

***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.

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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 *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 *G. communis* (Aymard, 1846) and *G. laubei* Schlosser, 1901; the last occurrence of the ‘gelocids’ is no younger than MP28 (Late Oligocene) with the occurrence of *Prodremotherium elongatum* Filhol, 1877 whose affinity with ‘Gelocidae’ is debated (e.g. Janis 1987). The genus *Prodremotherium* is also reported from the Early Oligocene of Kazakhstan (*P. fterowi* Trofimov, 1957), Mongolia (*P. sp.* of Vislobokova &

Daxner-Höck 2002) and Georgia (*P. trepidum* Gabunia, 1964), but the generic assignment of these Asiatic forms remains doubtful.

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 *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 *Prodremotherium* to be a basal eupecoran, close to Bovoidea (Jehenne 1977, 1985; Jehenne & Brunet 1992) or Cervoidea (Webb & Taylor 1980; Janis & Scott 1987). It has also been placed within Prodremotheriidae (Guo *et al.* 1999, 2000; Métais *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, *P. elongatum* is known only in the poorly dated old collections of the Phosphorites du Quercy (Filhol 1877; Jehenne 1977, 1985, 1987; Remy *et al.* 1987;

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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

MNHN: Muséum National d’Histoire Naturelle, Paris, France; **USTL**: Université des Sciences et Techniques du Languedoc, Montpellier, France; **UCBL**: Université Claude Bernard Lyon, France; **NMB**: Naturhistorisches Museum Basel, Switzerland; **MNBe**: Naturhistorisches Museum Bern, Switzerland.

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, MNBe, 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

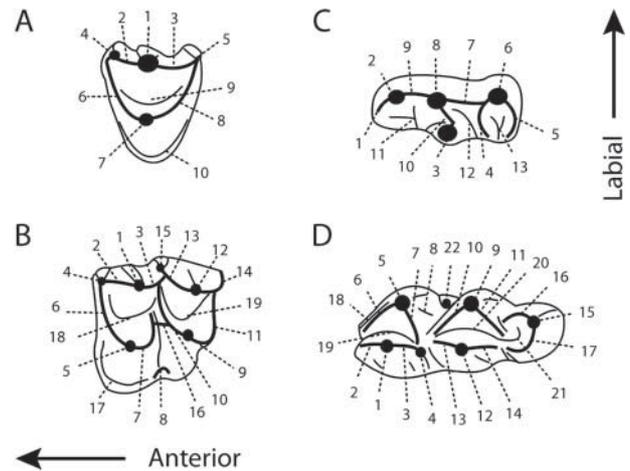


Figure 1. Nomenclature of the dentition. **A**, upper premolars: 1, anterolabial cone; 2, anterolabial crista; 3, posterolabial crista; 4, anterior style; 5, posterior style; 6, anterolingual crista; 7, lingual cone; 8, posterolingual crista; 9, fossa; 10, cingulum. **B**, upper molars: 1, paracone; 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, anterior styloid; 2, anterior conid; 3, mesolingual conid; 4, posterolingual conid; 5, posterior styloid; 6, posterolabial conid; 7, posterolabial cristid; 8, mesolabial conid; 9, anterolabial cristid; 10, transverse cristid; 11, anterior valley; 12, posterior valley; 13, back valley. **D**, lower molars: 1, metaconid; 2, premetacristid; 3, postmetacristid; 4, metastylid; 5, protoconid; 6, preprotocristid; 7, internal postprotocristid; 8, external postprotocristid; 9, hypoconid; 10, prehypocristid; 11, posthypocristid; 12, entoconid; 13, preentocristid; 14, postentocristid; 15, hypoconulid; 16, prehypococonulidcristid; 17, posthypococonulidcristid; 18, anterior cingulid; 19, anterior basin; 20, posterior basin; 21, back basin of m3; 22, ectostylid. Modified from Bärmann & Rössner (2011).

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, Catzefflis, & Douzery, 1997
Suborder **Ruminantia** Scopoli, 1777
Genus *Mosaicomeryx* gen. nov.

Type species. *Gelocus quercyi* Jehenne, 1987.

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.

