Mosaicomeryx gen. nov., a ruminant mammal from the Oligocene of Europe and the significance of ‘gelocids’

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The description of new material and the reassessment of specimens previously assigned to Gelocus quercyi lead us to propose a new genus for this species, Mosaicomeryx gen. nov. 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 40 dental, cranial and postcranial features highlights the misidentification of Gelocus quercyi and suggests that Mosaicomeryx gen. nov. is closely related to Prodremotherium elongatum. Mosaicomeryx quercyi and Prodremotherium elongatum form a monophyletic group of stem Pecora that first appeared in Western Europe by the late Early Oligocene (MP25–26), and Prodremotherium elongatum persisted up to MP28; following this time both taxa appear to be replaced by Dremotherium and Amphitragulus. This time interval covers two major Oligocene faunal and climate changes: Extinction 1 (MP24), associated with regression of the inner European sea, and Extinction 3/Migrations 3 (MP28), associated with Late Oligocene Warming.


Keywords: Ruminantia; Prodremotherium; systematics; phylogeny; Oligocene; Europe

Introduction

Most of the extant ruminant mammal groups (also known as crown Pecora or Eupecora, most of them bearing cranial appendages) diversified during the mid-Miocene (Gentry 1994; Gentry \textit{et al.} 1999; Hassanin & Douzery 2003). The basal radiation of Ruminantia occurred probably early in the Eocene, but Eocene ruminants remain poorly documented, except for a few key taxa such as Archaeomeryx (e.g. Webb & Taylor 1980). During the Late Eocene, ruminants are documented by several forms closely related to tragulids, while the Early Oligocene is marked by the first appearance of several forms of ‘pre-Pecora’, often included in the ‘wastebasket’ family Gelocidae. The type genus of Gelocidae, Gelocus, appears in the earliest Oligocene (MP21, European mammal reference level) with \textit{G. communis} (Aymard, 1846) and \textit{G. laubei} Schlosser, 1901; the last occurrence of the ‘gelocids’ is no younger than MP28 (Late Oligocene) with the occurrence of \textit{Prodremotherium elongatum} Filhol, 1877 whose affinities with ‘Gelocidae’ is debated (e.g. Janis 1987). The genus Prodremotherium is also reported from the Early Oligocene of Kazakhstan (\textit{P. flerowii} Trofimov, 1957), Mongolia (\textit{P. sp. of Vislobokova & Daxner-Höck 2002}) and Georgia (\textit{P. trepidum} Gabunia, 1964), but the generic assignment of these Asiatic forms remains doubtful.

\textit{Prodremotherium elongatum}, the suprageneric assignment of which is equivocal, is classically considered to belong to Gelocidae (Jehenne 1977, 1987; Janis 1987; Sudre & Blondel 1996; Blondel 1997; Métais & Vislobokova 2007; Mennecart \textit{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) have recognized that attribution to Gelocidae can be disputed, but have maintained it as useful in descriptive nomenclature. Other authors have considered \textit{Prodremotherium} to be a basal eupecoran, close to Bovoida (Jehenne 1977, 1985, 1987; Jehenne & Brunet 1992) or Cervoidea (Webb & Taylor 1980; Janis & Scott 1987). It has also been placed within Prodremotheriidae (Guo \textit{et al.} 1999, 2000; Métais \textit{et al.} 2000). Even the family name is matter of confusion because it literally means ‘before the Dremotheriidae’ while close affinities between these two ‘families’ have never been clearly shown. Moreover, \textit{P. elongatum} is known only in the poorly dated old collections of the Phosphorites du Quercy (Filhol 1877; Jehenne 1977, 1985, 1987; Remy \textit{et al.} 1987;
Jehenne & Brunet 1992) and in one well-dated locality, Pech Desse (MP28; Blondel 1997).

Gelocus quercyi Jehenne, 1987 is exclusively known from a few upper teeth from the Phosphorites du Quercy (Jehenne 1985, 1987; Blondel 1997). This species is assigned to Gelocus due to some primitive characteristics (bunoselenodont tooth 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.

Here we reassess the European fossil material referred to both P. elongatum and G. quercyi and test their phylogenetic relationships through a cladistic analysis including both European and Asian ‘gelocids’.

Material and methods

Institutional abbreviations

Material

The taxonomic revision and phylogenetic 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 1997), stored at MNHN, NMB, MNB, UCBL, and USTL. The identifications are based on anatomical features, comparative anatomy and biometrical measurements, following the ruminant dental terminology detailed in Figure 1. All measurements are given with a precision of 0.1 mm (Table 1). The biochronological framework used in this work is based on Berger (2011) and Scherler et al. (2013).

Synonymy and anatomical abbreviations

Synonymy 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.

Anatomical abbreviations: i, lower incisor; 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; sen., left.

Systematic palaeontology

Order Cetartiodactyla Montgelard, Catzeflis, & Douzery, 1997
Suborder Ruminantia Scopoli, 1777
Genus Mosaicomeryx gen. nov.

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

Diagnosis. The P1 is lost. The P2 and P3 are elongated, with a well-formed lingual cingulum on P4. The upper molars are selnodont, with a protocone and a metaconule few conical, and cristae elongated and curved. The post-protocrista ends between the paracone and the metacone. They possess a deep cingulum surrounding the protocone and a small entostyle on the metaconule. The metaconule of the M3 is well developed, giving a square shape to these teeth. There is a long diastema between c and p2. The p1 is absent; the p4 has a strong mesolinguin conid and four crests linguin orientated. There are neither external postprotocristid nor ‘Dorcatherium folds’ on lower molars but there is 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 gully closed.

This genus differs from Prodremotherium by the presence of a cingulum on the upper molars and being a little more bunodont. The upper premolars are more elongated in Mosaicomeryx than in Gelocus and the postprotocristid is elongated and labially orientated whereas it is short and distally orientated for Gelocus. This genus possesses a bony bridge closing the metatarsal gully, which is absent.

Table 1. Dental measurements of Mosaicomeryx quercyi 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 length and the second is width.

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http://doc.rero.ch
in Gelocus. The lower premolars are greatly elongated in comparison to Amphitragulus or Dremotherium, taxa which possess a total fusion of their metapodial bones.

*Mosaicomeryx quercyi* (Jehenne, 1987)

(Fig. 2A–G)

v pars 1861 *Palaeomeryx* Fischer-Ooster: 222.

