the tooth row p2-m2 and becomes concave at the level of the m3 (Fig. 3A). The *incisura vasorum* is well marked and enlarged. Its position can vary from just behind the m3 to far back from it, which is the most frequent case. The angular process is well marked and salient. The quite enlarged diastema begins with a constriction just on the anterior part of the p2. The mandible interalveolar crest is straight until the symphysis and becomes highly concave until the canine.

Skull MNHN Qu4640 (Fig. 3B). The specimen MNHN Qu4640 is a partly preserved skull of a juvenile of *Prodremotherium*, which has never been described before. Only the left side of the skull is preserved, and the facial, temporal, and occipital parts are lacking, so that no observation on the absolute length of the skull can be made. The lacrimal and postorbital areas are damaged, and the basicranium is missing. Interestingly, the skull preserves left deciduous teeth and an erupting upper canine. Although the posterior part of the cranium is missing, its left anterior part is well preserved (Fig. 3B1). The orbital area and the maxillary bone are well preserved. The lower part of the orbit is quadrangular in shape. Its anterior border reaches the mid-length of M2. The tooth row is complete with D2-M3. However, the upper part of the maxillary is broken and the anteorbital vacuity cannot be observed. There is no lacrimal fossa on the skull. A large *foramena ovalis* lies at the level D2. The anterior part of the jugal is preserved. The orbitasphenoid and presphenoid are present. The supraorbital area is highly vascularised such as on the other described skull of *Prodremotherium elongatum* (MNHN Qu4596, Jehenne 1977) and *Dremotherium feignouxi* (MNHN SG4303, Sigogneau 1968). The inner orbit is partly preserved on the parietal bones, and seems to possess only one large *lachrymal foramena* and a big *ethmoidal foramena*. The right part of the skull MNHN Qu4640 is badly preserved, and only a partial maxilla with P2 and P3 can be observed (Fig. 2B3). The left *foramena ovalis* is close to the adult check teeth, proving the partial destruction of the maxillary bone. The tusk-like canine is short and highly curved (Fig. 3B4). Its section is oval and laterally compressed. The nasal bone is elongated, straight, and narrow. The anterior left neocortex and olfactory bulb cavities are preserved but not prepared.

The deciduous premolars of MNHN Qu4640 are badly preserved and totally worn (Fig. 3B2). The D4 is trapezoidal and shows the same and smaller than M1. The P2 and P3 are almost similar in size and shape. The P3 possesses a large hypocone giving it a more triangular shape. The hypocone is posterior to the high paracone. The posthypocrista of the P2 is curved and elongated: it is straight and short on P3. The parastyle is enlarged on P2. The metacone is pinched. The paracrista are straight. The upper molars are square in outline and exhibit four main cusps. The protocone is large and crescentiform. Contrary to the anterior basin, the posterior basin can possess a neocrista. The parastyle is strong mesially salient. The postprotocrista is arc like, and it joins the distal bifurcation of the premetaconulecrista. The paracone possesses a strong labial rib without anterior groove. The paracone and the metacone are crescentiform and the metacone is slightly shifted labially with respect to the paracone. The premetacrista joins a columnar and globular mesostyle. The labial rib of the metacone is weak and it becomes reduced from M1 to M3. The straight postmetaconulecrista joins the base of the postmetacrista. The metaconule is oblique and is reduced in size on M3. The entostyle lying on the mesio-lingual side of the metaconule tends to become smaller from M1 to M3. The premetaconulecrista is curved and transversely oriented to join the labial wall between the metacone and the paracone.

Discussion. In regard to the morphology and size of its teeth, MNHN Qu4640 clearly belongs to *Prodremotherium elongatum*. This is the first time that a canine of *Prodremotherium* is found associated with a tooth row. This canine is not elongated and sabre-like as in *Dremotherium*, but rather shows a shorter and highly curved morphology as in traguloids.

The skull MNHN Qu4640 possesses a better-preserved anterior part than the adult MNHN Qu4596, described by Jehenne (1977). The skull of *Prodremotherium* is close to that of *Dremotherium*, including the neotype MNHN SG9660 described by Sigogneau (1968). The supraorbital area of the frontal bones is narrow and parallel to the axis of the skull on *Prodremotherium* and *Dremotherium* whereas this bone is fairly enlarged transversely, giving a triangular shape of this area on *Bachitherium* or *Floridameryx*. Thus, the orbits have different shapes: it is rounded on *Bachitherium* and *Floridameryx*, and more square-like on *Prodremotherium* and *Dremotherium.* The postorbital process of the frontal bone is highly constricted and the frontal crest extends anteriorly to the cranium on *Prodremotherium* and *Dremotherium* whereas this process is wide posteriorly and the frontal crest occurs more posteriorly, within the cranium, on *Bachitherium*. Moreover, *Bachitherium* and *Dremotherium* possess a larger cranium than *Prodremotherium*. As suggested by Jehenne (1977), the skull of *Prodremotherium* shows close affinities with that of *Dremotherium*, but several features appear to be more primitive (e.g., structure of the canine, apparent lack of lacrimal fossa).

6.4 Cladistic analysis

We propose three cladograms. The first one is a manual one and the other two are based on cladistic analyses. A range of 35 dental, mandibular, and postcranial features was selected (Annex 1), resulting from both direct observation and literature (Martinez & Sudre 1985, Janis & Scott 1987, Geraads et al. 1987, Blondel 1997, Vislobokova & Daxner-Hock 2002, Métais & Vislobokova 2007). The ingroup taxa cover the most documented species of ruminants known in Europe and Asia during the Oligocene. The outgroup is represented by *Lophiomeryx chalaniati*, which belongs to the most primitive ruminants in Europe (Métais & Vislobokova 2007). All characteristics are equally weighted without any ordering. The phylogenetic reconstruction is provided by TNT (Goloboff 1999). Convergences and reversion are allowed. The branch and bound algorithm is applied to find the optimal solution of the analysis. The most parsimonious tree is found by using a randomized stepwise addition.

The cladistic analysis generated 21 most parcimonious trees. Two trees are proposed in figure 5: the strict consensus (Fig. 5.1) and the majority rule consensus (Fig. 5.2). The topology of the strict consensus of the analysis supports that *Mosaicomeryx* and *Prodremotherium* do not belong to the Gelocidae (Fig. 5). These two genera are associated in an isolated branch and are the sister group of the Eupecora (represented by *Dremotherium* and *Amphitragulus*) and belong to the same clade. This intermediate position of *Prodremotherium* had already been shown in many phylogenies (Fig. 4). The fact that *Prodremotherium* and *Mosaicomeryx* are no Gelocidae is here accentuated by the position of the Bachitheriidae as sister group of the Eupecora and *Mosaicomeryx*/*Prodremotherium*. *Gelocus* is one of the most primitive ruminants considering Figure 5. This cladogram is consistent with our knowledge of the ruminant evolution. The oldest Lophiomerycidae are known during the Eocene (Guo et al. 2000, Métais et al. 2001) and are now considered as one of the most primitive families of ruminants (Métais & Vislobokova 2007). The true Gelocidae are only known from the Early Oligocene (see the following discussion). The Bachitheriidae appeared in Europe during MP23. *Mosaicomeryx* and *Prodremotherium* are known from MP25 to MP28. The Eupecora seem to have appeared during MP28, with the genera *Amphitragulus* and *Dremotherium*. The systematic position of the monotypic genus family Bachitheriidae is a little problematic. The phylogenetic relationships of *Bachitherium* with other Oligocene ruminants remain ambiguous, or at least not consensual in the literature (Fig. 4). This “moving” position of the monogeneric Bachitheriidae is probably linked to a convergent evolution of postcranial and dental features. *Bachitherium* is clearly primitive in retaining a caniniform p1 and a traguloid type of the astragalus (the distal and proximal pulleys are not aligned), but the selenodonty of the molars and the fusion of the carpal

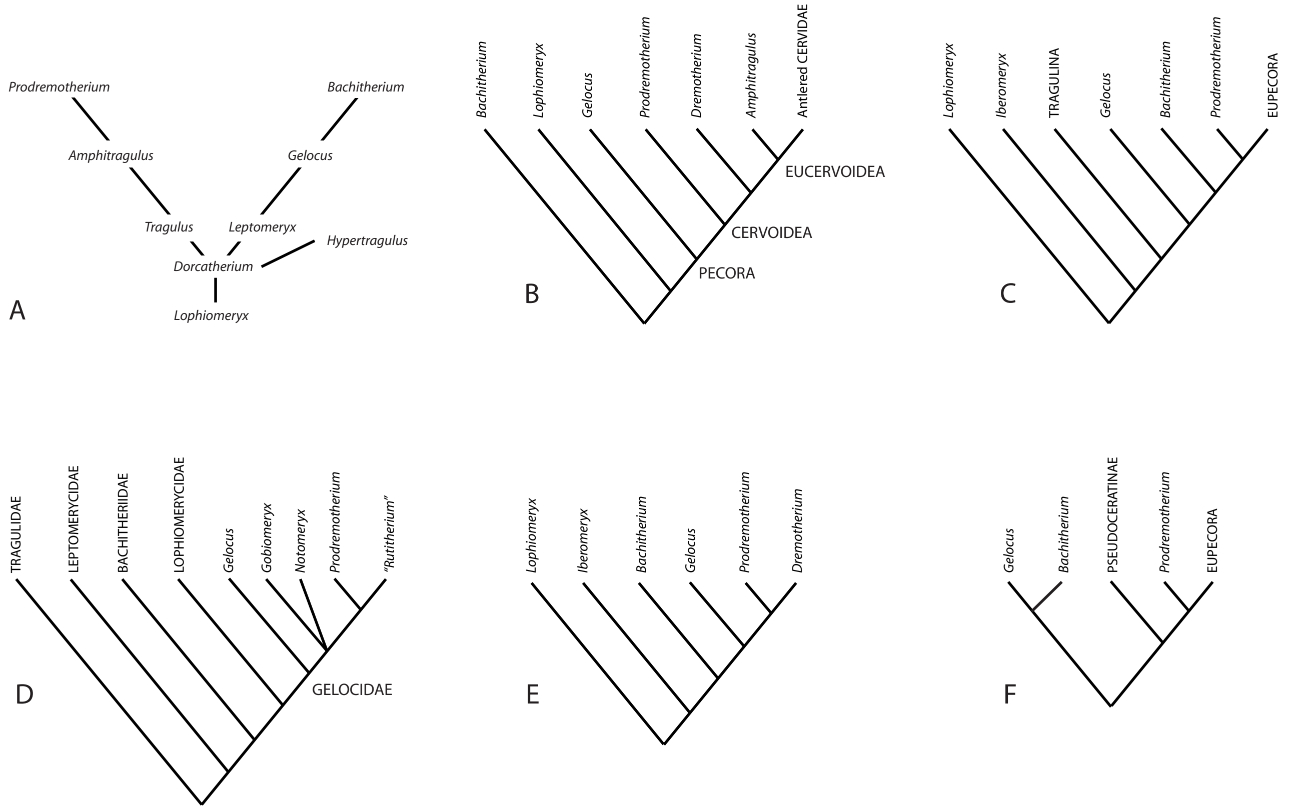

Figure 4: History of ideas on phylogenetic position of *Prodremotherium*. **A**. View of Cope (1887) with a linear evolution of various genera from the Oligocene and Miocene of Europe and Northern America. **B**. Composite diagram incorporating the view of Janis & Scott (1987). **C**. Simplified diagram of the view of Geraads et al. (1987). "Tragulina" includes the Leptomerycidae, with *Leptomeryx*, and the actual Tragulidae. "Eupecora" includes *Dremotherium*, and the actual ruminant families excluding the Tragulidae. **D**. Simplified diagram of the view of Janis (1987). "Tragulidae" includes the genus *Dorcatherium*. "Leptomerycidae" includes the genus *Leptomeryx*. "Bachitheriidae" includes the genus *Bachitherium*. "Lophiomerycidae" includes the genera *Lophiomeryx*, *Iberomeryx*, and *Cryptomeryx*. **E**. View of Blondel (1997) including only Oligocene European ruminants. **F**. View of Webb (2008). "Pseudoceratinae" includes *Pseudoceras* and *Floridameryx*. "Eupecora" includes *Dremotherium*.

bones probably result from convergent evolution. The (mis-) interpretation of this convergent features certainly explains the variety of trees published so far (Fig. 4), most of them being hand-made trees.

6.5 Discussion

6.5.1 Phylogeny

The Gelocidae classically contain numerous primitive Laurasian ruminant taxa, such as *Prodremotherium, Gelocus*, *Paragelocus*, *Pseudogelocus*, *Pseudomeryx*, *Floridameryx*, *Pseudoceras*, *Notomeryx*, *Gobiomeryx*, *Eumeryx*, *Rutitherium* (Janis 1987, Janis & Scott 1987, Webb 2000, Métais & Vislobokova 2007). The principal features unifying all those taxa are mostly symplesiomorphic such as brachyodont teeth, a small p1 separated from the p2 by a small diastema, a small metaconid on the premolars without postmetacristid, an incomplete postentocristid, presence of a cingulum/cingulid on molars, and a small metaconule on M3 (Janis 1987, Janis & Scott 1987). Bouvrain et al. (1986) reassessed the material referred to the genus *Rutitherium* and concluded that the type specimen of Filhol (1877) is in fact a synonym of *Gelocus communis* and the specimens from Pech Desse referred to *Rutitherium* by Sudre (1984) likely belong to *Amphitragulus quercyi*. *Mosaicomeryx* and *Prodremotherium* possess many synapomorphic features, which put them apart from Gelocids. The molars of *Gelocus* are clearly more bunodont than those of *Mosaicomeryx* or *Prodremotherium*. The upper molars of *Gelocus* display a smaller metaconule, giving them a more and less subtriangular outline; the cingulum is deep and also present on *Mosaicomeryx quercyi*. However, the retention of a lingual cingulum

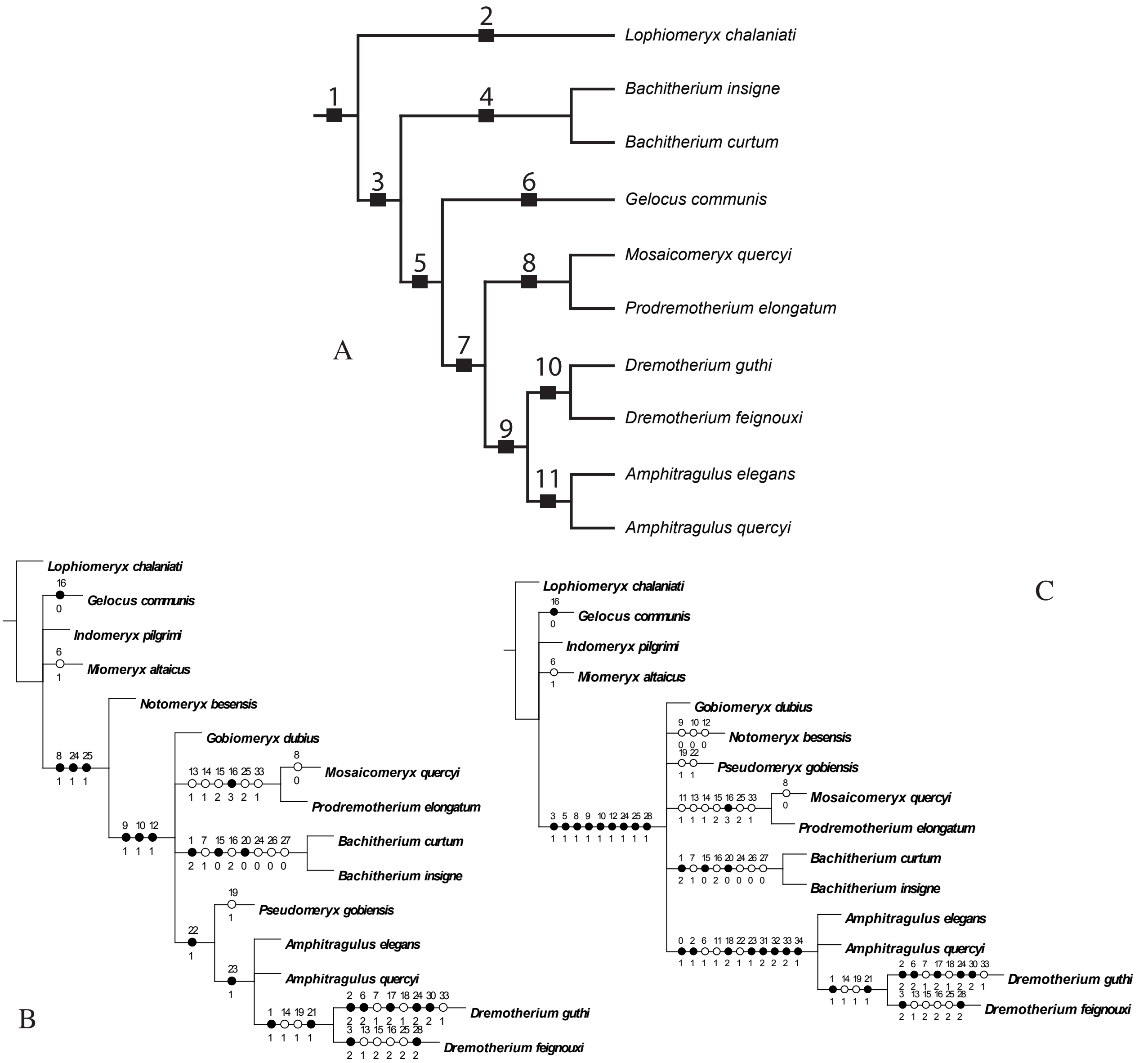

Figure 5: **A**. Manual cladogram showing hypothesized relationship within Oligocene-Early Miocene European ruminants. Main characteristics (defining each taxa) at nodes (after Martinez & Sudre 1985, Janis & Scott 1987, Geraads et al. 1987, Blondel 1997, Métais & Vislobokova 2007, this study). (1) Ruminantia: reduction and loss of upper incisors, inclusion of incisiform lower canines in incisor row, fusion of cuboid and navicular. (2) Lophiomerycidae: orbit apparently open posteriorly, small and noninflated auditory bullae, fenestrae vestibuli small, promontory sulcus absent, trigonid of lower molar open anterolingually, metatrsals separated. (3). Unnamed clade: intermediate fusion of the metapodial bones, lost of the crest at the cubo-navicular boundary, lost of the medial boundary sustentacular facet crest. (4) Bachitheriidae: postorbital bar formed mostly from jugal, ventral part of the mandible straight, bifurcated paracone of P4, large caniniform p1, talonid p3 and p4 consist of two parallel walls, metatarsals III and IV incompletely fused. (5) Pecora: astragalus shorter with parallel sides; stapedial artery lost; subarcuate fossa reduced; trapezium absent; fore and hind limbs almost equal in length. (6) Gelocidae: postorbital bar mostly from frontal, fenestra vestibule large, metatarsals III and IV fused with open gulley. (7) Unnamed clade: metastylids on lower molars, "*Dorcatherium* fold" totally lost, metaconule well developed, elongated of the postprotocrista. (8) Mosaicomerycidae: lost of p1, metatarsals III and IV proximally fused with an intermediately close gulley. (9) Eupecora: saberlike upper canine, "*Palaeomeryx* fold" in lower molars, premolars short, p4 with an elongated entocristid and a postmetacristid, central metapodial bones totally fused. (10) "Moschina": laterally enclose, subcentral tymponohyal vagina partially formed, remnant metatarsal bone V proximally fused. (11) "Eucervoidea": double lacrimal office on dorsal rim of orbit, posterior tuberosity on metatarsus. **B**. Strict consensus cladogramm (provided by TNT) of Eurasian ruminants from the Eocene to the Early Miocene (*Amphitragulus*, *Bachitherium*, *Dremotherium*, *Gelocus*, *Gobiomeryx*, *Indomeryx*, *Lophiomeryx*, *Miomeryx*, *Mosaicomeryx*, *Notomeryx*, *Prodremotherium*, *Pseudomeryx*) using the Annex 1 characteristics dataset. **C**. Majority rule consensus (provided by TNT) of Eurasian ruminants from the Eocene to the Early Miocene (*Amphitragulus*, *Bachitherium*, *Dremotherium*, *Gelocus*, *Gobiomeryx*, *Indomeryx*, *Lophiomeryx*, *Miomeryx*, *Mosaicomeryx*, *Notomeryx*, *Prodremotherium*, *Pseudomeryx*) using the Annex 1 characteristics dataset.

on upper molars is a symplesiomorphic feature that is also present in the Oligocene traguloid *Lophiomeryx* and *Iberomeryx*. The postprotocrista is curved and connects the premetaconulecrista near the centre of the molar: it is a derived feature shared by *Prodremotherium* and *Mosaicomeryx*. In *Gelocus,* the postprotocrista is short, straight, and extends labially, but rather tends to join the mesial wall of the metaconule. This configuration of the upper molars is similar to that of Lophiomericidae or Tragulidae. The mesostyle is more globular and less salient in *Mosaicomeryx* than on *Gelocus*. The hypocone of P3 is transversally compressed, lingually salient and posterior to the paracone in *Prodremotherium*. This P3 pattern is less prominent on *Mosaicomeryx*, but remains much more similar to *Prodremotherium* than to *Gelocus*. The premolars of *Mosaicomeryx* are much smaller than those of *Prodremotherium*. Unlike *Gelocus*, the p1 is lost in *Mosaicomeryx* and *Prodremotherium*. This simplification of the dentition can be more complete with the disappearance of the p2 (Fig. 3C).

The metatarsal bones are partly fused with a close gully on *Mosaicomeryx* and *Prodremotherium*. These genera display a mosaic of primitive (partly fused metapodial bones) and derived features (loss of p1). It is generally admitted that the Gelocidae represent a paraphyletic to polyphyletic assemblage of genera, which share some "protopecoran" features without any real autapomorphy (Geraads et al. 1987, Janis 1987, Janis & Scott 1987, Métais & Vislobokova 2007). *Prodremotherium elongatum* and *Mosaicomeryx quercyi* clearly do not belong to the Gelocid family, as it is currently "defined" (Fig. 5). Many authors suggested putting *Prodremotherium* apart from this family. For example, Janis (1987) explains that *Prodremotherium* is something different from the classical Gelocidae (i.e., *Gelocus*). However, she considered the "pre-pecora" morphological grade represented by Gelocidae as a useful tool for description, pending additional fossil data. Janis & Scott (1987) based on the presence of a closed metatarsal gully to argue that gelocids represent basal Cervoidea. However, these postcranial features may be highly variable in taxa other than Cervidae (Janis & Scott 1987, Hassanin & Douzery 2003) and may therefore be of limited interest for taxonomical purposes.

Prodremotherium is classically considered as the potential "ancestor" of *Dremotherium* (Filhol 1877, Jehenne 1977, 1985, 1987). However, *Prodremotherium* like *Mosaicomeryx* lack a p1. According to Jehenne (1987), 80% of the specimens referable to *Dremotherium guthi* known in latest Oligocene retain a p1, and some rare Aquitanian specimens of *Dremotherium feignouxi* from Montaigu-le-Blin in Central France also preserve a p1 (personal observation). Therefore it appears difficult to support the hypothesis of a direct phylogenetic link between *Prodremotherium* and *Dremotherium*. The structure of the p4 is quite similar on both *Gelocus,* and *Prodremotherium*, suggesting this morphology to be plesiomorphic. The p4 is much more complex and compressed in *Dremotherium* and *Amphitragulus*. The Upper Middle Eocene to Late Eocene Chinese Ruminant *Indomeryx*, *Notomeryx* and *Gobiomeryx* show close affinities with *Prodremotherium* (Guo et al. 1999, Guo et al. 2000). Like *Prodremotherium* and *Mosaicomeryx*, the specimens of *Notomeryx* from the latest Middle Eocene do not retain a p1 (V11483.1, Guo et al. 1999, Fig. 2). Guo et al. (1999) underline the necessity to split the Gelocidae into two families; the Gelocidae *sensu stricto* (with the genus *Gelocus*, *Pseudogelocus* and *Paragelocus*) and the new family Prodremotheriidae, in which they include *Prodremotherium* Filhol, 1877, *Indomeryx* Pilgrim, 1928, *Notomeryx* Qiu, 1978, and *Gobiomeryx* Trofimov, 1957. However, the dental morphology of *Indomeryx* is more primitive than the Middle Eocene genus *Archaeomeryx*, and should have been considered as a basal form among the ruminants (Métais et al. 2000). In add the monophyly of this group is not supported by our cladistic analysis (Fig. 5).

The oldest fossils referred to *Prodremotherium* are from Tchelkar-Teniz (*P. flerowi* MP22-24, Kazakhstan) and Benara (*P. trepidum* MP23, Georgia) (Trofimov 1957, Gabunia 1964, Vislobokova 1997, Lucas & Emry 1999, Métais & Vislobokova 2007). No direct observation by the authors allowed testifying the attribution to this genus of these Asian species. According to Gabunia (1968), the metapodial bones are totally fused in *P. trepidum* from Benara, which is not the case of the European species (Blondel 1997, this article). In addition, *P. trepidum* (MP23) displays a more complex structure of p4 than the *P. elongatum* (MP28) (Gabunia 1968). It is possible that the Georgian species belong to another genera.

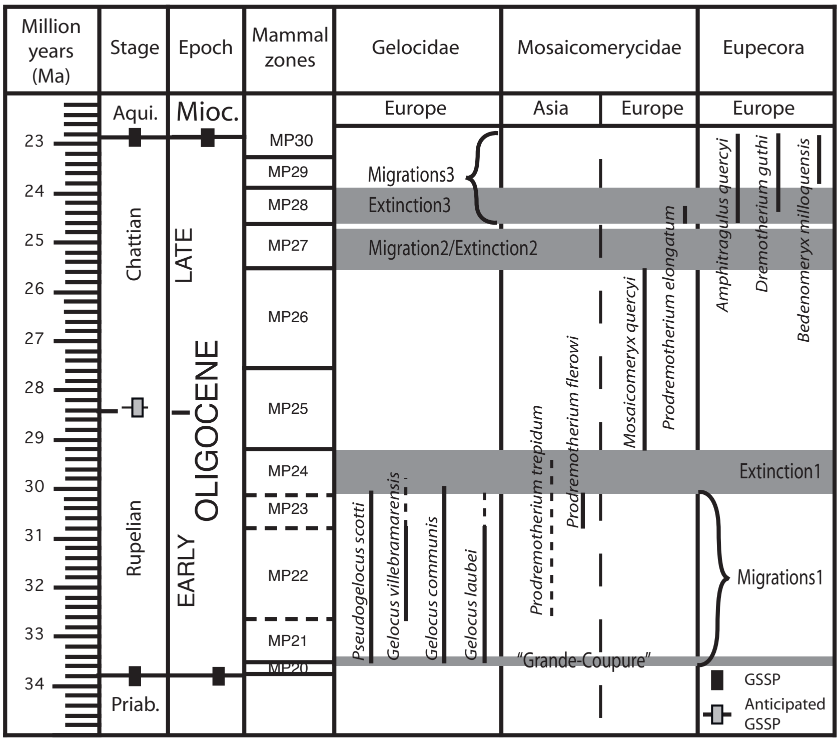

Figure 6: Biostratigraphy of the Gelocidae and Mosaicomerycidae. The chronostratigraphy and Mammal reference levels are based on Berger (2011). Migration and extinction events correspond to the majors European ruminant communities changes during the Oligocene. The time interval (ca. 33.6–33.4 Ma) of the "Grande-Coupure" event (Stehlin 1910) is based on the high-resolution stratigraphy in the Belgian Basin after Hooker et al. (2004, 2009). The biochronostratigraphical ranges are revised in accordance with Jehenne & Brunet 1992, Sudre & Blondel (1996), Biochrom. et al. (1997), Engesser & Mödden (1997), Vislobokova (1997), Guo et al. (1999), Lucas & Emry (1999), Ménouret & Guérin (2009), Vianey-Liaud & Schmidt (2009).

6.5.2 Biostratigraphy

Figure 6 illustrates a temporal and geographic range of the taxa discussed above. *Prodremotherium elongatum* is relatively rare in the Oligocene localities of Europe. The only well-dated locality yielding this taxon is Pech Desse from the Quercy, MP28 (Martinez & Sudre 1985, Remy et al. 1987, Blondel 1997). It has been tentatively reported in Cournon, Boujac and Sarèle in France (Hartenberger et al. 1970, Hugueney 1997). The Sarèle and Boujac localities are contemporaneous (Hartenberger et al. 1970) and have been dated either to MP27 (Biochrom. et al. 1997), or to MP28 (Hartenberger et al. 1970). Bonis et al. (1973), Jehenne (1987), and Jehenne and Brunet (1992) mentioned the presence of *Prodremotherium* in older localities (La Plante 2, Mas de Got, and Roqueprune 2). However, the fossils from La Plante 2 have been incorrectly determined, and confused with *Bachitherium curtum* (Blondel 1997). It could have been the same for the other localities. The ruminants from Bumbach, Saint André, and "Marseille" allow a clear distinction between *Prodremotherium elongatum* and *Mosaicomeryx quercyi*. Looking on the collections of the Universty of Lyon, the "Marseille" locality could have been in fact the Saint Henri locality. All these localities are correlated to MP25 and MP26 (Engesser & Mödden 1997, Biochrom et al. 1997). *Prodremotherium elongatum* has also been reported from Saint Géry (Tarn, France), which is stratigraphically in the Stampian *sensu stricto* deposits (Cavaillé 1971), a local stage corresponding to the late Rupelian (Foucault & Raoult 2001). Likewise, *Prodremotherium* cf. *elongatum* is reported from les Milles (Repelin 1916). These entire occurrences are consistent with an earlier occurrence (MP25-26) of *M. quercyi* than previously thought. In La Sauvetat and Antoingt, also correlated to MP25 (Hugueney 1997), *Dremotherium* sp. or *Dremotherium feignouxi* are reported (Giraud 1902, Lavocat 1951, Ginsburg 1967, Hugueney 1997). Elsewhere in Europe, *Dremotherium* first appeared during the late Chattian with the species *Dremotherium guthi* (Jehenne 1985, 1987, Blondel 1997), *Dremotherium feignouxi* being limited to the Aquitanian (Becker et al. 2010). These supposed early occurrences of *Dremotherium* may result from wrong identification of specimens that may actually be *Mosaicomeryx quercyi*, but this assumption requires further studies. Likewise, Early Oligocene occurrences of *Prodremotherium* species in several poorly sampled Asian localities remain fairly doubtful, and would require further geochronological evidences (Métais & Vislobokova 2007).

6.5.3 Evolution of the family

Mosaicomeryx and *Prodremotherium* probably arrived from Asia to Western Europe by the mid-Oligocene. Close relatives to these genera are reported in the Late Eocene of Asia (*Notomeryx*), but the arrival of *Mosaicomeryx and Prodremotherium* in Western Europe does not seem to have occurred during the "Grande-Coupure" (Fig. 6, Migrations1) as for Gelocidae (*sensu* Guo et al. 1999), and little later for the Tragulidae and Lophiomerycidae. The first occurrence of Mosaicomerycidae in Europe seems to be correlated with a major phase of Oligocene mammalian turnover in Europe, which corresponds to the definitive disappearance of *Gelocus* (Fig. 6, Extinction1), Tragulids (Mennecart et al. 2011), and the speciation of the Lophiomerycidae (Brunet & Sudre 1987). This could be related to climate changes (Oi2 glaciations, see Pekar et al. 2006). Some authors suggested that *Gelocus* survived until the Early Miocene in Africa and Asia with the species "*G.*" *whitworthi* and "*G.*" *gajensis* (Pilgrim 1912, Hamilton 1973, Métais & Vislobokova 2007). However, we agree with Métais et al. (2009) and Cote (2010) that "*G.*" *whitworthi* and "*G.*" *gajensis* do not belong to the *Gelocus* genus due to the presence of a double postentocristid on the former and extremely primitive lophiomerycid features on the other. The disappearance of the Mosaicomerycidae in Europe corresponds to the main phase of faunal renewal during the Oligocene (see Fig. 6, Migrations3/Extinction3; Jehenne & Brunet 1992, Mennecart et al. 2012). During this turnover, *Lophiomeryx* and *Bachitherium* are replaced by the first European Eupecora *sensu* Fig. 5a, such as *Dremotherium* and *Amphitragulus* (Jehenne 1987, Blondel 1997, Mennecart et al. 2012). This turnover can also be observed within the rodents (Vianey-Liaud et al. 1991), the Cainotheriidae (Berthet 2003, Blondel 2005), and the Anthracotheriidae with the first appearance of *Microbunodon* in Western Europe (Lihoreau et al. 2004, Scherler 2011). As suggested by Mennecart et al. (accepted), this faunal turnover could also be due to a climatic event since it correlates with Late Oligocene global warming recorded in the marine realm (Zachos et al., 2001). The postcranial remains of *Mosaicomeryx quercyi* suggest that this animal lived in wooded area (Hiard 2010), whereas more open habitat is argued for *Prodremotherium elongatum* (Blondel 1998). The analysis of the entire mammalian communities corroborates this shift toward more open and grassy habitats during MP27-28 (Legendre 1989, Vianey-Liaud 1991, Blondel 1998, Hiard 2010).

6.6 Conclusion

The description of new fossil material and the reassessment of the material previously referred to *Gelocus quercyi* leads us to propose a new genus *Mosaicomeryx* for this species. Previously assimilated into the Gelocidae or Prodremotheriidae, we have shown the necessity to rename this family into Mosaicomerycidae. This family, which presents a modular evolution, should have been considered as the sister group of the Eupecora and permits to improve the understanding of the global ruminant evolution. The study of a new skull of a juvenile *Prodremotherium* sheds light on the nonascendance between this genus and *Dremotherium*. Defining these specimens in well-dated localities permits to have a good idea about the biostratigraphic ranges of *Mosaicomeryx quercyi* (MP25-26) and *Prodremotherium elongatum* (MP28) in Europe. These time intervals seem to correspond to the major climate changes during this period: the glaciations Oi2 and the Late Oligocene warming.

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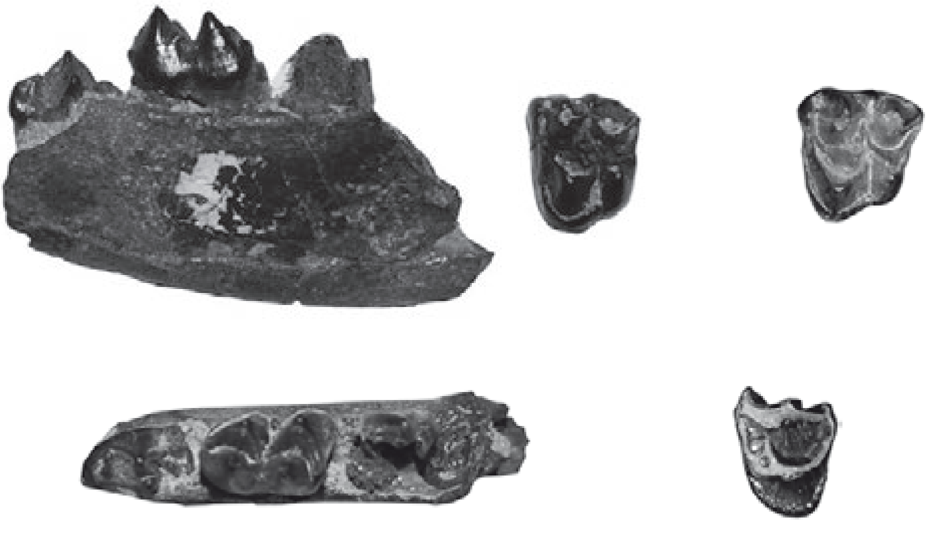
Annex 1

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**
Lophiomeryx chalaniati	?	?	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bachitherium curtum	0	2	0	1	1	1	0	1	1	1	1	0	1	0	0	0	2	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0
Bachitherium insigne	0	2	0	1	1	1	0	1	1	1	1	0	1	0	0	0	2	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0
Gelocus communis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	1	0	1	1	0	1	0	0
Mosaicomeryx quercyi	?	?	?	1	0	1	0	0	0	1	1	1	1	1	1	2	3	0	1	0	1	0	0	0	1	2	1	?	?	?	?	?	1	1	0
Prodremotherium elongatum	0	0	0	1	0	1	0	2	1	1	1	1	1	1	1	2	3	0	1	0	1	0	0	0	1	2	1	1	1	1	1	1	1	1	0
Dremotherium guthi	1	1	1	2	1	1	1	2	1	1	1	1	1	1	0	1	1	1	2	1	1	1	1	1	1	2	1	1	?	1	1	2	2	2	1
Dremotherium feignouxi	1	1	1	2	1	1	1	2	1	1	1	1	1	1	1	2	2	1	2	1	1	1	1	1	1	2	1	1	2	1	1	2	2	2	1
Amphitragulus elegans	1	0	1	1	1	1	1	2	1	1	1	1	1	0	0	1	1	1	2	0	1	0	1	1	1	1	1	1	1	1	1	2	2	2	1
Amphitragulus quercyi	1	0	1	1	1	1	1	2	1	1	1	1	1	0	0	1	1	1	2	0	1	0	1	1	1	1	1	1	?	1	1	2	2	2	1
Gobiomeryx dubius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	1	?	?	?	?	?	?	?	?
Notomeryx besensis	?	?	?	?	?	?	?	?	1	0	0	0	0	0	0	?	?	?	?	0	1	0	0	0	1	1	1	?	?	?	?	?	?	?	?
Indomeryx pilgrimi	?	?	?	?	?	?	?	?	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	0	0	0	1	?	?	?	?	?	?	?	?
Miomeryx altaicus	?	?	?	0	0	0	1	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pseudomeryx gobiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	0	1	0	1	1	1	?	?	?	?	?	?	?	?

Upper tooth row
1 Curve of the upper canine
(**1**) strong; (**2**) weak
2 Section of the upper canine on its half-high
(**1**) ovoid; (**2**) triangular; (**3**) circular
3 Size of the tusklike canine
(**1**) moderately elongated; (**2**) saberlike
4 Tooth crown
(**1**) bunoselenodont; (**2**) selenodont; (**3**) well-selenodont
5 Upper premolar
(**1**) elongated; (**2**) shortened
6 P3 hypocone size
(**1**) small; (**2**) big
7 Direction of the protocone on P3
(**1**) posteriorly situated and directed; (**2**) centrally situated and lingually directed
8 P4 cingulum
(**1**) present; (**2**) weak; (**3**) absent
9 Upper molars lingual cingulum
(**1**) present; (**2**) absent
10 Postprotocrista length
(**1**) short; (**2**) long
11 Postprotocrista
(**1**) straight; (**2**) curved
12 Metaconule size on M3
(**1**) small; (**2**) well-developed
13 Entostyle
(**1**) absent; (**2**) present
14 Premetaconulecrista
(**1**) simple; (**2**) bifurcated
Lower tooth row
15 p1
(**1**) present; (**2**) absent
16 p1
(**1**) tusklike; (**2**) leaflike; (**3**) absent
17 Diastema p1-p2
(**1**) distant to p2 by a short diastema; (**2**) coalescent to p2; (**3**) distant to p2 by a long diastema;
(**4**) absent
18 p2 and p3
(**1**) elongated; (**2**) shortened
19 p4 entocristid
(**1**) short; (**2**) elongated
20 Anterior bifurcation of the protoconulid
(**1**) absent; (**2**) present
21 Metaconid on p4
(**1**) absent; (**2**) present
22 Premetacristid on p4
(**1**) absent; (**2**) present
23 Postmetacristid on p4
(**1**) absent; (**2**) present
24 Molars *Palaeomeryx* fold
(**1**) absent; (**2**) present
25 Molars metastylid
(**1**) absent; (**2**) present
26 Molars postentocristid
(**1**) absent; (**2**) incomplete; (**3**) complete
27 Molars «*Dorcatherium* fold»
(**1**) present; (**2**) absent
Postcranial bones
28 Trochlea of astragalus
(**1**) nonaligned; (**2**) aligned
29 Fusion of remnant lateral metatarsals
(**1**) no; (**2**) one; (**3**) both
30 Crest at the cubo-naicular boundary
(**1**) present; (**2**) absent
31 Medial boundary sustentacular facet crest
(**1**) present; (**2**) absent
32 Fusion of the des metacarpal bones III and IV
(**1**) absent; (**2**) intermediate; (**3**) complet
33 Fusion of the metatarsal bones III and IV
(**1**) absent; (**2**) intermediate; (**3**) complet
34 Metatarsal gully
(**1**) open; (**2**) intermediate; (**3**) close
35 Complete distal metapodial keels
(**1**) yes; (**2**) no

III - LATEST OLIGOCENE



Hypodigm of *Babameryx engesseri* Mennecart, 2012

7 - LARGE MAMMALS FROM RICKENBACH (SWITZERLAND, REFERENCE LOCALITY MP29, LATE OLIGOCENE): BIOSTRATIGRAPHIC AND PALAEOENVIRONMENTAL IMPLICATIONS

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Abstract

Since the first exploitation of the Huppersandstones quarry of Rickenbach (Canton Solothurn, Switzerland) in 1898, many fossils of plants, molluscs, and vertebrates have been discovered. The study of the small mammals brought this locality to international recognition as the type locality for the European mammalian reference level MP29 (latest Oligocene). Our study reviews the terrestrial herbivorous mammals of Rickenbach and aims to reconstruct the palaeoenvironmental and palaeoclimatic conditions in which they lived. The perissodactyls and cetartiodactyls are described and identified: *Protapirus* sp. (Tapiridae), *Ronzotherium romani* and *Diaceratherium lamilloquense* (Rhinocerotidae), *Anthracotherium magnum* and *Microbunodon minimum* (Anthracotheriidae), *Palaeochoerus pusillus* (Suoidea), and *Dremotherium guthi*, "*Amphitragulus*" *quercyi*, "*Amphitragulus*" *feningrei*, and *Babameryx engesseri* gen. et sp. nov. (Ruminantia). Based on the updated faunal list, a cenogram of the locality of Rickenbach is established. We also performed ecomorphologic analyses on ruminants and rhinocerotids. The reconstructed palaeoenvironment of Rickenbach probably corresponded to a savannah woodland affected by a subtropical climate with clear seasonality.

7.1 Introduction

Since its discovery in 1897, and until it was recognised as the type locality for the European mammalian reference level MP29 by Schmidt-Kittler et al. (1987), Rickenbach (Canton Solothurn, Switzerland) has become one of the most important mammal localities in Western Europe. Additionally, Rickenbach is also:
– a locality studied by the "Basler School", from Hans Georg Stehlin to Johannes Huerzeler, and later Burkart Engesser;
– number CH/1088/2 in the "Register of the Tertiary Mammal-Bearing Localities of the Naturhistorisches Museum Basel" created and completed by J. Huerzeler, and later by B. Engesser;
– Rickenbach, Huerzeler, and Engesser, three names related to one small mammal, *Eomys huerzeleri*, the largest Eomyidae of the Oligocene, erected by Engesser in 1982 from Rickenbach.

It is a great pleasure for us to present this locality, where our dear colleague Burkart Engesser conducted a great part of his research, especially for its recognition as an international mammal level. We hope that he will enjoy this study, which shows that the large mammals of Rickenbach fully confirm the international interest of the

Table 1. Updated floral and faunal list of Rickenbach (MP29, Switzerland). The * indicate the taxa reviewed in this study. Other data are taken from the literature (Rollier 1910; Kehrer 1922; Stehlin 1922; Baumberger 1927; Helbing 1928; Erni and Ketelborn 1948; Viret and Zapfe 1951; Engesser 1982; Engesser and Mayo 1987; Mödden 1993; Engesser and Mödden 1997; Mödden and Vianey-Liaud 1997; Emery 2004; Emery et al. 2007).

PLANTAE

Pinus cones
Alnoid leaves
Cinnamomoid leaves
Salicoid-Myricoid leaves
Palm leaves

MOLLUSCA

Plebecula ramondi
Cepaea rugulosa
Parachloraea oxystoma
Melanopsis acuminata
Neritina sp.
Limnaea (Radix) subbullata
Limnaea (Radix) subovata
Limnaea pachygaster
Planorbis (Coretus) cornu
Unio (Iridea) subflabellatus
Unio vogti
Unio inaeguiradiatus

PISCES indet.

REPTILIA

Testudinidae indet.
Crocodilia indet.

AVES indet.

MAMMALIA

Amphiperatherium exile
Talpidae indet.
Amphechinus sp.
Dinosorex huerzeleri
Gliravus buijni
Microdyromys cf. *praemurinus*
Sciurus sp.
Steneofiber dehmi
Rhizospalax poirrieri
Eomys cf. *ebnatensis*
Eomys huerzeleri
Adelomyarion vireti
Eucricetodon praecursor
Eucricetodon cf. *dubius*
Melissiodon cf. *quercyi*
Plesiosminthus promyarion
Archaeomys helveticus
Archaeomys arvernensis
?Archaeomys laurillardi
Issiodoromys pseudanoema
Hyaenodon aff. *compressus*
Hyaenodon filholi
Cephalogale sp1
Cephalogale sp2
Amphicyon sp.
Haplocyon sp.
Plesictis sp.
Stenogale sp.
Viverridae indet.
*Ronzotherium romani**
*Diaceratherium lamilloquense**
Protapirus sp.*
*Microbunodon minimum**
*Anthracotherium magnum**
*Palaeochoerus pusillus**
Caenotherium sp1
Caenotherium sp2
*Dremotherium guthi**
*“Amphitragulus” quercyi**
*“Amphitragulus” feningrei**
Pecora nov. gen. nov. sp.*

locality. The present paper aims to describe the ungulate assemblage, spanning the orders of the perissodactyls (tapirids, rhinocerotids) and cetartiodactyls (anthracotheriids, suoids, ruminants), and to reassess the faunal list (Table 1) and the environmental significance of Rickenbach. The geological context is presented in Figure 1, and Figure 2 illustrates the stratigraphic frame.

7.2 Historical Background

The Rickenbach locality (Canton Solothurn, Switzerland) was a quarry mined in the first half of the 20th century to provide raw material (Huppersande, Eocene) for industrial production. Discovered by chance in 1897, the Huppersandstones were first exploited by the Glutz family (between 1898 and 1907), and then by the firm Kamber Bau AG until 1947. In 1956, the quarry was bought by the firm Hunziker for the deposit of construction waste. In 1964, the area was filled and covered with humus in order to create a biotope (Solothurnische Naturschutzverband). The “Biotopstiftung des Portlandcementwerk” was set in 1980, and is today managed by the “Biotop Stiftung Huppergrube” (since 2002). As a geological site, the quarry was included in 1996 in the “Inventar der geowissenschaftlichen schützenswerten Objekte des Kantons Solothurn” (under the number Ingeso-ooid 220), and more recently in the “Inventory of Geotopes of National Importance” (Number GIN 1201, see Berger et al. 2011).

On the 8th of July, 1905, and after several years of exploitation, R. Martin and H. G. Stehlin discovered the first fossil vertebrates in Rickenbach, associated with leaves and unionid bivalves (Martin 1906). The first geological profiles and pictures were documented by Martin (1906), Rollier (1910), Kehrer (1922), and Baumberger (1927). Additionally, a faunal list was established by Stehlin (1914). During the years 1916 to 1924, several collectors and palaeontologists (e.g., G. Schneider, E. Kuhn, J. Huerzeler) brought an important quantity of material to H. G. Stehlin. The latter stored most of these fossils in the Naturhistoriches Museum

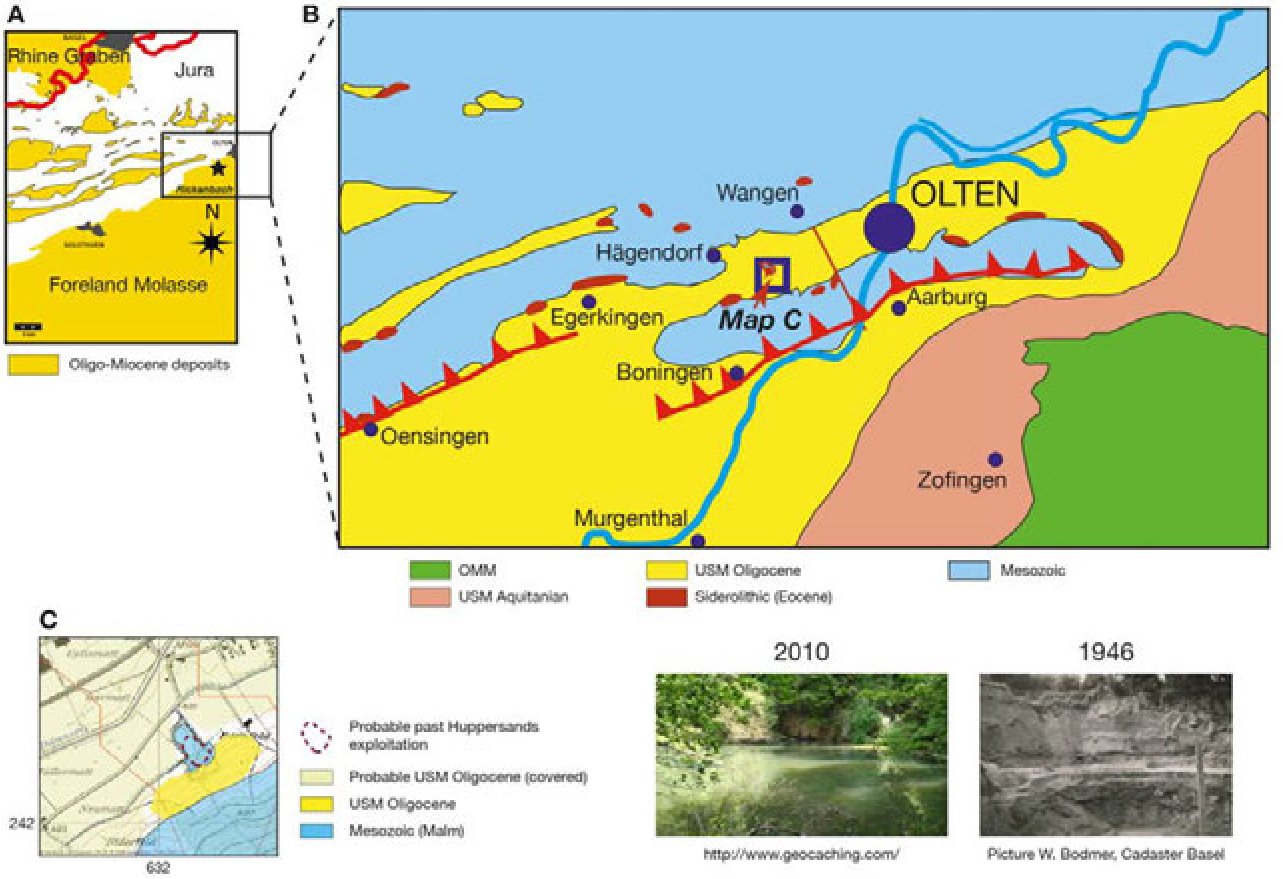

Figure 1. Geographical and geological location of Rickenbach (late Chattian, Switzerland). **A**, The Jura Molasse in Northwestern Switzerland (modified from Emery et al. 2007); **B**, geology of the region of Olten (according to Mühlberg, 1915; Kehrer 1922; Erni and Kelterborn 1948; Jordi et al. 2003; Swisstopo, unpublished map); **C**, detailed map of Rickenbach quarry. Pictures of the biotope taken in 2010, and of the old exploitation in 1946.

Basel, and many publications were edited (Helbing 1922, 1928; Kehrer 1922; Stehlin 1922; Schaub 1925, 1933; Baumberger 1927). A second important excavation was carried out in 1935, as attested by Froehlicher (1935) and Erni and Kelterborn (1948). A very important amount of vertebrates, this time stored in the Naturmuseum Olten, was collected during this period by E. Fey and T. Schweizer, particularly.

Except for the carnivores (Helbing 1928) and for part of the rhinocerotid material (e.g., Heissig 1969; Michel 1983; Emery et al. 2007), most of the large mammals collected in Rickenbach remained undescribed. The small mammals were however intensively studied by Viret and Zapfe (1951; *Heterosorex*), Stehlin and Schaub (1951; rodents and insectivores), and Hrubesch (1957; cricetids). Following the Congress of Paleogene in Bordeaux in 1962, Thaler (1965) published the first biostratigraphic scale based on European mammal levels for the Eocene and Oligocene. Rickenbach was considered for the first time in the international stratigraphic context as equivalent to the lower part of the Coderet level. Subsequently, diverse publications discussed the mammals from Rickenbach (e.g., Heissig 1969; Engesser 1975, 1982; Engesser et al. 1984), leading to the biozonation of Engesser and Mayo (1987). Since their publication in the “International Symposium on Mammalian Biostratigraphy and Palaeoecology” (Engesser and Mayo 1987), Rickenbach is definitively recognised as the European mammalian reference locality for level MP29. Remaining questions and arguments concerning the theridomorphs (e.g., Engesser and Mayo 1987; Vianey-Liaud and Schmid-Kittler 1987) were solved (e.g., Mödden 1993; Mödden and Vianey-Liaud 1997) and the eomyids were completely reviewed by Engesser (1990). In 1997, Engesser and Mödden published the official biozonation of the Swiss Molasse, confirming Rickenbach as the reference level for MP29.

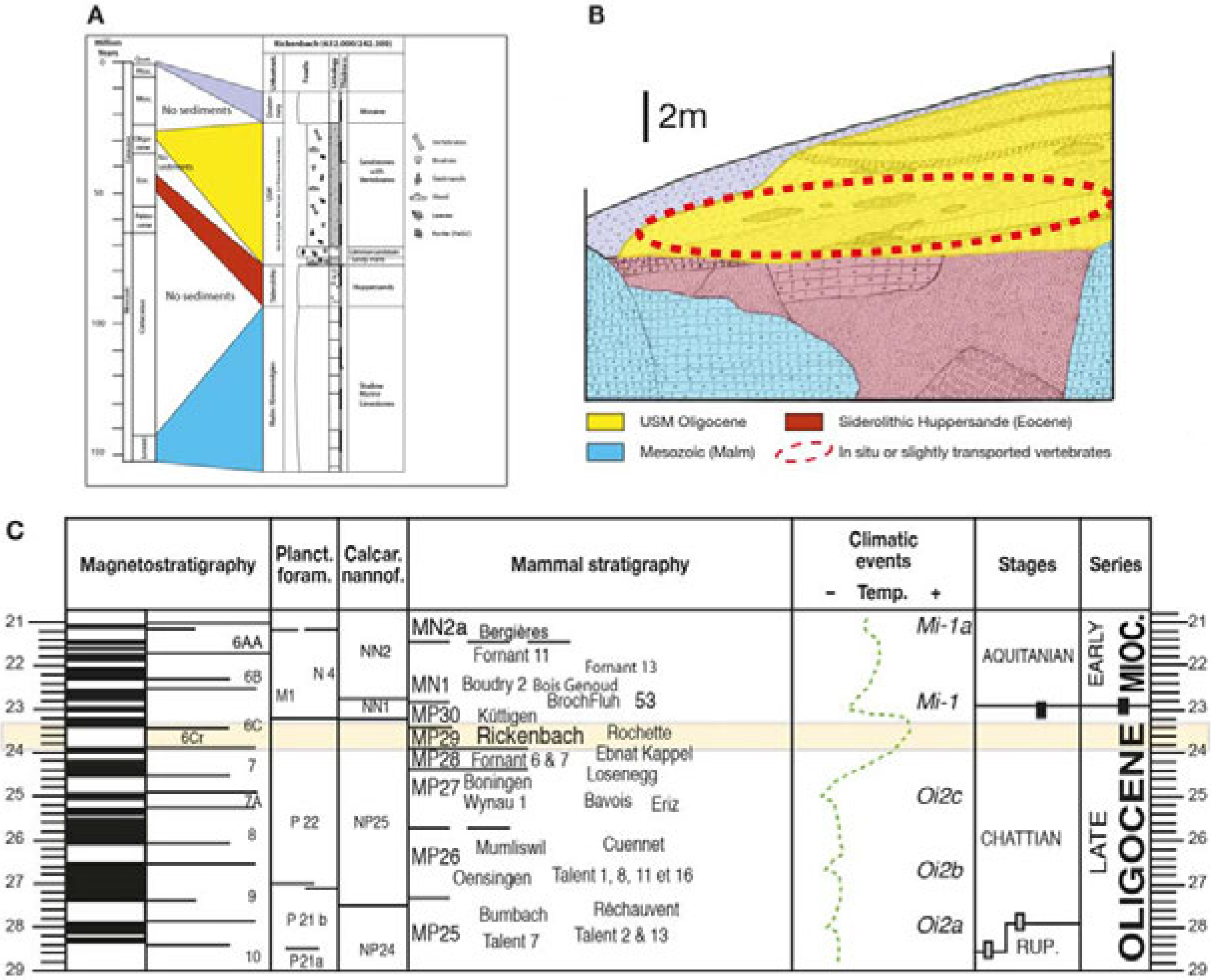

Figure 2. Stratigraphic context of Rickenbach (late Chattian, Switzerland). **A**, Sedimentological section (modified from Emery et al. 2007); **B**, drawing of the deposits, modified from unpublished picture from D. Fey, 1935 (Naturmuseum Olten); **C**, stratigraphic correlation of the Late Oligocene and earliest Miocene (modified from Berger 2011).

