geodiversitas

Memorial Stéphane Peigné – Carnivores of the Cenozoic –

Carnivora from the early Oligocene
of the 'Phosphorites du Quercy'
in southwestern France

Louis de BONIS, Axelle GARDIN & Cécile BLONDEL

MUSÉUM
NATIONAL D'HISTOIRE NATURELLE

PUBLICATIONS
SCIENTIFIQUES

Carnivora from the early Oligocene
of the 'Phosphorites du Quercy' in southwestern France

Louis de BONIS
Axelle GARDIN
Cécile BLONDEL
Palevoprim: laboratoire de Paléontologie, Évolution, Paléoécosystèmes, Paléoprimatologie,
Bâtiment B35 TSA51106, 6 rue Michel Brunet F-86073 Poitiers cedex 9 (France)
louis.debonis@univ-poitiers.fr
axelle.gardin@univ-poitiers.fr
cecile.blondel@univ-poitiers.fr

KEY WORDS
Caniformia,
Feliformia,
Amphicynodontidae,
Ursidae,
Mustelidae,
Nimravidae,
sabre-toothed
carnivorans,
Paleogene,
MP 22,
lectotypification,
new combination,
new genera,
new species.

ABSTRACT
The early Oligocene carnivorans from the Quercy phosphorites (southwestern France) studied herein come from three localities: Mas de Got, La Plante2 and Valbro, all in MP 22 of the European Paleogene Mammal stratigraphy scheme. These localities contain a rich carnivoran fauna with weasel-sized to tiger-sized species in diverse families, especially Amphicynodontidae (with four species of *Pachycynodon* and two of *Amphicynodon*) and Nimravidae. New taxa are described (*Wangictis* n. gen., *Peignictis pseudamphictis* n. gen., n. sp.). We note the absence of taxa often present in the sites of the Quercy phosphorites, such as the family Amphicyonidae and, in the Feloidea, the genera *Stenoplesictis* Filhol, 1880 and *Palaeoprionodon* Filhol, 1880. The fauna of the three localities is typical of the early Oligocene prior to a faunal turnover in the middle Oligocene. Future research in the Quercy will give more precision to the timing and mode of this faunal event.

MOTS CLÉS
Caniformia,
Feliformia,
Amphicynodontidae,
Ursidae,
Mustelidae,
Nimravidae,
carnivores à canines-en-
sabre,
Paléogene,
MP 22,
lectotypification,
combinaison nouvelle,
genres nouveaux,
espèce nouvelle.

RÉSUMÉ
Carnivores de l'Oligocène inférieur des 'Phosphorites du Quercy', sud-ouest de la France.
Les carnivores de l'Oligocène inférieur des phosphorites du Quercy (sud ouest de la France) examinés dans cette étude proviennent de trois localités Mas de Got, La Plante2 et Valbro, toutes dans l'unité MP 22 de l'échelle mammalienne du Paléogène. Elles contiennent une riche faune de carnivores, dont les tailles s'étagent depuis celle d'une belette jusqu'à celle d'un tigre, à travers diverses familles, en particulier celles des Amphicynodontidae (avec quatre espèces de *Pachycynodon* et deux d'*Amphicynodon*) et des Nimravidae. De nouveaux taxons sont décrits (*Wangictis* n. gen., *Peignictis pseudamphictis* n. gen., n. sp.). Nous notons également l'absence de certaines formes très souvent présentes dans les sites fossilifères des phosphorites du Quercy, comme la famille des Amphicyonidae et, parmi les Feloidea, les genres *Stenoplesictis* Filhol, 1880 et *Palaeoprionodon* Filhol, 1880. La faune de ces trois localités est typique de l'Oligocène inférieur avant un changement qui se produira vers le milieu de l'Oligocène. Les futures recherches dans le Quercy devront préciser la date et les modalités de cet évènement.

INTRODUCTION

The Quercy area is situated in southwestern France, near the city of Cahors. A large part of this area is covered by Jurassic limestone in which erosion hollowed fissures, caves and galleries to form a large karstic system. Through time, there was a succession of erosion and infilling by sediments. The sediments contain phosphate deposits and, during the last third of the 19th century, they were worked to extract the 'phosphorite', which was used as a fertilizer for cultivation and farming. In several localities the sediments were rich in diverse categories of plant, invertebrate and vertebrate fossils. In particular, countless thousands of vertebrate remains, comprising skulls, teeth and bones, were unearthed by the workers from many quarries lying across an area of hundreds of km². These fossils were sold or given to different people, amateurs and professionals, so that the fossils are now scattered in collections across the whole world. The geological age of the specimens extends from the early Eocene (Astruc *et al.* 2000) to the early Miocene (Sigé *et al.* 1991). Nevertheless, most of the fossils were deposited from the late Eocene to the late Oligocene but are today all mixed together. Therefore, the numerous paleontological studies of the old collections during the 19th could not work out problems of evolution and concluded that the fossils were mixed at every locality (see Bonis 2011 for more complete references).

The same has been the case concerning the Carnivora in more recent publications (Teilhard 1915; Piveteau 1931, 1942, 1962; Bonis 1966, 1971, 1981; Ginsburg 1966, 1979; Lange 1969, 1970; Wolsan & Lange-Badré 1996; Peigné & Bonis 1999; Peigné 2000, 2001, 2003), in which new genera and species were described but did not clear up the different lineages. At that time, many people thank thought all the fossil bearing fissures were emptied.

Another period began during the 1930th when new researches (Gèze 1938a, b) demonstrated that two Quercy localities had retained their sediment infills, including fossil fauna. Each of these fossil faunas was homogeneous, without any mixing. From the middle of the 1960s, a team of researchers from some French universities (Montpellier UM, Paris 6 [UPMC], Lyon 1 [Claude Bernard], Poitiers and the Muséum national d'Histoire naturelle, Paris) decided to carry out paleontological field campaigns in the Quercy area. Over the years, the results were published, bearing out the homogeneity of the sites (Vianey-Liaud & Legendre 1986) and describing hundreds of species from several orders of mammals. Some of these Quercy localities played a significant role in the creation of the European mammal stratigraphic scheme for the Paleogene numbered from MP 1 to MP 30, with the type levels MP 17b (Perrière), MP 19 (Escamps), MP 23 (Itardies), MP 25 (Garouillas), MP 26 (Mas de Pauffié) and MP 28 (Pech du Fraysse) all coming from the Quercy area (see Biochrom'97 1997).

Carnivores (Hyaenodonta and Carnivora) are present in most of the sites and have been the subject of several papers. In the present article we describe early Oligocene Carnivora specimens belonging to different taxa coming from localities of MP 22: La Plante2, Mas de Got, and Valbro.

MATERIAL AND METHODS

The studied material comes from several field campaigns in the Quercy. The fossils were obtained both by excavating and by washing-screening as well. Measurements were made by digimatic callipers to the nearest 1/100 mm and presented to the nearest 1/10. The new material was compared to the old collections of Quercy, containing most of the type specimens, as well as to fossils from other localities. The photographs were taken with a camera Nikon Coolpix 750 and processed in Adobe Photoshop.

ABBREVIATIONS

D	deciduous upper molar;
d	deciduous lower molar;
aac	anterior (mesial) accessory cusp;
aacd	anterior (mesial) accessory cuspid;
pac	posterior (distal) accessory cusp;
pacd	posterior (distal) accessory cuspid;
L	length;
w	width;
w1	mesial width;
w2	distal width;
tr	trigonid;
tl	talonid;
mts	metastyle;
MP	Mammal Paleogene reference levels.

Institutions

MNHN.F	Muséum national d'Histoire naturelle, Paris, collections de Paléontologie;
NHMB	Naturhistoriches Museum Basel;
UM	Université de Montpellier;
UP	Université de Poitiers.

MP 22 Localities

VD, VBO, VBOA	Valbro;
MGA, MGB	Mas de Got;
LPL	La Plante2.

Teeth
We use capitals for the upper teeth and lower case for lower teeth.

SYSTEMATICS

Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Parvorder URSIDA Tedford, 1976
Family AMPHICYNODONTIDAE Simpson, 1945

Genus *Amphicynodon* Filhol, 1881

TYPE SPECIES. — *Cynodon velaunus* Aymard, 1846 (by original designation).

DIAGNOSIS. — Amphicynodontidae with a relatively low skull with a faint sagittal crest slightly more developed distally; elongate muzzle; ossified bullae; shallow suprameatal fossa; alisphenoid canal present. Dental formula 3/3 I, 1/1 C, 4/4 P, 2-3/3 M. Simple premolars P1-P3 and p1-p3; short P4 with robust protocone and short metastyle; triangular M1 with tiny parastyle without para-

conule but with metaconule; M2 more or less reduced; p4 with pacd or not; grouped and not very tall trigonid of m1, horizontal wear of the cuspids, metaconid as high as the paraconid; not very elongate m2 with paraconid present or not, metaconid as high or higher than the protoconid; small rounded m3.

The genus is present in the old Quercy collections represented by several species but also in the new early Oligocene localities (Table 1).

REMARK

Aymard (1846) created the species *C. velaunus* for a fossil from the early Oligocene locality Ronzon (France) that he described a few years later (Aymard 1850). He added another species, *C. palustris* Aymard, 1853 for a hemi-mandible slightly larger than that of *C. velaunus*. Later (1881) Filhol, considering that *C. palustris* was very different from *C. velaunus*, created the new genus *Amphicynodon* for it. Finally, the name *Cynodon* being pre-occupied by a fish, Trouessart (1904) proposed the genus name *Aymardia*. However, following the rules of nomenclature, *Amphicynodon* Filhol, 1881 has priority, although Teilhard (1915), without taking into account either Filhol or Trouessart, continued using *Cynodon*. Later, several species of *Amphicynodon* were described, principally from the old collections of the Quercy, thus lacking biostratigraphic support. We shall here focus on the specimens from MP 22.

Amphicynodon typicus (Schlosser, 1888)
(Fig. 1B)

TYPE SPECIMEN. — Neotype by designation (Cirot & Bonis [1992: 121]): left hemi-mandible with p4-m2 UP PC46 from Pech Crabit, MP 23.

NEW MATERIAL. — Left-hemi-mandible UP VAL2; right hemi-mandible with m2 UM VD13.

DESCRIPTION

The left hemi-mandible UP VAL2 (Fig. 1B) preserves the tooth series p2-m3. The corpus is elongate with a convex lower border. The ascending ramus and the distal part of the mandible are broken off, leaving only the rostral part of the masseteric fossa. The teeth are unworn; the single-rooted p1 is missing. The p2 is asymmetric, the distal portion being very elongate, p3, separated by a short diastema, is larger and less asymmetric. The p4, the least asymmetric premolar, is tall, and pointed with a pacd and the base of the crown slightly upturned mesially and distally.

A faint cingulid underlines the base of the buccal side of m1; the protoconid, higher than the p4, is slightly bucco-lingually compressed; the paraconid, set slightly obliquely, extends the shearing blade of the trigonid; the conical, reduced metaconid is not visible in buccal view; a relatively short talonid displays a large and compressed hypoconid and a very low entoconid, in contact at their bases, creating a V-shaped talonid basin although most of the surface is occupied by the sloping lingual face of the hypoconid. This structure is seen in *A. typicus*.

The protoconid and metaconid of m2, the former being slightly the larger, enclose a well-developed mesial fovea. The distal fovea, enclosed by the hypocristid and entocristid, is more elongate. The buccal portion of m3 is partially broken off, the tooth seems to have had a circular flat basin enclosed by a swollen cristid. Two main characters present in UP VAL2 and *A. typicus* are the pointed p4 and the trenchant talonid of m1. They seem sufficient to allow us to place the specimen in this species.

The hemi-mandible UM VD13 is shallow and includes fragments of the roots of p3 and p4, alveoli of m1, m3 and an unworn m2. Its outline tapers distally. The preprotocristid of a well-developed protoconid runs to a tiny mesio-lingual bulge corresponding to the paraconid, which is separated by a notch from the metaconid. The latter, as high as the protoconid, is followed directly by the postmetacristid to join a globular hypoconid, enclosing a small but deep talonid basin. The trigonid occupies ⅔ of the crown.

Amphicynodon sp. 1
(Fig. 1A)

DESCRIPTION

Less complete than the former, another left hemi-mandible (UP VAL1) retains only p3-p4, m2 and alveoli of p1-2, m1, m3 (Fig. 1A). It is slightly larger than UP VAL2. The dentition is unworn, p1 and m3 are single rooted, and p3 is slender and asymmetric. The p4 is less asymmetric and includes a pacd, the crown terminating distally in a small upturn. Based on the alveoli the length of m1 is estimated to 8 mm. The structure of m2 is unusual with a large mesial fovea limited mesially by a cristid and, distally by the cristids of protoconid and metaconid, two pyramidal cuspids of similar size, with convex buccal and lingual and lingual faces respectively. There is a very long basin bordered by the hypocristid and entocristid, terminating in the hypoconid and entoconid respectively, followed by cristids distally closing the basin. An m2 that long is unusual in *Amphicynodon*. Without taking into account forms with an especially short m2 (*A. velaunus* and *A teilhardi*), the index (length m2/length m1) × 100 is 75 (the length of m1 measured from the alveoli). In the sample from the locality Itardies (MP 23), the same index is 44-62, mean 52. It is 54 for the type specimen of *A. crassirostris* (Filhol, 1876), 56 for *A. typicus* (Schlosser, 1888), 48 for *A. rossignoli* (Filhol, 1882) but 75 for *A. gracilis* (Filhol, 1874). Thus, the latter has the same proportions as UP VAL1 and we may place this specimen near *A. gracilis*. Nevertheless, there are some differences insofar as *A. gracilis* is smaller, there is no pacd in p4 and all the premolars have a marked cingulid. Thus, this identification is inappropriate and UP VAL1 remains *Amphicynodon* sp.