1902 *Dremotherium feignouxi* Giraud: 167.


v pars 1985 *Gelocus* quercyi Jehenne: 49, fig. 9a–e.


v 1987 *Bachitherium insigne* Engesser & Mayo: 73.

v pars 1987 *Gelocus* quercyi Jehenne: 132, fig. 1.


v 1997 *Prodremotherium elongatum* Engesser & Möddjen;Engesser & Möddjen: 483.

v 1997 *Bachitherium insigne* Engesser & Möddjen: 484.

**Holotype.** MNHN Qu4151, maxillary with the tooth row P2–M3 sen. (Jehenne 1985, fig. 9a, 1987, fig. 1).

**Type locality.** Quercy, Lot, France.

**Additional localities.** Saint André, ‘Marseille’ (Saint Henri, MP26), Saint Géry (MP26?), France; Bumbach (MP25), Réchaument (MP25), Talent1 (MP26), Mümliswil Hartberg (MP26), Veyron2 (MP27), Switzerland (Engesser & Mödden 1997, Weidmann *et al.* in press).

**Additional material.** NMB UM459a, fragmentary mandible with the tooth row p2–m3 (broken) dext., Bumbach (Switzerland); NMB UM459b, fragmentary mandible with tooth row p4–m3 (broken) sen., Bumbach; NMBe 5017072, P3 dext., Bumbach; NMBe 5017073 P4 sen., Bumbach; NMB UM2292, distal part of a metapodial bone, Mümliswil (Switzerland); NMB2317, fragmentary part of a toothless mandible, Mümliswil locality; NMB Mar667, fragmentary mandible with p3 and fragmentary p4 sen., m1 sen., fragmentary diastema, M2 sen., M3 sen., Saint André (France); NMB Mar640, fragmentary mandible with tooth row m2–3 dext., Saint André; USTL 9326, isolated m1, m2, m3 sen., and m3 sen., ‘Marseille’ (France); MNHN Qu4145, maxillary with tooth row M1–M3 sen., Phosphorites du Quercy (SW France); MNHN Qu4146, maxillary with tooth row M2–M3 dext., Phosphorites du Quercy; MNHN Qu4147, maxillary with tooth row M1–M3 dext. (Jehenne 1985, fig. 9c), Phosphorites du Quercy; MNHN Qu4149, maxillary with tooth row P4–M3 sen., Phosphorites du Quercy; MNHN Qu4150, maxillary with the tooth row M2–M3 sen., Phosphorites du Quercy; MNHN Qu4152, maxillary with the tooth row M1–M2 sen. (Jehenne 1985, fig. 9e), Phosphorites du Quercy; NMB Qu4153 maxillary with tooth row P4–M3 sen. (Jehenne 1985, fig. 9b) Phosphorites du Quercy; MNHN Qu4154, maxillary with tooth row M1–M3 dext., Phosphorites du Quercy; MNHN Qu4155, maxillary with tooth row P4–M3 sen. (Jehenne 1985, fig. 9d), Phosphorites du Quercy (SW France); NMB QuA644, maxillary with tooth row M2–M3, Phosphorites du Quercy; NMB QuA711, maxillary with tooth row M1–M3, Phosphorites du Quercy; NMB QuA710a, maxillary with tooth row P4–M3, Phosphorites du Quercy; NMB OT3, Metatarsal bones dext., Saint Géry (SW France).

**Diagnosis.** As for genus.

**Description.** The two mandibles from Bumbach seem to belong to the same individual due to the same stage of molar wear (Fig. 2C, D). These fossils also possess a well-developed anterolabial cingulid. This feature is smaller or 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 mandible is slender, being slightly deeper 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 mid-depth on the mandible. The fragmentary diastema does not possess an isolated p1 tooth socket.

**Lower adult dentition.** It does not appear that *Mosaicomeryx quercyi* had a p1. The anterior part of the p2 does not possess a contact surface with an anterior tooth (Fig. 2C), and an isolated fragment of diastema does not show the presence of an isolated p1 tooth socket. The three lower premolars possess the same occlusal pattern with an increasing 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 mesolabial conid lies in the mesial half of the tooth. It ends with the anterior conid bulge. The posterolabial cristid is anteriorly orientated. The anterolabial cristid is anteriorly orientated and forms the labial wall of the tooth. It ends with the anterior conid bulge. The posterolabial cristid makes the labial wall and joins the posterolabial conid, which is relatively prominent, but much less high than the mesolabial conid. It may be fused with the posterolabial conid when this feature is present. It forms the posterolabial edge of the tooth. The posterior cristid stops at the posterolabial and the posterior part of the tooth. The posterior valley is shallow and labially open. On the p3, the mesolabial conid is central and located on the labial face of the tooth. It possesses a
Figure 2. *Mosaicomeryx quercyi* from old collections from the Phosphorites du Quercy (undated, SW France), Bumbach (mid-Oligocene, Central Switzerland), ‘Marseille’ and Saint André (mid-Oligocene, SE France). A, ‘Marseille’, USTL 9326, isolated m1, m2, m3 sen., and m3 sen. in occlusal (1) and lingual (2) views. B, Phosphorites du Quercy, NMHN Qu4151, holotype, maxillary with the tooth row P2–M3 sen., occlusal view. C–E, Bumbach; C, NMB UM459a, fragmentary mandible with the tooth row p2–m3 dext., in labial (1), occlusal (2) and lingual (3) views; D, NMB UM459b, fragmentary mandible with the tooth row p4–m3 sen., in labial (1), occlusal (2) and lingual (3) views; E, NMBE 5017073, P4 sen., occlusal view. F, G, Saint André; F, NMB Mar667, fragmentary mandible with p3 and fragmentary p4 sen., m1 sen., fragmentary diastema, M2 sen., M3 sen., in labial (1), occlusal (2) and lingual (3) views; G, NMB Mar640, fragmentary mandible with the tooth row m2–3 dext., in labial (1), occlusal (2) and lingual (3) views. Scale bar = 1 cm.
posterior oblique transverse cristid, which joins the lingual edge of the p3, forming a groove between it and the mesiolabial conid. The p3 from Saint André (Fig. 2F) differs from that from Bumbach (Fig. 2C2) by the total absence of posterolingual conid and the presence of a bulge on the transverse cristid, which could be a small mesolingual conid. The anterior conid is more developed and transverse and the posterolabial conid is more globular on the p3 than on the p2. On the p4, the anterior conid is even stronger. From the transverse cristid, a lingual and strong mesolingual conid can be observed. There is a groove between this latter and the mesolabial conid. The posterolabial conid is absent. It has been replaced by the bifurcated transverse cristid. The posterior stylid makes the posterolabial angle of the tooth and the labial part of the p4 (Fig. 2C, D). The posterolingual conid is transverse. It joins the posterior stylid, making a posterior valley. The anterior conid is bigger and less oblique. The anterior valley is wider from the p2 to the p4. The back valley is narrower from the p2 to the p4 (Fig. 2C).

