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The hyaenodonts (Mammalia) from the French locality of Aumelas (Hérault), with possible new representatives from the late Ypresian

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ABSTRACT

We describe the carnivorous mammals from the Eocene French locality of Aumelas (Hérault, France). All the carnivores that have been recovered from the fossiliferous locality belong to the Hyaenodonta, a group that was very diverse during the Eocene of Europe. Three new species are described. *Matthodon peignei* n. sp. is intermediate in size between *M. menui* (Rich, 1971) and *M. tritens* Lange-Badré & Haubold, 1990. This is the first known occurrence of this genus in southwestern Europe. *Oxyaenoides aumelasiensis* n. sp. is distinct from other *Oxyaenoides* Matthes, 1967 species by its smaller size (15% smaller than *O. bicuspidens* Matthes, 1967). A third new species is proposed from Aumelas: *Leonhardtina meridianum* n. sp. The hyaenodonts from Aumelas appear to be morphologically similar to hyaenodonts from late Ypresian to early Lutetian of the northwestern Europe (European mammal reference level MP10 and MP11). These new species are incorporated into a phylogenetic analysis and are resolved within the clade Hyaenodontoidea. Our analysis interestingly recovered the Prionogalidae and *Thereutherium* as members of the Hyainailourinae. Based on the carnivorous faunal analysis, Aumelas is likely close to the Ypresian/Lutetian transition. However, because the hyaenodonts display unusual sizes that could result from provincialism, dates for Aumelas based on only these taxa should be treated cautiously, and will require confirmation based on a broader faunal analysis.

KEY WORDS
Europe,
Carnivores,
Paleogene,
Endemism,
Tethys,
new species.

RÉSUMÉ
Les hyénodontes (Mammalia) de la localité française d'Aumelas (Hérault), de possibles nouveaux repré-sentants de l'Yprésien tardif.
Nous décrivons les mammifères carnassiers de la localité française d'Aumelas (Hérault, France). Tous les fossiles découverts dans cette localité appartiennent au Hyaenodonta, un groupe de carnassiers très diversifié en Europe durant l'Éocène. Trois nouvelles espèces sont reconnues. *Matthodon peignei* n. sp. est morphologiquement similaire aux deux espèces précédemment référées à ce genre – *M. menui* (Rich, 1971) and *M. tritens* Lange-Badré & Haubold, 1990 – mais elle est intermédiaire en taille. Ceci est la première occurrence de ce genre particulier dans le sud-ouest de l'Europe. *Oxyaenoides aumelasiensis* n. sp. se distingue des autres espèces d'*Oxyaenoides* Matthes, 1967 par une plus petite taille (15 % par rapport à *O. bicuspidens* Matthes, 1967, la plus petite espèce du genre). La troisième espèce appartient au genre *Leonhardtina* Matthes, 1952: *L. meridianum* n. sp. Les hyénodontes d'Au-melas sont morphologiquement proches des hyénodontes connus à l'Yprésien tardif et au début du Lutétien (niveaux repères MP10 et MP11) dans le nord-ouest de l'Europe. Ces nouvelles espèces ont été incluses au sein d'une analyse phylogénétique des hyaenodontes ; il ressort qu'elles appartiennent au clade des Hyaenodontoidea. Cette analyse phylogénétique se distingue des précédentes en ce qu'elle conduit à envisager les Prionogalidae comme des membres des Hyainailourinae. Sur la base de la faune carnivore, un âge proche de la transition Yprésien/Lutétien pour les fossiles d'Aumelas apparaît possible, contrairement à ce qui avait été proposé jusqu'à présent. Cependant, étant donné que les hyénodontes d'Aumelas présentent des tailles inhabituelles, dues vraisemblablement à du provincialisme, la datation de la localité sur la seule base des hyénodontes demeure incertaine et demande confirmation.

MOTS CLÉS
Europe,
carnivores,
Paléogène,
endémisme,
Téthys,
espèces nouvelles.

INTRODUCTION

The fossil locality of Aumelas was discovered 20 km west of Montpellier (Hérault, France) by Mr. Gabinaud and was first reported by Hartenberger (1963). The first mammals described from this locality were *Propalaeotherium* sp. (cf. *parvulum*) and *Lophiodon isselensis*. These identifications were revised by Sudre (1980) and Rémy *et al.* (2016). Other mammals, notably the adapid primate *Anchomomys* aff. *gaillardi* (Hartenberger *et al.* 1969; later considered as *A.* cf. *gaillardi* by Godinot 1988) and the artiodactyl *Dichobune robertiana* (Sudre 1988; Sudre & Ginsburg 1993), suggested the locality was slightly older than Lissieu (France), or could be correlated to La Défense or Bouxwiller (France), and thus possibly be close to the MP13 reference-level (late Lutetian) (BiochroM'97 1997). The faunal list of Aumelas is being developed and is currently composed of crocodilians (Martin 2016), chelonians (Hervet 2004) and at least 19 mammalian taxa (marsupials, bats, rodents, lipothyphlan, primates, artiodactyls and perissodactyls; see Crochet 1979; Sudre 1980, 1988; Godinot 1988; Escarguel 1999; Maitre *et al.* 2006, 2008; Maitre 2014; Rémy *et al.* 2016, 2019).

This study is a contribution to a larger effort to review and revise the Aumelas fauna based on the collections at the University of Montpellier and new materials collected over the last decade. Sudre (1980) mentions that the first identification of the carnivorous mammals from Aumelas (Proviverrinae indet) was made by B. Lange-Badré. No carnivoraform has been discovered at Aumelas. We here describe three new hyaenodonts based on unpublished fossils from Aumelas. Comparisons with recently published material of Hyaenodonta (Solé *et al.* 2014a,

2015a) and the addition of this material to a recent phylogeny (Borths & Stevens 2019) allows us to assess the previously proposed age of Aumelas. These new materials also permit us to compare the composition of carnivorous faunas at different European Eocene localities

MATERIAL AND METHODS

FOSSIL SPECIMENS
The fossils described herein are all from the locality of Aumelas (Hérault, France). Fossil collecting at Aumelas began in 1960 and has continued under the auspices of a team from the University of Montpellier. The fossils are removed from the matrix using acid preparation, an effort lead by one of us (B.M.), with additional preparation at the Royal Belgian Institute of Natural Sciences. The fossils are deposited in the collection of the University of Montpellier under the acronym UM-AUMXXX.

DENTAL NOMENCLATURE AND MEASUREMENTS
The nomenclature of the teeth follows the dental terminology of Szalay (1969). The measurements (length × width in mm) follow Gingerich & Deutsch (1989).

TAXONOMY
Solé & Mennecart (2019) and Dubied *et al.* (2019) modified the Borths & Stevens (2017c) matrix. Their phylogenetic study refuted the monophyly of "Proviverrinae" *sensu* Solé (2013), resolving "proviverrines" as part of the hyaenodontine stem lineage. Because their results agree with those of Borths *et al.*

(2016), they proposed to consider the Proviverrinae as a clade that includes the last common ancestor of *Proviverra* and *Parvagula*. They thus applied the name Hyaenodontoidea to the clade that includes the last common ancestor of *Proviverra* and *Hyaenodon*. This resolves Hyaenodontidae and Proviverrinae within Hyaenodontoidea.

However, the combination here presented of the Solé & Mennecart (2019) matrix, with the one published by Borths & Stevens (2019), results in the exclusion of *Parvagula* from the Proviverrinae. Therefore, we here consider that Proviverrinae includes the following hyaenodont genera: *Proviverra*, *Morlodon*, *Allopterodon*, and *Lesmesodon*. This analysis also results in the exclusion of *Parvagula* from the Hyaenodontoidea.

Authorships of taxa are indicated in the Appendix 8.

PHYLOGENETIC ANALYSIS

We did not build a new character-taxon matrix but we combined the matrices published by Solé & Mennecart (2019), Dubied *et al.* (2019), and Borths & Stevens (2019). However, we have some disagreements with the coding of some European hyaenodonts in the character-taxon matrix created by Borths & Stevens (2017c, 2019). We thus decided to modify this matrix in order to reflect our observations (Appendix 1). It is worth noting that the Borths & Stevens (2019) matrix does not include the following taxa, which were however included in the Borths & Stevens (2017c) matrix: *Thereutherium thylacodes*, *Pakakali rukwaensis*, and the prionogalids *Namasector soriae* and *Prionogale breviceps*. We added these taxa into our matrix. We also added the new taxa described herein: *Matthodon peignei* n. sp., *Oxyaenoides aumelasiensis* n. sp., and *Leonhardtina meridianum* n. sp. Moreover, as in Solé & Mennecart (2019), three European hyaenodont OTUs (Operational Taxonomic Unit) *Matthodon menui*, *Prodissopsalis eocaenicus*, and the genus *Paracynohyaenodon* have been included in the matrix. The resulting character-taxon matrix includes 156 characters (Appendix 2) and 103 OTUs (Appendix 3). We also corrected the numerical ages used for the European hyaenodonts (Appendix 4).

The character-taxon matrix was assembled in Winclada (Nixon 2002). As in Borths & Stevens (2017c, 2019), nineteen multistate characters were treated as ordered, and all characters were treated as equally weighted. Phylogenetic analysis was performed using the Bayesian 'tip-dating' phylogenetic methods described by Beck & Lee (2014) and applied to hyaenodonts by Borths *et al.* (2016). This method simultaneously estimates branch length, rate, phylogeny and support for clades recovered in the analysis, a common approach for paleontological systematic analysis (e.g., Beck & Lee 2014; Dembo *et al.* 2015; Borths *et al.* 2016; Gorscak & O'Connor 2016; Lund *et al.* 2016; Turner *et al.* 2017). Bayesian 'tip-dating' analyses were performed in MrBayes (Ronquist *et al.* 2012). MrBayes formatted nexus files with all analytical parameters are included in the Appendix 5. Appendix 6 can be used to visualize the results (e.g., age estimates, rate of change) with FigTree.

BODY MASS

The body mass of each new species is estimated based on the methodology provided by Morlo (1999). The equation is

$\text{Log}^{10}(P) = [3.5104 \times \text{Log}^{10}((\Sigma M)/3)] - 2.3469$ where P is the estimated body mass (in grams) and ΣM the sum of the length of the three lower molars (in mm). All the values are available in Appendix 7.

ABBREVIATIONS

MNHN.F   Muséum national d'Histoire naturelle, Paris, Palaeontology collections;
RZ   collection from Rouzilhac, Aude, France;
UM   Université de Montpellier, France;
UM-AUM   Material from locality of Aumelas, Hérault, France deposited in the UM;
L   length;
n   number of specimens;
OR   observed range;
W   width.

SYSTEMATICS

Order HYAENODONTA Van Valen, 1967
Family HYAENODONTIDAE Leidy, 1869

Genus *Matthodon* Lange-Badré & Haubold, 1990

TYPE SPECIES. — *Matthodon tritens* Lange-Badré & Haubold, 1990.

OTHER SPECIES. — *Matthodon menui* (Rich, 1971); *Matthodon peignei* n. sp.

Matthodon peignei n. sp.
(Fig. 1)

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HOLOTYPE. — UM-AUM694, left mandible with p2-m3 and the alveoli for the canine and p1.

ETYMOLOGY. — Dedicated to the memory of Dr. S. Peigné (1972-2017), who described numerous carnivorous mammals from the Paleogene and Neogene of Eurasia and Africa.

REFERRED SPECIMENS. — UM-AUM268, left mandible with m2 and m3.

HORIZON AND AGE. — Lacustrine limestone of Montpellier, proposed as Lutetian in age in previous study but here considered possibly late Ypresian/early Lutetian in age

TYPE LOCALITY. — Aumelas, Hérault, France.

DIAGNOSIS. — *Matthodon peignei* n. sp. is intermediate both metrically and morphologically between *Matthodon menui* and *Matthodon tritens*: *M. peignei* n. sp. differs from *M. menui* by having longer premolars and molars and from *M. tritens* by having mesiodistally shorter premolars and molars. *Matthodon peignei* n. sp. differs from *M. tritens* by having less developed paraconids on p2, p3 and p4; the larger and more individualized metaconid on the molars; the longer talonid on the m1 and m2; and by shorter molars (4% for the m1, 8% for the m2 and m3), and longer p2 and p4 (respectively 9% and 5%). *Matthodon peignei* n. sp. differs from *M. menui* and *M. tritens* by the relative larger size of the p2, and narrower premolars.

MEASUREMENTS. — Table 1.

Locus		n	OR	Mean
c	L	1	14.4	–
	W	1	11.46	–
p1	L	1	6.06	–
	W	1	4.76	–
p2	L	1	9.32	–
	W	1	5.66	–
p3	L	1	9.67	–
	W	1	5.92	–
p4	L	1	11.81	–
	W	1	6.85	–
m1	L	1	11.59	–
	W	1	6.22	–
m2	L	2	12.56-12.89	12.75
	W	2	7.33-8.14	7.74
m3	L	2	12.31-13.00	12.66
	W	2	7.88-8.26	8.07
MD		1	26.27	–

Species	p2	p3	p4
Matthodon menui	0.65 (OR: 0.63-0.67, n=2)	0.66 (OR: 0.65-0.67, n=2)	0.6 (OR: 0.57-0.63, n=2)
Matthodon tritens	0.71 (OR: 0.69-0.73, n = 4)	0.67 (OR: 0.54-0.75, n = 5)	0.65 (OR: 0.59-0.68, n = 4)
Matthodon peignei n. sp.	0.61	0.61	0.58
	(n=1)	(n=1)	(n=1)

DESCRIPTION

UM-AUM 694 is almost a complete mandible that bears well-preserved teeth, except the i3, canine and p1, which are represented by their alveoli (Fig. 1A-C). The mandible is deep (26.3 mm below the m1). Two mental foramina are present: the first one opens below the posterior root of p2, while the second is present below the anterior root of p4. The masseteric fossa is very deep. A deep fossa for insertion of the temporal muscle is present along the anterior margin of the crest. The angular process is curved sharply dorsally and is relatively wide. The mandibular condyle is robust, and is mediolaterally wide.

The presence of an incisor (possibly the i3) is indicated by its tiny alveolus in front of the canine. The canine is buccolingually wide. The canine, premolars and molars are very close together. The p1 is single-rooted. The teeth display crenulated enamel. The p2 is simple with only the hypoconid present on the talonid. A small fold indicates the position of the paraconid. The p3 is mesiodistally longer and buccolingually wider than the p2. It differs by the presence of a paraconid, and by having three cuspids on the talonid: the larger corresponds to the hypoconid, while the other two are situated in the position of the entoconid. The p4 is more symmetrical in lateral view than the p3. The paraconid is much more developed. On the talonid, two cuspids are present: the hypoconid and the entoconid, which form a postfossid.

The three molars display similar morphologies. The m3 is slightly mesiodistally shorter than the m2, but this is due to the reduction of the talonid. The paraconid is prominent and located mesially. The anterior keel is well developed. The metaconid is lower than the paraconid and almost completely fused with the protoconid. The latter is distinctly the highest cusp. The talonid is mesiodistally short and narrow. The postfossid is narrow and surrounded by three bulbous cusps: entoconid, hypoconid and hypoconulid; the entoconid being the tallest one. The m3 differs from m1 and m2 in having a much more reduced talonid in which the talonid cusps can-

not be distinguished. The precingulid is short (limited to the paraconid) but is very wide, notably on m3.

DISCUSSION

The new fossils share with *Matthodon* species the peculiar distal positions of the mental foramina (the first is inferior to the distal margin of p1 and the second is inferior to p4), the presence of a single-rooted p1, a closely packed toothrow, and the poorly developed metaconid on molars. All these features distinguish *Matthodon* from the European Ypresian and Lutetian hyaenodonts. UM-AUM694 is among the best preserved mandibles ever found for *Matthodon*.

The genus *Matthodon* is represented by two species: *Matthodon menui* from Chavot, Monthelon, Mancy, and Grauves (Ypresian, MP10; France) and *Matthodon tritens* from Geiseltal-Untere Unterkohle (Lutetian, MP11; Germany).

The fossils from Aumelas differ from those of the Lutetian species, *Matthodon tritens*, by having less developed paraconids on p2, p3 and p4; the larger and more individualized metaconid on the molars; the longer talonid on the m1 and m2; and by shorter molars (4% for the m1, 8% for the m2 and m3), and longer p2 and p4 (respectively 9% and 5%). These differences are reminiscent of the Ypresian species *Matthodon menui*.

