PALÆO VERTEBRATA

ARTICLE

A new species of *Propalaeotherium* (Palaeotheriidae, Perissodactyla, Mammalia) from the Middle Eocene locality of Aumelas (Hérault, France)

Jean Albert REMY*, Gabriel KRASOVEC & Bernard MARANDAT

Institut des Sciences de l'Évolution (UM, CNRS, IRD, EPHE), c.c. 064, Université de Montpellier, Place Eugène Bataillon, 34095 Montpellier cedex 05, France
**Corresponding author: jean.a.remy@wanadoo.fr*

Abstract: A new *Propalaeotherium* species, clearly distinct from the genus *Eurohippus*, is described. It is characterized by having a similar size as *P. voigti* from the German Geiseltal localities (MP 11 to MP 13 reference-level), but differs in several features suggesting a slighty more derived morphology. It presents indeed less brachyodont crowns with less prominent and less elevated cingula, slightly larger relative surface of premolars, and a more marked metaconid splitting on cheek teeth. This new species is unknown from other European localities except the nearby Saint-Martin de Londres locality which has been considered older than the MP 13 level.

Keywords: Paleogene, Southern France, Europe, systematics, dental anatomy

Submitted 13 November 2015, Accepted 9 March 2016
Published Online 23 May 2016, doi: 10.18563/pv.40.2.e1

INTRODUCTION

The Aumelas locality, situated about 20 km west of Montpellier (Hérault, France), consists of lacustrine limestones that have yielded the gastropods *Galba aquensis michelini* and *Australorbis pseudoammonius*. It has therefore been attributed to the Lutetian stage (Hartenberger, 1963; Sudre, 1980; Crochet *et al.*, 1988). Many vertebrate remains have been extracted by acid dissolution of the carbonated matrix. A preliminary list of the resulting fauna was proposed by Sudre (1980) and is still largely incomplete today. It is composed of crocodilians, chelonians and mammals. Among the latter, it is possible to recognize marsupials, bats, rodents, lipothyphlan insectivores, primates, creodonts, artiodactyls and perissodactyls (Sudre, 1978, 1980, 1988; Crochet, 1979; Lalaï, 1982; Godinot, 1988; Escarguel, 1999; Maitre *et al.*, 2006, 2008; Maitre, 2014). The biochronological indications provided by diverse faunal elements have led authors to propose that this rich fauna is near the reference level MP 13 (Late Lutetian). A large amount of the collected material is nevertheless still unpublished. Here a new species of *Propalaeotherium* is described within the framework of an ongoing revision of the perissodactyls from Aumelas.

Abbreviations for institutions

UM: Université de Montpellier
GMH: Geiseltal Museum, Halle
HLMD: Hessisches Landesmuseum, Darmstadt
MBO: Muséum d'Histoire Naturelle, Bordeaux
MNHN: Muséum National d'Histoire Naturelle, Paris
NMB: Naturhistorisches Museum, Basel

Abbreviations for metric parameters

DPC: post-canine diastema = distance from P2 to M3 (upper or lower) at the bone level
H_{cing}: height of the cingulum / height of the highest cusp x100
I_H: index of hypsodonty (= height / width of the crown x100)
LRDJ: length of the tooth row from P2 to M3 (upper or lower)
MMM: lever arm of the masseter muscle (= vertical distance -referring to the occlusal plane of teeth- from the surface of the condyle to the ventral border of the angular process of the mandible)
MMT: lever arm of the temporal muscle (= horizontal distance -referring to the occlusal plane of teeth- from the rear of the condyle to the anterior side of the ascending ramus)
PMI: length ratio between (upper or lower) molar and premolar series (L_{P2-P4}/L_{M1-M3} x100)
S_P/S_M: surface of P2 to P4 / surface of M1 to M3 x 100
S_{P4}/S_{3M}: surface of P4 / surface of M1 to M3 x 100
%DPC: DPC/LRDJ x100
MP: Reference levels according to the European biochronologic scale of Palaeogene mammals (BiochroM'97).

Dental terminology follows Froehlich (2002). Poorly preserved teeth are indicated in brackets. All specimens from Aumelas are held in the UM collections. They are cited AUM XXX in reference to UM-AUM XXX to save space in text, tables and annexes.

SYSTEMATICS

Suborder HIPPOMORPHA Wood, 1937
Superfamily EQUOIDEA Hay, 1902
Family PALAEOTHERIIDAE Bonaparte, 1850 (*s. l.*)
PACHYNOLOPHINAE Pavlow, 1888
Genus *Propalaeotherium* Gervais, 1849

Emended diagnosis of genus (modified from Savage *et al.*, 1965; Franzen & Haubold, 1986; Franzen, 2006). Small to large equoids with estimated skull length from 120 to over 250 millimeters; dental formula: 3.1.4.3/3.1.4.3; brachylophodont dentition; upper molars with more or less pronounced mesostyle; upper premolars non-molariform, lacking hypocone; mesostyle on P3-4/ and entoconid on P/3-4 appearing in youngest species;

lower cheek teeth without paraconid; lower molars with rounded crescentic lobes and twinned prominent metaconid; lingual cingula on upper molars, usually weak or absent; lower cheek teeth with more or less developed labial cingula, but with weak or absent lingual cingula; rather short postcanine diastema. *Propalaeotherium* differs from *Eurohippus* by a wider skull and narrower ascending ramus with regard to its height.