The lower molars and the metaconid rib increase in size from m1 to m3 (Fig. 2A, C, D). The trigonid is closed. The talonid is a somewhat lingually opened, due to the posthypocristid, which does not fuse with a very weak postentocristid. The posthypocristid ends 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 for a small distance on the lingual part, forming a cingulid and an anterolingual stylid. The protoconid is strong and does not bear an external postprotocristid. The internal postprotocristid joins the posterior base of the metaconid, and fuses with the postmetacristid and the pretretoconid. The metaconid and the preentocristid are rectilinear. The protoconid and the hypoconid are similar in size. The internal postprotocristid changes orientation from being transverse on the m1, to becoming progressively more oblique posteriorly on the m2 and the m3. The prehypocristid is oblique, and the form of its ending is variable. It terminates at the level of the fusion of the three other cristids to the distal part of the internal 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 and forms a small column progressively distant from the postmetacristid from the m1 to the m3. The metastylid is elongated, forming a well-developed blade, an anterolingual cingulid. The anterior cingulid is progressively blurred from the m1 to the m3. The posterior cingulid is oblique and joins the posthypocristid on its labial part. The molars of *Mosaicomeryx* are a slightly more bunodont than those of *Bachitherium*. On the back fossa of the m3, the hypoconulid, which is highly variable in size and shape, often forms a compressed and oblique buckle. Its posthypoconulidcristid and prehypoconulidcristid 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 fully straight postentocristid. The entoconulid possesses a lingual rib with two tiny cristids.

**Adult upper dentition.** Specimen NMBe 5017072 is a broken P3. Only the labial part is preserved. The anterolabial cone and the anterior style are weak. Considering the size, this tooth might well belong to *Mosaicomeryx quericyi*. The P4 is triangular due to an anterolingual crista and a straight postlingual cristid (Fig. 2E). The lingual cone is fully selenodont. The anterolingual crista reaches the anterior style and the postlingual crista joins the base of the posterior style. The anterior style and the posterior style are prominent and form the labial edges of the tooth. The fully selenodont anterolabial cone possesses a large labial rib with a small anterior groove. The P4 has a large lingual cingulum.

The upper molars of the Saint André specimens (Fig. 2F) possess a very large cingulum around the protocone terminating at the base of the metaconule, as seen on the holotype (Fig. 2B). The molars are square. The protocone is large and selenodont. The anterior and posterior basins do not possess neocrista. The postprotocrista joins a strong and slightly curved parasyle. The paracone possesses a strong rib without an anterior groove. The paracone and the metacone are selenodont and are not in the same plane. The postprotocrista, which is elongated and regularly curved, reaches the premetaconulecrista before its end. The premetaconulecrista ends with a globular mesostyle. The metacone rib is weak to absent, and when present is progressively less defined from M1 to M3. The postmetaconulecrista joins a well-defined mesostyle, finishing a postlingual ‘cingulum’ of the metacone on the bigger specimens. The straight posthypocrista joins the base of the metaconulecrista. The metaconulecrista and the paracone are selenodont and possess a progressively smaller entostyle from M1 to M3. The prehypocrista is curved and ends between the metacone and the paracone. The postprotocrista may end at the level of the prehypocrista, or it may fuse with it and then return to the paracone to end within the basin. The postprotocrista never bifurcates.

**Metatarsal bones III and IV.** The NMB OT3 specimen is complete. These relatively stocky bones possess an unfused distal epiphysis. The condyles are slightly flattened dorsally. The articular facet is weakly developed. The enlarged gully is distally closed due to an unfused bony bridge.

**Discussion.** Jehenne (1985, 1987) considered ‘*Gelocus* quericyi’ 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 genera Lophiomeryx, Iberomeryx and Babameryx (Mennecart et al. 2011, 2012b). The upper molars of Mosaicomeryx differ from those of Gelocus in being more selendon (they are clearly bunoselendon in Gelocus): the postprotocrista is elongated, curved, and labially orientated, 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 selendon, not tetrahedral as in Gelocus communis. The P4 possesses straight cristae and they are not concave as in Gelocus communis and Gelocus villebramarensis Brunet & Jehenne, 1976. The lingual cusps of the upper premolars of Mosaicomeryx are much more prominent than those of Gelocus. The dental material previously referred to ‘Gelocus’ quercyi clearly differ from those 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 variant of the population of ‘Gelocus’ quercyi. This specimen is clearly reminiscent of Gelocus in having bunoselendon crowns, a short and straight postprotocrista, which is perpendicular to the premetaconulecrista, and a reduced metaconule. Specimens of Mosaicomeryx quercyi have been listed as Prodremotherium elongatum in various articles (Engesser & Mayo 1987; Engesser & Mödden 1997). Both genera possess derived 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 selendon than those of Mosaicomeryx, but the latter are more selendon than those of the Eocene Asiatic genera such as Notomeryx. As in Notomeryx, the molars of Mosaicomeryx possess a well-developed metastylid, lack a p1, and lack an external postprotocristid. Although the P3 lingual cone is less developed on Mosaicomeryx quercyi than on Prodremotherium elongatum, but more so than on Gelocus communis, it has a similar shape due to a posterior anterolabial cone and relatively laterally compressed prominent lingual cone. Moreover, Mosaicomeryx has a very strong lingual cingulum on its upper molars, which is absent in Prodremotherium. Mosaicomeryx has smaller premolars and a smaller entostyle than Prodremotherium. The mesostyle is less globular on Mosaicomeryx quercyi than it is on Prodremotherium elongatum.