Amphicynodon sp. 2
(Fig. 1D)

DESCRIPTION

A right M1 (UM VBO492) from Valbro (Peigné *et al.* 2014: fig. 22b) has an overall pattern indicating *Amphicynodon*

TABLE 1. — Measurements (in mm) of teeth of *Amphicynodon* Filhol, 1881, from the alveoli.

Amphicynodon	p2L	p2w	p3L	p3w	p4L	p4w	m1L	m1Ltr	m1wtr	m1wtl	m2L	m2wtr	m2wtl	m3L	m3w
UP VAL1	–	–	6.68	3.33	6.98	3.33	(8.1)	–	–	–	6.23	6.23	4.1	3.59	–
UP VAL2	4.86	2.3	4.61	2.33	7.09	2.82	7.99	5.56	4.17	3.83	4.27	3.47	2.89	2.43	2.01

	M1L	M1w1	M1w2
UM VBO492	6.5	9.2	8.8
UM VD49	6.9	10.3	8.3

morphology. Thus UM VBO492, shares with the M1 of *A. leptorhynchus* (Filhol, 1876) found in the locality Itardies (Cirot & Bonis 1992), a similar aspect of the trigon, the presence of a metaconule and a large lingual cingulum (Fig. 1D). On the other hand, it is narrower distally than mesially, indicating a reduction of the distal part of the jaw. This character is present in *A. velaunus* and *A. teilhardi*, but the outline of the tooth is different, with a greater length of the buccal border in those two species. We do not know if in our material there is a lower dentition corresponding to UM VBO492 and thus we cannot assign a species name to this M1, although *Amphicynodon typicus* could be a possibility.

Amphicynodon sp. 3
(Fig. 1C)

NEW MATERIAL. — Right M1 UM VD49.

DESCRIPTION

The right M1 UM VD49 (Fig. 1C) has a symmetrical outline like that of *A. leptorhynchus* (Cirot & Bonis 1992). Paracone and metacone are nearly identical in size and are on more or less a same longitudinal line. A thick cingulum runs along the buccal side without any style. The protocone is situated slightly lingually relative to the middle of the crown. The postprotocone and postmetaconule cristae fade out in contact with the distal face of the metacone. There is a huge lingual cingulum forming a true cusp. There are small wear facets on buccal cusps and large wear facets on metaconule, protocone and lingual cingulum. The morphology of this M1 differs from that of the left M1 UM VBO1212 (Peigné *et al.* 2014) which is more symmetrical, with both preprotocone and postprotocone cristae. But neither tooth can be firmly associated to a mandible of any named species.

Genus *Pachycynodon* Schlosser, 1888

TYPE SPECIES. — *Pachycynodon crassirostris* Schlosser, 1888 by original designation.

DESCRIPTION

Schlosser created the genus *Pachycynodon* for a P4 and M1 from the Quercy phosphorites (Schlosser 1988: pl. IX, fig. 2, 7, 9 and pl. IX, fig. 4 respectively) without any biostratigraphic context. He thought that these specimens were conspecific with *Cynodictis crassirostris* Filhol, 1876 (1876: figs 67, 69 and 72) but, in fact the Filhol's specimen, a mandible with c, p3, m1-m2, belongs to the genus *Amphicynodon*. Thus, the name *crassirostris* being conserved, the type species of the genus is *Pachycynodon crassirostris*. Later, several species were added to the genus and to the Amphicynodontidae, forming a group with robust dentition (more robust than that of *Amphicynodon*), mandible often deep, p4 as high or higher than the protoconid of m1, massive cuspids of the trigonid of m1, postmetaconid cristid sloping very obliquely toward the preentocristid, paraconid often present in m2. The robust P4 has a short metastyle and large plateau-like protocone. There is a trend in M1 toward an almost quadratic outline, without paraconule and disto-lingual metaconule and with a large cingulum around surrounding the protocone. The M2 is more or less reduced. The muzzle is elongated.

Pachycynodon crassirostris Schlosser, 1888

TYPE SPECIMEN. — Lectotype, right P4 in Schlosser 1888: 29, pl. IX, fig. 2 and 9 "Phosphorites du Quercy", BSP 1879XV40, Museum of Munich, by subsequent designation of Peigné *et al.* 2014.

DESCRIPTION

The type specimen of the species *Pachycynodon crassirostris* Schlosser, 1888, an isolated P4 comes from an unknown locality in the Quercy phosphorites, without any biostratigraphic indicators. This tooth is not frequent in the collections and, except for *P. boriei*, never associated with a mandible. The P4 is not a good diagnostic element for a species insofar as all type specimens of other species are mandibles and lower dentitions. Schlosser considered that the type could correspond to a mandible named *Cynodictis crassirostris* Filhol, 1882 but we don't know the criteria he used (see above). Later (1899) he figured other specimens from Quercy, a mandible and an m1 (Schlosser 1899: pl. VIII, figs 1, 8), which seemed to him match the upper tooth considered as the type specimen. Teilhard figured a Quercy mandible from the Museum of Montauban (Teilhard 1915: pl. IV, fig. 11) as *P. crassirostris*. The latter was synonymised by Cirot (1992) because of mandibular morphology with another Quercy species, *Cynodictis dubius* Filhol, 1882 (1882: pl. VIII, figs 11-13) of which type specimen, a mandible, is housed in the MNHN Paris (no. MNHN.F.QU3231). However an examination of this specimen (by LdeB) shows that it belongs in the genus *Pachycynodon* but differs from the Montauban mandible by its smaller size, relatively lower cuspids of m1 trigonid, relatively longer m2
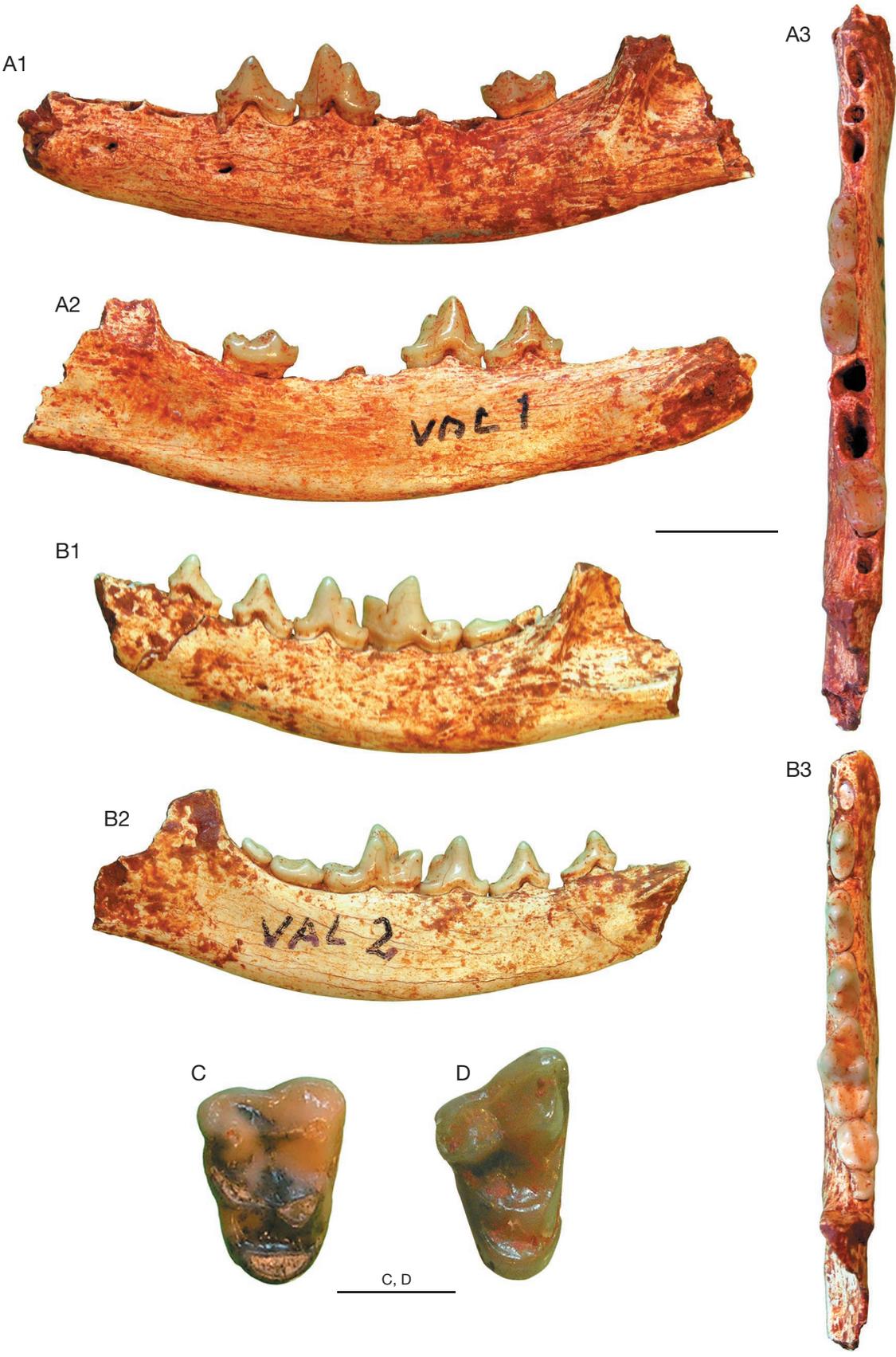
FIG. 1. — **A**, *Amphicynodon* sp. 1: left hemi-mandible UP VAL2, in buccal (**A1**), lingual (**A2**), and occlusal (**A3**) views; **B**, *Amphicynodon typicus*: left mandible UP VAL1, in buccal (**B1**), lingual (**B2**), and occlusal (**B3**) views; **C**, *Amphicynodon* sp. 3: right M1, UM VD49, in occlusal view; **D**, *Amphicynodon* sp. 2: right M1, UM VBO492, in occlusal view. Scale bars: A, B, 10 mm; C, D, 5 mm.

and shallower mandibular corpus. Thus, we think that *P. dubius* is really a different species. *Pachycynodon crassirostris* was recorded in Valbro (MP 22) by Peigné *et al.* (2014: fig. 26a) from a worn mandible whose wear is almost horizontal, probably indicating a hypocarnivorous diet (Peigné *et al.* 2014: fig. 20), but see below for *Pachycynodon amphictina* n. stat. Currently, the lower dentition of *P. crassirostris* is unknown.

Pachycynodon cf. *boriei* or *curvirostris* (Filhol, 1876)
(Fig. 2A)

New material. — d3-m1 (UP LPL13).

Diagnosis. — Large species of *Pachycynodon* (length of m1 = 12 to 13.5 mm), m1 with slightly open trigonid basin. The very robust p4 and high and spaced premolars seem to be characteristic of the species. Another specimen, smaller but with the same characters, figured under the name *Cynodictis leymeriei* (Filhol 1876: figs 55-57) could be a female of *P. boriei*. The occurrence of *P. boriei* in the new collections of the Quercy was indicated in La Plante2 (Cirot 1992) and definitively in Valbro (Peigné *et al.* 2014) from a fragment of an M1. The new specimens do not firmly verify the occurrence of this species in one of the new localities in the Quercy insofar as another species of *Pachycynodon*, *P. curvirostris* (Filhol, 1876), slightly smaller than *P. boriei*, differs in its elongated and constricted lower premolars, and smaller p4 relative to m1 (holotype, MNHN.F.QU9208; Filhol 1876: figs 52-54). Two other mandibles (MNHN.F.QU9210 and MNHN.F.QU9216) may be related to the same species.

Remark
Pachycynodon boriei (Filhol, 1874) was named and later figured (Filhol 1876: figs 33, 40) as "one of the largest Carnivora ever found into the phosphate localities"(LdeB translation). Filhol 1876: 72) chose as type a mandible (Filhol 1876: fig. 40) with an associated cranium (1876: fig. 34) that is probably from the same individual.

Description
The d3 (Fig. 2A4, A5) is single-cusped but two-rooted; the crown is slightly dissymmetric, the distal part being larger than the mesial one. It is slightly longer than high with a small medial edge ("protostylid") and a medium high, lingually situated pacd not along the sagittal cristid as is normally the case in premolars; both mesial and distal cristids are sharp and there is a small, flat and slightly upturned talonid around the distal crown (size: 6.3 × 2.9 mm).