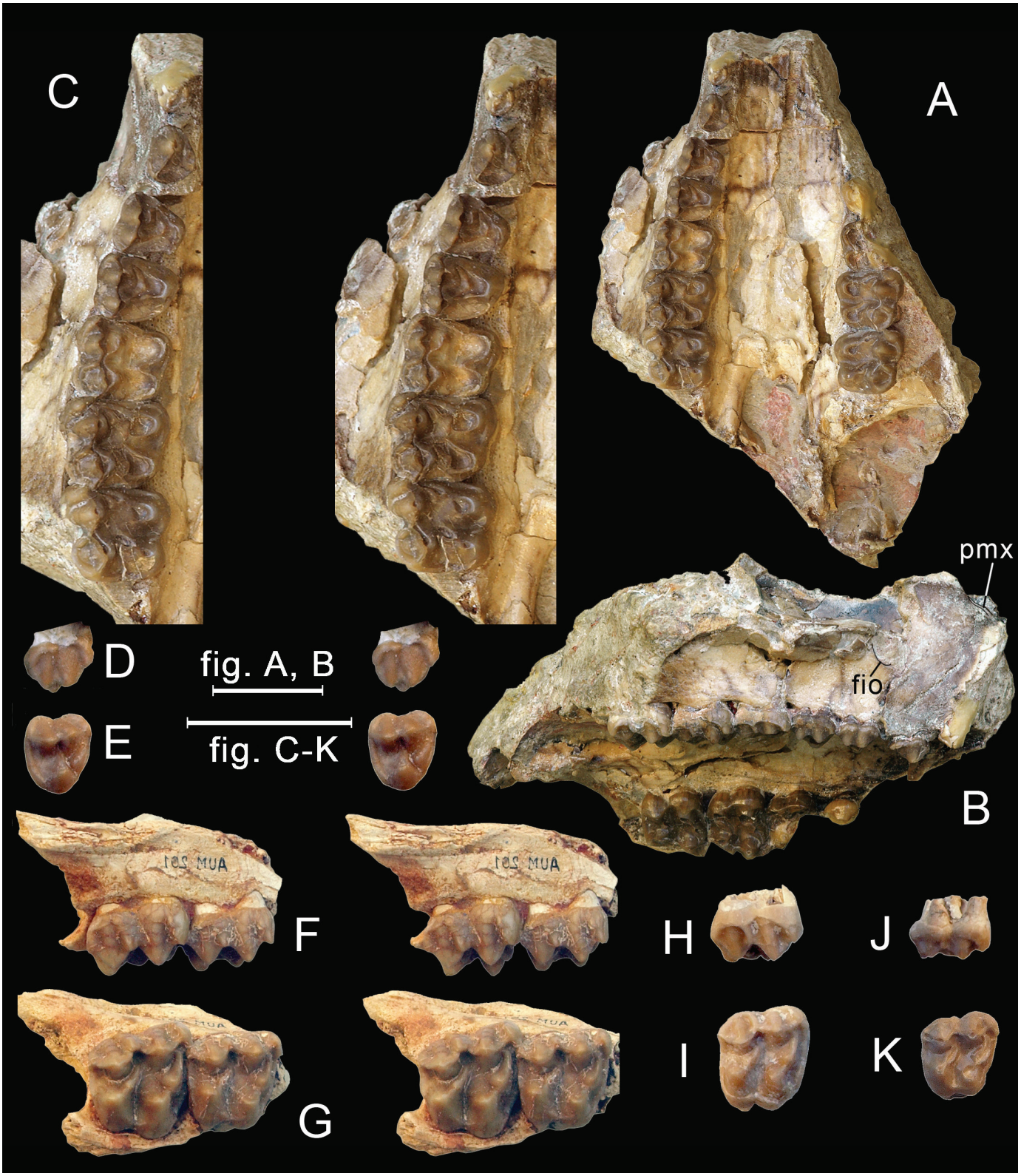

Figure 1. *Propalaeotherium sudrei* n. sp. **A-C**, AUM 181, holotype, palate bearing the right (P1/)-P2/-M3/ and left (P4/-M1/)-M2-3/; A, ventral view; B right lateral view; C, right cheek teeth (stereograph). **D-E**, AUM 207 (stereographs), right P3/; D, labial view; E, occlusal view. **F-G**, AUM 201 (stereographs), left maxillary fragment with M1-2/ (reversed); F, labial view; G, occlusal view. **H-I**, AUM 221, left M1/ (reversed); H, labial view; I, occlusal view. **J-K**, AUM 223, right DP4/; J, labial view; K, occlusal view. fio = opening of the infra-orbital foramen; pmx = tip of the premaxilla. Scale bars: 2 cm.

Type-species. *Propalaeotherium isselanum* (Cuvier, 1824)

Included species. *P. argentonicum* Gervais, 1849; *P. hassiacum* Haupt, 1925; *P. helveticum* Savage *et al.*, 1965; *P. voigti* Matthes, 1977.

Propalaeotherium sudrei n. sp.

(Figs. 1-4, 5e-g)

v *Propalaeotherium* sp. (cf. *parvulum*?) - Hartenberger, 1963.

v *Propalaeotherium* sp. - Remy, 1976.

v *Propalaeotherium* sp. - Sudre, 1980.

lsid:zoobank.org:act:A0A14476-C3FA-4B4D-89C1-7F66075A2D0B

Etymology. Dedicated to Jean Sudre who provided an essential contribution to the excavation of the Aumelas outcrop and found the type-specimen.

Holotype. AUM 181, a palate bearing right (P1/)-P2/-M3/ and left (P4/-M1/)-M2-3/. Montpellier University collections. Figure 1A-C.

Material. AUM 173, left M1/; AUM 174, left maxillary fragment with (P4/)-M1/; AUM 175, right maxillary fragment with P4/-M3/; AUM 201, left maxillary fragment with M1-2/; AUM 202, left M2/-(M3/); AUM 207, right P3/; AUM 221, left M1/; AUM 223, right DP4/; AUM 044, -045, left M/1-2; AUM 064, left (M/3); AUM 113, left M/3; AUM 163, left M/2-(M/3); AUM 165, right M/2-(M/3); AUM 171, left (P/2)-P/3-4; AUM 179, left mandible with P/4-M/3; AUM 180, left mandibular fragment with (M/3); AUM 182, left mandibular fragment with (D/3)-D/4-M/1 ((P/4)-M/1-2 in Hartenberger, 1963); AUM 183, left M/2-3 ; AUM 203, right M/3; AUM 205, right mandible with its angular area, ascending branch and M/3; AUM 206, right mandible with (alv. P/1-alv. P/2)-P/3-M/3; AUM 208, left mandible with (alv. P/2-alv. P/3)-P/4-M/1-(M/2)-M/3; AUM 212, left M/3; AUM 215, right M/3; AUM 218, right M/3; AUM 219, right M/2; AUM 220, right M/2; AUM 227, left M/3; AUM 228, right M/3; AUM 310, left mandibular fragment with P/4, M/2-(M/3).