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
		—	—	0.26/0.35	0.12/0.40	0.79/0.32	0.95/0.13

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 selenodont, 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 mesolingual conid and four crests lingually orientated. There are neither

external postprotocristid nor ‘*Dorcattherium* 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 postprotocrista 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

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 feignouxii* Giraud: 167.
v pars 1914 *Ruminantia* inc. sed. Stehlin: 185.
1916 *Prodremotherium* cf. *elongatum* Repelin: 102.
v 1983 *Bachitherium insigne* Mayo: 906.
v* pars 1985 *Gelocus quercyi* Jehenne: 49, fig. 9a–e.
v 1987 *Prodremotherium elongatum* Engesser & Mayo: 71.
v 1987 *Bachitherium insigne* Engesser & Mayo: 73.
v* pars 1987 *Gelocus quercyi* Jehenne; Jehenne: 132, fig. 1.
1997 *Dremotherium* sp. Hugueney: table 4.
v 1997 *Prodremotherium elongatum* Engesser & Mödden; Engesser & Mödden: 483.
v 1997 *Bachitherium insigne* Engesser & Mödden: 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), Réchauvent (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; NMB 5017072, P3 dext., Bumbach; NMB 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); NMHN Qu4145, maxillary with tooth row M1–M3 sen., Phosphorites du Quercy (SW France); NMHN Qu4146, maxillary with tooth row M2–M3 dext., Phosphorites du Quercy; NMHN Qu4147, maxillary with tooth row M1–M3 dext. (Jehenne 1985, fig. 9c), Phosphorites du Quercy; NMHN Qu4149, maxillary with tooth row P4–M3 sen., Phosphorites du Quercy; NMHN Qu4150, maxillary with the tooth row M2–M3 sen., Phosphorites du Quercy; NMHN Qu4152, maxillary with the tooth row

M1–M2 sen. (Jehenne 1985, fig. 9e), Phosphorites du Quercy; NMHN Qu4153 maxillary with tooth row P4–M3 sen. (Jehenne 1985, fig. 9b) Phosphorites du Quercy; NMHN Qu4154, maxillary with tooth row M1–M3 dext., Phosphorites du Quercy; NMHN 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 QJ80a, 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 (Fig. 2C2). Its posterolingual part possesses a small transverse cristid 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 posterolingual conid when this feature is present. It forms the posterolingual 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