Detailed correlations between Swiss mammal levels and magnetostratigraphy were additionally published by Schlunegger et al. (1996), who clearly correlated the Rickenbach level (=MP29) within the chron 6 Cr, which actually corresponds to the interval 23.4 to 23.9 Ma (Fig. 1; Berger 2011).

To sum up, earlier literature and additional unpublished documents from the "Register of the Tertiary Mammal-Bearing Localities of the Naturhistorisches Museum Basel" show that: 1) the Molasse deposits above the Huppersands are composed of 4 to 8 meters of alternating sands and sandy marls – with marly or micro-conglomeratic intercalations, representing a typical fluvial sedimentary pattern slightly discordant on the Jurassic limestone or the Eocene Huppersands; 2) no vertebrates were found in the Huppersands; 3) all vertebrates coming from these 4-to-8-meter layers were geologically contemporaneous (Fig. 2). Therefore, Engesser and Mödden's statement (1997: p. 489) that "[…] in comparison with other reference faunas definitively obtained from one level, an origin of the mammal remains from layers slightly different in age cannot be excluded in the case of Rickenbach […]" should be updated. Indeed, even though a short post-mortem transport of the specimens is probable, no indication concerning a reworking was ever observed, neither in the geological and sedimentological context, nor in the faunal diversity.

7.3 Material and Methods

7.3.1 Palaeontology

The fossils discovered in Rickenbach are represented by many (>2000) dental remains and isolated bones of

Table 2. Estimated body weights of the herbivore terrestrial mammals sensu lato from Rickenbach (type locality MP29, Switzerland) and La Milloque (MP29+, France). The faunal lists have been modified from Brunet et al. (1981) and Engesser and Mödden (1997).

Fauna from Rickenbach	Body weight estimate [g]	Fauna from La Milloque	Body weight estimate [g]
Ronzotherium romani	1’790’000	*Anthracotherium magnum*	1’400’000
Anthracotherium magnum	1’420’000	*Diaceratherium lamilloquense*	1’040’000
Diaceratherium lamilloquense	1’040’000	*Doliochoerus quercyi*	48’000
Protapirus sp.	43’000	*Protapirus aginensis*	43’000
Microbunodon minimum	40’000	*Microbunodon minimum*	40’000
Palaeochoerus pusillus	22’000	*Bedenomeryx milloquensis*	32’000
Dremotherium guthi	20’000	*Palaeochoerus gergovianus*	31’000
Ruminantia n. gen. n. sp.	16’000	*Dremotherium guthi*	18’000
“Amphitragulus” feningrei	13’000	*Amphitragulus quercyi*	8’000
“Amphitragulus” quercyi	8’000	*Amphilagus* sp.	2’700
Steneofiber dehmi	7’500	*Piezodus* sp.	1’800
Cainotherium sp. 2	2’500	*Cainotherium commune*	1’300
Archaeomys helveticus	1’000	*Archaeomys laurilardi*	1’050
Cainotherium sp. 1	700	*Melissiodon quercyi*	100
Archaeomys arvenensis	500	*Issiodoromys pseudanoema*	90
Amphechinus sp.	450	Lipotyphla sp.	70
Rhizospalax poirrieri	180	Marsupialia sp.	50
Melissiodon cf. *quercyi*	140	*Plesiosminthus schaubi*	40
Issiodoromys pseudanoema	125	*Eucricetodon praecursor*	30
Sciurus sp.	35	Lipotyphla sp.	22
Eucricetodon cf. *dubius*	30	*Pseudodryomys* sp.	21
Eucricetodon praecursor	25	*Adelomyarion vireti*	17
Amphiperatherium exile	21	Marsupialia sp.	16
Talpid indet.	20	*Eomys* sp.	15
Eomys cf. *ebnatensis*	20	*Glirudinus glirulus*	13
Eomys huerzeleri	20	*Pseudocricetodon* cf. *thaleri*	10
Adelomyarion vireti	18	*Rhodanomys* sp.	7
Dinosorex huerzeleri	15	*Peridyromys murinus*	7
Plesiosminthus promyarion	11	*Pseudotherydomys* sp.	6
Gliravus sp.	10		
Microdyromys cf. *praemurinus*	5		

terrestrial mammals. The specimens are housed in the Swiss institutions MHNG (Muséum d’histoire naturelle de Genève), NMB (Naturhistorisches Museum Basel), NMO (Naturmuseum Olten), and NMS (Naturhistorisches Museum Solothurn). Material for comparison is housed in UCBL–FSL (Université Claude Bernard, Faculté des Sciences de Lyon), MNHN (Muséum national d’histoire naturelle de Paris), and USTL (Université des Sciences et Techniques du Languedoc, Montpellier). The descriptions, measurements, and diagnostic characters follow Scherler et al. (2011) for tapirids, and Heissig (1969), Guérin (1980), Antoine (2002), and Antoine et al. (2010) for rhinocerotids. Lihoreau (2003) and Boisserie et al. (2010) determined the methodology for bunodont cetartiodactyls (anthracotheres and suoids), and the terminology and biometry for ruminants follow Bärmann and Rössner (2011) and Köhler (1993). The taxonomic identifications of the rhinocerotids and ruminants include postcranial elements, but those of the tapirids and bunodont cetartiodactyls are exclusively based on dental remains. Biometrical dimensions are expressed in millimetres (mm) and the measurements of teeth are indicated by L x W. Body weights are expressed in grams (g).

Abbreviations. **C/c**, upper/lower canine, **D/d**, upper/lower deciduous teeth, **I/i**, upper/lower incisor, **M/m**, upper/lower molar, **P/p**, upper/lower premolar; **Mc**, metacarpal, **Mt**, metatarsal; **H**, height, **L**, length, **W**, width; **APD**, anteroposterior diameter, **TD**, transverse diameter; **GI**, gracility index, **HI**, hypsodonty index.

7.3.2 Palaeoecology

We applied the cenogram method following Legendre (1989) to the mammal community of Rickenbach based on the terrestrial non-flying herbivores (in this study: Marsupialia, Lipotyphla, Glires, Rodentia, Perissodactyla, Cetartiodactyla). Table 2 lists the fauna of Rickenbach and the estimated body weights for each species used.

Body weights for perissodactyls and cetartiodactyls were evaluated using the regression of body mass (Legendre 1989) on the occlusal areas of m1s (L x W measurements). Body weights of mammals other than ungulates were taken from Legendre's data (1989). Furthermore, we compared our results with the contemporaneous fossil-community cenogram of La Milloque (MP29, France) and with five extant community cenograms (established by Legendre 1989) in order to qualitatively estimate the structure of the mammalian community in Rickenbach. The faunal list of La Milloque (Brunet et al. 1981) has been adapted with our personal observations, and the body weights of ungulates were re-evaluated. Relationships between extant community cenograms and the main environmental characteristics are based on Gingerich (1989), Legendre (1989), Rodriguez (1999), and Costeur and Legendre (2008). The slopes and gaps formed by three size classes (less than 500 g, more than 500 g but less than 250'000 g, and more than 250'000 g) give information on vegetation structure, annual precipitation, and temperature (Legendre 1989, Rodriguez 1999, Costeur and Legendre 2008). Comparing the shape of fossil-community structures with extant ones gives additional information on palaeoenvironments.

The ecomorphologic analysis of the ruminants is based on the morphology of the metapods and phalanges according to Köhler (1993). In the present study, the subdivisions of the habitats are simplified to two types: wooded (type A) and open (type B). Type A can be additionally divided into two: moderately humid (subtype A1) and very humid (subtype A2). The characterization of the palaeobiologic parameters of rhinocerotids mainly follows Becker et al. (2009), in order to define the anatomical types and the related environments by analogies with extant representatives. Body sizes are estimated by comparing the length of the metapods with the shoulder height of extant rhinoceroses. The estimated body weights are based on Legendre's aforementioned method and the regression of body mass on skull length (occipital condyles-premaxilla). Locomotion types (cursorial, mediportal, graviportal) are defined from the slenderness of the central metapods following the method of the GI (sensu Guérin 1980: TD diaphysis/L). The diets are evaluated by observing the occlusal patterns of the back teeth and by calculating the HI on the m3s (sensu Janis 1988: H/W). The feeding behaviour, or posture (head-holding down, intermediate, or up), is characterised from skulls by using the occipital side inclination and the angle of the occipital crest in lateral view (Bales 1996).

7.4 Systematic Palaeontology

Order Perissodactyla Owen, 1848
Family Tapiridae Gray, 1821
Genus *Protapirus* Filhol, 1877
Protapirus indet.

A unique fragmentary left m2 of *Protapirus* sp. (NMO–H10/64) has been discovered in the large amount of mammalian remains. It lacks its mesiolabial part, but its dimensions (18.5 x 11.0) and the presence of two vertical crests on the posterior side of the protolophid correspond to a Chattian species of the genus *Protapirus*. It is nevertheless not possible to discriminate between the two representatives of the Late Oligocene *P. bavaricus* (Oettingen-Spielberg, 1952) and *P. aginensis* (Richard, 1938).

Family Rhinocerotidae Gray, 1821
Subfamily Elasmotheriinae Bonaparte, 1845
Genus *Ronzotherium* Aymard, 1854
Ronzotherium romani Kretzoi, 1940
Figs. 3 and 4

The middle-sized, slender, and hornless rhinocerotid *Ronzotherium romani* is documented by 35 dental and postcranial remains. The most characteristic ones are a left I2 (NMB–UM6319), a fragmentary right i2 (NMB–UM807), a left D3 (NMO–I11/85), a left d1 (NMB–UM2574), a left P3 (NMB–Ri24), a fragmentary right maxilla P4-M1 (NMB–UM1840), two M1s (NMO–I12/24, NMO–I3/13), a mandible (NMB–UM3832), a distal fragment of a left humerus (NMO–K3/5), a distal fragment of a right McIII (NMB–UM2570), two astragali (NMO–I12/20, NMO–K3/9), two right MtIIIs (NMO–K3/13, NMO–H9/9), and a right MtIV (NMO–I10/103).

According to Heissig (1969) and Brunet (1979), the specimens in question show dimensions and a combination of characters that are typical for *Ronzotherium*: the sections of I2 and i2 are almond-shaped and oval, respectively. The cheek teeth are brachyodont with a strong lingual cingulum notched at the level of the medisinus, which joins the anterior and posterior ones. The ectoloph profile is somewhat waved with a smooth paracone fold, and weak mesostyle and metacone fold. The crochet and the antecrochet are usually absent on upper premolars, but there is a wide and deep postfossette. The upper molars bear a strong antecrochet and a straight posterior part of the ectoloph profile. The trigonid of the lower molars is angular and forms a right dihedron in occlusal view. The lingual opening of the posterior valley is U-shaped, and the hypolophid is transversely oriented. The D3 and D4 bear a marked paracone fold, well-developed parastyle and metastyle, and reduced lingual and labial cingula. Furthermore, the base of the corpus mandibulae is straight; the mandible has a weak incisura vasorum, a weakly developed angulus mandibulae, and a subvertical ramus.

From the referred humerus (TD distal extremity = 113.0; minimal TD diaphysis = 60.0), the median constriction of the trochlea is somewhat deep ("diabolo-shape" sensu Antoine 2002). The two referred astragali are broader than high (mean of TD/H = 1.08) and shallow (APD/H = 0.56). The fibular facet is sub-vertical and transversally flat, and the collum tali is high. The posteroproximal border of the trochlea is nearly straight, and the trochlea itself is very oblique in respect to the distal articulation. The lateral lip is prominent. The calcaneal facet 1 is concave and its laterodistal expansion is present, rather low and broad. Facet 2 is flat and higher than wide, and facet 3 is small and unconnected to facet 2. The documented metapods are slender (mean GI on MtIII = 0.236), with a shorter MtIV (L = 137.0) compared to the MtIII (mean L = 156.5). The insertions for the interossei muscles are long and marked down to the distal half of the shaft. The intermediate reliefs are usually high and acute, and the proximal border of the anterior side of MtIII is concave. There are two flat and well-developed MtII-facets on the medial side of the MtIII; the MtIV has independent facets and is lacking the cuboid facet on the lateral side. There is no distal widening of the diaphysis of the MtIII.

The specimens from Rickenbach differ from the primitive ronzotheres *R. velaunum* (Aymard, 1853) and *R. filholi* (Osborn, 1900) by a general reduction of the cingula on the cheek teeth, a more advanced molarisation and a weaker crista on upper premolars, and a weak paracone fold and constricted protocone on upper molars. P2 is molariform (sensu Heissig 1969) with joined protoloph and ectoloph that are curved posterolingually, and straight metaloph. P3 and P4 (P3 mean = 32.25 x 40.75; P4 mean = 39.0 x 50.5) are semi-molariform (sensu Heissig 1969) with a posterolingually curved protoloph, longer than the roughly S-shaped metaloph. The referred M1s (mean = 51.0 x 56.5) are characterised by the absence (or strong reduction) of labial and lingual cingula, and by the presence of a constricted protocone. D3 and D4 (D3 = 40.0 x 41.0; D4 mean = 44.0 x 46.75) exhibit a quadrangular occlusal shape, weak parastyle and metastyle, as well as straight and posterolingually oblique protoloph and metaloph. d1 (14.5 x 7.5) is one-rooted and it bears a wide postfossettid. Regarding the mandible, the posterior border of the symphysis reaches the middle of p3 and the foramen mentale is located below the level of p2-p3. Additionally, the lower premolar series is short with respect to the molar series (mean Lp3-4/Lm1-3 = 0.45), the probable absence of p1/d1 in adults (no corresponding alveoli are attested on the referred mandible), the reduction of p2 (curved paralophid without constriction, reduced paraconid, and closed posterior valley), the strongly reduced lingual and labial cingulids, and the developed external groove of the lower cheek teeth, impede referring the large rhino from Rickenbach to *R. filholi* or *R. velaunum*. Most morphological features aforementioned are consistent with those of *R. romani* (e.g., Heissig 1969; Brunet 1979; Becker 2009; Ménouret and Guérin 2009), however, being even more similar to the latest representatives of the concerned species, known from the latest Oligocene, as suggested by Brunet (1979) and Brunet et al. (1987).

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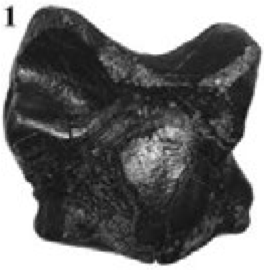

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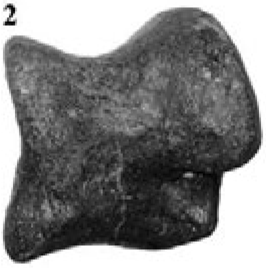

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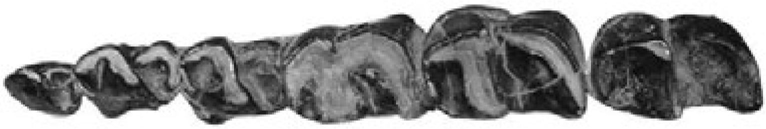

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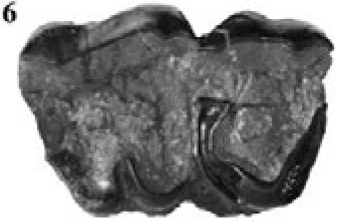

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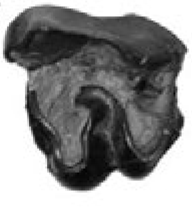

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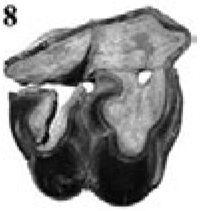

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Figure 3. (opposite page) Latest Oligocene rhinocerotids of Rickenbach (type locality MP29, Switzerland). *Ronzotherium romani*: **1**, left astragalus (NMO–K3/9), posterior view; **2**, left astragalus (NMO–I12/20), anterior view; **3**, sub-complete mandible (NMB–UM3832): right tooth row, occlusal view (**a**), left tooth row, occlusal view (**b**), left hemi-mandible, lateral view (**c**); **4**, left D3 (NMO–I11/85), occlusal view; **5**, left P3 (NMB–Ri24), occlusal view; **6**, right P4-M1 (NMB–UM1840), occlusal view; **7**, left M1 (NMO–I12/24), occlusal view; **8**, right M1 (NMO–I3/13), occlusal view; **9**, distal fragment of left humerus (NMO–K3/5), anterior view.
Diaceratherium lamilloquense: **10**, distal part of right humerus (NMB–UM973), anterior view; **11**, right D4 (NMB–UM971), occlusal view; **12**, right P2 (NMO–I1/104), occlusal view; **13**, right P3 (NMO–I12/23), occlusal view; **14**, left P3 (NMO–I11/73), occlusal view; **15**, left P4 (NMB–HR1), occlusal view; **16**, left M2 (NMB–Ri27), occlusal view. Scale bar equals 20 mm.

Subfamily Rhinocerotinae Gray, 1821
Genus *Diaceratherium* Dietrich, 1931
Diaceratherium lamilloquense Michel, 1983
Figs. 3 and 4

The small-sized and mediportal-graviportal diacerathere *Diaceratherium lamilloquense* Michel, 1983 is documented by relatively few remains: nine isolated teeth (fragmentary left i2, NMB–Ri22; right D4, NMB–UM971; right P2, NMO–I1/104; left P3, NMO–I11/73; right P3, NMO–I12/23; left P4, NMB–HR1; left M2, NMB–Ri27; left m2, NMO–I11/75; right m2, NMO–I1/93), right humerus (NMB–UM973), and three metapods (fragmentary left McIII, NMB–UM6801; left MtII, NMB–UM2565; left MtIII, NMO–unnumbered).

According to Heissig (1969), Brunet (1979), and Ménouret and Guérin (2009), the available specimens show some similarities with those attributed to *Ronzotherium romani* Kretzoi, 1940, such as a continuous lingual cingulum joined to the anterior and posterior ones, a reduced labial cingulum, a distinct crista, and a wide postfossette on upper premolars. On P2, the protocone is less developed than the hypocone, and the M2s bear a strong antecrochet, as well as a simple crochet, and a crista. The metapods have sharp intermediate reliefs and distinct MtIV facets on MtIII. However, most specimens from Rickenbach are smaller in size than those of *Ronzotherium romani*, and they further differ morphologically from the latter by having a triangular i2 in cross section, a stronger reduction of the labial cingulum, a smooth ectoloph profile with a developed paracone fold, and an onset of the crochet on upper premolars, which are molariform (sensu Heissig 1969: separated protocone and hypocone). The protoloph is interrupted on P2 (30.0 x 30.0), with nearly transverse and straight protoloph and metaloph, and straight and posterolingually oblique protoloph and metaloph on P3 and P4, with a slightly constricted protocone and an onset of crochet and antecrochet on the latter (P3 mean = 32.8 x 40.3; P4 = 38.0 x 49.5). The referred M2 (54.0 x 58.0) shows a concave posterior part of the ectoloph profile. The lingual and labial cingulids on m2s (mean = 45.5 x 27.5) are strongly reduced, with a well-marked external groove and a developed, somewhat constricted, entoconid. D4 (37.0 x 38.0) displays a stronger reduction of the cingula, a narrow postfossette, short parastyle and metastyle, and a marked anterior groove on the protocone. The metapods are stockier (GI on MtIII = 0.329) with short insertions for the interossei muscles that are restricted to the proximal half of the shaft. In anterior view, the magnum facet on McIII is visible and the MtIII displays a concave proximal border and a distal widening of the shaft. There are no MtII facets on the MtIII, and vice versa. The referred humerus (L = 404.0; TD distal extremity = 128.0; minimal TD diaphysis = 58.0) displays a shallow median constriction ("egg-cup shape" sensu Antoine 2002).

Most of these features recall those of the early teleoceratine diaceratheres from the Late Oligocene of Western Europe (e.g., Michel 1983; Brunet et al. 1987; Ménouret and Guérin 2009). The dimensions mainly match those of the smallest representative of the latest Oligocene diaceratheres of Europe, *D. lamilloquense* (MP29; Michel 1983; Brunet et al. 1987). The referred humerus only is around 15% larger than the humerus from the specimen of La Milloque (NMB–LM1161) and it has similar size and proportions to that of *Diaceratherium massiliae* (UCBL–FSL–9523; Ménouret and Guérin 2009: fig. 10.A). This may reveal wide metrical discrepancies within *D. lamilloquense* as noted in most of teleoceratines (e.g., Cerdeño 1993; Antoine 2002). Furthermore, the junior synonymy of *D. massiliae* Ménouret and Guérin, 2009 with *D. lamilloquense* Michel, 1983 could be questionable. Based on these observations, the concerned specimens, of which some have been misidentified as *R. romani* Kretzoi, 1940 in

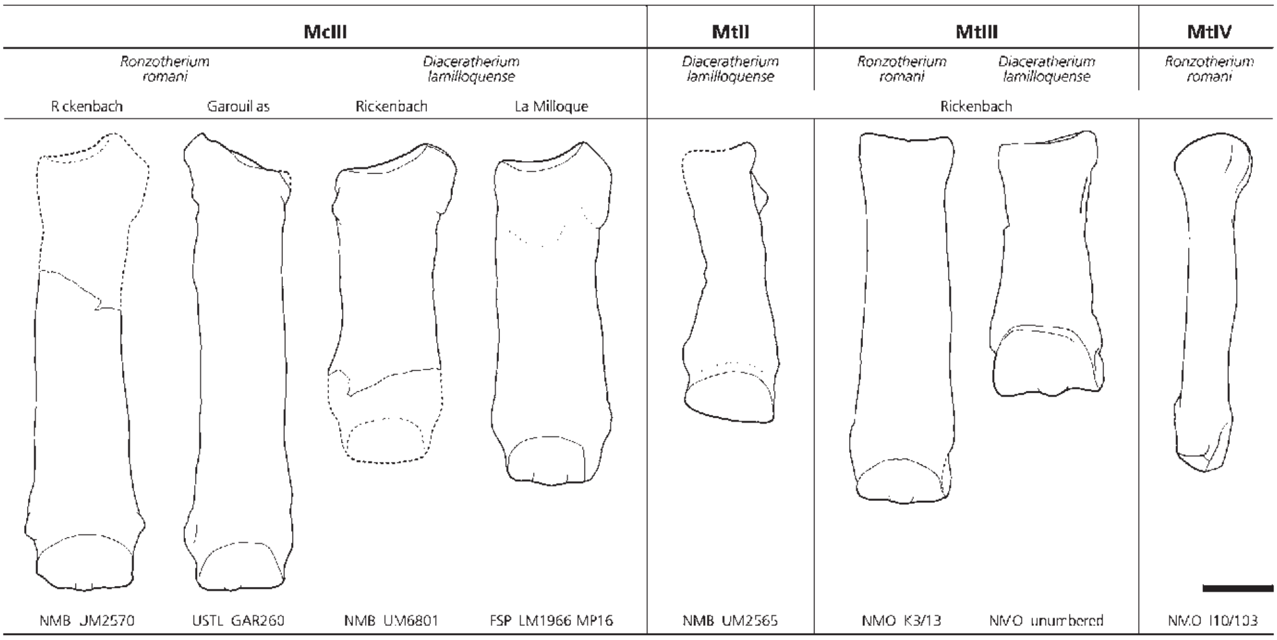


Figure 4. Metapods (McIII, MtII, MtIII, and MtIV) of *Ronzotherium romani* and *Diaceratherium lamilloquense* from Rickenbach (type locality MP29, Switzerland) compared to the McIII of *R. romani* from Le Garouillas (MP25, France) and to the McIII of *D. lamilloquense* from La Milloque (MP29+, France). Scale bar equals 30 mm.

former papers (e.g., left P4, NMB–HR1; Heissig 1969; Michel 1983; Becker 2003), are tentatively assigned to *D. lamilloquense*. A direct observation of the lost specimen of the NMB – fragmentary maxilla with M2-M3 illustrated by Michel (1983: pl. 8.f), coll. Heizmann – should support this assignation by showing a clearly concave posterior part of the ectoloph profile on M2 and fused ectoloph and metaloph on M3.

Order Cetartiodactyla Montgelard et al., 1997
Family Anthracotheriidae Leidy, 1869
Subfamily Anthracotheriinae Leidy, 1869
Genus *Anthracotherium* Cuvier, 1822
Anthracotherium magnum de Blainville, 1839-1864
Fig. 5

A complete review of the Swiss anthracotheres was recently presented by Scherler (2011). Dental remains (around 60) of the very large *Anthracotherium magnum* were discovered, represented almost only by isolated lower and upper teeth, along with a fragmentary left mandible (NMB–HR3). The canines (e.g., NMO–I12/35, NMO–I12/39) are large with a rounded section (mean = 36.5 x 31.0). The P2s (e.g., NMB–UM949, NMO–K2/27) and P3s (e.g., NMO–K2/29, NMO–K5/50) are sub-triangular without a real protocone, and their undifferentiated postparacrista and postmetacrista join the metastyle (P2 mean = 34.0 x 22.0; P3 mean = 36.5 x 28.0). Additionally, there is an accessory cusp on the distolingual side of the P3s. The P4s (e.g., NMB–UM948) are sub-rectangular with a well-developed cingulum almost all around the tooth (mean = 29.5 x 38.0). The trapezoidal upper molars (e.g., NMB–HR240, NMB–HR141, NMB–HR188) display a strong and oblique parastyle, and a metastyle shifted posteriorly. There is a mesiostyle, which is characteristic of the genus diagnosis (e.g., Lihoreau 2003), and a medium distostyle. Furthermore, the postprotocrista is isolated and distally directed, and does not join the premetacristule (M1 mean = 32.5 x 33.5; M2 = 52.5 x 59.0; M3 mean = 56.0 x 68.0). The p4s (e.g., NMB–HR3) are inscribed in a right-angled triangle, without any mesiostylid or distostylid, and their endoprotocristid is well developed and distolingually directed. Furthermore, there is a short lingual accessory cristid initiating from the preprotocristid and distally directed (33.5 x 21.5). The sub-rectangular m1s (e.g., NMB–HR3, NMB–HR144) and m2s (e.g., NMB–HR3) bear four bunodont cuspids with slightly developed mesial and distal cingulids. The prehypocristid is mesiolingually directed and joins the distal wall of the

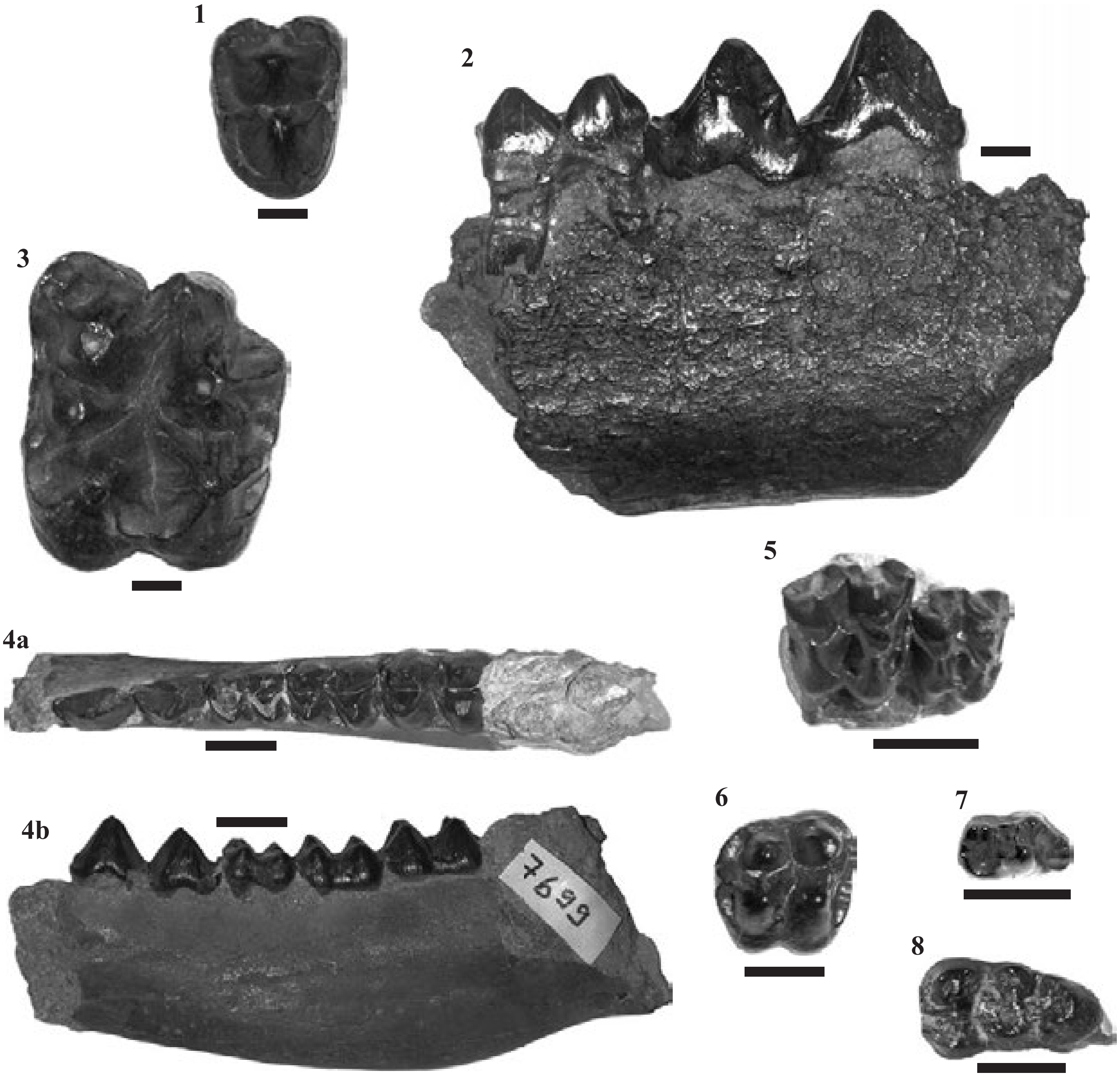


Figure 5. Latest Oligocene anthracotheres and suoids of Rickenbach (type locality MP29, Switzerland). *Anthracotherium magnum*: **1**, right P4 (NMB–UM948), occlusal view; **2**, fragmentary left mandible with p3-m1 (NMB–HR3), lingual view; **3**, right M3 (NMB–HR188), occlusal view. *Microbunodon minimum*: **4**, fragmentary left mandible with p3-m3 (NMS–7699), occlusal (**a**) and labial (**b**) views; **5**, right M1-M2 (NMO–I8/83), occlusal view. *Palaeochoerus pusillus*: **6**, right M2 (NMB–UM1330), occlusal view; **7**, left p4 (NMB–HR2590), occlusal view; **8**, left m3 (NMB–Ri63), occlusal view. Scale bars equal 10 mm.

postmetacristid, forming a large accretion in the middle of the sagittal valley (m1 mean = 37.0 x 28.0). The unique m3 (NMB–HR3) bears an additional talonid that shows a distinct entoconulid well separated from the hypoconulid. Along with the large size of the specimens (e.g., NMB–UM3184, left M3 = 56.5 x 68.5), these two latter features are diagnostic of *Anthracotherium magnum* de Blainville, 1839-1864 (Scherler 2011).

Subfamily Microbunodontinae
Lihoreau and Ducrocq, 2007
Genus *Microbunodon* Depéret, 1908
Microbunodon minimum (Cuvier, 1822)

Fig. 5

The small anthracothere *Microbunodon minimum* (Cuvier, 1822) is also mainly represented in Rickenbach by dental remains (around 90). It comprises many fragmentary maxillae (e.g., NMO–H11/98, NMO–K5/29, NMB–Ri1) and mandibles (e.g., NMB–Ri60, NMO–H11/30, NMO–I12/9) with upper and lower tooth rows, as well as isolated teeth. The canines (e.g., NMB–Ri56) are transversally compressed with mesial and distal careens, and they show sexual dimorphism marked by blade-like C in males (12.0 x 7.0). The molars are bunoselenodont. On the upper molars (e.g., NMO–H10/70, NMB–HR145), the parastyle is strong and sub-vertical, and the mesostyle is V-shaped (M1 mean = 12.0 x 13.5). There is a well-developed distostyle, but no mesiostyle. The labial cuspids of the lower molars are crescent-like compared to the lingual ones, which are more conical (m1 mean = 12.0 x 8.5; m2 mean = 14.0 x 10.5; m3 mean = 24.5 x 11.0). The m1s (e.g., NMB–UM1329, NMO–H10/92) and m2s (e.g., NMO–K9/100, NMS–7715, NMS–7709) are sub-rectangular, with short mesial and distal cingulids. Furthermore, the talonid of the m3s (e.g., NMB–HR146, NMO–K10/241) bears a single cuspid, the hypoconulid, which forms a loop-like hypolophid.

Superfamily Suoidea Gray, 1821
Family Palaeochoeriidae Matthew, 1924
Genus *Palaeochoerus* Pomel, 1847
Palaeochoerus pusillus Ginsburg, 1974
Fig. 5

The teeth of suoids from Rickenbach (around 20, see Scherler 2011) are referred to the small palaeochoerid species *Palaeochoerus pusillus*. The upper molars (e.g., NMB–UM1330, NMB–UM2588, NMO–K5/11) are bunodont and simple, with four main cuspids that are well-conical. They do not display any accessory cuspids. The mesial, distal, and labial cingula are strong, but there is no lingual cingulum. There is a weak entostyle and the distostyle is well developed (M1 = 12.5 x 11.0; M2 = 12.5 x 13.0; M3 = 13.0 x 13.5). The p4s (NMB–UM2590, NMB–HR242) bear a lingual metaconid well differentiated from the protoconid. The hypoconid is less developed, and there is no entoconid. The mesio- and distostylids are slightly developed (p4 mean = 11.25 x 6.75). The lower molars (e.g., NMB–Ri64, NMO–H10/74, NMO–K9/105) are simple bunodont teeth that only display a metaconulid as an accessory cuspid. There is a short and weak mesial cingulid, but no real stylids. The transverse valley is wide and continuous, as is the sagittal valley that separates the first lobe from the second (m2 mean = 12.0 x 8.5; m3 mean = 21.0 x 11.5). In comparison to *Doliochoerus quercyi* from La Milloque, the specimens from Rickenbach differ by the absence of any accessory cuspids on the upper molars, the absence of a real paraconid, and the absence of a prehypoconulid on the m3s. Indeed, the talonid of the m3s from Rickenbach is simple, without any accessory cuspid between the second lobe and the hypoconulid. This latter feature is characteristic of the species *Palaeochoerus pusillus*. Additionally, the specimens from Rickenbach display an intermediate size between the very small species *Palaeochoerus paronae* and the larger *P. gergovianus* and *P. typus*. These latter species display accessory cuspids on their upper molars that are not present on the specimens from Rickenbach. Further comparisons to the holotype of *P. pusillus* (MNHP–Qu15, Phosphorites du Quercy) figured by Hellmund (1992) confirm the assignment of the specimens from Rickenbach to *Palaeochoerus pusillus* Ginsburg, 1974.

Suborder Ruminantia Scopoli, 1777
Infraorder Pecora Flower, 1883

The ruminants are currently reviewed by Mennecart (in progress) in the frame of his PhD thesis. Latest Oligocene and Early Miocene familial attributions are mainly speculative and confusing, and will not be proposed for this article. All the ruminants collected in Rickenbach were initially stored under the name *Amphitragulus* sp.

Genus *Dremotherium* Saint-Hilaire, 1833
Dremotherium guthi Jehenne, 1987
Figs. 6 and 7

Dremotherium guthi is the most represented ruminant in Rickenbach with more than 50 remains. The material includes isolated upper teeth (e.g., NMB–UM2594, NMB–UM1331, NMO–L6/38), lower jaws (e.g., NMB–HR9, NMB–UM2595), and postcranial remains. The dental features are characteristic to *Dremotherium*. Indeed, these teeth are larger and more advanced in comparison to those of ruminants from the latest Oligocene (NMO–K4/31, m2 = 11.4 x 7.2, m3 = 15.5 x 7.0; NMO–I7/7, M2 = 11.4 x 12.8). The crowns are high and the cusps are well selenodont (NMB–HR162, NMO–L6/38). The quadratic upper molars bear a well-developed metaconule (NMB–UM1331, NMO–I7/37). The postprotocrista is long and highly curved, and the premetaconulecrista is distally forked. The paracone rib displays an anterior groove, and the metacone rib, when present, is weak. The mesostyle is well developed and aligned with the premetacrista and the postparacrista. The metastyle forms a small column and the entostyle is weak or absent. There is no lingual cingulum at the level of the protocone. The total length of the lower molar row is smaller than those of *D. feignouxi* and similar to those of the paratype *D. guthi* (for Rickenbach, L m1-m3 = 35.0; for La Milloque, L m1-m3 = 37.0). The p4 is laterally compressed and its well-developed mesiolingual conid possesses an anterolingual cristid (NMB–HR9, NMB–UM2595). The lower molars have widely open trigonid and talonid due to slightly backward oriented internal postprotocristid and posthypocristid (NMB–UM1603, NMO–I7/31, NMO–I7/64). The lingual wall is flat with large cristids, and the metaconid and entoconid ribs are reduced. The postentocristid does not reach the large and globular entoconulid, and this forms a small gap between these two features. The metastylid is small and salient, and a small spur is present on the anterolingual part of the lower molars. The external postprotocristid is present and usually very well marked.

Postcranial remains have been assigned to *Dremotherium guthi* due to their very large size in comparison to the other ruminants present in Rickenbach (Hiard 2010). With its aligned trochlea, the astragalus (e.g., NMO–K2/48) is characteristic to Pecora. The metapodial bones (e.g., NMB–2836) are elongated with weakly developed and slightly dorsally flattened condyles. The extensor tendon forms a long groove on the proximal part of the bone. The proximal phalanx (e.g., NMO–K2/52) is robust with a flattened outline of the distal articulation. The outline of the dorsal surface is slightly concave, and the external side of the bone is straight. The middle phalanx is short and broad with a thinner distal part. The proximal articular facet is slightly concave. The distal articular facet is wide and triangular with a distally oriented tuberosity.

Genus *Amphitragulus* Croizet in Pomel, 1846

The review of the species of the genus *Amphitragulus* and their relationships with *Pomelomeryx* and *Dremotherium* are still unresolved (Jehenne 1985; Blondel 1997; Mennecart in progress). Because the complete review is out of frame for the present contribution, we keep the name *Amphitragulus* for the species *quercyi* and *feningrei*, but with quotation marks.

"Amphitragulus" quercyi Filhol, 1887

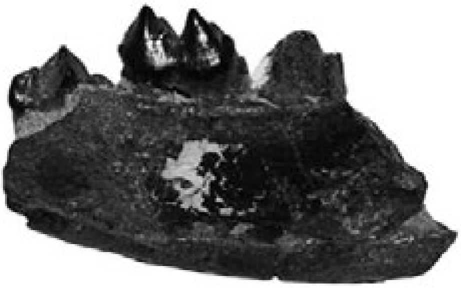
Fig. 6

The smallest ruminant from Rickenbach, *"Amphitragulus" quercyi*, is very rare and seems to be only represented by dental remains (5 fossils). The teeth are bunoselenodont with a low crown. The upper molars possess a reduced external postprotocrista (NMO–I9/48) and a slightly reduced metaconule. The paracone rib is salient, but there is no metacone rib. The para-, meso-, and metastyles are salient. The lingual cingulum, when present, is very weak. The lingual wall of the lower molars shows highly bulged cuspids (NMB–HR150). The internal postprotocristid and the very short posthypocristid are transversal one to each other and form a small trigonid and talonid. The metaconid and the entoconid are aligned, and the metastylid forms a large small column. The external postprotocristid is deep, and the third basin is small and pinched. The specimens from Rickenbach are similar in shape and size (NMB–HR150, m3 = 11.9 x 6.0) from those described by Blondel (1997) in Pech Desse (mean dimensions for m3s = 12.0 x 5.8) and Pech du Fraysse (mean dimensions for m3s = 11.8 x 5.7), and from the holotype of *Amphitragulus quercyi* (MNHN–Qu4771, m3 = 11.3 x 5.3).

"Amphitragulus" feningrei Schlosser, 1925-26

Fig. 6

Definitive and deciduous teeth (around 20) of the medium-sized ruminant "*Amphitragulus*" *feningrei* have been discovered. Their crowns are selenodont, but more brachyodont than those of *Dremotherium guthi* Jehenne, 1987. The upper molars are almost quadratic, slightly laterally compressed (NMB–HR164, NMO–I7/3, NMO–I7/4). The labial cusps are not aligned, and the metaconule



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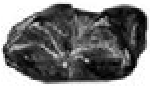

7a

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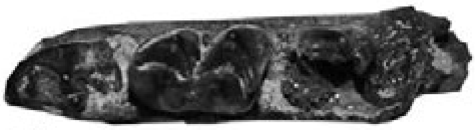
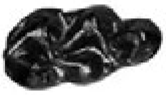


1b

3

8a

5a



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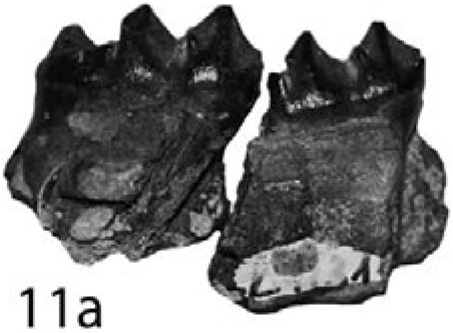

11a

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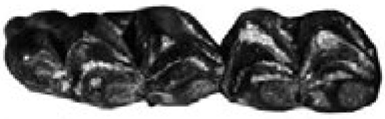

11b

14a

14b

Figure 6. Latest Oligocene ruminants of Rickenbach (type locality MP29, Switzerland). *Babameryx engesseri* gen. et sp. nov.: **1**, right fragmentary mandible (NMO–K5/7) with erupting p4 and m1, lingual (**a**) and occlusal (**b**) views; **2**, Holotype: left M1 (NMO–K11/15), occlusal view; **3**, left M3 (NMB–UM2833), occlusal view; **4**, right P4 (NMB–UM793), occlusal view. "*Amphitragulus*" *quercyi*: **5**, right m3 (NMB–HR150), lingual (**a**) and occlusal (**b**) views; **6**, left M1 (NMO–I9/48), occlusal view. "*Amphitragulus*" *feningrei*: **7**, right m2 (NMB–UM796), lingual (**a**) and occlusal views (**b**); **8**, left fragmentary mandible with d4-m1 (NMO–H11/64), lingual (**a**) and occlusal views (**b**); **9**, right M1 (NMB–HR164), occlusal view; **10**, right M3 (NMO–I7/4), occlusal view. *Dremotherium guthi*: **11**, left m2-m3 (NMO–K4/31), lingual (**a**) and occlusal (**b**) views; **12**, right M2 (NMO–I7/7), occlusal view; **13**, left M2 (NMO–L6/38), occlusal view; **14**, right mandible with p4-m3 (NMO–26578), lingual (**a**) and occlusal (**b**) views. Scale bar equals 10 mm.

is slightly reduced. The external postprotocrista is short and curved. The paracone is globular with a well-developed rib, but the metacone rib is absent. The para- and mesostyles are globular and form small columns, whereas the parastyle is anteriorly projected. There is no lingual cingulum. The lower molars possess small trigonid and talonid that form an acute angle (NMB–UM796, NMO–H11/64, NMO–K8/64). The lingual cuspids are sharp and laterally compressed, and their ribs are bulged. The entoconulid and metaconulid are both small, but the latter is more salient. Additionally, the external postprotocristid is very deep.

The holotype and paratypes of *Amphitragulus feningrei* Schlosser, 1925-26 from Peublanc (MP30) stored in Munich had been lost or destroyed during World War II (G. Rössner and K. Heissig, pers. comm.). The figured specimens of Schlosser (1925-26: fig. 14) are similar in size and shape (excluding fig. 14d, see *Babameryx engesseri* gen. et sp. nov. below) to those described and figured by Viret (1929: pl. 31, figs. 13-14) from Coderet (MP30; UCBL–FSL–97.731: d4 = 9.7 x 4.0, m1 = 8.9 x 5.1) and to the specimens from Rickenbach (MP29; NMO–H11/64: d4 = 9.8 x 4.5, m1, 8.3 x 5.7). This species is clearly different from the other *Amphitragulus* species in having more selenodont crowns. Moreover, the cusps are sharp and the parastyle is globular and anteriorly projected, which seems to be unique amongst the Oligocene and Early Miocene ruminants. Therefore, this species should probably be assigned to a new genus (Mennecart, in progress).

Genus *Babameryx* gen. nov.

Type species: *Babameryx engesseri*

Diagnosis: Medium-sized, brachyodont bunoselenodont Pecora; p4 compact and possessing well-formed mesolingual conid and anterior stylid; lower molar possessing highly bulged lingual cuspids without rib and a protoconid with an external postprotocristid; P4 stocky with a deep lingual cingulum and a central fold; upper molars with reduced metaconule, large and highly bulged paracone rib and metacone rib, and deep cingulum surrounding the protocone.

Etymology: From *Baba-*, "elder" or "patriarch" in eastern languages (Arabic, Russian, Slavic), and *-meryx*, Greek for "ruminants", in reference to the primitive features of this Eupecora.

Babameryx engesseri sp. nov.
Fig. 6

1914 v pars	Ruminantia incertae sedis Stehlin: 185.
1987 v pars	*Amphitragulus* sp. Engesser and Mayo: 76.
1997 v pars	*Amphitragulus* sp. Engesser and Mödden: 488.
2007 v pars	*Amphitragulus* sp. Emery et al.: 56, not fig. 10.

Holotype: NMO–K11/15, left M1 (8.9 x 10.7).

Paratype: NMO–K5/7, right fragmentary mandible with erupting p4 and m1 (8.2 x 4.2 and 9.3 x 6.4, respectively); NMB–UM2833, left M3 (10.0 x 11.6); NMB–UM793, right P4 (7.6 x 8.8).

Etymology: In tribute to our esteemed colleague and friend, Burkart Engesser, in recognition of his palaeontological investigations in the Swiss Molasse Basin, and especially in Rickenbach.

Stratum typicum: Sandstone bed of the Aarwanger Molasse of the USM (Lower Freshwater Molasse), European mammal reference level MP29.

Type locality: Rickenbach (NW Switzerland, Swiss coordinate grid: 632.200/242.300).

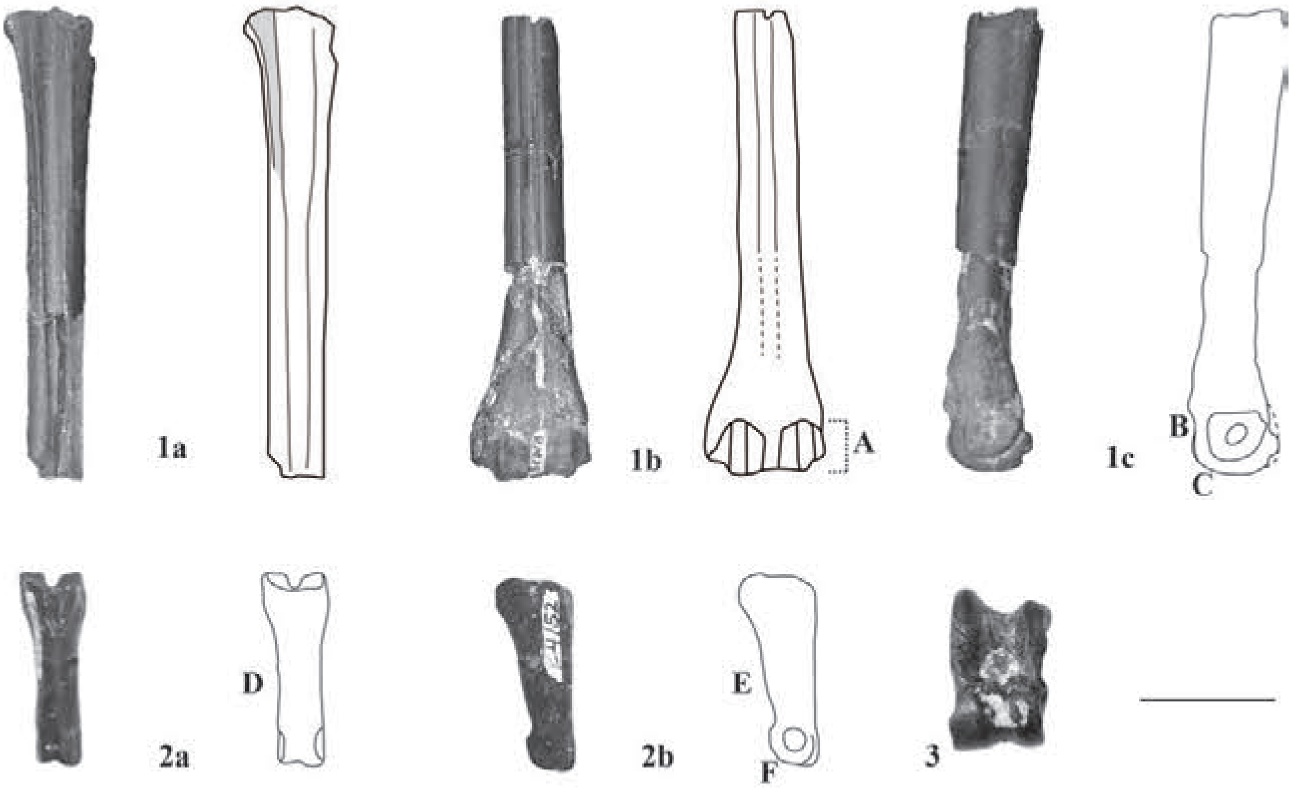

Figure 7. Postcranial remains of *Dremotherium guthi* of Rickenbach (type locality MP29, Switzerland). **1**, fragmentary right metatarsus (NMB–UM2836), proximal part in dorsal view (**a**), distal part in dorsal view (**b**), distal part in lateral view (**c**); **2**, left proximal phalanx (NMO–R4/52), dorsal (**a**) and lateral (**b**) views; **3**, right astragalus (NMO–R2/48), dorsal view (**3**). Light-grey area: long furrow for the lateral extensor tendon; **A**: low articular surfaces with well-individualised condyles; **B**: deep grooves; **C**: flattened outline of the condyle; **D**: straight outline of the external side; **E**: straight outline of the palmar side in lateral view; **F**: flattened dorsal articulation. Scale bar equals 20 mm.

Occurrence: Latest Oligocene (MP28–30) from Germany (Gaimersheim 1) and Switzerland (Rickenbach, Küttigen).

Diagnosis: Only known species of the genus.

Nomenclatural remark: This new species must be referred to as *B. engesseri* Mennecart, 2011, following article 50.1 and the "recommendation 50A concerning multiple authors" of the International Code of Zoological Nomenclature (ICZN, 1999:52, 182).

The scarce referred remains of a new medium-sized ruminant have been discovered in Rickenbach. The material includes upper and lower teeth that display extremely primitive and unique features amongst the Pecora from the Oligocene of Europe, with pretty bunodont and brachyodont crowns. The P4 is stocky (NMB–UM793), with salient and well-developed anterior style, posterior style, and central fold. A deep cingulum surrounds the lingual cone. The upper molars are triangular due to a reduced metaconule (NMB–UM791, NMB–793, NMB–3542, NMO–K11/15). The external postprotocrista is short and straight, and the paracone rib is large and highly bulged. The metacone is globular and highly bulged on the labial wall. The parastyle and mesostyle form globular small columns. A deep cingulum surrounds the protocone. The p4 is characteristic to Pecora in being compact and possessing a well-formed mesiolingual conid (NMO–K5/7). There are no postero- and anterolingual cristids, but there is an anterior stylid. The mesiolabial conid is high and well developed, forming a groove on its posterolabial part. The posterolingual conid is elongated. No cingulids can be observed. The lower molars possess a transverse labial cristid forming a small trigonid and a talonid (NMO–K5/7, NMO–K10/184). The postentocristid is very short, and the lingual cuspids are highly bulged and without rib, which gives a clear primitive aspect to the molars. However, the protoconid possesses an external postprotocrista. The metastylid is very weak; the ectostylid is weak when present; and the entoconulid, globular. Furthermore, the anterior cingulid is strong.

This species clearly differs from the older European pecoran genera *Gelocus* and *Prodremotherium* in having a deep external postprotocrista and a short and advanced p4. Moreover, the molars are highly bunodont; the metaconule and the external postprotocrista are reduced; a deep cingulum surrounds the protocone; and the lower molar lacks a metastylid. These primitive features clearly exclude an affiliation to the classical European Late Oligocene and Early Miocene genera *Amphitragulus*, *Dremotherium*, *Bedenomeryx*, *Andegameryx*, or *Oriomeryx*. The referred upper cheek teeth, however, could correspond to the destroyed upper dentition described as *Amphitragulus feningrei* by Schlosser (1925-26: fig. 14d). However, the holotype of *A. feningrei*, which is represented by a lower tooth row, is clearly different from this new species (see the above description of "*Amphitragulus*" *feningrei*). For these reasons, the referred specimens are assigned to *Babameryx engesseri* gen. et sp. nov. According to Menncart (in progress), this new taxa was also recorded in the contemporaneous localities of Gaimersheim 1 (MP28) and Küttigen (MP30). *Babameryx engesseri* gen. et sp. nov., just like the genera *Dremotherium* and *Amphitragulus*, does not possess direct phylogenetic links with older European ruminants (Mennecart pers. obs.). These mammals, along with the anthracotheriid *Microbunodon* (Lihoreau et al. 2004, Scherler 2011), probably came from a large Asiatic migration during MP28.

7.5 Palaeoecology

Diverse palaeoecologic proxies have been used on the fossils from Rickenbach in order to characterise the palaeoenvironment and palaeoclimate that prevailed in this region during the latest Oligocene. The results obtained from cenogram (Fig. 8) and ecomorphologic (Figs. 4 and 7) studies are summarised here, and the interpretations of the habitat, based also on literature data, are discussed in this section.