Material from other locality. Saint Martin de Londres (SMF) UM-SMF 63, left P4/-M3/; UM-SMF 64, right DP4/.

Probable other material. AUM 331, right mandible with P/1-4.

Diagnosis. Small species of *Propalaeotherium,* not very brachyodont; trapezoidal upper molars, distally narrow, with a slightly bulging mesostyle, reaching occlusal surface as a fairly thin crest; very deeply notched centrocrista, somewhat elongated conules; M3/ without hypostyle; premolar series relatively short and of low surface, not molariform, without mesostyle; short diastema between P1/ and P2/; P4/ relatively wide and devoid of a hypocone; cingula usually narrow though rather high, with lingual one often missing; crescents of lower molars fairly rounded with a well-defined splitting of the metaconid; P/4 without entoconid.

Differential diagnosis. Comparison with other *Propalaeotherium* species: smaller dimensions than most of these; less bunodont and less brachyodont teeth than those of *P. hassiacum*; upper premolars devoid of mesostyle unlike *P. helveticum*. Similar in size to *P. voigti* but with less marked brachyodonty, centrocrista of upper molars more indented, internal cusps and paraconules less rounded, relative surface of premolars slightly larger, metaconid splitting of lower cheek teeth more pronounced, and less high and less marked cingula. Comparison with *Eurohippus parvulus*: larger, especially at the molar level; area of the premolars relatively smaller; brachyodonty less pronounced; mesostyle of upper molars less bulbous; relatively wider palate; relatively lower temporal lever arm of the mandible.

Description. The type specimen belonged to an old individual (Fig. 1A-C); on M1/ the areas of exposed dentin are largely confluent whereas on other teeth the reliefs are heavily flattened. The dentition is rather lophodont and heterodont with slightly molarised premolars. But that lophodonty is likely to be due in part to the high degree of wear.

A rather notable size difference is observed between M1/ and both other molars ($S_{M3/}$ / $S_{M1/}$ = 1.33). But conversely, there is almost no morphological gradient from M1/ to M3/ for most of the structures. These teeth are fairly narrow at the rear because of the obliquity of the ectoloph and outward shifting of the hypocone. The paracone of the molars is not as lingually tilted as in very brachyodont forms, suggesting that these teeth were not very low. The paracone is underlined by a strong labial crest. The metacone is slightly recessed with respect to the paracone but it presents a barely less developed crest. Despite the wear, the centrocrista is deeply notched between paracone and metacone. The labial cingulum is rather thick and fairly high but it decreases in height and becomes thinner on M2-3/ at the rear of the paracone; the mesostyle is narrow and occlusally sharp, oblique to the back in a cervical direction, barely inflated towards the collar and merged with the metacone cingulum; it shows no basal widening anteriorly. The parastyle and metastyle are increasingly more pronounced towards the rear of the series but even on M3/ they barely exceed the alignment of the ectoloph. The elongated paraconule, which is not completely isolated from the protocone, is slightly inflated at its postero-lingual end. The protoloph is directed towards the parastyle but it leans labially to reach the ectoloph between the paracone and parastyle. The metaloph, on which a metaconule is fairly well defined, seems orientated towards the premetacrista. There is no well-pronounced hypostyle on M3/. The lingual cingulum, very thin but continuous on M1/, is attenuated to the rear; on M3/ it is almost missing, interrupted on the protocone and hypocone. The heterodonty is marked by a relatively short premolar series: the PMI ($L_{P2/-P4/}$ / $L_{M1/-M3/}$) only reaches 70, and premolars represent 43% of the surface of the molars (Table 1, Supp-data 1).

P4/ is somewhat transversely elongated (L/W ratio = 0.84), with a broadly rounded lingual outline. It bears two well-sepa-

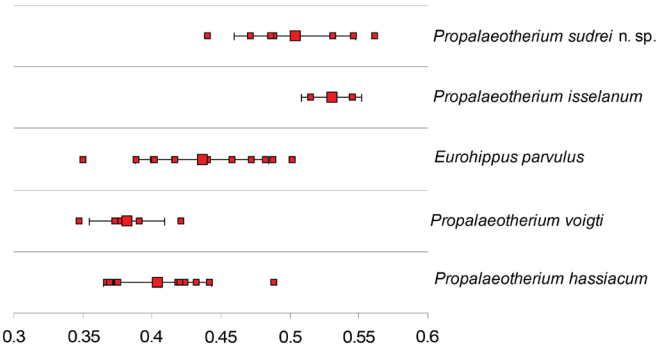

Figure 2. Graphical comparison of hypsodonty indices (I_H) in various propalaeotheres. Large square: mean; horizontal bars: +/- 1 SD (see also Supp-data 2).

rated labial cusps but no mesostyle. The parastyle and metastyle are low and poorly defined. They form a faint cervical bulge. There is a slight mesial displacement of the protocone which gives way to a rather wide, elongated posterior concavity with no trace of a hypocone. The protoloph, on which a paraconule cannot be distinguished, is straight and aligned with the parastyle. The metaconule is a little better developed and the metaloph is orientated towards the basis of the metacone. There is no lingual cingulum on the protocone.

P3/, slightly damaged and heavily worn at the posterior basin, has a similar structure to P4/ except that it is even less transverse and both labial cusps are closer together with a much shallower indentation of the ectoloph crista. The inner outline is narrower with a front edge that is slightly oblique and the protocone is not anteriorly displaced.