The fossils from Aumelas , are distinct from those referred to *Matthodon menui* by having longer premolars and molars: the molars are 6% longer, the p2 9% longer, and the p3 and p4 4% longer. The mesio-distal diameter of the alveolus of the p1 is also distinctly longer than those measured for *M. menui*. As indicated above, the teeth from Aumelas are morphologically more similar to those of *M. menui* than to those of *M. tritens*.

The mean width/length ratio of the p2, p3 and p4 differentiates *Matthodon peignei* n. sp. from *M. menui* and *M. tritens* by having narrower premolars (Table 2).

The fossils from Aumelas appear intermediate both metrically and morphologically between Ypresian *M. menui* and Lutetian *M. tritens*. It differs from the two previously described taxa by the relatively large size of the p2. This feature is highly characteristic because the relative size of the p2, which decreases from *M. menui* to *M. tritens*, can be considered as an indication of the reduction of the anterior dentition (p1 and p2). The larger size of the p2 in UM/AUM 694 thus can be regarded as a primitive feature. The same observation can be made for the narrowness of the premolars.
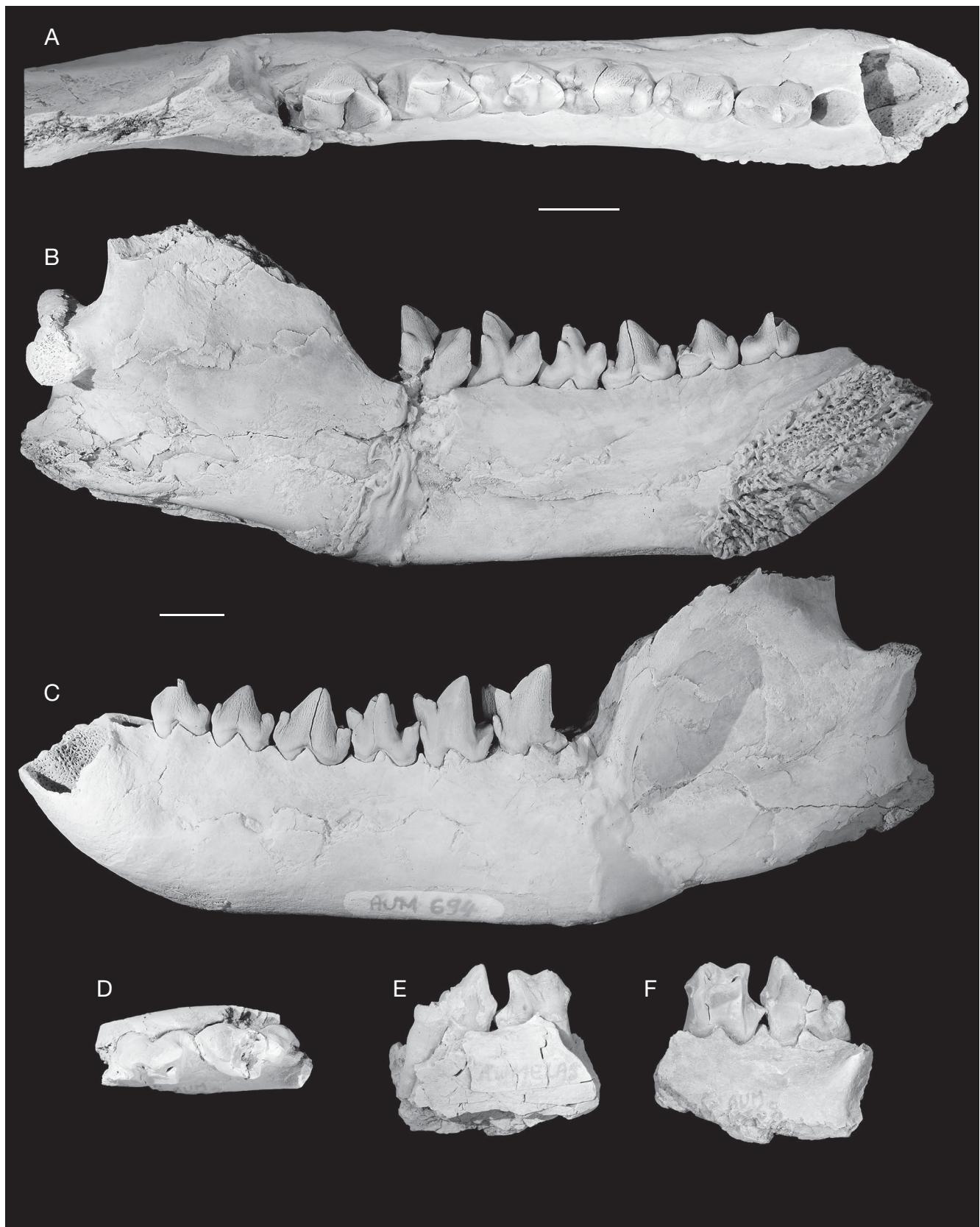
Fɪɢ. 1. — *Matthodon peignei* n. sp. from Aumelas (MP10-MP11?): **A-C**, UM-AUM694 (Holotype), left mandible bearing the p2-m3 and the alveoli of the canine and p1; **A**, occlusal view; **B**, lingual view; **C**, labial view; **D-F**, UM-AUM268, left mandible bearing the m2 and m3; **D**, occlusal view; **E**, lingual view; **F**, labial view. Scale bars: 1 cm.

TABLE 3. — Measurements (in mm) of *Oxyaenoides aumelasiensis* n. sp. from Aumelas (MP10-MP11?). *, based on roots and/or alveoli; Body mass (*c.* 4.24 kg) estimated after Morlo (1999).

Locus		n	OR	Mean
P3	L	2	9.88-11.10	10.49
	W	2	6.39-6.78	6.59
P4	L	2	11.28-11.55	11.42
	W	2	7.63-8.75	8.19
M1	L	2	9.39-9.52	9.46
	W	1	10.54	–
M2	L	1	8.32	–
	W	1	10.11	–
p2	L	1	5.88	–
	W	1	2.31	–
m1	L	1	8.71*	–
	W	1	4.65*	–
m2	L	1	7.74*	–
	W	1	5.16*	–
m3	L	1	9.24	–
	W	1	5.37	–
MD		1	16.68	–

Based on these comparisons the Aumelas specimen represents a new species of *Matthodon*, the first occurrence of the genus in the southwestern part of Europe.

Genus *Oxyaenoides* Matthes, 1967

TYPE SPECIES. — *Oxyaenoides bicuspidens* Matthes, 1967.

OTHER SPECIES. — *Oxyaenoides schlosseri* (Rütimeyer, 1891); *Oxyaenoides lindgreni* (Rich, 1971); *Oxyaenoides aumelasiensis* n. sp.

Oxyaenoides aumelasiensis n. sp.
(Fig. 2)

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HOLOTYPE. — UM-AUM693, left mandible bearing m3, the anterior root and talonid of the m1, the posterior alveolus of the p4, and the alveoli of m2.

ETYMOLOGY. — Latin, from Aumelas (type locality).

REFERRED SPECIMENS. — UM-AUM686, right M2; UM-AUM692, combination of a left maxillary fragment bearing the P2-M1, a right maxillary fragment bearing the P3-P4, the protocone of the M1 and the alveoli of the P2; UM-AUM695, labial part of a M1.

HORIZON AND AGE. — Lacustrine limestone of Montpellier, proposed as Lutetian in age in previous study but here considered possibly late Ypresian/early Lutetian in age

TYPE LOCALITY. — Aumelas, Hérault, France.

DIAGNOSIS. — The species is 15% smaller than *O. bicuspidens* and 25% smaller than *O. bicuspidens* and *O. schlosseri*. It differs from *O. lindgreni* and *O. bicuspidens* by a more buccally aligned metastyle on molars. It differs from *O. bicuspidens* and *O. schlosseri* by a less retroflexed protoconid.

DESCRIPTION

The P2 has a very small lingual fold that corresponds to an incipient parastyle. The metastyle is short and low (Fig. 2D, E). There is a small diastema between the P2 and P3 (Fig. 2F, G). The P3 and P4 are mesiodistally elongated. The P3 is characterized by the presence of a distinct parastyle and a strong metastyle. There is a large lingual bulge but no protocone. The P4 also displays a very large parastyle and metastyle; the latter is very tall. The protocone projects lingually and is mesiodistally narrow (Fig. 2D-G).

The two known molars have a very similar morphology (Fig. 2D, E, H, I). On M1, the parastyle is present and bulbous but is mesiodistally short and narrow. The metastyle is mesiodistally elongated. The paracone and metacone are partially fused; only the apexes are fully separated. The protocone is low. The protofossa is very mesiodistally short and narrow. The paraconule is present. The metaconule is absent. The M1 is morphologically identical to the M2 except that the parastyle is wider and the metastyle is less distally located.

The mandible is narrow. The masseteric fossa is deep. As in *Matthodon*, a deep fossa for insertion of the temporal muscle is present along the anterior margin of the coronoid crest. The latter is distally inclined and the angle between the coronoid crest and the body of the dentary is close to 120°.

UM/AUM693 is a fragment of a left mandible that bears the talonid of m1 and a complete m3 (Fig. 2A-C). The talonid of the m1 bears three distinct cusps (entoconid, hypoconid, and hypoconulid). The entoconid is lower than the hypoconulid, which is distally located, and lower than the hypoconid. Contrary to the m1, the m3 is complete. The paraconid is tall, long and well mesially located. There is no metaconid. The m3 is thus characterized by a cutting trigonid. The talonid is very mesiodistally short, low, and narrow with only one cusp (hypoconulid?) present. The precingulid is developed.

DISCUSSION

The fossils from Aumelas are characterized by a very cutting morphology (e.g., long metastyle on P4 and molars, absence of metaconid, long paracristid on m3). Only one hyaenodont genus known from the Ypresian and Lutetian of Europe has molars that are characterized by the absence of a metaconid, a hypercarnivorous feature: *Oxyaenoides* (MP10-?MP13) (Matthes 1967; Lange-Badré & Haubold 1990; Solé *et al.* 2014a). The teeth found at Aumelas share with *Oxyaenoides* mesiodistally short and narrow talonids bearing crestiform entoconids on molars. This genus is known both in northwestern (Matthes 1967; Lange-Badré & Haubold 1990; Solé *et al.* 2014a, 2015a) and southwestern Europe (Crochet *et al.* 1976).

Three species of *Oxyaenoides* are presently known: *Oxyaenoides lindgreni* from MP10 (Rich 1971; Solé *et al.* 2014a), *Oxyaenoides bicuspidens* from MP11 (Matthes
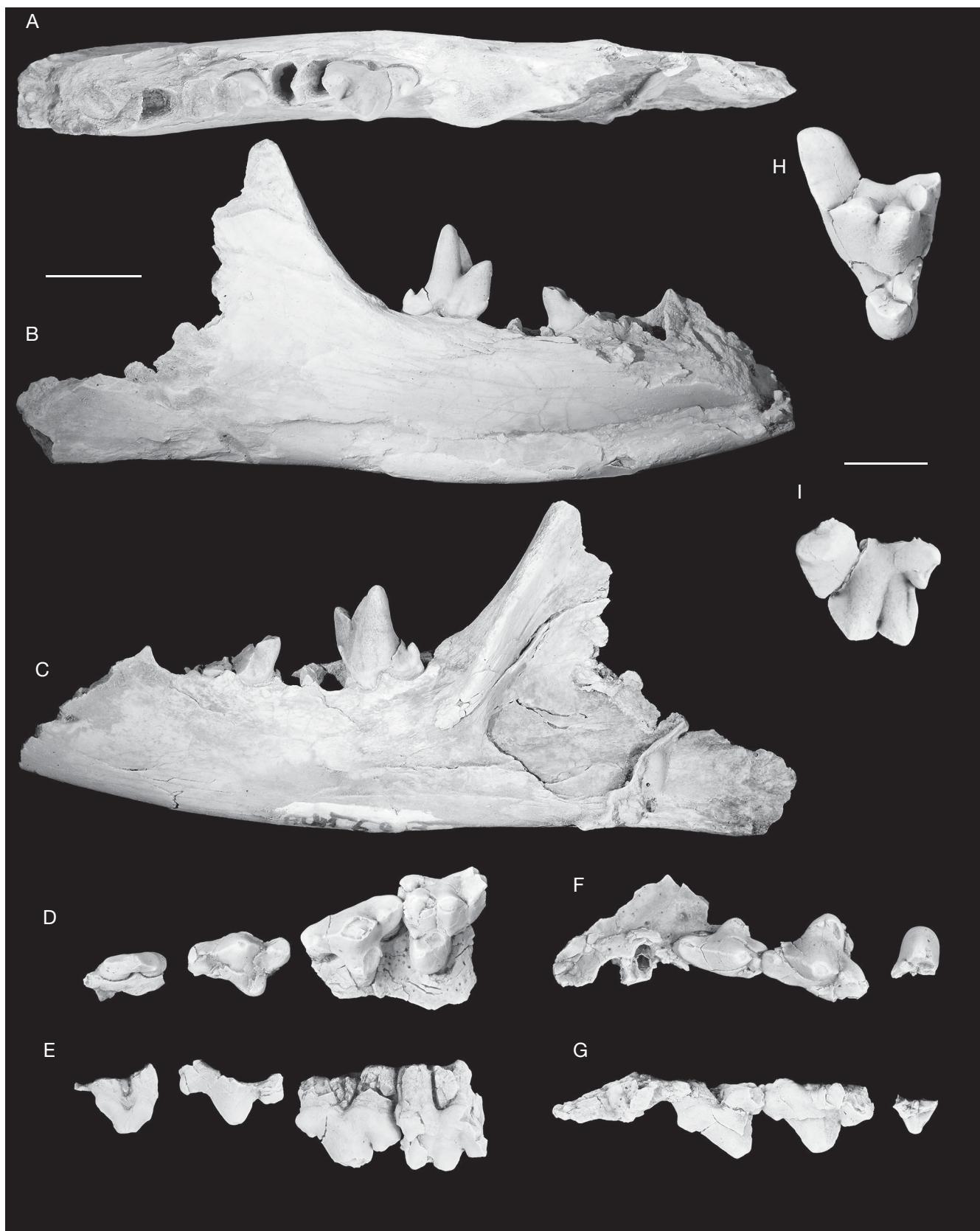
FIG. 2. — *Oxyaenoides aumelasiensis* n. sp. from Aumelas (MP10-MP11?): **A-C**, UM-AUM693 (Holotype), left mandible bearing m3, the anterior root and talonid of the m1, and the posterior alveolus of the p4, and the alveoli of m2; **A**, occlusal view; **B**, lingual view; **C**, labial view; **D-G**, UM-AUM692, combination of a left maxillary fragment bearing the P2-M1, a right maxillary fragment bearing the P3-P4, the protocone of the M1 and the alveoli of the P2; **D**, occlusal view of left maxillary; **E**, labial view of the left maxillary; **F**, occlusal view of the right maxillary; **G**, labial view of the right maxillary (reversed view); **H-I**, UM-AUM686, right M2; **H**, occlusal view; **I**, labial view. Scale bars: A-G, 1 cm; H, I, 50 mm.

Locus		*Leonhardtina meridianum* n. sp.			
		from Aumelas		from Rouzilhac	
		n	OR	n	OR
M2	L	1	4.96	0	–
	W	1	6.07	0	–
M3	L	1	2.91	0	–
	W	1	5.49	0	–
p2	L	0	–	1	6
	W	0	–	1	2.7
p3	L	1	6.5	1	7
	W	1	3.19	1	3.2
p4	L	1	5.39	1	5.4
	W	1	2.51	1	2.7
m1	L	1	4.95	0	–
	W	1	2.94	0	–
m2	L	1	5.49	0	–
	W	1	3.21	0	–
m3	L	1	5.78	1	5.9
	W	1	3.67	1	4
MD		1	10.48	1	10.68

1967; Crochet *et al.* 1976; Lange-Badré & Haubold 1990) and *Oxyaenoides schlosseri* from ?MP13 (Rütimeyer 1891; Lange-Badré 1972; Solé *et al.* 2015a). The syntypes of *O. schlosseri* are from Egerkingen γ (Lange-Badré 1972), but the MP reference-level of this site (possibly MP13) is uncertain (BiochroM'97 1997), as is Aigues-Vives 2 where a mandible of *O. schlosseri* was discovered (Solé *et al.* 2015a).