The d4 (Fig. 2A4, A5) is thin with a high protoconid that is clearly buccally convex but slightly lingually convex and moderately sloping distally. The very oblique paraconid appears smaller than the metaconid in lingual view; the latter is slightly distally located and has a triangular horizontal section. The metalophid is acute as are the premetaconid and postmetaconid cristid. The lingual face of the metaconid is slightly convex but the mesial and distal ones are almost flat. The talonid basin has a wide and flat bottom. The cristid obliqua joins the buccal part of the base of the protoconid to the moderately high and bucco-lingually compressed hypoconid. The postmetaconid cristid joins the preentoconid cristid without a notch; postentoconid and

posthypoconid cristids reach a small hypoconulid distally. A d4 from Valbro was previously described by Peigné *et al.* (2014). It is smaller and differs in its less pointed trigonid cuspids, lower protoconid and less transverse paraconid (size: 8 × 35 mm)

The m1 is a germ out of its crypt. Despite a fissure, the crown is very well preserved (Fig. 2A1-A3). The grouped cuspids of the trigonid are massive, with the protoconid slightly higher than the other cuspids and a part of the metaconid slightly visible in buccal view. The disto-lingual face of the metaconid is triangular and flat. The distal faces of both protoconid and metaconid are in almost the same plane, sloping distally at an angle of about 45°. There is a large hypoconid occupying the entire talonid basin and gently sloping to the base of the entocristid, the latter being a series of buds in which it is impossible to distinguish an entoconid (size: 12.3 × 5.8).

Judging by the size and morphology, the m1 of the mandible, UP LPL13 could be a small specimen of *P. boriei* but we cannot exclude, without more complete specimens and knowledge of the premolars, a large *P. curvirostris*.

Small species and sub-species of *Pachycynodon*
Several taxa of quite small size (length of m1 between about 7 and 9 mm) of *Pachycynodon* have been described, all from the old collections of the Quercy phosphorites:
    Pachycynodon dubius (Filhol, 1882);
    Pachycynodon filholi Schlosser, 1888;
    Pachycynodon vulpinus Schlosser, 1899;
    Pachycynodon tenuis Teilhard, 1915;
    Pachycynodon aff. *tenuis* Teilhard, 1915;
    Pachycynodon tenuis '*amphictoïde*' Teilhard, 1915;
    Pachycynodon filholi var. *amphictina* Teilhard, 1915;

All these taxa constitute a homogeneous group in which it is easy to recognize the genus characters but difficult to interpret the tenuous differences between the component species, with size playing a role in the distinctions. The above list of taxa represents almost half of the small *Pachycynodon* specimens housed in the MNHN. *Pachycynodon tenuis* is considered by Teilhard (1915: 36) as a model for the origin of the group because of its small size, p4 higher than m1 and the thinness of the latter despite the swollen cuspids of the trigonid. Nevertheless we believe that the narrow m1 is due to the small size of the specimen, since other m1s, although larger, have the same or lower breadth/length index of m1. Other features are cited by Teilhard, such as the sharp-edged cuspids, the hollow talonid of m1, the m2 beginning to be rounded and with a distinct paraconid, but these features also are present in other species (see below), more especially as the paraconid is not all that distinct. To this we may add an entoconid that is less enlarged than the hypoconid but high, and a reduced mesial fovea in m2. *Pachycynodon* aff. *tenuis* (Teilhard 1915: pl. 4, fig. 5), where the tips of the p4 and p3 cuspids are broken off, is characterized by a high and pointed p2 separated from p3 by a short diastema. *Pachycynodon tenuis* '*amphictoïde*' (Teilhard 1915: pl. IV, fig. 6) is a poorly preserved hemi-mandible with m1 and
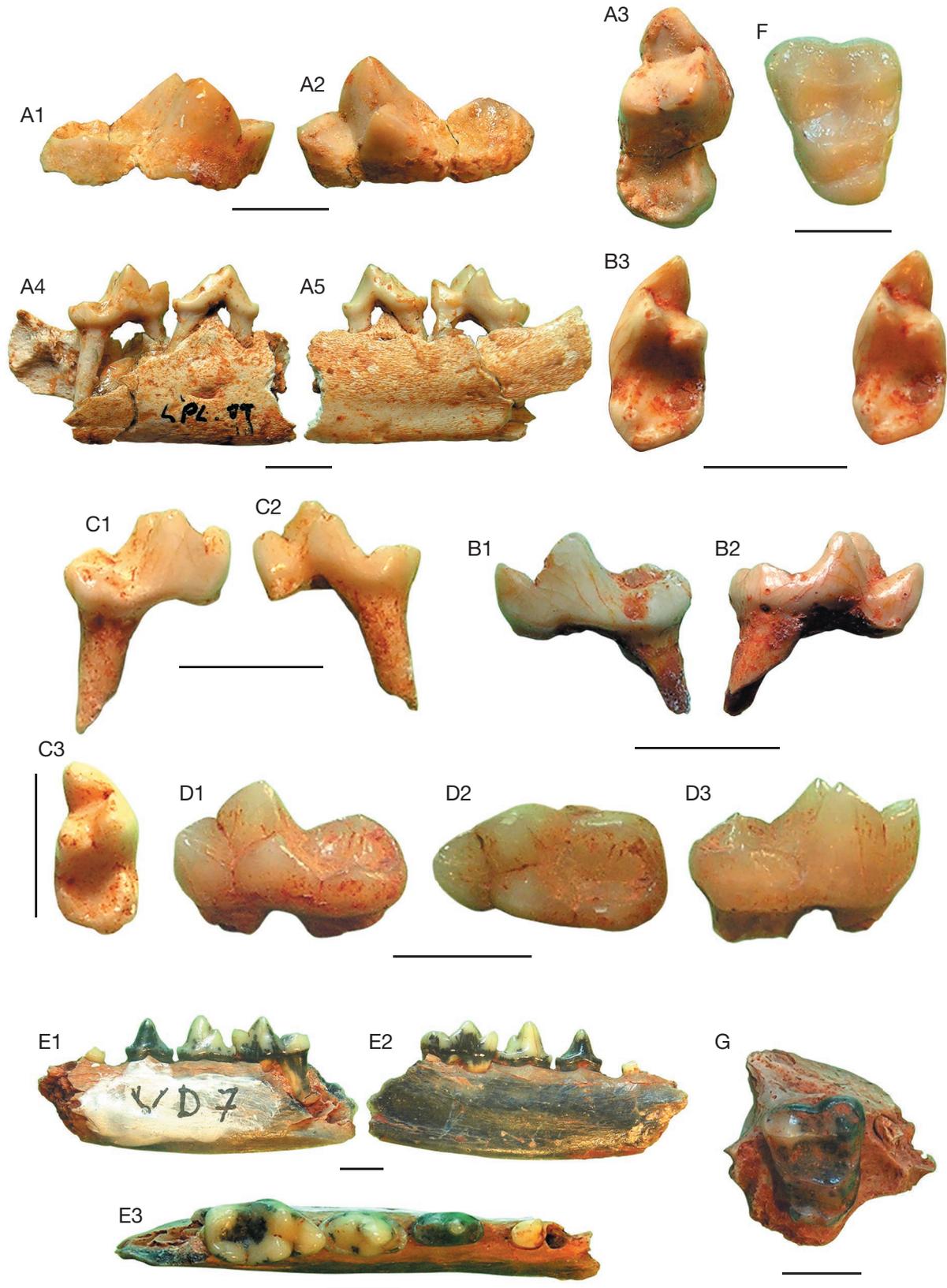
FIG. 2. — **A**, *Pachycynodon boriei* or *curvirostris* (Filhol, 1876): **A1**-**A3**, UP LPL13, right m1, in buccal (**A1**), lingual (**A2**), and occlusal (**A3**) views; **A4**, **A5**, d3-d4, in buccal (**A4**), and lingual (**A5**) views; **B**, **C**, *Pachycynodon* sp. 1; **B**, UP MGB9, left d4, in buccal (**B1**), lingual (**B2**), and occlusal (**B3**) views (stereo); **C**, UM VD16, right d4, in buccal (**C1**), lingual (**C2**) view, and occlusal (**C3**) views; **D**, *Pachycynodon* sp. 2, UM VD18, right d4; **D1**, lingual view, occlusal (**D2**), and buccal (**D3**) views; **E**, *Pachycynodon* cf. *filholi*, UM VD7, left hemi-mandible, in buccal (**E1**), lingual (**E2**), and occlusal (**E3**) views; **F**, *Pachycynodon* sp. 3, UM VD48 M1, in occlusal view; **G**, *Pachycynodon* sp. 4, UM VD50 M1, in occlusal view. Scale bars: 5 mm.

TABLE 2. — Measurements (in mm) of lower teeth of *Pachycynodon* Schlosser, 1888.

Pachycynodon	p1L	p1w	p2L	p2w	p3L	p3w	p4L	p4w	m1L	m1wtr	m2L	m2wtr	m3L	m3w
P. amphictina n. stat.	3.3	1.5	4.5	2.1	6.3	2.6	6.4	3.3	8.9	4.6	3.7	2.5	2.7	2.5
P. cf. *filholi* Schlosser, 1888				mean	6	3.2	5.6	3.2	8.7	4.5	4.7	–	–	–
				min	5.1	2.8	5.4	3.1	8.5	4.1	–	–	–	–
				max	6.2	3.1	5.8	3.2	9.1	5.1	–	–	–	–
				n	2	2	2	2	2	2	1	1	1	1
P. cf. *dubius* (Filhol, 1882)				mean	–	–	–	–	8.6	4.8	4.9	4.2	3.5	2.8
				min	–	–	–	–	8.2	4.5	4.7	4.1	–	–
				max	–	–	–	–	9.4	5.1	4.9	4.3	–	–
				n	–	–	–	–	3	3	3	3	1	1

alveoli of m2. There is no m3, like in *Amphictis*, but we cannot say anything else with so a poor material. *Pachycynodon dubius* was established on a hemi-mandible from the Quercy phosphorites with p2-m2 and part of the ascending ramus. According to Teilhard (1915) it is principally characterized by a very low m1, even taking into account the wear on the trigonid cuspids, and the diastemata between the premolars. The holotype of *P. vulpinus* comes, like the other species, from the phosphorites of Quercy. Its size is close to that of *P. dubius*, the m1 is low the premolars have diastemata between them. The p3 and the p2 are smaller than the p4. Comparing a cast of *P. vulpinus* with *P. dubius* no significant difference between the specimens can be seen, except that the size difference between p4 and the other premolars is more marked in the former. We believe them to be conspecific, as noted by Teilhard (1915: 39), with *P. dubius* (Filhol, 1882) having priority.

Pachycynodon cf. *filholi* Schlosser, 1888
(Figs 2E; 3B, H)

TYPE MATERIAL. — Lectotype by designation of Teilhard (Teilhard 1915: 38): fragment of left hemi-mandible with broken p2, p3-m1 (Schlosser 1888: 30, pl. IX, figs 1, 3, 5), "Phosphorites du Quercy" without any biostratigraphic information.

NEW MATERIAL. — UM VD7 left hemi-mandible with p3-m1; UM VD8 left hemi-mandible; UM VD10 small fragment of mandible with m2; UP LPL14 m2; UM VD5 hemi-mandible with p3-m2.

REMARKS
Schlosser (1888) established *P. filholi* on a fragment of mandible with p3-m1 from the "Phosphorites du Quercy" and he added a fragment of edentulous maxilla (Schlosser 1888: pl. IX, fig. 16) from the bulk of the Quercy specimens without any special link to the mandible.

Among the material from Valbro, some mandibular specimens seem to be close to this species. A hemi-mandible (UM VD7) with mesial alveolus and distal root of p2, and fresh p3-m1 is quite similar to a cast of the type of *P. filholi* (Fig. 2E1-E3). The almost symmetrical and pointed p3 displays small mesial and distal cingulids with a small, pointed mesial spur; its mesial and distal edges are sharp and pointed, with a profile that is slightly concave. The

p4 is clearly higher than p3 and the protoconid of m1, its mesial and distal cingulids are more developed than in p3 and the distal cingulid forms a true small talonid. A pacd is situated at mid-height of the distal cristid of p4. The low m1 has a small cingulid running along the base of the paraconid-protoconid blade, the former appears smaller than the metaconid in lingual view. The paraconid–metaconid contact at mid-height closes the trigonid valley. The latter is slightly shifted distally and can clearly be seen in buccal view behind of the protoconid, which is separated from the hypoconid by a large sinus. The hypoconid is quite large and slopes gently lingually to the base of the entoconid, which is fused into a slender entocristid slightly higher than the hypoconid. Medially, the entoconid is separated by a small notch from the metaconid and distally joins the hypocristid to close the talonid basin. The p2 and p3 (Teilhard 1915: pl. IV, figs 7-9) are sharp.

There is no m2 in the type specimen, but there is an m2 in the hemi-mandible VD5 that we identify as *P.* cf. *filholi* (Fig. 3B1-B3). The p3 of VD5 is partly broken off but was smaller than the thin and pointed p4 that displays a small pacd and a minute talonid. The m1 has a paraconid that is less oblique than that of *P. dubius* and thus the paraconid-protoconid shearing blade is more prominent. In the talonid of m1, the entoconid is partly broken off. In m2, which is rectangular, the trigonid occupies half of the surface of the crown; the protoconid and metaconid are subequal in size, both having a small wear facet on the dentine at the tip. In front of the protoconid and metaconid, a mesial cristid closes a mesial fovea. The protoconid is separated by a sinus from the hypoconid, which, in turn, is followed by a cristid running to the metaconid and closing a bowl-shaped basin.