P2/ is triangular. Only one labial cusp is observed but the large surface of wear on its rear part makes it impossible to see any potential lingual bulging of the postparacrista, which could indicate an incipient metacone. The oblique antero-lingual edge of the tooth is overhung by a small stretched cusp, a mere thickening of the cingulum.

The right P1/, only preserved by a distal fragment, is separated from P2/ by a small diastema. It is a narrow and elongated tooth, consisting of a single prominent central cusp with a strong lingual cingulum.

A few specimens assigned to the same taxon provide some additional information on upper cheek teeth with a glimpse of the morphological and quantitative variations of the species. The coefficients of variation for dental measurements are moderate, generally lower than eight (Table 1). Some I_H indices have been evaluated based on slightly worn teeth (Supp-data 2, Fig. 2), which are overall relatively high for a propaleothere:

***Propalaeotherium sudrei* n. sp.**

	P2/		P3/		P4/	
	L	W	L	W	L	W
N	1	1	2	2	2	2
mean	7.1	5.9	8.1	9.0	8.5	10.7
variation range			8.0-8.1	8.3-9.7	8.4-8.5	10.1-11.2

	M1/				M2/				M3/			
	L	W	D	d	L	W	D	d	L	W	D	d
N	6	6	6	6	4	4	4	4	3	2	3	3
mean	10.4	12.3	13.3	12.4	11.9	14.0	14.9	13.9	12.0	13.7	15.0	14.0
variation range	9.4-11.5	11.1-12.9	11.6-14.3	11.1-13.3	11.1-12.9	13.7-14.6	14.0-15.8	13.1-14.8	11.5-12.5	13.7-13.7	14.0-15.5	13.6-14.4
standard deviation	0.842	0.660	1.029	0.763	0.772	0.403	0.957	0.714	0.503		0.823	0.400
coeff. of variation	8.1	5.4	7.8	6.1	6.5	2.9	6.4	5.1	4.2		5.5	2.9

	DP4/			
	L	W	D	d
AUM 223	9.5	10.3	11.7	10.1

	$L_{P2-M3/}$	$L_{P2-P4/}$	$L_{M1-M3/}$	PMI
AUM 181	53.5	22.0	31.5	69.8

***Propalaeotherium sudrei* n. sp.**

	P/2			P/3			P/4		
	L	W_1	W_2	L	W_1	W_2	L	W_1	W_2
N	1	2	2	3	3	3	6	6	6
mean	7.8	3.9	4.3	8.1	5.1	5.6	9.1	6.4	6.6
variation range		3.7-4.1	3.7-4.9	7.4-8.7	4.0-5.6	5.4-5.8	8.2-10.1	6.0-7.3	5.9-7.5
standard deviation				0.651	0.416	0.208	0.684	0.496	0.593
coeff. of variation				8.1	8.1	3.7	7.5	7.8	9.0

	M/1			M/2			M/3			
	L	W_1	W_2	L	W_1	W_2	L	W_1	W_2	W_3
N	5	5	5	10	10	10	13	16	16	13
mean	10.2	7.4	7.5	11.4	8.2	8.0	16.4	8.4	7.5	5.6
variation range	9.7-10.6	7.0-7.8	6.9-8.2	10.1-12.2	6.9-8.6	7.4-9.0	15.3-17.4	7.3-9.2	6.6-8.4	5.1-6.0
standard deviation	0.434	0.305	0.513	0.613	0.513	0.485	0.666	0.484	0.484	0.344
coeff. of variation	4.3	4.1	6.9	5.4	6.3	6.0	4.1	5.8	6.5	6.1

	DP/3			DP/4			M/1		
	L	W_1	W_2	L	W_1	W_2	L	W_1	W_2
AUM 182			5.4	9.0	6.2	6.3	10.5	7.5	7.1

Table 1. Dental measurements of cheek teeth of *Propalaeotherium sudrei* n. sp. of Aumelas. **L**, length of ectoloph (upper teeth) or maximal length (lower); **W**, maximum width; $\mathbf{W_1}$, trigonid width; $\mathbf{W_2}$ talonid width; $\mathbf{W_3}$ hypoconulid width (M/3); **D**, maximum diameter from parastyle to hypocone; **d**, diameter perpendicular to D.

the cheek teeth were most likely not very low in this species, as already suggested. On AUM 175, the teeth are more bunodont than the type specimen, with smaller conules and their ectoloph is markedly notched between the paracone and metacone. Conversely, on AUM 202, the mesostyles are slightly wider near their apice than on other specimens, and the parastyles are slightly more developed. The paraconule of both molars also appears somewhat better isolated from the protocone. The labial cingula are very reduced and the lingual ones are almost absent on AUM 201 and -202. They are thick and high on AUM 175, very wide on the distal side of its M3/ whose lingual cingulum is almost continuous, only interrupted facing the hypocone. The P4/ of AUM 175 is also more transverse than on the holotype. The same is true for the P3/ AUM 207, which also shows a stronger separation between the protocone and the paraconule. Nevertheless, these differences are not sufficient enough to distinguish several taxa within this material since they correspond to the morphological variability already often noticed in propaleotheres (e.g. Stehlin, 1904:402; Franzen & Haubold, 1986:6; Hooker, 1986:345; Franzen, 2006:99; Remy, 2015:81).

Finally, the DP4/ AUM 173, fully molarized, is distinguished from molars by its lesser height and by a deep separation between the paraconule and the protocone.