The most striking feature of the fossils from Aumelas is their small size compared to other *Oxyaenoides* material. The teeth are 15% smaller than those of *O. lindgreni* and 25% smaller than those of *O. bicuspidens* and *O. schlosseri*. The size of the new taxon is actually almost equivalent to that of *Preregidens langebadrae* (Saint-Papoul; *c.* MP8+9).

Oxyaenoides aumelasiensis n. sp. differs from those of *O. lindgreni* and *O. bicuspidens* by a more buccally aligned metastyle on upper molars. It also differs from *O. bicuspidens* and *O. schlosseri* by a mesially oriented protoconid – this feature accommodates an elongate preprotocristid, a structure found on cutting molars. *Oxyaenoides aumelasiensis* n. sp. appears more primitive than northwestern species by having a buccally aligned metastyle on upper molars and the less retroflexed protoconid on molars.

To conclude, the fossils of *Oxyaenoides aumelasiensis* n. sp. share with the other *Oxyaenoides* species several features including: a reduced metaconid and reduced talonid morphology. However, based on the small size and distinctive features, we distinguish *O. aumelasiensis* n. sp. from previously described species of Oxyaenoides.

The fossils from Aumelas are important because they are the first to provide so much information on the morphology of the upper premolars of the genus *Oxyaenoides*. The fossils from Aumelas represent the smallest hypercarnivorous hyaenodont ever discovered in the Ypresian and Lutetian.

Genus *Leonhardtina* Matthes, 1952

TYPE SPECIES. — *Leonhardtina gracilis* Matthes, 1952.

OTHER SPECIES. — *Leonhardtina godinoti* Solé, Falconnet & Laurent, 2014; *Leonhardtina meridianum* n. sp.

Leonhardtina meridianum n. sp.
(Fig. 3)

urn:lsid:zoobank.org:act:DA2667CF-BFAD-4CFD-AFE0-E9B1416140D2

HOLOTYPE. — UM-AUM54, right mandible bearing p3 to m3.

ETYMOLOGY. — *Meridianum* (Latin) means from the Midi, the south. In reference to the fact that the species is recorded only in the southern part of France.

REFERRED SPECIMENS FROM AUMELAS. — UM-AUM530, right maxillary fragment bearing M2 and M3.

OTHER REFERRED SPECIMENS. — MNHN.F.RZ142, right mandible bearing p2-p4 and m3.

HORIZON AND AGE. — Lacustrine limestone of Montpellier, proposed as Lutetian in age in previous study but here considered possibly late Ypresian/early Lutetian in age

TYPE LOCALITY. — Aumelas, Hérault, France.

OTHER LOCALITY. — Rouzilhac, Aude, France (Ypresian-Lutetian?; MP10b, Godinot *et al.* 2018)

DIAGNOSIS. — The new species is smaller than *Leonhardtina godinoti* (5% based on the length of the molars) and *Leonhardtina gracilis* (20%). It also differs from these species by a narrower postfossid on molars, and by relatively larger p3 relative to p4.

MEASUREMENTS. — Table 4.

DESCRIPTION

The upper teeth are represented by the M2 and M3 (Fig. 3A, B). The M2 is characterized by the separation of the paracone and metacone. These cusps appear to be of similar height. The parastyle is well-developed. The metastyle is long and mainly buccally aligned. The protocone is extended buccolingually and mesiodistally short. The protofossa is worn. The M3 is buccolingually elongated. The parastyle is long. Only the paracone is visible; the metacone-metaconule area is broken. The protocone is almost as tall as the paracone. A paraconule is discernable.

The mandible is deep (Fig. 3C, D). The coronoid crest is slightly distally inclined; the angle between the coronoid crest and the body of the dentary is close to 100°. As in the two other hyaenodonts from Aumelas, a deep fossa for the insertion of the temporal muscle is present along the anterior margin of the coronoid crest.

The p3 is elongated mesiodistally and is longer than the p4 (Table 4). The tooth is too damaged to describe its morphology (Fig. 3F-H). The p4 probably had a paraconid, but the anterior part of the tooth is too damaged to be sure. The protoconid is robust. The talonid is short in
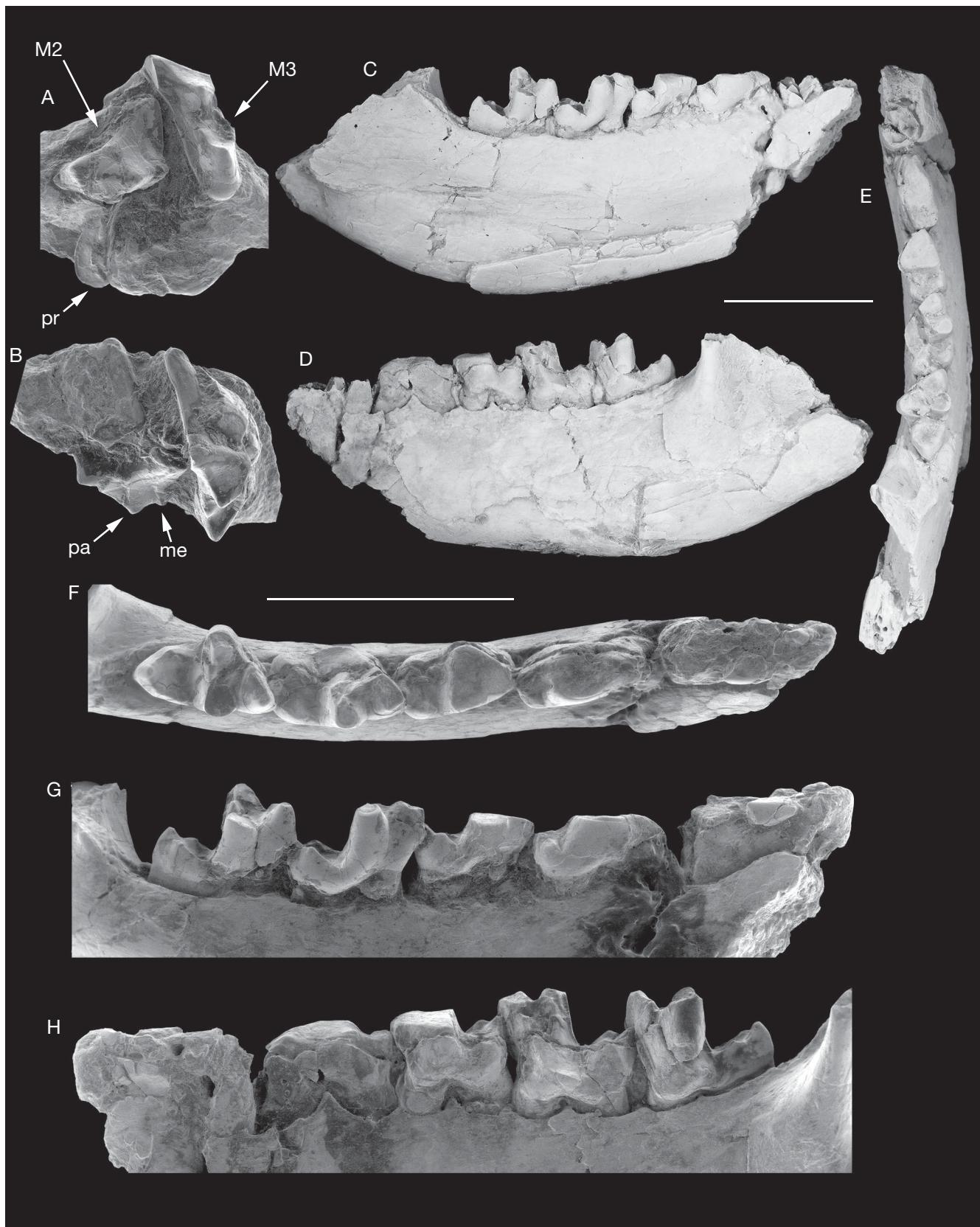
FIG. 3. — *Leonhardtina meridianum* n. sp. from Aumelas (MP10-MP11?): **A**, **B**, UM-AUM530, right maxillary fragment bearing M2 and M3; **A**, occlusal view; **B**, labial view; **C**-**H**, UM-AUM54 (Holotype), right mandible bearing p3 to m3; **C**, lingual view; **D**, labial view; **E**, occlusal view; **F**, occlusal close-up; **G**, lingual close-up; **H**, labial close-up. Abbreviations: **me**, metacone; **pa**, paracone; **pr**, protocone. Scale bars: 1 cm.

length and bears two cusps: a hypoconid and a lingually located entoconid. The molars are similar in morphology except the m3 has a narrower and more mesiodistally elongated talonid than m1 and m2 (Fig. 3F-H). The three teeth have a sharply pointed and mesiodistally compressed trigonid. The paraconid is lingually located relative to the protoconid. The metaconid is buccolingually aligned with the protoconid. The apexes of the metaconid and paraconid are worn preventing comparison of cusp height; the paraconid was however probably shorter in height than the metaconid. The talonid is almost as wide as the trigonid. The postfossid is narrow. The three talonid cusps are well individualized and bulbous. The talonid is labially oriented relative to the horizontal ramus as in primitive hyaenodonts (e.g., *Prototomus*, *Eoproviverra*). The hypoconulid is slightly taller than the two other talonid cusps. The hypoconulid and entoconid are close together. On the molars, the three talonid cusps are well-defined. The precingulid seems to have been present as well as an incipient postcingulid, but this is uncertain due to taphonomic processes. No ectocingulid is present.

DISCUSSION

The fossils of *Leonhardtina meridianum* n. sp. described differ from those of *Matthodon* and *Oxyaenoides* by their smaller size; the p3 longer than the p4; the wide talonid on the molars; and the sharply pointed and mesiodistally compressed trigonid of the molars.

According to our phylogenetic analysis (see below), *Leonhardtina* is closely related to *Preregidens langebadrae*. This latter species is only represented by one mandible discovered at Saint-Papoul (MP8+9; France) (Solé *et al.* 2015a). *Preregidens* shares with *Leonhardtina* the presence of mesiodistally short trigonid and buccolingually narrow postfossid on molars. However, *Preregidens* differs from *L. gracilis* and *L. meridianum* n. sp. by having buccolingually narrower talonid on molars, the absence of postcingulid on molars, shorter talonid on m3, and possibly the p3 shorter than the p4 (the p3 is only represented by its alveoli on the sole known fossil of *Preregidens*). *Preregidens* also differs from *L. gracilis* by having a higher and sharper p4.

The p3 longer than the p4, the wide talonid on the molars, and the sharply pointed and mesiodistally compressed trigonid of the molars are features that characterize the small hyaenodonts *Leonhardtina*, *Proviverra*, *Lesmesodon*, and *Allopterodon*, which form a clade in Solé *et al.* (2014a, 2015a). This clade is not recovered in the recent analyses (e.g., Borths & Stevens 2017c, 2019) nor in the phylogenetic analysis we performed (Fig. 4).

Leonhardtina meridianum n. sp. differs from *Proviverra*, *Lesmesodon* and *Allopterodon* by having weakly developed labial cingulids on the p4 and the molars; the latter are indeed well-developed in the three European hyaenodontoid genera, notably *Proviverra* (Lange-Badré 1981; Morlo & Habersetzer 1999). *Leonhardtina* further differs from these genera by having more oblique cristid obliqua, and narrower talonids and postfossids on the molars.

Some species of the genera *Cynohyaenodon*, *Paracynohyaenodon*, and *Quercytherium* are also close in size to *Leonhardtina*. However, these genera clearly differ from *Leonhardtina* by the p3 shorter than the p4 and a mesiodistally elongated trigonid on molars. These features also distinguish *Leonhardtina* from *Boritia*, a monospecific genus phylogenetically close to *Cynohyaenodon*, *Paracynohyaenodon*, and *Quercytherium*.

The weakly developed labial cingulids on the molars are also found in late Ypresian and early Lutetian genus *Leonhardtina*. This genus is represented by two species: *L. godinoti* from Grauves (Ypresian, MP10; Solé *et al.* 2014a) and *L. gracilis* from Geiseltal-Untere Mittelkohle and Geiseltal-Obere Mittelkohle (Lutetian, MP12-13; Matthes 1952; Lange-Badré & Haubold 1990). The fossils from Aumelas are smaller than other *Leonhardtina* species: 5% smaller than *L. godinoti* and 20% smaller than *L. gracilis*. The newly described fossils are 15-20% larger than those of *Proviverra typica*, which is found with *L. gracilis* in Geiseltal (Lange-Badré & Haubold 1990).

The new fossils also differ from the two species of *Leonhardtina* by having a relatively larger p3. The ratio of p3 length to p4 length equals 1.21 for *L. meridianum* n. sp. The ratio equals 1.04 in *L. godinoti* and 1.08 in *L. gracilis*. However, the ratio in *L. meridianum* n. sp. may be overestimated because the p3 and p4 are crushed, which probably results in lengthening the p3 measurement.

Godinot *et al.* (2018) described a mandible discovered in the locality of Rouzilhac (Aude, France; MP10b) that they referred to *Leonhardtina* cf. *gracilis*. The teeth preserved on the mandible are very close in size to those preserved on UM-AUM54 (Table 4). Moreover, the p4 and m3 are morphologically identical (e.g., talonid mesiodistally compressed on m3). Because of these similarities, we propose that MNHN.F.RZ142 and UM-AUM54 belong to the same taxon.

The p3 and p4 are better preserved on the fossil from Rouzilhac: the ratio p3 length/p4 length equals 1.3 in this specimen. This is consistent with *L. meridianum* n. sp. having a relatively large p3 compared to *L. godinoti* and in *L. gracilis*.

L. meridianum n. sp. differs from the other *Leonhardtina* species by having narrower talonids and postfossids and a more oblique cristid obliqua on the molars. The morphology of the talonids of the molars on UM-AUM54 are similar to the earliest European hyaenodonts such as *Eoproviverra* (Rians; Ypresian, *c.* MP7) and *Parvagula* (Palette, Fournes, Fordones; Ypresian, *c.* MP7) rather than *Leonhardtina*, *Allopterodon* or *Proviverra*.

The upper teeth (M2 and M3) are poorly preserved and not very diagnostic. However, they are morphologically similar to those of *Leonhardtina gracilis* in having a separated paracone and metacone; a buccally aligned metastyle; and a lingually elongated protocone.

To conclude, the *Leonhardtina* species found at Aumelas is smaller than the two *Leonhardtina* species known in northwestern Europe, and has the potentially primitive feature of a narrower talonid and postfossid on molars. However, *L. meridianum* n. sp. has the potentially derived feature of a relatively long p3.
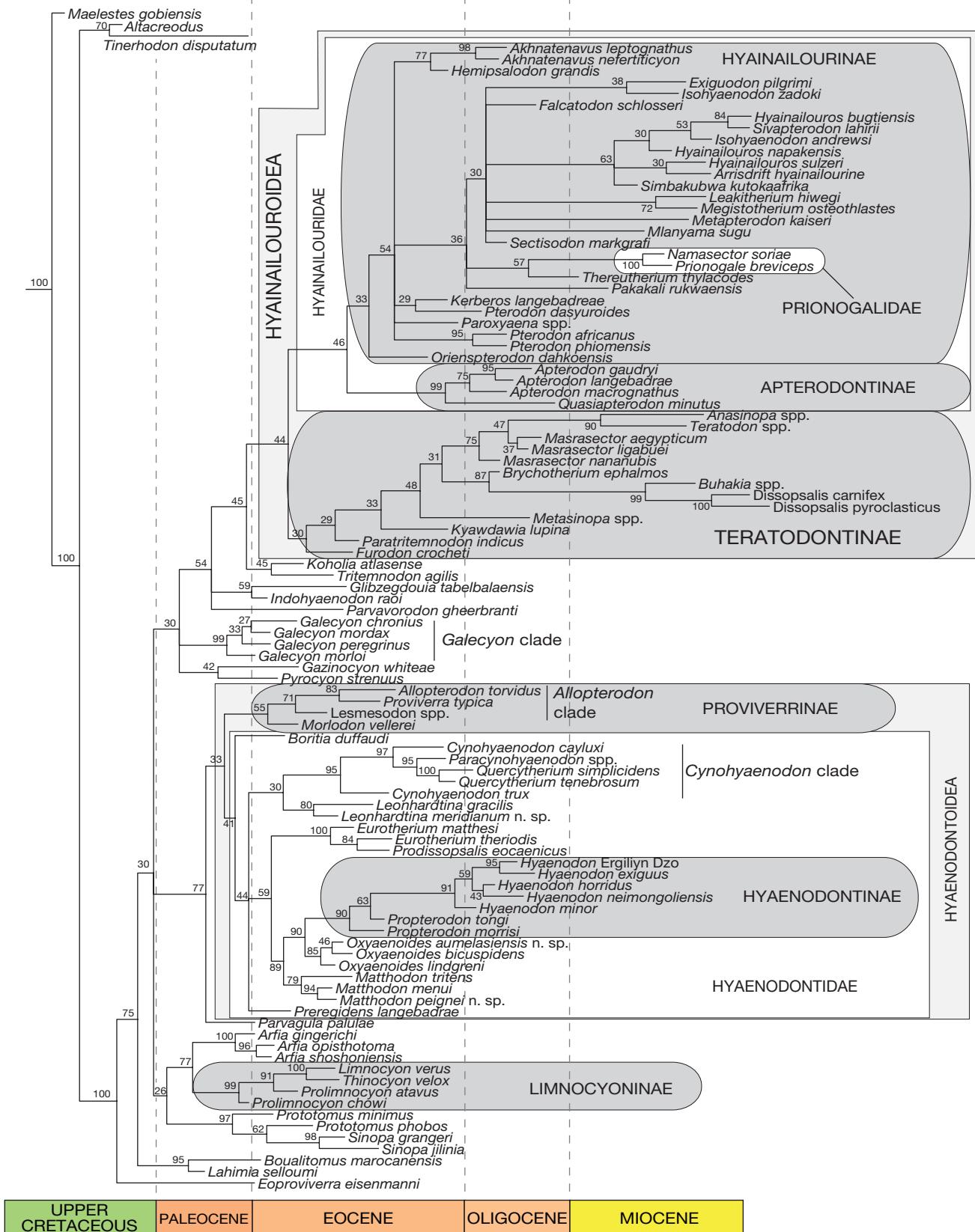
FIG. 4. — Results of the phylogenetic analysis of Hyaenodonta character-taxon matrix. Results are visualized as an "all compact" (majority rule plus compatible groups) consensus tree. Major, named clades recovered or discussed in this analysis and recovered in other analyses are illustrated. In bold: new hyaenodonts species described herein.