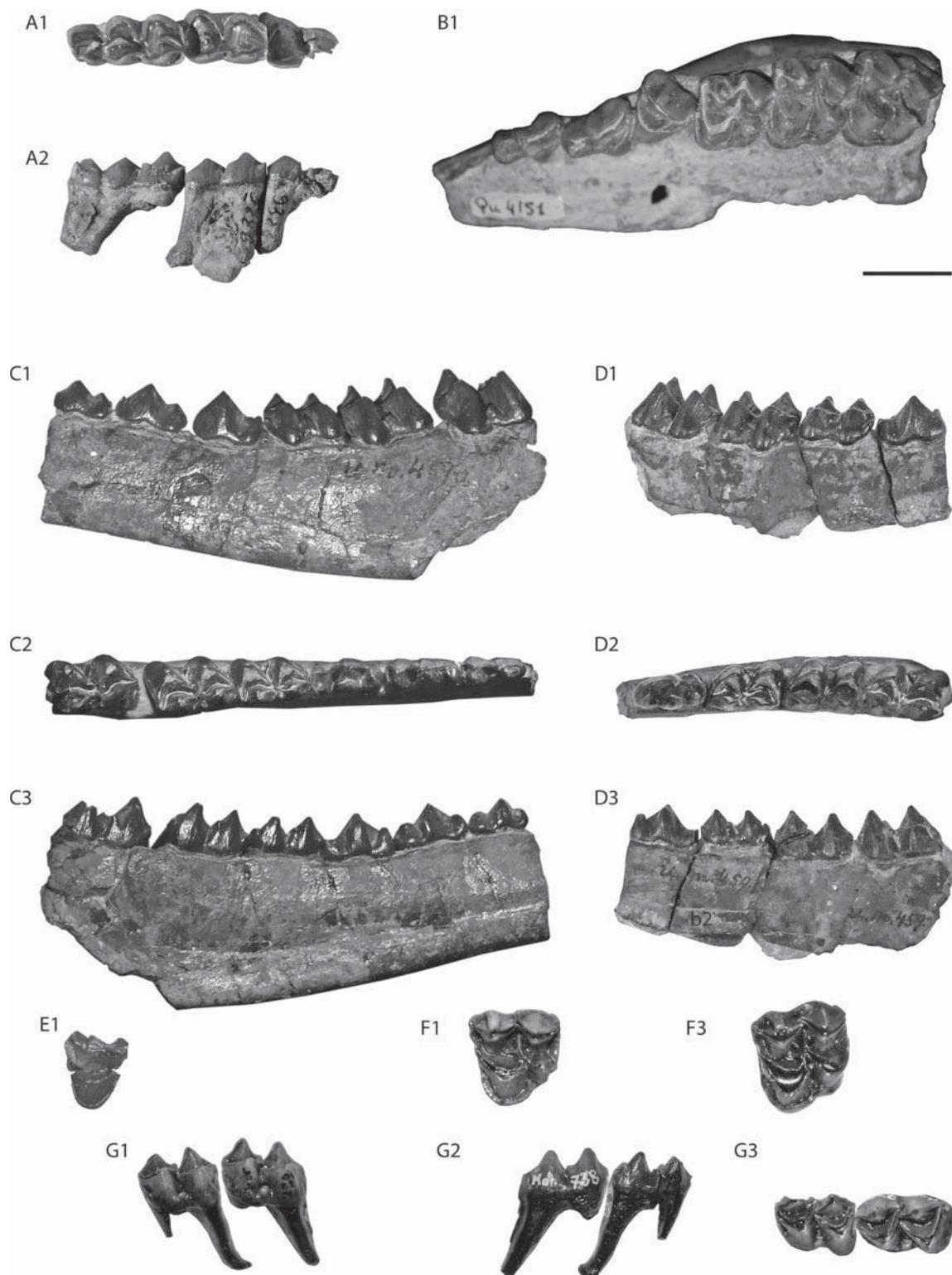


Figure 2. *Mosaicomeryx quercyi* from old collections from the Phosphorites du Quercy (undated, SW France), Bumbach (mid-Oligocene, Central Switzerland), ‘Marseille’ and Saint André (mid-Oligocene, SE France). **A**, ‘Marseille’, USTL 9326, isolated m1, m2, m3 sen., and m3 sen. in occlusal (1) and lingual (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 mesolabial 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 styloid 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 styloid, 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 styloid. 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 preentocristid. The metacristids 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 quercyi*. The P4 is triangular due to an anterolingual crista and a straight posterolingual crista (Fig. 2E). The lingual cone is fully selenodont. The anterolingual crista reaches the anterior style and the posterolingual 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 preprotocrista joins a strong and slightly curved parastyle. 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 premetacrista ends with a globular mesostyle. The metacone rib is weak to absent, and when present is progressively less defined from M1 to M3. The postmetacrista joins a well-defined 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. At the end of the large cingulum, the metaconule, at its base, possesses 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 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 genera *Lophiomeryx*, *Iberomeryx* and *Babameryx* (Mennecart *et al.* 2011, 2012b). The upper molars of *Mosaicomeryx* differ from those of *Gelocus* in being more selenodont (they are clearly bunoselenodont 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 selenodont, 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 bunoselenodont 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 selenodont than those of *Mosaicomeryx*, but the latter are more selenodont 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 bunoselenodont 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 anterolingual cristid) and are relatively elongated. The molars are selenodont. The postcranial 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.

Additional species. *Prodremotherium flerowi* Trofimov, 1957; *P. trepidum* Gabunia, 1964.

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 linguallly orientated. There are neither external postprotocristids nor *Dorcatherium* folds on the lower molars, but there is a distinct metastylid. The entoconid is transversally compressed and crested anteriorly and posteriorly. The preprotocristid closes the trigonid linguallly. 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 astragalus has a transversally extended sustentacular facet and parallel trochleae.

Remarks. This genus differs from *Gelocus* and *Mosaicomeryx* by the absence of cingula on the upper molars and in being more selenodont. 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*¹ pars 1877 *Prodremotherium elongatum* Filhol: 448, pl. 11, 258, 259, 263–268.

1883 *Prodremotherium elongatum* Filhol; Rüttemeyer: 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.
- 1970 *Prodremotherium* indet. Hartenberger *et al.*: table 3.
- 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.
- 1987 *Prodremotherium elongatum* Filhol; Janis: 200, fig. 4.
- 1987 *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. Huguency: 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. (Qu4646; 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, Cournon, Pech Desse, MP28 (Hartenberger *et al.* 1970; Remy *et al.* 1987; Blondel 1997; Huguency 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 posterolingual 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 vasorum* 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 orbitasphenoid and presphenoid are present. The supraorbital area is highly vascularized, like on the other described skull of *Prodremotherium elongatum* (MNHN Qu4596; Jehenne 1977) and in *Dremotherium feignouxii* (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 left *foramen ovalis* is close to the adult cheek teeth, deciduous 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