Twenty three mandible fragments or isolated lower cheek teeth can be assigned to the new taxon (Fig. 3). The molars have internal cuspids that are slightly taller than the external

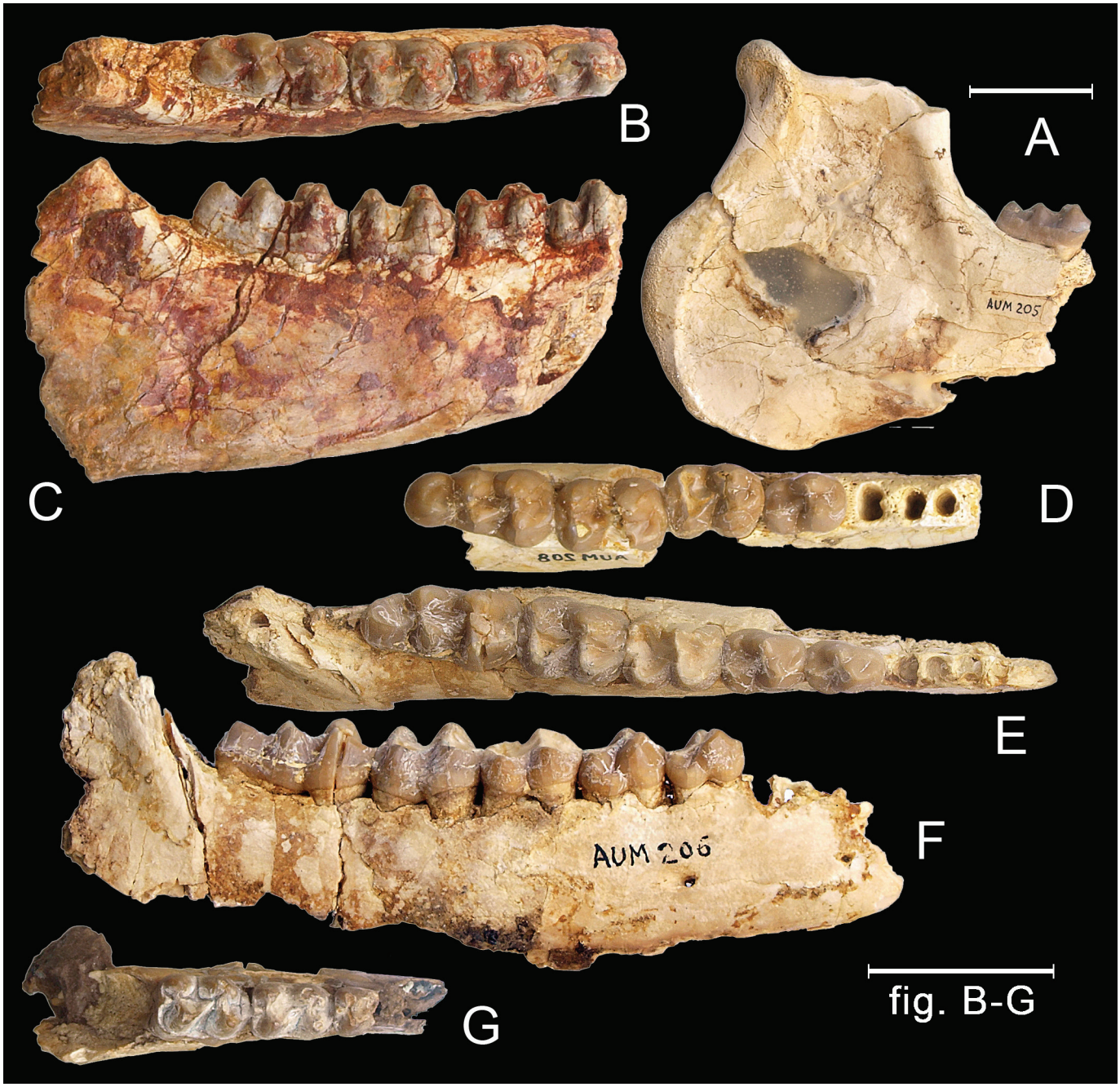

Figure 3. *Propalaeotherium sudrei* n. sp. **A**, AUM 205, right mandible with M/3, labial view. **B-C**, AUM 179, left mandible with P/4-M/3 (reversed); B, occlusal view; C, labial view. **D**, AUM 208, left mandible with (alv.P/2-P/3)-P/4-M/1-(M/2)-M/3 (reversed), occlusal view. **E-F**, AUM 206, right mandible with (alv.P/1-alv.P/2)-P/3-M/3; E, occlusal view; F, labial view. **G**, AUM 182, left mandibular fragment with (D/3)-D/4-M/1, (reversed), occlusal view. Scale bars: 2cm.

ones and they are somewhat bulbous. Their transverse lophids are marginally oblique and these are fairly U-shaped on unworn teeth. The crescents of the trigonid and talonid are more rounded than those of *Pachynolophus*. The former is relatively short and the curved, low paralophid bears no distinct paraconid. The metaconid is generally clearly split and the straight metalophid is inserted between both cuspids. There is a small median hypoconulid overhanging the distal cingulid. There is no cingulid on the lingual side and the labial one is rather variable, generally faint, not very high and interrupted where the cuspid bulges. The hypoconulid of M/3 is as long and nearly as wide as both other tooth lobes. Its rounded cristid reaches labially to the middle of the hypolophid and curves lingually to the base of the entoconid.

P/4 is somewhat inflated, with its trigonid being as wide and almost as long as the talonid. A faint paraconid appears. The talonid is low and there is no true hypolophid but a minute entoconid is present. The labial cingulid is poorly defined, limited to the opening of the medivallum. The P/3 is simpler: it tapers anteriorly on AUM 171, yet the crescent of the trigonid is fully developed with a metaconid that is well separated from the protoconid. The talonid is crossed by a low metalophid ending with a small hypoconid at the middle of the posterior side of the tooth. On the mandibular series AUM 331, unfortunately very worn and thus not certain to belong to the here described species, the hypoconid of P/3 remains in a more labial position. This specimen also shows the first two premolars. P/2 is elongated, tapering towards the front. It has a prominent protoconid displaced anteriorly. The metaconid is not as tall and shifted distally, while the relatively wide talonid has the same structure as on P/3. P/1 is a relatively long but very narrow tooth, with a prominent protoconid overhanging a short talonid.