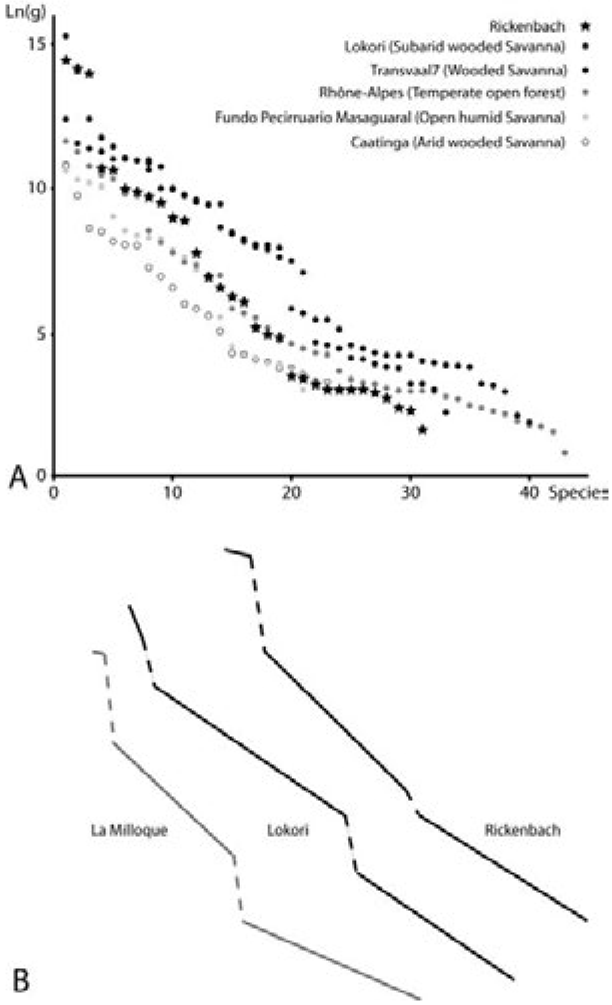

Figure 8. Cenogram from Rickenbach (the body weights of each species are proposed in Table 1) compared with: **A**, current savannah faunas (data from Legendre 1987, 1989); **B**, La Milloque (France, latest Oligocene) and Lokori (Kenya, present), with schematic representation of cenograms showing two breaks each.

7.5.1 Cenogram Analysis

The mammalian community of Rickenbach comprises 31 terrestrial herbivorous and non-flying species (Table 2) and gives an interesting range of body sizes, which allowed us to establish a cenogram for this community (Fig. 8). According to Legendre (1987), Costeur (2005a) classically considered five size classes to compose the mammalian communities (body weights in grams: class 1 = 0–12.5, very small; class 2 = 12.5–500, small; class 3 = 500–8'000 or 10'000, medium; class 4 = 8'000 or 10'000–250'000, large; class 5 = above 250'000, very large). The cenogram of Rickenbach possesses two main breaks separating three different mammal groups. The very large mammals (class 5) from Rickenbach are relatively diversified with three species. The first break is due to the lack of large mammals (between 50’000 and 250’000 g, class 4). Although the medium (class 3), small (class 2), and very small (class 1) mammals form a homogeneous group that is highly diversified with 28 species, the second and smaller break occurs between the small mammals (class 2) and the medium mammals (class 3). The first slope is additionally steeper than the second one.

The shape of the cenogram from Rickenbach is closely related to those of modern savannahs by the number of present mammals (Fig. 8). The habitat extrapolated from the mammalian community of Rickenbach is very similar to that of the wooded savannah of Lokori (Kenya) in the following points: very large mammals of class 5 (elephants and hippopotamuses), first break right after them, and second break. According to Rodriguez (1999), the fact that the second gap is smaller in Rickenbach than in Lokori could be due to a more wooded environment for the former. The similar number of small and very small mammals could indicate a similar warm climate (Legendre 1989). Lokori is dominated by dry conditions with seasonal rainfalls, but this 600-meter high sub-arid savannah may be less dense than the environment of Rickenbach due to the presence of more abundant large mammals (Legendre 1987, 1989).

The structure of the community from Rickenbach is characteristic of those of the latest Oligocene in Europe (MP28-30). The cenograms established for the French localities (e.g., La Milloque, MP29+) possess also two breaks due to a lack of medium-sized species (class 3) and a high number of small mammals (Fig. 8; Legendre 1987, 1989; Costeur 2005b). Legendre (1989) and Costeur (2005a) interpreted this shape of cenogram as corresponding to a quite arid and open environment. However, Rickenbach possesses more medium mammals and a smaller second break, which may indicate a more wooded environment than in La Milloque. The number of small mammal species is greater than that reported from older Oligocene localities (such as St-Henri, St-André, St-Menoux, and Mas de Pauffié, MP26). In this aspect, Rickenbach may correspond to a warmer climate (Legendre 1987) probably linked to the Latest Oligocene Warming. However, Rodriguez (1999) demonstrated that the slope of the micromammals, which is correlated to the number of species, does not seem to be associated with temperature.

7.5.2 Ecomorphologic Analysis

7.5.2.1 Ruminants

There are similar species of ruminant in Rickenbach and La Milloque (*Dremotherium guthi* and “*Amphitragulus*” *quercyi*). A microwear analysis on the mammals from La Milloque reveals that the smallest species fed mainly on leaves, whereas the largest were pure grazer (Novello et al. 2011). The appendicular skeleton of “*A*.” *quercyi* is similar to Cephalophini and animals of light forests (Blondel 1998).

The appendicular bones of *D. guthi* show a clear mixing of adaptations between the types determined by Köhler (1993) as wooded (type A) and open (type B) environments (Fig. 7). The metapods are elongated (type B) and become distally broader (type A). Deep grooves can be observed above the distal articular surface (type B). The distal articulation is low with dorsally flattened and well-individualised condyles (sub-type A1). The lateral view reveals that the outline above the articulation is dorsally convex and palmarly concave (type A). In the proximal part, the furrow for the lateral extensor tendon is long (type A). The proximal phalanges are robust (type A), with a flattened distal articulation on the palmar side (type B). External side is straight dorsally (type A), and the outline of the dorsal surface is slightly concave (type B). In lateral view, the outline of the palmar side is straight (type B). The middle phalanges are short and broad (type A), but become distally thinner (type B). The proximal articular surface is laterally slightly concave (type A). The distal articulation shows a triangular outline from its internal view, with the angle distally directed (type A). Furthermore, the articular surface is extensive dorsally and palmarly (type B).

According to this description, *D. guthi* probably lived in a mixed habitat, such as wooded savannah, or a thin wooded area along a river. Additionally, it is most probable that *D. guthi* had a different ecology from *D. feignouxi*, a later species of the same genus. Indeed, *D. feignouxi* shows a characteristic morphology of type B, and probably lived in a more open area (Becker et al. 2010). Furthermore, *D. guthi* was a mixed feeder

(Novello et al. 2011; Mennecart submitted), whereas *D. feignouxi*, with its elongated cervical vertebrae, was a leaf-eater (Viret 1929; Janis and Scott 1987; Mennecart submitted). *D. guthi* can be compared to the extant bovid *Tragelaphus angasii*, which has the same diet (Nowak 1999) and similar metapods in shape (but not in size). *T. angasii* lives on the edge of the forest by day and feeds in an open area by night (Nowak 1999): *D. guthi* may have a similar ecology. Such results confirm thus an environment ranging from light forest to more open areas for Rickenbach, such as suggested in La Milloque (Novello et al. 2011).

7.5.2.2 Rhinocerotids

The palaeoecologic parameters of *Ronzotherium romani* are close to those of *R. filholi* (mean L for McIII = 194.0; mean L for MtIII = 158.0; McIII GI = 0.212; MtIII GI = 0.222; Brunet 1979), even though the most recent representative of *R. romani*, in Rickenbach, is slightly less slender (mean L for McIII = 156.5; mean GI for MtIII = 0.236). Although the use of Legendre's method to estimate body weight is assumed for the cenogram construction in order to have a homogeneous data source, this method does not always seem adequate for the slender rhinocerotids (Becker et al. 2009), given an overestimation of body weights. By analogy with biometric data of extant rhinocerotids (Guérin 1980), *Ronzotherium romani* was probably of medium size, similar to *Diceros bicornis* (shoulder height of 1.6 m, Nowak 1999), and had a small body weight, similar to *Dicerorhinus sumatrensis* (800'000 g, Nowak 1999). In this regard and based on the regression of body mass on skull length (occipital condyle-premaxilla, Becker et al. 2009) of the specimen from Vendèze (MP24, France; Brunet 1979: tab. 52), the body-weight estimate of *Ronzotherium romani* is 780'000 g. One should notice that this comment on the estimation of ronzothere weights does not affect the general interpretation of the cenogram established in this study. The GI calculated from the metapods is low (McIII GI = 0.192, USTL–GAR260 from Le Garouillas; de Bonis and Brunet 1995; MtIII GI = 0.236, NMO–K3/13 and NMO–H9/9 from Rickenbach), corresponding to a cursorial locomotion type that does not exist in modern rhinoceroses. The low hypsodonty index (HI = 1.0, NMB–UM3832 from Rickenbach) and the down head posture evaluated by analogy with the skulls from Villebramar (*R. filholi*, MP22, France; Brunet 1979: fig. 13, pl. 10) and Vendèze (*R. romani*, MP24, France; Brunet 1979: fig. 15, pl. 18) seem to indicate that *R. romani* was a regular browser, probably feeding preferentially on short vegetation (Janis 1988; Becker et al. 2009).

The estimated body weight of *Diaceratherium lamilloquense* (1'043'000 g) is based on the m1 measurements of the holotype from La Milloque (Michel 1983: tab. 8). It corresponds to a small-to-medium body weight similar to *Diceros bicornis* (1'200'000 g, Nowak 1999). By comparing the MtIII lengths of the specimen from Rickenbach (MtIII L = 112.5, NMO–unnumbered from Rickenbach) with the smallest extant representative *Dicerorhinus sumatrensis* (mean of MtIII L = 149.28, Guérin 1980; shoulder height of 1.30 m, Nowak 1999), *D. lamilloquense* (MtIII L = 112.5, NMO–unnumbered from Rickenbach) can be considered as even smaller. Its locomotion type was mediportal to graviportal (McIII GI = 0.281, Michel 1983; MtIII GI = 0.329, NMO–unnumbered from Rickenbach), close to the locomotion type of *Ceratotherium simum* (McIII GI = 0.300 and MtIII GI = 0.280, Guérin 1980). The hypsodonty index, calculated on an m3 from La Milloque (HI = 0.89; Michel 1983: tab. 8, pl. 3), is very close to the HI of *Ronzotherium romani* and corresponds also to a brachyodont dentition (Janis 1988). Based on direct observations of diacerathere skulls (*D. lemanense*, *D. asphaltense*, *D. aginense*), we assumed an intermediate head posture as in *Diceros bicornis*. According to Becker et al. (2009), the combination of intermediate head-holding with brachyodont teeth points to a rather high-level browser, probably well adapted to feed on high vegetation (Janis 1988; Becker et al. 2009).

By analogies with extant representatives and following the aforementioned anatomical type and the feeding behaviour, the rhinocerotids of Rickenbach represent sympatric species covering two ecologic types. Although the anatomic type of *Ronzotherium romani* is unknown today, the latter is considered a regular browser living in bushland, in the transitional zone between forest and grassland, like *Diceros bicornis* (Nowak 1999). Moreover, the cursorial locomotion type of *R. romani* suggests commonness in open areas. *Diaceratherium* *lamilloquense* corresponds to a regular-to-high browser living in dense or slightly open forests close to waterbeds or swamps. This habitat is somewhat comparable to those of *Rhinoceros sondaicus* and *Dicerorhinus sumatrensis* (Nowak 1999).

Additionally, the sympatry of ronzotheres and diaceratheres, already mentioned by Ménouret and Guérin (2009), is confirmed. According to the latter, the oldest record of this co-occurrence is dated to the earliest Chattian in St-André (MP26, France) and corresponds to the FAD of the diaceratheres, with *Diaceratherium massiliae* (Ménouret and Guérin 2009). The locality of Rickenbach records here the youngest co-occurrence of these two rhinocerotids, which also corresponds to the LAD of the ronzotheres. To sum up, the co-occurrence, in Rickenbach, of *Ronzotherium romani* and *Diaceratherium lamilloquense* attests to a woodland-savannah landscape associated to patches of forested areas and tree-and-shrub savannah.

7.5.2.3 Comment on the Rodents

Even though the ecologic value of the rodent must be discussed with prudence (most of the fossils correspond in fact to rejection pellets of birds, meaning that they were sorted by the predators' tastes), the rodents suggest a typical mixed association as well, with forests (attested by the presence of eomyids and castorids) and more open and/or arid environments (according to the theridomorphs).

7.5.2 Biogeochemistry

In their short synthesis on the rhinocerotids of Rickenbach, Emery et al. (2007) performed biogeochemical analysis on several mammalian teeth (Rhinocerotidae, Anthracotheriidae, Suoidea, and Ruminantia) coming from this locality. They analysed the carbon and oxygen stable isotopes of the carbonate fraction of tooth enamel. They obtained relatively homogeneous $d^{18}O_{CO3}$ values (from -5.4 to -3.0 ‰) amongst the ungulates from Rickenbach, and they calculated a mean annual temperature of nearly 20°C, corresponding to a subtropical climate (Emery et al. 2007). Surprisingly, the $d^{18}O_{CO3}$ values obtained from two ruminants are significantly higher (from -0.9 to -0.5 ‰) than the average covered by the mammalian community. Emery et al. (2007) hypothesised that either 1) these animals fed on leaves that underwent strong vapour transpiration, or 2) they drank water from a different area compared to the other mammals. A third explanation may be the sampling method. When analysing the total crown height for mean isotopic values, differences in the enamel isotopic composition may depend on the tooth considered and on its growing time (e.g., Bryant et al. 1996). Indeed, Merceron et al. (2006) proved the existence of seasonality by analysing two ruminants from the Late Miocene, and they observed similar differences in their $d^{18}O$ values. In Rickenbach, the small brachyodont-toothed ruminants probably needed only three to four months to form the enamel of their whole crown, contrarily to larger mammals that need almost a whole year. The higher $d^{18}O_{CO3}$ values displayed by the ruminants may indeed indicate a warmer season during which their teeth were formed compared to the mean $d^{18}O_{CO3}$ values of the entire community. This confirms the results obtained here from the cenogram, which supposes seasonality during the latest Oligocene.

7.6 General Reconstruction

According to the aforementioned analyses, the palaeoenvironment of Rickenbach was probably a savannah woodland affected by a subtropical climate with clear seasonality. The mean annual temperature of around 20 degrees proposed by the biogeochemical analysis fits well with the floral assemblage, principally represented by palms and Lauraceous. The absence of taxads (joined to the presence of *Pinus)* may indicate a more arid environment as well.

The comparison of Rickenbach with other localities of the same age situated in the Swiss Molasse Basin shows that the palaeotopography of the basin certainly played an important role, both for flora and fauna. In the Subalpine Molasse (e.g., Rochette), the temperature was lower and the humidity clearly higher (Berger 1998). This was probably due to palaeoreliefs implying two main types of environments:

1) a humid swampy area along the early Alpine reliefs, marked by the deposit of the "Coal Molasse" (characteristic of the locality of Rochette);

2) a more arid and seasonal environment, marked by the deposit of lacustrine and evaporitic sediments in the distal part of the basin (e.g., "Calcaires delémontiens" and "Grès et Marnes gris à Gypse", Berger et al. 2005), sometimes drained by fluvial system ("Aarwanger Molasse", characteristic of the locality of Rickenbach).

The environment and climate of the latest Oligocene probably corresponded to the end of the Late Oligocene Warming (Zachos et al. 2001), right before the Mi-1 glaciation (Pekar et al. 2006). This period is marked by the "*Microbunodon* phase" of Stehlin (1922), dated to MP28-30, and the Rickenbach level corresponds to the beginning of the "Terminal Oligocene Crisis" (Becker et al. 2009), the faunal turnover "ETOFE-4" (Scherler 2011), and the phase "Extinction/Migration 3" observed from the ruminants (Mennecart in progress).

7.7 Conclusion

In this paper, we reassessed the faunal list of Rickenbach for the hoofed mammals. We described *Babameryx engesseri* gen. et sp. nov. (Ruminantia, Pecora), and highlighted for the first time the co-occurrence of *Diaceratherium lamilloquense* and *Ronzotherium romani* (Rhinocerotidae). We reconstructed the palaeoecology of the ungulates to determine the palaeoenvironment of Rickenbach as a savannah woodland affected by a subtropical climate with clear seasonality.

The present study emphasises the great interest of hoofed mammals for both biostratigraphy and palaeoecology. These taxa underline the important place of the locality of Rickenbach in the understanding of the Late-Oligocene history. In this respect, the continuation of researches and new excavations are highly expected to highlight both the huge collection of the Naturmuseum Olten and the promotion of the Olten area to the public.

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8 - *Late Oligocene Changes in Mammal Communities of Western Europe: Warming and Cooling Event ?*

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Numerous authors describe the European Oligocene as a quiet period with a relative faunal and climatic stability. Data from the deep-sea record, however, show that during the Late Oligocene (ca. 25.5 Ma) a huge decrease of the δ18O characterizes the well-known "Late Oligocene Warming". The δ18O amplitude could correspond to an increase of 4°C of ocean water in about two million years. This climatic change seems to be linked to a precipitation increase and a woodland expansion in Western Europe that contrasts with the more open environments of the Early Oligocene. Since MP28, the low hypsodont to brachyodont rodents diversify, and digging rodents appear. They testify to more forested and wet environments. In the same way, the ruminant fauna totally changes. Primitive Oligocene taxa with incomplete rumination (*Lophiomeryx*, *Bachitherium*, *Prodremotherium*) disappear and give away to modern Pecora (e.g., *Dremotherium*, *Bedenomeryx*) that will diversify during the Early Miocene. These faunal changes seem to be related to the "Late Oligocene Warming", which is hardly supported by the regional temperature peak recorded from paleofloral data of Central Europe. After this warming event, we observe in MP29 the disappearance of the typical Oligocene *Rozontherium* (Rhinocerotidae) and *Anthracotherium* (Anthrocotheriidae) genera and the migration of new large mammal taxa as *Diaceratherium* (Rhinocerotidae). At the same time, the Swiss Molasse Basin displays a modification in its sedimentary record with the appearance of evaporate deposits, and in its paleoflora with the disappearance of palms and taxads. These local shifts seem to emphasize new environmental conditions, starting in the latest Oligocene and marked by a general trend of aridity and cooling, and leading at the global scale to the Mi-1 Glaciation of the Oligo/Miocene boundary. These results suggest that the major part of the "Late Oligocene Warming" permitted the diversification of forest-dwelling mammals, whereas the end of this event and the transition to the Mi-1 Glaciation implied an environmental damage and new mammal occurrences.

9 - BIOSTRATIGRAPHY OF THE LATEST OLIGOCENE RUMINANTS FROM WESTERN EUROPE

In preparation for *Paleontographica*

9.1 Introduction

The time interval MP28-29 is a transitional period in Europe between the primitive and typical faunas from the Oligocene, and the modern taxa from the Miocene (Vianey-Liaud 1991, Berthet 2003, Becker et al. 2009, Scherler 2011, Scherler et al. 2011, Mennecart et al. 2012). The arrival of the Eupecora replaced the typical primitive Oligocene genera (e.g., *Lophiomeryx* and *Bachitherium*), implying a complete familial turnover within the Rumiantia (Jehenne 1987, Brunet & Jehenne 1992, Blondel 1997, Métais & Vislobokova 2007). This basal radiation of these "evolved" Pecora has been misunderstood for a long time and overlooked.

Usually, the European ruminants *Prodremotherium elongatum*, *Amphitragulus quercyi*, and *Dremotherium feignouxi* were associated with the latest Oligocene deposits (e.g., Viret 1929). Jehenne (1985) reassessed the European Pecora and developed a new taxonomical arrangement and a new biostratigraphy of the latest Oligocene and the Early Miocene ruminants. He differentiated two species of *Dremotherium*: *D. guthi* from the latest Oligocene, which fed on grass or on mixed grass and leaves and was characteristic of a wooded savannah habitat (Novello et al. 2010, Mennecart et al. 2011, Mennecart et al. 2012) and *D. feignouxi*, restricted to the Aquitanian, which was a folivore and lived in open areas (Becker et al. 2010, Mennecart et al. 2012, Mennecart et al. accepted). Jehenne (1988) also described *Bedenomeryx lamilloquensis* based on a complete skull and mandibles. *Amphitragulus quercyi*, *Dremotherium guthi*, and *Bedenomeryx lamilloquensis* were considered as the only ruminant species occurring during the terminal Oligocene (Jehenne 1987, Brunet & Jehenne 1992, Blondel 1997). Jehenne (1985) considered that *Prodremotherium elongatum* was characteristic of the Rupelian, based on undated fossils from the Quercy. Blondel (1997) corrected its biostratigraphy with fossils described in Pech Desse (MP28).

The latest Oligocene is well recorded in Europe with nearly 40 localities dated from MP28 (ca. 24.3 Ma) and MP30 (ca. 22.8 Ma) containing ruminant specimens (Tab. 1, Berger 2011). Blondel (1996, 1997, 1998) reviewed ruminants from the fissure fillings of Pech Desse and Pech du Fraysse (MP28, France). The fissure filling of Gaimersheim 1 (MP28, Germany) is full of ruminant remains, with than 100 fossils. However, the specimens of Gaimersheim 1 are not included in this work. The Rickenbach locality (MP29, Switzerland) has been published in detail by Mennecart et al. (2012; see chap. XX). La Milloque (MP29, France) was widely studied by the Poitiers University (Jehenne 1985, 1987, 1988, Brunet & Jehenne 1992, and Novello et al. 2010). The Coderet locality (MP30, France), located in the town of Bransat (or Branssat), has fossiliferous marly lenses within lacustrine limestone. Viret (1929) first published this locality. Stehlin & Schaub (1951) presented a study of rodents from this locality that they called "Coderet près de Branssat" and "Branssat". Then, Hugueney (1969) collected new specimens and published a complete study of the rodent assemblage. Pech du Fraysse, Rickenbach, and Coderet are the type localities of MP29, MP29 and MP30, respectively.

Mennecart et al. (2012) affirm that the "latest Oligocene and Early Miocene ruminant familial attributions are mainly speculative and confusing". Costeur (2011) confirms the difficulty of assigning these ruminants to a family, even if the specimen is a complete skull. Furthermore, many species from this period had been described under the genus *Amphitragulus*. However, *Amphitragulus* is an animal characterized by specific dental features

Table 1. Geographical and biostratigraphical distribution of the Western European Ruminantia localities during the latest Oligocene.

Species (*type species)	**Locality (* type locality, - direct observations)**	**Country**	**Mammal Zone (* Standard level)**	**References**
«Amphitragulus» quercyi	*Quercy-	France	Oligocene	Filhol 1887, Bouvrain et al. 1986
	Balstahl Bännli	Switzerland	MP28	Engesser pers. com.
	Brochene Flüh	Switzerland	MP30	Engesser & Mayo 1987, Engesser & Mödden 1997
	Cournon	France	MP28	Jehenne 1985, Jehenne 1987, Blondel 1997
	Cournon les Soumérous	France	MP28	Jehenne 1985, Blondel 1997
	Gaimersheim 1	Germany	MP28	Biochrom'97
	Küttigen	Switzerland	MP30	Engesser & Mayo 1987, Engesser & Mödden 1997
	La Milloque	France	MP29	Jehenne 1985, Blondel 1997
	Pech Desse-	France	MP28	Bouvrain et al. 1986
	Pech du Fraysse-	France	*MP28	Blondel 1997
	Réal	France	MP28-29	Jehenne 1985, Blondel 1997
	Rickenbach	Switzerland	*MP29	Engesser & Mayo 1987, Engesser & Mödden 1997, Emery et al. 2007, Mennecart et al. 2012
	Suscevaz	Switzerland	late Chattian	
	Vazzio	France	MP29	Ferrandini et al. 2000
	Vivel del Rio	Spain	MP28	Hugueney et al. 1987
«Amphitragulus» feningrei	*Peublanc	France	MP30	Schlosser 1925-26, Viret 1929, Hugueney 1997
	Basel St Jakob	Switzerland	MP29	Engesser & Mödden 1997
	Coderet	France	MP30	Viret 1929, Hugueney 1969, Hugueney 1997
	Quercy	France	Oligocene	
	Rickenbach	Switzerland	*MP29	Stehlin 1914, Engesser & Mayo 1987, Engesser & Mödden 1997, Emery et al. 2007, Mennecart et al. 2012
Amphitragulus primeavus	*Peublanc	France	MP30	Schlosser 1925-26, Viret 1929, Hugueney 1997
Babameryx engesseri	*Rickenbach	Switzerland	*MP29	Stehlin 1914, Engesser & Mayo 1987, Engesser & Mödden 1997, Emery et al. 2007, Mennecart et al. 2012
	Gaimersheim 1	Germany	MP28	Biochrom'97
	Küttigen	Switzerland	MP30	Engesser & Mödden 1997
Dremotherium guthi	*La Milloque	France	MP29	Jehenne 1987
	Brochene Fluh Waldenbuch	Switzerland	MP30	Engesser & Mödden 1997, Becker et al. 2002
	Les Chauffours	France	MP29	Hugueney 1997
	Chidrac	France	late Chattian	Hugueney 1997
	Coderet	France	MP30	Jehenne 1987
	Comberatière	France	MP29	Jehenne 1987
	Cournon	France	MP28	Jehenne 1987
	Cournon les Souméroux	France	MP28	Jehenne 1987
	Dieupentale	France	MP29	Jehenne 1987
	Ebnatt Kappel	Switzerland	MP28	Engesser & Mödden 1997
	Gaimersheim 1	Germany	MP28	Biochrom'97
	Küttigen	Switzerland	MP30	Engesser & Mayo 1987, Engesser & Mödden 1997
	Mathod près Yverdon	Switzerland	late Chattian	

Dremotherium guthi	Montgiscard	France	late Chattian	Richard 1946, Jehenne 1985, Jehenne 1987
(continued)	Mörigen	Switzerland	MP30	Engesser & Mödden 1997
	Möriken	Switzerland	latest Chattian	Scherler 2011
	Pech du Fraysse	France	*MP28	Blondel 1997
	Peublanc	France	MP30	Jehenne 1987
	Portal	France	MP28	Blondel 1997
	Réal	France	MP28-29	Jehenne 1987, Blondel 1997
	Rickenbach	Switzerland	*MP29	Stehlin 1914, Engesser & Mayo 1987, Engesser & Mödden 1997, Emery et al. 2007, Mennecart et al. 2012
	La Rochette	Switzerland	MP29	Engesser & Mayo 1987, Engesser & Mödden 1997, Berger 1998
	Romagnat	France	MP29	Hugueney 1997
	Rott	Germany	MP30	Mors 2002
	Thézels	France	MP30	Jehenne 1987
Bedenomeryx milloquensis	*La Milloque	France	MP29	Jehenne 1985, 1988
	La Comberatière	France	MP29	
	Dieupentale	France	MP29	Jehenne 1985, 1988
	Küttigen	Switzerland	MP30	Engesser & Mödden 1997
	Rennevile	France	?	
	Vénerque	France	late Chattian	

(see below). An uncertain affiliation to the genus *Amphitragulus* is expressed by quotation marks.

The reassessment of the European ruminants from the latest Oligocene allows the precise diagnosis and definition of the long-known genera *Amphitragulus* and *Dremotherium*. Furthermore, a new interpretation of the latest Oligocene taxonomy and diversity is proposed using at least 6 species of Eupecora, including the newly published *Babameryx engesseri* Mennecart, 2012. Their biostratigraphy and their evolutionary responses to biotic and abiotic events are explained in detail.

9.2 Materials and methods

9.2.1 Systematic palaeontology

The identifications are based on anatomical feature descriptions, comparative anatomy and biometrical measurements, following the ruminant dental terminology of Bärmann & Rössner (2011). All measurements are given with a precision of 0.1 mm. The biochronological framework is mainly based on the synthesis of Berger (2011).

9.2.2 Synonymy abbreviations

Conventional abbreviations used in front of the year in the synonymy list follow Matthews (1973): *, the work validates the species; ., the authors agree on the identification; v, the authors have seen the original material of the reference; ?, the allocation of the reference is subject to some doubt; non, the reference actually does not belong to the species under discussion; pars, the reference applies only in part to the species under discussion; no sign, the authors were unable to check the validity of the reference. Years in italics indicate a work without description or illustration.

9.2.3 Abbreviations

i, lower incisive; c, lower canine; p, lower premolar; m, lower molar; d, lower decidual premolar; C, upper canine; P, upper premolar; M, upper molar; D, upper decidual premolar; dext., right; sin.

9.2.4 Institutional abbreviations

BSPG, Bayerische Staatssammlung für Paläontologie und Geologie (München, Germany); IPHEP, Institut International de Paléoprimatologie, Paléontologie Humaine: Évolution et Paléoenvironnements, Université de Poitiers (France); MHNF, Musée d’histoire naturelle de Fribourg (Switzerland); MHNT, Muséeum d'histoire naturelle de Toulouse (France); MJSN, Musée jurassien des sciences naturelles (Switzerland); MNHN, Musée national d'Histoire naturelle (Paris, France); NMB, Naturhistorisches Museum Basel (Switzerland); NMBE, Naturhistorisches Museum der Burgergemeinde Bern (Switzerland); NMO, Naturmuseum Olten; NMSO, Naturmuseum Solothurn; UCBL, Université Claude Bernard (Lyon, France); USTL, Université des Sciences et Techniques du Languedoc (Montpellier, France).

9.3 Systematic palaeontology

Order **CETARTIODACTYLA** Montgelard, Catzeflis & Douzery, 1997
Suborder **RUMINANTIA** Scopoli, 1777
Infraorder **PECORA** *sensu* Webb and Taylor, 1980
Parvorder **EUPECORA** *sensu* Chapter 1
Genus ***Amphitragulus*** Croizet in Pomel, 1846

Type species. *Amphitragulus elegans* Pomel, 1846 from Saint-Gérand-le-Puy (Allier, France), MN2.

Further included species. "*Amphitragulus" quercyi* Filhol, 1887, *Amphitragulus primaevus* Schlosser, 1925-1926, "*Amphitragulus" feiningrei* Schlosser, 1925-1926.

Neodiagnosis. This inermous ruminant possesses saber-toothed canines that are ovoid in section. The brachyodont crowns are selenodont with a trend to the bunodonty. The upper molars have a relatively quadratic shape with a slightly reduced metaconule. The lingual wall of the metacone is concave. The paracone rib is bulged. The diastema between c and p1 is slightly elongated. The lower p4 possess a well-developed mesolingual conid without a posterolingual cristid. The anterior stylid is absent. On the lower molars, the postentocristid is shortened, the metastylid is small to absent, and the external postprotocristid is present.

Etymology. *Amphi* is the Greek word for around and *tragulus* is the scientific name of the chevrotain, which was first considered to be close to this genus.

"***Amphitragulus*" *quercyi*** Filhol, 1887
Fig.1

1887* v	*Amphitragulus quercyi* Filhol: 12.
1914 v	*Amphitragulus* sp.1 Stehlin: 185
1914 v pars	Ruminantia inc. sedis Stehlin: 185
1931 v	*Dremotherium tolosanum* Richard: 325, figs. 3-12.
1948 v	*Dremotherium tolosanum* Richard: 154.
1973 v	*Amphitragulus* (?) *nouleti* de Bonis et al.: tab. 2(4).
1981	"Dremotheriidés" sp. 3 Brunet et al.: 355.
1984 v	*Rutitherium nouleti* Sudre: fig. 14.
1985 v	*Dremotherium quercyi* Jehenne: 188, figs. 29-31.
1986 v	*Amphitragulus quercyi* Bouvrain et al.: 101, fig. 1.
1987 v	*Dremotherium quercyi* Remy et al.: 188, tab. 4c.
1987 v ?	*Dremotherium quercyi* Engesser and Mayo: 74.
1987 v pars	*Amphitragulus* sp. Engesser and Mayo: 76.
1987 v	*Dremotherium* sp. 3 Engesser and Mayo: 77.
1995 v	*Dremotherium* sp. A Martinez and Sudre: fig. J.
1997 v	*Dremotherium quercyi* Blondel: 580, figs. 4-5.
1997 v ?	Artiodactyl indet. Engesser and Mödden: 486.
1997 v pars	*Amphitragulus* sp. Engesser and Mödden: 488.
1997 v	*Dremotherium* sp. 3 Engesser and Mödden: 490.
1998 v	*Dremotherium quercyi* Blondel: 527.
2000	*Pomelomeryx boulangeri* Ferrandini et al.: 675, figs. 2-4.
2007 v pars	*Amphitragulus* sp. Emery et al.: 56.
2012 v	"*Amphitragulus*" *quercyi* Mennecart et al.: 174, figs. 6.5–6.6.

Holotype. Right mandible with p2-m3 (MNHN Qu 4771, Bouvrain et al. 1986: fig.1).

Species etymology. From the Quercy locality.

Type locality and horizon. Undated old collections of the Phosphorites du Quercy.

Occurrence. Latest Oligocene, From MP28 to MP30, of France (Cournon, Cournons les Souméroux, Grépiac, Gratentour, La Milloque, Pech Desse, Pech du Fraysse, Pechbonnieu, Réal, Vazzio), Switzerland (Balstahl Bännli, Brochene Flüh, Küttigen, Rickenbach, Suscevaz), and Germany (Gaimersheim 1).

Referred material. La Milloque (France): NMB CMB57, fragmentary mandible with m2-3; NMB LM226, fragmentary mandible with m2-3; NMB LM253, fragmen-

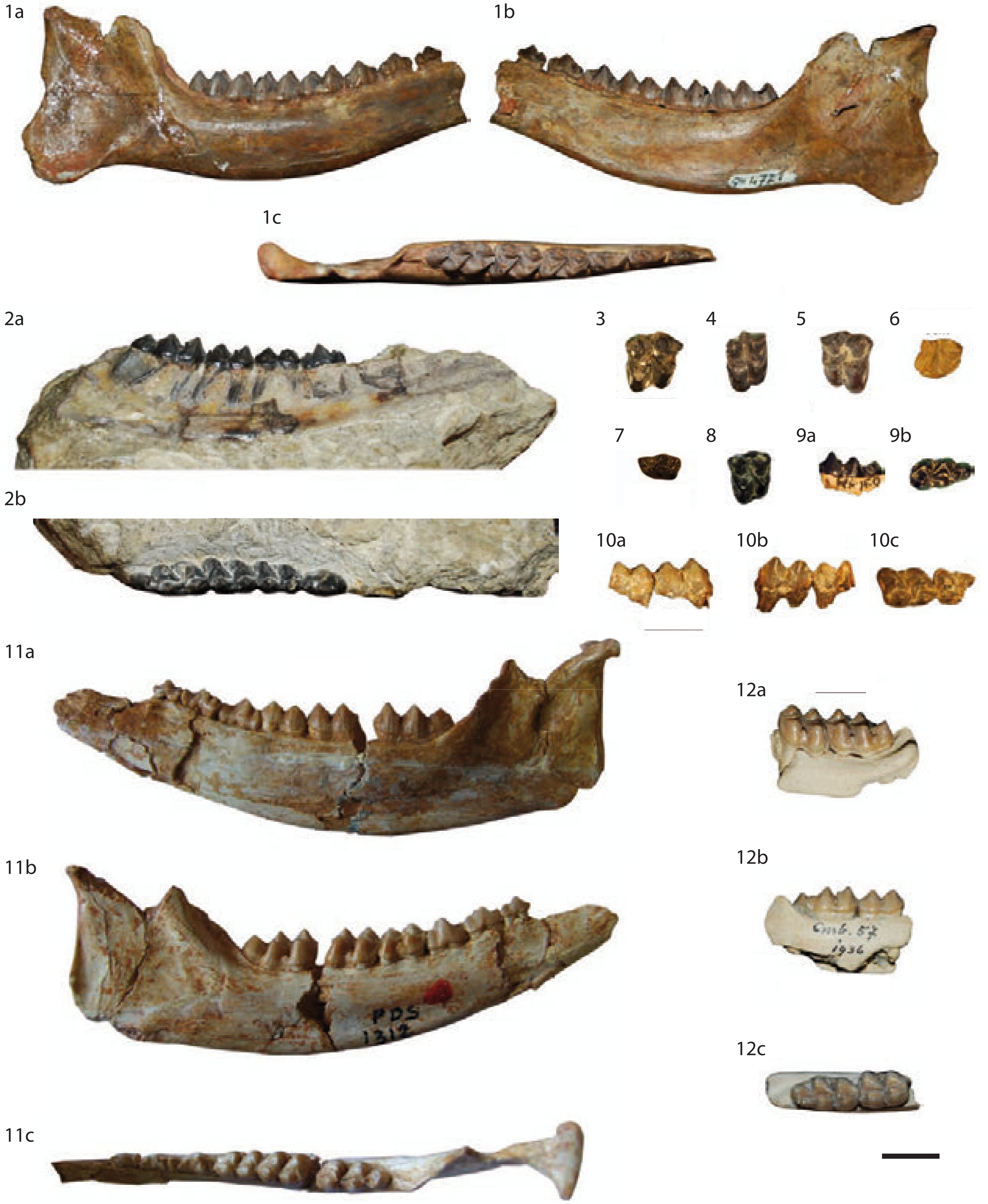


Figure 1. “*Amphitragulus*” *quercyi*: from old collections of the *Phosphorites du Quercy* **1** right mandible with p2-m3 (MNHN Qu 4771, Holotype), labial (**a**), lingual (**b**), and occlusal views (**c**); from *Balsthal “Bännli-Erzmatt”* **2** left complete *corpus mandibulae* with p4-m3 (NMSO 7685), lingual (**a**) and occlusal views (**b**); from *Küttigen* **3** left M2 (NMB UM3895), occlusal view; **4** left M3, (NMB UM3637), occlusal view; **5** right M2 (MNB HR969), occlusal view; **6** right m3 (NMB UM1807), occlusal view; **7** left p4 (NMB HR157), occlusal view; from *Rickenbach* **8** left M1 (MNO I9/48), occlusal view; **9** right m3 (NMB HR150), lingual (**a**), and occlusal views (**b**); from *Brochene Fluh Waldenbuch*: **10** left m1-2 (NMB UM2843), labial (**a**), lingual (**b**), and occlusal views (**c**); from *Pech Desse* **11** right mandible with p2–m3 (USTL PDS 1312), lingual (**a**), labial (**b**), and occlusal views (**c**); from *La Comberatière* **12** left mandible with m2–m3 (NMB Cmb57), labial (**a**), lingual (**b**), and occlusal views (**c**). Scale bar equals 10 mm.

tary mandible with m3; NMB LM255, fragmentary mandible with m3. Pech Desse (France): USLT PDS1312, left mandible with p2-m3, figured in Blondel (1997: 579, fig. 4c); USTL PDS 1342, fragmented left mandible with p4-m1; USTL PDS 1421, right maxillary with D2-4; USTL PDS 1441, left mandible with p2-m2; USTL PDS 1455, right p3-4; USTL PDS1803, right mandible with p2-m3, figured in Sudre 1984 page 17 fig.14; USTL PDS 2134, right mandible with p2-m1; USTL PDS 2135, left m1-2; USTL PDS 2136, right m2-3: USTL PDS 2137, left m1-m3; USTL PDS 2138, right fragmented mandible with p3-m1; USTL PDS 2139, left maxillary with P3-M3; USTL PDS 32151, left mandible with d3-4. Old collections of the Phosphorites du Quercy (France): MNHN Qu 4771 (holotype), right mandible with p2-m3; MNHN Qu4252, left m2-3. Balsthal "Bännli-Erzmatt" (Switzerland): NMSO 7685, left complete *corpus mandibulae* with p4-m3. Küttigen (Switzerland): NMB HR157, left p4; NMB HR969, right M2; NMB UM1807, right m3; NMB UM3637, left M3; NMB UM3895, right M2; NMB UM6164, left M3. Rickenbach (Switzerland): NMB HR150, right m3, figured in Mennecart et al. (2012: 173, fig. 6.5); NMB UM966, left M; NMB UM968, right p4; NMB UM1850, left m, NMO H12/4, right imprint of p3-m3 with preserved m2-3; MNO I9/48, left M1, figured in Mennecart et al. (2012: 173, fig. 6.6); NMB UM3186, right p4; NMSO 7718, fragmented right mandible with p4-m3. Brochene Fluh Waldenbuch (Switzerland): NMB UM2843, left m1-2. Suscevaz (Switzerland): NMB Vd93, right M2.

Amended diagnosis (adapted from Jehenne 1985, Bouvrain et al. 1986, and Mennecart et al. accepted). Small-sized ruminant, older than *Pomelomeryx gracilis* and *P. boulangeri* and more primitive. The premolars are not well molarized. p1 is separated from the p2 by a short diastema. The mesolingual conid is well developed on p4. On the lower molars, the trigonid is large. The postentocristid is present but incomplete. The mesostylid is weak such as the external postprotocristid. The upper molars possess a reduced external postprotocrista and a slightly reduced metaconule. The paracone rib is salient, but there is no metacone rib. The para-, meso-, and metastyles are salient. The lingual cingulum is lacking to very weak.

Description

Mandibles. Only one well-preserved *corpus mandibulae* has been referred (Balsthal, NMO 7685; fig. 1.2). However, the specimen USTL PDS1312 (Blondel 1997, fig. 4c; fig. 1.11) is a nearly complete mandible showing a high gracility of the *corpus mandibulae*. There is little variation in the height of this bone below the check-teeth. The ventral profile is very concave. The diastema c-p1 possesses a small vertical constriction. The *incisura vasorum* is weakly marked, blurred, and relatively far from the m3. The *ramus* is slightly backward oriented and enlarged. The condylar process is quite low.

Lower adult dentition. The lower premolars are relatively simple and compact. The mesolingual conid is very high and strong. The presence of anterolingual and posterolingual cristids seems variable. They are absent on the specimens of Pech Desse, but present on the specimens of Gaimersheim 1 and Balsthal. That gives a different shape to the anterior valley. The latter is nearly closed when the anterolingual cristid is present and widely opened when absent. The anterior conid can be absent (Pech Desse) or present (Gaimersheim 1 and Balsthal) forming a forked anterolabial cristid. The back valley is ovoid and closed by the partial fusion of the posterolingual conid and the posterior stylid.

On the lower molars, the trigonid and the talonid are closed. The cuspids are bunoselenodont. The preprotocristid is oblique and joins the premetacristid in the axis of the tooth. The premetacristid is more elongated on m3 than on m1. The anterior part of m1 is less bulged from m1 to m3, forming a pinched anterior part of the tooth. The internal postprotocristid is longer from m1 to m3, forming a wider trigonid. The external postprotocristid is deep. The oblique prehypocristid is relatively thin and salient. It ends against the postprotocristid. The metastylid is small and salient. The ectostylid is present but smaller from m1 to m3. The talonid is bigger from m1 to m3 due to a longer posthypocristid. The posthypocristid is located side by side to the entoconid, but not fused. The lingual cuspids are relatively laterally compressed. They are not in exactly the same axis. As for the entocristids, the premetacristid is longer than the postmetacristid. All the lingual crests are straight. The postentocristid is very short and does not join the posthypocristid. The back fossa is elongated, narrow, and pinched. The hypoconulid

Table 2. Dental measurements (in mm) of the “*Amphitragulus*” *quercyi*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	Reference	p2		p3		p4		m1		m2		m3	
Amphitragulus quercyi														
La Milloque	NMB CMB57										8.4	6.1	10.6	5.7
	NMB LM226										9.0	5.9	11.5	5.6
	NMB LM253												11.3	6.1
	NMB LM255												10.7	
Pech Desse	USLT PDS1312				7.4	3.5								
	USTL PDS 1441								7.8	5.5	7.9	6.2	11.8	5.6
	USTL PDS1803				8	3.3	7	3.9	7.7	5.2	8.0	5.6	11.5	5.5
	USTL PDS 2134				7.6	3.0			7.2	5.2				
	USTL PDS 2137				7.5	2.8			7.8	5.6	8.0	5.5		
Old collections of Quercy	MNHN Qu 4771		4.9	2.4	6.4	2.8	6.5	3.8	7.3	5.1	8.3	5.5	11.3	5.2
	MNHN Qu4252												11.0	4.9
Balsthal «Bannli-Erzmatt»	NMSO 7685						6.9	4.0	7.4	5.0	8.4	5.4	11.4	5.5
Küttigen	NMB HR157						7.5	4.1						
	NMB UM1807													6.8
	NMB UM3895										8.8	6.4		
Rickenbach	NMB HR150												11.9	6.0
	NMB UM968							4.3						
	NMB UM1850								7.0					
	NMB UM3186						6.5	3.6						
	NMSO 7718						7.6	4.8	7.3	6.0				6.2
Brochen-Flüh Waldenbuch	NMB UM2843										8.2	6.1		
Suscevaz	NMB Vd93										8.2	6.1		
Pech Desse	mean value	Blondel 1997	5.7	2.3	6.7	3.2	7.1	3.9	7.7	5.3	8.3	5.7	12.0	5.7
Pech du Fraysse	mean value	Blondel 1997	5.5	2.5	6.5	3.2	6.7	3.8	7.6	5.2	8.0	6.0	11.8	5.7
La Milloque	mean value	Jehenne 1985	5.3	2.5	6.0	3.1	6.4	4.0	7.4	5.3	8.0	6.0	10.8	5.7

Locality	Inventory number	Reference	d3		d4	
Pech du Fraysse	mean value	Blondel 1997	6.3	2.5	8.7	3.8

Locality	Inventory number	Reference	P2		P3		P4		M1		M2		M3	
Küttigen	NMB HR969										8.9	10.3		
	NMB UM3637													9.5
	NMB UM6164												9.1	
Rickenbach	NMO I9/48													
Pech Desse	mean value	Blondel 1997			7.5	5.4	5.6	7.2	7.2	8.4	8.0	9.2	8.6	9.9
Pech du Fraysse	mean value	Blondel 1997			7.4	6.0	6.1	7.7	7.8	8.9	8.9	10.0	8.3	10.5
La Milloque	mean value	Jehenne 1985	7.2	4.8	7.1	6.4	6.0	7.4	7.3	8.5	8.4	9.8	8.2	9.5

Locality	Inventory number	Reference	D2		D3		D4	
Pech Desse	mean value	Blondel 1997	7.1	3.7	8.5	6.0	7.3	7.8

forms the edge of the latter. The anterior cingulid is variable, from weak to very strong. The posterior cingulid is quite small.

Upper adult dentition. The upper molar cusps are relatively bunodont. They have a reduced and straight external postprotocrista and a slightly reduced metaconule. The premetaconulecrista and the fossae are simple without neocrista. The paracone rib is salient, but there is no metacone rib. The para-, meso-, and metastyles are salient. The lingual cingulum is very weak to absent.

Taxonomical attribution

Even if the teeth are not as bunoselenodont as in *Amphitragulus elegans*, the referred specimens have quite primitive features, such as the absence of lingual cristid on lower premolar, and a highly reduced metastylid, a low crown, a small postentocristid, and, although laterally compressed, bulged lingual cuspids on lower molars. All of these characteristics exclude an affiliation with either the *Dremotherium* or *Bedenomeryx* genus. Furthermore, the extremely small size of "*Amphitragulus" quercyi* is a distinguishing feature for the latest Oligocene ruminants of Europe.

"*Amphitragulus" quercyi* has been listed in Boningen (type locality for MP27; Engesser & Mayo 1987) this could be the oldest record for this species. However, the referred specimens of this locality are too badly preserved to be identified (Engesser & Mödden 1997, personal observation).

Vislobokova (1997) presents a small species *Amphitragulus* attributed to *A*. cf. *quercyi* (also written *Amphitragulus* cf. *querey* in Vislobokova 1996 and Devyatkin et al. 2002) in the latest Oligocene Yagan Tologoi locality in Mongolia (MP28-30). Vislobokova & Daxner-Höck (2002) also described another small *Amphitragulus* sp. from the Ikh Argalatuyn locality (Mongolia), which could be closer to "*A*." *quercyi*. An Asiatic origin for this species, such as *Dremotherium guthi* (see below) is suggested, but the resolution of the age of these localities remains approximate.

Ferrandini et al. (2000) identified, on the basis of the size, the imprint of an upper dentition from the Vazzio locality (Corsica, France), as *Pomelomeryx boulangeri*. However, they could not compare this unusual specimen with "*Amphitragulus" quercyi* due to the lack of an upper dentition description of the latter (Blondel 1997). The recent publication of Mennecart et al. (2012) presents the first description of upper dentition of "*A." quercyi* in Rickenbach. The specimen from Vazzio is similar in size and shape and probably belongs to this species. Jehenne (1985) and Blondel (1997) suggested a likely affiliation between "*A." quercyi* and the genus *Pomelomeryx*. If a speciation phase clearly occurred at the Oligocene/Miocene limit within the ruminant lineages *Dremotherium*, *Amphitragulus* and *Bedenomeryx* and the lineages of other mammal groups (e.g., Becker et al. 2009), the case of the lineage of "*A." quercyi* remains unclear. A strong size reduction seems to occur between "*A." quercyi* and the various species of *Pomelomeryx*, but, in some aspects, more advanced characteristic occurred on lower molars of the older "*A." quercyi*, such as laterally compressed lingual cuspids and the development of the metastylid. Furthermore, the specimens from Pech Desse and the holotype MNHN Qu 4771 from the Phosphorites du Quercy are slightly different from those of Gaimersheim 1 and Balsthal. The presence of only one species with a large intraspecific variability or the record of two different small species of ruminants during the latest Oligocene cannot be excluded.

"*Amphitragulus*" *feningrei* Schlosser, 1925-26
Fig. 2

1914 v pars	Ruminantia inc. sedis div. Stehlin: 185.
1925-26	*Amphitragulus feningrei* n. sp. Schlosser: 387, pl. XII, figs. 15-16.
1929 v	*Amphitragulus feningrei* Viret: 229, pl. XXXI, figs. 14-15.
1969 v	*Amphitragulus feningrei* Hugueney: 194.
1985v pars	*Dremotherium guthi* Jehenne: 173.
1987 v pars	*Amphitragulus* sp. Engesser and Mayo: 76.
1997	*Amphitragulus feningrei* Hugueney: 421.
1997 v	*Amphitragulus feningrei* Hugueney: 426.
1997 v pars	*Amphitragulus* sp. Engesser and Mödden: 488.
2007 v pars	*Amphitragulus* sp. Emery et al.: 56.
2012 v	"*Amphitragulus*" *feningrei* Mennecart et al.: 174, figs. 6.8–6.10.

Lectotype. Left fragmentary mandible with p2-m3 (Schlosser 1925-26: pl. XII, fig. 14a). The specimen was lost during the Second World War.

Parlectotype. Left fragmentary maxillary with P2-M3 (Schlosser 1925-26: pl. XII, fig. 14d). The specimen was lost during the Second World War.

Species etymology. In tribute to the archaeologist and palaeontologist Mr. A. Feningre.

Type locality and horizon. Peublanc (Auvergne, France), MP30.

Occurrence. Latest Oligocene, from MP29 to early MP30, of France (Coderet, Dieupentale, Quercy) and Switzerland (Basel St Jakob, Rickenbach).

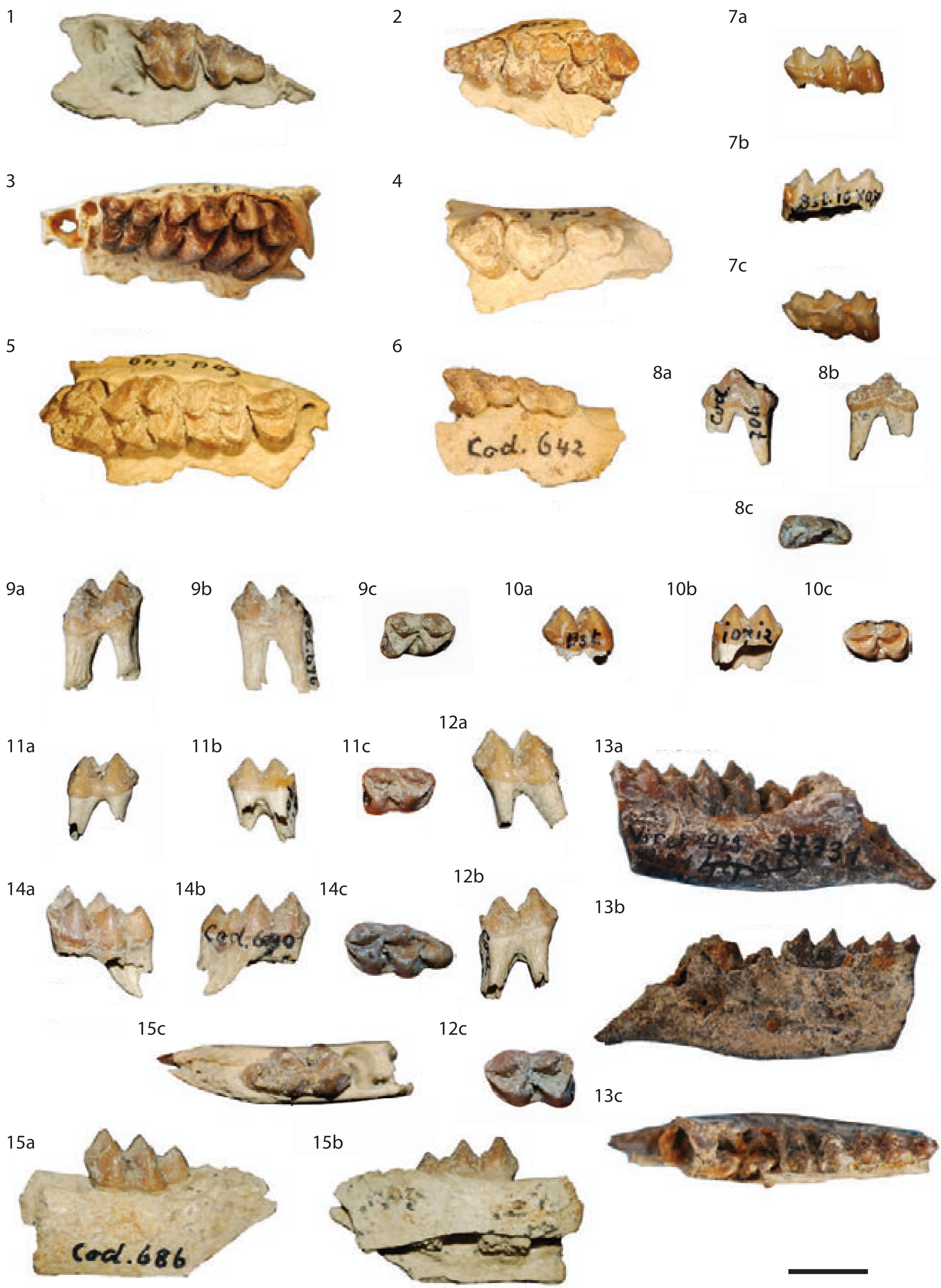
Referred material. Coderet (France): NMB Cod4486, right P3; NMB Cod4484, left m1; NMB Bst705, left m1; NMB Bst704, left m2; NMB Bst703, broken left m3; NMB Bst10690, fragmentary right maxillary with D3-4; NMB Bst10691, fragmentary left maxillary with P4-M1; NMB Bst10692, fragmentary left maxillary with D4; NMB Bst10693, left P4; NMB Bst10694, left M1; NMB Bst10695, right M1; NMB Bst10697, left M1; NMB Bst10698, left M2; NMB Bst10699, left M2; NMB Bst10700, left M1; NMB Bst10701, left M2; NMB Bst10702, left M3; NMB Bst10703, right M1; NMB Bst10704, broken left m; NMB Bst10705, right m3; NMB Bst10706, left m3; NMB Bst10708, right m2; NMB Bst10709, right m1; NMB Bst10711, right D4; NMB Bst10712, left m1; NMB Bst10714, left m1; NMB Bst10715, broken right m3; NMB Bst10716, left P3; NMB Bst10718, left D3; NMB Bst10719, right P3; NMB Cod640, fragmentary right maxillary with P4-M3; NMB Cod641, fragmentary right maxillary with P2-4; NMB Cod642, fragmentary right maxillary with D2-3; NMB Cod643, fragmentary left maxillary with D3-M1; NMB Cod644, fragmentary right maxillary with D4; NMB Cod686, left m3; NMB Cod688, left d4; NMB Cod690, left m3; NMB Cod691, right d4; NMB Cod693, right d4; NMB Cod695, left m2; NMB Cod696, right m2; NMB Cod698, right m1; NMB Cod699, right m1; NMB Cod700, right d2; NMB Cod701, right m1; NMB Cod702, left m3; NMB Cod703, left m2; NMB Cod703, right m2; NMB Cod704, right p2; NMB Cod706, left p3; NMB Cod707, left d4; NMB Cod708, left d3; NMB Cod709, right m1; NMB Cod710, right d4; NMB Cod711, left p3; NMB Cod712, right P2; NMB Cod712, right m1; NMB Cod713, right d3; NMB Cod714, left p4; NMB Cod715, right d3; NMB Cod716, right d4; NMB Cod718, left D2; NMB Cod726, right d3; UCBL FSL 97730, left maxillary with D4-M2, figured in Viret 1929 pl.(XXXI fig. 13); UCBL FSL 97731, left mandible with d4-m1, figured in Viret 1929 (pl. XXXI fig. 14). Mouillac, old collections of the Phosphorites du Quercy (France): NMB QuB144, fragmentary left mandible with m1-3. Basel St Jakob (Switzerland): NMB OB531, broken right d4. Rickenbach (Switzerland): NMO H11/64, left d4-m1; NMO I7/3, right M2; NMO I7/4, right M3; NMO I9/48, left M1; NMO K4/35, mandible mandible with m1; NMO K8/64, right m; NMO K11/95, right m2; NMB HR9, left mandible with p3-m3; NMB HR164, right M2; NMB HR180, right p4; NMB HR928, right M1; NMB UM2592, left M1; NMB UM796, right m2; NMB UM1849, left mandible with p4-m3; NMB UM1852, right M1; NMB UM7926, broken right M.