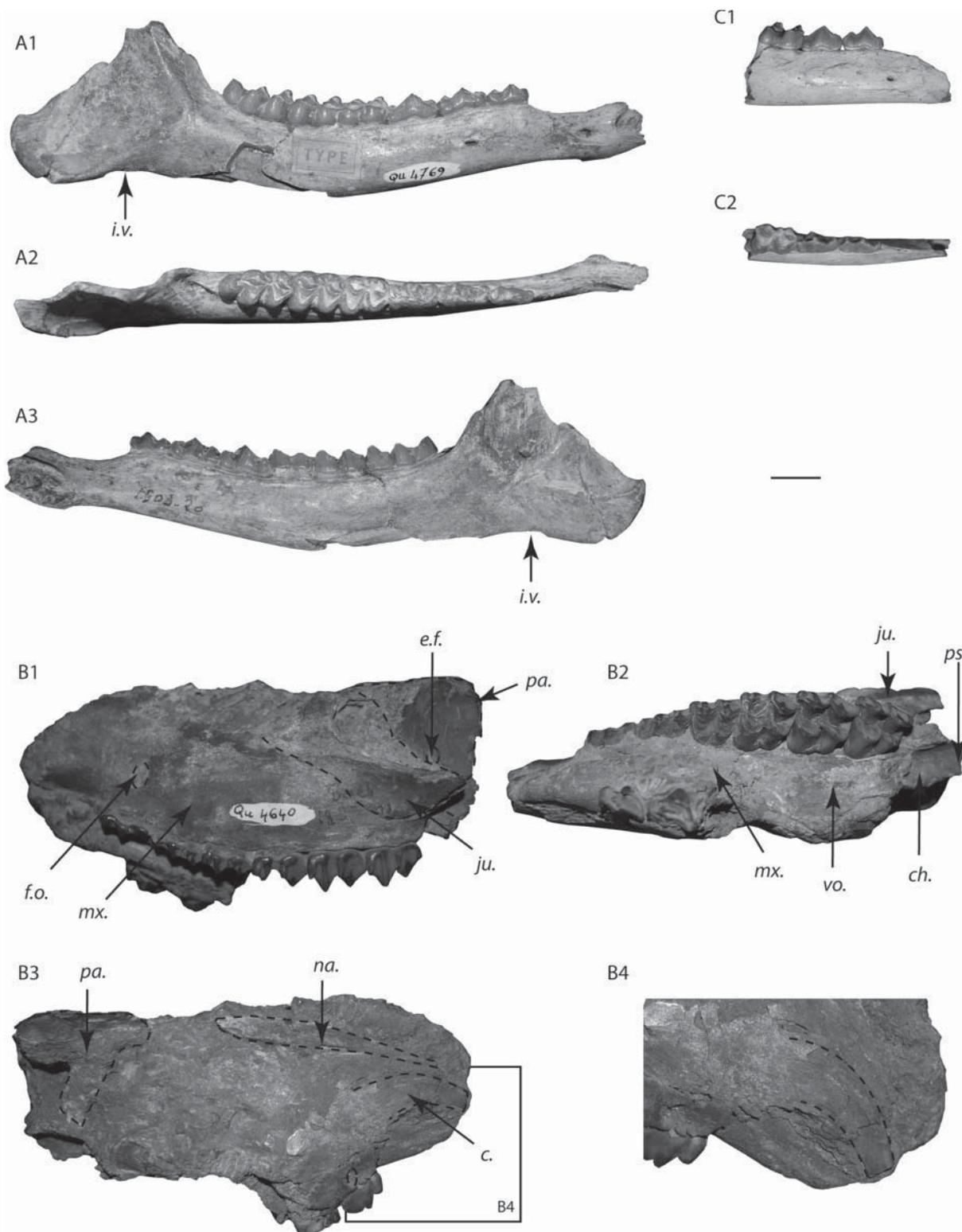


Figure 3. *Prodremotherium elongatum* from old collections from the Phosphorites du Quercy (undated, SW France). **A**, MNHN Qu4769, holotype, mandible with the tooth row p2–m3 dext., in labial (1), occlusal (2) and lingual (3) views. **B**, MNHN Qu4640, partial skull of a juvenile with D2–M3 sen. and 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.*, ethomoidal 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 posterolingual crista 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 cristae 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 premetaconule-crista. 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 postmetaconulecrista 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 premetaconulecrista 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 (Madison & 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

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; Menecart 2012; Scherler *et al.* 2013).