PHYLOGENETIC ANALYSIS

The character-taxon matrix that forms the basis of the present analysis has been used – and improved – in several studies of hyaenodonts systematics (Borths *et al.* 2016; Borths & Seiffert 2017; Borths & Stevens 2017a, b, c, 2019; Solé & Mennecart 2019; Dubied *et al.* 2019). The analysis ("all compact" consensus tree; Fig. 4; Appendix 6) recovered all the clades found in the previous phylogenetic analyses.

The "all compact" consensus tree shows the monophyly of the Hyainailouroidea (Posterior Probability = 44%), the Hyainailouridae (PP = 46%), as well as that of the Teratodontinae (PP = 30%), Hyainailourinae (PP = 33%), and Apterodontinae (PP = 99%), three subfamilies of the Hyainailouroidea. These values are close to those found by Borths & Stevens (2019). The relationships among Hyainailouroidea have been extensively discussed by Borths *et al.* (2016), Borths & Seiffert (2017), and Borths & Stevens (2017a, b, 2019). The clades established by our analysis are similar to those found by Borths & Stevens (2019). However, numerous polytomies within the Hyainailourinae are present in the resulted tree of our analysis (Fig. 4), which was not the case in the previous published phylogenetic analyses.

The most dramatic difference with the previous phylogenetic studies is the presence of the enigmatic *Thereutherium* and of the prionogalids *Namasector* and *Prionogale* within the Hyainailourinae – the clade Prionogalidae+*Thereutherium* is supported by a PP of 57%, while the Prionogalidae is supported by a PP of 100%. This position differs from the results of Solé & Mennecart (2019): indeed, they were resolved as sister taxa of Hyaenodontinae by this analysis. A close relationship with Hyaenodontinae was also found by Borths & Stevens (2017c) when the characters were ordered. When the characters were unordered, the Prionogalidae (i.e., *Namasector* and *Prionogale*) were located within the Hyainailourinae, but *Thereutherium* was still closely related to the Hyaenodontinae (Borths & Stevens 2017c). Therefore the presence of both Prionogalidae and *Thereutherium* among the Hyainailourinae was unexpected.

This result questions the relationships of the Prionogalidae and *Thereutherium*, which highlights in addition the difficulty to understand the origin of these enigmatic hyaenodonts. Because the prionogalids have been only found in Africa (Schmidt-Kittler & Heizmann 1991; Morales *et al.* 2008; Borths & Stevens 2019), their presence among Hyainailourinae, which in all probability originated in Africa (Solé *et al.* 2014b, 2015b; Borths & Stevens 2019), is biogeographically logical. The case of *Thereutherium* is more complex, this small-bodied hypercarnivorous hyaenodont being only known in the Oligocene of Europe (Lange-Badré 1979). Based on the present topology, one can imagine that this hyaenodont dispersed from Africa into Europe in the earliest Oligocene. Such dispersal (i.e., from Africa to Europe in the early Oligocene) of a hyaenodont has been already proposed for *Apterodon* (Simons & Gingerich 1976; Lange-Badré & Böhme 2005; Grohé *et al.* 2012).

Some polytomies are also present at the nodes located closely to the Hyainailouroidea. A polytomy is also present close to the base of the Hyaenodonta: this node actually groups the Hyainailouridae and related taxa (e.g., *Galecyon* clade), the Hyaenodontoidea+*Parvagula*, and the Limnocyoninae and related taxa (*Arfia*, *Prototomus*, and *Sinopa*).

Besides the position of *Thereutherium* and Prionogalidae within the Hyainailourinae, the second striking difference with the previous phylogenetic studies is the very basal position of the Moroccan hyaenodonts *Lahimia* and *Boualitomus*; only the European hyaenodont *Eoproviverra* is more basally located than these hyaenodonts. This position is surprising because these carnivorous mammals were generally found to be close to the Hyainailouroidea (Borths *et al.* 2016, Borths & Seiffert 2017; Borths & Stevens 2017a, b, c). However, one can remember that *Lahimia* and *Boualitomus* were more basally located in Borths & Stevens (2019) (i.e., before the split between the Hyaenodontidae and the Hyainailouroidea). The basal position of these two hyaenodont genera is interesting because the presence of *Lahimia* in the Paleocene of Morocco, has been notably used as an argument for an African origin of the Hyaenodonta by Solé *et al.* (2009) and Solé (2013); Gheerbrant (1995) and Gheerbrant *et al.* (2006) also proposed this hypothesis but before the discovery of *Lahimia*. This hypothesis has been notably criticized by Borths *et al.* (2016) and Borths & Stevens (2019). However, the issue of the geographic origin of the hyaenodonts is beyond the present research and should be analyzed only based on biogeographic analysis such as those performed by Borths *et al.* (2016) and Borths & Stevens (2019).

Contrary to the previous phylogenetic analyses (Borths & Seiffert 2017; Borths & Stevens 2017a,b,c), but similarly to Solé & Mennecart (2019), some of the "proviverrines" *sensu* Solé (2013) (i.e., *Proviverra*, *Lesmesodon*) are not located at the base of the hyaenodont clade, but are more deeply nested in the present phylogenetic tree. Therefore, our analysis is significant in that it recovers almost all the "proviverrine" taxa *sensu* Solé (2013) within the same clade except *Eoproviverra* (Fig. 4). In the present analysis *Eoproviverra* is the earliest-diverging hyaenodont (Fig. 4).

In the previous analyses (Borths *et al.* 2016; Borths & Seiffert 2017; Borths & Stevens 2017a, c), the Proviverrinae is a clade located at the base of the Hyaenodonta and generally included the European genera *Proviverra*, *Eoproviverra*, *Lesmesodon*, *Parvagula*, and *Morlodon*. This group also included *Allopterodon* in Borths *et al.* (2016), but this genus is closer to the Hyaenodontinae in the other analyses.

Comparably to the results of Solé & Mennecart (2019) and Dubied *et al.* (2019), we found a clade (PP = 55%) that gathers the European hyaenodont genera *Proviverra*, *Allopterodon*, *Lesmesodon*, and *Morlodon*. As discussed in Solé & Mennecart (2019), this clade partially corresponds to the concept of Proviverrinae of Borths *et al.* (2016). Borths *et al.* (2016) and Solé & Mennecart (2019) considered that the Proviverrinae is a clade that includes the common ancestor

of *Proviverra* and *Parvagula*. However, in the present analysis, *Parvagula* is outside this clade and is the sister taxon to a clade that groups the Proviverrinae and Hyaenodontidae (Fig. 4). Therefore, we here propose that the Proviverrinae is a clade that includes the common ancestor of *Proviverra* and *Morlodon*. From the recent phylogenetic analyses, it seems that the content of the *Proviverrinae* is susceptible to vary in the future, but we think that this concept is useful and should be conserved.

As in Solé & Mennecart (2019) and Dubied *et al.* (2019), the clade Proviverrinae is not located at the base of the Hyaenodonta but is the sister clade of the Hyaenodontidae. This result supports the concept of Hyaenodontoidea proposed by Solé & Mennecart (2019) to designate the clade formed by the common ancestor of *Proviverra* and *Hyaenodon* (Fig. 4).

Among the Proviverrinae, the *Allopterodon* clade (*Allopterodon*, *Proviverra*, *Lesmesodon*) of Solé *et al.* 2014a is partially recovered (PP = 71%). Contrary to Solé & Mennecart (2019), the genera *Lesmesodon* and *Proviverra* are not sister taxa; the proviverrines *Allopterodon* and *Proviverra* are indeed more closely related (PP = 83%).

All the other "proviverrine" taxa *sensu* Solé (2013) are located among the Hyaenodontidae (PP = 41%), as most of the previous phylogenetic analyses (e.g., Borths *et al.* 2016; Borths & Stevens 2019; Solé & Mennecart 2019). In this clade, only the hyaenodontines (i.e., *Propterodon* and *Hyaenodon*) are not "proviverrine" taxa *sensu* Solé (2013). The Hyaenodontinae, which contains the genera *Propterodon* and *Hyaenodon*, is supported by a PP of 90% (Fig. 4). The genera *Cynohyaenodon*, *Paracynohyaenodon*, and *Quercytherium* form the *Cynohyaenodon* clade (according to Solé *et al.* 2014a) (PP = 95%); the genus *Cynohyaenodon* is not monophyletic (Fig. 4). This clade is closely related to *Leonhardtina* (PP = 30%). This – poorly supported – relationship was not found neither in Solé & Mennecart (2019) nor in Dubied *et al.* (2019). The new *Leonhardtina* species described herein is closely related to *Leonhardtina gracilis* (PP = 80%).

There is a clade (PP = 59%) that contains the Hyaenodontinae and the hyaenodontids *Eurotherium*, *Prodissopsalis*, *Matthodon*, and *Oxyaenoides*. *Eurotherium* and *Prodissopsalis* are closely related (PP = 100%) and constitute the most basal clade. One can note that the genus *Eurotherium* is not monophyletic: *E. theriodis* is closely related to *Prodissopsalis* (PP = 84%) (Fig. 4).

The other hyaenodontids are in a clade that has a PP of 89%. The next clade to diverge is *Matthodon* (PP = 79%) (Fig. 4). The new species, *M. peignei* n. sp., is closely related to *Matthodon menui* (PP = 94%). This supports the generic referral of the new hyaenodont from Aumelas to this genus. *Oxyaenoides* (PP = 85%) is the hyaenodontid genus most closely related to Hyaenodontinae. The new species, *O. aumelasiensis* n. sp. is closely related to *O. bicuspidens* (PP = 46%) (Fig. 4). As for *Leonhardtina* and *Matthodon*, the phylogenetic analyses confirm our observations based on dental material discovered at Aumelas. It is worth noting that the hyaenodontines, *Matthodon*, and *Oxyaenoides* display hypercarnivorous dentition characterized by the loss of the metaconid and reduction of the talonid, an adaptation that appeared several times among Hyaenodontinae (Borths *et al.* 2016).

Finally, one can note the presence of a clade (PP = 26%) that gathers the Limnocyoninae (PP = 99%), and the genera *Arfia*, *Prototomus*, and *Sinopa*. This clade is commonly recovered in the phylogenetic analyses that deal with the relationships within Hyaenodonta.

DISCUSSION

Implications of the hyaenodont fauna concerning the age of Aumelas

The carnivorous mammals from Aumelas are represented by three new species, representing three previously described genera – *Oxyaenoides*, *Leonhardtina*, and *Matthodon*. It is important to note that no carnivoran is known from this locality. This is not surprising because in localities close to the MP10, MP11 (except Messel, Germany, where two carnivorans are known; Springhorn 1980, 2000), MP12, MP13, and MP14 reference-levels, carnivorans are rarer and less diverse than the hyaenodonts.

If the number of carnivorous taxa is low, the morphological disparity shown by the fossils is high: *Matthodon* and *Oxyaenoides* represent large (*Matthodon*: 15 kg) and medium-sized (*Oxyaenoides*: 4 kg) hypercarnivorous predators, while *Leonhardtina* represents a small – probably insectivorous – predator (843 g).

Specimens referred to *Oxyaenoides* have been discovered at several localities in southwestern Europe: Palassou (Crochet *et al.* 1976), Aigues-Vives 2 (Solé *et al.* 2015a), and Rouzilhac (Godinot *et al.* 2018). *Leonhardtina* was only recently discovered in the south of France (*Leonhardtina* cf. *gracilis* in Godinot *et al.* 2018 but *Leonhardtina meridianum* n. sp. herein). This is the first occurrence of *Matthodon* from the southwestern Europe, a genus that was previously only known from the northwest (Lange-Badré & Haubold 1990; Solé *et al.* 2014a). *Oxyaenoides* and *Leonhardtina* have been discovered together in the locality of Rouzilhac. The *Leonhardtina* species at Rouzilhac is similar to *L. meridianum* n. sp., but the *Oxyaenoides* species (*O. bicuspidens*) is larger than *Oxyaenoides aumelasiensis* n. sp. found at Aumelas and is closer in size to the *Oxyaenoides* species known from the northwestern Europe (Godinot *et al.* 2018).

The occurrence of these three hyaenodonts at Aumelas has interesting implications for relative age of the site. *Oxyaenoides* and *Leonhardtina* have long stratigraphic ranges: the former is known from localities close to the MP10, MP11 and ?MP13 reference-levels (Lange-Badré & Haubold 1990; Solé *et al.* 2014a, 2015a), while the latter is known from localities close to the MP10, MP12 and MP13 reference-levels (Lange-Badré & Haubold 1990; Solé *et al.* 2014a). The stratigraphic record of *Matthodon* is shorter, having only been reported from localities close to the MP10 and MP11 reference-levels (Lange-Badré & Haubold 1990; Solé *et al.* 2014a). Its particular ecology as a

TABLE 5. — Hypothetical correlations between the two mammalian successions of the Northwestern and Southwestern European provinces during the Ypresian and earliest Lutetian, with indication of the hyaenodonts recorded for the Northwestern and Southwestern provinces localities. Correlations based on BiochroM'97 (1997) and Marandat *et al.* (2012). PE biozones are from Hooker (1996, 1998). In bold: localities and fossils described and discussed in the present article: *, taxa not recorded in the type-locality of the reference–level. Note: the age of Aumelas and Rouzilhac is uncertain as the two localities are considered to be close to MP10 and MP11 reference–levels with uncertainty (see text); they are here grouped in a MP10b level, intermediate in age between MP 10 and MP 11, as proposed by Godinot *et al.* (2018) for Rouzilhac. Authorships of taxa are indicated in the Appendix 8.