DP/4 and the talonid of DP/3 are retained on AUM 182. These teeth are fully molariform: DP/4 is smaller, narrower, and slightly lower than M/1, with a metastylid well-separated from the metaconid and a marked hypoconulid. The talonid of DP/3 shows the same structure.

The palate, as observed on the holotype, is relatively wide. The anterior limit of the choanae, highlighted by a thick torus, is aligned with the mid M3/. The maxilla tuberosity is low and relatively short. The infraorbital foramen opens 10 mm above the alveolar plane. Its posterolateral edge is aligned with P3/. Despite the bad preservation of the fossil at the level of the nasal opening, it seems that it was notched at least up to P1/ and that the premaxilla ended in a very fine tip slightly anterior to the P1/. This configuration could allow the maxillary to participate to the bony edge of the nose notch.

According to AUM 205 (Fig. 3A), the angular process of the mandible is strongly developed ventrally and posteriorly. In relation to its height, the ramus is not very wide and so the lever arm of the temporal muscle is rather short compared to that of the masseter (MMT/MMM = 49.5; Supp-data 3B). This reveals the relative importance of the latter in the chewing process. The mandibular condyle, located 25 mm above the occlusal plane of M/3, is somewhat short (19 mm), moderately oblique relatively to the horizontal ramus and posteroventrally slanted.

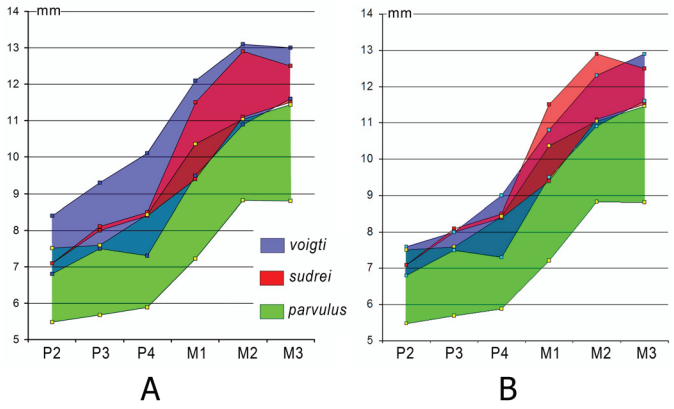

Figure 4. Compared variation ranges of upper cheek teeth ectoloph lengths in *Eurohippus parvulus*, *Propalaeotherium voigti* and *P. sudrei* n. sp. (cf. Supp-data 4, 7). **A**, for *P. voigti*: Geiseltal all loci merged; **B**, Geiseltal only mUK to oMK.

DISCUSSION

A comparison with the known species of propaleotheres leads to the conclusion that this material represents a new taxon.

Compared to the monospecific genus *Eurohippus* (*sensu* Franzen, 2006), the new taxon differs first by its larger size. The upper molar of the Argenton-sur-Creuse locality, type of the species *Eurohippus parvulus* (Laurillard, 1849), is now lost according to Savage *et al*. (1965: 66). However, at least six upper molars from Argenton have been referred to this taxon: the M1/ or M2/ MBO 2012.G.1512 (probably corresponding to figure 25 in Stehlin, 1904) and the others stored at the MNHN. These teeth are on average 10% smaller than those of Aumelas but they are too few specimens to render these differences actually significant.

However, more abundant specimens from several other deposits are attributed to *Eurohippus parvulus*, mainly from Messel (*E. p. messelensis* [Haupt, 1925]), from the Geiseltal and Egerkingen (*E. p. parvulus* [Laurillard, 1849]), or from Robiac (*E. parvulus* in Remy, 2015).

These materials confirm that the upper molars of *P. sudrei* are significantly larger than those of *E. parvulus* (Supp-data 4). Nevertheless, this difference is less marked on the premolars, provided that the meager sample of Aumelas premolars allows this assertion (Fig. 4). This would correspond to a difference in the proportions between the premolar and molar series

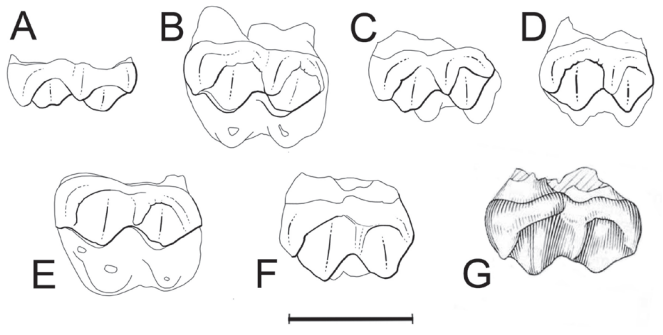

Figure 5. Shape of mesostyles of upper molars of *Propalaeotherium sudrei* n. sp. compared to that of *Eurohippus parvulus*. A-D, *Eurohippus parvulus*; **A**, GMH Leo7-8004, left M2/; **B**, MNHN AGT-426, right M3/ (reversed); **C**, NHMB Mt-217, left M1/ or M2/; **D**, UM-RbN 5681, left M2/. E-G, *Propalaeotherium sudrei* n. sp.; **E**, UM-AUM 181, left M3/; **F**, UM-AUM 221, left M1/; **G**, UM-SMF 63, left M3/ (from Crochet *et al*., 1988, fig. 18). Scale = 1 cm.

compared to *Eurohippus parvulus*; this trend is even more marked in the Robiac morphotype (Remy, 2015). Indeed the premolar area represents 46 to 55% of the surface of the molar sector in *Eurohippus parvulus*, 53 to 55% in the Robiac morphotype, but only 43 to 44% in *P. sudrei* from Aumelas (Supp-data 1). Similar differences in size can be observed on the lower teeth (Supp-data 5).