Taxon	Main reference	Type locality	Biostratigraphy
<i>Archaeomeryx optatus</i>	Matthew & Granger (1925b)	Shara Murun (late Middle Eocene, Mo)	Late Middle Eocene
<i>Leptomeryx evansi</i>	Leidy (1853)	South Dakota (Early Oligocene, USA)	Orellan (Early Oligocene)
<i>Hypertragulus calcaratus</i>	Cope (1873)	South Dakota (Late Eocene, USA)	Chadronian (Late Eocene)
<i>Lophiomeryx chalianati</i>	Pomel (1853)	La Sauvetat (M25, Fr)	MP24–MP28
<i>Lophiomeryx mouchelini</i>	Brunet & Sudre (1987)	Villebramar (MP22, Fr)	MP22–MP24
<i>Archeotragulus krabiensis</i>	Métais <i>et al.</i> (2001)	Wai Lek lignite pit (Late Eocene, Th)	Late Eocene
<i>Iberomeryx minor</i>	Filhol (1882)	Quercy (undated, Fr)	MP23–MP24
<i>Miomeryx altaicus</i>	Matthew & Granger (1925a)	Erguulin-Dzo (Late Eocene, Mo)	Late Eocene
<i>Gobiomeryx dubius</i>	Trofimov (1957)	Erguil Obo (Late Eocene, Mo)	Late Eocene
<i>Indomeryx cotteri</i>	Pilgrim (1928)	Yarshe Kyitchaung (late Middle Eocene, My)	Middle Eocene
<i>Notomeryx besensis</i>	Qiu (1978)	Baise (latest Middle Eocene, Ch)	Middle and Late Eocene
<i>Pseudomeryx gobiensis</i>	Trofimov (1957)	Tatal-Gol (Early Oligocene, Mo)	Early Oligocene
<i>Prodremotherium elongatum</i>	Filhol (1877)	Quercy (undated, Fr)	MP27?–MP28
<i>Prodremotherium trepidum</i>	Gabunia (1964)	Benara (MP23?, Go)	Early Oligocene
<i>Prodremotherium flerowi</i>	Trofimov (1957)	Tchelkar-Teniz (Early Oligocene, Kz)	Early Oligocene
<i>Mosaicomeryx quercyi</i>	Jehenne (1987)	Quercy (undated, Fr)	MP25–MP27
<i>Gelocus communis</i>	Aymard (1846)	Ronzon (MP21, Fr)	MP21–MP24
<i>Gelocus villebramarensis</i>	Brunet & Jehenne (1976)	Villebramar (MP22, Fr)	MP21–MP22
<i>Gelocus laubei</i>	Schlosser (1901)	Eselberg (MP21–22, Ge)	MP21 (MP22?)
<i>Pseudogelocus/Paragelocus scotti</i>	Schlosser (1902)	Hochberg/Oerliner Thal (MP21, Ge)	MP21–MP23
<i>Bachitherium curtum</i>	Filhol (1882)	Quercy (undated, Fr)	MP22–MP27
<i>Bachitherium insigne</i>	Filhol (1882)	Quercy /undated, Fr)	MP22–MP27
<i>Dremotherium feignouxii</i>	Saint-Hilaire (1833)	Saint-Gérard-le-Puy (MN2, Fr)	MN1–MN2
<i>Dremotherium guthi</i>	Jehenne (1987)	La Milloque (MP29, Fr)	MP28–MP30
<i>Amphitragulus elegans</i>	Pomel (1846)	Saint-Gérard-le-Puy (MN2, Fr)	MN1–MN2
<i>Amphitragulus quercyi</i>	Filhol (1887)	Quercy (undated, Fr)	MP28–MP30

Abbreviations: Ch, China; Fr, France; Ge, Germany; Go, Georgia; Kz, Kazakhstan; Mo, Mongolia; My, Myanmar; Th, Thailand.

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), Menecart *et al.* (2011) and Menecart (2012).

The majority rule (50%) consensus (Fig. 5A), as with the implied weighting consensus tree (Fig. 5B), groups *Gelocus communis* and *Lophiomeryx chalianati* 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 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 hypertragulids and leptomerycids. *Mosaicomeryx* and *Prodremotherium* do not belong to Gelocidae (Fig. 5) but group

together with *Amphitragulus* and the poorly known Asiatic *Gobiomeryx* and *Pseudomeryx* as stem Pecora (below the level of crown Pecora clade, here represented by *Dremotherium* 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 carpal 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; Mennecart *et 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