ELMA	Ma	Biozone	MP	Reference-locality	Northwestern Province	Southwestern Province	Hyaenodonts from Northwestern Province	Hyaenodonts from Southwestern Province
Robiacian	–	–	14	Egerkingen α+ß	Le Guépelle Geiseltal Oberkohle	Lissieu Issel	*Prodissopsalis eocaenicus*; *Eurotherium theriodis*; *Allopterodon torvidus*; *Proviverra typica*; *Cynohyaenodon trux*; *C. ruetimeyeri*	*Prodissopsalis eocaenicus*; *Eurotherium theriodis*
Geiseltalian	44	–	13	Geiseltal-Obere Mittelkohle	?Egerkingen γ La Défense Bouxwiller	?Aigues-Vives 2	*Prodissopsalis eocaenicus*; *Leonhardtina gracilis*; *Proviverra typica*; *Cynohyaenodon trux*; *Allopterodon torvidus**; *Oxyaenoides schlosseri**; *Eurotherium theriodis**; *Alienetherium buxwilleri**; *Praecodens acutus**; *Cartierodon egerkingensis**	cf. *Oxyaenoides schlosseri**; *Proviverra typica.**; *Oxyaenoides schlosseri**; *Eurotherium theriodis**,
	–	–	12	Geiseltal-Untere Mittelkohle	–	–	*Prodissopsalis eocaenicus*; *Leonhardtina gracilis*; *Proviverra typica*; *Cynohyaenodon trux*	–
	47-48	–	11	Geiseltal-Untere Unterkohle	Messel	Palassou	*Oxyaenoides bicuspidens*; *Matthodon tritens*; *Eurotherium matthesi*; *Lesmesodon edingeri**; *L. behnkeae**	*Oxyaenoides bicuspidens*;
Grauvian	–	–	10b	–	–	?Rouzilhac ?Aumelas	–	*Oxyaenoides bicuspidens*; *Oxyaenoides aumelasiensis* n. sp.*; *Leonhardtina meridianum* n. sp.*; *Matthodon* peignei n. sp.*
	–	–	10a	Grauves	Cuis, Chavot, Mancy, Monthelon	–	*Oxyaenoides lindgreni**; *Matthodon menui*; *Protoproviverra palaeonictides**; *Leonhardtina godinoti*	–
Neustrian	–	PE V	8+9	Avenay	–	Saint–Papoul/ La Borie	*Morlodon vellerei*;	*Boritia duffaudi**; *Preregidens langebadrae**
	–	PE IV	8+9	–	Mutigny	–	*Minimovellentodon russelli**	–
	55.12	PE III	8+9	–	Abbey Wood	–	*Prototomus minimus*; *Prototomus girardoti*;	–
	–	PE II	–	–	Soissons	Rians, Palette, Fournes, Fordones	*Prototomus girardoti*	*Eoproviverra eisenmanni**; *Parvagula palulae**; *Galecyon gallus**
	55.8	PE I	7	Dormaal	Le Quesnoy	–	*Arfia gingerichi*; *Prototomus minimus*; *Prototomus girardoti*; *Galecyon morloi*	–

possible bone-cracking predator (Solé *et al.* 2014a) might be related to its short stratigraphic distribution, but only further studies on the ecology of the Eocene carnivorous mammals could validate this hypothesis.

The locality of Aumelas has generally been considered close to the MP13 reference-level. This hypothesis is consistent with the range of *Oxyaenoides* and *Leonhardtina*, but conflicts with the range of *Matthodon* (Table 5). The
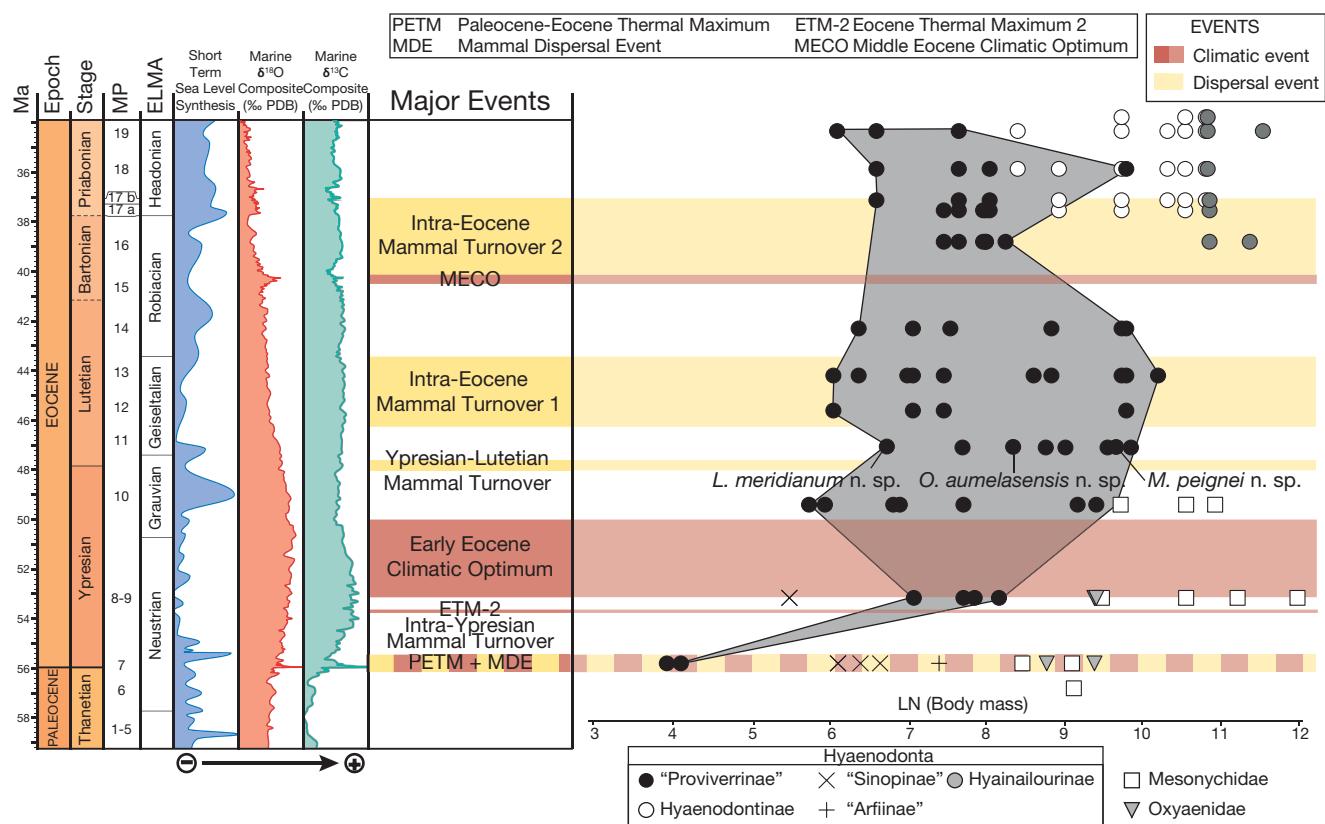
FIG. 5. — Values of the Ln (body mass) of mesonychids, oxyaenids, and hyaenodonts ("Proviverrinae" *sensu* Solé (2013), "Sinopinae", "Arfiinae", Hyaenodontinae, and Hyainailourinae) from MP7 to MP19 with particular attention on hyaenodonts from Aumelas. Aumelas is here represented to be close to the MP11 reference-level. Abbreviations: **ELMA**, European Land Mammal Ages; **EMP**, Mammal Palaeogene. Values are available at Appendix 6.

only reference-levels that could include all three genera are the MP10 and MP11. The genera are known from Paris Basin localities close to the MP10 and around MP11 in the Geiseltal area. *Oxyaenoides* and *Matthodon* are both recorded in Geiseltal-Untere Unterkohle (MP11) (Table 5), but not *Leonhardtina*, which is only known in Geiseltal-Untere Mittelkohle (MP12) and Geiseltal-Obere Mittelkohle (MP11) in the Geiseltal area. Because this genus is known in MP10 localities, it may have been present around MP11 in Geiseltal. It is interesting that only large and middle-sized hyaenodonts are known from Geiseltal-Untere Unterkohle.

The specimens referred to *Oxyaenoides*, *Matthodon*, and *Leonhardtina* from Aumelas are distinctive enough from specimens discovered in the northwestern Europe that we designated three new species at Aumelas. These species each possess relatively primitive characters with respect to other younger species in the genus; however, they present also probable derived features.

The presence of a species of *Matthodon* as well as the primitive features of the new *Matthodon*, *Oxyaenoides*, and *Leonhardtina* species at Aumelas suggests an age close to the MP10 and MP11 reference-levels (maybe closer to MP10 reference-level) rather than the MP13 age previously proposed based on other mammalian groups (Bio-chroM'97 1997).

THE EVOLUTION OF EUROPEAN HYAENODONTS

The new topology of the phylogenetic tree (close relationship between the Proviverrinae and Hyaenodontidae) supports the hypothesis of Solé *et al.* (2014a) that the hyaenodonts had a radiation in Europe around the Ypresian/Lutetian transition (see Solé *et al.* 2014a for an extensive description of this radiation during the Eocene of Europe). Therefore, it is interesting to look at the evolution of the ecology of the European hyaenodonts.

The body mass of extinct carnivorous mammals is important for understanding their ecological "guild" (*sensu* Root 1967). Reconstructing the body mass of extinct carnivores also facilitates examination of larger evolutionary trends. Following Solé *et al.* (2014a, 2015a), we estimated the body mass of the new hyaenodonts found at Aumelas and compared them to those of other European hyaenodonts in a chronostratigraphic context (Fig. 5). The body masses of the new hyaenodonts fit with the general pattern observed in European hyaenodonts, which shows a body mass increase through the Ypresian and Lutetian (see also Solé & Mennecart 2019).

We specially focused on the hyaenodonts recorded from the MP10, MP11 and MP12 reference-levels (Fig. 6). The body mass of *Oxyaenoides aumelasiensis* n. sp. (4.2 kg) is smaller than its relatives found in the northwestern Europe, as discussed above: 9.7 kg for *O. lindgreni*; 14.2 kg for *O. bicuspidens* and 16.9 kg for *O. schlosseri*. The body mass of *O. bicuspidens* recorded
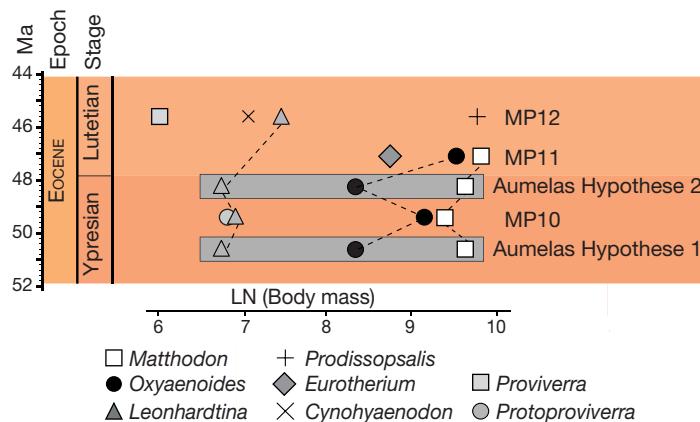
FIG. 6. — Comparison of the range of body masses (in LN) of the hyaenodonts from Aumelas with those recorded from the MP10 (Cuis, Grauves, Monthelon, Mancy), MP11 (Geiseltal-Untere Unterohle) and MP12 (Geiseltal- Untere Mittelkohle) reference-levels in a chronostratigraphic context. Two hypotheses are shown: **Hypothesis 1**, Aumelas is close to MP10 reference-level (Ypresian); **Hypothesis 2**, Aumelas is close to MP11 reference-level (Lutetian). The hypothesis 1 is based on the primitive features displayed by the fossils from Aumelas; the hypothesis 2 is based on the intermediate size of *Matthodon peignei* n. sp. between *Matthodon menui* (MP10) and *Matthodon tritens* (MP11). Note: the range of body masses provided for the MP10 level combines the data available from Grauves (reference-locality), Cuis, Chavot, Mancy, and Monthelon. Authorships of taxa are indicated in the Appendix 8.

at Rouzilhac is 14.1 kg. Because the three other *Oxyaenoides* species have been reconstructed as hypercarnivorous predators (Morlo 1999; Solé *et al.* 2014a, 2015a), and *O. aumelasiensis* n. sp. is part of this genus, it likely was also a hypercarnivorous mammal. However, because of the difference in body mass, *O. aumelasiensis* n. sp. likely had a different ecological role than the three other *Oxyaenoides* species. Compared to the faunas recorded in MP10-MP12 localities, *O. aumelasiensis* n. sp. is close in size to the hyaenodont species *Eurotherium matthesi* recorded in Geiseltal-Untere Unterkohle (MP11) (Fig. 6). *E. matthesi* is reconstructed as a hypercarnivorous mammal (Morlo 1999) with an estimated body mass close to 6.5 kg. Therefore, it seems possible that in southwestern Europe, the genus *Oxyaenoides* filled two distinct ecological niches: the one it occupied in northwestern Europe (i.e., as a large hypercarnivorous predator as evidenced at Rouzilhac), but also the one occupied by *Eurotherium* (i.e., as a fox-sized meat-eating predator).

Matthodon peignei n. sp. has a body mass (*c.* 15 kg) close to that of the MP10 and MP 11 *Matthodon* species recorded in northwestern Europe. *Matthodon* may have been a durophagous hyaenodont, based on the size of its premolars (see Solé *et al.* 2014a, but see Morlo 1999 for a different opinion). Because the new species is close in size and morphology to the northwestern species, these species likely belonged to the same guild: large meat/bone eater – it is important to note that 'large' herein is relative to the overall body mass of the carnivorous mammals from the Ypresian and Lutetian and does not correspond to the concept of 'large' carnivores in the physiological sense of Carbone *et al.* (2007). Finally, the *Leonhardtina* species (*c.* 850 g) filled the same ecological niche in northwestern and southwestern Europe (i.e., small meat/non-vertebrate eater). Therefore, only *O. aumelasiensis* n. sp. is occupying unexpected niche-space among the hyaenodonts from the southwestern and northwestern Europe.

The hyaenodont specimens from Aumelas suggest mammalian predator faunas in northwestern and southwestern Europe were homogeneous at the genus level around the Ypresian/Lutetian transition. This differs from the biogeographic generic diversity of faunas during the early Ypresian described by Marandat (1997) and Marandat *et al.* (2012) (see Solé *et al.* 2014a, 2015a for a discussion concerning the case of Hyaenodonta).

The overall bodymass disparity of the hyaenodonts is similar between the two European areas (Fig. 6); in contrast, the mesonychids have different body masses between the two European areas (the southern mesonychids have twice the body mass of the northern mesonychids; see Solé *et al.* 2018). Furthermore, the case of *Oxyaenoides* shows that the ecological niches occupied by this genus were probably different between the northwestern and southwestern Europe.

These two observations indicate that the European carnivorous faunas were probably not ecologically identical despite an homogeneity at the genus level. However, it is worth keeping in mind that the evolution of carnivorous communities during the Paleogene of Europe has not been comprehensively analyzed.

CONCLUSION

Three new carnivorous mammals referred to Hyaenodonta are now known from Aumelas. They provide information on the radiation of the hyaenodonts in Europe around the Ypresian/Lutetian transition, when specialized ecomorphotypes – like hypercarnivorous *Oxyaenoides* and the durophageous *Matthodon* (Solé *et al.* 2014a) – appeared.

This new material demonstrates that the northwestern and southwestern European faunas were homogenous (i.e., presence of the same genera in the two areas), in contrast to the faunas in the early Ypresian (Marandat 1997; Marandat *et al.* 2012). However, minor differences in the composition of the carnivore fauna (i.e., ecological niches occupied by *Oxyaenoides*) are intriguing and must be investigated in the future.

The presence of these hyaenodonts, especially *Matthodon*, supports a reclassification of Aumelas as close to Ypresian/Lutetian boundary rather than close to the MP13 reference-level (middle Lutetian). This stratigraphic hypothesis requires further research on the rest of the fauna preserved at Aumelas.

Acknowledgements

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APPENDIX 1. — List of the modifications to the matrix of Borths & Stevens (2019). **Character**, previous coding → new coding.

Allopterodon torvidus
14: 1 → 0
16: 0 → 1
25: 0 → 1
64: ? → 0

Boritia duffaudi
15: 0 → 1
21: 0 → 1
31: 1 → 0
36: 0 → 1

Cynohyaenodon cayluxi
26: 0 → 1
84: 0 → 1
87: 1 → 2
105: 1 → 0

Cynohyaenodon trux
87: 1 → 2
105: 1 → 0

Eurotherium matthesi
31: 1 → 0
57: 1 → 0
58: 1 → 0
93: 1 → 0
94: 1 → 0

Eurotherium theriodis
7: ? → 1
18: 1 → 0
31: 1 → 0
57: 1 → 0
58: 1 → 0
93: 1 → 0
94: 1 → 0

Galecyon morloi
Characters 19 to 29 are coded '?' because no P_4 is known for this species (see Zack 2011)

Leonhardtina gracilis
21: 0 → 1
43: 1 → 0

Lesmesodon spp.
42: 0 → 1

Matthodon tritens
57: 1 → 0
60: 1 → 0

Morlodon vellerei
11: 0 → 1
16: 0 → 1
21: 0 → 1
26: 0 → 1
42: 0 → 1
45: 0 → 1
78: 0 → ?
79: 0 → ?
84: 0 → 1
93: 1 → 0

Oxyaenoides bicuspidens
10: 1 → 0
60: 1 → 0

Oxyaenoides lindgreni
36: 0 → 1
100: X → ?
104: X → ?
107: X → ?