Mosaicomeryx possesses a clear mixture of primitive (very large cingulum, somewhat bunoselendon tooth crowns, elongated and simple lower premolars) and derived dental features (no p1, elongated and curved cristae on upper molars, a flat metacone rib, an enlarged metaconule, and a strong metastylid). The lower premolars are simple, without additional cristids (such as the anterior cristid or the anterolinguinal cristid) and are relatively elongated. The molars are selendon. The postcaninal remains show metatarsal bones only proximally fused, with a closed metatarsal gully. All these morphological features allow a generic distinction between the former ‘Gelocus’ quercyi and other species referred to the genus Gelocus. In sum, Mosaicomeryx shows a ‘transitional stage’ between the primitive Gelocidae (represented by Gelocus) and the Late Oligocene crown Pecora (Dremotherium).

Genus Prodremotherium Filhol, 1877

Type species. Prodremotherium elongatum Filhol, 1877.


Diagnosis. (modified after Métais & Vislobokova 2007). The P1 is lost. The P2 and P3 are elongated, with a very weak or absent 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 mesolingual conid and four crests lingually orientated. There are neither external postprotocristids nor Dorcatherium folds on the lower molars, but there is a distinct metastylid. The entostylid is transversally compressed and crested anteriorly and posteriorly. The preprotocristid closes the 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 are not functional. The metatarsal bones III and IV are proximally fused, with a closed metatarsal gully. The astragalarus has a transversally extended sustentacular facet and parallel trochlea.

Remarks. This genus differs from Gelocus and Mosaicomeryx by the absence of cingula on the upper molars and in being more selendon. The postprotocrista is elongated and labially orientated, whereas it is short and distally orientated in Gelocus, and the upper premolars are more elongated in Prodremotherium than in Gelocus. Prodremotherium possesses a bony bridge closing the metatarsal gully, absent on Gelocus. The lower premolars are very elongated in comparison to Amphitragulus or Dremotherium, which show total fusion of their metapodial bones.

Prodremotherium elongatum Filhol, 1877
(Fig. 3A–C)

v pars 1877 Prodremotherium elongatum Filhol: 448, pl. 11, 258, 259, 263–268.
1883 Prodremotherium elongatum Filhol; Rütimeyer: 68, pl. 7, figs 20, 21, pl. 8, figs 30–38.
1896 *Prodremotherium elongatum* Filhol; Röse & Bartels: 96, figs 20, 21.

v non 1929 *Prodremotherium* sp. Viret: 229, pl. 31, fig. 15a, b.


v non 1973 *Prodremotherium elongatum* Filhol; Bonis et al.: 109, table 2(4).

v 1977 *Prodremotherium elongatum* Filhol; Jehenne: 233, pl. 1.

v 1985 *Prodremotherium elongatum* Filhol; Jehenne: 75, figs 12–19.

v 1987 *Prodremotherium elongatum* Filhol; Janis: 200, fig. 4.

v 1997 *Prodremotherium elongatum* Filhol; Janis & Scott: fig. 11.

v pars 1987 *Prodremotherium elongatum* Filhol; Remy et al.: 188, table 4c.

v 1995 *Prodremotherium elongatum* Filhol; Martinez & Sudre: fig. H.

v 1997 *Prodremotherium elongatum* Filhol; Blondel: 576, figs 2, 3.

1997 *Prodremotherium* sp. Hugueney: 426

v 1998 *Prodremotherium elongatum* Filhol; Blondel: 527.

**Syntypes.** The fossils illustrated by Filhol (1877, figs 260–268). Unfortunately, these specimens have not been studied. However, two specimens are currently stored in the MNHN: a mandible with the tooth row p2–m3 dext. (Qu4769; Filhol 1877, pl. 11, figs 265, 266) and a maxillary with the tooth row P3–M3 dext. (Qu4596; Filhol 1877, pl. 11, figs 267, 268).

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

**Additional localities and biochronological range.** Sarèle, Boujac, Courmon, 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. (Filhol 1877, pl. 11, figs 265, 266; Jehenne 1985, fig. 17a); Qu4640, partial skull of a juvenile with D2–M3 sen. and C-P3 dext.; Qu4596, partial skull with P3–M3 dext. (figured by Jehenne 1977, 1985, figs 12–14); Qu4415 right mandible with the tooth row p3–m1 dext.

**Diagnosis.** (modified from Jehenne 1985). Medium-sized ruminant possessing three elongated upper and lower premolars. The upper molars are quite elongated, giving a square shape to these teeth. The upper molars are fully selenodont. The protocone and the metacone are not very conical, possessing elongated and curved cristae. The postprotocrista ends between the paracone and the metacone. 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 tragus-like, highly curved and laterally compressed.

**Remarks.** This species differs from the smaller *Prodremotherium trepidum* by the structure of the p4 with a posteroingual conid less developed and total fusion of the metapodial bones. *P. flerowi* is larger than the type species and possesses a more complete fusion of the metatarsal bones III and IV.

**Description**

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

**Skull.** Specimen MNHN Qu4640 (Fig. 3B) is the partly preserved skull of a juvenile of *Prodremotherium*, previously undescribed. Only the left side of the skull is preserved, and the facial, temporal and occipital portions are lacking. 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. 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 *foramen ovalis* lies above the D2. The anterior part of the jugal is preserved. The orbitosphenoid and prephenoid are present. The supraorbital area is highly vascularized, like on the other described skull of *Prodremotherium elongatum* (MNHN Qu4596; Jehenne 1977) and in *Dremotherium feignouxi* (MNHN SG4303; Sigogneau 1968).

The inner orbit is partly preserved on the parietal bones, and appears to possess only one large *lacrimal foramen* and a large *ethmoidal foramen*. 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 *foramen ovalis* is close to the adult cheek teeth, decidual teeth being missing, indicating the partial destruction of the maxillary bone. The tusk-like canine is short and highly curved (Fig. 3B4). Its section is oval and laterally...
Figure 3. Prodremotherium elongatum from old collections from the Phosphorites du Quercy (undated, SW France). A, MNHN Qu4769, holotype, mandible with the tooth row p2–m3 dext., in labial (1), occlusal (2) and lingual (3) views. B, MNHN Qu4640, partial skull of a juvenile with D2–M3 sen. and C–P3 dext., in left (1), occlusal (2) and right (3) views, and magnification of the upper canine (4). C, MNHN Qu4415, fragmentary mandible with the tooth row p3–m1 dext., in labial (1) and occlusal (2) views. Abbreviations: c., canine; ch., choanes; e.f., ethmoidal foramea; f.o., foramen ovalis; i.v., incisura vasorum; ju., jugal bone; mx., maxillary bone; na., nasal bone; pa., parietal bone; ps., presphenoid; vo., vomer. Scale bar = 1 cm.
compressed. The nasal bone is elongated, straight and narrow. The anterior left neocortex and olfactory bulb cavities are preserved but have not been prepared.