Neodiagnosis. The crowns are brachyodont and selenodont. The upper molars are almost quadratic, slightly laterally compressed with a slightly reduced metaconule. The external postprotocrista is short and curved. The paracone is globular with a well-developed rib, but the metacone rib is absent. The para- and mesostyles are globular and form small columns, whereas the parastyle is anteriorly projected. There is no lingual cingulum. The lower molars possess small trigonid and talonid basins due to an acute angle of the protoconid and the hypoconid. The lingual cuspids are sharp and laterally compressed, and their ribs are bulged. The entoconulid and metaconulid are small, but the latter is more salient. Additionally, the external postprotocristid is very well-marked.

Description

Mandibles. The mandible is slender and the ventral outline is concave. The height of the *corpus mandibulae* is quite similar from below d4 to m2. Below m3, there is an inflection that could be the *incisurae vasorum*. The lingual groove is weakly marked. The labial part is bulged.

Lower decidual dentition. The decidual lower premolars are more molarized from d2 to d4. d2 is very narrow and low-crowned. The cuspids are in the axis of the tooth. The tranverse cristid is weak. The posterior cristid joins the posterolingual edge of the crown. The posterior valley is very weak. The anterior part of d3 is sharp and sa-


1
2
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Cod. 690
Cod. 686

Figure 2. “*Amphitragulus*” *feningrei*: from *Coderet* **1** right maxillary with D3-4 (NMB Bst10690), occlusal view; **2** left maxillary with D3-M1 (NMB Cod643), occlusal view; **3** left maxillary with D4-M2 (UCBL FSL 97.730), occlusal view; **4** right maxillary with P2-4 (NMB Cod641), occlusal view; **5** right maxillary with P4-M3 (NMB Cod640), occlusal view; **6** right maxillary with D2-3 (NMB Cod642), occlusal view; **7** left d4 (NMB Bst10707), labial (**a**), lingual (**b**), and occlusal views (**c**); **8** left p3 (NMB Cod706), labial (**a**), lingual (**b**), and occlusal views (**c**); **9** right m2 (NMB696), labial (**a**), lingual (**b**), and occlusal views (**c**); **10** left m1 (NMB Bst10712), labial (**a**), lingual (**b**), and occlusal views (**c**); **11** right m1 (NMB Cod701), labial (**a**), lingual (**b**), and occlusal views (**c**); **12** left m2 (NMB Cod695), labial (**a**), lingual (**b**), and occlusal views (**c**); **13** left mandible with d4-m1 (UCBL FSL 97.731), labial (**a**), lingual (**b**), and occlusal views (**c**); from *Rickenbach* **14** left m3 (NMB Cod690), labial (**a**), lingual (**b**), and occlusal views (**c**); **15** mandible with left m3 (NMB Cod686), occlusal (**a**), labial (**b**), and lingual views (**c**); **16** M1 (NMB HR928), occlusal view; **17** M2 (NMB HR164), occlusal view; **18** M3 (NMO I7/4), occlusal view; **19** M1 (NMB UM1852), occlusal view; **20** M2 (NMO I7/3), occlusal view; **21** M1 (NMB UM2592), occlusal view; **22** right m2 (NMB UM796), labial (**a**), lingual and (**b**) occlusal views (**c**); **23** left mandible with d4-m1 (NMO H11/64), labial (**a**), lingual and (**b**) occlusal views (**c**); **24** left mandible with p3-m3), labial (**a**), lingual (**b**), and occlusal views (**c**); from old collections of the *Phosphorites du Quercy* **25** left mandible with m1-m3 (NMB QuB144), labial (**a**), lingual (**b**), and occlusal views (**c**). Scale bar equals 10 mm.

lient. Its anterior conid is high, transverse, and well developed. Its anterior cristid is slightly oblique and can have a well-developed anterior stylid (NMB Cod715) forming a huge anterior valley. The anterior conid is clearly separated from the mesolabial conid, but linked to it at its base by an oblique anterolabial cristid. The anterior valley is widely opened, without cingulid. The transverse cristid joins the lingual edge of the tooth. The posterolingual conid is high, transverse, and slightly removed from the posterolabial cristid. The posterolabial conid possesses a weak cristid. It forms the posterolabial edge of the tooth. The posterior stylid is lingual. The posterior valley is narrow, weakly lingually opened. On d4, the cristids are short and straight. The preprotocristid joins the posterior cristid of the anterolabial conid and the premetacristid joins the posterior cristid of the anterolingual conid. The anterolabial conid and the anterolingual conid are anteriorly oriented and highly laterally compressed. The anterior conid bears an external posterior cristid. The anterior cristid of the anterolabial conid and the anterior cristid of the anterolingual conid join together on the anterior axis of the tooth. The metaconid is slightly oblique with straight metacristids. The preprotocristid is oblique. The protoconid and the hypoconid are relatively high and slightly proclivous. The protoconid possesses a well-marked external postprotocristid. The lingual cusps are laterally compressed. The internal postprotocristid is transverse. The metacristids are aligned. There is quite a big metastylid at the base of the postmetacristid, forming a link with the preentocristid. There are two ectostylids, one on the base of the protoconid and the other on the base of the anterior conid. The prehypocristid is oblique joining the base of the preentocristid. The posthypocristid is transverse and does not fuse with the postentocristid, forming a gap on the lingual part of the tooth between the entoconid and the posthypocristid. The latter ends with a well-developed entoconulid. The posterior cingulid is weakly developed. The anterior cingulid is very elongated and ends in the axis of the protoconid.

Lower adult dentition. The lower premolars are more molarized, larger, and higher from p2 to p4. p2 is highly laterally compressed. p3 is just a little bit smaller than p4. On the p2, the anterior conid is anteriorly oriented and possesses an anterior cristid. On the other premolars, the anterior conid is more oblique. The mesolabial conid is well developed and located in the centre of the tooth. The transverse cristid is posteriorly oriented, forming a small posterior valley. p2-3 do not possess a mesolingual conid. p2 possesses neither developed posterolabial conid nor posterolingual conid. The posterolabial conid is better developed on p4 than on p3. On p3, the posterolingual conid cannot be distinguished and the posterolabial conid joins the oblique posterolingual conid, closing the posterior basin. p4 has a mesolingual conid posterior to the mesolabial conid. This mesolingual conid is quite big and joins the mesolabial conid by the transverse cristid on its posterolabial part. The posterolabial cristid is elongated and joins the unindividualised posteriror stylid, only visible on the labial part by a rib and an anterior groove. Its posterolabial cristid constitutes the posterolabial angle of the tooth. Its posterior stylid closes the posterior part of p4. Between the mesolingual conid and the posterolabial conid, the posterolingual conid is latterly compressed and oblique. It can be linked to the posterolabial cristid. The posterior cristid is curved and joins the posterolingual angle of the tooth, without closing the posterior basin. The anterior cingulid is missing.

The lower molars become larger from m1 to m3. The metastylid is bulged on m1 to narrow on m3. There is no anterior conid. The molar cristids are short and straight. The metaconid is slightly oblique with straight metacristids. The preprotocristid is oblique. The protoconid and the hypoconid are relatively high and slightly proclive. The protoconid possesses a well- marked external postprotocristid. The lingual cusps are laterally compressed. The internal postprotocristid is transverse. It ends at the base of the metaconid. The metacristids are aligned. The metastylid is quite big. Between the protoconid and the hypoconid, there is a very strong ectostylid. The prehypocristid is oblique. It joins the base of the preentocristid. The posthypocristid is transverse and does not fuse with the postentocristid, forming a gap on the lingual part of the tooth. The latter ends with an entoconulid more or less developed. The posterior cingulid is weakly developed, whereas the anterior one is very well marked. It is very elongated and ends in the axis of the protoconid. On m3, the entoconulid is weakly developed to absent. Its oblique postentocristid is long and well developed. It ends at the opening of the back fossa of m3, without any fusion. The hypoconulid forms the posterolabial angle of m3. The back fossa of m3 is narrow and oblique. The

Table 3. Dental measurements (in mm) of the "*Amphitragulus*" *feningrei*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	Reference	p2		p3		p4		m1		m2		m3	
Amphitragulus feningrei														
Coderet	NMB Bst10705												12.5	6.2
	NMB Bst10706												13.8	6.6
	NMB Bst10708										9.5	6.4		
	NMB Bst10709								8.7	5.7				
	NMB Bst10712								8.6	5.5				
	NMB Bst10714								8.5	5.4				
	NMB Bst10715													5.7
	NMB Bst703													6.4
	NMB Bst704										9.8	6.5		
	NMB Bst705								8.8	5.6				
	NMB Cod4484								8.8	6.1				
	NMB Cod686												12.6	6.0
	NMB Cod690												13.1	6.1
	NMB Cod695										9.8	6.3		
	NMB Cod696										9.7	6.1		
	NMB Cod698								9.0	6.0				
	NMB Cod699								8.9	5.7				
	NMB Cod701								8.6	5.5				
	NMB Cod702												13.7	6.4
	NMB Cod703											6.4		
	NMB Cod703										9.5	6.5		
	NMB Cod704		6.1	2.9										
	NMB Cod709								9.0	6.0				
	NMB Cod711				7.4	3.4								
	NMB Cod712								9.1	5.8				
	NMB Cod713				8.0	3.1								
	NMB Cod714						8.2	4.7						
	NMB Cod715				8.2	3.5								
	NMB Cod726				7.6	3.0								
	UCBL FSL 97731						9.7	3.9	9.0	5.1				
Mouillac	NMB QuB144								8.6	5.7	9.4	6.2	13.4	5.9
Rickenbach	NMB HR9				8.3	4.0	9.1	5.1	9.5	6.4	9.4	7.0	13.2	6.8
	NMB UM796										10.6	5.9		
	NMB UM1849						8.1		9.2		9.2		13.3	
Quercy	NMB QuB144								8.1	5.7	8.4	6.0	12.7	5.8
Peublanc	mean value	Schlosser 1925-26					9.0						12.5	

Locality	Inventory number	Reference	d2		d3		d4	
Coderet	NMB Cod688						10.2	4.7
	NMB Cod691						10.3	4.6
	NMB Cod693						10.0	4.3
	NMB Cod700		7.6	2.7				
	NMB Cod707						10.2	4.4
	NMB Cod708				7.8	3.1		
	NMB Cod710						10.1	4.1
	NMB Cod716						9.7	4.1
Peublanc	mean value	Sclosser 1925-26					10.0	

Table 3 (continued). Dental measurements (in mm) of the "*Amphitragulus*" *feningrei*, in each row, the first d set of ata is the length and the second is the width.

Locality	Inventory number	Reference	P2		P3		P4		M1		M2		M3	
Coderet	NMB Bst10693						6.9	8.5						
	NMB Bst10694								8.7	10.7				
	NMB Bst10695								8.8	10.0				
	NMB Bst10697								9.1	10.4				
	NMB Bst10698									10.9				
	NMB Bst10699										9.5	10.5		
	NMB Bst10700								8.8	9.6				
	NMB Bst10701										9.4			
	NMB Bst10702												10.0	10.4
	NMB Bst10703								8.6	10.6				
	NMB Bst10716				8.3	6.8								
	NMB Bst10719				7.0	5.7								
	NMB Cod4486					6.5								
	NMB Cod640						5.7	7.2	8.1	8.8	9.5	9.3	9.2	9.4
	NMB Cod641		7.4	4.6	8.1	7.2	6.5	7.8						
	NMB Cod643								9.3					
	NMB Cod712		7.7	4.6										
	UCBL FSL 97730								8.5	9.5	9.4	10.4		
Rickenbach	NMB HR164										9.6	12.2		
	NMB HR928									9.9				
	NMB UM2592								9.2	10.2				
	NMB UM1852									10.1				
Peublanc	mean value	Schlosser 1925-26							10.3	10.6				

Locality	Inventory number	Reference	D2		D3		D4	
Coderet	NMB Bst10692						8.3	8.7
	NMB Bst10711						7.5	8.8
	NMB Bst1090				8.9	5.6	8.2	8.1
	NMB Cod642		7.5	3.7	9.5	5.1		
	NMB Cod643				8.7	5.5	8.0	8.3
	NMB Cod644						8.2	8.3
	UCBL FSL 97730						8.1	7.8
Peublanc	mean value	Schlosser 1925-26			8.0		8.0	7.5

prehypocristulid joins the flank of the posthypocristid. The posthypocristulid joins the entoconulid, such as the postentocristid.

Maxillary. The maxillary bone possesses a big infraorbital foramen at the level of P2 or D2, depending on the age of the specimen. The maxillary interalveolar crest begins just posterior to D2. It is highly curved, this could indicate that the diastema is very short.

Upper decidual dentition. D2 is much more compressed than P2, with a much more anterior metaconule. The paracone is bulged on the anterior part. The parastyle is small. The posterior part of this tooth is pinched, while the anterior part is rounded. The metaconule forms a small bulge on the lingual face. D3 is a triangular tooth. The metacone possesses a small labial rib. The mesostyle is salient. The paracone is oblique and more salient than the metacone. The metaconule is oblique and tetrahedron-shape due to the posterolabial postmetaconulecrista, the labial premetaconulecrista, and an anterior crista forming a small basin. The postmetaconulecrista is low. The premetaconulecrista ends between the paracone and the metacone. The anterior part of the D3 forms a buckle. D4 is molar-shaped, but much smaller. This tooth is trapezoidal with only 3 roots. The protocone is vertical, whereas the metaconule is backwards. The anterior fossa is wider than the posterior fossa, due to the preprotocrista, which is straight and oblique, and the curved postmetaconulecrista. The preprotocrista reaches the base of the well-developed parastyle. It forms a globular small column on the anterolabial edge of D4. The postprotocrista ends at the half part of the premetaconulecrista and does not fuse with it. The premetaconulecrista is bifurcated, with a smaller branch going inside the anterior fossa and the other joining the anterior base of the metacone. The postmetaconulecrista reaches the base of the postmetacrista. The labial cusps are not aligned but parallel. The globular paracone possesses a strong paracone rib with a small anterior groove. The preparacrista is straight and reaches the parastyle. The postparacrista is very short without any fusion. The mesostyle is very strong and globular, forming a small column. The metacristae are curved forming a concave metacone with a small metacone rib. The postmetacrista ends with a metastyle. The anterior cingulum is weak.

Upper adult dentition. P2 is stocky and rounded, with an ellipsoid shape. The anterolabial cone is anterior and globular. The anterior style is not as salient as on P3. The anterolingual cone is weakly salient and posterior to the anterolabial cone. There is a weak anterolingual cingulum linked to the anterolingual crista and a strong posterolingual one linked to the posterolingual crista. P3 is stocky with an anterior style, pinched and salient. The short and straight anterolabial crista links the anterior style to the anterolabial cone. The short anterolingual crista ends before the anterolingual cone. The latter is globular and very salient. The latter separates the fossa in two small basins. The curved posterolingual crista joins the straight posterolabial crista. The anterolabial cone is bulged on its anterior part forming a groove between it and the anterior style. There is a weak posterior cingulum. P4 is massive, relatively high-crowned, and possesses a low anterolabial cone with an anterior groove. The anterior style is globular. The central fold is weak. The anterolingual cone is very selenodont. The anterolingual crista joins the apex of the anterior style. There is a bulged posterior style. The posterolingual crista joins the posterolabial crista at a low height. The anterolabial crista and the posterolabial crista are aligned. There is no cingulum.

The upper molars are quadrangular with main cusps occasionally bearing interne ribs starting from the apex (Schlosser 1925, NMO I9/48). They are bigger from M1 to M3. The anterior and posterior fossae are narrow, with an anterior fossa, which is generally wider than the posterior one. The protocone and the metaconule are slightly anteriorly proclivous. The preprotocrista is transverse and joins the parastyle. It possesses a distal notch deeper from M1 to M3. The postprotocrista can be straight and oblique, ending at the middle of the premetaconulecrista and forming a wide anterior fossa (NMO I9/48 and NMO I7/4), or it can be highly curved and ended at the base of the posterolingual part of the paracone without connecting the premetaconulecrista (UCBL FSL 97730, Schlosser 1925, NMO I7/3). The ectostylide is very weak. The premetaconulecrista is elongated and oblique, and ends between the paracone and the metacone without connecting them. This crista can be distally bifurcated (NMO I7/4). The postmetaconulecrista is more transverse. The parastyle forms the anterolabial edge of the upper molars. It forms a small column that weakens from M1 to M3. It is joined to the paracone by a small and straight preparacrista. The paracone is high and globular. The paracone rib is less prominent, with anteriorly blurred groove, from M1 to M3. The mesostyle forms a small column that weakens from M1 to M3. The metacone is oblique, concave, and is not aligned with the paracone. The metacone rib is more blurred from M1 to M3.

Taxonomical attribution

“*Amphitragulus” feningrei* is clearly different from the other known ruminants during the latest Oligocene and the Early Miocene in Europe. This medium-sized ruminant, between the size of the large *Dremotherium guthi* and the small “*Amphitragulus” quercyi*, is the most common ruminant from Coderet (type locality MP30). Its cheek teeth are more bunodont than the various species of *Dremotherium* or *Bedenomeryx*, but more selenodont than the species of *Amphitragulus, Pomelomeryx, Friburgomeryx*, and *Oriomeryx*. On its lower premolars, the posterolingual conid is often isolated. Its lower molars possess narrow cuspids, whereas in *Prodremotherium*, *Dremotherium* and *Amphitragulus* they are quite large. The metaconid rib is bulged as in *Prodremotherium*, whereas *Dremotherium* possesses a salient metaconid rib. The latter is lacking in *Amphitragulus* and *Pomelomeryx*. The entoconid does not possess a rib, such as *Prodremotherium*. Contrary to *Amphitragulus*, the entoconulid and the metaconulid are well developed and individualized on lower molars. The dental crowns of *Dremotherium* and *Bedenomeryx* are clearly more hypsodont than those of “*A.” feningrei* and the size of the teeth are larger. The lingual cristids of *Dremotherium* remain quite high, whereas they end at the base of the lingual conids in “*A.” feningrei*. The *Dremotherium* metastylid is inserted into the lingual wall without a big recess. Contrary to *Dremotherium*, the metastylid of “*A.” feningrei* is salient. However, the specimens of Bransat possess a less developed mesostylid than those of Rickenbach. In *Dremotherium*, there is a big gap between the entoconulid and the end of the entoconid, due to the postentocristid, which stops on the upper part of the entoconid. In “*A.” feningrei*, the postentocristid stops at the level of the entoconulid, enclosing this gap. Contrary to *Prodremotherium*, *“A.” feningrei* possesses a well-developed external postprotocristid on the lower molars. On the upper molars, the paracone is globular with a well-developed rib, but the metacone rib is absent. The para- and mesostyles are globular and form small columns, whereas the parastyle is anteriorly projected. The aspect of the upper molars is more primitive than those of *Dremotherium*.

For all these above-mentioned reasons, “*Amphitragulus*“ *feningrei* is a valid species. Furthermore, a new genus will be assigned to this species, increasing the importance of the mammalian response to the latest Oligocene faunal turnover in Europe.

The specimens referred to “*Amphitragulus*“ *feningrei* in the original description of Schlosser (1925-26) were lost during the Second World War (Gertrud Rössner and Kurt Heissig, comm. pers.). However, the illustrations are precise and cover the lower and upper adult and deciduous tooth rows. “*Amphitragulus*“ *feningrei* is much more abundant than *Amphitragulus primaevus* in the type locality Peublanc (Schlosser, 1925-26). Viret (1929, pl. XXXI, figs. 14–15) also described and illustrated the latter ruminants in Coderet. The specimens, stored at the Faculté des Sciences de Lyon (France), are similar in size and shape to the specimens of “*Amphitragulus” feningrei* from Peublanc. Furthermore, additional specimens were excavated by the Naturhistorisches Museum Basel (Switzerland) during the 1940’s and stored under the name Bransat or Branssat (Hugueney 1969). The fossil collection from this locality is quite important, and is composed of only two species of ruminants. “*Amphitragulus*“ *feningrei* clearly dominates with numerous dental and postcranial remains.

Amphitragulus primaevus Schlosser, 1925-26

Fig. 3

1925-26*	*Amphitragulus primaevus* n. sp. Schlosser: 387, figs. 2 and pl. XII, figs. 13.
1929 v non	*Amphitragulus primaevus* Viret: 229.
1969 v non	*Amphitragulus primaevus* Hugueney: 194.
1997	*Amphitragulus primaevus* Hugueney: 421.

Lectotype. Left p2 and p4-m3 (Schlosser 1925-26: pl. XII, fig. 14a). The specimen had been lost during the Second World War.

Parlectotypes. Left P2 P4-M3 P2 (Schlosser 1925-26: fig. 2), left P2 (Schlosser 1925-26: pl. XII, fig. 13a), left

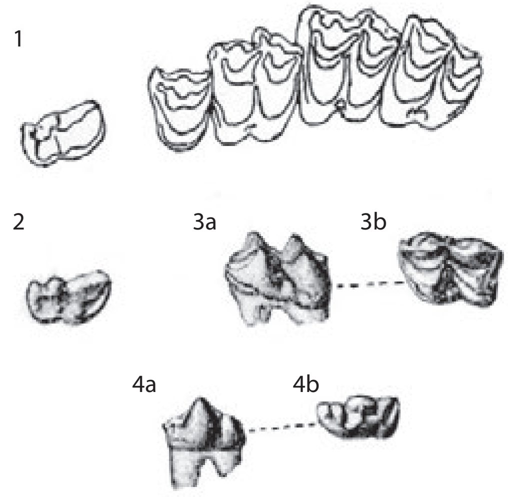


Figure 3. *Amphitragulus primaevus* published by Schlosser (1925-26): from *Peublanc* **1** left P2, P4-M3 (Schlosser 1925-26, Fig.2), occlusal view; **2** left P2 (Schlosser 1925-26, Fig. 13a, Tab. XII), occlusal view; **3** left m2 (Schlosser 1925-26 , Fig. 13b, Tab. XII), labial (**a**) and occlusal views (**b**); **4** left p4 (Schlosser 1925-26, Fig. 13c, Tab. XII), labial (**a**) and occlusal views (**b**).

m2 (Schlosser 1925-26: pl. XII, fig. 13b), and left p4 (Schlosser 1925-26: pl. XII, fig. 13c). The specimens had been lost during the Second World War.

Species etymology. Latin word for juvenile.

***Type locality and horizon*.** Peublanc (Auvergne, France), MP30.

Discussion

The remains of this taxon have not been observed directly in this study. Following the description and drawing of Schlosser (1925-26) (Fig. 3), the molars are relatively bunoselenodont. The metaconule is not reduced and the anterior cingulum is small to absent. The paracone and the metacone are aligned. p4 possesses a big and bulged mesolingual conid without posterolingual cristid. The lower molars seem to lack a metastylid.

Amphitragulus primaevus differs from *Babameryx engesseri* by the absence of a huge anterior cingulum surrounding the protocone and the reduction of the metaconule on the upper molars, which are bunodont. However, the teeth are more primitive than those of "*Amphitragulus*" *feningrei* and *Dremotherium guthi*. Looking at the p4 morphology, the size of the metasytlid, the bunoselenodonty, an attribution to the genus *Amphitragulus* seems coherent. Furthermore, the smaller size of this taxon, in comparison to the younger *Amphitragulus elegans*, and the larger size than the contemporaneous "*A.*" *quercyi*, confirms that *A. primaevus* is different from the other *Amphitragulus* species.

Viret (1929), confirmed by Hugueney (1969) in a faunal list, attributed specimens to *Amphitragulus primaevus* in Coderet. However, in her listing from 1997, *A. primaevus* was replaced by *Dremotherium guthi*, due to a synonymisation in Jehenne (1985). Viret (1929) attributed a left M1 and a right d2 to *A. primaevus* due to the presence of a big ectostylid. However, this characteristic is also present in *D. guthi*, but these fossils have not been found in the collections. Furthermore, no remains of *A. primaevus* were found in the collections of Basle and Lyon.

Schlosser (1925-26) and Viret (1929) postulated that "*A.*" *feningrei* and *A. primaevus* were the ancestors of *A. lemanensis* and *A. elegans*, respectively. The first proposition seems to be inadequate, due to the probable synonymisation of *A. lemanensis* with *A. elegans* (Loïc Costeur and Gertrud Rössner, comm. pers.) and a more advanced grade considering the tooth morphology of "*A.*" *feningrei*. However, the possible affiliation between *A. primaevus* and *A. elegans* has to be kept in mind.

Babameryx Mennecart, 2012

Type species. *Babameryx engesseri*

Diagnosis. Medium-sized, brachyodont bunoselenodont Pecora; p4 compact and possessing well-formed mesolingual conid and anterior stylid; lower molars possessing highly bulged lingual cuspids without a rib and a protoconid with an external postprotocristid; P4 stocky with a deep lingual cingulum and a central fold; upper molars with reduced metaconule, large and highly bulged paracone rib and metacone rib, and deep cingulum surrounding the protocone.

Etymology. From *Baba*, "elder" or "patriarch" in eastern languages (Arabic, Russian, Slavic), and *meryx*, Greek for ruminants, in reference to primitive eupecoran features.

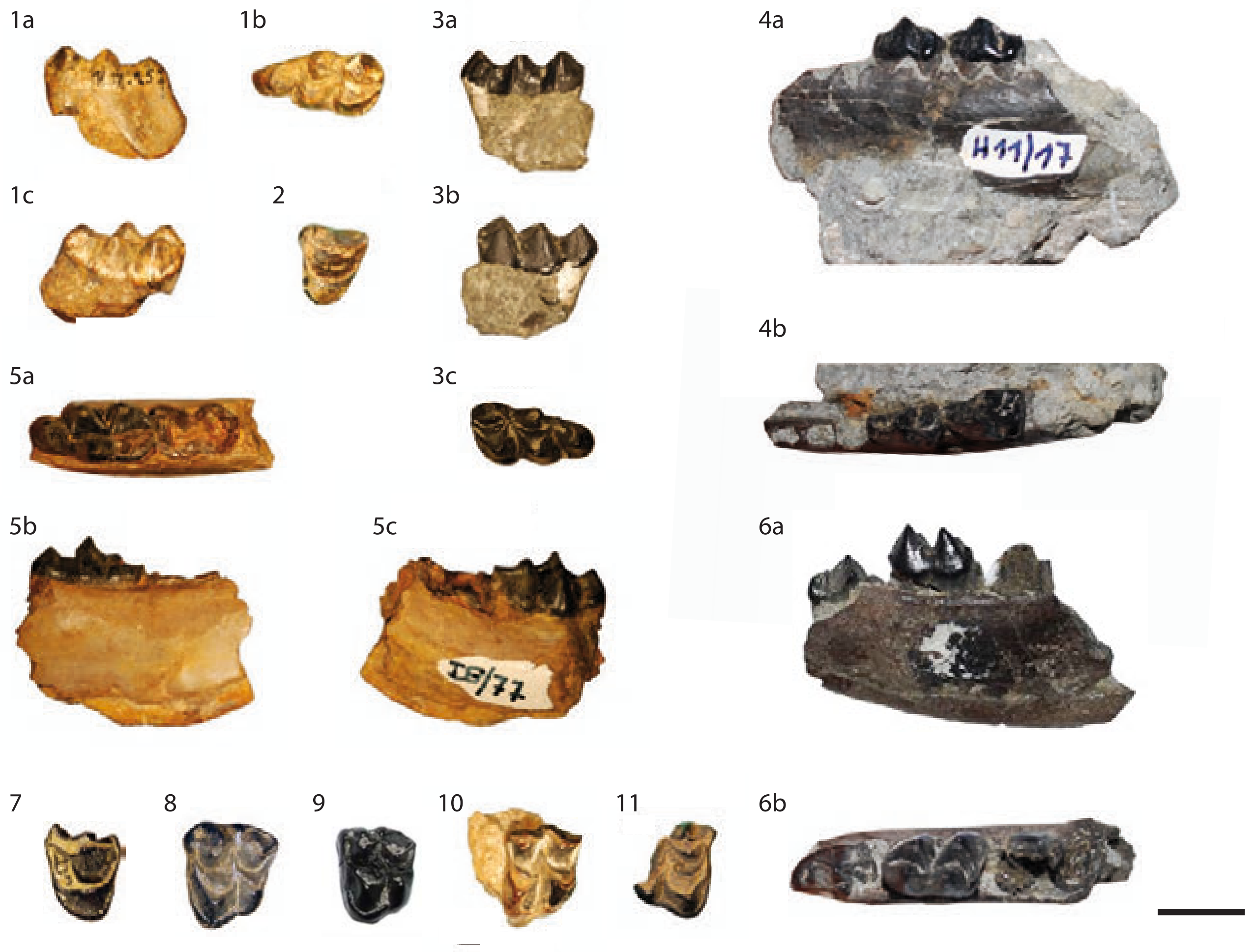


Figure 4. *Babameryx engesseri*: from *Küttigen* **1** right m3 (NMB), labial (**a**), lingual (**b**), and occlusal views (**c**); **2** left P4 (NMB), occlusal view; from *Rickenbach* **3** left m3 (NMB), labial (**a**), lingual (**b**), and occlusal views (**c**); **4** left mandible with p3-4 (NMO H11/17), labial (**a**), occlusal views (**c**); **5** left m3 (NMO I8/77), occlusal (**a**), lingual (**b**), and labial views (**c**); **6** right mandible with p4-m1 (NMO K5/7, paratype), lingual (**a**) and occlusal views (**b**); **7** right P4 (NMB UM793, paratype), occlusal view; **8** left M3 (NMB UM2833, paratype), occlusal view; **9** left M1 (NMO K11/15, holotype) occlusal view; **10** left M2 (NMB UM791), occlusal view; **11** right M (NMB UM3542), occlusal view. Scale bar equals 10 mm.

Babameryx engesseri Mennecart, 2012
Fig. 4

1914 v pars	Ruminantia incertae sedis Stehlin: 185.
1987 v pars	*Amphitragulus* sp. Engesser and Mayo: 76.
1997 v pars	*Amphitragulus* sp. Engesser and Mödden: 488.
2007 v pars	*Amphitragulus* sp. Emery et al.: 56, not fig. 10.
2012 v	*Babameryx engesseri* gen. et sp. nov. Mennecart et al.: 174, figs. 6.1–6.4.

Holotype. NMO K11/15, left M1 (8.9 x 10.7) (Mennecart et al. 2012: 172, fig. 6.2).

Paratypes. NMO K5/7, right fragmentary mandible with erupting p4 and m1 (Mennecart et al. 2012: 172, fig. 6.1); NMB UM2833, left M3 (Mennecart et al. 2012: 172, fig. 6.3); NMB UM793, right P4. (Mennecart et al. 2012: 172, fig. 6.4).

Species etymology. In tribute to Burkart Engesser, in recognition to his palaeontological investigations in the Swiss Molasse Basin and especially in Rickenbach.

Type locality and horizon. Rickenbach (Solothurn, Swiss coordinate), European mammal reference level MP29.

Occurrence. Latest Oligocene, from MP28 to MP30, of *Germany* (Gaimersheim 1) and Switzerland (Rickenbach, Küttigen).

Table 4. Dental measurements (in mm) of the *Babameryx engesseri*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	p3	p4	m1	m2	m3
Babameryx engesseri						
Küttigen	NMB UM257					13.5 6.6
Rickenbach	NMO H11/17	8.1 4.7	8.8 5.0			
	NMO H11/32			10.0 6.7		
	NMO I8/77				9.0	13.8 6.6
	NMO K5/7			9.5 6.4		
	NMO K10/134					15.3 6.6
	NMB HR12		8.8 4.9			
	NMB Ri74					13.6 7.0
	NMB UM794				11.0 7.5	13.0 6.6

Locality	Inventory number	P4	M1	M2	M3
Küttigen	NMB UM253	8.1 9.3			
Rickenbach	NMO K11/15			8.4 10.9	
	NMB UM791			8.4 10.6	
	NMB UM793	7.6 8.8			
	NMB UM2594				11.2 12.2
	NMB UM2833				10.0 11.6
	NMB UM3542				12.5

Referred material. Küttigen (Switzerland): NMB UM253, left P4; NMB UM257, right m3. Rickenbach (Switzerland): left M1; NMO H11/17, left mandible with alveoli of p1-2 and the teeth p3-4; NMO H11/32, right mandible with m1; NMO I8/77, left mandible with alveoli of m2 and the tooth m3; NMO K5/7, right fragmentary mandible with erupting p4 and m1 (Mennecart et al. 2012: 172, fig. 6.1); NMO K11/15, left M1 (Holotype, Mennecart et al. 2012: 172, fig. 6.2), left m3; NMB HR12, left p4; NMB Ri74, left m3; NMB UM791, left M2; NMB UM793, right P4 (Mennecart et al. 2012: 172, fig. 6.4); NMB UM794, left m2-3; NMB UM2594, right M; NMB UM2833, left M3 (Mennecart et al. 2012: 172, fig. 6.3); NMB UM3542, left fragmented M.

Diagnosis. Same as that of the genus.

Description

The scarce referred remains of this new medium-sized ruminant have been discovered in Rickenbach and Küttigen. The material includes upper and lower teeth that display extremely primitive and unique features amongst the Pecora from the Oligocene of Europe, with quite bunodont and brachyodont crowns. The following descriptions are mainly based on Mennecart et al. (2012).

Upper dentition. P4 is stocky (NMB UM793), with salient and well-developed anterior style, posterior style, and central fold. A deep cingulum surrounds the lingual cone. The upper molars are triangular due to a reduced metaconule (NMB UM791, NMB 793, NMB–3542, NMO K11/15). The external postprotocrista is short and straight, and the paracone rib is large and highly bulged. The metacone is globular and highly bulged on the labial wall. The parastyle and mesostyle form small globular columns. A deep cingulum surrounds the protocone.

Lower dentition. Considering the tooth socket of the p1 is not separated from p2 (NMO H11/17). p3 and p4 have basically the same shape. However, p4 is larger than p3 and the mesolingual conid is lacking on p3. p4 is compact and has a well-developed mesolingual conid (NMO K5/7). There are no postero- and anterolingual cristids, but there is an anterior stylid. The mesiolabial conid is high and well developed, forming a groove on its posterolabial part. The posterolingual conid is elongated. No cingulids can be observed. The lower molars possess a transverse posterolabial cristids forming a small trigonid and talonid (NMO K5/7, NMO K10/184). The postentocristid is very short, and the lingual cuspids are highly bulged and without ribs, giving a clear primitive aspect to the lower molars. However, the protoconid possesses an external postprotocrista, the metastylid is very weak, the ectostylid is weak to absent, and the entoconulid is globular. The hypoconulid is large, forming a relatively large back fossa on m3. Furthermore, the anterior cingulid is strong.

Taxonomical attribution

This species clearly differs from the older European pecoran genera *Gelocus* and *Prodremotherium*, and the Early Miocene *Friburgomeryx* in having a strong external postprotocrista and a short and advanced p4. Furthermore, the molars are highly bunodont, the metaconule and the external postprotocrista are reduced, a strong cingulum surrounds the protocone, and the lower molars lack a metastylid. These primitive features clearly exclude an affiliation to the classical European Late Oligocene and Early Miocene genera *Amphitragulus*, *Dremotherium*, *Bedenomeryx*, *Andegameryx*, or *Oriomeryx*. On the other hand, the referred upper cheek teeth could correspond to the destroyed upper dentition described as "*Amphitragulus" feningrei* by Schlosser (1925-26: fig. 14d). However, the holotype of "*A." feningrei*, which is represented by a lower tooth row, is clearly different from this new species (see the above description of "*Amphitragulus*" *feningrei*). For these reasons, the referred specimens are assigned to *Babameryx engesseri*. *Babameryx engesseri*, in the same way as *Dremotherium* and *Amphitragulus*, does not possess direct phylogenetic links with older European ruminants.

Genus **Dremotherium** Saint-Hilaire, 1833

Type species. *Dremotherium feignouxi* Saint-Hilaire, 1833 from Saint-Gérand-le-Puy (Allier, France), MN2.

Further included species. *Dremotherium guthi* Jehenne, 1987, *Dremotherium cetinensis* Ginsburg, Morales & Soria, 1994.

Neodiagnosis. This inermous ruminant possesses saber-toothed canines, which are triangular in section. The diastema between c and p1 is elongated. The very-selendont crowns of the cheek teeth are relatively high. The upper molars are quadratic with a large metaconule. The lingual wall of the metacone is concave. The posterior fossa can have a metaconule fold. The premetaconulecrista is often forked. There is no cingulum. p4 possesses a well-developed mesolingual conid with a posterolingual cristid. The presence of an anterior stylid forms a forked anterior conid. On the lower molars, the postentocristid ends before joining the posthypocristid. The metastylid and the external postprotocristid are present.

Etymology. *Dremo* means running in Greek and *therium* means beast in Greek, because Saint-Hilaire presumed that the absence of elongated canines meant that this taxon could not climb mountains, unlike its cousin the extant *Moschus*, thus it was a beast of the plains.

Dremotherium guthi Jehenne, 1987
Fig. 5

1925 v	*Dremotherium* sp. Schlosser: 385, fig1.
1925 non	*Amphitragulus primaevus* n. sp. Schlosser: 387, pl. XII, fig. 13
1929 v	*Prodremotherium* ? sp. Viret: 229, pl. XXI, figs. 15-16.
1929 v	*Amphitragulus primaevus* Viret: 229, pl. XXXI, figs. 13-14.
1931 pars	*Dremotherium feignouxi* Richard: 319, pl. XVI, figs. 7-8.
1931 pars	*Dremotherium nanum* Richard: 321, pl. XVII, fig. 1 (not fig. 2).
1948	*Dremotherium nanum* Richard: 154.
1948	*Dremotherium feignouxi* Richard: 154.
1948	*Amphitragulus elegans* Richard: 165.
1948 non	*Dremotherium nanum* Richard: 172.
1969 v	*Amphitragulus primaevus* Hugueney:194.
1969 v	*Prodremotherium* sp. Hugueney:194.
1979 pars	*Dremotherium* sp. Brunet: 183.
1981	"Dremotheriidés" sp.2 Brunet et al.: 355.
1984 v	*Amphitragulus* sp. Engesser et al.: 14.
1985 * pars	*Dremotherium guthi* n. sp. Jehenne: 173, figs. 26-28.
1987 v pars	*Amphitragulus* sp. Engesser et Mayo: 76.
1987 v pars	*Dremotherium* sp.1 Engesser et Mayo: 77.
1987 *	*Dremotherium guthi* n. sp. Jehenne: 133, figs. 2-3.
1995 v	*Dremotherium* sp.B Martinez and Sudre: fig. K.
1996	*Dremotherium* cf. *guthi* Vislobokova:
1997 v	*Dremotherium guthi* Blondel: 582, fig. 6.
1997 v pars	*Amphitragulus* sp. Engesser et Mödden: 488.
1997 v pars	*Dremotherium* sp.1 Engesser et Mödden: 490.
1998 v	*Amphitragulus* sp. Berger: tab. 1.
2002 ?	*Dremotherium* sp. Mörs: 182.
2002	*Dremotherium* cf. *guthi* Vislobokova: 223.

2007 v pars	*Amphitragulus* sp. Emery et al.: 56, fig. 10.
2012 v	*Dremotherium guthi* Mennecart et al.: 171, figs 6.11–6.14 and 7.

Holotype. Right partial maxillary with P3-M3 (FSL LM.1968.MA.40, Jehenne 1987: 134, fig.2).

Paratype. Right mandible with p3-m3 (LM.1968.MA.1, FS Poitiers, Jehenne 1987: 134, fig.3).

Etymology. In tribute to the Professor Chr. Guth who was first to excavate the La Milloque locality again.

Type locality and horizon. La Milloque (Lot-et-Garonne, France), MP29.

Occurrence. Latest Oligocene, from MP28 to MP 30, of France (Coderet, Comberatière, Cournon, Cournon-les-Souméroux, Dieupentale, Grépiac, Montgiscard, Pech du Fraisse, Pechbonnieu, Peublanc, Portal, Réal, Thézels), Switzerland (Brochene-Fluh Waldenburg, Ebnatt Kappel, Küttigen, La Rochette, Mathod près Yverdon, Möriken, Rickenbach), and Germany (Gaimersheim 1).

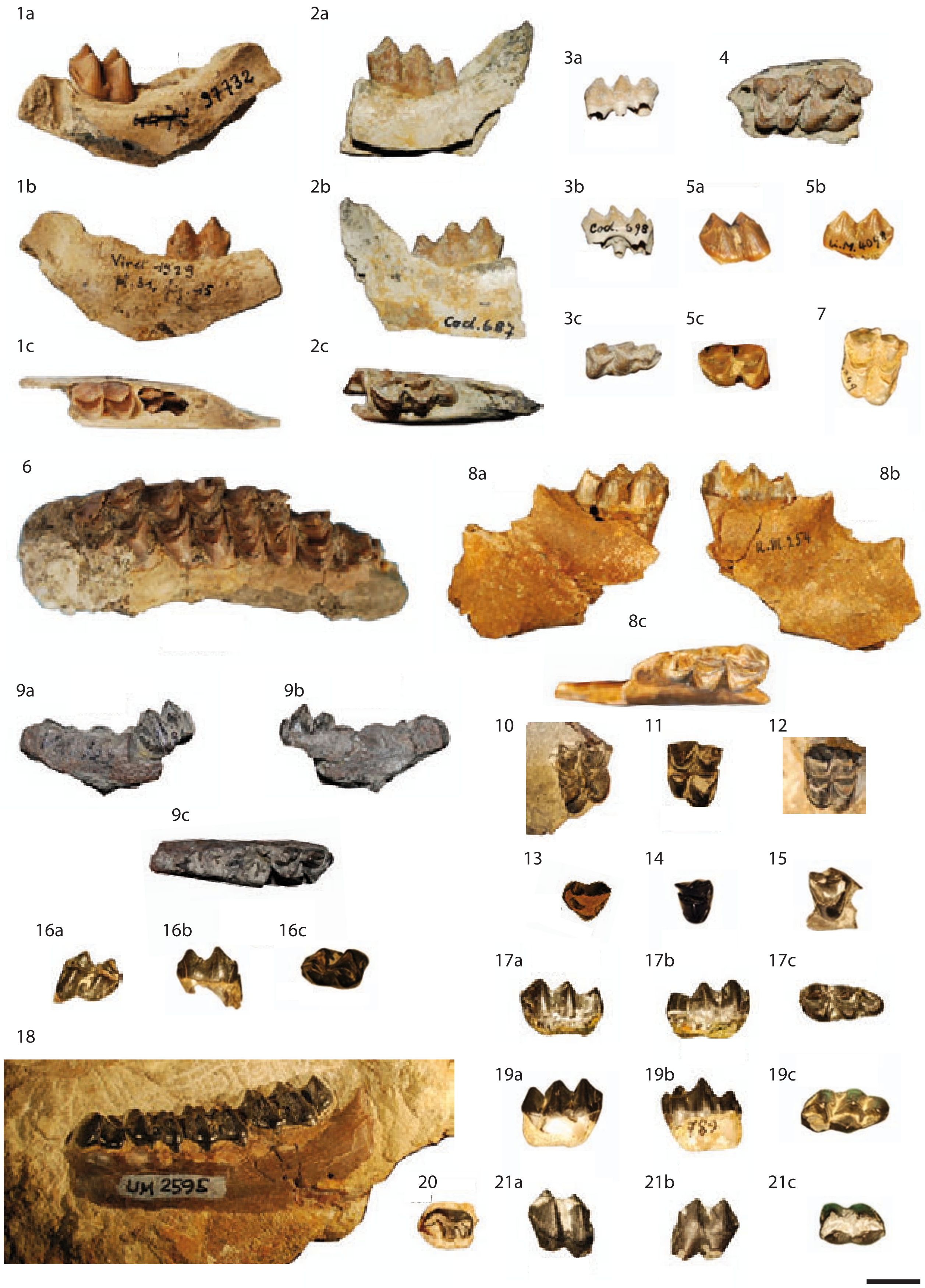
Referred material. Coderet (France): NMB Bst698, right M; NMB Bst700, left P4; NMB Bst701, left P2; NMB Bst10710, right D4; NMB Cod639, fragmentary maxillary with D4-M1; NMB Cod687, left m3; NMB Cod692, right d4; NMB Cod698, right d4; NMB Cod705, right d3; NMB Bst10707, left d4; UCBL FSL97732 fragmentary left mandible with m1 and an erupting m2. La Milloque (France): NMB LM220, mandible with p2-m3, NMB LM221, mandible with p3-m3; NMB LM222, mandible with p3-m3; NMB LM224, fragmentary mandible with m1-3; NMB LM225, mandible with p4-m3; NMB LM232, fragmentary mandible with m2-3; NMB LM233, mandible with p3-m3; NMB LM234, mandible with p4-m3; NMB LM235, fragmentary maxillary with P2-M3; NMB LM238, fragmentary mandible with m1-3; NMB LM239, fragmentary mandible with m1-3; UCBL FSL 97.732, left fragmentary mandible with m2 and erupting m3 (Viret 1929: 229, pl. XXXI fig. 15) . Thézels (France): UCBL 3794, fragmentary right mandible with m1-3; UCBL 3795, M; UCBL 3796, right m3; UCBL 9841, Fragmentary right maxillary P3-M3; UCBL 9842, Fragmentary left maxillary P4 and M2-3. Pech du Fraysse (France): USTL PDS 1485, right m3. Brochene-Flüh Waldenburg (Switzerland): NMB UM2843, left M1-2. Küttigen (Switzerland): NMB HR155, left m3; NMB HR968, right M1; NMB HR970, left P4; NMB UM249, right M3; NMB UM250, right M2; NMB UM251, left M1; NMB UM252, left M; NMB UM254, right m3; NMB UM255, left m3; NMB UM1803, right d3; NMB UM1804, right M3; NMB UM1805, left M2; NMB UM1806, left M3; NMB UM3894, left M2. La Rochette (Switzerland): NMB Vd122, fragmentary left mandible with m1. Mathod près Yverdon (Switzerland): NMB Vd75, left p3. Möriken (Switzerland): NMB UM4098, left m2. Rickenbach (Switzerland): NMB HR162, left m2; NMB HR243, right M1; NMB HR245, right m1; NMB Ri28, left p3; NMB Ri33, right P4; NMB Ri73, right M2; NMB Ri76, right P4; NMB UM789, right m3; NMB UM790, right M1; NMB UM959, right M1; NMB UM960, fragmentary right p3; NMB UM962, right p3; NMB UM1331, right M2; NMB UM1603, left m3; NMB UM1604, left m2; NMB UM1851, left P3; NMB UM2046, right m1; NMB UM2595, left *corpus mandibulae* with p4-m3; NMB UM2601, fragmentary left p3; NMB UM2602, fragmentary left m2; NMB UM3131, left M3; NMB UM3568, right M3; NMO H11/6, left mandible with m2-3; NMO K4/31, left m2-3; NMO K10/184, m3; NMO K11/95, right m1; NMO L6/38, left M2.

Diagnosis (modified from Jehenne 1987). *Dremotherium* are older and smaller than *D. feignouxi*. P2-3 are stockier and not strongly molarized. The lower premolars are well molarized. The lower molars are quite hypsodont with relatively weak developed metastylid.

Description

Mandibles. The diastema between the tooth socket of c and p1 is relatively elongated. The *corpus mandibulae* is slender and the lower outline is concave. The incisura vasorum is marked and large. The mandible process is large such as the ramus. The condylar process is slightly backwards oriented. The coronoid process is enlarged and backwards.

Lower adult dentition. The crowns are high and the cusps are very selenodont. p4 is short and laterally compressed, and its anterior part can be bifurcated due to the presence of an anterior stylid and conid. Its well-developed meso-


1a
2a
3a
4
97732
1b
2b
3b
5a
5b
Cod. 698
Cod. 687
1c
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8a
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U.M. 254
8c
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9c
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16a
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18
19a
19b
19c
UM 2595
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21a
21b
21c

Figure 5 (opposite page). *Dremotherium guthi*: from *Coderet* **1** left fragmentary mandible with m2 and erupting m3 (UCBL FSL 97.732), labial (**a**), lingual (**b**), and occlusal views (**c**); **2** left m3 (NMB Cod687), labial (**a**), lingual (**b**), and occlusal views (**c**); **3** right d4 (NMB Cod698), labial (**a**), lingual (**b**), and occlusal views (**c**); **4** fragmentary maxillary with D4-M1 (NMB Cod639), occlusal view; **5** left m2 (NMB UM4098), labial (**a**), lingual (**b**), and occlusal views (**c**); from *La Milloque* **6** right M3 (NMB UM249), occlusal view; from *Küttigen* **7** right mandible with m3 (NMB UM254), labial (**a**), lingual (**b**), and occlusal views (**c**); **8** fragmentary right maxillary P3-M3 (UCBL 9841), occlusal view; from *La Rochette* **9** fragmentary left mandible with m1 (NMB UM Vd122), labial (**a**), lingual (**b**), and occlusal views (**c**); from *Rickenbach* **10** left M3 (NMB UM3131), occlusal view; **11** right M1 (NMB HR243), occlusal view; **12** right M2 (NMB Ri73), occlusal view; **13** left P3 (NMB UM1851), occlusal view; **14** right p4 (NMB Ri76), occlusal view; **15** (NMB Ri33), occlusal view; **16** right m1 (NMB UM2046), labial (**a**), lingual (**b**), and occlusal views (**c**); **17** left m3 (NMB UM1603), labial (**a**), lingual (**b**), and occlusal views (**c**); **18** left mandible with p3-m3 (NMBUM2595), occlusal view; **19** right m3 (NMB UM789), labial (**a**), lingual (**b**), and occlusal views (**c**); **20** right p3 (NMB UM962), occlusal view; **21** left m2 (NMB HR162), labial (**a**), lingual (**b**), and occlusal views (**c**). Scale bar equals 10 mm.

Table 5. Dental measurements (in mm) of the *Dremotherium guthi*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	p2		p3		p4		m1		m2		m3	
Dremotherium guthi													
Coderet	NMB Cod687											15.4	7.0
	NMB Cod706					9.4	4.2						
	UCBL FSL97733							12.0	7.0				
La Milloque	NMB LM220	6.2		8.4	4.0	8.5	5.3	9.6	7.2	13.0	8.4	18.3	8.1
	NMB LM221			8.1	3.9	8.6	5.0	9.6	7.1	10.7	7.6	16.3	7.3
	NMB LM222			8.2	3.2	9.2	4.5	10.6	6.6	11.9	7.0	16.0	6.8
	NMB LM224							9.9	6.9	11.8	7.3	15.5	6.8
	NMB LM225					9.0	5.5	8.8	6.9	11.6	7.8	16.0	7.6
	NMB LM232									10.9	6.5	16.7	7.4
	NMB LM233			8.5		8.5		10.8		12.4		15.3	
	NMB LM234					8.8	4.8	10.7	6.6	11.9	7.2	14.7	6.7
	NMB LM238							11.6	6.9	12.1	7.3	15.6	7.4
	NMB LM239							10.9	6.2	11.6	7.8	16.4	7.2
Thézels	UCBL 3794											15.0	7.5
	UCBL 3796											15.9	
Küttigen	NMB HR155											15.7	8.4
	NMB UM254											16.5	7.5
	NMB UM255											16.8	7.2
Romagnat	NMB Au1452							9.5	5.5				
	MNHN LIM327							9.4		10.5		15.5	
	MNHN LIM504				3.8	7.5	4.7	8.9	6.0	10.2	6.8	14.5	
	MNHN LIM501			7.6	3.5	8.1	4.8	10.2	6.6	11.6	7.1	16.7	6.7
	MNHN LIM502			7.7	3.9	8.0	5.0	9.8	6.9	11.2	7.6	16.8	7.6
Les Chauffours	MNHN LIM640							9.5	6.1	11.1	6.8		6.3
Cournon	MNHN LIM340	5.5		7.7		9.0		10.7		12.4		16.8	
La Rochette	NMB Vd122							10.7					
Mathod près Yverdon	NMB Vd75			7.4	3.8								
Möriken	NMB UM4098									12.0	7.6		
Rickenbach	NMB HR162									11.9	7.3		
	NMB HR180					9.0	4.5						
	NMB HR245							10.8	7.0				
	NMB Ri28			8.3	4.1								
	NMB UM789											14.8	6.5

Table 5 (continued). Dental measurements (in mm) of the *Dremotherium guthi*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	references	p2		p3		p4		m1		m2		m3	
Rickenbach	NMB UM960					3.7								
continued	NMB UM962				8.8	5.0								
	NMB UM1603												15.3	6.7
	NMB UM1604										11.1			
	NMB UM2046								10.8	7.1				
	NMB UM2595						10.0		10.5		11.0		16.2	
	NMB UM2601					3.5								
	NMO H11/6										10.8	6.6	15.4	6.0
	NMO K4/31										11.1	6.9	15.8	6.8
	NMO K11/95								8.7	5.4				
	NMO L6/38												14.7	7.6
	NMO K10/134												15.3	6.6
La Milloque	mean value	Jehenne 1987			7.8	3.9	8.4	4.7	10.5	6.8	11.6	8.2	15.5	7.8
Pech du Fraysse	mean value	Blondel 1997			7.9	3.6	8.1	4.3	9.8	6.3	9.7	7.3		
	mean value	Jehenne 1985	6.4	2.9	7.9	4.1	8.5	4.8	9.7	6.5	11.2	7.6	15.6	7.5

Locality	Inventory number	d3		d3		d4	
Coderet	NMB Bst10707					13.0	5.4
	NMB Cod692					13.5	5.4
	NMB Cod698					13.0	5.4
	NMB Cod705			8.7	3.7		
	UCBL FSL97733					12.5	5.4
Les Chauffours	MNHN LIM640			9.2		11.3	5.0
Küttigen	NMB UM1803			9.6	4.3		
Romagnat	NMB Au1452	7.0	2.5	8.1	3.0	12.0	5.0

Locality	Inventory number	P2		P3		P4		M1		M2		M3	
Coderet	NMB Bst698										12.7		
	NMB Bst700					7.0	8.0						
	NMB Bst701	8.8	4.5										
	NMB Cod639							10.7	11.8				
La Milloque	NMB LM235	7.8	4.5	8.0	6.6	7.6	8.7	10.1	11.0	12.4	13.1	11.8	12.4
	UCBL 9841			9.7	7.4	7.8	9.3	10.4	13.3	12.9	14.1	12.4	13.8
	UCBL 9842					7.7	9.7			12.7	14.2	12.5	13.8
Brochene-Flüh Waldenburg	NMB UM2843							9.8	11.8	11.5	13.2		
Küttigen	NMB HR968							9.7	12.4				
	NMB HR970					7.8	9.7						
	NMB UM249											12.0	13.8
	NMB UM250									11.3	13.0		
	NMB UM251								12.5				

Table 5 (continued). Dental measurements (in mm) of the *Dremotherium guthi*, in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	references	P2		P3		P4		M1		M2		M3	
Küttigen	NMB UM1804												12.0	13.0
	NMB UM1805										11.6			
continued	NMB UM1806												11.6	12.7
	NMB UM3894										11.2	12.6		
Rickenbach	NMB HR243								9.9	12.0				
	NMB Ri33						7.1	8.5						
	NMB Ri73										11.1	12.2		
	NMB Ri76						7.2	8.1						
	NMB UM790								9.5	12.2				
	NMB UM959								11.1	13.8				
	NMB UM1331										11.2	13.3		
	NMB UM1851				9.1	7.3								
	NMB UM3131													13.7
	NMB UM3568												11.0	14.0
La Milloque	mean value	Jehenne 1987			8.7	7.0	7.2	9.0	9.9	11.6	12.5	13.0	12.3	12.9
Pech du Fraysse	mean value	Blondel 1997			9.1	7.3	9.1	10.1	11.8					

Locality	Inventory number	references	D3		D4	
Coderet	NMB Bst10710				8.6	8.4
	NMB Cod639				10.0	10.3
	UCBL FSL97732					
Pech du Fraysse	mean value	Blondel 1997	9.8	6.8	8.7	9.1

lingual conid possesses an anterolingual cristid. The posterolingual conid is straight and joins the posterior stylid on the posterolabial edge of the tooth, closing the back valley.