Parvagula palulae
42: ? → 0

Preregidens langebadrae
11: 0 → 1
28: 0 → 2
31: 1 → 0
36: 0 → 1

Proviverra typica
11: 0 → 1
16: 0 → 1
21: 0 → 1
26: 0 → 1
44: 0 → 1
102: 0 → 2
105: 1 → 0

Quercytherium simplicidens
36: 0 → 1
39: 0 → 2
60: 1 → 0
93: 1 → 0
94: 1 → 0
114: 0 → 1

Quercytherium tenebrosum
36: 0 → 1
93: 1 → 0
94: 1 → 0

APPENDIX 2. — Descriptions of characters and character states used in the phylogenetic analysis.

The characters are from Borths & Stevens (2019) without modification.

LOWER DENTITION
Deciduous Lower Dentition

1. dP3 paraconid height: paraconid indistinct (0); paraconid present lower than talonid (1);paraconid present and taller than talonid (2).
2. dP3 protostylid between protoconid and talonid: present (0); absent (1). (New Character relative to Borths & Stevens 2017c).
3. dP4 paraconid height: lower than half protoconid height (0); half protoconid height or taller (1).
4. dP4 metaconid height: lower than half paraconid height (0); half paraconid height or taller (1); metaconid absent (2). (compare with Bastl *et al.* 2014: character 12).
5. dP4 talonid basin cusps: Entoconid and hypoconid present (0); Only hypoconid present (1). (compare with Bastl *et al.* 2014: character 13).
6. dP4 talonid length proportion: More than ⅓ length of entire tooth (0); less than ⅓ length of entire tooth (1).

Adult Lower Dentition

7. First mental foramen position: inferior to P1 (0); inferior to P2 (1). (Solé *et al.* 2014b: character 0).
8. Second mental foramen position: inferior to P3 (0); inferior to P4 (1). (Solé *et al.* 2014b: character 1).
9. P1: present (0); absent (1). (Solé *et al.* 2014b: character 2).
10. P1 root number: two roots (0); one root (1). (Polly 1996: character 13; Zack 2011: character 2; Solé *et al.* 2014b: character 2).
11. P2 talonid mesiodistal length: absent to short (0); elongate with distinct inflection separating postprotocristid from talonid (1). (modified Polly 1996: character 3; Egi *et al.* 2005: character 34; Solé *et al.* 2014b: character 5).
12. P2 to P3 relative mesiodistal length: P2 shorter than P3 (0); P2 as long or longer than P3 (1). (Egi *et al.* 2005: character 29; Solé *et al.* 2014b: character 6).
13. P3 inclination: perpendicular to horizontal ramus, tooth forms isosceles triangle in buccal view (0); tooth inclines distally, preprotocristid mesially convex (1).
14. P3 buccolingual width relative to mesiodistal length: width 33% of length (0); width 50% of length (1); width more than 50% of length (2).
15. P3 paraconid morphology: absent or small (0); developed with distinct postparacristid (1). (modified Polly 1996: character 6; Egi *et al.* 2005: character 35; Solé *et al.* 2014b: character 7).
16. P3 talonid mesiodistal length: short, cusp-like (0); long, distinct inflection separating postprotocristid from talonid (1). (modified Polly 1996: character 4; Egi *et al.* 2005: character 37; Solé *et al.* 2014b: character 8).
17. P3 entoconid: absent (0); present (1). (Solé *et al.* 2014b: character 9).

18. P3 to P4 relative mesiodistal length: P3 shorter than P4 (0); P3 as long or longer than P4 (1). (Egi *et al.* 2005: character 31; Solé *et al.* 2014b: character 10).
19. P4 inclination: perpendicular to horizontal ramus, tooth forms isosceles triangle in buccal view (0); tooth inclines distally, preprotocristid mesially convex (1).
20. P4 orientation: talonid and protoconid aligned with horizontal ramus (0); talonid and protoconid at oblique angle to horizontal ramus (1). (New Character relative to Borths & Stevens 2017c).
21. P4 paraconid morphology: present but poorly developed (0); paraconid well-developed (1); paraconid indistinct to absent (2). (modified Polly 1996: character 7; Solé *et al.* 2014b: character 11).
22. P4 metaconid: absent (0); present, usually weakly developed or ridge-like (1). (modified Solé *et al.* 2014b: character 12).
23. P4 entoconid: absent (0); present (1). (Solé *et al.* 2014b: character 14).
24. P4 hypoconulid: present and distinct (0); absent or indistinct from entoconid (1). (New Character relative to Borths & Stevens 2017c).
25. P4 hypoconid height: short, less than 33% of protoconid height (0); tall, more than 33% protoconid height (1). (modified Solé *et al.* 2014b: character 16).
26. P4 talonid basin: buccolingually compressed and shallow (0); buccolingually wide and deep (1); absent (2).
27. P4 precingulid and postcingulid: absent (0); present (1). (modified Solé *et al.* 2014b: character 18).
28. P4 relative height: mesiodistally longer than height (0); mesiodistally shorter than height (1); mesiodistal length and height subequal (2).
29. P4 height relative to molars: shorter than all molars (0); taller than M1 only (1); taller than M2 (2).
30. P5 presence: present (0); absent (1).
31. M1 and M2 entoconid morphology: well developed or bulbous (0); crestiform with visible apex (1); undifferentiated entocristid (2). (modified Zack 2011: charcter 23; Solé *et al.* 2014b: character 27).
32. M1 and M2 talonid depth: deep (0); shallow (1). (modified Zack 2011: character 25; Solé *et al.* 2014b: character 29).
33. M2 entocristid in lingual view: parallels hypocristid (0); present, stops before metaconid (lower than hypocristid) (1); weak ridge or absent (2).
34. M3 entocristid: parallels hypocristid (0); present, stops before metaconid (lower than hypocristid) (1); weak ridge or absent (2).
35. M1 and M2 talonid buccolingual width: narrow, less than 80% width of trigonid (0); wide, greater than 80% trigonid (1). (modified Solé *et al.* 2014b: character 28).
36. M1 mesiodistal length relative to M2: M1 length subequal or longer than M2 (0); M1 length less than M2 (1). (modified Zack 2011: character 26; Solé *et al.* 2014b: character 31).

37. M1 relative to M2 mesiodistal length: M1 greater than or equal to M2 trigonid length (0); M1 greater than M2 paraconid length (1); M1 equal to or shorter than M2 paraconid length (2). (New Character relative to Borths & Stevens 2017c).
38. M1–M3 trigonid height relative to talonid: trigonid tall on all molars, talonid less than 50% of trigonid height (0); trigonid low on all molars, talonid more than 50% of trigonid height (1); trigonid low on M1 and M2 (2). (modified Solé *et al.* 2014b: character 32).
39. M3 postprotocristid distal trend in buccal view: slopes mesial to distal (0); perpendicular to alveolus (1); slopes distal to mesial (overhangs talonid) (2).
40. M2 cristid obliqua orientation relative to mesiodistal axis: lingual to buccal trend (0); parallel to mesiodistal axis (1); buccal to lingual trend (2). (compare to Zack 2011: character 21).
41. M2 and M3 paraconid position relative to protoconid, angle defined relative to mesiodistal axis of mandible: directly mesial to protoconid,15 degrees (0); slightly lingual paraconid, 15.1 to 45 degree angle (1); strong lingual position, 45.1 to 60 degrees (2). *Ordered.*
42. M3 postparacristid mesial to distal trend: steep slope to preprotocristid ("V" shaped acute angle) (0); shallow slope to preprotocristid (forms right angle with preprotocristid) (1); forms obtuse angle with preprotocristid (2). *Ordered.*
43. M2 and M3 paraconid height relative to protoconid: paraconid significantly shorter than protoconid (0); paraconid slightly shorter than protoconid (1); paraconid and protoconid subequal in height (2).
44. M3 talonid buccolingual width in lingual view: postparacristid shorter than premetacristid (0); postparacristid subequal to premetacristid (1); postparacristid longer than premetacristid (2).
45. M3 postparacristid length to preprotocristid in buccal view (carnassial blade proportions): postparacristid much shorter than preprotocristid (30%) (0); postparacristid half length of preprotocristid (1); postparacristid more than half preprotocristid length (2); subequal lengths (3).
46. M2 and M3 metaconid expression: connate and connects to paraconid base (0); connate, separated from paraconid (1); fold or ridge (2); absent (3). *Ordered.*
47. M1 metaconid: taller than paraconid (0); subequal to paraconid (1); shorter than paraconid or absent (2). *Ordered* (compare to Polly 1996: character 18).
48. M2 metaconid: taller than paraconid (0); subequal to paraconid (1); shorter than paraconid or absent (2). *Ordered* (compare to Polly 1996: character 18).
49. M3 metaconid: taller than paraconid (0); subequal to paraconid (1); shorter than paraconid or absent (2). *Ordered* (compare to Polly 1996: character 19).
50. M2 mesiodistal length to M3 length: M2 shorter than M3 (0); M2 subequal to M3 (1); M2 longer than M3 (2); M3 absent (3). *Ordered* (compare to Zack 2011: character 30).
51. M2 talonid mesiodistal length (% of total mesiodistal length): >40% (0); 40% to 30% (1); 29% to 21% (2); <20% (3). *Ordered.*
52. M3 talonid mesiodistal length (% of total mesiodistal length): >40% (0); 40% to 30% (1); 29% to 21% (2); <20% (3). *Ordered.*
53. M3 talonid: present, bears hypoconid and hypoconulid (0); present, only one distinct cusp (1); absent (2). *Ordered.*
54. M2 buccal talonid margin: steep slope distal to mesial (0); shallow slope distal to mesial (1); parallel to alveolus (2); slopes mesial to distal (3). *Ordered.*
55. M3 buccal talonid margin angle from highest point to lowest: steep slope distal to mesial (0); shallow slope distal to mesial (1); parallel to alveolus (2); slopes mesial to distal (3). *Ordered.*
56. M1–M3 ectocingulid: weakly expressed to absent (0); distinct (1). (modified Solé *et al.* 2014b: character 34)
57. M1–M3 postcingulid: absent (0); present (1). (modified Solé *et al.* 2014b: character 35).
58. M1–M3 ectocingulid to postcingulid connection: separated (0); fused (1). (modified Solé *et al.* 2014b: character 36).
59. M3 talonid buccolingual width relative to M2 talonid width: equal (0); narrower (1).
60. Mandible inflection anterior to angular process (Solé *et al.* 2015b): present (0); absent (1).
61. Angular process morphology: distinct process with medial inflection (0); gently curved process in line with mandibular corpus (1); ventral inflection (2).
62. Mandibular condyle position: superior to M3 alveolus (0); directly distal to M3 alveolus (1); inferior to M3 alveolus (2).
63. Coronoid process shape: tall, anterior and posterior slopes similar (0); tall, posterior slope concave (1); low, rounded (2).
64. Anterior coronoid angle relative to horizontal ramus: near vertical, 90 to 100 degrees (0); slight posterior inclination, 100 to 110 degrees (1); strong posterior inclination, greater than 110 degrees (2).
65. Masseteric fossa depth: deeply excavated with strong anterior angle, inferior margin welldefined (0); rounded anterior margin, little inferior definition (1); deep fossa but poorly defined inferior margin (2).

UPPER DENTITION
Deciduous Upper Dentition
66. dP3 parastyle mesiodistal length: more than half metastyle length (0); less than half metastyle length (1).
67. dP3 metacone-paracone fusion: metacone distinct cusp (premetacrista slopes to metacone apex; See *Pterodon dasyuroides*) (0); metacone fused to paracone (premetacrista subhorizontal; See *Apterodon*) (1).

APPENDIX 2. — Continuation.

68. dP3 paracone morphology: pre- and postparacrista similar in slope (apex isosceles triangle inbuccal view) (0); preparacrista distally inclined (apex closer to right triangle in buccal view) (1).

69. dP3 metastyle notch: Small inflection between post-metacrista and metastyle (0); deep notch between post-metacrista and metastyle (1).

70. dP3 Protocone prominence: mesiodistal length shorter than buccolingual width (narrow) (0); mesiodistal length equal to or longer than buccolingual width (wide) (1). (modified from Bastl *et al.* 2014: character 2).

71. dP3 lingual cingulum: present (distinct lingual connection between parastyle and protocone) (0); absent (faint or no connection between parastyle and protocone) (1). (modified from Bastl *et al.* 2014: character 4).

72. dP4 main cusp height: paracone taller than metacone (0); Paracone subequal to metacone (1); Paracone shorter than metacone (2). *Ordered* (Modified from Bastl *et al.* 2014: character 6).

73. dP4 protocone orientation: Protocone projects mesially to parastyle margin (0); Protocone projects lingually and does not align with parastyle (1).

74. dP4 ectoflexus: Deep and distinct inflection between metacone and metastyle (0); Indistinct or shallow inflection between metacone and metastyle (1).

Adult Upper Dentition

75. Upper incisor count: 3 or more (0); 2 or fewer (1).

76. Lateral-most upper incisor: incisiform, similar to mesial incisor (0); caniniform (1).

77. Upper canine alveolar cross-section: distally tapers with mesiodistal axis more than 20% buccolingual axis (0); rounded with mesiodistal axis less than 20% buccolingual axis (1). (New Character relative to Borths & Stevens 2017c).

78. P3 lobe of the protocone or protocone alveolus: absent (0); present but small and alveolus merged lingual alveoli (1); protocone well-developed, individuated and alveolus distinct from lingual alveoli (2). (modified Polly 1996: character 9; Egi *et al.* 2005: character 4; Solé *et al.* 2014b: character 39; modified relative to Borths & Stevens 2017c).

79. P3 root number: two roots (0); three roots (1). (Solé *et al.* 2014b: character 40).

80. P3 contact with P4 parastyle: P3 contacts or aligned with P4 parastyle (0); P3 framed by P4 parastyle (1).

81. P4 parastyle: distinct (0); very reduced to absent (1). (modified Egi *et al.* 2005: character 8; Zack 2011: character 34; Solé *et al.* 2014b: character 41).

82. P4 protocone alignment: transversely aligned with paracone (0); mesially shifted relative to paracone (1). (Zack 2011: character 36; Solé *et al.* 2014b: character 42).

83. P4 protocone morphology: bulbous and distinct from paracone (0); weak separation from paracone, shelf to cingulum-like (1). (modified Polly 1996: character 10; Egi *et al.* 2005: character 6/7; Solé *et al.* 2014b: character 43).

84. P4 metastylar blade (=postmetacrista): short (0); elongate (1). (modified Egi *et al.* 2005: character 9; Zack 2011: character 35; Solé *et al.* 2014b: character 45).

85. P4 metastyle contact with M1: P4 metastyle braced buccally by M1 parastyle (0); P4 metastyle contacts mesial aspect of M1 parastyle (1).

86. M1 and M2 metastyle blade curvature: straight with carnassial notch (0); postmetacrista arcuate, no carnassial notch (1). (Zack 2011: character 42; Solé *et al.* 2014b: character 46).

87. M1 and M2 metastyle blade length: short, carnassial blade shorter than postmetacrista (0); intermediate, subequal to slightly longer than postmetacrista (1); elongate, greater than 1.5xlength of postmetacrista (2). *Ordered* (Egi *et al.* 2005: character 21; Solé *et al.* 2014b: character 47).

88. M1 and M2 metastyle robusticity (length divided by width): robust or 1.0 or greater (0); moderate or between 0.71 and 0.99 (1); gracile or 0.70 or less (2). (New Character relative to Borths & Stevens 2017c).

89. M1 postmetacrista to metastyle angle: Angle less than 130 degrees (0); Angle between 131 and 144 degrees (1); Angle greater than 145 degrees (2).

90. M1 mesiodistal length relative to M2: M1 subequal or longer than M2 (0); M1 shorter than M2 (1). (modified Solé *et al.* 2014b: character 50).