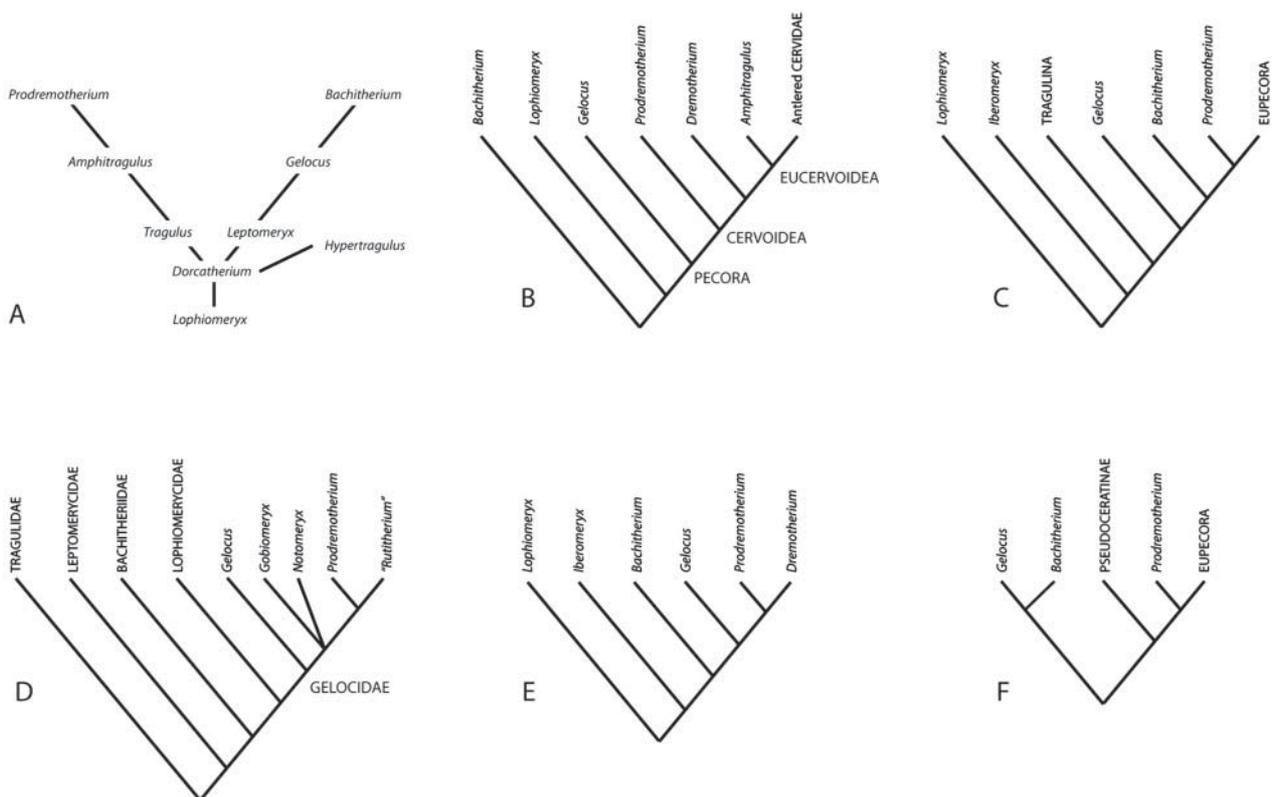


Figure 4. History of ideas on the phylogenetic position of *Prodremotherium*. **A**, view of Cope (1887) with a linear evolution of various genera from the Oligocene and Miocene of Europe and northern America. **B**, composite diagram incorporating the view of Janis & Scott (1987, figs 17–19). **C**, simplified diagram of the view of Geraads *et al.* (1987); ‘Tragulina’ includes Leptomerycidae, with *Leptomeryx*, and true Tragulidae, ‘Eupecora’ includes *Dremotherium* and true ruminant families excluding Tragulidae. **D**, simplified diagram of the view of Janis (1987); ‘Tragulidae’ includes *Dorcatherium*, ‘Leptomerycidae’ includes *Leptomeryx*, ‘Bachitheriidae’ includes *Bachitherium*, and ‘Lophiomerycidae’ includes *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*.