The lower molars have widely open trigonids and talonids due to slightly posteriorly oriented internal postprotocristid and posthypocristid. The lingual wall is flat with large cristids, and the metaconid and entoconid ribs are reduced. However, the metaconid and the entoconid are not exactly in the same axis, the entoconid is farther inside than the other conid. The postentocristid does not reach the large and globular entoconulid, forming a small gap. The metastylid is small and salient, and a small spur is present on the anterolingual part of the lower molars. The external postprotocristid is present and usually very well marked. However, some specimens described in La Milloque do not possess such cristid. When it is present, it gets shorter from m1 to m3. The hypoconulid is high and forms the more posterolabial part of m3. The back fossa on m3 is pinched and oblique. The quite strong anterior cingulid is bigger than the posterior cingulid.

Upper adult dentition. P4 is relatively molarized. The lingual cone is enlarged and well-rounded. The anterolabial cone possesses a rib with a small anterior groove. The anterior and posterior stylids are relatively well-formed.

The quadratic upper molars bear a well-developed metaconule, but are slightly smaller than the protocone. The cusps are very selenodont. Even if a quite important variability was observed, no additional folds were detected. The preprotocrista and the postmetaconulecrista are labially oriented and quite straight. The postprotocrista is long and highly curved. It can be totally isolated or fused to the premetaconulecrista. These two cristae do not reach the paracone and the metacone. The latter are aligned. The paracone rib displays an anterior groove and the metacone rib is weak to absent. The mesostyle and parastyle are well developed and aligned with the premetacrista and the postparacrista. They form globular small columns. The mesostyle is larger from M1 to M3. The entostyle is weak to absent. There is neither lingual cingulum surrounding the protocone nor real meastyle forming a well-developed cuspid. However, small anterior and posterior cingulums are present.

Taxonomical attribution

The referred dental specimens are more advanced and larger in comparison to those of other ruminants from the latest Oligocene (Jehenne 1987, see table 2, 3, 4, and 5). The crowns are high and more selenodont than in the other Oligocene genera. The teeth are relatively complex with quadratic upper molars due to a well-developed metaconule, postprotocrista is elongated and highly curved, and the premetaconulecrista is distally forked (Jehenne 1987). There is no lingual cingulum at the level of the protocone. The laterally compressed p4 possesses a well-developed mesolingual conid and an anterolingual cristid. The well-molarized p4 permits us to distinguish *Dremotherium* from *Amphitragulus* (Costeur 2011). The lingual wall of the lower molars is flat, with large cristids, and the metaconid and entoconid ribs are reduced. The postentocristid does not reach the large and globular entoconulid, forming a small gap. The metastylid is small and salient. The external postprotocristid is present and usually very well marked.

Dremotherium guthi is supposed to be the ancestor to the Aquitanian and the larger *D. feignouxi* (Jehenne 1985, 1987, Blondel 1997, Mennecart et al. 2012). The *Dremotherium* sp. from Peublanc was synonymised with *Dremotherium guthi* by Jehenne (1985). The *Prodremotherium*? of Viret (1929, pl. 31 fig. 15-16), is clearly a *Dremotherium guthi* by its shape and size.

Similarly to **“***Amphitragulus” quercyi*, *Dremotherium guthi* has been observed in the Asian localities of Yagan Tologoi and Taatsiin Gol in *Mongolia* (Vislobokova 1996, Vislobokova & Daxner-Höck 2002, Devyatkin et al. 2002). However, even if “*A.” quercyi* appears to be recorded in latest Oligocene deposits, an older age (early Late Oligocene) is suggested for the Asiatic *D. guthi*. This specimen could be the oldest representative of this species (Vislobokova & Daxner-Höck 2002), confirming the Asiatic origin of Eupecora.

Genus **Bedenomeryx** Jehenne, 1988

Type species. *Bedenomeryx milloquensis* Jehenne, 1988 from La Milloque (Lot-et-Garonne, France) MP29.

Further included species. *B. paulhiacensis* Jehenne, 1988, *B. truyolsi* Ginsburg et al., 1994, *B. validus* (Dehm, 1935).

Diagnosis (adapted from Jehenne 1988). Inermous primitive ruminant characterized by a skull bearing two lacrymal foramina on the inner wall of the orbit. The upper canines are long and saber-like. All cheek teeth are covered by pleated enamel. The upper premolars are massive and dumpy. The upper molars have shallow anterior and posterior fossae. The external postprotocristid is constant on the lower molars and the posterior entoconid’s wing is developed and complete. The anterior central groove of the metatarsus is distally closed and a diarthrodial facet is present at the proximal extremity.

Etymology. The genus name *Beden* was given as a tribute to the palaeontologist Michel Beden and *meryx* is the Greek word for ruminant.

Bedenomeryx milloquensis Jehenne, 1988

*1985	*Bedenomeryx milloquensis* – Jehenne: 200, figs. 32-37.
1987 v pars	*Dremotherium* sp.2 – Engesser and Mayo: 77.
*1988	*Bedenomeryx milloquensis* – Jehenne: 1991, figs. 1-3.
1997 v pars	*Dremotherium* sp.2 – Engesser and Mödden: 490.

Holotype. Complete skull (IPHEP L.M. 1967-MA-8, Jehenne 1988: 1993, fig. 1).

Etymology. From the type locality La Milloque.

Type locality and horizon. La Milloque (Lot-et-Garonne, France) MP29.

Occurrence. Latest Oligocene, from MP29 to MP30, of France (Dieupentale, Renneville) and Switzerland (Küttigen).

Referred material. Renneville (France): UCBL9780, fragmentary right mandible with broken d4 and erupting m2. Küttigen (Switzerland): NMB HR156, left p3.

Diagnosis (adapted from Jehenne 1988). Species of rather large size. The skull is characterized by an elongated postorbital region and a strong sagittal crest. The anterior rim of the orbit is situated straight above the anterior edge of M2. The p1 is reduced and variable. The cheek teeth are massive and the upper premolars are relatively more molarized than the lower premolars.

Description

Specimen NMB HR156 is an isolated and relatively worn p3. It is very elongated. The anterior conid is gently oblique. The anterior cristid is elongated and straight. The anterior valley is wide. The large mesolabial conid possesses a posterolabial groove separating this conid from the posterolabial conid. The oblique transverse cristid ends on the lingual part of the tooth, without mesolingual conid. The posterolingual conid is oblique too and joins the posterolingual edge of the tooth. The medial valley is narrow and deep.

The specimen UCBL9780 is bigger than those of *Dremotherium feignouxi*. The lower molars are relatively high, very selenodont with a trigonid slightly anteriorly opened and a talonid posteriorly opened. The external postprotocristid is lacking. The mesostylid is stronger from m1 to m3. The metastylid forms a spur. The lingual cusps are laterally compressed and not aligned. The lingual wall of the entoconid is bulged and a rib is present on the metaconid. The metacristids are large. The posthypocristid does not join the postentocristid, implying an open trigonid. The postentocristid is high and does not join the base of the entoconid and the posthypocristid, forming a gap. The entoconulid is absent. The anterior cingulum is strong, whereas the posterior one is absent. The ectostylid is strong.

Taxonomical attribution

p3 NMB HR156 is characteristic of an evolved Eupecora lower premolar. It possesses three valleys. Its size is very big. By its molarization and its size, much larger than *Dremotherium guthi*, the other « big » latest Oligocene ruminant (Jehenne 1985, 1988), this specimen is similar to the p3 specimens of *Bedenomeryx* from La Milloque. Furthermore, the lower molar structure is more primitive than those of *Dremotherium*. *Bedenomeryx milloquensis* is only known in the type locality La Milloque.

9.4 Discussion

9.4.1 The familial attribution of the latest Oligocene-Early Miocene ruminants: problem of a basal radiation

Nowadays, the appendages, the cheek teeth, the skulls and the postcranial bones allow us to easily differentiate the six extant ruminant families. However, only hornless taxa with saber-like canines and tooth patterns strongly similar to primitive ruminants existed until the Early Miocene. As a result, the western European Oligocene and Early Miocene ruminants were for a long time mainly identified either as *Dremotherium* or *Amphitragulus* (e.g., Pomel 1853, Engesser & Mayo 1987, Engesser & Mödden 1997). At least 17 species have been described up to the beginning of the 20th century, five of them have Saint-Gérand-le-Puy as the type locality (Pomel 1853, Filhol 1881). The reassessment of these species leads to 5 different categories:

1) the species is valid;
2) the species is not valid and is a variability of a valid *Amphitragulus* species;
3) the species is valid but belongs to a another valid genus;
4) the species is valid but belongs to a new genus.
5) the species is not valid.

The type species *Amphitragulus elegans* Pomel, 1846 is well-known in Aquitanian deposits of Western Europe (Engesser et al. 1993, Gentry et al. 1999, Costeur 2011). This taxon is known by its skull and postcranial remains (Viret 1929, Jehenne 1985, Janis &Scott 1987). However, its ecology remains relatively poorly known (Gentry 1994, Costeur 2011). Furthermore, the larger *A. lemanensis* Pomel, 1853 seems to be an intraspecific variation of *A. elegans* (Costeur in progress).

Amphitragulus primaevus Schlosser, 1925-26 is described as the ancestor of *A. lemanensis*, whereas "*Amphitragulus" feningrei* Schlosser, 1925-26 is considered as the ancestor of *A. elegans*. However, *A. elegans* and *A. lemanensis* are synonyms as mentioned above. *Amphitragulus primaevus* clearly displays primitive features, such as bulged cuspids with a trend to the bunodonty on molars and a shortened postentocristid on lower molars. From these characteristics, this taxon clearly belongs to *Amphitragulus*. *Amphitragulus primaevus* is smaller, more primitive and older, it probably represents the old-

est *Amphitragulus* species of Europe (fig. 6).
Amphitragulus minoensis Matsumoto, 1918 belongs to the Burdigalian Hiramaki mammalian fauna close to Kyushu in Japan (Tokunaga 1933, Takai 1961). This is a quite big *Amphitragulus* with an estimated weight of nearly 50 kg (Watanabe & Matsukawa 2006). However, neither direct nor indirect observations of this species have been made.

The attribution of "*Amphitragulus" feningrei* Schlosser, 1925-26 to the genus *Amphitragulus* is still under discussion. For nearly a century, this species had been "forgotten" and not described, figured, or mentioned except for Peublanc (Schlosser 1925-26), Coderet (Viret 1929, and Hugueney 1969, 1997 in Tables), and Rickenbach (Mennecart et al. 2012). Mennecart et al. (2012) argued, on the basis of the specimens from Rickenbach, that "*Amphitragulus" feningrei* is clearly different from a classical *Amphitragulus*" in having more selenodont crowns (…) the cusps are sharp and the parastyle is globular and anteriorly projected". This association of characteristics seems to be unique among the ruminants of the Oligocene and Early Miocene. Furthermore, "*Amphitragulus" feningrei* possesses a typical compact Eupecora p4 and more advanced cheek teeth than those of *Amphitragulus*, *Bedenomeryx*, and *Babameryx*, but more primitive than those of *Dremotherium*. The cheek teeth of the latter are more hypsodont with wider lingual cuspids. The mesostylid is larger (in *Amphitragulus* it is almost absent) and the lingual metaconid rib is salient (in "*A*." *feningrei* it is globular) on lower molars. Also, the posterolingual conids are separated from the posterolabial cristid on lower premolars of "*A*." *feningrei*. The latter feature seems to be variable, but highly frequent in "*A*." *feningrei* in comparison to the other contemporaneous ruminants. The small mesolingual conid of the p4 is located on the posterior back part of the tooth. Therefore, according to Mennecart et al. (2012), it is suggested that this species should be assigned to a new genus.

In 1989, Ginsburg and Morales defined the genus *Pomelomeryx* for the two small species *Pomelomeryx* (*Amphitragulus*) *boulangeri* Pomel, 1853 and *Pomelomeryx* (*Amphitragulus*) *gracilis* Pomel, 1853. These species are distinguished by their skulls and complete tooth rows (Viret 1929, Jehenne 1985, Rössner & Rummel 2001). Gentry et al. (1999) and Prothero (2007) defined *Pomelomeryx* by the following characteristics: "relatively primitive low crown, poorly developed selenodonty, with conical cusps, fewer and weaker internal crests on the check teeth, less-rounded lingual wall, as well as slender P3 and p3". *Amphitragulus meminoides* Pomel, 1853 was described as a slightly smaller species than *Pomelomeryx boulangeri* with shorter and slender lower premolars, and *Amphitragulus pomeli* Filhol, 1881 as a smaller species of *Amphitragulus* with teeth more bunodont than the type species (Filhol 1881). However, Rütimeyer (1883) and Viret (1929) concluded with intraspecific variability and synonymized these two species, and also synonymized *Palaeomeryx medius* Meyer, 1834, with *Pomelomeryx boulangeri*.

"Amphitragulus" quercyi Filhol, 1887 (*A. querey* of Vislobokova 1996 and Devyatkin et al. 2002 and *Dremotherium quercyi* of Jehenne 1985, 1987, Blondel 1997) is considered to be a direct ancestor of *Pomelomeryx gracilis* (Jehenne 1985, Blondel 1997). "*Amphitragulus" quercyi* possesses more primitive premolars with a small postentocristid on lower premolars. However, these characteristics seem highly variable (Blondel 1997). Furthermore, a general trend during the latest Oligocene shows a reduction in size. After Blondel (1997), the relationship between these two species (fig. 7) can be confirmed. "*Amphitragulus" quercyi* is clearly different from *A. primaevus* in having more laterally compressed lingual cuspids, more advanced premolars, and a more salient metastylid on lower molars. Having established the relationship between "*A." quercyi* and *P. gracilis*, we should consider "*A." quercyi* to be the oldest representative of *Pomelomeryx* in Europe.

Ginsburg (1985) defined the genus *Oriomeryx* in reference to the large and primitive species *Amphitragulus major* Viret, 1929. *Amphitragulus validus* Dehm, 1935 was reassessed by Ginsburg et al. (1994) and placed within the genus *Bedenomeryx.*

First described under the name *Amphitragulus communis* Aymar, 1846, due to the primitive bunodont aspect of the molars, Aymar (1855) proposed the new genus *Gelocus* for this species. Referring to a left mandible with p2-m3 from the Phosphorites du Quercy, Filhol (1876) defined the new genus and species *Rutitherium nouleti*. Then, Filhol (1877) suggested an attribution to *Dorcatherium nouleti* due the primitive aspect of the lower molars with the presence of a kind of *Dorcatherium* fold. *Rutitherium nouleti* had also been described in Pech Desse by Sudre (1984). Finally, Bouvrain et al. (1986) concluded that the holotype of *Rutitherium nouleti* is a junior synonym of *Gelocus communis* and the specimens described in Pech Desse belong to "*Amphitragulus" quercyi* (*Dremotherium quercyi* in Blondel 1997).

Mayet (1908) defined the species *Amphitragulus aurelianensis* based on a hemi-mandible with p3-m3 and a palate with left P2-M3 and right P3-M3 from Artenay (France). Gentry (1994) underlined the difficulty to distinguish *A. aurelianensis* from *Procervulus* (such as *P. praelucidus* first described as *P. aurelianensis* by Mayet 1908). The main characteristic discriminating the latter genus is the presence of antlers, being the most distinctive hard parts of the advanced Cervidae (Gustafson 1985; Gentry 1994; Rössner 1995; Gentry et al. 1999). However, females seem to be hornless (Gentry 1994) and Gentry et al. (1999) concluded a synonymy between *A. aurelianensis* and *Procervulus dichotomus*.

Similar observations can be made with the genus *Dremotherium*. Only two species are considered to be valid, the type species *Dremotherium feignouxi* Saint Hilaire, 1833 and *Dremotherium guthi* Jehenne, 1987. These two taxa are fairly well known from skulls and postcranial remains, they have been discussed in recent publications (Becker et al. 2010, Novello et al. 2010, Costeur 2011, Mennecart et al. 2011, Mennecart et al. 2012a, b). Also, a different ecology is depicted. The late Chattian small grazer (or mixed-feeder) *D. guthi* lived in wooded savannah, whereas the Aquitanian leaf eater *D. feignouxi* was characteristic of open environments.

Dremotherium nanum Saint Hilaire, 1833 and *D. traguloides* Pomel, 1853 are described as being slightly smaller *Dremotherium* than *D. feignouxi* and *D. cetinensis* Ginsburg et al., 1994, which possess more hypsodont dentition and show intraspecific variability (Jehenne 1985, Gentry et al. 1999). The small *D. tolosanum* Richard, 1931 is an intermediary between "*A." quercyi* and *Pomelomeryx* species (Jehenne 1985, pers. obs.). The small and inermous Moschidae *Micromeryx flourensianus* was wrongly changed into *Dremotherium flourentianum* Deperet, 1887.

Jehenne (1985, 1987), Blondel (1996, 1997, 1998), and Novello (2010) suggested that all the ruminants from the late Chattian and Aquitanian belong to the genus *Dremotherium* (synonymising *Amphitragulus* with *Dremotherium*), except for two new genera described by Jehenne (1985, 1988) based on the skull: *Bedenomeryx* (two species associated with mandible specimens) and *Hydropotopsis*. By the general aspect of the teeth and the length of the premolar row, *Bedenomeryx* is clearly different from *Dremotherium*. *Hydropotopsis* remains much more problematic. Its skull has 2 lacrymal fossae instead of one as generally occurs in *Amphitragulus* and *Dremotherium*. However, Costeur (2011) noted that this characteristic may be variable and *Hydropotopsis lemanensis* could be synonymised with *Amphitragulus elegans*. However, the aforementioned differences are too important to assume the occurrence of only one genus.

9.4.2 Biostratigraphy

Figure 6 summarizes the biostratigraphy of the ruminants of the latest Oligocene. During the time interval MP28 to MP30 (ca. 2 My), nine valid species of ruminants are recorded in Europe. Based on the results of this study, the occurrence within this time interval is new for eight of them. Three different cases can be distinguished.

Lophiomeryx chalaniati is a species relic from the typical Oligocene fauna. The last occurrence of this species corresponds to MP28 in Cournon (even if this locality is not precisely dated, Hugueney 1997) and Pech Desse (Brunet & Sudre 1987, Blondel 1997). However, the remains of *L. chalaniati* are extremely rare in these two latter localities: only two specimens in Cournon (Brunet et Sudre 1987) and one in Pech Desse (Brunet et Sudre 1987, pers. obs.) were identified without any doubt. Furthermore, Blondel (1997) referenced 33 astragalus bones from Pech Desse, according to the data of Martinez & Sudre (1985). However, no postcranial remains from this locality were clearly described and consistently identified. Regarding the dental specimens, the specific attribution of *Lophiomeryx* remains quite complicated, because the teeth show

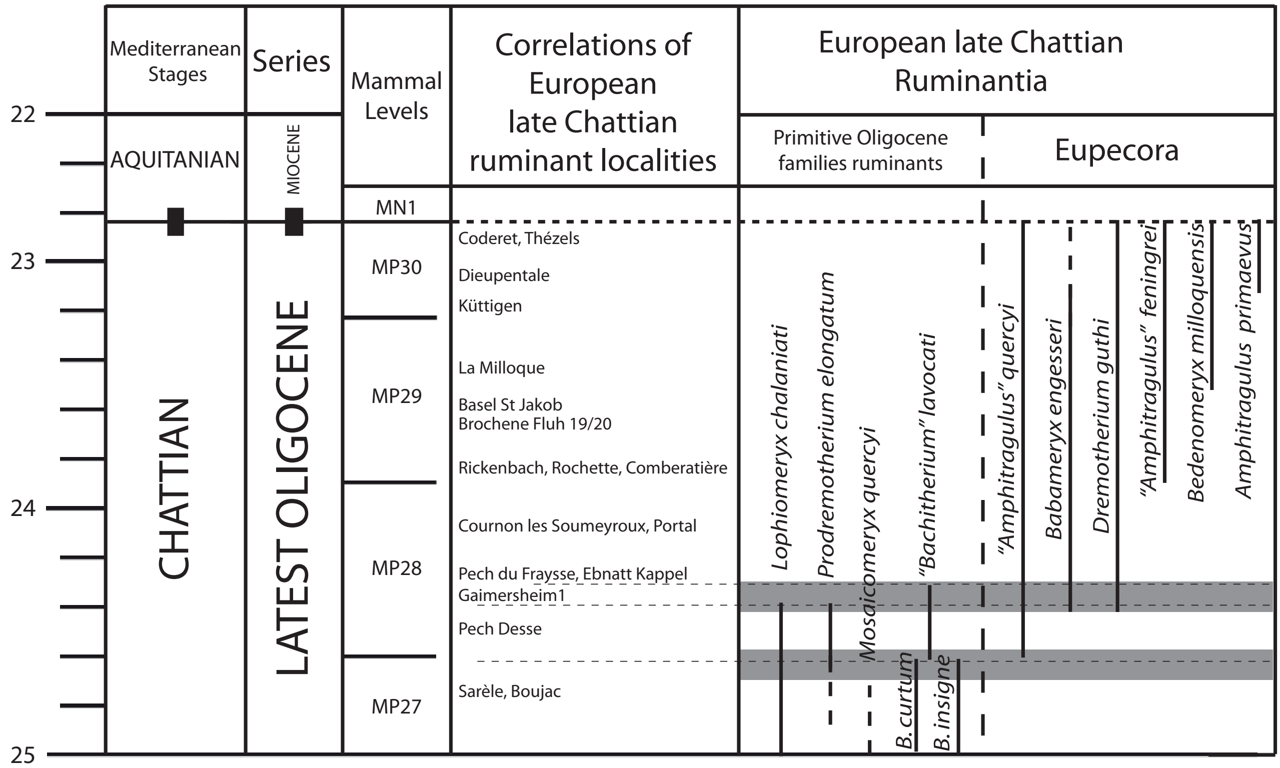

Figure 6. Biostratigraphy of the European latest Oligocene ruminants.

very simple patterns and an interspecific monotony, and the interspecific discrimination is mainly based on population size differences (Brunet & Sudre 1987).

A second category is composed of new taxa belonging to families already present in Europe during the major part of the Oligocene. The Bachitheriidae *Bachitherium lavocati* and the Mosaicomerycidae *Prodremotherium elongatum* are highly restricted in time. They only occurred during a time interval of ca. 300 000 years, possibly late MP27 and undoubtedly MP28, in Sarèle, Boujac, Pech Desse and Gaimersheim 1. This assemblage seems to correspond to transitional forms between the primitive ruminants of the mid-Oligocene and the Eupecora (highly evolved ruminants).

The occurrence of new families belonging to the true Pecora (Eupecora), characterized by a highly derived lower premolar structure (short and large p4 possessing a well-developed mesolingual conid), composes the third category. "*Amphitragulus" quercyi* is the first representative of the Eupecora in Europe. It appeared at the same time as *Bachitherium lavocati* in Pech Desse. "*A." quercyi*, such as *Dremotherium guthi*, was already present in Asia (Vislobokova 1997).

Regarding the biostratigraphy, only three different families occurred during the mid-Oligocene: Lophiomerycidae (*Lophiomeryx chalaniati*), Bachitheriidae (*Bachitherium curtum* and *B. insigne*), and Mosaicomerycidae (*Mosaicomeryx quercyi*). Their related species disappeared during MP27-28 and gave way to new species of Bachitheriidae (*Bachitherium lavocati*) and Mosaicomerycidae (*Prodremotherium elongatum*).

The immigration of Eupecora into Europe coincides with the first occurrence of "*A." quercyi* and with the last representative of *Lophiomeryx* and *Prodremotherium* in Pech Desse. Then, a huge and unexpected diversification of the Eupecora is observed. The last representative of the Bachitheriidae from Gaimersheim 1 concurred with the first representives of *Dremotherium guthi* and *Babameryx engesseri*. Then at the base of MP29, "*Amphitragulus" feningrei* appeared in Rickenbach. During the late MP29, *Bedenomeryx lamilloquensis* is present in La Milloque. The last species appearing during the terminal Oligocene is *Amphitragulus primaevus* (Peublanc, MP30). This huge migration occurred until the Aquitanian with at least 6 new genera and species during the latest Oligocene and 3 more genera during the Aquitanian (*Oriomeryx*, *Friburgomeryx*, *Andegameryx*).

The latest Oligocene corresponds to a major faunal renewal among the mammalian communities, such as the rodents (Vianey-Liaud 1992), the artiodactyls (Berthet 2003, Mennecart et al. 2011, Scherler 2011), and the perissodactyls (Becker et al. 2009, Mennecart et al. 2011, Scherler et al. 2011), but also among the reptiles, such as the booids (Rage & Szyndlar 2005). The biozone MP29 coincides with the last occurrence of the emblematic Oligocene taxa *Anthracotherium* (anthracotheriid) and *Ronzotherium* (Rhinocerothid) (Mennecart et al. 2011). Indeed, the time interval MP27-MP30 (ca. 24.3 and 22.9, Berger 2011) is marked by huge global changes. It began with the Late Oligocene warming and ended with the Mi1 glaciation (Berger 2011), which characterizes the Oligocene-Miocene transition. The seawater temperature increased by 2 to 4°C and the temperature on the continents by nearly 10°C (Vianey-Liaud 1991, Zachos et al. 2001, De Man & Van Simaeys 2004). The surviving taxa of the Early Oligocene first disappeared in Europe at the beginning of the Late Oligocene warming; these were replaced by species from the same families. The palaeoecology of the mammal community also changed. Considering the postcranial remains, the mid-Oligocene species are characteristic of wooded environments, contrary to the latest Oligocene ones, which lived in more open habitats (Blondel 1998, Hiard 2010, previous chapter on Mosaicomerycidae). Similar palaeoecological changes have also been observed among the rodents during the same time interval (Vianey-Liaud 1991). Within the Molasse Basin, no changes of the sedimentary context have been observed.

After the Late Oligocene warming, during MP28, a second turnover occurred that stratigraphically corresponds to sedimentary changes in Switzerland. The deposit of coal in La Rochette characteristic of wet environments, and gypsum deposits in the Jura Molasse characteristic of dry environments, are separated by a few hundreds of kilometres (Berger 1998, Berger et al. 2005a, b). These local differences are probably due to palaeotopography. The original altitude of the la Rochette mines is estimated at 500 m (Berger 1998). The Late Oligocene warming, associated with the Alpine orogenesis, gave birth to changes sedimentation and probably the climate and vegetation cover (Berger 1989, 1990a). Accordingly, these new environmental conditions led to a major faunal renewal and competition between the primitive families and the Eupecora, which possessed a more efficient metabolism and were better adapted to dry habitats. By comparing the fossil Tragulina (Bachitheriidae and Lophiomerycidae) with the extant Tragulidae, Janis (1989) considered that the primitive European Tragulina are mainly distinguished by forestomach fermentation without real rumination during the Oligocene. Nowadays, the Tragulidae only live in the tropical forests of Africa and South-East Asia (Rössner 2007). The opening of the environment with less forests during the latest Oligocene could have been fatal for the primitive ruminants.

9.4.3 Evolution and speciation during the Oligocene-Miocene transition

After the first familial renewal during MP28, unusual changes occurred in the European ruminant community at the Oligocene-Miocene transition. Regardless of the complete renewal at the species level, numerous lineages persisted and genera survived until the end of the Aquitanian. Only *Babameryx engesseri* and "*Amphitragulus*" *feningrei* do not seem to have progressed to new species and did not survive this transition. Nevertheless, "*Amphitragulus*" *quercyi* currently does not belong to the genus *Pomelomeryx*, but appears to be an ancestor to the latter

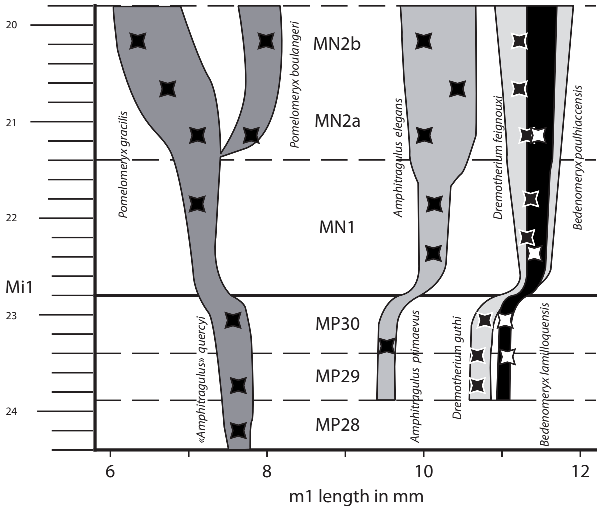

Figure 7. First lower molar size evolution trough time of the ruminant genera surviving the Paleogen/Neogene boundary. The data including measured specimens from Gaimershiem 1, Rickenbach, La Milloque, Küttigen, Coderet, Montaigu le Blin, Paulhiac, Saint Gérand le Puy, Barbotan le Thermes, Lausanne, La Chaux 7, Tavannes Sous le Mont and from Schlosser 1925–26, Jehenne 1985, 1987, 1988; Ginsburg & Morales 1989, Blondel 1997; Rössner & Rummel 2001.

Aquitanian genus (see above). During the Aquitanian, a general increase in size of various medium-sized species can be observed (*Dremotherium*, *Amphitragulus* and *Bedenomeryx*; fig. 7). On the other hand, the smallest species became even smaller (*Pomelomeryx*).

Regarding *Dremotherium*, whose palaeoecology is well documented, a characteristic anatomical change can be highlighted. The smallest species possess postcranial features characteristic of a mixed environment between forest and open area (Mennecart et al. 2012), whereas the larger species clearly lived in an open environment (Becker et al. 2010). Concerning the palaeodiet, the Oligocene *D. guthi* was a grazer to mixed feeder, according to dental microwear and geometric morphometrics analyses (Novello et al. 2010, Mennecart et al. 2012), whereas the Miocene *D. feignouxi*, which possesses a slender mandible and elongated cervical vertebra such as in *Litocranius walleri*, was probably folivore (Becker et al. 2010, Mennecart et al. 2012, accepted). Accordingly, two different modes of life can be distinguished: the probably nocturnal small grazer *D. guthi* living on the edges of the forest such as the extant *Tragelaphus angasii* (Mennecart et al. 2012) and the larger folivore *D. feignouxi* living in wooded savannah (Mennecart et al. 2012). The presence of mixed areas during the latest Oligocene (Vianey-Liaud 1992, Costeur 2005) is also attested by the structure of the cenogram of the mammal community of Rickenbach (Mennecart et al. 2012) and the coocurrence of strictly grazer (*D. guthi* and *B. milloquensis*) and folivore ("*A." quercyi*) ruminants (Novello et al. 2010). Considering the palaeoecology of "*A." quercyi*, based on postcranial remains, Blondel (1998) concluded that this species lived in a lightly forested environment, probably corresponding to the palaeoenvironment of Rickenbach (Mennecart et al. 2012).

During the Aquitanian, the environment seems to be more open (Costeur 2005, Becker et al. 2010, Chapters 11 and 12). The transition between the Paleogene and the Neogene is marked by the cooling event Mi-1 (Zachos et al. 2001, Pekar et al. 2006, Berger 2011) and an opening of the environment (Costeur 2005, Becker et al. 2009). This increase in grassland appears to well-correlated with the increase in size of the medium-sized ruminants and a reduction in size of the smallest ones (Fig. 7).

9.5 Conclusion

The latest Oligocene is an interesting period considering the ruminant communities in Europe. During MP28, the immigration of the Eupecora marked the last occurrence of the primitive and typical Tragulina Lophiomerycidae, Bachitheriidae, and Mosaicomerycidae. Due to the record of similar Eupecora species in older Asiatic localities, we assume a migration from Asia. This event correlates with the end of the major climatic change of the Late Oligocene warming. It seems to highlight that a migration and competition event imply faunal changes at familial level within a mammal community.

This early eupecoran community, composed only of ruminants possessing saber-like upper canines, persisted until the end of the Aquitanian. Their diversity was minimized. The presence of 6 new genera (*Amphitragulus*, *Dremotherium*, *Bedenomeryx*, *Babameryx*, new genera related to *"Amphitragulus" feningrei* and "*Amphitragulus*" *quercyi*) of Eupecora during the latest Oligocene attests that the turnover within the Ruminantia community was earlier and stronger than previously thought. Many genera crossed the Oligocene-Miocene transition. However, no Oligocene species seem to have survived up to the crisis marked by the Mi1 glaciation. During the Aquitanian, a speciation phase occurred with the diversification from medium-sized ruminants living in forests to larger ruminants living in more open environments. Later, the migration of the ruminants possessing cranial appendages probably initiated the decline of these primitive Eupecora during the Early Burdigalian.

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IV - EARLY MIOCENE (AQUITANIAN)

MNHN SG4304 *Dremotherium feignouxi* (Neotype)

10 - LATE AQUITANIAN MAMMALS FROM ENGEHALDE (MOLASSE BASIN, CANTON BERN, SWITZERLAND)

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Abstract

The construction of the Neufeld tunnel in Bern city (2006–2008) led to the discovery of fossil mammals in the vicinity of the historical site of Engehalde. The study of the whole available sample led to the distinction of two mammal assemblages: (1) the historical level with the rhinocerotids *Diaceratherium lemanense* and *D. aginense*, and the ruminant *Andegameryx* cf. *laugnacensis*; (2) the Neufeld level with the artiodactyls *Dremotherium feignouxi* and *Cainotherium* sp., the carnivore *Plesiogale angustifrons*, and the glires *Eucricetodon* cf. *aquitanicus*, *Peridyromys* sp., and *Prolagus vasconiensis*. These two assemblages attest to a latest Aquitanian age (MN2b) for the last deposits of the 'Lower Freshwater Molasse' in the area. The palaeoecological analysis of the faunas indicates either the co-occurrence or the very short-termed succession of assorted terrestrial environments, ranging from forested habitats nearby water bodies or nearby steady rivers to open well-drained habitats within the hinterland.

Résumé

Mammifères de l'Aquitanien supérieur d'Engehalde (Bassin molassique, Suisse, Canton de Berne). Les travaux du tunnel de Neufeld en ville de Berne (2006-2008) ont permis la découverte de mammifères fossiles à proximité du site historique d'Engehalde. L'étude de l'ensemble du matériel a permis de mettre en évidence deux associations de mammifères : (1) le niveau historique, avec les rhinocérotidés *Diaceratherium lemanense* et *D. aginense* et le ruminant *Andegameryx* cf. *laugnacensis* ; (2) le niveau de Neufeld, avec les artiodactyles *Dremotherium feignouxi*, *Cainotherium* sp., le carnivore *Plesiogale angustifrons* et les glires *Eucricetodon* cf. *aquitanicus*, *Peridyromys* sp. et *Prolagus vasconiensis*. Quoique distinctes, ces associations attestent toutes d'un âge Aquitanien terminal (MN2b) pour les derniers dépôts de la « Molasse d'eau douce inférieure » dans la région. L'analyse paléoécologique des faunes indique la coexistence ou la succession à très court terme d'environnements forestiers en bordure de plans d'eau ou de cours d'eau de faible énergie et d'environnements d'arrière-pays plus ouverts à sol bien drainé.

10.1 Introduction

Since its discovery in 1850, the Early Miocene locality of Engehalde (Canton Bern, Switzerland) has become one of the most important large mammal localities in the Swiss Molasse Basin. Studer (1853) first reported bone and dental remains assigned to *"Rhinoceros incisivus*" and *"Palaeomeryx minor*". Rütimeyer (1860) confirmed the occurrence of *"Palaeomeryx minor*" and described the skull, mandible and dentition of two rhinocerotids, *"Aceratherium gannatense*" and *"Rhinoceros sansaniensis*". Ooster and von Fischer-Ooster (1871) illustrated the main rhinocerotid specimens identified by Rütimeyer (1860), among which a complete skull associated to a mandible assigned to *"Acerotherium gannatense*". Additionally, Studer (1895) illustrated a fragmentary juvenile upper dentition attributed to the ruminant *Dremotherium feignouxi* Saint-Hilaire, 1833. The latest faunal list of Engehalde, published by Stehlin (1914), included the suoid *Palaeochoerus typus* Pomel, 1847, the ruminants *Amphitragulus* cf. *elegans* Pomel, 1853 and "*A. lemanensis*", and only one rhinocerotid, "*Aceratherium lemanense*". Eversince, no review of the Aquitanian Engehalde fauna has been undertaken, with the exception of Becker et al. (2009), who briefly reviewed the famous rhinocerotid skull and assigned it to *Diaceratherium* cf. *lemanense* (Pomel, 1853).

Recently, due to the construction of the Neufeld tunnel in Bern city (2006–2008), a team of the Natural History Museum Bern discovered a new mammal level in Engehalde, in the vicinity of the historical one (Menkveld-Gfeller and Becker, 2008). The new material consists mostly in ruminant remains, but a mustelid specimen was also unearthed, as well as small mammals, turtles, amphibians, gastropods (Helicidae and *Limnaea*), and charophytes (*Stephanochara* gr. *praeberdotensis*). In the present work, we revise the mammal specimens from both the historical and the Neufeld levels of Engehalde, which in turn allows us to discuss their biostratigraphical range and the palaeoenvironmental significance of Engehalde within the Swiss Molasse Basin.

10.2 Geological setting and taphonomy

The two fossiliferous levels of Engehalde are located in the Enge quarter of Bern city, along the left bank of the Aar River. Mammals, reptiles, gastropods, and charophytes were trapped in sandy and marly deposits of the *'Obere Bunte Mergel'* (Aquitanian, top of the 'Lower Freshwater Molasse': USM; Habicht 1987). In the Early Miocene, the sedimentation of the 'Plateau Molasse' was controlled by Alpine alluvial fans, the eastward drainage system of the *'Genferseeschüttung'*, and the eastward diachronic transgression of the Burdigalian sea ('Upper Marine Molasse': OMM) occurring from MN2a to MN2b (Berger et al., 2005) (Fig. 1).

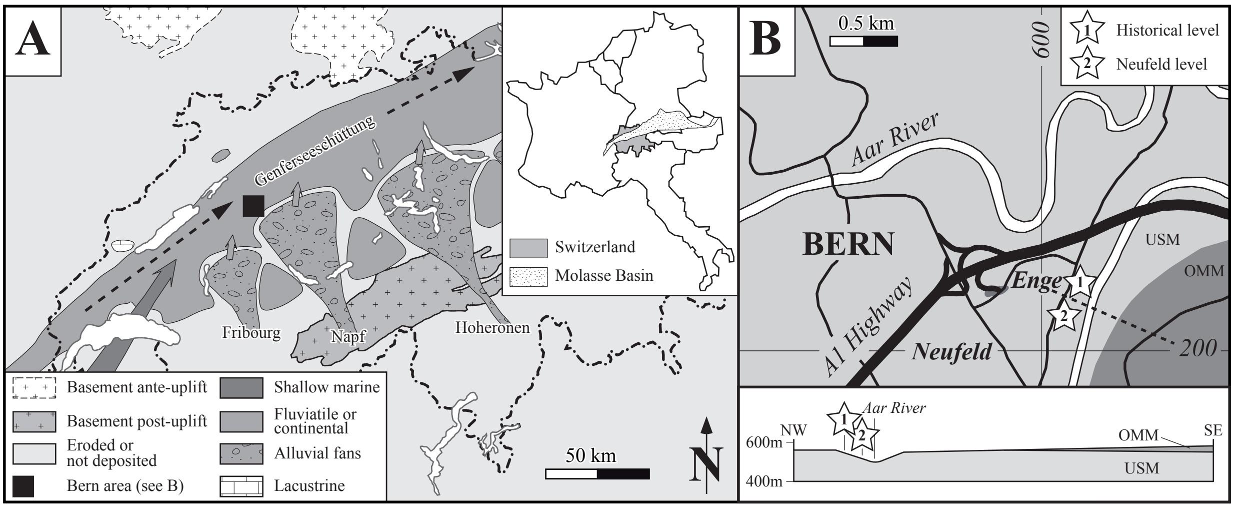


Fig. 1. General setting of the late Aquitanian (MN2) mammal localities of Engehalde (Molasse Basin, Canton Bern, Switzerland). **A,** palaeogeographical map (after Berger et al., 2005); **B,** geographical and geological (dashed line: geological section) location of the historical and Neufeld levels (after Kellerhals et al., 2000).

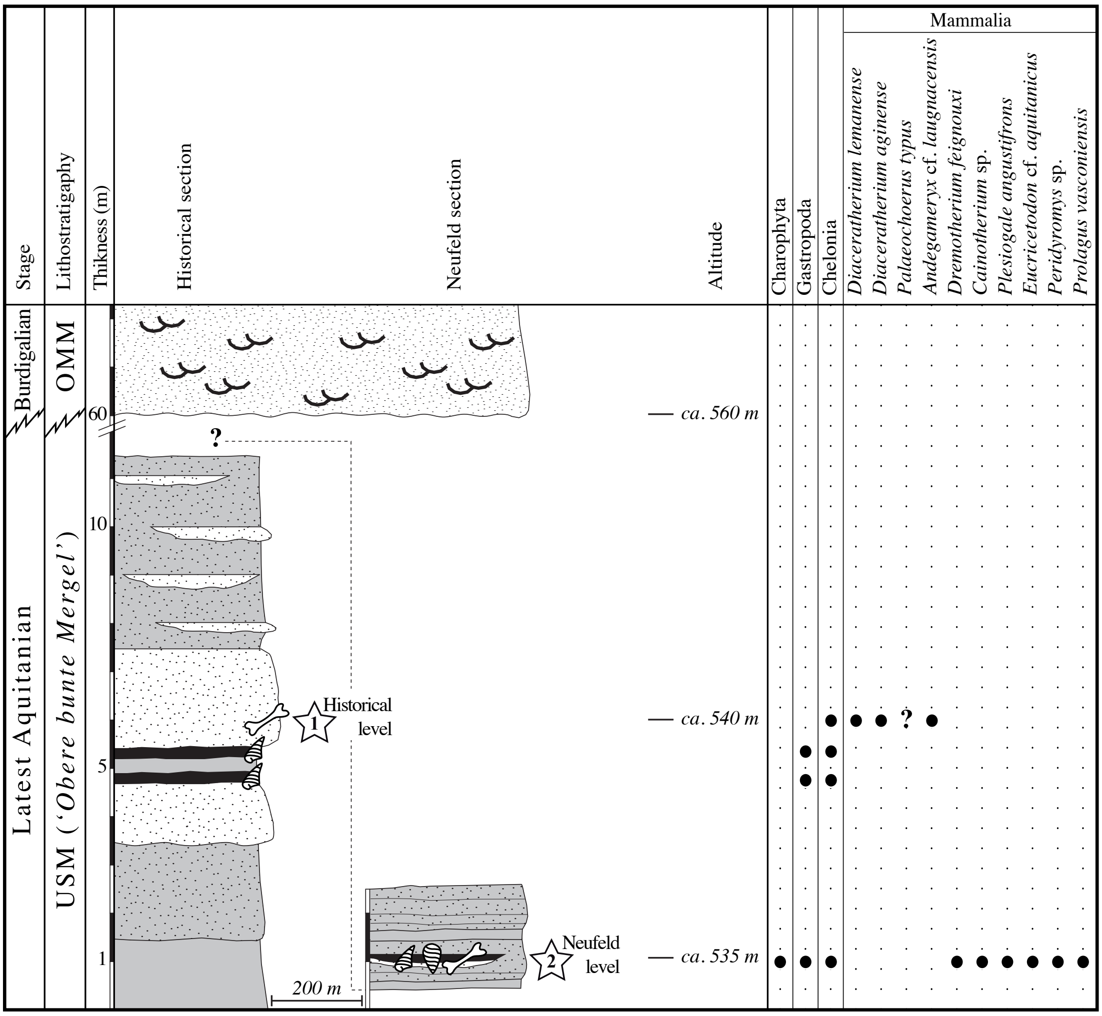


Fig. 2. Synthetic stratigraphical section of the late Aquitanian deposits of Engehalde (Molasse Basin, Canton Bern, Switzerland) and fossil content of both the historical and Neufeld levels. The lithostratigraphic position of the localities is based on Studer (1853) and new field data.

According to the description of the historical outcrop (Studer, 1853), and in agreement with the recent Neufeld field data, the two levels are situated at 200m one from the other and they are almost laterally equivalent. The short synthetic sedimentary series is defined by floodplain deposits 8m-thick, situated at the top of the last freshwater deposits of the USM, ca. 50m below the earliest deposits of the Burdigalian marine transgression (OMM) (Fig. 2). The historical level corresponds to a massive fine sand of river deposits and the Neufeld level to fines of an abandoned crevasse channel fill. The latter is lithostratigraphically situated above the historical level, but, due to erosion processes of the sedimentary system and local dip (ca. 5-7º), topographically located a few meters below (Fig. 2).

The two fossiliferous levels are bone beds rich in scattered and unworn remains of mammals without long *post mortem* transports. They result from occasional flood events that were responsible for the transport and sorting of mainly isolated hemi-mandibles and their deposition in the floodplain (either in the crevasse splay for the historical level or in the abandoned channel fill for the Neufeld level). However, articulated lumbar vertebrae of a rhinocerotid (*Diaceratherium* sp.) and associated limb bones of a ruminant (Ruminantia indet.) have been discovered in the historical level, as well as associated teeth and incomplete disarticulated fore and hind limbs of a ruminant (*Dremotherium feignouxi*) in the Neufeld level. Thus, the whole reported material illustrates a large range of biostratinomic patterns recognisable in mammal accumulations, indicating several taphonomical processes, such as transport by traction, lag deposits, and maybe mixture resulting from short time averaging (Behrensmeyer and Hook, 1992).

10.3 Materiel and methods

The referred material is stored in the collection of the Natural History Museum Bern (*'Naturhistorisches Museum der Burgergemeinde Bern'*). Large mammal remains were quarried out of the historical and Neufeld levels and small mammal teeth were discovered by screen-washing of the fine-grained deposits of the Neufeld fossiliferous level (ca. 50 kg of sandy marl). The mammal specimens from Engehalde (historical and Neufeld levels) have been reviewed by means of anatomical descriptions, comparative anatomy, and biometrical measurements. The dental terminology for rhinocerotids and the sequence of anatomical features described follow Antoine (2002), while dental and skeletal measurements were taken according to Guérin (1980). For the artiodactyls, terminology and measurements follow Gentry et al. (1999) and Köhler (1993) (Ruminantia), and Berthet (2003) (Cainotheriidae). For other groups, the dental terminology is that of Ginsburg (1999) (Carnivora), Hugueney (1999) (Cricetidae), Daams (1999) (Gliridae), and López-Martínez (1989) (Lagomorpha). All dimensions are in mm and those between brackets are estimated.

The biochronological framework is based on chronological correlations of the European Land Mammal Zones (MN-Zones) (Mein, 1999; Steininger, 1999) and the Swiss Reference Faunas (Engesser and Mödden, 1997; Kempf et al., 1997), and the Paleogene and Neogene geological time scale (Lourens et al., 2004; Luterbacher et al., 2004). The boundary MN2a/MN2b is used in this paper at the Swiss Molasse Basin scale (Engesser and Mödden, 1997), although this subdivision inside of MN2 is not longer applied at the European scale because of a diachronic faunal turnover (Mein, 1999).

Abbreviations

c lower canine, **d** lower deciduous teeth, **i** lower incisor, **M/m** upper/lower molar, **P/p** upper/lower premolar. **APD** antero-posterior diameter, **H** height, **L** length, **TD** transversal diameter, **W** width. **NMBE** *'Naturhistorisches Museum der Burgergemeinde Bern'* (Switzerland); **NMB** *'Naturhistorisches Museum Basel'* (Switzerland).

10.4 Systematic Palaeontology

10.4.1 Historical level

Order PERISSODACTYLA Owen, 1848
Family RHINOCEROTIDAE Gray, 1821
Genus *Diaceratherium* Dietrich, 1931

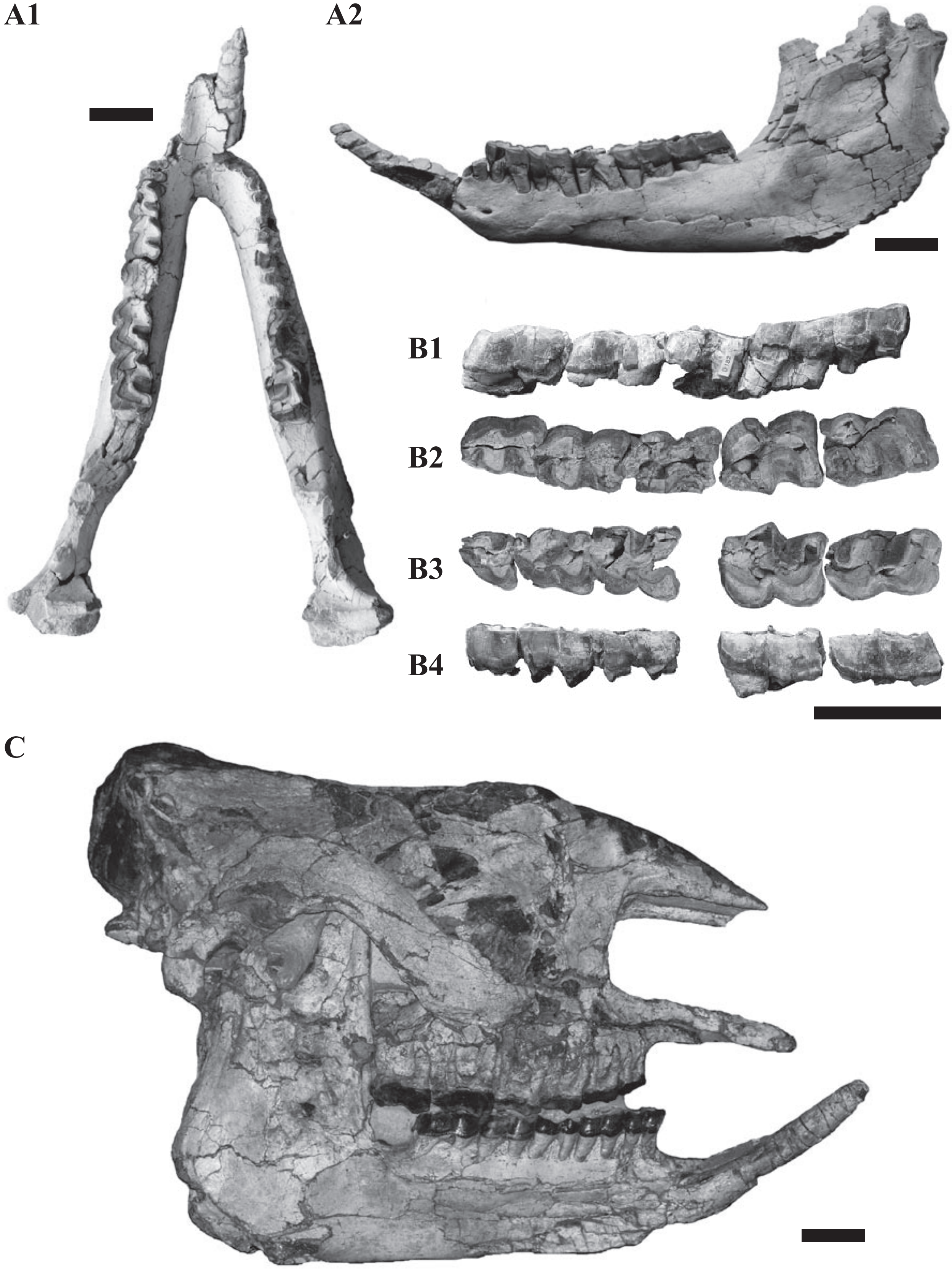
Diaceratherium lemanense (Pomel, 1853)

Referred specimens (Fig. 3A–C): slightly deformed adult skull and mandible with right P2-M3, right i2 and p3-m3, and left i2 (fragment), p4 and m3, and lingual imprints of p3 and m1-2 (NMBE–5016763); adult mandible with right i2, p2-m1 (roots), m2 (fragment) and m3, and left i2 (root), p2 (roots), p3-4, m1 (fragment) and m2-3 (NMBE–5016766); adult tooth rows with right p3-m3 (NMBE–5016764), and left p2-p4 and m2-m3 (NMBE–5016765). Measurements of the skull NMBE–5016763 are reported in Becker et al. (2009: tab. 6, previously numbered as NMBE–D3193), those of the other specimens in Table 1.