An isolated rectangular and elongate m2 from the site of La Plante2 (UP LPL14) is too small to fit *P. boriei* or *P. curvirostris* (Fig. 3H). It displays a complete trigonid, a faint cingulid is present along the base of a small but clear paraconid displaying a small pit of dentine at its tip. The paraconid cristids close the minute trigonid basin mesially. Both protoconid and metaconid display a wear facet at the tip. This facet is larger in the latter. The proto- and metalophids separate the trigonid and talonid basins, while distally a post-hypocristid and entocristid close the bowl-shaped talonid basin.
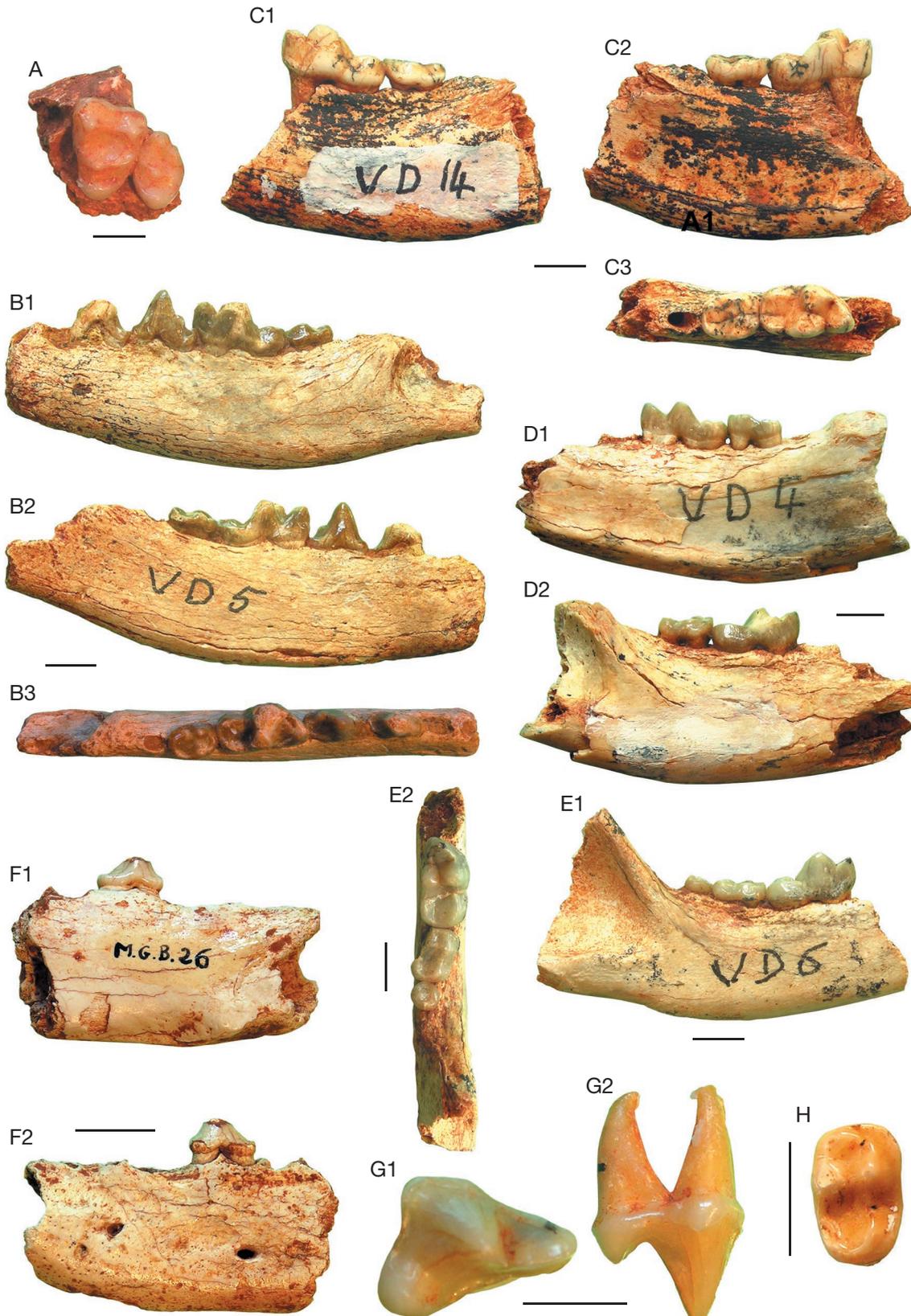
Fig. 3. — **A**, *Pachycynodon* sp. 3, left M1-M2, UM VD47, in occlusal view; **B**, *Pachycynodon* cf. *filholi*, UM VD5, left hemi-mandible, in buccal (**B1**), lingual (**B2**), and occlusal (**B3**) views; **C-E**, *Pachycynodon* cf. *dubius*; **C**, left hemi-mandible UM VD14, in buccal (**C1**), lingual (**C2**), and occlusal (**C3**) views; **D**, right hemi-mandible UM VD4, in lingual (**D1**) and buccal (**D2**) views; **E**, right hemimandible VD6, in buccal (**E1**), and occlusal (**E2**) views; **F**, *Cephalogale* sp., left mandible UP MGB26, in lingual (**F1**), and buccal (**F2**) views; **G**, *Pachycynodon* sp. 5, left P4 UP VD51, in occlusal (**G1**), and mesial (**G2**) views; **H**, *Pachycynodon* cf. *filholi*, right m2, UP LPL14, in occlusal view. Scale bars: 5 mm.

The corpus mandibulae of UM VD8 is shallow and tapering rostrally. There are two small mental foramina, one below p2, and another below p3. The m1, in which part of the trigonid is missing, has a morphology similar to that of UM VD7. Some isolated m1s could belong to the same taxon.

We hesitantly add to these remains a fragment of mandible (UM VD10) with m2. Its crown is partially worn but we can see the large wear pit of the protoconid, the less marked metaconid and, mesially, the small well with dentine that would may correspond to the paraconid. There is a sinus between the protoconid and the hypoconid. The hypoconid and the entoconid are worn with large appearance of dentine. The talonid tapers distally and the basin is narrow.

Pachycynodon cf. *dubius* (Filhol, 1882)
(Fig. 3C-E)

TYPE SPECIMEN. — Holotype by monotypy: hemi-mandible with p2-m2 (Filhol 1882: 48-52, pl. VII, figs 11-13), MNHN.F.QU9231.

NEW MATERIAL. — Hemi-mandible with m1-m2, UM VD4; hemi-mandible with m1-m3, UM VD6; hemi-mandible with m1-m2, UM VD14.

REMARK
The name *dubius* is due to doubts by Filhol that it belonged in *Cynodictis* because of the grouped trigonid of m1, which differs from that of other species of the genus. Teilhard (1915) reassigned the specimen to *Pachycynodon*. This species is smaller than *P. boriei* and *P. curvirostris*, its size being closer to that of *P. filholi*. It differs from the latter by its slightly larger size, the greater height of the dentary, p2-3 (absent in our material) lower relative to p4 and with blunt mesial and distal edges, a broad p4 with a larger pacd and more inflated cuspids of the trigonid, m1 paraconid more oblique relatively to the sagittal plane, metaconid larger and higher than the paraconid, distal cristid of the metaconid joining, after a gentle slope, the preentocristid by uninterrupted connection or after a small notch, hypoconid slightly higher than the entoconid, talonid basin often with enamel wrinkling and distally open, m2 without or with a tiny paraconid and low mesial cristid enclosing a small fovea (Fig. 3C, D). Like in *P. filholi*, m3 has a small circular crown (Fig. 3E1, E2). We include, with some hesitation, the isolated m2 UM VBOA3-9 (Fig. 5G). It is unworn and less elongate than in *P. filholi*. The metaconid is larger and especially higher than the protoconid. These two cusps are separated and there is no mesial fovea, but a long basin extends from the mesial to the distal cristid. A clear paraconid is present in front of the metaconid. The protoconid is followed by a slight sinus and a cristid joining the postmetacristid, separates the trigonid from the talonid basin. It differs from the proportions of m2 in *P. filholi* but is smaller than m2 in UM VD4 or VD14. The lack of complete specimens prevents a definitive identification.

Pachycynodon amphictina Teilhard, 1915 n. stat.

Pachycynodon filholi var. *amphictina* Teilhard, 1915: 38, pl. IV, fig. 8.

Pachycynodon crassirostris Schlosser, 1888: 253. — Peigné *et al.* 2014: 33, fig. 20a.

REMARK
Teilhard (1915: pl. IV, fig. 10) figured a mandible from the phosphorites of Quercy (MNHN.F.QU9224) as *Pachycynodon filholi* Schlosser, 1888 var. *amphictina*. It is a small *Pachycynodon* (m1 = 8.8/4.5 mm; m2 = 4.3/4.1 mm) with p1-p2, p4-m3, the three first premolars being spaced in the mandible. The p1 is single-rooted and asymmetric, the complete mesial half of the crown being projected forward out of the root.

After a short diastema p2 is less asymmetric although the mesial face is almost vertical while the distal face is oblique and, distally, a faint cingulid forms a minute talonid. The p3 is broken off. The p4 is higher than the protoconid of m1 and less asymmetric than p2. A faint cingulid produces a minute mesial basin and a larger one around the distal border. A pacd is situated at midheight of the crown. The low trigonid of m1, with a small height difference between the cuspids, displays a vertical wear facet along the para- and protoconids. The distal face is oblique, with a small notch between metaconid and entocristid and a large one between protoconid and prehypocristid. The m2 is rectangular with a distinct paraconid on the mesio-lingual corner, and a mesially open trigonid basin. The protoconid slightly larger than the metaconid, both with wear facets to the dentine at the tip, but not in contact together, thus leaving an aperture between trigonid and talonid basins. There are wear facets on the mesio-buccal faces of the hypo- and entoconid. The m3 is small and rounded. The two posterior molars, especially m3, are implanted in the ascending ramus of the mandible. We may observe these characters in the mandible with p1-m3 from Valbro (UM VBO 456) figured in Peigné *et al.* (2014: 32, 33, fig. 20a), in which the m3 is located higher than the protoconid of m1. There is an original shortening of the mandible by the distal part, re-enforcing the pressure on m1 because there is no pressure in m2 and m3 Thus, m1 is worn down while m3 is still unworn. The two specimens differ from the type of *P. filholi*, which has less a globular metaconid of m1, more symmetrical p3 and p4, a shorter and more pointed p4 with a pacd located lower, and we consider that they belong to a separate species with the name originally given by Teilhard for a variant.

Pachycynodon indet. lower dentition

Pachycynodon sp. 1
(Fig. 2B, C)

NEW MATERIAL. — UP MGB9, left d4; UM VD16, right d4.

Pachycynodon sp. 2
(Fig. 2D)

NEW MATERIAL. — UM VD18, right d4.

REMARKS
Specimen UP MGB9 (Fig. 2B1-B3) is a small left d4 with elongate crown and low trigonid. thre is a small height difference between the trigonid cuspids, and distal wall of the protoconid gently sloping distally. The inflated metaconid is looking larger than the paraconid in lingual view and almost as high as the protoconid, and gently sloping distally. The thinner paraconid is less inflated than in other species of *Pachycynodon*, and projected up and mesially. The contact between paraconid and metaconid is at the base of the crown, and thus the trigonid valley is open lingually. The talonid is long and broad with a flat bottom. The hypoconid is developed as a small cuspid connected to the protoconid by a very low and non-oblique cristid obliqua. The bucco-lingually compressed entoconid is connected without interruption to the metaconid by a low preentocristid. There is a small hypoconulid distally. Specimen UM VD16 is a small right d4 similar to MGB9 (Fig. 2C1-C3). The third d4, UM VD18 (*Pachycynodon* sp. 2), is slightly different in its more swollen cuspids, exaggerating the characters of *Pachycynodon*, but the overall pattern is the same (Fig. 2D1-D3). The low trigonid with swollen cuspids, amongst which the heights are similar, is a character of *Pachycynodon*. The talonid differs by the higher and more robust hypoconid (size: MGB9 = 6.5 × 3 mm; VD16 = 5.4 × 2.7; VD18 = 8 × 4.2 mm).

These d4s differ from all m1 of *Pachycynodon* by their smaller size (Table 2), the shape of the paraconid, the low contact between paraconid and metaconid and the shape of the broad talonid. Compared to the d4 LPL13 (Fig. 2A4, A5) they display the same pattern but are smaller (MGB9 and VD16) and relatively thicker (VD18). It is at present not possible to identify the species of *Pachycynodon* corresponding to these milk teeth.

Pachycynodon indet. upper dentition

REMARKS
Some upper molars and one P4 belong to *Pachycynodon* with a high probability but at present, we cannot refer any of them to a known mandible because, as noted above, only the upper dentition of the large *P. boriei* was found associated with lower teeth.

Pachycynodon sp. 3
(Fig. 3A)

DESCRIPTION
Pachycynodon sp. 3 is a piece of left maxilla with M1-M2 (UM VD47). The M1 (size = 6.7 × 8.6 mm)differs from *Amphicynodon* by its larger buccal length relative to the bucco-lingual diameter and the relatively lingually situated metaconule (Fig. 3A). The features are less expressed than in *P. boriei*. The M2 (size = 4.3 × 7) is oval, smaller but close to the pattern of *P.* 'gryei' (Filhol, 1976). The M1 UM VD48 (Fig. 2F) is similar to VD47 and likely belongs to the same species (size = 7 × 8.6 mm).