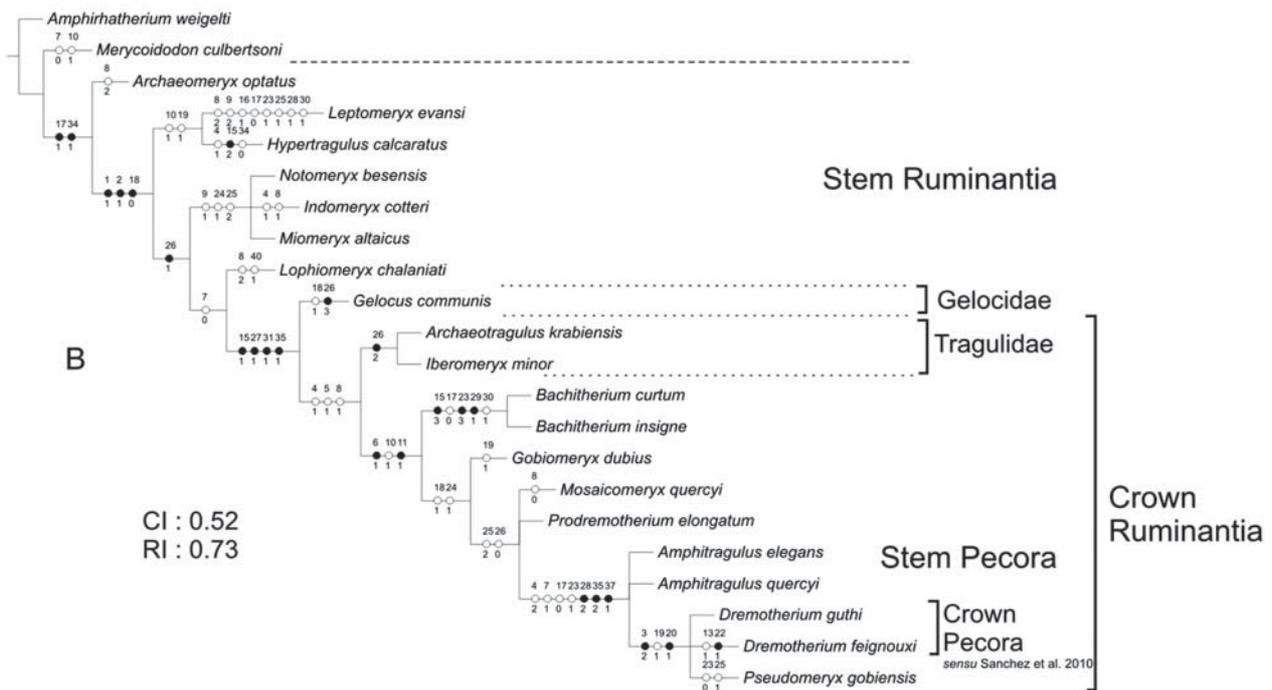
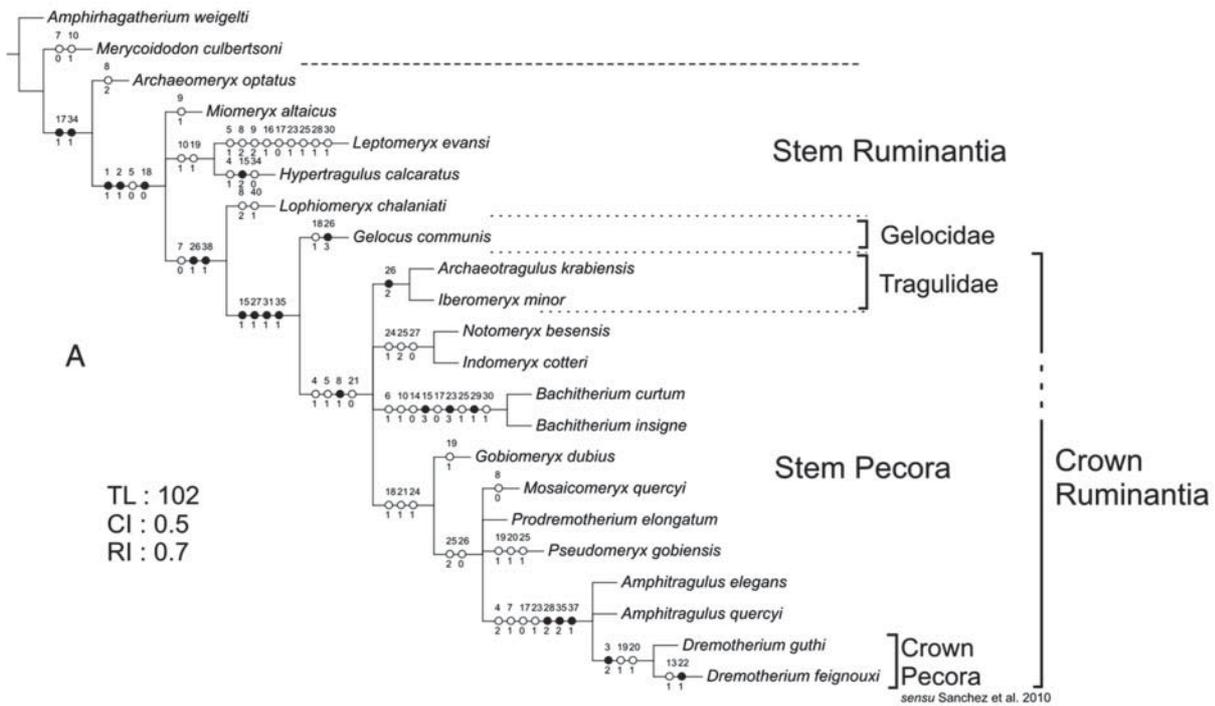