The deciduous premolars of MNHN Qu4640 are poorly preserved and completely worn (Fig. 3B2). The DP4 is trapezoidal and is of a smaller size than M1 but has a similar pattern. The P2 and P3 are almost identical in size and shape. The P3 possesses a large lingual cone giving it a more triangular shape. The lingual cone is posterior to the high anterolabial cone. The posteroconular cista of the P2 is curved and elongated: it is straight and short on P3. The anterior style is enlarged on P2. The posterior style is pinched. The labial cistae are straight.

The upper molars are square in outline and exhibit four main cusps. The protocone is large and crescentiform. Contrary to the condition in the anterior basin, the posterior basin may possess a neocrista. The parastyle is strong and mesially prominent. The postprotocrista is arc-like, and it joins the distal bifurcation of the premetacrista. The paracone possesses a strong labial rib without an 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 postmetacrista joins the base of the postmetacrista. The metaconule is oblique and is reduced in size on M3. The entostyle lying on the mesiolingual side of the metaconule tends to become smaller from M1 to M3. The premetacrista-entostyle is curved and transversely orientated to join the labial wall between the metacone and the paracone.

Discussion. The morphology and size of the teeth show that MNHN Qu4640 clearly belongs to Prodremotherium elongatum. This is the first time that a canine of Prodremotherium has been found associated with a tooth row. This canine is neither elongated and sabre-like, as in Dremotherium, nor extremely short and relatively straight, such as proposed by Filhol (1877), but rather shows a thin and highly curved morphology as in traguloids.

The skull MNHN Qu4640 possesses a better-preserved anterior part than the adult specimen MNHN Qu4596 described by Jehenne (1977, 1985). The skull of Prodremotherium is similar in morphology 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 in Prodremotherium and Dremotherium, whereas in Bachitherium (Geraads et al. 1987) and Floridameryx (Webb 2008) this bone is fairly enlarged transversely, giving a triangular shape to this area. Thus, the orbits have different shapes: they are rounded in Bachitherium and Floridameryx but squarer in Prodremotherium and Dremotherium. The postorbital process of the frontal bone is highly constricted and the frontal crest extends anteriorly to the cranium in Prodremotherium and Dremotherium, whereas in Bachitherium this process is wide posteriorly and the frontal crest occurs more posteriorly, within the cranium. Moreover, Bachitherium and Dremotherium possess a larger cranium than Prodremotherium. As suggested by Jehenne (1977), the skull of Prodremotherium shows close affinities to that of Dremotherium, but several features appear to be more primitive (e.g. the structure of the canine, and the apparent lack of a lacrimal fossa).

Phylogenetic relationships

In order to propose a hypothesis regarding the phylogenetic affinities of Mosaicomeryx, we compiled a matrix of 40 dental, mandibular and postcranial features (Supplemental Appendix 1) known in several Oligocene ruminants from both direct observation and the literature (Supplemental Appendices 3 and 4), scored in a character–taxon matrix (Supplemental Appendix 2). Taxa included in the analysis are 20 ruminant species representing a large range of European and Asiatic ‘gelocids’, bachitheriids and several species of Late Oligocene or Early Miocene ‘Pecora’ belonging to *Amphitragulus* and *Dremotherium* (Table 2). Lophiomerycids, tragulids, *Leptomeryx* and *Archaeomeryx*, and *Hypertragulus* were also scored. In all analyses, the choeropotamid *Amphirhagatherium weigelti* Heller, 1934 and the merycoidodontid *Merycoidodon culbertsoni* Leidy, 1848 were set as outgroup taxa.

The data matrix was assembled in Mesquite 2.75 (Maddison & Maddison 2010). All multistate characters were treated as unordered. The morphology dataset was analysed using TNT version 1.1 (Goloboff et al. 2000, 2008). Searching was performed with traditional search including 1000 RAS+TBR. The phylogenetic trees with morphological character state optimizations were generated by Winclada v.1.00 (Nixon 2002). For each node, the list of non-ambiguous synapomorphies is given in Figure 5; the upper numbers indicate the character rank in the matrix of characters (Supplemental Appendix 1) and the lower numbers indicate the state number for this feature. All characters are equally weighted without any ordering. Some characters were coded as polymorphic when the two character states are known in a given species. Convergences and reversion are allowed. The branch and bound algorithm was applied to find the optimal solution of the analysis. The most parsimonious tree was found by using a randomized stepwise addition.

In an initial analysis, the character–taxon matrix was analysed with the equal weighting search, producing 45 equally parsimonious cladograms of 102 steps. The consistency index of the most parsimonious cladograms excluding uninformative characters (CI) is 0.5 and the retention index (RI) is 0.7. The strict consensus of 45 MP
trees is poorly resolved, and consequently the majority rule (50%) consensus tree is shown in Figure 5A.

In a second analysis, the character–taxon matrix was analysed with the implied weighting option (k = 3) of TNT; two trees (CI = 0.52; RI = 0.73) were generated, and the strict consensus tree is shown in Figure 5B.

The topology of the strict consensus is poorly resolved: Archaeomeryx optatus appears as the first offshoot of a highly pectinate topology including all the remaining ingroup taxa. However, two clades are supported in this highly pectinate topology: the two species of Bachitherium form a monophyletic group, as do Archeotragulus krabiensis and Iberomeryx minor. This association supports the interpretation of Iberomeryx minor as probably a primitive tragulid, as suggested by Sudre (1984), Mennecart et al. (2011) and Mennecart (2012).