Pachycynodon sp. 4
(Fig. 2G)

DESCRIPTION
Pachycynodon sp. 4 (Fig. 2G) is a little smaller and more thick-set (size = 6.5 × 8.1). It looks more like the pattern of *P. boriei*, which, nevertheless, is far larger.

Pachycynodon sp. 5
(Fig. 3G)

DESCRIPTION
Pachycynodon sp. 5 is a P4 (UM VD51) which displays characteristics and measurements of UM VBO1207 figured in Peigné *et al.* 2014. We note only a slightly higher paracone (5.9 mm for the latter and 6.4 for our specimen) (Fig. 3G1, G2).

Genus *Wangictis* n. gen.

urn:lsid:zoobank.org:act:BB1F314F-5373-48DA-AC87-80C87E8816D7

TYPE SPECIES. — *Pachycynodon tedfordi* Wang & Qiu, 2003.

DIAGNOSIS (as the type species modified from Wang & Qiu 2003). — Medium-sized Amphicynodontidae; mandible height tapering medially; two mental foramina, one under the distal root of p3 and another, very large, under p1 and p2; premolars low; p1-p3 very asymmetrical and mesially inclined; presence of diastemas before and after p4, the latter tooth with well-developed pacd; m1 low with a short paraconid and a relatively reduced metaconid; relatively long m2 without paraconid; no notch between protoconid and cristid obliqua in one hand and between postmetaconid cristid and preentoconid cristid in the other hand.

ETYMOLOGY. — From *ictis* (latin: weasel) and dedicated to Xiaoming Wang for his work on Carnivora.

REMARKS
Wang & Qiu (2003) described a new species allocated to the genus *Pachycynodon* recovered during a field campaign to Nei Mongol by the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing (IVPP). Comparing this taxon to European representatives of the *Pachycynodon*, it appears that it belongs to a new genus that we here name *Wangictis* n. gen.

Wangictis tedfordi (Wang & Qiu, 2003) n. comb.

Pachycynodon tedfordi Wang & Qiu, 2003: 117.

TYPE MATERIAL. — Holotype: left hemi-mandible with c-m2 by monotypy.

TYPE LOCALITY. — Ulanmannei, east of Saint-Jacques, Nei Mongol, China.

TYPE HORIZON. — Early Oligocene.

DIAGNOSIS. — That of the genus.

REMARKS
The type hemi-mandible was described (Wang & Qiu 2003) as *Pachycynodon*. Nevertheless, despite the relatively swollen cheek teeth, as in all Amphicynodontidae, it differs from the species of the genus *Pachycynodon* by the p4, which is lower than the protoconid of m1, the reduced metaconid of m1 and the very short paraconid, the shape of the premolars, and the reduction of p1-p3, which seems to indicate a shorter muzzle. This fossil may belong in the family Amphicynodontidae but not into the genus *Pachycynodon*. The occurrence in Asia of *W. tedfordi* (Wang & Qiu, 2003) n. comb. indicates a larger splitting of the family than previously thought.

Family URSIDAE Fischer von Waldheim, 1817
Subfamily HEMICYONINAE Frick, 1926

TRIBE CEPHALOGALINI Bonis, 2013

REMARKS
The Cephalogalini were present in Western Europe from the Oligocene to the early Miocene (MN3). Like the Hemicyoninae as a whole, they are considered to be pursuit predators with a canid-like way of life (Hunt 1996: 493; 2009: 4). They are represented by hundreds of mandibles in the old Quercy collections but are less frequent in the new ones, except for a few places like Pech du Fraysse and Pech Desse (Bonis 2013), two localities of the late Oligocene (MP 29). The type genus of the tribe, *Cephalogale* Jourdan, 1862, is founded on the species *C. geoffroyi* Jourdan, 1862 from an Oligocene locality of central France. The genus is common from the late Oligocene to the lower Miocene, with several species but is less common in the early Oligocene. Nevertheless, *Cephalogale* was doubtfully reported in Valbro (Peigné *et al.* 2014: fig. 19b) on the basis of a buccal piece of M1 and cited in Mas de Got (Rémy *et al.* 1987) as *Cephalogale minor*. The tribe is definitively present in the latter locality.

Cephalogale sp.
(Fig. 3F)

NEW MATERIAL. — Piece of hemi-mandible, UP MGB26, with p3, alveoli of c, p1, p2 and p4.

DESCRIPTION AND COMPARISON
The mandible (Fig. 3F1, F2) belongs to a medium sized carnivoran. The corpus height under p3 is 19.7 mm and the thickness 4.25 mm. There are two mental foramina, one under the roots of p2, another under the distal root of p3. The size of the tooth (L = 8.45, w = 4.25) is within the range of *Cyonarctos dessei* Bonis, 2013, with length = 7.6 to 11.1 mm and width 3.15 to 5.71 (Bonis 2013: table 1) but the shape is different. The profile of the crown is slightly asymmetrical, the distal part being larger than the mesial one. The buccal face is convex but the lingual one is separated into two parts by a vertical median pillar, with both parts being slightly concave. A weak cingulid runs along the lingual base and, to in a lesser extent, the buccal one, to distally enclose a small and very shallow talonid basin.

The morphology of MGB 26 is far from that of the shearing premolars of the nimravids. It is the same, judging from the shape of P4, with the small amphicyonid *Goupilictis* Ginsburg, 1969. Thus, MGB 26 fits the Cephalogalini better. *Adelpharctos* Bonis, 1971 is larger. The p3 is missing in the holotype of the nominal species, but the shape and size of p4, large, high, and nearly symmetrical, may give an idea of the p3 morphology. However, the tooth is present in *A. ginsburgi* Bonis, 2011 and confirms the deduction. *Phoberogale* Ginsburg & Morales, 1995 displays a very low and elongate p3 with a more robust cingulid and a clear pacd. *Cyonarctos* Bonis, 2013 differs by the higher and more pointed p3 without cingulid and talonid basin. The closest genus seems to be *Cephalogale* with the closest species being *C. brevirostris* (Croizet *in* Blainville, 1845) (Blainville 1845: 122) and *C. gergoviensis* Viret, 1929. Thus we cannot provide a specific attribution, and then the fossil is identified as *Cephalogale* sp.

Parvorder MUSTELIDA Tedford, 1876
Family MUSTELIDAE Fischer Von Walldheim, 1817

Genus *Mustelictis* Lange, 1969

TYPE SPECIES. — ?*Plesictis robustus* Filhol *in* Teilhard, 1915 (1915: 58, pl. VII, fig. 13), by original designation.

REMARKS
The genus *Plesictis* Pomel, 1846 was created for small mustelids from late Oligocene and lower Miocene localities of France. Several species were described, especially in Europe, and among them some specimens from the old collections of the Quercy phosphorites. However, some of them do not bear all the characters of *Plesictis*. Thus, an isolated skull from the old collection, and considered as a *Plesictis,* was assigned to a new genus, *Mustelictis,* by Lange (1969, 1970). However, it was described without any comparison either with other specimens or with the literature (Lange 1970), although it was figured by Teilhard as *Plesictis robustus* (Teilhard 1915: pl. VII, fig. 13, 13a). Teilhard noted that this skull was similar to another skull figured by Filhol (1890) as *Viverra schlosseri*. We could not find the latter and thus *V. schlosseri*, without type specimen, becomes a nomen dubium. However, the skull did not bear the characters of *Plesictis*. In particular, it does not display the double fronto-parietal crests that are characteristic in *Plesictis* (see for instance Viret 1929) as can readily be seen
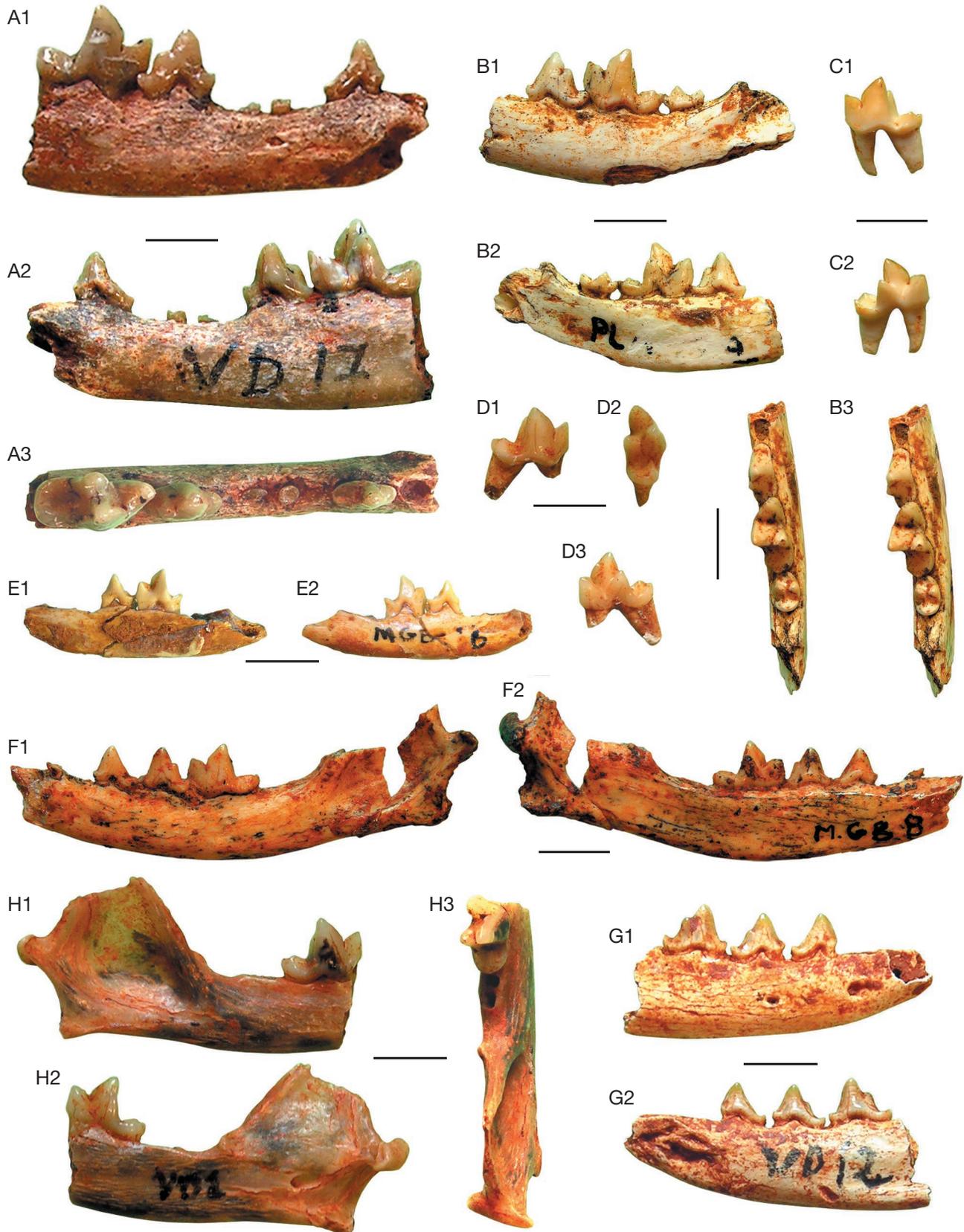
FıG. 4. — **A**, *Mustelictis* cf. *major*, right hemi-mandible with p2-p4-m1, UM VD17, in buccal (**A1**), lingual (**A2**), and occlusal (**A3**) views; **B**, *Mustelictis* aff. *olivieri*, left hemi-mandible with p4-m2, UP LPL12, in buccal (**B1**), lingual (**B2**), and occlusal (**B3**) views; **C**-**E**, *Mustelictis* aff. *olivieri*; **C**, left m1, UP LPL11, in buccal (**C1**), and lingual (**C2**) views; **D**, right m1, UM VBOA3-4, in buccal (**D1**) view, occlusal (**D2**) view, and lingual (**D3**) views; **E**, right hemi-mandible with d3-d4, UP MGB6, in lingual (**E1**), and buccal (**E2**) views; **F**, *Mustelictis olivieri*, left mandible with p3-m1, UP MGB8, in buccal (**F1**), and lingual (**F2**) views; **G**, *Mustelictis* aff. *olivieri*, right hemi-mandible with p2-p4, UM VD12, in buccal (**G1**) view, and lingual (**G2**) views; **H**, *Peignictis pseudamphictis* n. gen., n. sp., right hemimandible with m1, UM VD1, in buccal (**H1**), lingual (**H2**), and occlusal (**H3**) views. Scale bars: 5 mm.

TABLE 3. — Measurements (in mm) of lower teeth of *Mustelictis* Lange, 1969.

Mustelictis		p2L	p2w	p3L	p3w	p4L	p4w	m1L	m1w	m2L	m2w
M. olivieri	MGB7	2.8	1.3	3.3	1.4	3.8	1.6	5	2.5	2.4	1.8
	MGB8	–	–	3.2	1.4	3.8	18	5.2	2.7	–	–
	MGB9	–	–	–	–	–	–	–	–	–	–
M. aff. *olivieri*	LPL11	–	–	–	–	–	–	5.6	2.5	–	–
	LPL12	–	–	–	–	4.1	1.9	5.4	2.4	3	2
	VD12	3.1	1.3	3.2	1.5	4.1	1.8	–	–	–	–
M. cf. *major*	VD17	4.43	2.22	–	–	5	2.16	8.19	5.15	3.8	3.3

in Teilhard's figure, even if the parietal bones had been removed, probably to observe the brain endocast before Lange's study and thus it truly belongs to a different genus.