Figure 5. Trees resulting from the cladistic analysis of 40 dental, cranial and postcranial features (character definitions are listed in the Online Supplementary Material). All characters are non-additive. Taxon–matrix characters were processed with the traditional search (rule 3) of TNT version 1.1 (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 quercyi*. *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 quercyi* (character 9). However, the retention of a lingual cingulum on the upper molars is a symplesiomorphic feature that is also present in the Oligocene traguloids *Lophiomeryx* and *Iberomeryx* (Mennecart *et al.* 2011) and the derived stem pecoran *Babameryx* (Mennecart *et al.* 2012b). A curved postprotocrista connecting to the premetaconulecrista near the centre of the molars 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 Lophiomericidae 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 ‘protopecoran’ features without any truly autapomorphic features (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 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 Cervoidea 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 Hilaire, 1833 from Montaignu-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* Qiu, 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. flerowi* 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 Sarèle in France (Hartenberger *et al.* 1970; Huguency 1997). The Sarèle 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 Stampian *sensu stricto* (Cavaillé 1971), a local stage corresponding to the late Rupelian (Foucault & Raoult 2001) and late Suevoian 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

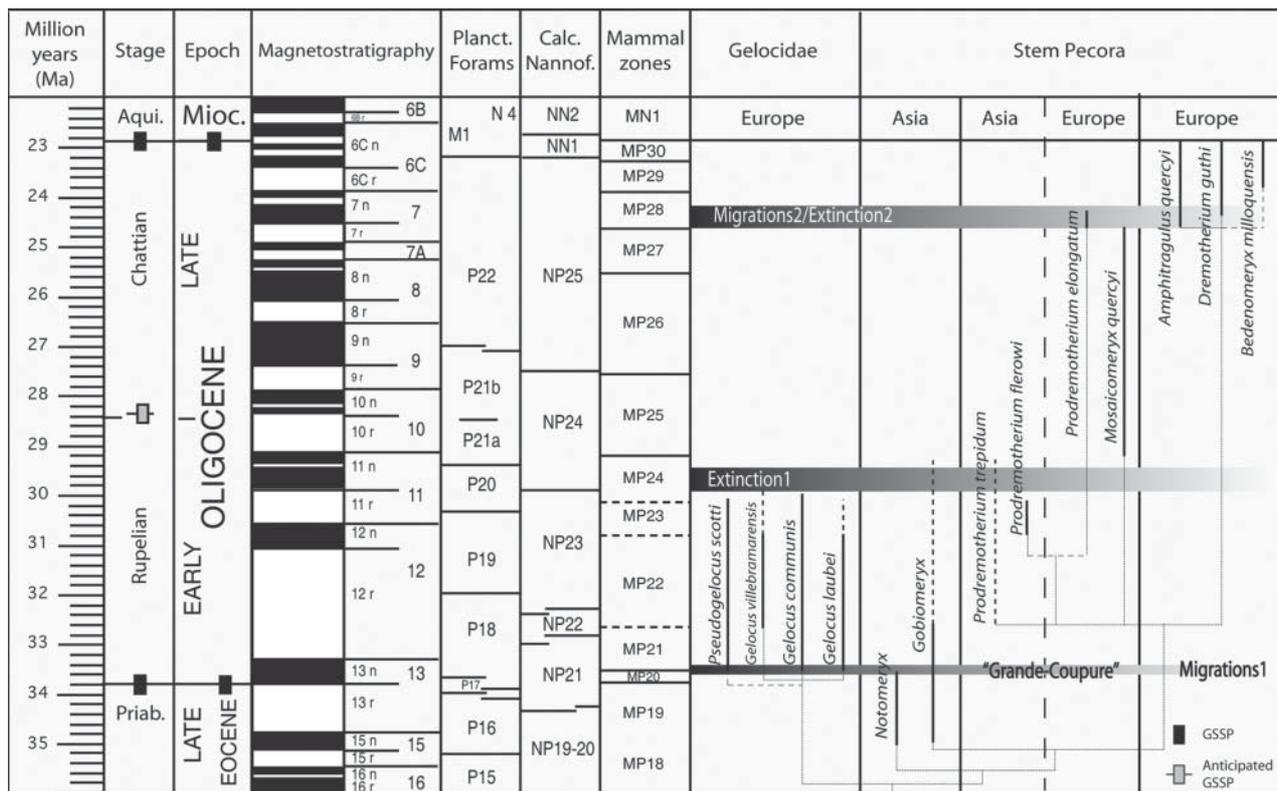


Figure 6. Biostratigraphy of Gelocidae and stem Pecora. The chronostratigraphy and biostratigraphy are based on Berger (2011). Migration and extinction events correspond to the major European ruminant community changes during the Oligocene. The time interval (c. 33.6–33.4 Ma) of the 'Grande-Coupure' event (Stehlin 1910) is based on high-resolution stratigraphy of the Belgian Basin after Hooker *et al.* (2004, 2009). 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) and Vianey-Liaud & Schmidt (2009).

(Huguéney 1997), *Dremotherium* sp. or *D. feignouxi* are reported (Giraud 1902; Lavocat 1951; Ginsburg 1967; Huguéney 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. *Amphitragulus* 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 *Amphitragulus* (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 premetaconulecrista 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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