91. M1 and M2 premetaconule crista: present (0); absent (1). (modified Solé *et al.* 2014b: character 51).

92. M1 and M2 conules: metaconule and paraconule present (0); only paraconule present (1); metaconule and paraconule absent (2) (modified Solé *et al.* 2014b: character 53).

93. M1 and M2 precingulum and postcingulum: absent (0); present (1). (modified from Polly 1996: character 20; Egi *et al.* 2005: character 26; Solé *et al.* 2014b: character 54).

94. M1 and M2 precingulum and postcingulum connection: separated (0); fused lingually (1). (Solé *et al.* 2014b: character 55).

95. M1 and M2 protocone morphology: Triangular, mesial and distal margins angled (0); parallel mesial and distal margins (1). (modified Egi *et al.* 2005: character 14).

96. M1 protocone position relative to paracone and metacone: centered (0); directly lingual to the parastyle (1); mesial to the parastyle (2). *Ordered* (modified Egi *et al.* 2005: character 15; Solé *et al.* 2014b: character 56; State 2 added to Borths & Stevens 2017c).

97. M1 protocone lingual projection, measured as the ratio of the protocone buccolingual length divided by the length of the bases of the paracone and metacone: long, ratio greater than 0.9 (0); intermediate, ratio between 0.9 and 0.61 (1); short, ratio less than 0.6 (2).

98. M1 and M2 metacone mesiodistal length relative to paracone: shorter (0); subequal (1); longer (2). (modified Egi *et al.* 2005: character 12).

99. M1 and M2 metacone coronal cross section: circular (0); ovoid, slightly compressed buccolingually (1); ellipsoid, strong buccolingual compression (2).

100. M2 paracone compression: conical, rounded base (0); ovoid (slight buccolingual compression) (1); ellipsoid (strong buccolingual compression) (2).

101. M1 and M2 paracone and metacone separation: separated to base (0); fused between base and half of height (1); almost completely fused (2). *Ordered* (modified Polly 1996: character 28; Egi *et al.* 2005: character 10; Zack 2011: character 40).

102. M1 and M2 paracone height: paracone taller than metacone (0); paracone as tall as metacone (1); paracone shorter than metacone (2). *Ordered* (modified Egi *et al.* 2005: character 11; Zack 2011: character 41; Solé *et al.* 2014b: character 48).

103. M1 and M2 protocone height: shorter than paracone/metacone separation (0); same height as paracone/metacone separation (1); subequal to paracone/metacone apices (2). (compare to Zack 2011: character 49).

104. M2 parastyle: absent (0); present and shelf-like (1); present, single distinct cusp (2); present multiple distinct cusps (3). (modified from Egi *et al.* 2005: character 19 and Borths & Stevens 2017c).

105. M1 parastyle compared to M2: M1 parastyle relatively shorter than M2 parastyle (0); parastyle on M1 and M2 similar (1).

106. M1 and M2 buccal cingulum: absent (0); weak ridge along metastyle base (1); prominent shelf forms shallow basin between metastyle and cingulum (2). (modified Egi *et al.* 2005: characters 16/17).

107. M2 ectoflexus: strong, strong indentation (0); weak, slight curve (1); absent, straight (2). (modified Egi *et al.* 2005: character 18).

108. Ectoflexus depth on M1 and M2: M1 ectoflexus shallower than M2 (0); same relative depth between M1 and M2 (1); M2 lacks metastyle (no ectoflexus) (2). *Ordered* (compare to Zack 2011: character 52).

109. M3 metacone: present (0); absent (1). (modified Polly 1996: character 15; Zack 2011: character 53; Solé *et al.* 2014b: character 58).

Cranial characters

110. Nuchal crest morphology: medial to lateral trend from apex to mastoid (0); dorsolateral margin tapers medially with thin connection to exoccipital (1); lateral margins trend medially, very weak ridge connects to exoccipital (2). *Ordered* (modified Polly 1996: character 35).

111. Facial wing of the lacrimal: extensive (larger than orbit diameter) (0); moderate (slightly longer than orbit diameter) (1); reduced (shorter than orbit diameter) (2). (modified Polly 1996: character 36).

112. Foramen rotundum size: slightly larger than foramen ovale (0); much larger than foramen ovale (1). (Polly 1996: character 39).

113. Palatal rugosity or torus at distal margin of palate: well-expressed (0); smooth (1).

114. Zygomatic arch contact: short contact between zygomatic and squamosal (0); extensive contact between zygomatic and squamosal (1).

115. Superior squamosal morphology: superior and inferior margins parallel (0); torsion along superior margin (1).

116. Foramen ovale orientation: anterior orientation (0); palatal orientation (1).

117. Exoccipital condyle position: tall, lateral placement around foramen magnum (0); ventral placement around foramen magnum (1).

118. Notch between occipital condyles: ring-like with no rostral excavation (0); rounded indentation with condyles meeting medially below foramen magnum (1); deep excavation with occipital "processes" following notch (2).

119. Postmandibular process: vertical orientation (0); strong anterior curvature (1).

120. Posterior orbital process: present, strong expression (0); present, weak with frontal "peaked" (1); absent (2).

121. Frontal furrow: absent or indistinct (0); present and well-defined (1).

122. Palatine and pterygoid medial contact: parallel posterior to palatine torus (0); palatines trend medially or partially fuse (1); fused entire extent of palatines (2).

123. Pterygoid size: broad, ventral projection anteriorly extensive (0); short anterior extent, trends medially (1).

124. Frontoparietal suture in dorsal view: steep constriction (0); gentle curvature (1).

125. Lateral expansion of the mastoid process (Solé *et al.* 2015b): projects to midpoint of mandibular fossa (0); projects beyond mandibular fossa (1).

126. Mastoid/paroccipital process: short tubercle (0); well-defined, prong-like process (1).

127. Process at maxilla/jugal suture (Solé *et al.* 2015b): present (0); absent (1).

128. Squamosal constriction in dorsal view: present, squamosal does not extend laterally (0); absent, squamosal expanded laterally (1).

129. Squamosal ventral projection: same transverse plane as petrosal (0); ventral to petrosal (1).

130. Posterior braincase: broad lateral expansion (0); narrow (1).

131. Subarcuate fossa morphology (Polly 1996): cup-shaped (see *Pterodon*) (0); shallow and horseshoe-shaped (see *Hyaenodon*) (1).

132. Bridge of the stylomastoid foramen primitivum: absent or slender (0); robust (1); roofed over with secondary stylomastoid foramen (2). (Polly 1996: character 40)

133. Mastoid sinus lateral to foramen stylomastoid primitivum: absent (0); present (1). (Polly 1996: character 41).

134. Ridge of bone dividing posterior petrosal sinus from foramen stylomastoid primitivum (Polly 1996): present (0); reduced to absent (1). (Polly 1996: character 42)

135. Posterior petrosal sinus: absent (0); small (1); greatly inflated (2). (Polly 1996; character 43).

APPENDIX 2. — Continuation.

POSTCRANIA

Humerus

136. Humerus cross-section above brachial flange: triangular (0); rounded (1). (Polly 1996: character 44).

137. Brachial flange expression: medium (0); enlarged (1); reduced (2). (Polly 1996: character 47).

138. Entepicondylar foramen: present, rounded (0); present, elongate (1); absent (2).

139. Medial epicondyle: large (bulbous) (0); reduced (elongate) (1).

140. Capitulum morphology: rounded, clearly separated (0); cylindrical (1).

141. Greater tubercle of the humerus: prominent, taller than humeral head (0); subequal to height of humeral head (1).

Ulna

142. Proximal trochlear notch orientation: lateral position on shaft (0); medial position on shaft (1).

143. Radial notch orientation: curved and faces laterally (0); flattened and faces anteriorly (1). (Polly 1996: character 47).

144. Olecranon process length: longer than trochlear notch (0); subequal or shorter than trochlear notch (1).

145. Olecranon process orientation: projects medially (0); projects ventrally (1).

Femur

146. Third trochanter of femur: large (0); small (1). (modified Polly 1996: character 50).

Astragalus

147. Astragalar foramen: large (0); reduced (0). (Polly 1996: character 51).

148. Astragalar condyles divided by: shallow depression (0); well-defined fossa or groove (1).

149. Astragalar condyle orientation: oblique relative to astragalar neck (0); parallel to astragalar neck (1).

150. Astragalar head relative to condyles: horizontal orientation (0); slight vertical orientation (1). (Polly 1996: character 53).

151. Sustentacular facet connection to astraglar head: clearly separated from astragalar head (0); grades into articulation of astragalar head (1).

152. Sustentacular facet position on astragalar neck: plantar astragalar neck (0); medial astragalar neck (1).

Calcaneum

153. Peroneal tubercle: distinct and separated from cuboid facet (0); part of a flange that grades to cuboid facet (1).

154. Cuboid facet inclination: perpendicular to calcaneal neck (0); plantar inclination (1).

155. Calcaneal neck trend: dorsal and plantar margins parallel (0); tapers proximally to calcaneal tuberosity (1).

156. Astragalar facet angle: oblique orientation to calcaneal neck (0); parallels calcaneal neck (1). (modified Polly 1996: character 58).

APPENDIX 3. — List of all the taxa and specimens added to the matrix of Borths & Stevens (2017c, 2019), along with information on age and locality data.

Matthodon menui
Formation: Sables à Unios et Térédines *sensu stricto*;
Locality: Chavot, Monthelon, Cuis, Mancy and Grauves;
Geological Age: MP10;
Absolute Age: 51-48.6 Ma;
Country: France;
Citation: Solé *et al.* 2014a;
Specimens observed: MNHN.F.1939-586 (Holotype), left mandible with M_3 and roots of M_2 and distal root of M_1; MNHN.F.Cui14838, LP_4; MNHN.F.CHO14799, right mandible with canine, P_2 to M_2, and alveolus of P_1; T.S. 914, right maxillary with P^3 and P^4; T.S. 374, right mandible with complete P_2-P_4, and M_3, fragmentary M_1 and M_2, and alveolus of P_1; MNHN.F.Ma14832, RP_4; MNHN.F.L-68-GR, left mandible with M_1 and alveoli of P_2 to P_4 and M_2; MNHN.F.L-58-Ma, RM^2.

Paracynohyaenodon magnus
Formation: Quercy;
Locality: Robiac and Le Bretou;
 Geological Age: MP16;
Absolute Age: 51-48.6 Ma;
Country: France;
Specimens observed: BRT 939 (Holotype), right maxillary bearing P^4 to M^2; RBN 5434, maxillaries bearing right P^1 to P^4, and alveoli of the canines and left P^1 to P^3; Rbn-NM 1018, right P^4; right mandible bearing M_1 to M_3; LAV 1310, left maxillary bearing P^3 to M^2; LAV 1312, left maxillary bearing M^2 and M^3; BRT 936, right mandible bearing P_2 to M_2; RBN 5434, right mandible bearing the canine, and P_1 to P_4 and left mandible bearing M_2 and M_3; LAV 1314, right mandible bearing P_4 to M_2;
Citation: Lange-Badré 1979; Crochet 1991.

Paracynohyaenodon schlosseri
Formation: Quercy;
Locality: Robiac, Le Bretou, Lavergne, La Bouffie, Les Pradigues, Les Clapiès;
Geological Age: MP16-MP17a;
Absolute Age: 40-33.9 Ma;
Country: France;
Specimens observed: Qu B 393 (Holotype), right mandible bearing M_1 to M_3; LAV 1310, left maxillary bearing P^3 to M^2; LAV 1312, left maxillary bearing M^2 and M^3; Ma Pq 60, right mandible bearing P_1 to M_3; MNHN.F.QU8539, right mandible bearing P_4 and M_1; PLV 117, left mandible bearing P_3 to M_2;
Citation: Lange-Badré 1979; Crochet 1991.

Matthodon peignei **n. sp.**
Formation: Lacustrine limestone of Montpellier, proposed as Lutetian in age in previous study but here questioned as late Ypresian/early Lutetian in age;
Locality: Aumelas, Hérault, France;
Geological Age: MP10-MP11?
Absolute Age: 51-40.4 Ma;
Country: France;
Specimens observed: UM-AUM694, left mandible bearing the p2-m3 and the alveoli of the canine and p1; UM-AUM268, left mandible bearing the m2 and m3.

Oxyaenoides aumelasiensis **n. sp.**
Formation: Lacustrine limestone of Montpellier, proposed as Lutetian in age in previous study but here questioned as late Ypresian/early Lutetian in age;
Locality: Aumelas, Hérault, France;
Geological Age: MP10-MP11?
Absolute Age: 51-40.4 Ma;
Country: France;
Specimens observed: UM-AUM693, left mandible bearing m3, the anterior root and talonid of the m1, and the posterior alveolus of the p4, and the alveoli of m2; UM-AUM686, right M2; UM-AUM692, combination of a left maxillary fragment bearing the P2-M1, a right maxillary fragment bearing the P3-P4, the protocone of the M1 and the alveoli of the P2; UM-AUM695, labial part of a M1.

Leonhardtina meridianum **n. sp.**
Formation: Lacustrine limestone of Montpellier, proposed as Lutetian in age in previous study but here questioned as late Ypresian/early Lutetian in age;
Localities: Aumelas, Hérault, France; Rouzilhac, Aude, France;
Geological Age: MP10-MP11?
Absolute Age: 51-40.4 Ma;
Country: France;
Specimens observed: UM-AUM54, right mandible bearing p3 to m3; UM-AUM530, right maxillary fragment bearing M2 and M3; MNHN.F.RZ142, right mandible bearing p2-p4 and m3.

Prodissopsalis eocaenicus
Formation: Karst fillings in an aberrant siderolitic facies
Locality: Geiseltal-Untere-Mittelkohle, Geiseltal-Obere Mittelkohle, Egerkingen γ;
Geological Age: MP12-MP13? (possibly MP14);
Absolute Age: 48.6-40.4 Ma;
Countries: Germany, Switzerland;
Specimens observed: Leo III-394; skull bearing the right P1-P4 and M1-M3, left P3-P4 and M1-M3, and the alveoli of the I2, I3, and canines; XXXV-327, left mandible bearing canine, p3-p4 and m1-m3; XXXVI-255, right mandible bearing p3-p4 and m1-m3.
Citation: Van Valen 1965 ; Lange-Badré & Haubold 1990.

APPENDIX 4. — Stratigraphic range (MP levels) of the European hyaenodonts and numerical ages for the MP levels.

RANGE (MP LEVEL) OF THE EUROPEAN HYAENODONTS

Allopterodon torvidus MP13-MP14
Apterodon gaudryi .... Rupelian
Arfia gingerichi MP7
Boritia duffaudi .... MP8+9
Cynohyaenodon cayluxi MP16-MP17a
Cynohyaenodon trux MP12-MP14
Eoproviverra eisenmanni MP7
Eurotherium matthesi MP11
Eurotherium theriodis MP13-MP14
Galecyon morloi MP7
Hyaenodon exiguus MP22-MP30
Hyaenodon minor MP17a-MP18
Kerberos langebadreae MP16
Leonhardtina gracilis MP12-MP13
Leonhardtina meridianum n. sp. MP10-MP11
Lesmesodon spp. MP11
Matthodon tritens MP11
Matthodon menui MP10
Matthodon peignei n. sp. MP10-MP11
Morlodon vellerei .... MP8+9-MP10
Oxyaenoides aumelasiensis n. sp. MP10-MP11
Oxyaenoides bicuspidens MP11
Oxyaenoides lindgreni MP10
Paracynohyaenodon spp. MP16-MP17a
Paroxyaena spp. MP16-MP17b
Parvagula palulae MP7
Preregidens langebadrae .... MP8+9
Prodissopsalis eocaenicus MP12-MP14
Prototomus minimus .... MP7-MP8+9
Proviverra typica MP12-MP14
Pterodon dasyuroides MP18-MP20
Quercytherium simplicidens MP17a-MP18
Quercytherium tenebrosum MP16-MP17a
Thereutherium thylacodes MP23-MP26

NUMERICAL AGES FOR EACH MP LEVEL

Numerical ages were extracted from Escarguel *et al.* (1997) and Vandenberghe *et al.* (2012).