The same skull is also *de facto* holotype of a new species, *M. piveteaui* Lange, 1969, but what can we say about the species name? *Viverra schlosseri* is a *nomen dubium* and the other name, *Plesictis robustus* Pomel, 1848, was created for late Oligocene and early Miocene carnivores that are true *Plesictis* and is not available for this Quercy specimen. Unfortunately, Teilhard did use the binomen *Plesictis robustus* for fossils from the Quercy. In fact, true *Plesictis* existed in late Oligocene localities in Quercy but not in the early Oligocene ones. The first *robustus* is a hemi-mandible considered *Plesictis robustus* by Filhol (1877: 49, 50). Filhol later (1882) changed his mind and called this specimen *Cynodictis leptorhynchus viverroides* (1882: 59-62, pl. VI, figs 3-5, pl. VII, figs 7-10). These specimens were figured again by Teilhard (1915: pl. VIII, figs 9, 10) and are housed in the MNHN Paris. We designate here the mandible of Teilhard (1915: pl. VIII, fig. 9), MNHN.F.QU9233, as lectotype of *Mustelictis robustus*.

The mandible corresponding to the skull is at present unknown, but another species, *Mustelictis olivieri* Bonis, 1997 was described from a skull associated with mandibular remains and may help in elucidating the morphology of the lower teeth of other species of *Mustelictis*. The new material includes a mandible probably belonging to the same genus as the type and adds new specimens of *M. olivieri*.

Mustelictis cf. *major* (Teilhard, 1915)
(Fig. 4A)

TYPE SPECIMEN. — Holotype by monotypy in Teilhard 1915: 60, pl. V, fig. 9; MNHN.F.QU9133.

NEW MATERIAL. — UM VD17 part of right hemi-mandible with alveolus of p1, p2, fragments of p3 roots, p4-m1.

DESCRIPTION
The right hemi-mandible VD17 is broken off in front of the p1 alveolus and behind the m1. The mandibular corpus is relatively shallow with a small mental foramen under the missing p3. The p2 is high, slender, elongate and asymmetric, similar in morphology to that of *M. olivieri*, although larger. The p4 is also high and slender, with a well-marked pacd and

two upturned spurs mesially and distally. The m1 has a high and trenchant protoconid, a smaller paraconid and a reduced but not distally placed metaconid; the talonid displays a moderately trenchant hypoconid, a low and thin entocristid and a slightly concave basin that is open distally.

These characters match those of a species of *Mustelictis*. Nevertheless, we are facing the recurring problem of identifying lower dentitions based on upper ones, and vice-versa. *Mustelictis piveteaui* is a skull and we do not know the mandible, whereas *M. olivieri* is too small. Some species have been identified as "*Plesictis*" in the Quercy and most of them would fit *Mustelictis*. *Mustelictis crassirostris* (Teilhard, 1915) was established on the specimen described by Filhol as *Cynodictis crassirostris* viverroïde (Filhol 1882: 58, 59) retaining the same name because the species *Cynodictis crassirostris* is still considered valid. Compared to the type specimen (MNHN.F.QU9135), VD17 differs in the shallower dentary, the relatively smaller p4 and the less trenchant talonid of m1. It also differs from *M. robustus* (Filhol, 1877) in the higher p2 and p4 relative to m1 and the pointed p2. The closest species seems to be *M. major* (Teilhard, 1915) which displays a pointed p2 and a similar p4. Thus, we identify this hemi-mandible as *Mustelictis* cf. *major*. A definitive identification will be probably possible with more complete specimens, especially with m2 (Table 3).

Mustelictis aff. *olivieri* Bonis, 1997
(Figs 4C-E, G; 5F)

TYPE SPECIMEN. — Holotype: skull, UP MGB60, by author designation; paratype: hemi-mandible, UP MGB7.

NEW MATERIAL. — Left m1, LPL11; left fragment of hemi-mandible, UP LPL12; right m1, UM VBOA3-4; fragment of right hemi-mandible p2-p4, UM VD12; left P4, VBO494.

REMARKS
The holotype and paratype of the species come from Mas de Got (MP 22). A skull and a hemi-mandible (paratype) were figured by Bonis (1997: figs 1, 2). New research has recovered additional specimens in other localities.

DESCRIPTION
The premolars are present in UP LPL12 and UM VD12 and all of them have cutting mesial and distal edges. The p2 is dissymmetric, the mesial part being smaller than the distal

one and having a more sloping mesial edge, the distal one finishing by a small upturned spur at its base. The p3, less dissymmetric than p2, displays a mesial spur; distally there is a small talonid with a small fovea surrounded by a low cristid; there is also a small pacd at mid-height on the distal edge (Fig. 4G1, G2). The p4 is similar to p3 but is larger. The carnassial is very similar to that of the type of *M. olivieri* but the talonid is less narrow. The m2 is larger than in the type in both absolute size and relative to m1; it has a complete trigonid with high protoconid and metaconid and small but clear paraconid, and a narrow talonid (Fig. 4B). The isolated P4 (VBO 494) figured by Peigné *et al.* (2014: fig. 22a) is close to that of the type specimen from Mas de Got, with a mesio-lingually elongate protocone finishing by a conic cusp, a buccal cingulum and a small mesial bulging representing a parastyle (Fig. 5F). These remains are close to the material of *M. olivieri* (Fig. 4F1, F2) but the small differences lead us to be cautious about the identification. They could be due to a small difference in the geological age between two localities of MP 22.

Family indet.

Peignictis n. gen.

urn:lsid:zoobank.org:act:D0A7BD46-4A31-4346-B31A-2EC645AF3720

TYPE SPECIES. — *Peignictis pseudamphictis* n. sp. by monotypy.

DIAGNOSIS. — Small Mustelida. Shallow corpus mandibulae, deep masseteric fossa distally to the level of m2 but more shallow in its upper part and gently diminishing; broad ascending ramus at its base but the distal border being oblique forward, it is narrowing up to the condyle before being broken off. Condyle situated high; small, medially advanced and slightly down directed angular process. High trigonid of m1 with protoconid far higher than the other cuspids and with an almost vertical distal face; protoconid and paraconid provide a clear buccal shearing surface; metaconid pointed and higher than the paraconid but not especially reduced or distally displaced.

ETYMOLOGY. — From latin *ictis* (weasel) and dedicated to the late Stéphane Peigné for his work on Carnivora.

Peignictis pseudamphictis n. gen., n. sp.
(Fig. 4H)

urn:lsid:zoobank.org:act:C96DF1A3-816B-4BD7-9635-28223CFDA804

TYPE SPECIMEN. — Holotype: posterior part of hemi-mandible, UM VD1.

DIAGNOSIS. — That of the genus

TYPE LOCALITY. — Valbro (Lot, France).

GEOLOGICAL AGE. — Early Oligocene (MP 22)

ETYMOLOGY. — Parallelism with *Amphictis* in the lack of m3 and elongate m2.

DESCRIPTION

UM VD1 from Valbro is a piece of hemi-mandible broken in front of m1 and with an unworn m1 and alveoli of m2, (length of m1 = 5.3 mm; w of trm1 = 2.8 mm; w of tlm1 = 2; height of the corpus under m1-m2 = 5.1; length of m2 from the alveoli = 2.5 mm). The ascending ramus, whose tip is broken off, is broad at the level of the condyle but narrowing upwards because the distal border is mesially oblique (Fig. 4H1-H3). The large and deep masseteric fossa extends mesially to the level of m2 and dorsally it diminishes gently without any trace of a boundary. The condyle is situated high (38 mm higher than the base of the angular process compared with 28 mm higher in *Mustelictis olivieri* of similar size). The angular process is flat, mesially situated relative to the condyle and not distally projected. The m1 trigonid is high with a vertical distal wall, while the protoconid and paraconid form a shearing blade. The pointed metaconid is higher than the paraconid but not clearly reduced nor distally displaced. The talonid basin is flat and surrounded by a low uninterrupted cristid in which we cannot distinguish the cuspids. Buccally, there is a well-marked notch between protoconid and hypocristid. Two alveoli, the mesial being the larger, indicate the length of m2. It is very long for an early Oligocene carnivoran. This is a parallelism with the geologically younger *Amphictis*. However, the overall morphology of the latter is different in having a lower and less pointed m1 trigonid. Thus, VD1 exhibits some contradictory characters, e.g., a cutting trigonid associated with a grinding talonid. We don't know any evolutionary history of this structure. The closest genus to *Peignictis* n. gen. is *Mustelictis*, which differs in having a slightly lower m1 trigonid, a more shearing m1 talonid and a shorter m2.

Suborder FELIFORMIA Kretzoi, 1945
Family NIMRAVIDAE Cope, 1880

Nimravus Cope, 1879

TYPE SPECIES. — *Machaerodus brachyops* Cope, 1878 by original designation.

REMARKS
The genus was created by Cope (1879) for the species *M. brachyops* from the Oligocene of Nebraska, United States (Cope 1878). One year later, he changed the generic name to *Nimravus*. The type species is widespread in North America in the middle to late Oligocene (Toohey, 1959). A European species, *Nimravus intermedius* (Filhol 1872a) has characters that are so close to those of *N. brachyops* that Toohey wrote, "I cannot, with the available materials and excellent figures in Piveteau's study, distinguish any consistent morphological differences between *N. brachyops* and *N. intermedius*". (Toohey 1959: 95). In Europe, *Nimravus* was present in early and middle Oligocene strata.

Nimravus intermedius (Filhol, 1872)
(Fig. 5E, H-J)

TYPE SPECIMEN. — Holotype by monotypy: left hemi-mandible with m1, MNHN.F.QU9551, in Filhol 1873.

NEW MATERIAL. — Right p4 UP LPL5; left P4 UP LPL4; right m1 UP LPL1711.

REMARKS
This species is common in the old Quercy collections and constitutes the largest sample of Quercy nimravids. It is present in the three MP 22 localities, La Plante2, Mas de Got and Valbro. The number of specimens recovered from all the Quercy localities provides an overall view of the species and a good idea of the intra-specific size variation (see Peigné 2003). For example, in lion m1 length (data from Turner 1984) the extreme values are 25.2 and 30.8 mm for a mean of 28.1, the index (difference divided by mean) × 100 = 19.9. In *N. brachyops* the indices are 19.9 for P4 and 23.8 for m1. In *N. intermedius* the indices are 32.7 (P4) and 50.35 (m1), both higher than in *N. brachyops*. A major part of the sample of *N. intermedius* is recorded in the old Quercy collections without any biostratigraphic data and extends over several million years. One explanation may be a progressive change in the size during this time, with the oldest specimens being smaller than the more recent ones. An increase in size of the p4 was also noted (Peigné *et al.* 2014: 28). Perhaps future researches will confirm the increase in size in *N. intermedius*, although in North America a larger range of time did not show a similar increase in *N. brachyops.*

DESCRIPTION
The p4 LPL5 is relatively small and low (L =11.7, w = 4.2 mm) when compared to other specimens of *N. intermedius* (range: L = 10.9-19.4, w = 4.5-19.2 mm in Peigné 2003). The pacd is larger than the aacd and the buccal base is underlined by a clear cingulid (Fig. 5H1, H2). The relatively small size of a lower Oligocene tooth could confirm the probable increase of size at younger localities. The P4 (UP LPL4) with L = 18.8 mm, w = 9.85, Lmts = 7, wmst = 4.7, is within the range of the smaller P4 of *N. intermedius* (Fig. 5E, I). The lower carnassial (UP LPL1711), with a length of 15.7 mm (Fig. 5J1-J3), is slightly smaller than the smallest m1 (L = 16 mm) in Peigné (2003).

Genus *Dinailurictis* Helbing, 1922

TYPE SPECIES. — *Dinailurictis bonali* Helbing, 1922 by original designation.

REMARKS
The genus was created by Helbing (1922) for fossils found in La Tuque (Lot & Garonne, France) in a molassic continental level which could be dated to the middle Oligocene. The remains consisted of a large scimitar-like upper canine, a P3 and a P4 most likely from the same animal. He added to the same sample a root of a large upper canine from Moissac whose size is similar to that of the La Tuque canine, but the geologic age of which is unknown because there are several levels from the middle and late Oligocene to the early Miocene in the Moissac area. Later, a fragment of maxilla with P3-P4 from the old Quercy collection was described as *Nimravus intermedius major* Piveteau, 1931. The latter author did not cite Helbing and probably was not aware of his article. The specimen was revised by Ginsburg (1979) and considered as the type species of the new genus *Quercylurus* Ginsburg, 1979. The main difference between the two genera was the size, *Quercylurus* being larger than *Dinailurictis*. The other characters (elongated protocone of P4, irregular minute pleating of the mesial crest of the paracone, m1 more robust) are linked to the larger size (slight allometry) or are also present in *Dinailurictis.*

Dinailurictis bonali Helbing, 1922
(Fig. 5A-D)

TYPE SPECIMEN. — Lectotype, left upper canine (NMB-AGN 618) NHMB, from La Tuque, France, was designated by Kretzoi (1929: 1320).

NEW MATERIAL. — UM VD46, fragment of lower canine; UM VBOA3-15, distal right humerus; UM VBOA3-17, distal left ulna; UM VBOA3-16, proximal of piece right femur.