Moreover, the upper cheek teeth of Aumelas seem less brachyodont, as already noted, with a I_H averaging 0.50 instead of 0.44 in *Eurohippus* (Supp-data 2, Fig. 2). Some other morphological features also separate *Propalaeotherium sudrei* from *Eurohippus*. The molar mesostyle is thus generally less bulging at the cervical level and it reaches the centrocrista as a narrower ridge (Fig. 5). The groove between the protocone and the paraconule is generally shallower. Concerning the premolars, due to the morphological variability observed in *Eurohippus parvulus* (see Remy, 2015: 81), the new species falls within the range of this taxon.

Beside its dental discriminant peculiarities, the genus *Eurohippus* is characterized according to Franzen (2006) by the slender proportions of the skull as well as of the postcranial skeleton, all data which are missing on the material of Aumelas. Nevertheless, given the available material, a slenderness index of the skull is here proposed by the ratio of the width of the palate on the M1/-M3/ length (Supp-data 3A). The width of the palate is here by convention the greatest distance between the protocones of both M2/ or M3/, after estimation of any eventual crushing of the skull. It appears that this relative width of the palate is effectively narrower in *Eurohippus* than that of other propalaeotheres. From this point of view, *Propalaeotherium sudrei* fits well with these latter.

Moreover, as for the mandible, due to a lesser width of the ramus relative to its height, the ratio between the lever arms of the temporal muscle (MMT) and the masseter muscle (MMM) is lower in *P. sudrei* than in *Eurohippus parvulus*, being of 50 as opposed to 57-65, and close to that is observed in other *Propalaeotherium* species (Supp-data 3B). This may indicate that the chewing process of *P. sudrei* is closer to that of other *Propalaeotherium* species, and distinct to that of *Eurohippus*.

Consequently, with regard to these considerations, the material from Aumelas should not be attributed to the genus *Eurohippus* but instead bears characters seen in *Propalaeotherium*. Among the various species of this genus, the dimensions of the new species are at least 20% smaller than those of *P. hassiacum*, *P. isselanum* and *P.* cf. *isselanum* (Geiseltal) or *P. helveticum*. Even larger is *P. argentonicum*. In addition, *P. hassiacum* is more brachyodont, very bunodont and *P. helveticum* bears mesostyle on its premolars.

P. sudrei would be closer in size with the species of the Geiseltal *P. voigti* (Supp-data 6, Fig. 3), especially if one only takes into account the specimens from sites post-uUk, namely the last Unterkohle and Mittelkohle from where the type specimen originates.

Indeed the specimens of the uUK assigned to *P. voigti* are significantly larger than those of the subsequent levels of the Geiseltal (Supp-data 6), and have upper premolars which are more transversally elongated (it may suggest the existence of two different species within the *P. voigti* material). *P. voigti* is nevertheless clearly distinguishable from *P. sudrei* by its cusps which are more slanted and by an I_H averaging 0.38 only (ranging from 0.35 to 0.42). In this way, *P. voigti* is even more brachyodont than *Eurohippus*. Moreover, the centrocrista is more indented on the Aumelas molars, the internal cusps and paraconule are less rounded and the groove between the paraconule and the protocone is usually not as deep. The relative premolar area also seems slightly smaller (Supp-data 1). Concerning the mandibular dentition, the splitting of the metaconid seems more pronounced and the cingula generally not as high as that of *P. voigti.* Despite some other morphological similarities, these discrepancies are sufficient to conclude that the form of Aumelas must be excluded from *P. voigti*, and that it consequently represents a new species.

The question arises whether this form is present elsewhere. The St-Martin de Londres locality (Herault, France) has yielded four maxillary teeth P4/-M3/ and a DP4/, which have been formerly described as *Propalaeotherium* cf. *parvulum* by Crochet *et al.* (1988). These authors noticed that this material could not be completely related to this taxon since it was somewhat larger. Moreover, they noticed its similarities with *P. voigti*. Indeed the dimension of Saint Martin de Londres specimens fall within the range of those from Aumelas and they offer most of the diagnostic features of *P. sudrei*, such as faint mesostyles (Fig. 5), increased length of conules and shallowness of the groove between them. Slight discrepancies arise in the narrower lingual outline of P4/ and the somewhat more pronounced lingual cingulum, but such peculiarities are usual within propaleotheres and can be considered as individual variations. Therefore it appears that the new species is present in this locality, which has been considered older than the MP 13 level (Crochet *et al.*, 1988).

The fissure fillings of Lissieu have also yielded teeth formerly attributed to *Propalaeotherium parvulum* by Stehlin (1904: 440). These teeth are generally smaller than those of the Aumelas species. Furthermore, their enamel structure is quite different, with Hunter-Schreger bands that are more developed, not as wide and more regularly ordered (Remy, 1976: pl.4, fig.1-4, "*Propalaeotherium parvulum* Lissieu"; fig.6, "*Propalaeotherium* sp. Aumelas").

In the French localities of La Défense, Bouxwiller, Le Guépelle and in the Swiss localities of Mormont, there are no specimen with size close to *P. sudrei* (i.e., intermediate in size between *E. parvulus* and *P. isselanum*).

As for the teeth of Le Bretou, attributed to "*Propalaeotherium parvulum*" (Remy, 1988), they fall within the range of *Eurohippus* and are too poorly documented to justify attempts to compare them with *P. sudrei.*

Finally, concerning the remains found at Creechbarrow and attributed to *Propalaeotherium* aff. *parvulum* by Hooker (1986: 343), their very transversely elongated molars point to a special form which probably deserves a different taxonomic status, clearly separate from *P. sudrei*.

CONCLUSION

As in most European Eocene fossil localities, the Perissodactyla are an important component in the vertebrate fauna of Aumelas. Besides the lophiodontids, prevailing due to their large size, palaeotheriids appear to be rather diversified. *Propalaeotherium sudrei* is the best represented species of this family in the locality. Several other palaeotheriids have been identified; they will be the subject of a future publication.