Description and comparison: Ooster and von Fischer-Ooster (1871) first illustrated the specimens NMBE–5016763 (pl. 1-2), NMBE–5016764 (pl. 3, fig. 2) and NMBE–5016765 (pl. 3, fig. 1) under the identification "*Acerotherium gannatense*" (junior synonym of the teleoceratine *Diaceratherium lemanense* (Pomel, 1853)), and the specimen NMBE–5016766 (pl. 3, fig. 4) under the identification "*Rhinoceros sansaniensis*" (i.e., the late Early-early Late Miocene rhinocerotine *Lartetotherium sansaniense* (Lartet, 1837)). Additionally, the skull NMBE–5016763 was reviewed by Becker et al. (2009: fig. 4b, previously numbered as NMBE–D3193) and assigned to *D.* cf. *lemanense*.

The skull is slightly flattened transversely. The most noticeable characters are long and fine nasals, a deep U-shaped nasal notch reaching the level of the middle of P3 (in lateral view), a developed and curved forward postglenoid apophysis, in contact with the posttympanic apophysis, a slight posterior elevation and enlargement of the zygomatic arch, weakly separated sagittal crests,

Fig. 3. Late Aquitanian mammals of Engehalde (Molasse Basin, Canton Bern, Switzerland). Historical level. **A,** *Diaceratherium lemanense* (Pomel, 1953); mandible (NMBE–5016766), occlusal view (1), lateral view (2). **B,** *D. lemanense*; lower tooth rows, right lateral (1) and occlusal (2) view (NMBE–5016764), left occlusal (3) and lateral (4) view (NMBE–5016765). **C,** *D. lemanense*; skull and mandible (NMBE–5016763), lateral view. Scale bars: 5 cm.


A1
A2
B1
B2
B3
B4
C

	D. lemanense Capdevieille	Engehalde			Montaigu
Lower teeth	Roman (1912) pl. VII, fig. 1	NMBE–5016763	NMBE–5016766	NMBE–5016764 5016765	NMB–SG18480
i2		23.0/29.0/–	14.5/20.5/–		
p2	19.0/–/–			[21.0]/22.0/–	25.5/17.0/– 24.0/16.0/–
p3	25.0/–/–	31.0/[21.0]/–	32.5/25.5/–	31.5/25.5/– 31.5/22.5/–	32.5/23.0/– 33.5/22.5/–
p4	29.0/–/–	34.0/–/–	35.0/29.0/–	37.0/29.0/– 38.0/[24.5]/–	36.5/25.5/– 35.5/24.5/–
m1	41.0/–/–	35.5/–/–	[33.0]/[29.0]/–	[40.0]/[26.5]/–	39.0/26.5/– 40.5/27.5/–
m2	47.0/–/–	42.5/–/–	41.5/30.5/– [39.0]/–/–	43.0/29.0/– – /29.0/–	47.0/27.0/– 45.0/27.0/–
m3	48.0/–/–	47.5/–/–	46.0/31.0/– 46.5/31.0/–	46.0/25.5/– [43.5]/26.5/–	49.0/28.0/– 49.0/25.0/–
Lp3-4	56.0	62.5	62.0	64.0 65.0	61.0 63.0
Lm1-3	130.0	122.5	113.0	124.0	122.0 126.0
H*corpus* p4/m1	58.0	83.0	45.5		67.0
H*corpus* m1/m2	61.0	85.0	51.0		73.0
H*corpus* back m3	68.0	87.0	65.5		82.0

Table 1 Comparative dimensions of lower teeth (length/width/height; mm) and mandibles of the rhinocerotid *Diaceratherium lemanense* (Pomel 1953) from the late Aquitanian of Engehalde, historical level (Molasse Basin, Canton Bern, Switzerland). The dimensions between brackets are estimated and those in italics are from literature.

and a strong and almost continuous labial cingulum on upper cheek teeth. The dorsal profile is mainly flat and characterised by a slight dome on the nasal posterior edge, a shallow frontal depression, and a very slight occipital elevation.

Only the labial side of the upper cheek teeth of NMBE–5016763 are visible (LP2 = 25.5; LP3 = 29.5; LP4 = 35.2; LM1 = 40.5; LM2 =46.5; LM3 = 43.5; LP3-4 = 65.5; LM = 120.0; L_{P3-4} / L_{M1-3} x 100 = 54.58). They bear a thin continuous labial cingulum running all along the cervix, getting slightly stronger backwards. The upper premolars are characterised by a rather flat ectoloph with a marked, paracone folding and a very weak metacone folding, and without mesostyle. The ectoloph profile of the upper molars is depressed bakwards (wing-shaped). The paracone folding is bulging, the parastyle and metastyle are elongated, and the mesostyle and metacone folding are very smooth.

The mandibles bear a thick symphysis, slightly upraised (< 30° with respect to the *corpus mandibulae*), and without constriction at the diastema level. The posterior border of the symphysis reaches the middle of p3, and the *foramen mentale* is located below p2/p3 level. No median sagittal groove (*sulcus mylohyoideus*) is present on the lingual side of the *corpus mandibulae*. The latter displays an anterior plate with a constant height below p3-p4, and then it gets regularly higher until m3 with a straight ventral border. The *spatium intermandibulare* is narrow to medium near the symphysis, and the horizontal branches deviate regularly. The *incisura vasorum* is weakly marked, the *angulus mandibulae* not much developed, the molar backspace rather long, and the *ramus mandibulae* slightly inclined forward and upward. The lower premolar series is long with respect to the molar series (L_{p3-4} / L_{m1-3} x 100 > 50; mean = 52.50). The i2 is tusk-like and roughly triangular in cross-section with a pronounced neck, a smooth mesiolabial crest and a weak mesiolabial cingulum. The presence of i1 and p1/d1 is attested neither by teeth nor by corresponding alveoli, thus the lower dental formula is 1i-3p-3m. The lower cheek teeth are low-crowned (brachyodont) and they bear distinct roots. The labial cingulum is present. It is always strong on lower premolars and variable on lower molars, but most of time reducing backwards. The lingual cingulum is weakly developed. The anterior cingulum runs lingually towards the opening of the anterior valley. The ectolophid groove is marked but it vanishes before the neck. The talonid valley is narrow and V-shaped in lingual view. In occlusal view, the trigonid is angular and it forms an acute dihedron. The paralophid is lingually reduced. This transversal reduction of the trigonid on lower premolars is accentuated by a concave labial side. The p2 is two-rooted, with a smooth anterior groove, a curved paralophid without constriction, and a somewhat developed paraconid.

The assignment of the skull and mandible NMBE–5016763 to the genus *Diaceratherium* is unequivocal, notably by the structure of the nasals (long and fine, deep U-shaped notch). According to Répelin (1917: pl. I, fig. 1-2), the skull differs from that of *Diaceratherium aginense* (Répelin, 1917) by a flatter dorsal profile of the skull, without a marked occipital elevation, and a straight ventral profile of the *corpus mandibulae*. The set of cranial characters points to *D. lemanense*, and NMBE-5015763 is very close to the specimen from Gannat illustrated by Roman (1912: pl. VIII, fig. 1). However, morphometrical data as well as many morphological characters are highly variable (e.g., cingulum development) or subject to sexual dimorphism and/or ontogenetical discrepancies (e.g., size, nasal horn development) in *Diaceratherium* (de Bonis, 1973; Michel, 1983; Brunet et al., 1983). Also, the intrageneric evolutionary characters cited by Michel (1983) are hardly relevant for specific identifications (e.g., reduction of the external groove, lowering of lingual valley openings on the lower cheek teeth). On the other hand, the mandible and lower teeth share a combination of features (straight posterior base of the *corpus mandibulae* with horizontal branches regularly deviated, long molar backspace, *ramus mandibulae* slightly inclined forward, i2 tusk-like, absence of i1 and d1/p1, smooth ectolophid anterior groove of p2, concave labial side of the trigonid of lower premolars) permitting an attribution to *D. lemanense* with confidence (de Bonis, 1973; Michel, 1983; Brunet et al., 1983; Boada-Saña, 2008). However, the *D. lemanense* mandibles from Gannat (Roman 1912: pl. VIII, fig. 1b) and Lamothe-Capdevieille (Roman 1912: pl. VII, fig. 1) differ somewhat by a completely straight ventral profile of the *corpus mandibulae* (i.e., without anterior plate), a reduced *angulus mandibulae*, a reduced paraconid of p2, and a shortened lower premolars series ($L_{p3-4} / L_{m1-3} \times 100 < 50$). The anterior plate of the ventral profile of the *corpus mandibulae* and the quiet developed paraconid of p2 are rather similar to the specimen NMB–SG18480 of Montaigu (MN2a; Hugueney, 1987), considered by Brunet et al. (1987) as an evolved form of *D. lemanense*. For these reasons, the latter characters permit to assign with confidence the reported specimens to *D. lemanense*.

Diaceratherium aginense (Répelin, 1917)

Referred specimens (Fig. 4A): young adult mandible in two parts (NMBE–5016767): symphysis with right and left i2 (alveoli), right *corpus mandibulae* with d1-m2 and m3 (alveolus), and left *corpus mandibulae* (fragment) with d1-p2, and left *corpus* and *ramus mandibulae* (fragment) with p3-m1 (roots), m2 (fragment) and m3 (alveolus); fragment of adult mandible in three parts (NMBE–5016768): symphysis with i1 (alveoli) and i2 (roots), right *corpus mandibulae* (fragment) with p2-4 (roots) and left *corpus mandibulae* (fragment) with d1-p4 (roots) and m1-3 (fragments; LxW m2 = 43.5x28.0); fragment of adult mandible in two parts (NMBE–5016769): symphysis (fragment) and left and right *corpus mandibulae* (fragments; H*corpus* m1/2 = 69.0) with p2-m1 (roots). Measurements are reported in Table 2.

Description and comparison: Ooster and von Fischer-Ooster (1871) first illustrated the specimens NMBE–5016767 (pl. 3, fig. 3) and NMBE–5016768 (partly, pl. 3, fig. 5) under the identifications "*Acerotherium gannatense*" and "*Rhinoceros sansaniensis*", respectively. The symphysis is thick and upraised (about 30° with respect to the *corpus mandibulae*), without constriction at the diastema level. The posterior border of the symphysis reaches the middle of p2 and the *foramen mentale* is located below the contact between d1 and p2. A sharp sagittal ridge runs on the dorsal border throughout the diastema and joins the lingual side of the d1. The *spatium intermandibulare* is narrow near the symphysis and the horizontal branches are almost parallel. A median sagittal groove (*sulcus mylohyoideus*) is present on the lingual side of the *corpus mandibulae*. The latter has a constant height from p3 until p4/m1 with a straight ventral border (anterior plate) that gets regularly convex until a marked *incisura vasorum*. The *angulus mandibulae*, incomplete, is quiet salient and the *ramus mandibulae* vertical. The lower premolar series is long with respect to the molar series ($L_{p3-4} / L_{m1-3} \times 100 > 50$; value of 54.44 on NMBE–5016767). The presence of a small i1 is revealed by an alveolus located in the antero-lingual border of the i2. The i2 is developed, curved upwards, and triangle-shaped in cross-section. A persistent one-rooted d1 is present at least until a subadult age. Thus, the lower dental formula is 2i-4p-3m. The lower cheek teeth are low-crowned (brachyodont) and they bear partly joined roots in biradiculate p2s. The latter display a constricted paralophid (spur-like) and a developed paraconid, an open posterior valley, as well as marked anterior and external grooves of the ectolophid. The labial cingulum is strong and continuous with vertical external roughnesses on p2, but it is reduced to a small ridge closing the external groove of the ectolophid on p3-m3. This sharp groove vanishes before the neck. The lingual cingulum is reduced on p2 (strong ridges at the entrance of lingual valleys) and formed by an oblique continuance of the anterior cingulum until the entrance of the anterior valley on p3-m3. The trigonid is rather rounded and it forms

	D. aginense Engehalde	Laugnac	***D. asphaltense*** Wischberg	Pyrimont-Challonges
Lower teeth	NMBE–5016767	Répelin (1917) pl. I, fig. 2 (skull B)	NMBE–D771	Depéret and Douxami (1902) pl. II, fig. 2
i2	17.0/24.0/–		26.0/33.5/81.5	*22.0/35.0/116.0*
d1	12.0/8.5/12.5			
p2	24.0/19.0/25.0 25.5/18.5/–	*25.5/15.5/27.0*	30.0/21.0/–	*30.0/21.0/–*
p3	30.0/23.0/29.5	*33.0/22.0/33.0*	36.5/25.5/–	*36.0/25.0/–*
p4	34.0/25.5/35.5	*39.0/28.0/37.0*	39.0/29.5/–	*39.0/29.5/–*
m1	37.0/ [23.5]/30.5	*45.0/31.0/36.0*	43.0/29.0/–	*43.0/29.0/–*
m2	41.0/ [29.0]/33.0 –/27.0/–	*45.0/30.0/37.0*	48.5/32.5/–	*48.5/32.5/–*
m3			52.0/29.0/–	*52.0/29.0/–*
Lp3-4	67.5		76.0	*70.0*
Lm1-3	[124.0]		139.0	*133.5*
H*corpus* p4/m1	61.5		91.0	
H*corpus* m1/m2	64.5		94.0	
H*corpus* back m3	[60.5]		93.5	

Table 2 Comparative measurements of lower teeth (length/width/height; mm) and mandibles of *Diaceratherium aginense* (Répelin, 1917) from the late Aquitanian of Engehalde, historical level (Molasse Basin, Canton Bern, Switzerland). The dimensions between brackets are estimated and those in italics are from literature.

an almost right dihedron with a rather developed lingual branch of the paralophid in occlusal view. The talonid valley is narrow and V-shaped on p3-m3.

Compared with the mandible and dental features observed in both *D. lemanense* and *D. aginense* from Gannat, Lamothe-Capdevieille, Paulhiac, and Laugnac localities (Roman, 1912; Répelin, 1917; de Bonis, 1973; Michel, 1983; Brunet et al., 1997), the present material displays comparable dimensions and it shares many similarities (e.g., upraised symphysis, i2 triangle-shaped, deep lingual valley openings on lower cheek teeth). However, it differs from *D. lemanense* by a vertical *ramus mandibulae*, horizontal branches of the mandible almost parallel, a *sulcus mylohyoideus* present, a ventral profile of the *corpus mandibulae* anteriorly straight (anterior plate) and posteriorly convex (with a marked *incisura vasorum*), a posterior border of the symphysis and a *foramen mentale* reaching the p2, i2 curved upwards, i1 and d1 persistent, rounded trigonid with lingually more developed paralophid on lower cheek teeth, p without concave labial side of the trigonid, and a marked anterior groove of the ectolophid on p2 (spur-like paralophid). In fact, the combination of these characters is very close to newly established diagnostic characters of *D. aginense* (Boada-Saña, 2008). Remarkably, the mandible from Laugnac figured by Répelin (1917: pl. III, fig. 6) is strongly similar to the referred specimen NMBE–5016767. Thus, the referred material can be confidently referred to *D. aginense*.

Additionally, we note strong similarities (e.g., i2 curved upwards, spur-like paralophid and a developed paraconid on p2, short posterior border of the symphysis, a ventral profile of the *corpus mandibulae* anteriorly straight and posteriorly convex) with the mandibles of Pyrimont-Challonges (type locality) and Wischberg (NMBE–D771), attributed to *Diaceratherium asphaltense* Depéret and Douxami, 1902 by Depéret and Douxami (1902: pl. II, fig. 2) and Schaub and Hürzeler (1948), respectively. Contrary to the results of Boada-Saña (2008) and of Boada-Saña et al. (2008), suggesting *D. asphaltense* may be a junior synonym of *D. lemanense*, the synonymy of *D. asphaltense* with either *D. lemanense* or *D. aginense* is still questionable.

Diaceratherium spp.

Referred specimens: left p3-4 (ectolophid fragments; Lp4 = 37.0) (NMBE–5016770); right p4 (ectolophid fragment) (NMBE–2971); fragmentary left humerus (L > 325.0; TDtuberosity = 107.5; TDdiaphysis = 39.0; TDdistal = 121.0; APDdistal = 77.0), fragmentary left radius-ulna (Lradius = 300.0; APDdiaphysis radius = 19.0; TDdiaphysis radius = 33.0) and ribs and a series of five articulated lumbar vertebrae (NMBE–5016771).

Description and comparison: The fragmentary teeth are only represented by parts of lower premolar ectolophids. The labial cingulum is reduced. The ectolophid groove is developed and it vanishes before the neck.

The postcranial specimens, poorly preserved, allow only a short description. The distal articulation of the humerus bears a high *fossa olecrani* and a shallow median constriction (egg-cup shape). The scar on the trochlea and the distal gutter on the epicondyle are absent. The radius and ulna are in contact. On the radius, the medial border of the diaphysis is straight, the insertion of the muscle *biceps brachii* shallow, and the proximal ulna-facets are fused. The angle between the diaphysis and the olecranon is open on the ulna. The lumbar vertebrae display a long body with respect to the height (mean L

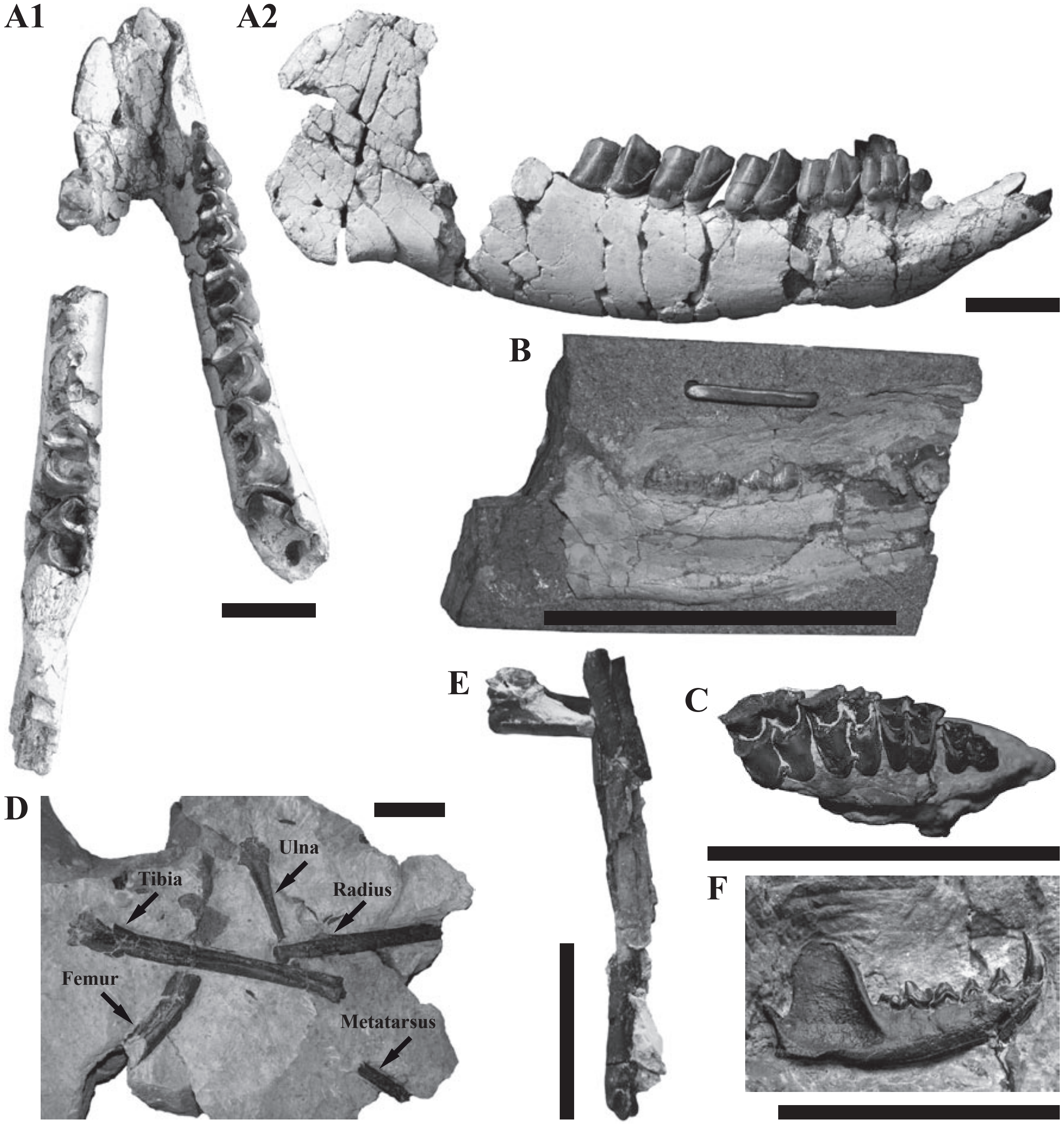


Fig. 4. Late Aquitanian mammals of Engehalde (Molasse Basin, Canton Bern, Switzerland). Historical level. **A,** *Diaceratherium aginense* (Répelin, 1917); right hemi-mandible with preserved symphysis (NMBE–5016767), occlusal view (1), lateral view (2). **B,** *Andegameryx* cf. *laugnacensis* Ginsburg and Morales, 1989; right hemi-mandible (NMBE–5016762), lateral view. Neufeld level. **C,** *A.* cf. *laugnacensis*; right juvenile maxilla with D3-M2 (NMBE–5014565), occlusal view. **D,** *Dremotherium feignouxi* Saint-Hilaire, 1833; postcranial bones (NMBE–5016761). **E,** *D. feignouxi*; right metacarpus (NMBE–5016761), anterior view. **F,** *Plesiogale angustifrons* Pomel, 1853; left hemi-mandible (NMBE–5016757), medial view. Scale bars: 5 cm.

= 65.0-70.0; mean H = *ca.* 50.0), as well as a shallow, vertical and constricted spinal process.

According to Répelin (1917), Michel (1983), de Bonis (1973), and Boada-Saña (2008), the dimensions and main morphological features (such as a developed ectolophid groove on lower premolars, a huge deltoid tuberosity, a high *fossa olecrani* and a shallow median constriction of the distal articulation of the humerus) allow referring all these specimens to *Diaceratherium lemanense* and/or to *D. aginense.* However, no diagnostic character allows identifying them at species level.

Order CETARTIODACTYLA Montgelard, Catzeflis and Douzery, 1997

Suborder RUMINANTIA Scopoli, 1777

Family ANDEGAMERYCIDAE Ginsburg and Morales, 1989

Genus *Andegameryx* Ginsburg, 1971

Andegameryx cf. *laugnacensis*

Referred specimen (Fig. 4B–C): fragmentary left adult mandible with p3, p4 (fragment), m2-m3 (Lp3 = 8.8; Lp4 = [9.2]; Lm1 = [9.5]; Lm2 = 10.6; Lm3 = 16.1) (NMBE–5016762); fragmentary right juvenile maxilla with D3-M2 (LxW D3 = 10.9x7.4; LxW D4 = 10.8x9.9; LxW M1 = 11.2x12.1; LxW M2 = 12.4x13.5) (NMBE–5014565).

Description and comparison: Studer (1895) (pl. 1, fig. 7-8) first illustrated the reported specimen NMBE–5014565 as *Dremotherium feignouxi* Saint-Hilaire, 1833. Only the lingual side of the mandible NMBE–5016762 is visible. The *corpus mandibulae* is relatively well preserved, whereas the *ramus mandibulae* is lacking and the *masseterica fossa* is only partly observable by its imprint. It is a middle-sized ruminant. The *corpus mandibulae* is slender, with a curved ventral profile. The *incisura vasorum* is relatively flat and begins at the level of the middle of m3. The lingual groove is well marked. The molar backspace is quite short. Dental crowns (badly preserved) display brachydont cheek teeth. A well-marked anterior valley groove and a posterior valley in small relief characterize the p3. The p4 shows a well-marked protoconulid and a well-developed metaconid close to the protoconid . The lower molars are bunoselenodont and they show a lingual wall without ectostylids. The *Palaeomeryx*-fold is absent. In NMBE–5014565, the upper cheek teeth are high-crowned, with a rough lingual base. D3 and D4 are worn, whereas M1 and M2 are not. D3 is triangular in occlusal view, with a protocone forming blade pins against the paracone and the paraconule. The mesostyle is more developed than the parastyle. The metastyle appears like a little spur. The paracone is smaller than the metacone and a little spur occurs between the parastyle and the paracone. D4 displays the same pattern as M1-2, i.e. a strong mesostyle, forming a square keel in cross section, a parastyle forming a small column oriented frontward (smaller on M1-2), a metastyle absent or only formed by a little spur, a trigonid larger than the talonid, a paracone and a metacone bearing large vertical ribs (with an anterior groove on the paracone rib), a postprotocrista not joining the praehypocrista, weak anterior and posterior cingula, but without additional crest obstructing the protocone and hypocone basins. On M1-2, the paracone rib is larger than the metacone rib. The entostyle gets more developed from D4 to M2.

According to Ginsburg and Morales (1989) and Becker et al. (2001), the specimens from Engehalde undoubtedly display the main characters of *Andegameryx* (no lingual stylids; no *Palaeomeryx*-fold on lower cheek teeth; postprotocrista separate from the praehypocrista on upper cheek teeth). By their dimensions, they are bigger than *Andegameryx andegaviensis* Ginsburg, 1971 from Beaulieu and La Brosse (Ginsburg et al., 2000; Ginsburg, 2005) and quite smaller than the series referred to *Andegameryx laugnacensis* from Laugnac and Barbothan-les-Thermes (Ginsburg and Morales, 1989; Ginsburg et al., 1991). However, the intraspecific variability is not documented in *A. laugnacensis* yet. As a consequence, the reported specimens are tentatively assigned to *A*. cf. *laugnacensis*.

Ruminantia indet.

Referred specimen: associated postcranial bones (NMBE–5016772): fragmentary left humerus (TDdistal = 29.2; TDdiaphysis = [19.0]; W of the *fossa olecrani* = 14.0), fragmentary radius-ulna, and fragmentary tibia.

Description and comparison: these reported postcranial bones are too badly preserved to allow valuable descriptions. They are slender and belong probably to a small-sized ruminant.

Superfamily SUOIDEA Gray, 1821
Family TAYASSUIDAE Palmer, 1897
Genus *Palaeochoerus* Pomel, 1847

Palaeochoerus typus Pomel, 1847

Remark: no trace of material belonging to Suoidea was found in the NMBE collection. Thus, it is impossible to testify to the presence of the palaeochoerid *Palaeochoerus typus* mentioned by Stehlin (1914). However, we have maintained this taxon as indicative within the faunal list of the historical level of Engehalde (Fig. 2).

10.4.2 Neufeld level

Order CETARTIODACTYLA Montgelard, Catzeflis and Douzery, 1997
Suborder RUMINANTIA Scopoli, 1777
Family MOSCHIDAE Gray, 1821
Genus *Dremotherium* Saint-Hilaire, 1833

Dremotherium feignouxi Saint-Hilaire, 1833

Referred specimens (Fig. 4D–E): fragmentary right P3 (NMBE–5016758); fragmentary left M2 (L = [9.9]) (NMBE–5016759); left M3 (LxW = [8.3]x13.0) (NMBE–5016760); incomplete and disarticulated fore and hind limbs (NMBE–5016761): fragmentary right radius (TDproximal = 14.0; TDdiaphysis = 15.0; APDdiaphysis = 9.0), fragmentary right ulna (APDdiaphysis = 26.5), right metacarpus (L = [160.0]; TDproximal = 19.4; APDproximal = 12.2; TDdiaphysis = 12.5; APDdiaphysis = [8.0]; TDdistal = [17.0]; APDdistal = 12.0), fragmentary femur (TD of the femoral head = [20.0]; TDdiaphysis = [23.0]), right tibia (L =200.0; TDproximal = 29.0; TDdiaphysis = 15.0; TDdistal = 19.2), and fragmentary metatarsus; metacarpus diaphysis (NMBE–5016782); proximal phalanx (NMBE– 5016783); intermediate phalanx (NMBE– 5016784); fragmentary right astragalus (NMBE–501681); lumbar vertebrae (NMBE–5016785).

Description and comparison: the referred teeth and bones belong probably to a single individual. P3 displays a small crest cutting in two parts the hypocone basin. In occlusal view, M2 is square and M3 rectangular. The postprotocrista of molars is distally forked and it joins the praehypocrista in its central part. On M2, the metacone is also postero-lingually forked by a large spur and the entostyle is weak. On M3, the parastyle is well developed, the mesostyle forms a small column well individualized, and the bottom of both the anterior and posterior fossettes displays a rib. The anterior and posterior cingula are deeper on M2 than on M3. The astragalus shows a plantar trochlea in posterior view, the diaphysis of the metapods are fully fused and the phalanxes are slender (thin and elongated). The right metacarpus and the right tibia are the most complete available postcranial elements. The metacarpus is long, with a constant anteroposterior diameter. The only preserved distal articular surface is high and narrow with a strong and sharp joint pulley. The latter has a rounded outline, in lateral view. It is limited by an abrupt constriction (palmar and dorsal grooves) and it bears a middle-sized protuberance for the insertion of the interossei ligaments. The tibia is long and it is antero-posteriorly slightly flattened in its distal part. The furrows for the insertion of flexor tendons of digits are deep and deep and elongated. The two grooves of the distal articular surface are nearly parallel to the antero-posterior cross-section of the diaphysis. The lateral one is larger than the medial one.

The reported specimens are too large to be assigned to *Pomelomeryx* Ginsburg and Morales, 1989 and too small to be referred to *Oriomeryx* Ginsburg, 1985. According to Becker et al. (2001), they differ from *Friburgomeryx* Becker et al., 2001 by the lack of a strong connected cingulum on upper molars. Their dimensions are consistent with those of *Amphitragulus elegans* Pomel, 1853, *Bedenomeryx validus* (Dehm, 1935), and *D. feignouxi* (Viret, 1929; Becker et al., 2001). The M3 seems to be more rectangular and the upper molars more advanced than in *Amphitragulus* and *Bedenomeryx* (Janis and Scott, 1987; Becker et al., 2001). On the other hand, the forked postprotocrista is also present in a figured specimen of *Dremotherium feignouxi* (Janis and Scott, 1987: fig.13B). The latter character is considered as diagnostic and it allows identifying the concerned specimens as *D. feignouxi* unambiguously. The postcranial elements presented here bear common features of ruminants (e.g. fully fused metapod diaphysis, plantar trochlea on astragalus). However, following Janis and Scott (1987), the latter are not diagnostic characters. We assign the concerned bones to *D. feignouxi* because of their association with diagnostic teeth.

RUMINANTIA indet.

Referred specimen: right capitato-trapezoïd (DT = 10.0; DAP = 11.0) (NMBE–5016786).

Description and comparison: this isolated postcranial bone is not associated to any diagnostic material. However, the fusion of the carpal bones III and II in a capitato-trapezoïd is typical of the ruminants. Based on this character and its dimensions, the reported specimen is identified as a small-sized Ruminantia indet.

Superfamily ANOPLOTHERIOIDEA Gray, 1821
Family CAINOTHERIIDAE Cope, 1821
Genus *Cainotherium* Bravard, 1828

Cainotherium sp.

Referred specimen: fragmentary upper molar (NMBE–5016780).

Description and comparison: the fragmentary square and five-cusped selenodont upper molar, with a backwardly displaced protocone, is typical of the small cainotheriid artiodactyl *Cainotherium*, according to Berthet (2003).

Order CARNIVORA Bowdich, 1821
Family MUSTELIDAE Fischer, 1817
Genus *Plesiogale* Pomel, 1846

Plesiogale angustifrons Pomel, 1853

Referred specimen (Fig. 4F): right mandible with c, p2-m2 (Lmandible = 55.0; Lp2 = 5.0; Lp3 = 5.0; Lp4 = 6.0; Lm1 = 9.0; Lm2 2.5; H*corpus* m1 = 14.0) (NMBE–5016757).

Description and comparison: only the lingual side of the mandible is visible. The symphysis is strongly upraised, the ventral profile of the *corpus mandibulae* slightly convex to straight, and the *ramus mandibulae* low and strongly inclined backward. The canine is almost vertical, long and acute, with a distal crest. The lower premolars are rather smooth. The p4 displays an anterior accessory cusp (paraconid) and a high first posterior accessory cusp (deuteroconid = hypoconid). On m1, there is no metaconid, the trigonid is relatively low, the distal side of the paraconid is only slightly inclined and the talonid is smooth. The m2 is two-rooted and short.

The present specimen differs from the remains referred to *Palaeogale* by smooth lower cheek teeth and from *Plesictis* by the absence of an upraised posterior crest of the talonid on m1. On the other hand, it bears a combination of characters, such as the absence of metaconid and a low trigonid on m1, which is diagnostic of *Plesiogale angustifrons* (de Bonis, 1973; Ginsburg, 1999). Besides, its size and morphology are very comparable to the specimen of Laugnac illustrated by de Bonis (1973: pl. 10, fig. 4a), which allows us referring the present mandible to as *Plesiogale angustifrons.*

Grandorder GLIRES Linnaeus, 1758
Order RODENTIA Bowdich, 1821
Family CRICETIDAE Rochebrune, 1883
Genus *Eucricetodon* Thaler, 1966

Eucricetodon cf. *aquitanicus*

Referred specimens (Fig. 5A–D): left M1 (L×W = 2.29×1.72) (NMBE–5016774), fragmentary left m1 (NMBE–5016779), left m2 (L×W = 1.84×1.58) (NMBE–5016899), and right m3 (L×W = 1.65×1.36) (NMBE–5016773).

Description and comparison: the left M1 NMBE–5016774 from Neufeld level is very much advanced showing a distinctly posteriorly directed protoloph (Fig. 5A). The latter joins the entoloph clearly behind the protocone. Posterosinus and posteroloph are pretty reduced. The anterocone is distinctly divided. All these characters are found in *E. aquitanicus* and in *E. infralactorensis* as well. Unusual on the left M1 from Neufeld level is the connection of the anterior branch of protocone with the anterocone, situated more lingually than in *E. aquitanicus* and *E. infralactorensis*. In contrast to the latter two species, the crest running from the anterocone back lingually, enclosing together with the anterior branch of protocone the protosinus, is completely lacking.

The hypolophid of m1 is anteriorly directed, joining the ectolophid in front of the hypoconid, immediately behind the mesoconid (Fig. 5B). The mesoconid is developed as a distinct cusp. From this one a short ectomesolophid is running into the sinusid. On m2, the ectomesolophid is still stronger than on m1. Such a crest cannot be observed in *E. aquitanicus* and *E. infralactorensis*. Advanced characters of m2 are the anteriorly directed metalophid and the consequently very much reduced first synclinid

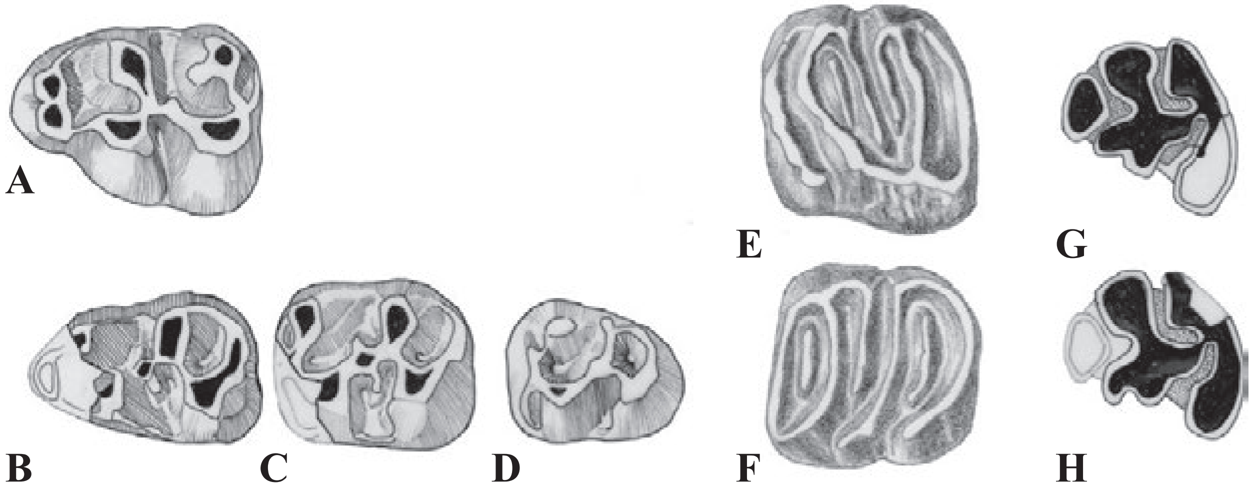


Fig. 5. Late Aquitanian Glires of Engehalde, Neufeld level (Molasse Basin, Canton Bern, Switzerland). **A–D,** *Eucricetodon* cf. *aquitanicus*, occlusal view, scale: □12.5. **A,** left M1 (NMBE–5016774). **B,** left m1 (NMBE–5016779). **C,** left m2 (NMBE–5016899). **D,** dext m3 (reverse) (NMBE–5016773). **E–F,** *Peridyromys* sp., occlusal view, scale: □25. **E,** left M1 (NMBE–5016777). **F,** right m2 (reverse) (NMBE–5016778). **G–H,** *Prolagus vasconiensis* Viret 1930, occlusal view, scale: □12.5. **G,** left p3 (NMBE–5016775). **H,** right p3 (reverse) (NMBE–5016776).

(Fig. 5C). As in m1 the hypolophid joins the ectolophod far in front of the hypoconid. The m3 is so far advanced, that the metalophid is very short and extending anteriorly. The lingual anterior cingulum and the first syncline are almost completely reduced.

The dental specimens of *Eucricetodon* from Neufeld level are distinctly larger and more advanced than those of *E. gerandianus* from La Chaux 7. As far as can be stated on the basis of the three measurable molars, *Eucricetodon* from Neufeld level has about the size of *E. aquitanicus* from Laugnac (Fig. 6). Thus it is smaller than the average size of *E. infralactorensis* Viret, 1930 from Estrepouy and *E.* aff. *infralactorensis* from Vully 1. The evolutionary level of *Eucricetodon* from Neufeld level coincides with that of both *E. aquitanicus* and *E. infralactorensis.* On average *E. infralactorensis* is somewhat larger than *E. aquitanicus*, but the former species is known to have larger size variability. The teeth from Neufeld level are in the size range of both species, but as they correspond quite well to *E. aquitanicus* from Laugnac, they are assigned to *E.* cf. *aquitanicus*.

Family GLIRIDAE Thomas, 1897

Genus *Peridyromys* Stehlin and Schaub, 1951

Peridyromys sp.

Referred specimens (Fig. 5E–F): left M1 sin. (LxW = 1.00x1.10) (NMBE–5016777) and right m2 (LxW = 1.04x0.97) (NMBE–5016778).

Description and comparison: the dental remains referred to *Peridyromys* sp. display diagnostic characters for this genus, such as a protocone and a lingual end of the posteroloph fused on the M1, and a well-developed mesolophid on m2 (Daams, 1999). The referred specimens from Neufeld level are morphologically close to *P. brailloni* (Thaler, 1966) from Laugnac (de Bonis, 1973: fig. 8.11–14). They share similar posterior centroloph on M1 and anterior extra ridge on m2, which are shorter than anterior centroloph and posterior extra ridge on M1 and m2, respectively. However, the present sample is not diagnostic enough to allow any identification at species level.

Order LAGOMORPHA Brandt, 1855

Family OCHOTONIDAE Thomas, 1897

Genus *Prolagus* Pomel, 1853

Prolagus vasconiensis Viret, 1930

Referred specimens (Fig. 5G–H): left p3 (NMBE–5016775) and right p3 (NMBE–5016776).

Description and comparison: the two referred p3s are triangular in occlusal view and they show both distinct protoflexid and anterioflexid. These characters, typical for the *P. praevasconiensis/vasconiensis* group, are much less pronounced, or even absent for the protoflexid, in *P. praevasconiensis* Ringeade, 1979. *Prolagus* from Neufeld level is quite similar to *P. vasconiensis* of Vully

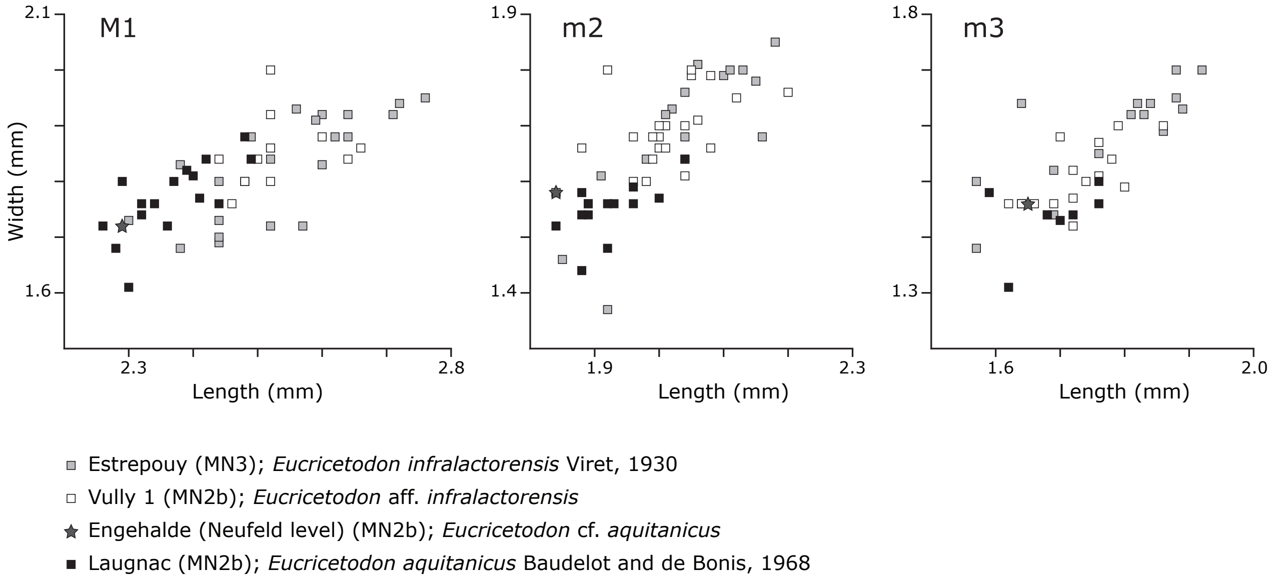


Fig. 6. Length-width (mm) diagrams of M1, m2, and m3 of *Eucricetodon* of Laugnac, Engehalde (Neufeld level), Vully 1, and Estrepouy.

1 (Berger, 1985: fig. 40.7), and it seems to be somewhat more evolved than *P. praevasconiensis* of Mèbre 698 (Engesser et al., 1993; fig. 10c). The corresponding specimens are assigned to *P. vasconiensis.*

10.5 Biostratigraphy and palaeoenvironment

The two mammal faunas from Engehalde attest to a late Aquitanian age (MN2), but they originate from two distinct levels (Fig. 2). The co-occurrence of *Diaceratherium lemanense* and *D. aginense* was already attested in early Aquitanian French localities (Gannat and Paulhiac; Boada-Saña, 2008; Boada-Saña et al., 2008). Besides, *D. lemanense* is recorded in Montaigu and *D. aginense* is abundant in late Aquitanian localities, such as Laugnac or the *'Molasse grise de Lausanne'* localities (MN2; de Bonis 1973; Engesser et al., 1993, Becker et al., 2009). In addition, *Andegameryx laugnacensis*, also known in Laugnac in France (Ginsburg and Morales, 1989), Wallenried in Switzerland (as *A.* cf. *laugnacensis*; Becker et al., 2001), and Loranca in Spain (Gentry et al., 1999), seems to be restricted to the MN2 (Ginsburg, 1999). Accordingly, *Palaeochoerus typus* ranges throughout the Aquitanian (MN1–2) (Hünermann, 1999). To sum up, the mammal assemblage of the historical level coincides with confidence to the European Land Mammal Zone MN2 (Fig. 7).

According to the small mammal assemblage, a maximum age of the fauna of the Neufeld level is given by the occurrence of the ochotonid *Prolagus*. This genus, together with *Lagopsis*, has its first local occurrence in the Swiss Molasse at Mèbre 698 (late MN2a; Engesser & Mödden 1997). The size and evolutionary stages of *Eucricetodon* cf. *aquitanicus* and *Prolagus vasconiensis* from Neufeld fit best within the latest Aquitanian Molasse mammal faunas of Wallenried and Vully 1 (Engesser & Mödden, 1997; Becker et al., 2001). More widely, they correspond to the European Land Mammal Zone MN2b, typified by Laugnac, in SW France. According to the sedimentation rate of the Aquitanian *'Obere Bunte Mergel'* (ca. 200m / Ma) and the related time interval, the historical level fauna could be slightly older, but it certainly still dated from MN2b (Figs. 2 and 7). These biostratigraphical results are concordant with the stratigraphical range of the *'Obere Bunte Mergel'*, which are a lateral equivalent of the *'Molasse grise de Lausanne'* from western Switzerland, but with a slightly younger extension (until Vully 1 instead of La Mébre 698) due to the diachronous W-E transgression of the OMM within the Swiss Molasse Basin (Berger et al., 2005).

The dominating lithofacies of the *'Obere Bunte Mergel'* deposits (fine sand, and massive silt and mud) indicate mainly deposits of overbank sheet flow, floodplain ponds and swamps, and abandoned channel fills typical of

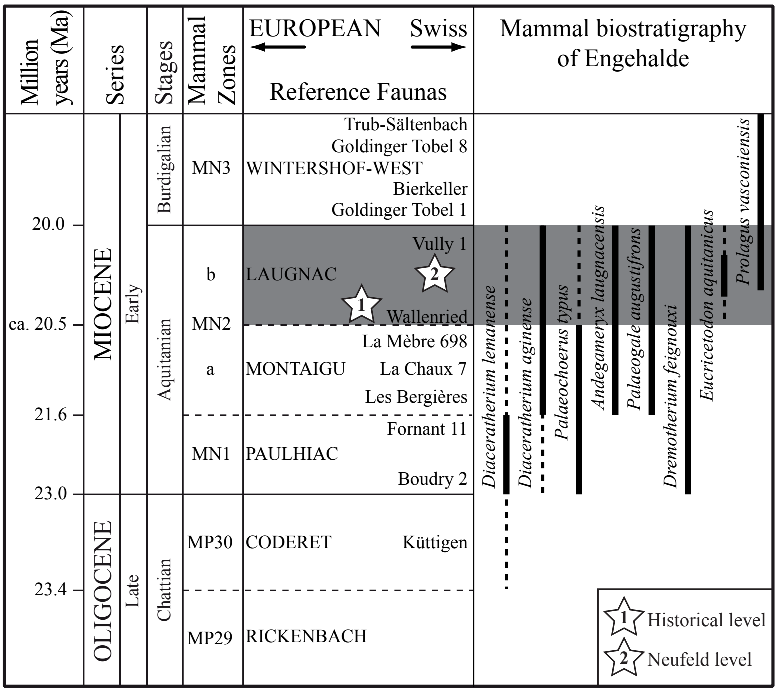


Fig. 7. Biostratigraphy of the mammal assemblages of Engehalde (Molasse Basin, Canton Bern, Switzerland), according to the European (capital) and Swiss (regular) reference faunas (Engesser and Mödden, 1997; Gentry et al., 1999; Ginsburg, 1999; Hünermann, 1999; Mein, 1999; Steininger, 1999; Boada-Saña et al., 2007; Becker et al., 2001, 2009).

the fine-grained meandering river style (Miall, 1996). Regarding the palaeosynecology, the present mammal assemblages do not permit an accurate characterization of the environment of the Bern area during the late Aquitanian. The identified taxa from the historical level would testify to the occurrence of humid forests (*Palaeochoerus typus*; Fortelius et al., 1996) to wooded habitats with moist and soft grounds (*Andegameryx* cf. *laugnacensis*; Becker et al., 2001) in the surroundings of water bodies (*Diaceratherium*; Becker et al., 2009). Based on the work of Köhler (1993), the main morphological characters of the metacarpus of *D. feignouxi* (NMBE–5016761: elongated metacarpus, deep dorsal and palmar grooves separating the diaphysis from joint pulleys, and high and well-rounded condyles) tends to indicate an open, flat, and well-drained habitat within the hinterland for the Neufeld level. According to Demarcq et al. (1983), Berger (1985), and Hugueney (1999), the presence of Cricetidae and especially of Lagomorpha could suggest a relatively dry and warm climate, confirming the habitat interpreted from *D. feignouxi*. Additionally, the Gliridae (forest dwellers) indicate the occurrence of wooded areas in the close surroundings.

10.6 Conclusion

The teleoceratine rhinocerotid *Diaceratherium* is the dominating taxon of the historical level of Engehalde (number of remains = 34; minimum number of individuals = 7). The corresponding dental and mandibular remains are referred to both *D. lemanense* and *D. aginense*. Their association with the ruminant *Andegameryx* cf. *laugnacensis* indicates a late Aquitanian age (MN2). The Engehalde historical level attest to the stratigraphically youngest co-occurrence of *D. lemanense* and *D. aginense* documented so far. Moreover, the main dental and mandible characters (e.g., the ventral profile of the *corpus mandibulae* anteriorly straight and posteriorly convex) typifying *D. aginense* pinpoint the question of a *pro parte* synonymy with *D. asphaltense*. The Neufeld level, lithostratigraphically slightly above the historical level, is dated by small mammals (*Eucricetodon* cf. *aquitanicus*, *Prolagus vasconiensis*) to MN2b. This locality therefore represents one of the last continental sedimentary records prior the Burdigalian marine transgression within the Swiss Molasse Basin.

Both the sedimentological and palaeontological interpretations tend to indicate distinct habitats for the two levels of Engehalde: a humid wooded habitat close to steady rivers and swamp areas for the historical level; a more distal well-drained floodplain, partly wooded, with open high-grassland and seasonal floods for the Neufeld level. These two types of habitats could be successive on a 10^4 year time-scale, but could also testify to the co-occurrence of assorted terrestrial environments.

Acknowledgements

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11 - *First evidence of Aquitanian deposits in the South-Central Jura Molasse (Tavannes, Canton Bern, Switzerland)*

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As a chapter for a publication in *Swiss Journal of Geosciences*

11.1 Introduction

The highway construction through the Jura Mountains (Cantons Bern and Jura, Switzerland) yielded numerous new molassic outcrops. These discoveries were essentially made by the Paléontologie A16 of Porrentruy, along the Canton Jura section of this motorway (e.g., Becker et al. 2004, 2009, Mennecart et al. 2011, Scherler 2011). Recent investigations along the canton Bern section, led by the University of Fribourg and the Paléojura project (Porrentury), brought attention to new Aquitanian deposits, which until recently were unknown in the Jura Molasse (e.g., Picot 2002, Becker 2003).

In 2008, a new mammalian locality was found at the north-eastern entrance of the tunnel Sous le Mont in Tavannes (Bern Canton, Fig. 1). Over a period of 3 years, systematic excavations revealed three distinctive fossiliferous levels separated by a few meters. More than 400 vertebrate remains were discovered. The material is composed mainly of ruminant and rhinocertid teeth and postcranial bones. Additionally, dental and postcranial specimens of small mammals (especially the taxon *Ritteneria* nov. sp. already mentioned in the Aquitanian locality of Montaigu), non-ruminant Cetartiodactyla (*Cainotherium* and Suoidae), Carnivora, birds, turtles and crocodiles, as well as the remains of charophytes and terrestrial plants were discovered. The localities dated to the Aquitanian are very rare within the Jura Molasse. Most of them, belonging to the *Calcaires Delémontiens*, are from the extreme base of the Aquitanian (MN1). No earlier Aquitanian deposits, except the local *Calcaires de la Chaux* (MN2a), are recorded in the Jura Molasse, forming the "Aquitanian gap" (Becker 2003).

The study of this new mammal assemblage, especially the Ruminantia *Dremotherium feignouxi* and *Pomelomeryx gracilis*, allows us to discuss the biostratigraphical and the palaeoenvironmental significance of Sous le Mont within the Swiss Molasse Basin. It should also allow us to reconsider the classical "Aquitanian gap" within the Jura Molasse (e.g., Picot 2002, Becker 2003, Berger et al. 2005a, b).

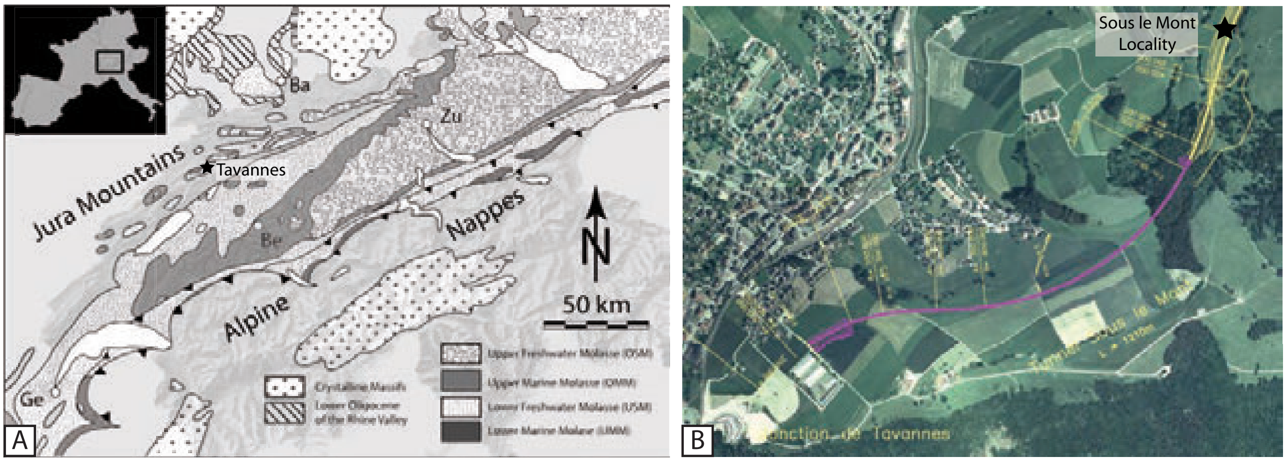

Figure 1 Geological and geographical location of Tavannes Sous le Mont (Late Aquitanian, Switzerland). **A** The geology of the Swiss Molasse Basin and location of Tavannes, **B** The Sous le Mont tunnel location in Tavannes with the mammalian Aquitanian locality (map courtesy of http://www.a16.ch).

11.2 Geological Setting

Located at the northern portal of the Sous le Mont tunnel (583’193/230’368), this outcrop consists of a section 16 meters thick of molassic sediments: 3 meters of calcareous and marly-calcareous deposits (*Calcaires delémontiens*), 7 meters of marly deposits rich in caliche, and 6 meters of grey sandy and marly deposits with an erosive base (Fig. 2). Classically, marly and sandy deposits above the *Calcaires delémontiens* are considered as marine deposits from the OMM (Obere Meeresmolasse = Upper Marine Molasse) (Berger, pers. comm.). Also, typical OMM deposits rich in marine fauna such as shark teeth were identified a few meters above this section (Zulliger 2008). However, the sandy and marly deposits at the top of the Sous le Mont section present no evidence of marine fauna, but are typical fluvial deposits associated with three fossilerous levels rich in terrestrial fossil assemblages (mammals, reptiles, birds and charophytes). Numerous lenses up to 50 cm thick, very rich in mud-pebbles and vertebrate remains, form the base of the sandy and marly series and the first fossiliferous level. The vertebrate specimens discovered in these lenses can be either fragmented and rounded attesting to a long transport, or they are very well preserved. Within larger lenses, mainly postcranial and dental remains of rhinocerotids were discovered. In the middle of the sandy series, a 10 cm thick bed, rich in caliche, yielded fragments of rounded bones and teeth. This bed forms the second fossiliferous layer. At the top of the series, the sediments are more marly and are somewhat mottled, which could correspond with a low energy environment, such as a lake. In this third fossiliferous level, the specimens discovered are well preserved and unworn.