MP	Start	End	ICS stages
30	23.2	23.03	Chattian
29	23.9	23.2	Chattian
28	24.6	23.9	Chattian
27	25.4	24.6	Chattian
26	27.3	25.4	Chattian
25	28.8	27.3	Chattian-Rupelian
24	30	28.8	Lutetian
23	30.9	30	Rupelian
22	32.5	30.9	Rupelian
21	33.9	32.5	Priabonian
20	34	33.9	Priabonian
19	35	34	Priabonian
18	37	35	Priabonian
17b	37.5	37	Priabonian
17a	37.8	37.5	Priabonian
16	40	37.8	Bartonian
15	41.2	40	Lutetian
14	43.5	41.2	Lutetian
13	44.9	43.5	Lutetian
12	46.3	44.9	Lutetian
11	47.8	46.3	Lutetian
10	50.8	47.8	Ypresian
8+9	55.2	50.8	Ypresian
7	56	55.2	Ypresian
6	57.2	56	Thanetian

APPENDIX 5. — Input file for the Bayesian phylogenetic analysis, formatted for MrBayes.

http://sciencepress.mnhn.fr/sites/default/files/documents/en/g2020v42a13_appendix_5.txt

This file is the input code used to perform the analysis that includes 19 ordered characters (listed after "ctype ordered" near the end of the file). It also lists all parameters input into MrBayes, including clock rate, burn-in period, and number of replications. The file can be used directly to run the analysis in MrBayes. With the MrBayes window open, type in the command "execute", type a quotation ("), then drag the tip-dating analysis file, close with a second quotation mark ("); you should see "MrBayes > execute"location_on_ the_computer_with_file_name" on the MrBayes window. Then push the "enter" button to perform the analysis.

APPENDIX 6. — 'Allcompat' summary tree formatted for FigTree.

http://sciencepress.mnhn.fr/sites/default/files/documents/en/g2020v42a13_appendix_6.txt

The following method follows the one proposed by Borths & Stevens (2017c: supplementary file 3).

This file contains the tree and all summary tree statistics output as part of the summary tree file inferred from the analysis performed in MrBayes. You can open the file directly in the tree-viewing software FigTree to open the tree.

To adjust the age estimates to an absolute timescale rather than an internal hyaenodont timescale, subtract the age (mean or median) listed for the fixed taxon (*Pakakali*) from 25 (the fixed age used for *Pakakali*) and add the result to each age. For example, to calculate the median date of the divergence of *Prionogale* from *Namasector*: calculate the difference between the fixed age of *Pakakali* (25 Ma) from the age of *Pakakali* on the tree (13.61 Ma) which is 11.39 Ma. Add 11.39 Ma to the age of the node that unites Prionogalidae (12.82 + 11.39) to get the estimated, absolute divergence date between *Prionogale* and *Namasector* (24.21 Ma).

To calculate evolutionary rate of change select "ratelgrBrlens_mean" or "ratelgrBrlens_median." These display the relative rate of evolutionary change for the tree. To convert the relative evolutionary rate into absolute evolutionary rate (% change/site/Ma), multiply the "ratelgrBrlens" value by the mean or median clockrate ouput in the .pstat file from MrBayes. In the case of the ordered analysis, the median clockrate is 0.007547 and the mean clockrate is 0.01022. Multiply the "ratelgrBrlens" by the clockrate value then multiply by 100 to express absolute % change/site/Ma. For example, to calculate the median % change/site/Ma for the branch supporting Prionogalidae: $1.14 \times 0.007547 \times 100 = 0.86$ % change/site/Ma.

APPENDIX 7. — Estimations of the body mass of selected hyaenodonts, oxyaenids, and mesonychids.

Taxa 1	Taxa 3	Species	Bodymass (kg)	Bodymass (g)	Ln bodymass	FAD mp	LAD mp
Hyaenodonta	Proviverrinae	*Alienetherium buxwilleri*	5.5	5500	8.612503371	13	13
Hyaenodonta	Proviverrinae	*Allopterodon bulbosus*	0.73	730	6.593044534	17b	19
Hyaenodonta	Proviverrinae	*Allopterodon minor*	2.1	2100	7.649692624	16	19
Hyaenodonta	Proviverrinae	*Allopterodon torvidus*	0.58	580	6.363028104	13	14
Hyaenodonta	Arfiinae	*Arfia gingerichi*	1.63	1630	7.396335294	7	7
Hyaenodonta	Proviverrinae	*Boritia duffaudi*	2.58	2580	7.855544678	8	9
Hyaenodonta	Proviverrinae	*Cartierodon egerkingensis*	28.65	28650	10.26290872	13	13
Hyaenodonta	Proviverrinae	*Cynohyaenodon blainvillei*	0.44	440	6.086774727	19	19
Hyaenodonta	Proviverrinae	*Cynohyaenodon cayluxi*	1.73	1730	7.455876687	16	17a
Hyaenodonta	Proviverrinae	*Cynohyaenodon lautricensis*	3	3000	8.006367568	16	16
Hyaenodonta	Proviverrinae	*Cynohyaenodon rutimeyeri*	1.89	1890	7.544332108	14	14
Hyaenodonta	Proviverrinae	*Cynohyaenodon trux*	1.17	1170	7.064759028	12	14
Mesonychia	Mesonychidae	*Dissacus blayaci*	39.08	39080	10.57336611	10	10
Mesonychia	Mesonychidae	*Dissacus europaeus*	9.25	9250	9.132378831	6	6
Mesonychia	Mesonychidae	*Dissacus filholi*	16.89	16890	9.73447701	10	10
Mesonychia	Mesonychidae	*Dissacus progressus*	56.59	56590	10.94358757	10	10
Mesonychia	Mesonychidae	*Dissacus raslanloubatieri*	13.14	13140	9.483416292	8	9
Mesonychia	Mesonychidae	*Dissacus rougierae*	9.01	9014	9.106573419	7	7
Hyaenodonta	Proviverrinae	*Eoproviverra eisenmanni*	0.05	50	3.912023005	7	7
Hyaenodonta	Proviverrinae	*Eurotherium matthesi*	6.47	6470	8.774931387	11	11
Hyaenodonta	Proviverrinae	*Eurotherium theriodis*	6.88	6880	8.836373931	13	14
Hyaenodonta	Sinopinae	*Galecyon gallus*	0.77	770	6.646390515	7	7
Hyaenodonta	Sinopinae	*Galecyon morloi*	0.6	600	6.396929655	7	7
Hyaenodonta	Hyaenodontinae	*Hyaenodon brachyrhynchus*	17.06	17060	9.744491821	17	23
Hyaenodonta	Hyaenodontinae	*Hyaenodon gervaisi*	50.36	50360	10.82695249	17b	29
Hyaenodonta	Hyaenodontinae	*Hyaenodon heberti*	30.53	30530	10.32646509	17b	19
Hyaenodonta	Hyaenodontinae	*Hyaenodon minor*	7.65	7650	8.942460927	17a	18
Hyaenodonta	Hyaenodontinae	*Hyaenodon requieni*	38.3	38300	10.55320518	17a	20
Hyaenodonta	Hyaenodontinae	*Hyaenodon rossignoli*	4.48	4480	8.407378325	18	19
Hyaenodonta	Hyainailourinae	*Kerberos langebadreae*	87.69	87690	11.38156315	16	16
Hyaenodonta	Proviverrinae	*Leonhardtina godinoti*	0.99	990	6.897704943	10	10
Hyaenodonta	Proviverrinae	*Leonhardtina meridianum* n. sp.	0.84	840	6.733401892	10	10
Hyaenodonta	Proviverrinae	*Leonhardtina gracilis*	1.73	1730	7.455876687	12	13
Hyaenodonta	Proviverrinae	*Lesmesodon behnkeae*	8.31	8310	9.025214888	11	11
Hyaenodonta	Proviverrinae	*Lesmesodon edingeri*	2.21	2210	7.700747795	11	11
Hyaenodonta	Proviverrinae	*Matthodon menui*	12.31	12310	9.418167219	10	10
Hyaenodonta	Proviverrinae	*Matthodon peignei* n. sp.	15.75	15750	9.664595644	10	10
Hyaenodonta	Proviverrinae	*Matthodon tritens*	19.15	19150	9.860057995	11	11
Hyaenodonta	Proviverrinae	*Minimovellentodon russelli*	1.18	1180	7.073269717	8	9
Hyaenodonta	Proviverrinae	*Morlodon vellerei*	2.25	2250	7.718685495	8	10
Oxyaenidae	Oxyaeninae	*Oxyaena gulo*	12.3	12300	9.417354541	8	9
Oxyaenidae	Oxyaeninae	*Oxyaena woutersi*	6.48	6480	8.776475789	7	7
Hyaenodonta	Proviverrinae	*Oxyaenoides aumelasiensis* n. sp.	4.24	4240	8.352318548	10	10
Hyaenodonta	Proviverrinae	*Oxyaenoides bicuspidens*	14.19	14190	9.56029277	11	11
Hyaenodonta	Proviverrinae	*Oxyaenoides lindgreni*	9.71	9710	9.180911561	10	10
Hyaenodonta	Proviverrinae	*Oxyaenoides schlosseri*	16.93	16930	9.736842475	13	14
Mesonychia	Mesonychidae	*Pachyaena* cf. *gracilis*	38.98	38980	10.57080397	8	9
Mesonychia	Mesonychidae	*Pachyaena* cf. *ossifraga*	74.89	74890	11.22377565	8	9
Mesonychia	Mesonychidae	*Pachyaena gigantea*	162.44	162440	11.99806398	8	9
Hyaenodonta	Proviverrinae	*Paenoxyaenoides liguritor*	18.02	18020	9.799237531	18	18
Oxyaenidae	Ambloctinae	*Palaeonictis gigantea*	12.04	12040	9.395989719	7	9
Hyaenodonta	Proviverrinae	*Paracynohyaenodon magnus*	3.85	3850	8.255828427	16	16
Hyaenodonta	Proviverrinae	*Paracynohyaenodon schlosseri*	2.97	2970	7.996317232	16	17a
Hyaenodonta	Hyainailourinae	*Parapterodon lostangensis*	103.62	103620	11.54848564	19	19
Hyaenodonta	Hyainailourinae	*Paroxyaena galliae*	52.78	52780	10.87388761	16	17b
Hyaenodonta	Proviverrinae	*Parvagula palulae*	0.06	60	4.094344562	7	7
Hyaenodonta	Proviverrinae	*Praecodens acutus*	1.09	1090	6.993932975	13	13
Hyaenodonta	Proviverrinae	*Preregidens langebadrae*	3.53	3530	8.16905315	8	9
Hyaenodonta	Proviverrinae	*Prodissopsalis eocaenicus*	18.02	18020	9.799237531	12	14
Hyaenodonta	Proviverrinae	*Protoproviverra palaeonictides*	0.91	910	6.8134446	10	10
Hyaenodonta	Sinopinae	*Prototomus girardoti*	0.45	450	6.109247583	7	9
Hyaenodonta	Sinopinae	*Prototomus minimus*	0.24	240	5.480638923	7	9
Hyaenodonta	Proviverrinae	*Proviverra typica*	0.42	420	6.040254711	12	13
Hyaenodonta	Hyainailourinae	*Pterodon dasyuroides*	51.56	51560	10.85050146	18	20
Hyaenodonta	Proviverrinae	*Quercytherium simplicidens*	3.12	3120	8.045588281	17a	18
Hyaenodonta	Proviverrinae	*Quercytherium tenebrosum*	2.89	2890	7.969011781	16	17a

APPENDIX 8. — Authorships of the taxa cited in the article (species and genera).

Alienetherium buxwilleri Lange-Badré, 1981
Allopterodon Ginsburg, 1978
Allopterodon bulbosus (Lange-Badré, 1979)
Allopterodon minor (Filhol, 1877)
Allopterodon torvidus (Van Valen, 1965)
Anchomomys Stehlin, 1916
Apterodon gaudryi Fischer, 1880
Apterodon intermedius Lange-Badré & Böhme, 2005
Arfia gingerichi Smith & Smith, 2001
Aumelasia gabineaudi Sudre, 1980
Boritia duffaudi Solé, Falconnet & Laurent, 2014
Cartierodon egerkingensis Solé & Mennecart, 2019
Cynohyaenodon Filhol, 1873
Cynohyaenodon blainvillei Brunet, 1977
Cynohyaenodon cayluxi Filhol, 1873
Cynohyaenodon lautricensis Lange-Badré, 1978
Cynohyaenodon rutimeyeri Van Valen, 1965
Cynohyaenodon trux Van Valen, 1965
Dichobune robertiana Gervais, 1848
Dissacus blayaci Stehlin, 1926
Dissacus europaeus Lemoine, 1891
Dissacus filholi (Lemoine, 1891)
Dissacus progressus Crusafont Pairó & Golpe-Posse, 1968
Dissacus raslanloubatieri Solé, Godinot, Laurent, Galoyer & Smith, 2019
Dissacus rougierae Solé, Godinot, Laurent, Galoyer & Smith, 2019
Eoproviverra eisenmanni (Godinot, 1981)
Eurotherium Polly & Lange-Badré, 1993
Eurotherium matthesi (Lange-Badré & Haubold, 1990)
Eurotherium theriodis (Van Valen, 1965)
Galecyon Gingerich & Deutsch, 1989
Galecyon gallus Solé, Gheerbrant & Godinot, 2013
Galecyon morloi Smith & Smith, 2001
Gazinocyon vulpeculus (Matthew & Granger, 1915)
Hyaenodon brachyrhynchus de Blainville, 1839
Hyaenodon exiguus (Gervais, 1872)
Hyaenodon gervaisi Martin, 1906
Hyaenodon heberti Filhol, 1876
Hyaenodon minor Gervais, 1852
Hyaenodon requieni Gervais, 1848-1852
Hyaenodon rossignoli Lange-Badré, 1979
Kerberos langebadreae Solé, Amson, Borths, Vidalenc, Morlo & Bastl, 2015
Leonhardtina Matthes, 1952
Leonhardtina godinoti Solé, Falconnet & Laurent, 2014
Leonhardtina gracilis Matthes, 1952
Leonhardtina meridianum n. sp.
Lesmesodon Morlo & Habersetzer, 1999
Lesmesodon behnkeae Morlo & Habersetzer, 1999

Lesmesodon edingeri (Springhorn, 1982)
Lophiodon isselensis Fischer, 1929
Lophiodon parisiense
Matthodon Lange-Badré & Haubold, 1990
Matthodon menui (Rich, 1971)
Matthodon peignei n. sp.
Matthodon tritens Lange-Badré & Haubold, 1990
Minimovellentodon russelli Solé, Falconnet & Laurent, 2014
Morlodon Solé, 2013
Morlodon vellerei Solé, 2013
Namasector Morales, Pickford & Salesa, 2008
Namasector soriae Morales, Pickford & Salesa, 2008
Oxyaena gulo Matthew & Granger, 1915
Oxyaena woutersi (Lange-Badré & Godinot, 1982)
Oxyaenoides Matthes, 1967
Oxyaenoides aumelasiensis n. sp.
Oxyaenoides bicuspidens Matthes, 1967
Oxyaenoides lindgreni (Rich, 1971)
Oxyaenoides schlosseri (Rütimeyer, 1891)
Pachyaena Cope, 1874
Pachyaena gigantea Osborn & Wortman, 1892
Paenoxyaenoides liguritor Lange-Badré, 1979
Pakakali Borths & Stevens, 2017
Pakakali rukwaensis Borths & Stevens, 2017
Palaeonictis gigantea de Blainville, 1842
Paracynohyaenodon magnus Crochet, 1988
Paracynohyaenodon schlosseri Martin, 1906
Parapterodon lostangensis Lange-Badré, 1979
Paroxyaena galliae Filhol, 1881
Parvagula Lange-Badré, 1987
Parvagula palulae Lange-Badré, 1987
Praecodens acutus Lange-Badré, 1981
Preregidens Solé, Falconnet & Vidalenc, 2015
Preregidens langebadrae Solé, Falconnet & Vidalenc, 2015
Prionogale Schmidt-Kittler & Heizmann, 1991
Prionogale breviceps Schmidt-Kittler & Heizmann, 1991
Prodissopsalis eocaenicus Matthes, 1952
Protoproviverra palaeonictides (Lemoine, 1880)
Prototomus girardoti Smith & Smith, 2001
Prototomus minimus Smith & Smith, 2001
Proviverra Rütimeyer, 1862
Proviverra typica Rütimeyer, 1862
Pterodon dasyuroides de Blainville, 1839
Quercytherium simplicidens Lange-Badré, 1975
Quercytherium tenebrosum Filhol, 1880
Simbakubwa kutokaafrika Borths & Stevens, 2019
Thereutherium Filhol, 1876
Thereutherium thylacodes Filhol, 1876