Since it is a new species, *Propalaeotherium sudrei* does not provide any conclusive argument concerning the dating of the outcrop of Aumelas currently assigned, as already mentioned, to the MP 13 level (BiochroM'97). Only consideration of the

fauna as a whole would help clarify this question, on the basis of new data collected. A synthesis work is in progress with the aim of providing an updated faunal list and more accurately date the locality. Paleoenvironmental and paleogeographical implications could subsequently be inferred.

ACKNOWLEDGMENTS

We are very grateful to the anonymous referees who agreed to read the manuscript and whose constructive comments have helped to improve it. All the specimens from Aumelas housed in the collections of the University of Montpellier come from excavations episodically realized on the deposit since 1963 by the team of the paleontology laboratory of the University.

BIBLIOGRAPHY

BiochroM'97 (collective), 1997. Synthèses et Tableaux de corrélations. In: Aguilar, J.-P., Legendre, S., Michaux, J. (Eds.), Actes du Congrès BiochroM'97. Mémoires et Travaux de l'EPHE, Institut de Montpellier, 769-805.

Crochet, J.-Y., 1979. Diversité systématique des didelphidés (Marsupiala) européens tertiaires. Géobios 11 (3), 365-378.

Crochet, J.-Y., Godinot, M., Hartenberger, J.-L., Remy, J. A., Sigé, B., Sudre, J., 1988. Découverte dans le bassin de St-Martin-de-Londres (Hérault, Sud de la France) d'un gisement à vertébrés continentaux d'âge Eocène moyen. Courier Forschungsinstitut Senckenberg 107, 419-434.

Escarguel G. 1999. Les Rongeurs de l'Eocène inférieur et moyen d'Europe occidentale. Systématique, phylogénie, biochronologie et paléobiogéographie des niveaux-repères MP 7 à MP 14. Palaeovertebrata 28 (2-4), 89-351.

Franzen, J. L., 2006. *Eurohippus* n. g., a new genus of horses from the Middle to Late Eocene of Europe. Senckenbergiana Lethaea 86 (1), 97-102.

Franzen, J. L., Haubold, H., 1986. Revision der Equoidea aus den eozänen Braunkohlen des Geiseltales bei Halle (DDR). Palaeovertebrata 16 (1), 1-34.

Froehlich, D. J., 2002. Quo vadis eohippus? The systematics and taxonomy of the early Eocene equids (Perissodactyla). Zoological Journal of the Linnean Society 134, 141-256. doi: 10.1046/j.1096-3642.2002.00005.x

Godinot, M., 1988. Les primates adapidés de Bouxwiller (Eocène Moyen, Alsace) et leur apport à la compréhension de la faune de Messel et à l'évolution des Anchomomyini. Courier Forschungsinstitut Senckenberg 107, 383-407.

Hartenberger, J.-L., 1963. Un gisement de la zone de Mammifères d'Issel (Eocène moyen) dans les calcaires lacustres d'Aumelas (Hérault). Comptes-rendus sommaires de la Société Géologique de France 9, 321-322.

Hooker, J. J., 1986. Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England. Bulletin of The British Museum (Natural History) Geology 39 (4), 191-478.

Lalaï, D., 1982. Étude systématique du *Lophiodon* du gisement d'Aumelas, Unpublished Master thesis, Université de Montpellier, Montpellier, 1-79.

Laurillard, C. L., 1849. [Various articles on fossil vertebrates]. In: D'Orbigny, C. (Ed.), Dictionnaire universel d'histoire naturelle, Paris.

Maitre, E., 2014. Western European middle Eocene to early Oligocene Chiroptera: systematics, phylogeny and palaeoecology based on new material from the Quercy (France). Swiss Journal of Palaeontology 133, 141-242. doi: 10.1007/s13358-014-0069-3

Maitre, E., Sigé, B. Escarguel, G., 2006. Amphilemuridae (Lipotyphla, Mammalia) éocènes d'Europe occidentale : nouvelles données taxonomiques. Comptes Rendus Palevol 5, 813-820.

Maitre, E., Escarguel, G., Sigé, B., 2008. Amphilemuridae éocènes d'Europe occidentale - Nouvelles données, formes affines, systématique et phylogénie. Palaeontographica Abteilung A 283 (1-3), 35-82.

Remy, J. A., 1976. Étude comparative des structures dentaires chez les Palaeotheriidae et divers autres Périssodactyles fossiles. Unpublished PhD thesis, Université Strasbourg I.

Remy, J. A., 1988. Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertébrés de l'Eocène supérieur. VIII. Périssodactyles. Palaeontographica A 205, 155-172.

Remy, J. A., 2015. Les Périssodactyles (Mammalia) du gisement Bartonien supérieur de Robiac (Éocène moyen du Gard, Sud de la France). Palaeovertebrata 39 (1e), 1-98.

Savage, D. E., Russell, D. E., Louis, P., 1965. European Eocene Equidae (Perissodactyla). University of California Publications in Geological Sciences 56, 1-94.

Stehlin, H. G., 1904. Die Säugetiere des schweizerischen Eocaens. Critisher Catalog der Materialen. 2er Teil. Abhandlungen der schweizerischen paläontologischen Gesellschaft 31, 154-445.

Sudre, J., 1978. Les Artiodactyles de l'Eocène moyen et supérieur d'Europe occidentale (systématique et évolution). Mémoires et Travaux de l'E.P.H.E., Institut de Montpellier 7, 1-229.

Sudre, J., 1980. *Aumelasia gabineaudi* n.g. n.sp. nouveau Dichobunidae (Artiodactyla, Mammalia) du gisement d'Aumelas (Hérault) d'âge Lutétien terminal. Palaeovertebrata, Mémoire Jubilaire R. Lavocat, 197-211.

Sudre, J., 1988. Apport à la connaissance du *Dichobune robertiana* Gervais, 1848-1852 (Mammalia, Artiodactyla) du Lutétien: considération sur l'évolution des Dichobunidés. Courier Forschungsinstitut Senckenberg 107, 409-418.