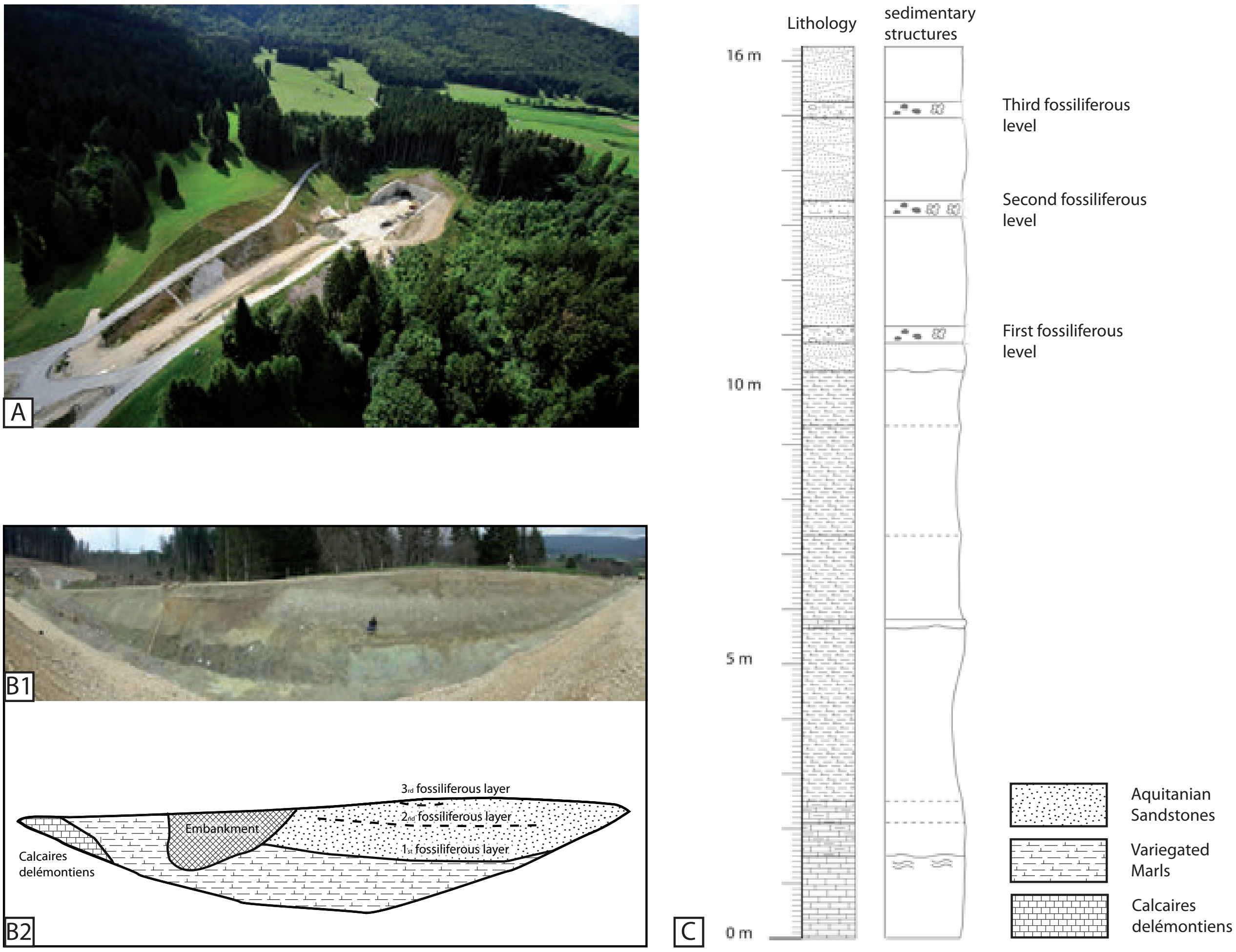

Figure 2 The Tavannes Sous le Mont locality. **A** Picture of the outcrop taken in 2010 (http://www.a16.ch). **B1** Picture of the outcrop taken in 2008 and **B2** profile of the outcrop. **C** Log of the Tavannes Sous le Mont locality.

11.3 Material and Methods

11.3.1 Palaeontology

The referred material is stored in the collection of Musée jurassien des sciences naturelles (MJSN) of Porrentruy (Canton Jura, Switzerland). The ruminant specimens from Sous le Mont have been studied using anatomical descriptions, comparative anatomy, and biometrical measurements.

The other specimens of mammals, crocodiles, turtles, and charophytes are still under study. However, a preliminary faunal and floral list is presented in Table 1. The earliest identification of the small mammals comes from Burkart Engesser (pers. com.), the rhinocerotids from Damien Becker (pers. com.), the suoids from Laureline Scherler (pers. com.), the postcranial specimens of ruminants partially from Florent Hiard (pers. com.), the cainotheriids from myself, and the charophytes (*Rhabdochara* gr. *langerii*, *Nitellopsis* (*Tectochara*) gr. m*erianii*, *Stephanochara* gr. *praeberdotensis*, and Chara indet.) from Jean-Pierre Berger (pers. com.).

The faunal composition is similar amongst all three fossiliferous levels.

The ruminant terminology and measurements follow Bärmann & Rössner (2011, dentition), Mennecart et al. (2011, mandible), Martinez & Sudre (1995, astragalus), and Köhler (1993, phalanges and metapodial bones). The ecomorphologic analysis of the ruminants is based on the morphology of the metapods and phalanges according to Köhler (1993). In the present study, the subdivisions of the habitats are simplified to two types: wooded (type A) and open (type B). Type A can be further divided into: moderately humid (sub-type A1) and very humid (sub-type A2). All dimensions are in mm. They are given with a precision of 0.1 mm.

Tavannes Sur le Mont	Age	MN2b
Marsupialia	Didelphidae	Indet.
Eulipotyphla	Talpidae	Indet.
	Sciuroidea	*Heteroxerus* sp.
Rodentia	Sciuridae	*Blackia* sp.
	Gliridae	Gliridae1
		Gliridae2
	Cricetidae	*Eucricetodon* cf. *quadratus*
	Eomyidae	*Ritteneria* nov. sp.
		Rhodanomys sp.
	Castoridae	*Steneofiber* sp.
Lagomorpha		Lagomorpha1
		Lagomorpha 2
Carnivora		?Carnivora indet.
Artidactyla	Suidae	*Palaeochoerus* sp.
		?*Hyotherium* sp.
	?Moschidae	*Dremotherium feignouxi*
		Pomelomeryx gracilis
	Cainotheriidae	*Cainotherium* cf. *lintillae*
Perissodactyla	Rhinocerotidae	*Diaceratherium* cf. *asphaltense*
Charophyta	*Nitellopsis* (*Tectochara*) gr. *merianii*	
	cf. *Rhabdochara* gr. *langerii*	
	Stephanochara gr. *praeberdotensis*	
	Chara indet.	

Table 1 Preliminary faunal and floral list of Tavannes Sous le Mont (MN2b, Switzerland).

The biostratigraphical framework is mainly based on Berger (2011).

11.3.2 Abbreviations

c lower canine, **d** lower deciduous teeth, **i** lower incisor, **M/m** upper/lower molar, **P/p** upper/lower premolar. **Mc** Metacarpal bones, **Mt** Metatarsal bones. **APD** antero-posterior diameter, **H** height, **L** length, **TD** transversal diameter, **W** width. **MJSN** Musée jurassien des sciences naturelles (Porrentruy, Switzerland); **NMB** Naturhistorisches Museum Basel (Switzerland).

11.4 Systematic Palaeontology

Order **CETARTIODACTYLA** Montgelard, Catzeflis & Douzery, 1997
Suborder **RUMINANTIA** Scopoli, 1777
Infraorder **PECORA** *sensu* Webb and Taylor, 1980
Genus ***Dremotherium*** Saint Hilaire, 1833
Type species ***Dremotherium feignouxi***
Saint Hilaire, 1833

Figs. 3.1 to 3.11 and Figs. 4. to 4.

Referred specimens. MJSN SLM008-15, left m1; MJSN SLM008-18, fragmentary right m; MJSN SLM008-29, left astragalus; MJSN SLM008-31, fragmentary left m; MJSN SLM008-42, fragmentary right P2; MJSN SLM008-51, right proximal phalanx; MJSN SLM008-56, right proximal phalanx; MJSN SLM008-59, left complete mandible with d3-m2, unerupted m3; MJSN SLM008-64, left p4; MJSN SLM008-65, metatarsal bone; MJSN SLM008-68, left proximal phalanx; MJSN SLM008-72, fragmentary left M; MJSN SLM008-75, metapodial bone; MJSN SLM008-91, left P4; MJSN

SLM008-99, left p3; MJSN SLM008-100, right proximal phalanx; MJSN SLM008-101, metapodial bone; MJSN SLM008-102, left intermediate phalanx; MJSN SLM008-108, right astragalus; MJSN SLM008-109 left p3; MJSN SLM008-114, metapodial bone; MJSN SLM008-116, right astragalus; MJSN SLM008-128, right proximal phalanx; MJSN SLM011-6, fragmentary right m3; MJSN SLM011-10, right m1; MJSN SLM011-13, right p4; MJSN SLM011-30, left i1; MJSN SLM011-37, fragmentary left d4; MJSN SLM011-38, right P2; MJSN SLM011-41, right tibia; MJSN SLM011-63, right tibia; MJSN SLM011-75, left p4; MJSN SLM011-80, fragmentary left m; MJSN SLM011-108, left m1; MJSN SLM011-110, right M; MJSN SLM011-111, right m3; MJSN SLM011-112, right p4; MJSN SLM011-118, right astragalus; MJSN SLM011-123, left P3; MJSN SLM011-125, left p4; MJSN SLM011-126, right m; MJSN SLM011-129, left proximal phalanx; MJSN SLM011-130, right m3; MJSN SLM011-134, right cubo-navicular; MJSN SLM011-143, right d3; MJSN SLM011-149, right calcaneus; MJSN SLM011-152, right i2; MJSN SLM011-157, right m3; MJSN SLM011-160, right calcaneus; MJSN SLM011-164, left cubo-navicular; MJSN SLM011-165, left M1; MJSN SLM011-173a, left astragalus; MJSN SLM011-173b, right astragalus; MJSN SLM XX XX1, metacarpal bone; MJSN SLM XX XX2, left astragalus.

Description

Dremotherium feignouxi is the most abundant species in Sous le Mont with more than 60 recognizable dental and postcranial remains. The measurements of the dental and postcranial specimens are summarized in Tables 2 and 3, respectively.

Mandible. The nearly complete juvenile left mandible MJSN SLM008-59 bears d3-m1, m2 still erupting and m3 observable on the lingual part of the specimen (Fig. 3.1). The *corpus mandibulalae* is slender, slightly concave with a well-marked *incisura vasorum*. The enlarged ramus is perpendicular to the *corpus mandibulalae*. The condylar process is small and the coronoid process is broken. The angular process is fragmented, but it does not appear to be enlarged. Even though the d2 is lacking, there is no d1 and the diastema between the alveoli of the d2 and the beginning of the mandible symphysis is elongated (19.5 mm). A second mandible is still under preparation.

Lower deciduous teeth. d3 are laterally compressed, very elongated and simple (Fig. 3.1). The anterior conid is not bifurcated and forms the anterolingual edge. The mesolabial conid is central and it is the highest cuspid. The transverse cristid is short and backwards oriented, without a mesolingual conid. The posterior stylid and the posterolingual conid are separated from the posterolabial conid. They are joined together on the posterolingual corner forming a circular back valley. On d4, a small mesostylid and metastylid are present (Fig. 3.1). The lingual cuspids are laterally compressed. The metaconid is sharp. The anterior cristid of the anterolingual conid is fused with the anterior cristid of the anterolabial conid on the most anterior part of the tooth. No anterior cingulid and anterior cingulid can be distinguished. The fossae are small. The posthypocristid does not reach the postentocristid. The ectostylids are small.

Lower adult teeth. i1 is enlarged and possesses quite a straight upper part (Fig. 3.2). i2 is more laterally compressed, oblique and is characterized by a rounded upper part (Fig. 3.3).

p2 is small and simple. No cristids, excluding the anterolabial and pasterolabial cristids, can be observed. p3 possesses a triangular outline. The anterior conid is

Figure 3 (opposite page) Late Aquitanian ruminant teeth of Tavannes “Sous le Mont” (MN2b, Switzerland). *Dremotherium feignouxi*: **1** left complete mandible with the tooth row d3-m1, m2 erupting, and m3 still in the mandible (MJSN SLM008-59), lingual (**a**), occlusal (**b**), and labial views (**c**). Scale bar equals 50 mm. **2** left i1 (MJSN SLM011-30), labial (**a**) and lingual (**b**); **3** right i2 (MJSN SLM011-152), labial (**a**) and lingual (**b**); **4** left p4 (MJSN SLM011-125), lingual (**a**), labial (**b**), and occlusal views (**c**); **5** right p4 (MJSN SLM011-112), lingual (**a**), labial (**b**), and occlusal views (**c**); **6** right p4 (MJSN SLM011-13), lingual (**a**), labial (**b**), and occlusal views (**c**); **7** right m1 (MJSN SLM011-10), lingual (**a**), labial (**b**), and occlusal views (**c**); **8** right fragmentary m3 (MJSN SLM011-6), lingual (**a**), labial (**b**), and occlusal views (**c**); **9** right m3 (MJSN SLM011 130), lingual (**a**), labial (**b**), and occlusal views (**c**); **10** left P3 (MJSN SLM011-123), occlusal view; **11** left P4 (MJSN SLM008-91), occlusal view. *Pomelomeryx gracilis*: **12** left m1 (MJSN SLM008 64), lingual (**a**), labial (**b**), and occlusal views (**c**); **13** left P4 (MJSN SLM011-17), occlusal view; **14** left m1 (MJSN SLM011-135), lingual (**a**), labial (**b**), and occlusal views (**c**); **15** right M1 (MJSN SLM011-27), occlusal view; **16** right M (MJSN SLM011-169), occlusal view. Scale bar equals 10 mm.


1a
1b
1c
2a
2b
3a
3b
4a
4b
4c
5a
5b
5c
6a
6b
6c
7a
7b
7c
8a
8b
9a
9b
9c
8c
10
11
12a
12b
12c
13
14a
14b
14c
15
16

Table 2 Dental measurements (in mm) of the *Dremotherium feignouxi*; in each row, the first set of data is the length and the second is the width.

Inventory number	p2		p3		p4		m1		m2		m3	
Dremotherium feignouxi												
MJSN SLM 08 15							10.2	6.7				
MJSN SLM 08 18												
MJSN SLM 08 31												
MJSN SLM 08 59							10.9	7.2				
MJSN SLM 08 64												
MJSN SLM 08 99				3.8								
MJSN SLM 08 109			9.2	4.2								
MJSN SLM 11 6												7.2
MJSN SLM 11 10							11.5	7.5				
MJSN SLM 11 13					10.2	5.7						
MJSN SLM 11 30												
MJSN SLM 11 38	8.6											
MJSN SLM 11 75						5.8						
MJSN SLM 11 80												
MJSN SLM 11 108							11.7	7.8				
MJSN SLM 11 111												7.5
MJSN SLM 11 112					10.3	5.8						
MJSN SLM 11 123			9.7	7.6								
MJSN SLM 11 125					9.6	5.0						
MJSN SLM 11 126								7.1				
MJSN SLM 11 130											16.4	8.2
MJSN SLM 11 152												
MJSN SLM 11 157												7.1

Inventory number	d3		d4	
MJSN SLM 08 59	9.1	3.9	12.9	6.4
MJSN SLM 11 143	9.0	3.0		

Inventory number	P2		P3		P4		M1	
MJSN SLM 08 42	9.1	4.8						
MJSN SLM 08 91					7.4	8.6		
MJSN SLM 11 165							10.0	11.5

usually bifurcated, forming a small lingual spur. The mesolingual cuspid is high and central on the lingual wall. The elongated and backward oriented transverse cristid does not end with a mesolingual conid. The posterolabial conid is located between the mesolabial conid and the posterior edge of the tooth. The posterior conid and the posterior stylid are quite transverse, forming a U-shaped back valley, which can be partly closed. p4 is compact (Figs. 3.4 to 3.6). The anterior conid is always bifurcated. The separation between these two small cristids is highly variable. From the high mesolabial conid, the transverse cristid reaches a well-developed mesolingual conid. The latter possesses a posterolingual cristid, closing the posterior valley. The posterior cristid and the posterior stylid are transverse and very close, forming a very narrow and closed back valley.

The molars (Figs. 3.7 to 3.9) possess quite high crowns. The labial cuspids are very selenodont. The external postprotocristid is deep. The fossae are quite large. The lingual cuspids are laterally compressed. The metaconid

Table 3 (opposite page) Postcranial bones measurements. Astragali measurements (following Plummer et al. 2008) **Ast1**, lateral length; **Ast2**, medial length; **Ast3**, minimal length; **Ast4**, distal width; **Ast5**, depth of the lateral portion of the tarsal articulation; **Ast6**, maximum thickness; **Ast7**, depth of lateral portion of the tibial articulation; **Ast8**, intermediate width; **Ast9**, depth of medial portion of tarsal articulation; **Ast10**, proximal width; **Ast11**, medial length of the tibial articulation; **Ast12**, lateral length of the posterior calcaneal facet; **Ast13**, minimum length of the tibial articulation; **Ast14**, lateral length of the tibial articulation; **Ast15**, depth of the distal lateral calcaneal facet; **Ast16**, width of the medial portion of the tarsal articulation. Metapodial bones measurements (following Scott 1985) **MD1**, total length; **MD2**, proximal width; **MD3**, proximal thickness; **MD4**, distal width; **MD5**, distal thickness; **MD6**, intermediate width; **MD7**, intermediate thickness. Proximal phalanges measurements following Degusta and Vrba (2005) **PP1**, midline length; **PP2**, proximal width; **PP3**, intermediate width; **PP4**, distal width; **PP5**, proximal height; **PP6**, intermediate height; PP7, distal height. Intermediate phalanx measurements (following Degusta and Vrba 2005) **PI1**, superior length; **PI2**, inferior length; **PI3**, proximal width; **PI4**, distal width; **PI5**, proximal lateral height; **PI6**, proximal medial height; **PI7**, distal height.

Figure 4 Late Aquitanian ruminants postcranial bones of Tavannes “Sous le Mont” (MN2b, Switzerland). *Dremotherium feignouxi* **1** metacarpus (MJSN SLM XXX1), lateral (**a**) and dorsal views (**b**); **2** right tibia (MJSN SLM 011 63), dorsal view; **3** right astragalus (MJSN SLM 08 116), dorsal view; **4** left astragalus (MJSN SLM 08 29), dorsal view; **5** right proximal phalanx (MJSN SLM 08 128), dorsal (**a**) and interdigital views (**b**); **6** left intermediate phalanx (MJSN SLM 08 102), dorsal (**a**) and interdigital views (**b**). *Pomelomeryx elegans* **7** right astragalus (MJSN SLM 08 63) dorsal view, **8** left astragalus (MJSN SLM 119), dorsal view. Scale bar equals 3 cm.

Locality	Inventory number	Ast1	Ast2	Ast3	Ast4	Ast5	Ast6	Ast7	Ast8	Ast9	Ast10	Ast11	Ast12	Ast13	Ast14	Ast15	Ast16
Dremotherium feignouxi																	
Tavannes Sur le Mont	MJSN SLM 008 108	21.2	20.3	17.8	13.1	8.1	10.6	7.5	12.3	10.3	13.12	11.1	11.2	6	8.9	-	5
	MJSN SLM 008 29	22.2	-	18.2	14.2	-	11	8.2	12.8	10.7	-	-	-	6	11.1	6.1	-
	MJSN SLM 008 116	24.7	23	19.3	-	-	12.7	8.6	14.6	12.5	15.2	13.8	-	6.5	13	8.9	6.2
	MJSN SLM 011 118	-	23.7	19.1	13.7	8.7	11.8	9	12.4	11.6	-	13.9	14.6	5.9	-	8.3	5.7
	MJSN SLM 011 173a	23	20.9	18.7	13.3	8.3	11.8	7.8	12.7	-	13.6	-	14	6.3	12.2	-	5.7
	MJSN SLM 011 173b	21.3	20.8	18.5	-	-	10.6	6.9	11.9	-	12.8	10.7	13.4	6.2	10.6	-	-
	TAV 2011 N	24.3	22.7	19.3	14.5	10.1	11.6	9.2	13.3	11.6	13.6	12.7	15	6	13.1	7.7	-
	TAV 2011 Q	24.6	22.7	20	13.4	9.6	10.9	8.2	12.7	11	13.6	11.8	14.3	6.9	12.5	-	5.9
		MD1	MD2	MD3	MD4	MD5	MD6	MD7									
	MJSN SLM 008 65	-	-	-	-	-	9.14	-									
	MJSN SLM 008 75	-	-	-	17	-	-	-									
	MJSN SLM 008 101	-	-	-	-	-	-	-									
	MJSN SLM 008 114	-	-	-	18	11	-	-									
	MJSN SLM XX XX1	-	-	-	19.2	12.3	11.2	12									
		PP1	PP2	PP3	PP4	PP5	PP6	PP7									
	MJSN SLM 008 100	23.3	9.9	6.7	7.1	9.8	7.9	5.6									
	MJSN SLM 008 128	24.8	9.7	6.4	7.3	9.6	7.7	5.4									
	MJSN SLM 008 56	-	-	-	7.4	-	-	5.7									
		PI1	PI2	PI3	PI4	PI5	PI6	PI7									
	MJSN SLM 008 102	15.1	14.4	7.7	5.7	6.8	5.6	6.8									
		Ast1	Ast2	Ast3	Ast4	Ast5	Ast6	Ast7	Ast8	Ast9	Ast10	Ast11	Ast12	Ast13	Ast14	Ast15	Ast16
Pomelomeryx gracilis																	
Tavannes Sur le Mont	Tav 2011 B	13.9		11.1		5.7	6.8	5	7.9		8						
	Tav 2011 H	13.4	12.3	11			6.7	4.5	7.2		8.1						
	Tav 2001 P																
	MJSN SLM 008 119	14	-	11.1	7.9	6	6.8	4.7	8.3	6.8	-	-	7.6	4	7.7	5	3.5
	MJSN SLM 008 63	14.5	13.5	11.7	9.4	6.6	7.1	5.6	9.1	7.2	9.4	7.9	8.1	4.2	8.3	5.1	3.8

Table 4 Comparison of measurements of the lower teeth of *Dremotherium feignouxi*. The data from Barbotan les Thermes, Lausanne, and Laugnac come from literature (respectively Ginsburg et al. 1991, Engesser et al. 1993, and Ginsburg & Morales 1989). All measurements of the following specimens are in mm.

Locality	Inventory number	Reference	p2		p3		p4		m1		m2		m3	
Dremotherium feignouxi														
Tavannas Sous le Mont	mean value		8.6		9.5	5.2	10.0	5.6	11.1	7.3			16.4	7.5
Barbotan les Thermes	mean value	Ginsburg et al. 1991			9.3	4.9		6.2	11.4	8.5	12.5	8.6		
Lausanne	mean value	Engesser et al. 1993	7.4	3.0	8.9	4.6	11.0	5.3	11.4	7.1	11.4	7.8	16.8	7.6
Montaigu le Blin	mean value		8.1	4.4	10.1	4.7	10.2	5.6	11.4	7.8	12.6	8.4	17.0	8.2
Laugnac	mean value	Ginsburg & Morales 1989	9.7	4.2	11.4	5.6	11.3	6.4	12.2	8.2	13.1	9.0	18.1	8.6

and the entoconid are not aligned. They possess a lingual rib, bigger on the metaconid than on the entoconid. The elongated postentocristid does not fuse with the posthypocristid, forming a small gap between these two cristids. The metastylid is always present, but quite small. The entostylid seems lacking. The anterior and the ectostylid cingulid are large. The back fossa of m3 is lingually opened due to the absence of entoconulid. The hypoconulid forms the posterolabial edge of m3.

Upper adult teeth. The anterolabial cone is well developed and located on the anterior half to the middle of the tooth from P2 to P4. It possesses a large and salient rib. The anterior style is large and forms a small transverse ridge on P2 and P3. The P2 is highly laterally compressed. However, even if the fossa is pinched, a central fold can be observed. The lingual cone is very small on P2, forming a slide on the labial ridge of the tooth. P3 is morphologically similar to P2 (Fig. 3.10). It is wider and the lingual cone is integrated to the lingual wall. P4 is highly laterally compressed due the enlargement of the lingual cone and possesses reduced styles and an anterolabial cone rib (Fig. 3.11). The central fold is well developed.

No complete upper molars have been found in Sous le Mont. However, the fragments imply that they are very selenedont. They possess a metaconule fold. The parastyle and the mesostyle are developed and quite salient. The paracone rib is reduced and absent on the metacone. The entostyle is small. The postprotocrista and premetaconulecrista are highly variable. The postprotocrista is often short and ends in the middle of the length of the premetaconulecrista. In some cases, an additional labially oriented neocrista completes this crista. The premetaconulecrista can also possess a neocrista.

Astragalus. The referred astragali are generally well preserved. The two trochleas are aligned and equilibrated in size. There is no crest at the cubo-navicular boundary. The mediolateral shape of the sustentacular facet is concave with a rounded ridge at the lateral edge, but without a crest at the medial edge.

Metapodial bones. Most of the referred metapodial bones correspond only to distal condyles. Only one of them is almost complete (MJSN SLMXXX-XX1) but it is damaged in two different places. This relatively elongated bone exhibits high, sharp, and well-rounded condyles. The latter are dorsally separated from the shaft by grooves and they end abruptly in the palmar face.

Proximal phalanx. The proximal phalanges are slender. The incision for the metapodial condyle is strong. The external side is straight in the dorsal view. The *sulcus* for the interosseus tendon is absent. The outline of the dorsal side is straight. The facet of the distal articulation is not visible in dorsal view. The distal articulation is flattened on the distal volar side.

Intermediate phalanx. The referred intermediate phalanx MJSN SLM008-102 is complete but rounded. Thus, some characteristics cannot be described. The phalanx is strong and short. The postarticular plateau and the dorsal extensor process are both short. The volar surface shows a well-marked insertion of the *Flexor Digitorum Superficialis*. In its interdigital view, the outline of the distal articular surface is triangular with a distally oriented angle.

Discussion

The morphology of the referred specimens is characteristic of the *Dremotherium* genus by having an elongated diastema, an absence of p1, quite high and very-selenodont cheek teeth, laterally compressed lingual cuspids with salient stylids and styles on lower cheek teeth, and a posterolingual cristid and a bifurcated anterior conid on p4 (Janis & Scott 1987, Gentry 1994). The variability of the crista on upper cheek teeth has already been observed on the specimens from Engehalde (Becker et al. 2010) and is also present on the holotype from Saint Gérand-le-Puy (pers. obs.). The tooth sizes of the population from Sous le Mont clearly reflect to the variability of *Dremotherium feignouxi* (Table 4). Also, regarding this variability in size, the notion of subspecies defined by Ginsburg & Morales (1989) and Ginsburg et al. (1991) should not be considered.

Genus ***Pomelomeryx*** Ginsburg & Morales, 1989
Pomelomeryx gracilis (Pomel, 1853)

Figs. 3.12 to 3.16 and Figs. 4. to 4.

Referred specimens. MJSN SLM008-23, right m1; MJSN SLM008-64, left m1; MJSN SLM008-64, right p2; MJSN SLM011-17, left P4; MJSN SLM011-24, left with alveoli p2-p4; MJSN SLM011-27, right M1; MJSN SLM011-127, left m3; MJSN SLM011-135, left m1; MJSN SLM011-137, fragmentary right m; MJSN SLM011-153, right m; MJSN SLM011-169, right M; MJSN SLM Tav2011B, astragalus; MJSN SLM Tav2011H, astragalus; MJSN SLM Tav2011P, astragalus; MJSN SLM008-119, astragalus; MJSN SLM008-69, astragalus.

Description

Pomelomeryx gracilis is relatively abundant at Sous le Mont with 11 dental specimens and XX postcranial specimens. The crown is brachyodont. The size of the specimens is summarized in Tables 5 and 6 for the dental and postcranial remains, respectively.

Lower adult dentition. The lower molars are bunoselenodont (Figs. 3.12 and 3.14). The lingual wall is bulged without a rib on the metaconid and the entoconid. The anterior fossa is smaller than the posterior one. The space between the metaconid and the entoconid is important, forming a gap. The metaconid possesses a rounded and high metastylid. The postentocristid is complete, joining the posthypocristid. The external postprotocristid is present but variable, from well developed to smooth. The ectostylid is small to absent.

Upper adult dentition. P4 is laterally strongly compressed (Fig. 3.13). The anterolabial cone and the anterior style are poorly developed. The lingual part of the tooth is quite symmetric with a well-rounded lingual cone.

The upper molars are bunoselenodont (Figs. 3.15 and 3.16). Even if the metaconule is smaller than the protocone, it is well developed. The paracone is globular with a large paracone rib. The metacone does not have a rib. The mesostyle and the parastyle are large, forming small columns. The metastyle is salient. The paracone and the metacone are in the same axis and joined at the level of the mesostyle. No neocrista were observed on the referred specimens. The entostyle is present. The specimen MJSN SLM011-27 possesses a small lingual cingulum (Fig. 3.15).

Table 5 Dental measurements (in mm) of the *Pomelomeryx gracilis*; in each row, the first set of data is the length and the second is the width.

Inventory number	p2		p3		p4		m1		m2		m3	
Pomelomeryx gracilis												
MJSN SLM 08 64							6.6					
MJSN SLM 08 64	4.2	2.2										
MJSN SLM 11 127												5.6
MJSN SLM 11 135							7.2	4.9				
MJSN SLM 11 137								4.7				
MJSN SLM 11 153							6.6					

Inventory number	P4		M1		M2	
MJSN SLM 11 17	5.1	6.8				
MJSN SLM 11 27			6.6	7.4		
MJSN SLM 11 169					7.2	8.8

Discussion

The referred specimens clearly belong to the genus *Pomelomeryx* due to their minute size and diagnostic characteristics such as brachyodont-selenodont cheek teeth (Rössner & Rummel 2001). The lingual cuspids of the molars are quite conical (Rössner & Rummel 2001). The metastylid is weak. Within the *Pomelomeryx* genus, the two species *P. gracilis* and *P. boulangeri* differ by their size, the level of selenodonty, and the accessory neocrista (Rössner & Rummel 2001). Moreover, it seems that in the case of *P. boulangeri* the paracone and the metacone are often not in the same axis (Ginsburg et al. 1991). Comparing the sizes with those given by Rössner & Rummel (2001, Tab. 6) and the morphology, the referred specimens belong to the species *P. gracilis*. This taxon has previously been identified in Switzerland (La Chaux 7, Engesser & Mayo 1987).

11.5 Discussion

11.5.1 Biostratigraphy

The Sous le Mont locality only possesses ruminants with saber-like upper canines, but without cranial appendages. The association of these ruminants is characteristic of the Aquitanian (Gentry et al. 1999, Becker et al. 2001, 2010). *Dremotherium feignouxi* is well-known during the Aquitanian of Western Europe (France, Germany, Spain, and Switzerland). *Pomelomeryx* appears to be uncommon but occurred until MN3 (Gentry et al. 1999). Moreover, the presence of *Ritteneria* nov. sp. (similar to that of Montaigu) confirms a Late Aquitanian age and the small mammal assemblage (Tab. 1) is characteristic of a younger age than La Chaux, close to the level of Vully 1 (MN2b) (Burkart Engesser, pers. com.).

11.5.2 The "Aquitanian gap"

The *Calcaires delémontiens* were considered for a long time to be exclusively Oligocene. During the last fifteen years, Picot et al. (1999), Picot (2002), and Becker (2003) have shown that the top of this Jura Molasse formation reaches the basal Aquitanian in some rare outcrops. However, the dating was mainly based on charophyte assemblages. Only the locality of SE Pré Godat (Canton Jura) and Waldenburg-Humbel (Canton Basel Land) were ascribed to the biozones MP30-MN1 on the basis of small mammal remains (Theiler 1998, Engesser & Mödden 1997). Additionally, Mojon et al. (1985) and Engesser & Mödden (1997) mentioned the well-known Aquitanian localities of Boudry (MN1) and La Chaux 7 (MN2a). These localities belong respectively to the *Grès et Marnes grises à Gypse* and the *Calcaires de La Chaux* formations, belonging to the USM (Untere Süsswassermolasse = Lower Freshwater Moasse) of the Plateau Molasse and of a local formation within the South-West Jura Molasse, respectively. Thus, the top of the Sous le Mont section is amongst the youngest and most northern records of USM deposits within the South-Central Jura Molasse. The thinness of these deposits, in comparison to the Plateau Molasse deposits, attests to a bevel effect towards the north, related to an early palaeo-relief of the Jura Mountain (Braillard 2006). The peculiar age and location of this formation should allow us to reconsider the classical "Aquitanian gap" within the Jura Molasse (Berger et al. 2005a, b, Braillard 2006). Probably, the uplift of the Aquitanian described by Braillard (2006) was not homogeneous, permitting local incursions of fluvial sedimentation from the Plateau Molasse to the Jura Molasse, as well as the persistence of lacustrine environments as demonstrated by the local Aquitanian records of *Calcaires Delémontiens* and *Calcaires de La Chaux*.

11.5.3 Palaeoecology and palaeoenvironment

The elongation of long bones (such as the tibia) and the general morphology of the metapodial bones and of the proximal phalanges of *D. feignouxi* (high, sharp and well-rounded condyle, abrupt end of the condyle in the palmar face and dorsal grooves on metapods; slender aspect, strong incision for the metapodial condyle, absence of the sulcus of the interosseus tendon, non-visible facet of the distal articulation in dorsal view, and flattened distal articulation on proximal phalanges) correspond to the morphological type B (= open, flat and dry habitats) of Köhler (1993). However, the intermediate phalanx shows a combination of characteristics from the type A (short and strong phalanx, short dorsal extensor process, well-marked insertion of the *flexor digitorum superficialis*, and triangular outline of the distal articular surface with a distally oriented angle) and from the type B (short postarticular plateau). However, considering the whole appendicular skeleton of *D. feignouxi*, this taxon corresponds to a ruminant living in an open habitat of the

Table 6 Ruminantia specific richness of some well-known Western European Aquitanian localities. Some data have been provided by the literature (*Lausanne*: Engesser et al. 1993; *Pauliac*: Jehenne 1988 and pers. obs.; *La Chaux*: Engesser & Mayo 1987 and pers. obs.; *Ulm-Westtangente*: Costeur et al. 2012; *Montaigu-le-Blin*: Pomel 1853, Filhol 1881, Gentry et al. 1999, Rössner & Rümmel 2001, and pers. obs.; *Saint Gérand-le-Puy*: Pomel 1853, Filhol 1881, Gentry et al. 1999, Rössner & Rümmel 2001, and pers. obs.; *Barbotan-les-Thermes*; Ginsburg et al. 1991 and pers. obs.; *Laugnac*: Ginsburg & Morales 1989).

	Tavannes Sous le Mont	Lausanne	Paulhiac	La Chaux	Ulm-Westtangente	Montaigu-le-Blin	Saint Gérand-le-Puy	Barbotan-les-Thermes	Laugnac
Age	MN2b	Aquitanian	MN1	MN2a	MN2a	MN2a	MN2a	MN2b	MN2b
Species									
Dremotherium feignouxi	X	X	X	X	X	X	X	X	X
Pomelomeryx gracilis	X	X		X	X	X	X	X	X
Pomelomeryx boulangeri			X	X	X	X	X	X	
Amphitragulus elegans		X	X	X	X	X	X	X	
Oriomeryx major			X				X		X
Andegameryx laugnacensis								X	X
Bedenomeryx paulhiacensis			X	?					

type B of Köhler (1993). This result is consistent with the description of the specimens of *D. feignouxi* from Engehalde (MN2, Canton Bern, Switzerland) (Becker et al. 2010). Also, according to Janis & Scott (1987), Mennecart et al. (2012), and Mennecart et al. (accepted), *D. feignouxi* is considered as a folivore associated with elongated cervical vertebra close to the anatomical type of *Litocranius walleri* (extant ruminant living in the African tree and shrub savannah).

In comparison with other localities from a similar age (e.g., Montaigu-le-Blin, Saint Gérand-le-Puy, Barbotan-les-Thermes, Laugnac, La Chaux), which contain many ruminant remains, the ruminant diversity of Tavannes Sous le Mont remains quite low (Table 6). This could indicate a less diverse environment in Tavannes during the Late Aquitanian, in comparison with the afore mentioned localities. The fossils from La Chaux, Montaigu-le-Blin, and Saint Gérand-le-Puy were found in many different layers (Berger, pers. comm. and Costeur, pers. comm.). In Ulm-Westtangente, a mosaic of lakes, rivers, forests, and grassland has been described (Costeur et al. 2012). In Tavannes, the sandstone indicates the presence of a river surrounded by a wooded savannah, attested by the presence of *Dremotherium feignouxi*.

11.6 Conclusion

The mammal assemblage discovered in the Sous le Mont locality opens a new window on a time interval in the Jura Molasse that was previously poorly understood. It allows us to be more cautious with the tendency to generalize the "Aquitanian gap" within the Jura Montains. This area could have been connected to the Plateau Molasse, when the western part, in La Chaux, was already sedimentologically independent.

The high diversity of small mammals limits the age of this locality to MN2b, similar to that of Vully 1 (Switzerland). The two species of ruminants are well represented with nearly 100 specimens. However, in comparison with other localities from a similar age (e.g., Barbotan-les-Thermes, Ulm-Westtangente), the diversity remains quite low. This could indicate a less diverse environment in Tavannes Sous le Mont than in other Aquitanian ruminant localities. Finally, the study of the postcranial remains permits the definition of the anatomical type of *Dremotherium feignouxi* and the interpretation of an open habitat.

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12 - *New data on ruminants at the Aquitanian Wallenried locality (Canton Fribourg, Switzerland)*

As a chapter for a publication in *Swiss Journal of Geosciences*

12.1 Introduction

The Wallenried quarry (574.45/192.45) is located 10 km north of Fribourg (Fig.1.1 and 1.2). The extraction of sandy and marly material is currently used to make bricks for the construction industry. These sediments are part of the Aquitanian Molasse grise de Lausanne Formation (USM = Untere Süsswassermolasse) within the Plateau Molasse (Becker et al. 2001; Becker 2003).

The locality was first studied by Becker (1996) and was dated to MN2b by a small mammal assemblage (*Peridyromys murinus*, *Eucricetodon* aff. *Gerandianus*, *Prolagus praevasconiensis*) found in some layers (WI.1, WI.2, WIII.1, and Channel; Becker et al. 2001). The large mammal assemblage, found in the layers "WI.2" and "channel", is composed of only two species of ruminants. A fragmentary lower molar was attributed to *Andegameryx* cf. *laugnacensis*, taxon relatively common in Western Europe (Gentry et al. 1999; Ginsburg 1999; Becker et al. 2010). Additionally, a new genus and species, *Friburgomeryx wallenriedensis*, has been described for most of the other ruminant remains. Following Becker et al. (2001), Prothero (2007) proposed a familial attribution to Moschidae. However, Wallenried is the only locality yielding this taxon and some doubt persists as to its taxonomic validity (L. Costeur, com. pers.). The hypodigm material of *Friburgomeryx wallenriedensis* is composed of 2 fragmentary maxillae with M1-3 (including the holotype MHNF 28449), a fragmentary anterior part of a mandible with p1-3, and a fragmentary lower molar.

During a field visit by the University of Fribourg, a complete fish was discovered in a marly level (named WallA; Fig. 1.3), just below the historical excavation. Following a recent palaeontological excavation campaign and the screen washing of nearly one tonne of fine sediment from this level, a new well-preserved and well-diversified fauna can be described. The association of these two fossiliferous levels permits a new insight into taphonomical processes (Fig. 1.4). Furthermore, a third fossiliferous level (WallE; Fig. 1.5) yielded an interesting and different faunal assemblage, possibly with Suoidea remains. Nearly one tonne from this level has also been sampled. Finally, a last level (WallF, Fig. 1.6) provided one tooth of *Ritteneria* sp. in nearly 20 kg of sediment. A new and preliminary faunal and floral list of the Aquitanian from Wallenried is proposed in Table 1.

This work focuses on the ruminant remains from the old and new excavations. Of particular importance is the level WallA, rich in gastropods with preserved pigments, which yielded numerous postcranial remains of the enigmatic *Friburgomeryx* (astragalus, juvenile mandible with lower molars). On the other hand, new dental remains of *Andegameryx* allowed the occurrence of this genus in Wallenried to be reassessed.

12.2 Material and Methods

12.2.1 Palaeontology

A huge fauna and flora, notably represented by nearly 620 dental remains in WallA and 125 in WallE, have been found (Fig. 2). However, only ruminants are described in this work. The identification and the description of the other fossils are still in progress. All specimens referred to in this work are stored at the Musée d'histoire naturelle de Fribourg (MHNF), in Switzerland.
Identification is based on anatomical feature descriptions,

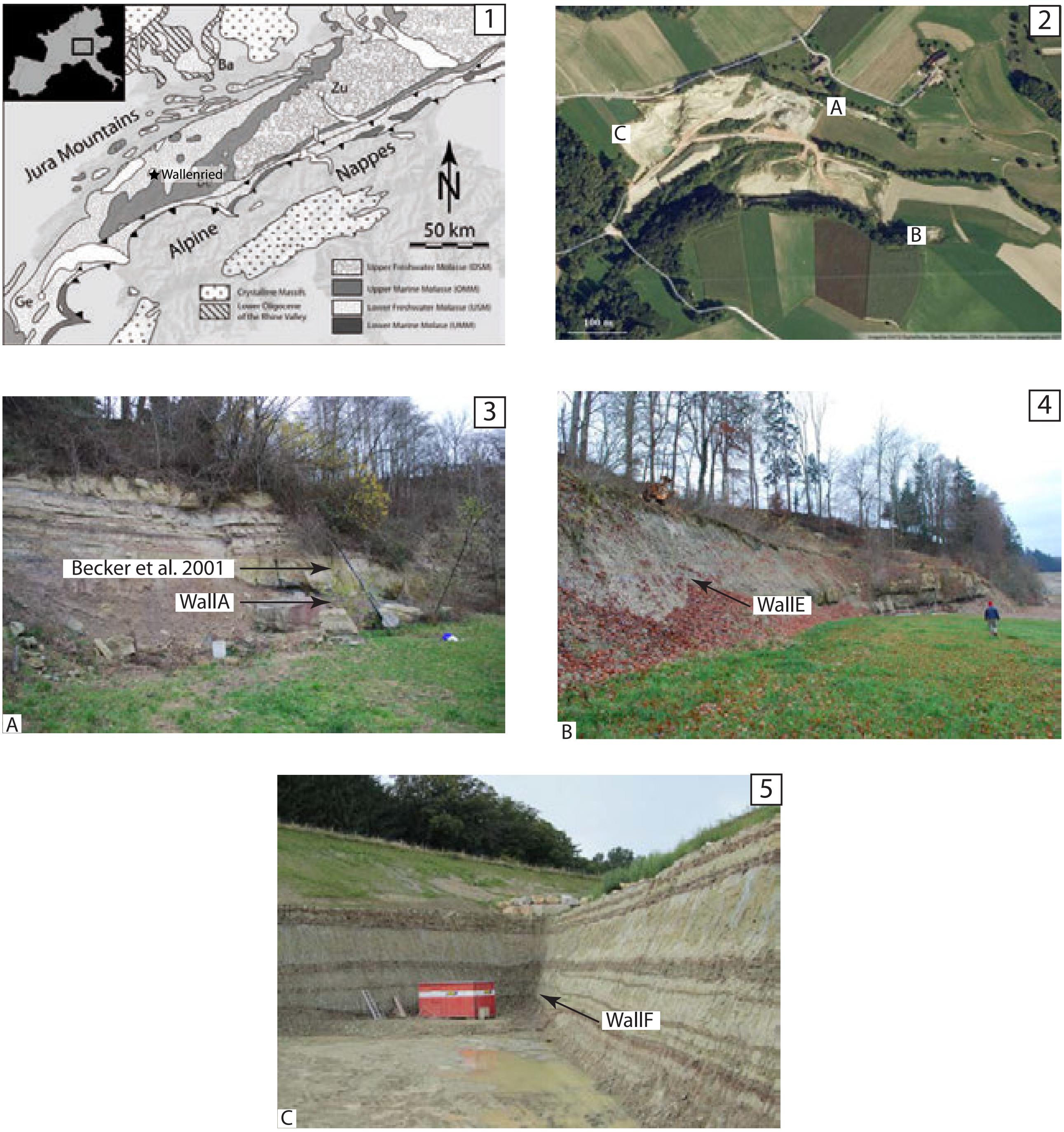


Figure 1 Location of the Wallenried fossiliferous localities. **1** The geology of the Swiss Molasse Basin and location of Wallenried; **2** The Wallenried quarry with the new mammalian layers (A: WallA, C: WalE, and D: WallF); **3** Picture of the WallA locality with the position of the old locality; **4** Picture of the WallE locality; **5** Picture of the WallF locality.

comparative anatomy and biometrical measurements, following the ruminant dental terminology of Bärmann & Rössner (2011). All measurements are given with a precision of 0.1 mm. The biochronological framework is based on the synthesis of Berger (2011).

12.2.1 Abbreviations

i, lower incisive; c, lower canine; p, lower premolar; m, lower molar; C, upper canine; P, upper premolar; M, upper molar; Mc, Metacarpal bones; Mt, Metatarsal bones.

Table 1 Preliminary faunal and floral list of Wallenried (MN2b, Switzerland).

Wallenried	2001	WallA	WallE	WallF
Marsupiala		X		
Insectivora		X		
Gliridae	(*Peridyromys murinus*)	?*P. murinus*	?*P. murinus*	
		X	X	
Cricetidae	*Eucricetodon* aff. *gerandianus*	?*E*. aff. *gerandianus*	?*E*. aff. *gerandianus*	
		?*Pseudocricetodon*		
Melissiodontidae			*Melissiodon* sp.	
Eomyidae	X	*Ritteneria* sp.	*R*. sp.	*R*. sp.
		X	X	
Aplodontidae		?		
Lagomorpha	*Prolagus praevasconiensis*	?*P. praevasconiensis*	?*P. praevasconiensis*	
		?*Titanomys* sp.	?*T*. sp.	
Cetartiodactyla	*Friburgomeryx wallenriedensis*	*F. wallenriedensis*		
	Andegameryx andegaviensis			
	Ruminantia3			
		Cainotherium sp.		
			?Suoidea	
Crocodilia	X	X		
Squamata	*Ophisaurus* sp.	*Ophisaurus* sp.	*Ophisaurus* sp.	
	X	X		
Testudina	X			
Fish	(Cyprinidae)	Cyprinidae	Cyprinidae	
Helicidae	X	X	X	
Limacella	X	X	X	
Ostracoda		X	X	
Charophyta	(X)	X	X	
Seed		X	X	
Coal	(X)	X	X	X

12.3 Palaeontology

Order **CETARTIODACTYLA** Montgelard, Catzeflis & Douzery, 1997
Suborder **RUMINANTIA** Scopoli, 1777
Infraorder **PECORA** *sensu* Webb and Taylor, 1980
Parvorder **Eupecora***sensu* Chapter 1
Genus ***Andegameryx*** Ginsburg, 1971
Andegameryx andegaviensis Ginsburg, 1971
Fig. 2

Referred specimens. MHNF 28453 (old number Wr.3; Becker et al. 2001: 559, pl.1 fig.5), partial *corpus mandibulae* with m2 (first reported and figured in Becker et al. 2001 as "left m1"); MHNF 31286, left mandible with m1-3; MHNF 31287, left D4.

Table 2 Preliminary inventory (number of specimens) of the mammals found in WallA and WallE.

	WallA	WallE
Marsupiala & Insectivora	38	0
Gliridae	61	21
Cricetidae	65	1
Melissiodontidae	0	4
Eomyidae	17	50
Aplodontidae	3	0
Lagomorpha	427	49
Artiodactyla	10	1

Description

The measurements are summarized in Table 2.

Lower adult dentition. The crowns are brachyodont and relatively selenodont. The fossae are relatively narrow. The protoconid and the hypoconid are enlarged. The outline of these cuspids is relatively circular, with the postprotocristid and the posthypocristid transversally oriented. No external postprotocristid can be observed. The space between the postprotocristid and the prehypocristid is relatively important. The metaconid is relatively laterally compressed when the entoconid is more globular. However, they remain relatively bulbous on their lingual face. The postentocristid is small but present. It closes the talonid. Even if it is broken on the specimens studied , we can observe that, contrary to the posterior cingulid, the anterior one is strong, forming a mesostylid. The metastylid and the entostylid are absent. The ectostylid is small.

Upper juvenile dentition. D4 possesses selenodont and large cusps, a strong mesostyle, forming an enlarged small column, and a big parastyle oriented frontward. The metastyle forms a little spur at the end of the elongated postmetacristid. The trigonid is larger than the talonid due to a very narrow metaconule. The paracone and the metacone bear large ribs, with a small anterior groove on the paracone rib. The cingulum is weak on the anterior part of the tooth and seems absent on the posterior part. No neocrista obstruct the fossae.

Discussion

This medium-sized ruminant possesses relatively simple molars for an Eupecora (bulged lingual cuspids and absence of metastylid). Such characteristics are also present in *Amphitagulus* and *Friburgomeryx*. However,

Figure 2 Late Aquitanain *Andegameryx andegaviensis* of Wallenried (MN2b, Switzerland). **1** left mandible with m1-3 (MHNF 31286), labial (**a**), lingual (**b**), and occlusal views (**c**); **2** partial *corpus mandibulae* with m2 (MHNF 28453), labial (**a**), lingual (**b**), and occlusal views (**c**); **3** left D4 (MHNF 31287), occlusal view. Scale bar equals 10mm.

Table 3 Dental measurements (in mm) of the *Andegameryx andegaviensis* and comparison with other species of this genus; in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	Reference	p1		p2		p3		p4		m1		m2		m3	
Andegameryx andegaviensis																
Wallenried (old locality)	MHNF 28453	Becker et al.2001											10.5	7.9		
	MHNF 31286										9.0	7.2	10.9	8.0	15.5	7.7
Engehalde	NMBE-5016762	Becker et al. 2010					8.8		9.2		9.5		10.6		16.1	
La Brosse	mean value	Ginsburg et al. 2000			4.6		8.2	4.1	9.2	5.7	9.6	7.4	10.3	7.5	14.7	7.1
Chiteney	mean value	Ginsburg et al. 2000					8.6	4.9	8.8	5.8	9.4	7.4	10.7	8.3	15.5	7.9
Andegameryx laugnacensis																
Laugnac	mean value	Ginsburg & Morales 1989	6.9	2.9	8.87	4.4	9.9	5.4	10.4	6.7	10.9	7.7	12.0	8.9	17.5	8.6
Andegameryx sp.																
La Encinilla	mean value	Quiralte & Morales 2006					10.7	5.8	11.0	6.6	12.7	8.1	14.8	10.6	19.3	9.5

Locality	Inventory number	Reference	D4	
Andegameryx andegaviensis				
Wallenried (old locality)	MHNF 31287		11.9	10.9
Engehalde	NMBE-5014565	Becker et al. 2010	10.8	9.9
Andegameryx laugnacensis				
Laugnac	mean value	Ginsburg & Morales 1989	11.7	10.2

the latter possess an external postprotocristid on lower molars (Becker et al. 2001, pers. obs.), absent on those of *Andegameryx* (Ginsburg 1999). Moreover, the gap between the postentocristid and the posthypocristid is reduced in *Andegameryx* in comparison to the previous genera. D4 is similar to that of the specimen NMBE–5014465 from Engehalde, identified as *A.* cf. *laugnacensis* by Becker et al. (2010). However, it is a little larger, but it should not belong to *Friburgomeryx*, because of a lacking extremely enlarged lingual cingulum, as is present in upper molars of *Friburgomeryx*.

Three different species of *Andegameryx* are defined. They are mainly based on size differences and biostratigraphy (Ginsburg 1999). *Andegameryx serum* is the smallest and the youngest and *A. laugnacensis* the largest and the oldest. Becker et al. (2001) attributed their unique specimen (Becker et al. 2001, Fig. 5, MHNF 28453) to a m1 of *Andegameryx* cf. *laugnacensis*, based on an incorrect anatomic, the specimen corresponding indeed to a m2. Regarding the new discoveries, the descriptions, and the size comparisons (Table 3), the referred specimens clearly belong to *A. andegaviensis*. In light of this new identification, the specimens attributed to *A.* cf. *laugnacensis* in Engehalde (Becker et al. 2010) should also be considered as *A. andegaviensis*.

Even if Ginsburg (1999) proposed that *A. andegaviensis* was strictly restricted to MN3, we agree with Gentry et al. (1999) and confirm a biostratigraphy extended to MN2b.

Genus **Friburgomeryx** Becker et al., 2001

Friburgomeryx wallenriedensis Becker et al., 2001

Fig. 3

Emended diagnosis. Small to medium-sized ruminant with selenobrachyodont dentition with more conical than crescent-shaped cusps. The upper molars possess a neocrista and strong parastyle, paracone, and mesostyle as well as a strong connected cingulum. The lower molars show a strong external postprotocristid and a rounded lingual wall of the metaconid. The lower premolars include p1. They are wide and bulky and poorly molarized. On p3, a short posterolabial cristid and anterolabial cristid are developed. p2 has a short postprotocristid and entocristid. The bunoselenodont lower molars bear an incomplete postentocristid and an enlarged mesostylid.

Referred specimens. MHNF 28450 (old number Wr.1; Becker et al. 2001: 556, pl.1 fig.1) *Paratype*, partial right maxilla with M1-3 weakly to strongly worn; MHNF 28449 (old number Wr.2; Becker et al. 2001: 556, pl.1 fig.2) *Holotype*, partial right maxilla with M1-3 moderately to strongly worn; MHNF 312888 (old number Wr.4; Becker et al. 2001: 556, pl.1 fig.3) *Paratype*, partial right *corpus mandibulae* with p1-3 moderately to strongly worn; MHNF 31282 (old number Wr.5; Becker et al. 2001: 556, pl.1 fig.4) *Paratype*, fragmentary left angular process and corpus with fragmentary m3 (first reported in Becker et al. 2001 as "left m1, m2 or m3"; more material of this fossil had been refound labelled as turtle remains); MHNF Wr.6, totally worn right mandible with m1-3; MHNF 28452, left mandible with m2-3; MHNF 31284, right nearly complete mandible with alveoli of the d2, the tooth row d3-m1, and m2 erupting; MHNF 31285, highly fragmented left mandible with badly preserved d3, d4, m1, and, m2; MHNF 28454, fragmented upper canine.

Description

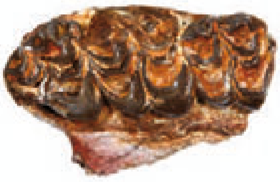
The measurements are summarized in Table 4.

Mandible. The *corpus mandibulae* is relatively massive. There are no diastema between p1 and p2. The height of the corpus becomes higher from p1 to m3. The *incisura vasorum* is very enlarged and smooth. The angular process is not prominent. The ramus is slightly reduced. The condylar process is not projected backwards. The coronoid process is relatively short, curved, and highly orientated backwards.