The majority rule (50%) consensus (Fig. 5A), as with the implied weighting consensus tree (Fig. 5B), as groups Gelocus communis and Lophiomeryx chalaniati as stem Ruminantia (below the crown Ruminantia). However, although they appear to be closely related in the trees obtained here, Lophiomeryx and Gelocus can be easily distinguished on post-cranial features (characters 27, 31, 35), and Gelocus is clearly determined to have a pecoran-like post-cranial morphology as suggested by Janis (1987) and Janis & Scott (1987). This relatively basal position of Gelocus communis suggests that the term gelocid should not be restricted to the genus Gelocus as suggested by Guo et al. (2000). The oldest Lophiomerycidae are known during the Eocene (Guo et al. 2000; Métais et al. 2001) and Lophiomerycidae is now considered as one of the most primitive families of ruminants (Métais & Vislobokova 2007). The true Gelocidae are only known in the Early Oligocene (see discussion below). In all analyses, Archaeomeryx optatus appears as the most basal offshoot of stem ruminants, followed by the North American hyptragulids and leptomerycids. Mosaicomeryx and Prodremotherium do not belong to Gelocidae (Fig. 5) but group

Table 2. Basic data for ruminant species used in the phylogenetic analysis and biostratigraphy (Brunet & Sudre 1987; Vislobokova 1997; Webb 1998; Lucas & Emry 1999; Métais et al. 2000; Métais & Vislobokova 2007; Mennecart 2012; Scherler et al. 2013).

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<th>Main reference</th>
<th>Type locality</th>
<th>Biostratigraphy</th>
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<td>Archaeomeryx optatus</td>
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<td>Shara Murun (late Middle Eocene, Mo)</td>
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<td>La Sauvetat (M25, Fr)</td>
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<td>Filhol (1882)</td>
<td>Quercy (undated, Fr)</td>
<td>MP22–MP27</td>
</tr>
<tr>
<td>Bachitherium insigne</td>
<td>Filhol (1882)</td>
<td>Quercy /undated, Fr</td>
<td>MP22–MP27</td>
</tr>
<tr>
<td>Dremotherium feignouxi</td>
<td>Saint-Hilaire (1833)</td>
<td>Saint-Gerard-le-Puy (MN2, Fr)</td>
<td>MN1–MN2</td>
</tr>
<tr>
<td>Dremotherium guthi</td>
<td>Jehenne (1987)</td>
<td>La Milloque (MP29, Fr)</td>
<td>MP28–MP30</td>
</tr>
<tr>
<td>Amphitragulus elegans</td>
<td>Pomel (1846)</td>
<td>Saint-Gerard-le-Puy (MN2, Fr)</td>
<td>MN1–MN2</td>
</tr>
<tr>
<td>Amphitragulus quercyi</td>
<td>Filhol (1887)</td>
<td>Quercy (undated, Fr)</td>
<td>MP28–MP30</td>
</tr>
</tbody>
</table>

Abbreviations: Ch, China; Fr, France; Ge, Germany; Go, Georgia; Kz, Kazakhstan; Mo, Mongolia; My, Myanmar; Th, Thailand.
together with Amphitragulus and the poorly known Asiatic Gobiomeryx and Pseudomeryx as stem Pecora (below the level of crown Pecora clade, here represented by Dreemotherium if we follow Sanchez et al. 2010). This intermediate position of Prodremotherium had already been shown in many phylogenies (Fig. 4).

The systematic position of the monogeneric family Bachitheriidae is somewhat problematical. The phylogenetic relationship of Bachitherium with other Oligocene ruminants remains ambiguous, or at least is not consensual in the literature (Fig. 4). This ‘moving’ position of the monogeneric Bachitheriidae is probably linked with 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 trochleae are not aligned), but the selenodonty of the molars and the fusion of the carpals bones probably result from convergent evolution. The misinterpretation of these convergent features almost certainly explains the variety of trees published so far (Fig. 4), most of them being done by hand. Although documented by a complete skeleton (Geraads et al. 1987), this phylogenetic position of this genus with respect to the crown Ruminantia (i.e. below or above Tragulidae) remains unstable. Further investigation of basicranial morphology (including the inner ear) may well provide interesting key features to constrain better the evolutionary history of bachitheriids.

Gelocidae classically contains numerous primitive Laurasian ruminant taxa (Table 2), such as Prodremotherium, Gelocus, Paragelocus, Pseudogelocus, Pseudomeryx, Floridameryx, Pseudoceras, Notomeryx, Gobiomeryx, Eumeryx and Rutitherium (Webb & Taylor 1980; Janis 1987; Janis & Scott 1987; Métais & Vislobokova 2007; Webb 2008; Mennecaet al. 2012a), and is a vast wastebasket. The principal features unifying all these taxa are mostly symplesiomorphic, such as brachyodont teeth, a small p1 separated from the p2 by a small diastema, a small mesolingual conid on the premolars without a posterolingual cristid, an incomplete postentocristid, the presence of a cingulum/cingulid on molars, and a

Figure 5. Trees resulting from the cladistic analysis of 40 dental, cranial and postcranial features (character definitions are listed in the Online Supplementary Material). All characters are non-additive. Taxon–matrix characters were processed with the traditional search (rule 3) of TNT version 1.1 (Goloboff et al. 2008). For each node the list of the non-ambiguous synapomorphies is given, each synapomorphy being represented by a black circle (strict synapomorphy) or an open white circle (homoplastic synapomorphy). The upper numbers indicate the character number and the lower numbers indicating the states for these characters. A, majority rule (50%) consensus tree of 45 most parsimonious trees obtained from an unweighted search (CI = 0.5; RI = 0.71). B, strict consensus tree of two most parsimonious trees resulted from a parsimony analysis using implied weighting method (k = 3) (CI = 0.53; RI = 0.74).
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 quericy. Mosaicomeryx and Prodremotherium possess many synapomorphic features that put them apart from the gelocids (Fig. 5). 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 or less subtriangular outline; the cingulum is deep and is also present in Mosaicomeryx quericy (character 9). However, the retention of a lingual cingulum on the upper molars is a synapomorphy feature that is also present in the Oligocene traguloids Lophiomeryx and Iberomeryx (Mennecart et al. 2011) and the derived stem pecoran Babameryx (Menne-cart et al. 2012b). A curved postprotocrista connecting to the premetacrista is a derived feature shared by Prodremotherium and Mosaicomeryx (character 10). In Gelocus, the postprotocrista is short, straight, and extends labially, and tends to join the mesial wall of the metaconule. This configuration of the upper molars is similar to that of Lophiomerycidae or Tragulidae. The mesostyle is more globular and less prominent in Mosaicomeryx than in Gelocus. The lingual cone of P3 is transversely compressed, lingually prominent and placed posterior to the anterolabial cone in Prodremotherium (characters 5 and 6). The P3 occlusal pattern is less prominent in Mosaicomeryx, but remains much more similar to that of Prodremotherium than of Gelocus. The premolars of Mosaicomeryx are much smaller than those of Prodremotherium, but remain elongated (character 4). Unlike the condition in Gelocus, the p1 is lost in Mosaicomeryx and Prodremotherium (character 13). This simplification of the dentition can be more complete with the disappearance of the p2 in Prodremotherium (Fig. 3C). Moreover, the lower molars of Mosaicomeryx and Prodremotherium display a postentocristid, a metastylid, absent in Gelocus, and a systematic absence of a bifurcation of the postmetacristid (characters 24, 25 and 26). The metatarsal bones are partly fused with a closed gully (characters 35 and 36) in Mosaicomeryx and Prodremotherium. These genera display a mosaic of primitive (partly fused metapodial bones) and derived features (loss of p1) (characters 13, 28 and 35).