DESCRIPTION
The lower canine (UM VD46), of which part of the root and part of the crown are broken off (Fig. 5D), displays the large size and crenulated trenchant distal carena that is typical of a large sabre-toothed cat. *Eofelis*, *Nimravus*, and *Eusmilus* are too small for this canine. We think that it belongs to *Dinailurictis bonali*.

UM VBOA3-15, distal right humerus, has only a part preserved, the epitrochlear arch is lacking (Fig. 5A). The size is intermediate between lion and leopard. The medial lip of the trochlea is less projecting than in modern large cats. It is may be an indication of a different way of running, *Dinailurictis* being less cursorial, a projected lip fixing better the elbow joint in cranio-caudal movements. The cranial fossa for receiving the olecranon process of the ulna is quite deep. The size fits *Dinailurictis bonali*.

UM VD-45, a distal left ulna (Fig. 5C), whose size is intermediate between lion and leopard, is characterized by a high and sharp interosseous crest.

UM VBOA3-16, a proximal right femur (Fig. 5B), consists of a small part of femur whose size is also intermediate between those of leopard and lion. The inter-trochanteric crest is well developed and the trochanteric fossa is deep. The small trochanter projects well laterally.

Genus *Eusmilus* Gervais, 1876

TYPE SPECIES. — *Machaerodus bidentatus* Filhol, 1872 by original designation.
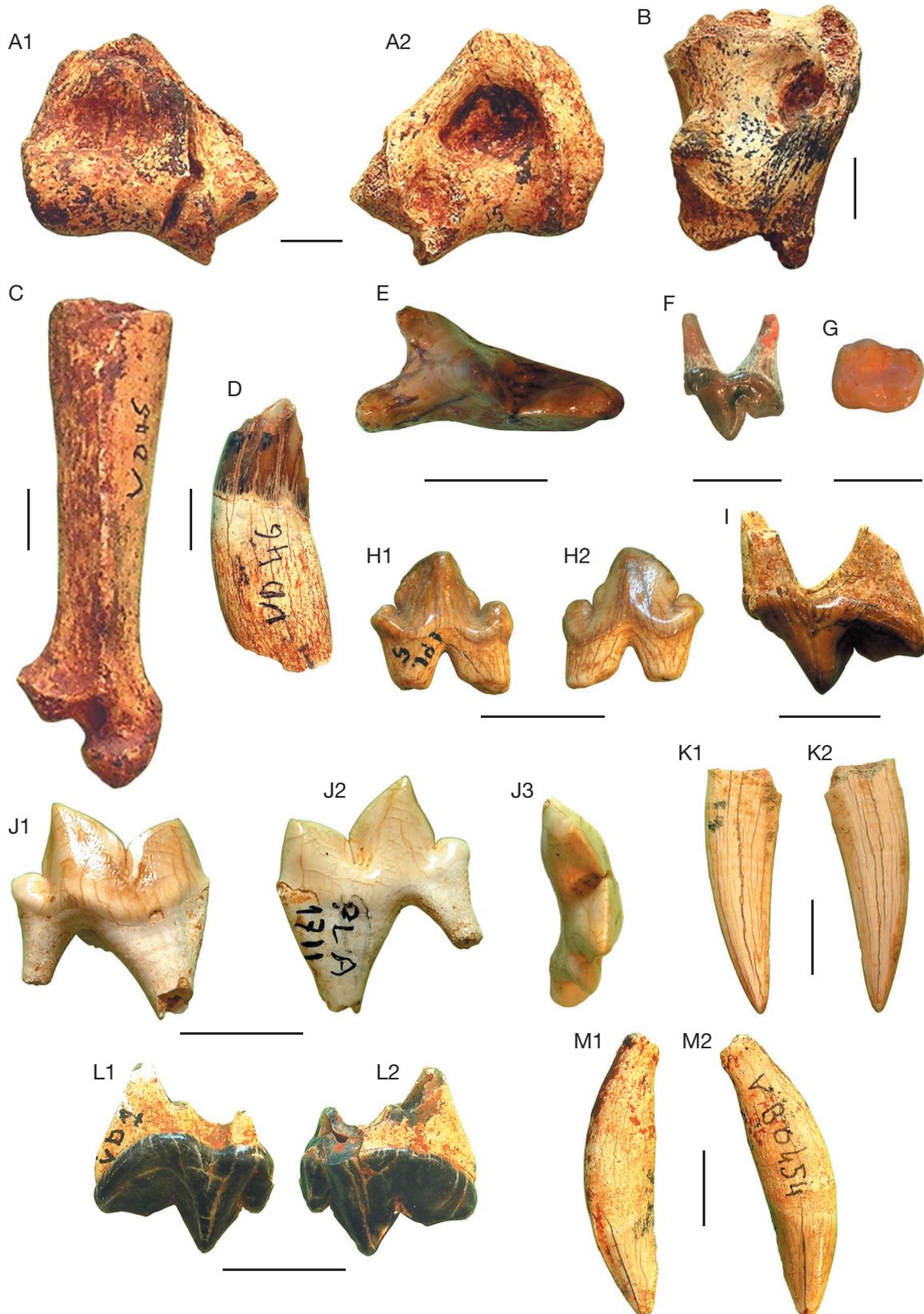
Fig. 5. — **A-D**, *Dinailurictis bonali* Helbing, 1922: **A**, right distal humerus UM VBOA3-15 in cranial (**A1**), and caudal (**A2**) views; **B**, piece of right proximal femur, UM VBOA3-16, cranial view; **C**, left distal ulna, UM VD45, cranial view; **D**, left lower canine, UM VD46, buccal view; **E**, **H-J**, *Nimravus intermedius*; **E**, left P4 UP LPL4, in occlusal view; **H**, right p4 UP LPL5, in buccal (**H1**), and lingual (**H2**) views; **I**, left P4, UP LPL4, in buccal view; **J**, right m1, UP LPL1711, in buccal (**J1**), lingual (**J2**), and occlusal (**J3**) views; **F**, *Mustelictis* aff. *olivieri*, left P4 UM VBO494, in buccal view; **G**, *Pachycynodon* cf. *dubius*? m2, UM VBOA3-9, in occlusal view; **K**, **L**, *Eusmilus bidentatus*, right upper canine, UM VD3, in lingual (**K1**), and buccal (**K2**) views; **L**, right P4, UM VD2, in buccal (**L1**), and lingual (**L2**) views; **M**, *Eofelis edwardsi*, right upper canine, UM VBO454, in lingual (**M1**), and buccal (**M2**) views. Scale bars: A, B, C, D, I, M, 5 mm; E, H, J, K, L, 10 mm.

Eusmilus bidentatus (Filhol, 1872)
(Fig. 5K, L)

RERMARKS
Part of the tip of an elongate and bucco-lingually much compressed canine with mesial and distal trenchant and crenulated carenae is characteristic of a sabre-toothed carnivore (Fig. 5K1, K2). It is impossible to know if it is a milk tooth or a permanent one because these are very similar (Peigné & Brunet 2001). Too small to belong to *Dinailurictis,* smaller and more elongated than that of *Nimravus*, it fits the genus *Eusmilus*. The latter, first described as *Machairodus* (Filhol 1872a) includes two European species, *E. villebramarensis* Peigné & Brunet, 2001 from early Oligocene deposits (MP 22) and *E. bidentatus* (Filhol, 1872) from undated old collections of Quercy and from Soumailles (MP 21), where a complete skeleton was recovered (Ringeade & Michel 1994a, b). The canines of the first species, whether permanent or milk teeth, are larger (Peigné & Brunet 2001) and UM VD3 is closer to *E. bidentatus.*

An isolated P4 (Fig. 5L1, L2) of which the protocone is broken off corresponds to a medium-sized feloid-like carnivoran (L = 15 mm; Wmts = 5.2; Lmts = 6.7). It has a robust parastyle and an elongate metastyle. It differs from *Proailurus*, which is smaller and lacks a large parastyle. *Eofelis edwardsi* (Filhol, 1872) is too small and does not have a parastyle. The P4 of the larger *Eofelis* species, *E. giganteus* Peigné, 2000, is unknown but probably did not have parastyle, like in the smaller species. *Nimravus* does not have parastyle and *Dinailurictis* is too large. The size and the robust parastyle indicate *Eusmilus*. By its size we may refer this carnassial to *E. bidentatus*. Taking into account the occurrence of the large *E. villebramarensis* in Villebramar (MP 22), which is not far away, we conclude that two different species were present in the same area and at the same time.

Genus *Eofelis* Kretzoï, 1938

Eofelis edwardsi (Filhol, 1872)
(Fig. 5M)

REMARKS
This small feloid-like carnivoran was noted by Filhol (1872a) based on a mandible and described by the same author (Filhol 1872b) based on several specimens. Peigné (2000), in a revision of the genus, identified a total of 52 remains of *E. edwardsi* in many collections but only three from the upper jaw, with only one canine. Until now we had not found any remains of *Eofelis* in more than fifty years of excavations in the Quercy. Thus, the new discovery UM VBO4511 is significant. This canine is slightly curved, bucco-laterally compressed (mesio-distal diameter = 8.8 mm, bucco-lingual = 5.6 mm; ratio L/W = 1.57) the height from the tip of the crown to the base of the root is 37.3 mm (Fig. 5M1, M2). The buccal surface of the crown is slightly convex and the lingual one is quite flat. There are slight crenulations or serrations on the distal edge as indicated by Filhol (1872b: 6) for the lower canine of *E. edwardsi* and Peigné (2000: 657) for the lower and upper canines of the same species. The ratio L/W for the upper canine is close to that given by Peigné (2000: table 1) for *E. edwardsi* (1.5). The size is slightly greater than that of a specimen figured by Ginsburg (1979: fig. 10a, b) but the shape is similar. Another species, *E. giganteus* Peigné, 2000, is much larger and although its upper canine is unknown, cannot fit our specimen. Thus, we attribute UM VBO454 to *E. edwardsi* which is firmly dated for the first time.

Family indet.

Genus *Palaeogale* Meyer, 1846

Palaeogale sectoria (Gervais, 1848-1852)

REMARKS
The history of *Palaeogale* is complicated (see Bonis 1981). At present, two species are recognized in Western Europe: the Oligocene *P. sectoria* and the early Miocene *P. minuta*. The former was identified in Valbro (Peigné *et al.* 2014: fig. 22C) from a P4. It is at present the oldest known occurrence of the species.

CONCLUSION

The guild of early Oligocene carnivorans in the phosphorites of Quercy corresponds to a quite complete fauna, from the small *Palaeogale sectoria* probably occupying a niche similar to that of a weasel, to the tiger-sized *Dinailurictis bonali*.

In size from smallest to largest, from a weasel-like to a tiger-like:

Palaeogale sectoria
Peignictis pseudamphictis n. gen., n. sp.
Mustelictis olivieri
Mustelictis cf. *major*
Pachycynodon cf. *filholi*
Pachycynodon cf. *dubius*

Pachycynodon amphictina n. stat.
Amphicynodon sp.
Amphicynodon typicus
Pachycynodon boriei-curvirostris
Cephalogale sp.
Eofelis edwardsi
Eusmilus bidentatus
Nimravus intermedius
Dinailurictis bonali

The species of *Pachycynodon* have a dentition with inflated cusps or cuspids and a special type of wear. The shearing part of the teeth, particularly the protoconid-paraconid blade of m1, is not especially worn buccally but rather at the tip of the cuspids, more or less horizontally, like the dentition of omnivorous carnivorans such as the extant palm civets. The diet of the small *Pachycynodon* was probably based in a large part on fruits and seeds, even if insects or small vertebrates contributed to add some protein to the diet. This ecology implies with high probability a tropical forest where this kind of food is abundant and where these small carnivorans would help in the maintenance of the system by dispersion of the seeds. These results strengthen the conclusions from the study of the flora (Franceschi *et al.* 2006) regarding the Mediterranean and sub-tropical characters of the plants.

The number of species of carnivorans (13) and that of Hyaenodonta (2 or 3), all carnivorous even if some of them could have been partially herbivorous, indicates the richness of the prey. A tropical forest seems to be the right environment to contain a large diversity of available prey. Few of the Orders of putative prey have been studied but one of them, Rodentia, encompassed 11 species in the locality Valbro (Peigné *et al.* 2014). If we add the artiodactyls, small like the Cainotheriidae (Blondel 2005), or larger, the reptiles (Augé 2006; Claude & Tong 2006), amphibians and birds (Mourer-Chauviré 2006) that are normal inhabitants of forests, the painting is complete. However, we should note the absence of taxa, which are present in old Quercy collections. For the small carnivorans, if the absence of scarce taxa like *Haplogale* Filhol, 1882 or *Palaeoprionodon* Filhol, 1880 is not surprising, that of *Stenoplesictis* Filhol, 1880 is astonishing because it is common in other Oligocene localities. It is the same for the family Amphicyonidae which includes more than 15 genera and more than 20 species (double if we take into account the sub-species; Springhorn 1977). The explanation could be ecological for the three studied localities, with amphicyonids perhaps living in more open environments although their skeleton, except that of the Daphoeninae, indicates that they were not good runners (Argot 2010). Another possibility is temporal and we may suppose they were later immigrants in Western Europe: all would "late travellers of the great Stampian migration" (Viret 1929). The early Oligocene carnivoran fauna is intermediate between the upper Eocene one with a few taxa, such as *Paramiacis, Cynodictis* and *Simanphycyon*, and the assemblages of middle and late Oligocene. Future research will try to pinpoint up the precise level of the changes between MP 22 and MP 26.