Lower juvenile dentition. Only the alveoli of d1 is preserved. d2 and d3 are very similar in shape, but d3 is larger. They are blade-like shaped. The anterior conid is oblique and ends the tooth. From the central and high mesolabial conid, there is a long anterolabial cristid, ending at the base of the posterolingual conid. The posterior valley is extremely narrow. The posterolabial conids are located on the labial face. The posterolingual conid and the posterior stylid are transverse and form a narrow back valley. On d3, there is a neocrista in the back valley. d2 and d3 don't have cingulid. d4 is basically of a similar shape to that of the lower molars. However, it possesses relatively low crowns. The anterior stylid is missing. The anterior conid is rounded

1a

2



3

4

5a

5b

6a

6b

7a

7b

7c

Figure 3 (opposite page) Late Aquitanain *Friburgomeryx wallenriedensis* of Wallenried (MN2b, Switzerland). **1** right nearly complete mandible with alveoli of the d2, the tooth row d3-m1, and m2 erupting (MHNF 31284), labial (**a**), lingual (**b**), and occlusal views (**c**); **2** partial right maxilla with M1-3 weakly to strongly worn (MHNF 28450, *Paratype*), occlusal view; **3** partial right maxilla with M1-3 moderately to strongly worn (MHNF 28449, *Holotype*), occlusal view; **4** fragmented upper canine (MHNF 28454), lateral view; **5** partial right *corpus mandibulae* with p1-3 moderately to strongly worn (MHNF 31288, *Paratype*), labial (**a**), and occlusal views (**b**); **6** fragmentary left angular process and corpus with fragmentary m3 (MHNF 31282, *Paratype*), labial (**a**), lingual (**b**), and occlusal views (**c**); **7** left mandible with m2-3 (MHNF 28452), labial (**a**), lingual (**b**), and occlusal views (**c**). Scale bar equals 20mm.

Table 4 Dental measurements (in mm) of the *Friburgomeryx wallenriedensis*; in each row, the first set of data is the length and the second is the width.

Locality	Inventory number	Reference	p1		p2		p3		p4		m1		m2		m3	
Friburgomeryx wallenriedensis																
Wallenried (old locality)	MHNF 31288 Paratype	Becker et al.2001	7.8	3.2	9.8	4.9	10.3	5.8								
	MHNF 31282 Paratype	Becker et al.2001													17.3	8.5?
	MHNF 31289												13.0?	9.5		9.5
	MHNF 28452												13.5?	9.3	17.5	8.2
Wallenried (new locality)	MHNF 31284										11.5	7.2				
	MHNF 31285												13.5	9.3		

Locality	Inventory number	d2		d3		d4	
Wallenried (new locality)	MHNF 31284	7.6	3.2	8.7	3.9	13.8	5.8
	MHNF 31286						5.5

Locality	Inventory number	Reference	M1		M2		M3	
Wallenried (old locality)	MHNF 28450 Paratype	Becker et al.2001	11.1	12.6	12.9		12.0	13.7
	MHNF 28449 Holotype	Becker et al.2001	11.1		13.8	15.3	12.5	14.9

and surrounded by an anterior cingulid. At its base, there is a large anterior ectostylid. All the lingual cuspids are laterally compressed and aligned in the same axis. The postentocristid is relatively elongated, even if it does not reach the posthypocristid. The latter ends with a well-developed entostylid. The internal postprotocristid and the posthypocristid are transverse, forming a small and acute mesofossa and posterior fossa. The external postprotocristid is missing and the ectostylid is small.

Lower adult dentition. The lower molars are relatively bunodont. The internal postprotocristid and the posthypocristid are orientated relatively backwards. On m3, there is a small ridge below the internal postprotocristid that could be the external postprotocristid. However, on the other specimens, it is clearly absent. Even if the lingual cuspids are relatively laterally compressed, they are bulged on the lingual side. They are aligned and their upper parts are quite sharp. The entoconid is more globular than the metaconid. The postentocristid is long on m1 and shorter on m2. It does not fuse with the posthypocristid, forming a gap. The metastyild is small to absent. However, on m2-3, the mesostylid is prominent, forming a small cingulum. The third lobe of m3 is relatively simple, only the hypoconulid being present. The orientation of the back fossa of m3 is oblique. The lingual part can possess a very small cristid, the ectostylid is small, and the anterior and the posterior cingulids are relatively large.

Upper adult dentition. The upper canine is elongated, large, curved, laterally flattened with an ovoid section. No new upper molars have been found. However, these teeth are characterized by a very strong lingual cingulum, large parastyle, paracone, and mesostyle, and a metaconule reduced only on M3, giving a triangular shape to the tooth.

Discussion

The new material attributed to *Friburgomeryx wallenriedensis* shows very primitive features. The cuspids are highly bunodont, the external postprotocristid is small, the postentocristid is incomplete, and the gap between the entoconid and the posthypocristid is wide. Some of these features (the weak metastylid and rounded metaconid) were already described on MNHF 31282 (Becker et al. 2001, Fig.4) and the dimensions are similar (Tab. 4). Moreover, p1 is elongated and in contact with p2, contrary to *Andegameryx* that shows a diastema between p1 and p2 (Ginsburg & Morales 1989).

The presence of an enlarged mesostylid and a huge lingual cingulum on lower molars is relatively uncommon for Aquitanian ruminants. Quiralte & Morales (2006) described an enlarged *Andegameryx* sp. (larger than *A. laugnacensis* and *F. wallenriedensis*; Tab. 2 and 3) in the Burdigalian of Spain. The latter possesses a big mesostylid, however the upper molars are without cingulum. *Babameryx engesseri* from the latest Oligocene of Switzerland is a Eupecora possessing a big lingual cingulum on its upper molars (Mennecart et al. 2012). However, no mesostylid is observed on lower molars and the metaconule on the all upper molars is reduced.

Eupecora indet.

Referred specimens. MHNF 31283, two fragments of lower molar.

Description and discussion

These two small fragments of molars belong to quite a small ruminant, smaller than *Andegameryx* and *Friburgomeryx*. The presence of enlarged stylids (metastilid or entostylid) confirms that this ruminant cannot be ascribed to the previously described ruminants from Wallenried.

12.4 Discussion

The preliminary results based on the fauna and the sedimentology could indicate that the fossils from the historic level described by Becker et al. (2001) have been reworked from WallA. Even if both levels possess gastropods with a similar preservation, WallA and WallE present a different faunal composition in different proportions (Tab. 2). If WallA and WallE are synchronous, the concentration of Eomyidae in WallE is probably due to bird predation such as in Mebre 698 (J.-P. Berger, comm. pers.). The mammal diversity from Wallenried is relatively important with 17 species and is comparable with other Aquitanian localities of the Swiss Molasse Basin (Tab. 5). The huge diversity from La Chaux 7 (with more than 40 species) could be due to a local mosaic environment, including woodlands and savannahs surrounding a lake. WallA would be more representative of the palaeofauna than WallE. The high concentration of Lagomorpha and the absence of Sciuridae suggest an open environment. After the study of postcranial remains, Becker et al. (2001) proposed that the ruminants from Wallenried lived in a subtropical forest. However, Köhler (1993) does not make any distinction between a humid forest habitat and a swampy environment. The presence of a lot of Helicidae, and the total absence of Sciuridae, confirms an open swampy environment rather than a wooded savannah, with a clear seasonality for Wallenried during the Late Aquitanian.

The ruminants from Wallenried are relatively abundant (with the presence of a third undefined species). They possess very primitive features on the teeth (bunodont to bunoselenodont), short postentocristid on lower molars, p1 present, and elongated upper canine. These characteristics belong to the primitive Eupecora. They existed in Europe between MP28 and MN3. However, the largest forms are only from the Miocene. *Andegameryx andegaviensis* is restricted to MN2b and MN3 (Gentry et al. 1999) and does not invalidate the MN2b age suggested by the small mammal assemblage (Becker et al. 2001). The identification of the new specimens of small mammals will precisely locate the biostratigraphic position of Wallenried in comparison to Mèbre 698 and Vully1.

12.5 Conclusions

The discovery of new specimens and the reassessment of old materials from Walleried provides new information on the ruminants from this locality. The description of the specimens referred to as the enigmatic *Friburgomeryx* (including lower juvenile dentition and lower molars) confirms that this ruminant is clearly different from the other genera known in Europe. It possesses a unique association of features such as a huge lingual cingulum on upper molars, the presence of an elongated p1, and a large metastylid on lower molars. However, the metaconule is relatively well formed on upper molars contrary to *Babameryx*. No phylogenic links can be proposed without further information. The reassessment of the specimen of *Andegameryx* from the historical level, associated with new fossils, permits us to correct

Table 5 Comparative faunal list of Swiss Aquitanian localities : Wallenried MN2b ; Les Bergières MN2a ; La Chaux7 MN2a ; Mèbre698 MN2a ; Vully1 MN2b ; Tavannes Sous le Mont MN2b (modified after Engesser & Mödden 1997 ; Becker 2003 ; Chapter 11).

	Wallenried	Les Bergières	La Chaux7	Mèbre698	Vully1	Tavannes Sur le Mont
Age	MN2b	MN2a	MN2a	MN2a	MN2b	MN2b
Marsupialia	X	Didelphid indet.	*Amphiperatherium* sp.	*Amphiperatherium* sp.		Didelphidae indet.
Eulipotyphla	X	cf. *Crocidosorex* sp.	*Paratalpa* cf. *micheli*	*Paratalpa* sp.	Tapid indet.	Talpidae indet.
			Crocidosorex antiquus	Talpid 2 indet.	Soricid indet.	
			Soricid indet.	Soricid indet.		
			Heterosorex neumayrianus			
			Dimylus paradoxus			
			Plesiosorex sp.			
Chiroptera			Chiroptera indet.	Chiroptera indet.		
Sciuroidea			*Palaeosciurus feignouxi*			*Heteroxerus* sp.
			Heteroxerus cf. *pauliacensis*			*Blackia* sp.
			Heteroxerux lavocati			
			Blackia cf. *ulmensis*			
Gliridae	*Peridyromys murinus*	*Peridyromys murinus*	*Microdyromys* cf. *hildebrandti*	*Microdyromys* sp.	*Glirudinus* aff. *gracilis*	Gliridae1
	X	*Plesiodyromys toriformis*	*Vasseuromys* sp.	*Peridyromys* cf. *brailloni*	*Peridyromys murinus*	Gliridae2
			Glirudinus cf. *modestus*	*Peridyromys occitanus*		
			«Glirudinus» glirulus			
			Peridyromys sp.1			
			Peridyromys murinus			
			Peridyromys sp.3			
			Plesiodyromys toriformis			
			Pseudodryomys aff. *aljaphi*			
			Pseudodryomys sp.2			
			Bransatoglis infractolensis			
			Bransatoglis aff. *concavidens*			
			Heteromyoxus wetzleri			
Cricetidae	*Eucricetodon* aff. *gerandianus*	*Eucricetodon* aff. *gerandiunus*	*Eucricetodon gerandianus*	*Eucricetodon gerandianus*	*Eucricetodon aff. aquitanicus*	*Eucricetodon* cf. *quadratus*
	?Pseudocricetodon sp.		*Eucricetodon haslachensis*			
			Pseudocricetodon thaleri			
Melissiodontidae	X		*Melissiodon* aff. *schlosseri*			
			Melissiodon cf. *dominans*			
Eomyidae	*Ritteneria* sp.	*Ritteneria molinae*	*Ritteneria manca*	*Ritteneria manca*		*Ritteneria* nov. sp.
	X		*Pseudotheridomys* aff. *lacombai*	*Pseudotheridomys* aff. *lacombai*	*Pseudotheridomys* aff. *lacombai*	*Rhodanomys* sp.
Castoridae			*Steneofiber* sp.			*Steneofiber* sp.
Aplodontidae	?					
Lagomorpha	*Prolagus praevasconiensis*	*Titanomys*	*Titanomys calmaensis*	*Lagopsis* cf. *spiracensis*	*Lagopsis* cf. *cadeoti*	Lagomorpha1
	X			*Prolagus praevasconiensis*	*Prolagus vasconiensis*	?Lagomorpha2
Carnivora			Mustelid sp.			Carnivora indet.
Cetartiodactyla	Suoidea indet.		*Palaeochoerus* sp.	Cetartiodactyl indet.		*Palaeochoerus* sp.
						Hyotherium sp.
	Friburgomeryx wallenriedensis		*Dremotherium feignouxi*			*Dremotherium feignouxi*
	Andegameryx andegaviensis		*Pomelomeryx boulangeri*			*Pomelomeryx boulangeri*
	Ruminantia3		*Pomelomeryx gracilis*			
			Amphitragulus elegans			
			Bedenomeryx sp.			
	Cainotherium sp.					*Cainotherium* cf. *lintillae*
Perissodactyla			*Tapirus* sp.			*Diaceratherium* cf. *asphaltense*
			Protaceratherium minutum			
			Diaceratherium agenense			

the previous attribution to the large *A.* cf *laugnacensis* into the medium-sized *A. andegaviensis*.

WallA and WallE are very rich fossiliferous levels. Their composition is different. This could be due to diachronism or predation concentration. The second case would imply that the fauna from WallA is closer to a palaeobiocene than the taphocenose of WallE.

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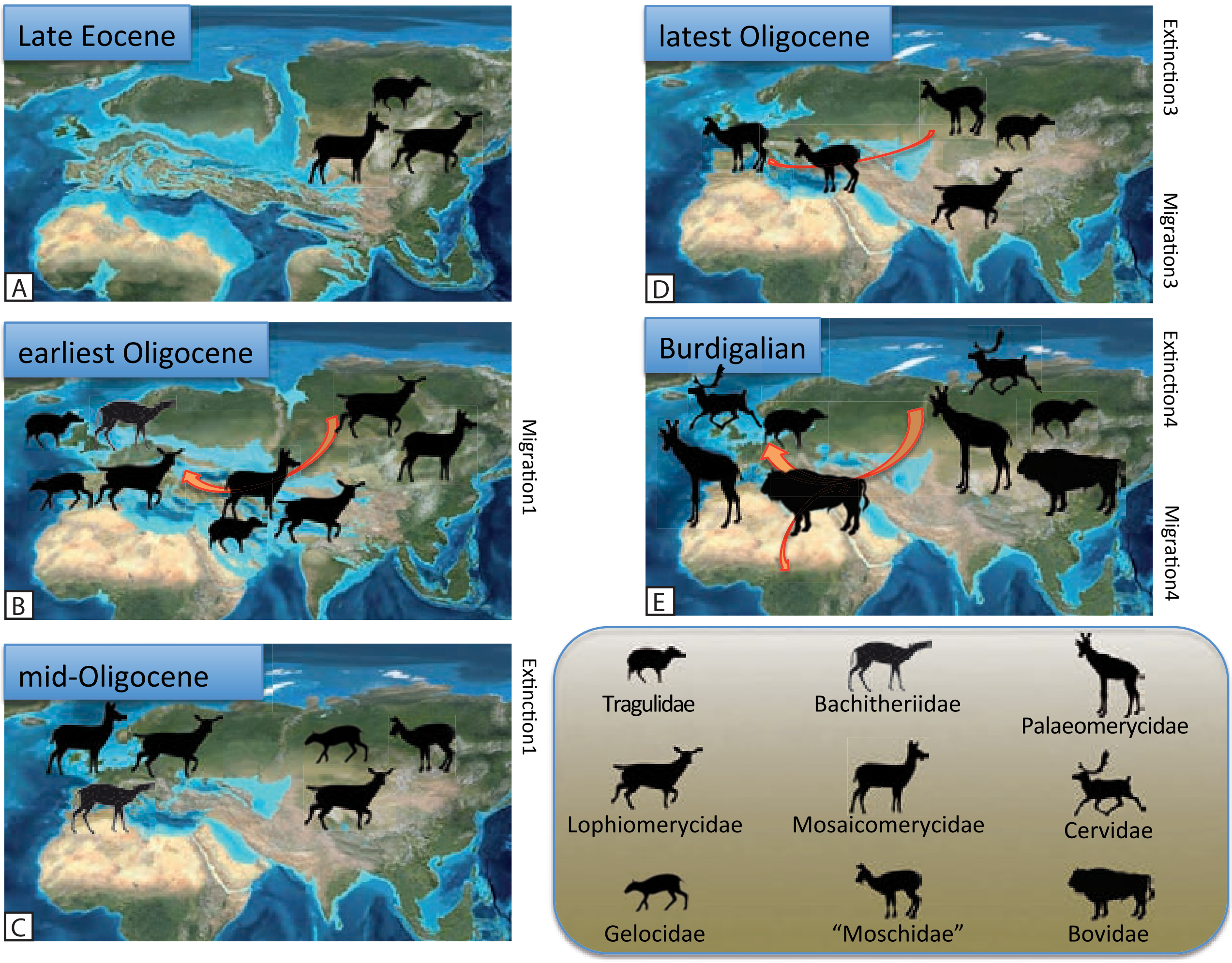
V - Conclusion



Palaeobiogeographyic maps of the Old World
ruminants during the Eocene and Early Miocene
(modified from http://jan.ucc.nau.edu/)

13 - CONCLUSION & PERSPECTIVES

12.1 Conclusion

Nowadays, the ruminants are the most diverse, ecologically dominant group of the hoofed mammals. Including nearly 190 species, they occur from deserts to tropical forests, have a body weight from 3 kg to 2 tons, and cover feeding habits from selective browser to grazer (Mennecart et al. accepted). Although primitive Tragulidae already occur in the Early Oligocene (Mennecart et al. 2011), the diversification of the current families in Europe seems to have occurred during the late Early to Middle Miocene with the Tragulidae (*Dorcatherium guntianum* and *D. crassum*; FAD at MN4), the sabertoothed Moschidae (*Micromeryx flourensianus*; FAD at MN5), the antlered Cervidae (*Procervulus praelucidus* and *Ligeromeryx praestens*; FAD at MN3), and the horned Bovidae (*Brachyotragus artenensis*; FAD at MN4) (Gentry et al. 1999; Hassanin & Douzery 2003).

The primitive European Oligocene ruminants are mainly enigmatic and belong to extinct families, or are uncertainly assigned to the extant families (Mennecart et al. 2012). Many authors suggest that the first ruminants appeared in Europe during the Late Eocene (e.g., Jehenne 1987; Sudre & Blondel 1996; Blondel 1997; Métais & Vislobokova 2007). However, the work of the latter authors is related to isolated, poorly located, and lost specimens, probably discovered in surrounding Oligocene localities (Chapter 5). Additionally, the European Oligocene ruminant diversity was related most of the time to a regional evolution with few migrations (Jehenne 1987; Jehenne & Brunet 1992; Sudre 1995; Blondel 1997). Based on the review of ruminants from 281 localities (Chapter 3), this study offers a new insight into the diverse evolutionary pattern of European ruminants during the Oligocene and the Early Miocene.

The first true ruminants appeared in the Middle and Late Eocene in North America and Asia (Gentry et al. 1999; Gentry 2000; Métais & Vislobokova 2007; Fig. 1A). Fossils of Lophiomerycidae, Tragulidae, and Mosaicomerycidae (new family including the Eurasian genus *Prodremotherium*; Chapter 6) are described in Asia (e.g., Guo et al. 1999; Guo et al. 2000; Métais et al. 2001). Europe was isolated from Asia by the Turgai Strait. European Eocene Artiodactyla are mainly endemic without later descendants (Erfurt & Métais 2007). The earliest occurrence at MN21 of an undeniable European ruminant (Chapter 5; Fig. 2, Migrations1), *Gelocus communis*, was related to the two co-occurring events, the “Grande-Coupure” (MP20/21) and the Oi1 glaciation (ca. 33.5 My; Stehlin 1909; Zachos 2001; Berger 2011). The general sea level dropped, drying out the Turgai Sea and forming land bridges between Asia and Europe, permitting the invasion of the Asian fauna in Europe. This decrease in temperature (nearly 10°C on the continents resulting in a warm month mean of ca. 20°C) was linked to the opening of the Tasmanian–Antarctic passage (Vianey-Liaud 1991; Zachos et al. 2001). European fauna suffered a huge faunal turnover with the disappearance of emblematic endemic taxa such as the omomyid and adapid Primates, cebochoerid and xiphodontid artiodactyls, and anchilophid and lophiodontid perissodactyls (Prothero & Schoch 1987; Bloch et al. 2007; Erfurt & Métais 2007). Related to this extinction/origination event, the earliest European ruminant families Lophiomerycidae, Bachitheriidae and Gelocidae arrived and diversified rapidly, with some arriving later. At MP23 the family of Tragulidae migrated from Asia (ca. 30.5 My; Chapters 4 & 5; Fig.

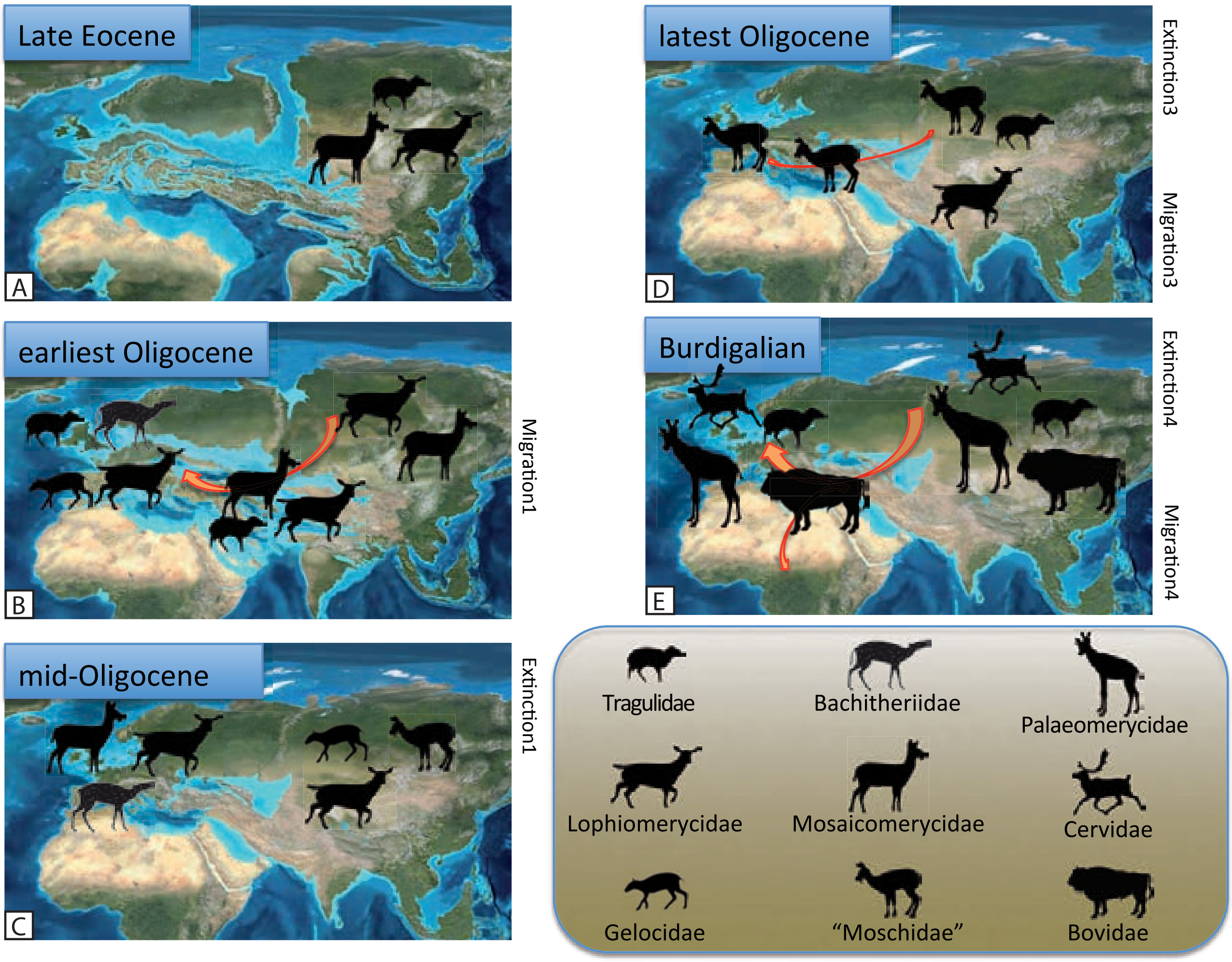


Figure 1 Palaeogeographic maps with ruminant palaeobiogeographical repartition and likely Migrations ways. **A** Late Eocene; **B** earliest Oligocene; **C** mid-Oligocene; **D** latest Oligocene; **E** Burdigalian (maps modified from http://jan.ucc.nau.edu/).

1B; Fig. 2, Migrations1; Fig. 3). Similarly, the earliest Rhinocerotidae, Tapiridae, and Suoidea reached Europe (Prothero & Schoch 1987; Becker 2009; Scherler 2011; Scherler et al. 2011).

At the beginning of MP24, a global change coinciding with the Oi2 glaciation event occurred (Zachos et al. 2001; Berger 2011). The latter may be correlated with the Drake Passage aperture between Antarctica and South America, creating an acute circumpolar current reinforcing the atmospheric and ocean cooling (Zachos et al. 2001) that generated a generally drier climate and a continental faunal renewal (Vianey-Liaud 1991; Legendre 1989; Chapter 5). In Switzerland, it coincided with the regression of the UMM (Untere Meeresmolasse = Lower Marine Molasse) and the Renish Sea, as well as drastic changes of the sedimentological context (Berger 2011; Fig. 3). Within the European ruminant community, the Gelocidae and the Tragulidae disappeared and only larger species of Bachitheriidae and Lophiomerycidae survived (Fig. 2, Extinction1; Fig. 3; Mennecart et al. 2011; Mennecart et al. 2012). Also, the family Lophiomerycidae shows an unsuspected diversity with at least 4 species. However, the co-occurrence of *L. mouchelini* and *L. chalaniati,* suspected at the base of MP24 (Antoine et al. 2011), seems to underline an anagenetic lineage within the genus *Lophiomeryx*. Similar observations can be made on other large mammal groups. Among the rhino-cerotoids, Becker (2009) shows the disappearance of the genus *Epiaceratherium* and the speciation of *Ronzontherium*, *Cadurcotherium* and *Eggysodon*. However, Becker (2009) did not mention this important faunal turnover event. Scherler (2011) characterized the speciation of the Antracotheriidae *Elomeryx* during this period.

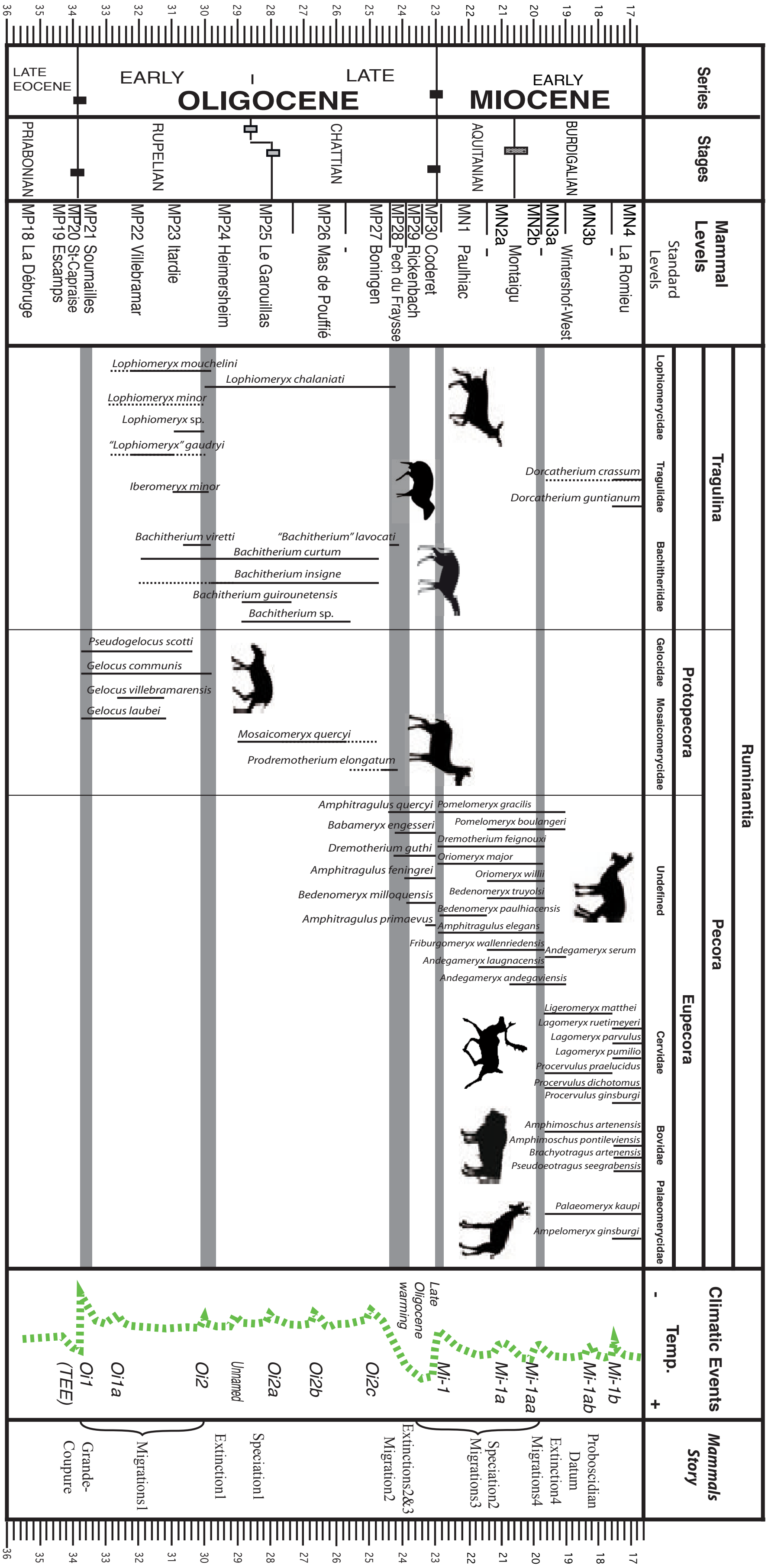


Figure 2 Synthesis of the biostratigraphy of the European Ruminantia species during the Oligocene and the Early Miocene related to major global faunal and climatic events. The chronostratigraphy is based on Berger 2011. Due to the huge number of ruminant species during the Burdigalian, they are not all recorded in this figure.

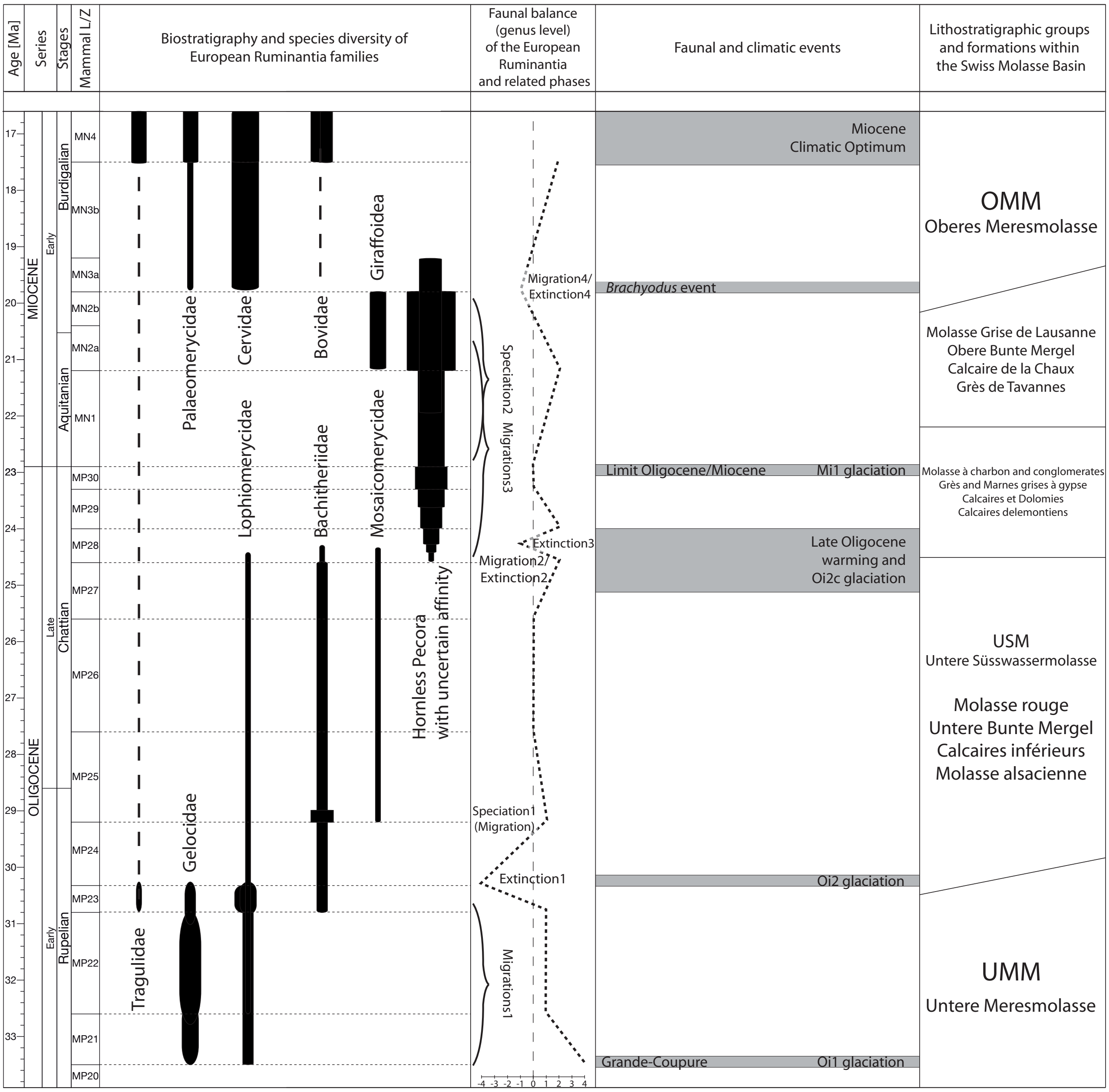


Figure 3 Biostratigraphy and faunal balance of the European Ruminantia at the genus level related to major global faunal and climatic events, and to the Swiss lithostratigraphic record within the Molasse Basin. The phases plotted along the faunal balance curve are defined with respect to the dominant causes of the recorded faunal changes between migration, extinction and speciation.

During MP24-25 (ca. 29.2 My), the Bachitheriidae diversified into many species and the ruminant Mosaicomerycidae, the anthracotheriid *Elliotherium*, and the rhinocerotid *Molassitherium* appeared in Europe (Chapter 5 & 6; Becker 2009; Scherler 2011; Becker et al. accepted; Fig. 1C; Fig. 2, Speciation1; Fig. 3). Within the Lophiomerycidae, only *L. chalaniati* persisted. Thereafter, the European mammal evolution was relatively quiet and steady until MP27. The environment was generally wooded, and the sedimentation in the Swiss Molasse was typically dominated by fluvial processes (Berger 2011; Fig. 3).

Around MP28, large changes occurred in the faunal communities (Vianey-Liaud 1991; Blondel 1997; Berthet 2003). The end of the Late Oligocene warming (end of MP27 to MP29; Berger 2011) was marked by an increase in the continental temperature that reached a mean annual value of ca. 20°C with a temperature for the warm month mean of ca. 30°C (De Man & Van Simaeys 2004). This period appears to be correlated with a tectonic plate reorganisation and the uplift of the Andean mountains (Zachos 2001). Simultaneously, it coincided in Switzerland with sedimentological changes involving the formation of gypsum related to a drier climate, and high-altitude deposits of coal, proving the active Alpine orogeny (Berger 1998; Berger 2011; Fig. 3). The diverse evolutionary pattern of the ruminants can be precisely defined for this period, thanks to the record of numerous rich and stratigraphically well-defined localities (Chapters 3 & 9). First, a specific renewal resulted in the dominance of ruminants in more open habitats (Chapters 5 & 6; Fig. 2, Extinction2 and Migration2; Fig. 3). The Bachitheriidae, the Lophiomerycidae, and the Mosaicomerycidae persisted during this very short time interval, but with new representatives (Migration2). *Bachitherium curtum*, *B. insigne*, and *Mosaicomeryx quercyi* gave way to *Bachitherium lavocati* and *Prodremotherium elongatum*. Also, the last occurrences of the anthracotheriid *Elliotherium* and *Elomeryx* are recorded (Scherler 2011). The Aquitanian *Elomeryx* aff. *borbonicus* from Pyrimont-Challonges and Wischberg (Hellmund 1991; Van der Made 1999) should probably be attributed to another genus (L. Scherler, pers. comm.). Next, a sudden extinction occurred, related to the emergence of new migrants, the Eupecora (Migrations3; Fig. 1D; Fig. 3). An explosion of diversity occurred, with at least 6 new genera and species ("*Amphitragulus*" *quercyi*, "*Amphitragulus*" *feningrei*, *Amphitragulus primaevus*, *Dremotherium guthi*, *Bedenomeryx milloquensis*, *Babameryx engesseri*; (Chapter 9; Fig. 2, Extinction3 and Migrations3). An Asiatic origin for these ruminants seems to be attested by the discovery of similar species in the mid-Oligocene of Mongolia (Vislobokova & Daxner-Höck 2002). This period also corresponds to the first occurrence of the small anthracotheriid *Microbunodon* (Scherler 2011). The last emblematic rhinocerotid *Ronzontherium* and anthracotheriid *Anthracotherium* still persisted until MP 29, or even MP30 (Hugueney 1997, Mennecart et al. 2012).

The Oligocene-Miocene transition (ca. 22.9 My) was marked by the Mi1 glaciation event (Zachos 2001; Berger 2011) that coincided with the acceleration of the Tibetan Plateau uplift and the Red Sea rift (Zachos et al. 2001), and also the general fragmentation of the environments in Europe (Costeur 2005). The latest Oligocene ruminants were renewed by anagenesis within surviving genera (Fig. 2, Speciation2; Fig. 3). A general trend highlights size changes; the small-sized species evolved into even smaller species and the medium-sized species into larger ones (Chapter 9). Additionally, the Migrations3 seems to continue with the arrival of the new genera *Andegameryx*, *Friburgomeryx*, and *Oriomeryx*, resulting in a huge diversity of hornless saber-toothed ruminants recorded in MN2 (Gentry et al. 1999; Fig. 2). Their affiliation with extant families remains doubtful (Costeur 2011; Mennecart et al. 2012). Considering the mandible outlines, the morphology was inbetween the protopecoran *Gelocus* and the extant families, contrary to the true antlered Cervidae from the Burdigalian, such as *Procervulus* and *Lagomeryx*. The latter exhibit a mandible shape variation ranging within that of the extant Cervidae (Chapters 2 & 4). The latest Oligocene and Aquitanian European Eupecora were maybe primitive inermous forms of extant families, but too basal to be recognized as such. They could also belong to new families corresponding to the basal radiation of the Eupecora. Rhinocerotid *Mesaceratherium* (MP27-MN2) and *Diaceratherium* (MP26-MN4) were also characteristic taxa of this transitional period of diversification and speciation, whereas rhinocerotoid *Eggysodon* and anthrocotheriid *Microbunodon* disappeared at the Oligocene-Miocene boundary (Becker et al. 2009).

The *Brachyodus* event, at the beginning of the Proboscidean datum (MN3a, ca. 19.8 My), coincided with the closing of the Tethys Ocean and, in Switzerland, with the transgression of the OMM (Rögl 1999; Berger 2011; Fig. 3). These major climate and faunal changes led to the disappearance of the primitive Eupecora taxa and the emergence of the extant families of Eupecora, such as the Cervidae and the Bovidae (Fig. 1E; Fig. 2, Extinction4 and Migration4). The newly created land bridge between Eurasia and Africa allowed important faunal exchanges. The first proboscids (*Deinotherium*, *Gomphotherium*, *Zygolophodon*) and the last anthracotheriids (*Brachyodus*) reached Europe, whereas the first ruminants and rhinocerotids arrived in Africa (Mein 1999). Also, the appearance of appendages in various groups, such as the rhinoceros and the ruminants, seems to be generalized. Notably, since this period, the Cervidae had antlers, the Bovidae had horns, and the Palaeomerycidae had ossicones.

Comparison with previous studies on the diversity of the European ruminants highlights the inaccuracy of the interpretations. As opposed to the theory of a regional European evolution that suggested few migrations (Jehenne 1987; Sudre 1995; Blondel 1997), this study highlights an evolutionary pattern marked by several important Asiatic immigrations, strongly related to global changes (clearly defined in the local sedimentological record in Switzerland) and punctuated by speciation phases. The extinction events directly linked to climate changes without migration were followed by anagenetic evolution and reduction in the diversity without new genera (Extinction1 and Speciation1). The extinction events linked to climate changes and migrations led an increase in the biodiversity with more drastic faunal renewal, sometimes at the familial level (Extinction3 and Extinction4). To sum up, Europe should be considered more as a Dead End area with an evolution of the mammal communities mainly influenced by climatic events and Asiatic migrations combined with extinctions, rather than an area with a normal evolutionary diversification causing speciations. This phenomenon of Dead End area related to migrations and extinctions is particularly accentuated by the peninsular shape of Europe.

13.2 Perspectives

13.2.1 Palaeontology

The Gaimersheim 1 fissure filling (MP28, Germany) is a key locality for understanding the transition between the primitive and derived ruminants in Europe. The material stored at the Bayerische Staatssammlung für Paläontologie (München, Germany) is composed of more than 100 dental remains, not included in this work. A preliminary analysis of the material suggests a high similarity between *Bachitherium lavocati* (with a complete skull and some other broken skulls) and "*Amphitragulus*" *quercyi* (probably with a partial skull), and the rare remains of *Babameryx engesseri* and *Dremotherium guthi*. These preliminary results indicate a transitional assemblage, situated between the exclusively primitive ruminants from Pech Desse (MP28, France) and the exclusive Eupecora from Pech du Fraysse (MP28, France) (Blondel 1997).

The study of the poorly known Oligocene ruminants from Central and Eastern Europe (Serbia, Roumania, Turkey) could improve our understanding of the link between the newly well-referred Western European fauna and the Asiatic ruminants, that are the topic of many recent discoveries and publications. Based on the good biostratigraphic resolution of the Carpathian Basin, for example, a study of the synchronism or diachronism of the East–West migrations of the ruminants could be performed. Also, a systematic analysis should be done to evaluate whether these ruminants are more closely related to Western Europe, or to Asia, or , wether they represent a high local endemism.

13.2.2 Ecomorphology

The Geometric Morphometrics analysis based on the shape of the mandible provided good preliminary results on the phylogeny and ecology of fossil (until the Burdigalian) and extant ruminants (Mennecart et al. 2011, Mennecart et al. accepted). A similar analysis based on whole extant ruminants is in progress. Superimposing the phylogeny on the plots of the analysis permits us to test (with a permutation test) if the phylogeny is supported by the graph or not, and if the mandible shape possesses a strong phylogenetic signal (Fig. 4). A canonical analysis defines *a posteriori* the possibility of easily separating feeding habits as a function of the mandible shape and to predefine some feeding characteristics of the mandible (Fig. 5). A modularity test, using the minimum of covariance between the two anatomical complexes, completes the morphofunctionality of the mandible, depending on the feeding habit. To include the fossils in this analysis, a quantitative analysis of the crown microwear should be taken into account. A multiregression test, based on the mandible morphology, quantitative analysis of crown microwear, and the toughness index of the eaten food (only for extant specimens) could indicate a general trend in ruminant evolution through time and their ecomorphological strategy in response to environmental changes.

Chapters 7, 10, and 11 underline that the ecomorphology of the postcranial remains of ruminants is a good proxy to define environments. A systematic analysis of the ecomorphology of the European ruminant postcranial remains, associated to cenograms (Legendre 1989; Costeur 2005) and palaeoflora analyses (e.g., De Man & Van Simaeys 2004), could give a good idea of the climatic and environmental changes through time.

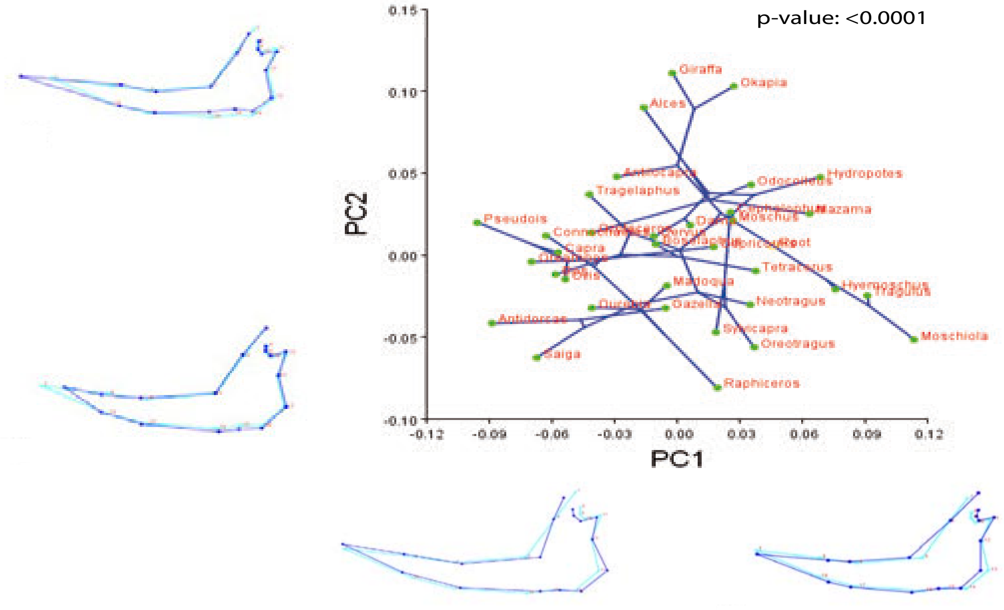


Figure 4 Phylogeny superimposed on the Principal Component Analysis of a geometric morphometrics analysis based on the mandible morphology of extant ruminant genera. The permutation test against the null hypothesis of no phylogenetic signal (with 10000 randomization rounds) provides a P-value inferior to 0.0001, indicating a strong impact of the phylogeny on the plotting area of the genera. Tree length = 0.10618029.

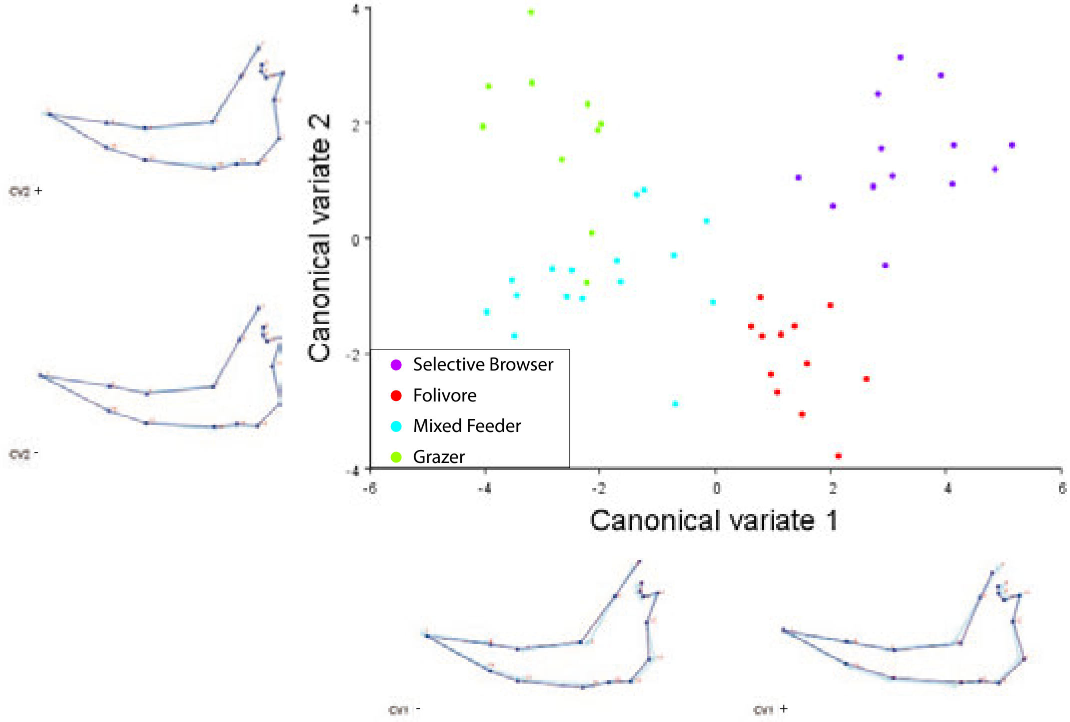


Figure 5 Canonical analyses based on the feeding habit and the shape of the ruminant mandible.

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2012.06: Lecteur et coorganisateur Excursion 3e année Bachelor « Excursion Géologique Générale » à l'université de Fribourg.
2012.04 : Lecteur Cours Master « Paléontologie » à l'université de Fribourg.
2012.04 : Lecteur Cours « Bassin Molassique et fossé rhénan » à l'université de Fribourg.
2012.03 : Lecteur Cours 3e année de Bachelor « Travail de Séminaires » à l'université de Fribourg.
2011.04: Assistant Excursion 2^{e} année « Iles Eoliennes » à l'université de Fribourg.
2011.09: Cafés scientifiques radiodifusés sur le thème de « l'histoire de la biodiversité » et « les enjeux de la biodiversité ».
2009 – en cours: Fouilles systématiques du site de Wallenried (Suisse) sous ma direction.
2009.09 – 2011.06: Assistant TP 2^{e} année Licence « Paléontologie » à l'université de Fribourg.
2009.08: Basecamp à Neuchatel, vulgarisation scientifique sur le thème « Paléontologie et Evolution ».
2009.07: Conférence Branféré (France) sur le thème « L'histoire des grands reptiles et des mammifères ».
2009.01: Présentations scientifiques de l'exposition « Paléomania » au Muséum d'Histoire Naturelle de Fribourg.
2008 – en cours: Collaborateur scientifique avec l'université de Franche Comté sur la thématique « rupture et extension de l'occupation du sol pendant l'Antiquité Tardive, étude diachronique de l'occupation du sol dans la basse vallée de la Cèze (Plaine et opida), sous la direction de Mr Canillos.

2008.06 – 2012.06: Assistant et coorganisateur Excursion 3e année Licence « Excursion Géologique Générale » à l'université de Fribourg.
2008 – 2011: Présentations scientifiques en congrès internationaux (EAVP, Molasse Meeting, RCNPS, SVP, SVPCA, Swiss Geosciences Meeting, Swiss Sed, Symposium on Lithographic Limestone and Plattenkalk).
2008 – 2011: Fouilles systématiques du site de Tavannes Sous le Mont (Suisse) sous ma direction.
2008.04 – 2012.04: Assistant Excursion Master « Paléontologie » à l'université de Fribourg.
2008.04– 2012.04: Assistant Excursion Master « Bassin Molassique » à l'université de Fribourg.
2007.09 – 2011.06: Assistant TP 1er année Licence « Géologie générale » à l'université de Fribourg.
2007.07-08: Présentations scientifiques au Musée parc des dinosaures de Mèze.
2006.07: Fouille systématique du site de Cherves de Cognac (France) sous la direction du Pr Mazin.
2005 – 2006: Inventaire paléontologique du Muséum d'Histoire Naturelle de Blois (France).
2005.06-07: Fouille systématique du site Unesco de Miguasha (Canada) sous la direction du Dr Desbiens.
2001– 2007.07-08: Assistant géomètre au cadastre de Blois (France).

Bourses:

2012: Ecole doctorale « Earth Surface Processes and Palaeobiosphere » (travel grant).
2008-2011: Société Paléontologique Suisse (travel grant).
2007-2011: Fond National de Recherche Suisse (PhD grant).
2006-2007: Université de Poitiers (Bourse sur mérite universitaire).

Cours 3e cycle pour Doctorant:

2012.01: 3D Geometric Morphometrics (ICP, Sabadell en Espagne).
2011.09: Geometric Morphometrics and Phylogeny (ICP, Sabadell en Espagne).
2011.03: Human paleopathology (Archéométrie avancée , université de Fribourg en Suisse).
2010.02: Tropical Marine Ecology: A case study at the Maldives, Magoodhoo, Faafu Atoll (CUSO).
2008.04: Taphonomy (CUSO).

Publications:

Scherler, L., ***Mennecart, B.***, Hiard, F., & Becker, D. (to be submitted). Large mammal evolution during the Oligocene-Miocene transition in Europe. Swiss Journal of Geosciences.

Hiard, F, ***Mennecart, B.***, & Becker, D. (to be submitted). The ruminant astragalus shape, a useful palaeoecological and palaeoenvironmental tool. International Journal of Geosciences.

Mennecart, B. & Métais, G. (to be submitted). Mosaicomeryx quercyi, new comb. ruminant from the Oligocene of Europe, and the significance of "gelocids". Journal of Systematic Palaeontology.

Londeix L. & ***Mennecart, B.*** (in press). Aperçu des mammifères continentaux aquitaniens en Aquitaine. in Londeix, L. (Ed.) Stratotype Aquitanien, collection Patrimoine géologique, MNHN & Biotope (co-éd.), 11 p., 13 fig., 1 tabl., 2 pl.

Mennecart, B., Scherler, L., Hiard, F., Becker, D., & Berger, J.-P. (2012). Large mammals from Rickenbach (Switzerland, Reference-Locality MP29, Late Oligocene): biostratigraphic and paleoenvironmental implications. Swiss Journal of Palaeontology. 131, 161–181.

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Mennecart, B., Becker, D., & Berger, J.-P. (2011). Iberomeryx minor (Mammalia, Artiodactyla) from the Early Oligocene of Soulce (Canton Jura, NW Switzerland): systematics and palaeodiet. Swiss Journal of Geosciences, 104 (suppl 1), S115–S132.

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Sauvage, J.-P. & ***Mennecart, B.*** (2006). L'utilisation des faluns pour la construction dans le canton de Contres. Annales de l'université du 3e age, session de printemps 2006. 68–81.

Mennecart, B. & Costeur, L. (2010). First description of the skull of Amphimoschus (Mammalia, ???Bovidae???) and taxonomy of the genus. Mésogée, 66, 71.

Hiard, F., ***Mennecart, B.***, & Berger, J.-P. (2010). Morphological and Biometrical study of the postcranial remains of Ruminants: a proxy for environmental changes (Swiss Molasse Basin, Oligo-Miocene transition). Mésogée, 66, 64.

Mennecart, B. & Becker, D. (2009). Palaeobiology of Iberomeryx minor (Mammalia, Artiodactyla) from the Lithographic Limestones of Soulce (Early Oligocene, Jura Switzerland). Société jurassienne d'émulation, actes 2009bis, 59.

Mennecart, B., Scherler, L., Becker, D., & Berger, J.-P. (2009). Late Oligocene changes in mammal communities of western Europe: warming and cooling event ? Journal of Vertebrate Paleontology, 23(supplement3), 147.

Associations:

European Association for Vertebrate Palaeontologists.
Société Paléontologique Suisse.
Greenpeace France et Suisse.
Pro Natura Suisse.

Langues:

Français (maternelle), Anglais (Couramment)

Hobbies:

Rugby (pratique du haut niveau en France entre 1999 et 2006 à Blois, Orléans et Poitiers ; 2011-2012 en Suisse à Fribourg), Voyager, Plonger, Pratiquer le snowboard, Etudier et observer les ruminants à dent de sabre.

Already published:

Vol. 1 **HILLGÄRTNER, Heiko** (1999) The evolution of the French Jura platform during the Late Berriasian to Early Valanginian: controlling factors and timing (203 pp.).

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