It is generally admitted that Gelocidae represent a paraphyletic or polyphyletic assemblage of genera, which share some ‘pre-pecora’ features without any truly autapomorphic features (Geraads et al. 1987; Janis 1987; Janis & Scott 1987; Métais & Vislobokova 2007). Prodremotherium elongatum and Mosaicomeryx quericy clearly do not belong to the gelocid family, as it is currently ‘defined’ (Fig. 5). Many authors have suggested the placement of Prodremotherium away from this family. For example, Janis (1987) explained that Prodremotherium is somewhat different from members of 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) suggested that Prodremotherium, Rutitherium and Gelocus whitworthi represent basal Cervoida based on the presence of a closed metatarsal gully. However, none of these taxa belong to Gelocidae (see discussion about the evolution of early Western European stem Pecora) and these postcranial features may be highly variable in taxa other than Cervidae (Janis & Scott 1987; Hassanin & Douzery 2003) and therefore of limited use for systematic purposes.

Prodremotherium is classically considered as the potential ‘ancestor’ of Dremotherium (Filhol 1877; Jehenne 1977, 1985, 1987). However, like Mosaicomeryx, Prodremotherium lacks a p1. According to Jehenne (1987), 80% of the specimens referable to Dremotherium guthi Jehenne, 1987 known in the latest Oligocene of Western Europe retain a p1, and some rare Agenian specimens of Dremotherium feignouxi Saint Hilare, 1833 from Montaigu-le-Blin (earliest Miocene, MN2) in central France also preserve a p1. Therefore, it is difficult to support the hypothesis of a direct phylogenetic link between Prodremotherium and Dremotherium. The structure of the p4 is quite similar in both Gelocus and Prodremotherium, suggesting that this morphology is plesiomorphic. The p4 is much more complex and compressed in Dremotherium and Amphitragulus. According to Guo et al. (1999, 2000), the late Middle Eocene to Late Eocene ruminants reported from eastern Asia such as Indomeryx, Notomeryx and Gobiomeryx share close affinities with Prodremotherium. Like Prodremotherium and Mosaicomeryx, the specimens of Notomeryx from the latest Middle Eocene do not retain a p1 (e.g. V11483.1: Guo et al. 1999, fig. 2). Guo et al. (1999) underlined the necessity of splitting Gelocidae into two families: Gelocidae sensu stricto (with the genera Gelocus, Pseudogelocus and Paragelocus), and the new family Prodremotheriidae, in which they included Prodremotherium Filhol, 1877, Indomeryx Pilgrim, 1928, Notomeryx Qui, 1978, and Gobiomeryx Trofimov, 1957. However, the dental morphology of Indomeryx is more primitive than the Middle Eocene genus Archaeomeryx, and it should be considered as a basal form amongst the ruminants (Métais et al. 2000). In addition 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. fierowi MP22-24, Kazakhstan) and Benara (P. trepidum MP23, Georgia) (Trofimov 1957; Gabunia 1964; Vislobokova 1997; Lucas & Emry 1999; Métais & Vislobokova 2007). No direct observations by the authors support the attribution of these Asian
species to this genus. According to Gabunia (1966), the metapodial bones are completely fused in *P. trepidum* from Benara, which is not the case in the European species (Blondel 1997; this article). In addition, *P. trepidum* (MP23) displays a more complex p4 structure than *P. elongatum* (MP28) (Gabunia 1966). It is possible that the Georgian species belongs to another genus.

**Stratigraphical range and geographical distribution of early Western European stem Pecora**

*Prodremotherium elongatum* is relatively rare in the Oligocene localities of Europe (Fig. 6). The only well-dated locality yielding this taxon is Pech Desse, Quercy from MP28 (Remy *et al.* 1987; Martinez & Sudre 1995; Blondel 1997). This taxon has been tentatively reported in Cournon, Boujac and Sarèlè in France (Hartenberger *et al.* 1970; Huguene 1997). The Sarèlè and Boujac localities are contemporaneous (Hartenberger *et al.* 1970) and have been dated either to MP27 (BiochroM’97 1997) or MP28 (Hartenberger *et al.* 1970). Bonis *et al.* (1973), Jehenne (1987) and Jehenne & 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 were incorrectly identified and confused with *Bachitherium curtum* Filhol, 1882 (Blondel 1997). This may be the same for the other localities. The ruminants from Bumbach, Saint André, and ‘Marseille’ allow a clear distinction between *P. elongatum* and *Mosaicomeryx quercyi*. Examining the collections of the University of Lyon, the ‘Marseille’ locality could in fact have been Saint Henri. All of these localities are correlated to MP25 and MP26 (Engesser & Mödden 1997; BiochroM’97 1997). Moreover, new data provided by new discoveries in the Swiss Molasse Basin show the last occurrence of *M. quercyi* during MP27 (Weidmann *et al.* in press). *P. elongatum* has also been reported from Saint Géry (Tarn, France), which is Stampaian *sensu stricto* (Cavaillé 1971), a local stage corresponding to the late Rupelian (Foucault & Raoult 2001) and late Suevian European Land Mammal Age. Likewise, *P. cf. elongatum* is reported from les Milles (Repelin 1916). All of these occurrences are consistent with an earlier occurrence (MP25–27) of *M. quercyi* than previously thought. In La Sauvetat and Antoingt, also correlated to MP25
(Hugueney 1997), Dremotherium sp. or D. feignouxi are reported (Giraud 1902; Lavocat 1951; Ginsburg 1967; Hugueney 1997). Elsewhere in Europe, Dremotherium first appeared during the late Arvernian (latest Oligocene, MP28) with the species D. guthi (Jehenne 1985, 1987; Blondel 1997; Mennecart 2012; Mennecart et al. 2012b), D. feignouxi being limited to the Agenian (earliest Miocene, MN1–2, Gentry et al. 1999; Becker et al. 2010; Mennecart 2012). These supposed early occurrences of Dremotherium may result from the misidentification of specimens that may actually be of M. quercyi, but this possibility requires further investigation. Likewise, Early Oligocene occurrences of Prodremotherium species in several poorly sampled Asian localities remain fairly doubtful, and would require further evidence (Métais & Vislobokova 2007). Gelocidae, Bachitheriidae, Lophiomerycidae, Tragulidae are typical post-Grande Coupure immigrants, having their first occurrence between MP21 and MP23 (Mennecart et al. 2011; Mennecart 2012). Mosaicomeryx and Prodremotherium arrived later and are known from MP25 to MP28. Amphitragus and Dremotherium first appeared in Europe during MP28 (Mennecart et al. 2012b).

**Evolution of early Western European stem Pecora**

Mosaicomeryx and Prodremotherium probably arrived in Western Europe from Asia by the mid-Oligocene. Close relatives of these genera are reported in the Late Eocene of Asia (Gobiomeryx), but the arrival of Mosaicomeryx and Prodremotherium in Western Europe seems to have occurred long after the ‘Grande-Coupure’, during MP24 (Fig. 6, Migrations 1). Gelocidae (sensu Guo et al. 1999), and slightly later Tragulidae and Lophiomerycidae, are typical post-Grande-Coupure immigrants (respectively at MP21 and MP22–23). The first occurrence of stem Pecora in Europe seems to be correlated with a major phase of Oligocene mammalian turnover in Europe, which corresponds with the definitive disappearance of Gelocus (Fig. 6, Extinction 1) and tragulids (Mennecart et al. 2011), and the diversification of Lophiomerycidae (Brunet & Sudre 1987) and Bachitheriidae (Sudre 1995). This may be related to environmental changes (Oi2 glaciations: see Pekar et al. 2006; European inner sea regressions: see Berger 2011). Some authors have suggested that Gelocus survived until the Early Miocene in Africa and Asia with the species ‘G.’ whitworthi Hamilton, 1973 and ‘G.’ gajensis Pilgrim, 1912 (Pilgrim 1912; Hamilton 1973; Métais & Vislobokova 2007). However, we agree with Métais et al. (2009), Cote (2010) and Mennecart et al. (2012a) that ‘G.’ whitworthi and ‘G.’ gajensis do not belong to the genus Gelocus due to the presence of a double postentocristid in the former species and extremely primitive lophiomerycid features in the latter. The disappearance of Mosaicomeryx and Prodremotherium in Europe corresponds to the main phase of faunal renewal during the Oligocene (see Fig. 6, Migrations 3/Extinction 3; Jehenne & Brunet 1992; Mennecart et al. 2012b). During this turnover, Lophiomeryx and Bachitherium gave way to derived crown Pecora and stem Pecora such as Dremotherium and Amphitragus (Jehenne 1987; Blondel 1997; Mennecart et al. 2012b). This turnover can also be observed within the rodents (Vianey-Liaud et al. 1991), Cainotheriidae (Berthet 2003; Blondel 2005), and Anthracotheriidae with the first appearance of Microbunodon in Western Europe (Lihoreau et al. 2004; Scherler 2011). As suggested by Mennecart et al. (2012b), the faunal turnover could also be due to a global climatic event since it correlates with Late Oligocene global warming recorded in the marine realm (Zachos et al. 2001) named the ‘Microbunodon event’ (Scherler et al. 2013).

Postcranial remains of Mosaicomeryx quercyi suggest that this animal lived in wooded areas (Scherler et al. 2013), whereas a more open habitat is argued for Prodremotherium elongatum (Blondel 1998). The analysis of the entire mammalian communities corroborates this shift towards more open and grassy habitats during MP27–28 (Legendre 1989; Vianey-Liaud 1991; Blondel 1998; Scherler et al. 2013).

**Conclusions**

The description of new fossil material and reassessment of material previously referred to Gelocus quercyi leads us to propose a new genus — Mosaicomeryx — for this species. Mosaicomeryx quercyi displays a mixture of primitive (relatively elongated lower premolars, strong cingulum surrounding the upper molar protocone, metatarsal bones partly fused) and derived (p1 lost, postprotocrista curved and connected to the premetaconeulicrista near the centre of the molar, mesostyle globular and few salient, bony bridge on the distal part of the metatarsal bones) features that set it apart from all hornless ruminant taxa described so far. Phylogenetic analysis shows that Gelocus and Mosaicomeryx are not closely related, Mosaicomeryx appearing more closely related to Prodremotherium elongatum, suggesting two distinct episodes of migration of stem Pecora from Asia to Western Europe. Defining these specimens in well-dated localities allows us to have a good understanding of the biostratigraphical ranges of Mosaicomeryx quercyi (MP25–27) and Prodremotherium elongatum (MP28) in Europe. These time intervals seem to correspond to the major climatic changes during this period: regressions of the European inner sea (linked to the Oi2 glaciations?) and the Late Oligocene Warming.
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Supplemental material

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References


Heller, F. 1934. Anthracobunodon weigelti n.g. et n.sp., ein Artiodactyl aus dem Mitteleozee der Halle a. S. Paläontologische Zeitschrift, 16, 147–263.


Mennecart, B. 2012. Le Ruminantia (Mammalia, Cetartiodac- tyla) from the Oligocene to the Early Miocene of Western Europe: systematics, palaeoecology and palaeobiogeography. GeoFocus, 32, 1–263.


Nixon, C. K. 2002. WRY: Hidden (Version 1.00.08. Published by the author, Ithaca, USA.