REFERENCES

ARGOT C. 2010. — Morphofunctional analysis of the post cranium of *Amphicyon major* (Mammalia, Carnivora, Amphicyonidae) from the Miocene of Sansan (Gers, France) compared to three extant carnivores: *Ursus arctos*, *Panthera leo* and *Canis lupus*. *Geodiversitas* 32 (1): 65-106. https://doi.org/10.5252/g2010n1a2

ASTRUC J.-G., ESCARGUEL G., MARANDAT B., SIMON-COINÇON R. & SIGÉ B. 2000. — Floor-age constraining of a tectonic paroxysm of the Pyrenean orogen. Late middle Eocene mammal age of a faulted karstic filling of the Quercy phosphorites, southwestern France. *Geodinamica Acta* Paris, 13: 271-280. https://doi.org/10.1016/S0985-3111(00)01047-0

AUGÉ M. 2006. — Répartition des tailles chez les lézards des phosphorites du Quercy. *Strata,* série 1, 13: 69-78.

AYMARD A. 1842-1846. — Essai monographique sur un nouveau genre de mammifère fossile trouvé dans la haute vallée de la Loire et nommé *Entelodon*. *Annales de la Société d'Agriculture, Sciences, Arts et Commerce du Puy* 12: 227-267. https://gallica.bnf.fr/ark:/12148/bpt6k408328n/f230.item

AYMARD A. 1850. — Du *Cynodon*, mammifère carnassier fossile trouvé dans les calcaires marneux de Ronzon, près du Puy. *Annales de la Société d'Agriculture, Sciences, Arts et Commerce du Puy* 15: 92-122. https://gallica.bnf.fr/ark:/12148/bpt6k2293835/f95.item

BIOCHROM'97 1997. — Synthèses et tableaux de corrélations in Acts of the Congress Biochrom'97. *Mémoires et Travaux de l'EPHE* 21: 769-805.

BLAINVILLE H. M. D. DE 1841-1864. — *Ostéographie ou description iconographique comparée du squelette et du système dentaire des mammifères récents et fossiles pour servir de base à la zoologie et à la géologie*. Tome 2. *Carnassiers*. J. B. Baillère, Paris. https://doi.org/10.5962/bhl.title.127351

BLONDEL C. 2005. — New data on the Cainotheriidae (Mammalia, Artiodactyla) from the early Oligocene of south-western France. *Zoological Journal of the Linnean Society* 144 (2): 145-166. https://doi.org/10.1111/j.1096-3642.2005.00166.x

BONIS L. DE 1966. — Arrière-crânes et moulages endocrâniens de Carnivores fossiles. *Annales de Paléontologie* 52 : 143-162.

BONIS L. DE 1971. — Deux nouveaux carnassiers des Phosphorites du Quercy. *Annales de Paléontologie* 57 (1): 117-127.

BONIS L. DE 1974. — Premières données sur les carnivores fissipèdes provenant des fouilles récentes dans le Quercy. *Palaeovertebrata* 6: 27-32.

BONIS L. DE 1981. — Contribution à l'étude du genre *Palaeogale* Meyer (Mammalia, Carnivora). *Annales de Paléontologie* 67 (1): 37-56.

Bonis L. de 1997. — Précisions sur l'âge géologique et les relations phylétiques de *Mustelictis olivieri* nov. sp. (Carnivora, Mustelidae), carnassier de l'Oligocène inférieur (MP 22) des phosphorites de Quercy (France). *Geobios* M.S. 20: 55-60. https://doi.org/10.1016/S0016-6995(97)80009-5

Bonis L. de 2011. — A new species of *Adelpharctos* (Mammalia, Carnivora, Ursidae) from the late Oligocene of the "Phosphorites du Quercy" (France). *Estudios Geológicos* 67 (2): 179-186. https://doi.org/10.3989/egeol.40553.181

Bonis L. de 2013. — Ursidae (Mammalia, Carnivora) from the late Oligocene of the "Phosphorites du Quercy" (France) and a reappraisal of the genus *Cephalogale* Geoffroy, 1862. *Geodiversitas* 35 (4): 787-814. https://doi.org/10.5252/g2013n4a4 https://doi.org/10.5252/g2013n4a4

Bonis L. de, Crochet J. Y., Rage J. C., Sigé B., Sudre J. & Vianey-Liaud M. 1973. — Nouvelles faunes de vertébrés oligocènes des phosphorites du Quercy. *Bulletin du Muséum national d'Histoire naturelle, 3ème série, Sciences de la Terre,* 174: 103-113 (Sciences de la Terre 28).

Cirot E. 1992. — *Étude phylogénétique de quelques genres d'Arctoidea de l'Oligocène eurasiatique. Comparaisons des données morphologiques et moléculaires*. PhD University of Poitiers (Unpublished).

Cirot E. & Bonis L. de 1992. — Révision du genre *Amphicynodon*, carnivore de l'Oligocène. *Palaeontographica* 220 (4-6): 103-130.

Cirot E. & Bonis L. de 1993. — Le crâne d'*Amphictis ambiguus* (Carnivora, Mammalia) : son importance pour la compréhension de la phylogénie des Mustéloïdes. *Comptes rendus de l'Académie des Sciences, Série 2, Mécanique, Physique, Chimie, Sciences de l'Univers, Sciences de la Terre* 316: 1327-1333. https://gallica.bnf.fr/ark:/12148/bpt6k6316609v/f349.item

Claude J. & Tong H. 2006. — Les faunes chéloniennes fossiles du Quercy : mise à jour des connaissances. *Strata,* série 1, 13: 79-84.

Cope E. D. 1878. — Vertebrate fauna of the Miocene of Oregon. *Paleontological Journal* 30: 1-16.

Cope E. D. 1879. — On the genera of Felidae and Canidae. *Proceeding of the Academy of Natural Sciences, Philadelphia* 31: 168-194. https://www.jstor.org/stable/4060308

Cope E. D. 1880. — On the extinct cats of America. *The Amerian Naturalist* 14 (12): 833-858. https://doi.org/10.1086/272672

Filhol H. 1872a. — Sur les Carnassiers et les Chéiroptères dont on trouve les débris fossiles dans les gisements de phosphorites de Caylux, Frégols, Concots. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences* 75: 92-94. https://gallica.bnf.fr/ark:/12148/bpt6k30321/f94.item

Filhol H. 1872b. — Recherches sur les mammifères fossiles des dépôts de phosphate de chaux dans les départements du Lot, du Tarn, et de Tarn-et-Garonne. Première partie : carnassiers et chiroptères. *Annales des Sciences géologiques* 3 (7): 1-31.

Filhol H. 1873. — Sur les vertébrés fossiles trouvés dans les dépôts de phosphate de chaux du Quercy. *Bulletin de la Société philomathique de Paris, série 6,* 8-10: 85-89. https://biodiversitylibrary.org/page/31641365

Filhol H. 1876-1877. — Recherches sur les phosphorites du Quercy. Études des fossiles qu'on y rencontre et spécialement des mammifères. *Bibliothèque de l'École des Hautes Études, Section des Sciences naturelles*. Première partie, 15 (4): 1-220. Deuxième partie 16 (1): 1-338.

Filhol H. 1880. — Sur la découverte de mammifères nouveaux dans les dépôts de phosphate de chaux du Quercy. *Comptes rendus hebdomadaires des séances de l'Académie des Sciences* 90: 1579-1580. https://biodiversitylibrary.org/page/3716419

Filhol H. 1882. — *Mémoires sur quelques mammifères fossiles des phosphorites du Quercy*. Vialelle et Cie, Toulouse: 1-140. https://doi.org/10.5962/bhl.title.86309

Filhol H. 1890. — Description d'une espèce nouvelle de *Viverra* fossile. *Bulletin de la Société philomathique de Paris*, sér. 8 II: 139-142. https://biodiversitylibrary.org/page/31965626

Franceschi D. de, Le Gall C., Escarguel, G., Hugueney M., Legendre S., Simon-Coinçon R., Pélissié T. & Sigé B. 2006. — Une paléoflore des phosphatières karstiques du Quercy (sud-ouest de la France) : première découverte, résultats et perspectives. *Strata,* série 1, 13: 97-101.

Gèze B. 1938a. — Contribution à la connaissance des Phosphorites du Quercy. *Bulletin de la Société géologique de France* 5 (8) : 123-146.

Gèze B. 1938b. — La genèse des phosphorites du Quercy. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences* 206: 759-761. https://gallica.bnf.fr/ark:/12148/bpt6k3158p/f759.item

Gèze, B., Rage J. C., Vergnaud-Grazzini C., Broin F. de, Buffetaud E., Mourer-Chauviré C., Crochet J. Y., Sigé, B., Sudre J., Remy J. A., Lange-Badré B., Bonis L. de, Hartenberger J. L. & Vianey-Liaud M. 1978. — La poche à phosphate de Sainte-Néboule (Lot) et sa faune de vertébrés du Ludien supérieur. *Palaeovertebrata* 8 (2-4): 167-326.

Ginsburg L. 1966.— Les Amphicyons des Phosphorites du Quercy. *Annales de Paléontologie* (*Vert.*) 52 (1): 23-44.

Ginsburg L. 1979. — Révision taxonomique des Nimravini (Carnivora, Felidae) de l'Oligocène des Phosphorites du Quercy. *Bulletin du Muséum national d'Histoire naturelle* Paris 1 (1): 35-49. https://biodiversitylibrary.org/page/55498108

Ginsburg L. & Morales J. 1995. — *Zaragocyon daamsi* n. gen. n. sp., Ursidae primitif du Miocène inférieur d'Espagne. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences*, série IIa, 321: 811-815. https://doi.org/10.1016/SO753-3969(98)80003-7

Kretzoi M. 1929. — *Materiale zur phylogenetischen Klassifikation der Aeluroiden*. 10th International Zoological Congress, Budapest, 2: 1293-1355.

Lange B. 1969. — Un nouveau musteliné des Phosphorites du Quercy, *Mustelictis piveteaui*. *Comptes rendus hebdomadaires des séances de l'Académie des sciences, Série D, Sciences naturelles* 268: 2870-2872. https://gallica.bnf.fr/ark:/12148/bpt6k6293308f/f761.item

Lange B. 1970. — *Mustelictis piveteaui*, mustélidé nouveau des Phosphorites du Quercy. *Annales de Paléontologie* 56 (1): 3-16.

Helbing H. 1922. — *Dinailurictis* nov. gen., ein eigenartiger Felidentypus aus dem Oligocän. *Eclogae geologicae Helvetiae Basel* 16 (5): 568-575.

Hunt R. M. Jr 1996. — Biogeography of the order Carnivora, *in* Gittleman T. L. (ed.), *Carnivora Behavior Biology and Evolution*. Cornell University Press, New York: 485-541.

Hunt R. M. Jr 2009. — Long-legged pursuit carnivorans (Amphicyonidae, Daphaeninae) from the early Miocene of North America. *Bulletin of the American Museum of Natural History* 318: 4-93. http://hdl.handle.net/2246/5948

Mourer-Chauviré C. 2006. — The avifauna of the Eocene and Oligocene phosphorites du Quercy (France): an updated list. *Strata,* série 1, 13: 135-147.

Peigné S. 2000. — A new species of *Eofelis* (Carnivora: Nimravidae) from the Phosphorites of Quercy, France. *Comptes Rendus de l'Académie des Sciences Paris* 330 (9): 653-658. https://doi.org/10.1016/S1251-8050(00)00199-3

Peigné S. 2001. — A primitive nimravine skull from the Quercy fissures, France. Implications for the origins and evolution of Nimravidae (Carnivora). *Zoological Journal of the Linnean Society* 132 (4): 401-410. https://doi.org/10.1111/j.1096-3642.2001.tb02467.x

Peigné S. 2003. — Systematic review of European Nimravinae (Mammalia, Carnivora, Ninravidae) and the phylogenetic relationships of Palaeogene Nimravidae. *Zoologica Scripta* 32: 199-229. https://doi.org/10.1046/j.1463-6409.2003.00116.x

Peigné S. & Bonis L. de 1999. ——Le premier crâne de *Nimravus* (Mammalia, Carnivora) d'Eurasie et ses relations avec *N. brachyops* d'Amérique du Nord. *Revue de Paléobiologie* 18 (1): 57-67.

Peigné S. & Brunet M. 2001. — Une nouvelle espèce du genre *Eusmilus* (Carnivora: Nimravidae) de l'Oligocène (MP 22) d'Europe. *Geobios* 34 (6): 657- 672. https://doi.org/10.1016/S0016-6995(01)80027-9

Peigné S., Vianey-Liaud M., Pélissié T. & Sigé B. 2014. — Valbro : un nouveau site à vertébrés de l'Oligocène inférieur (MP22) de France (Quercy). I – Contexte géologique ; Mammalia : Rodentia, Hyaenodontida, Carnivora. *Annales de Paléontologie* 100: 1-45. https://doi.org/10.1016/j.annpal.2013.11.002

Piveteau J. 1931. — Les chats des Phosphorites du Quercy. *Annales de Paléontologie* 20: 107-163.

Piveteau J. 1942 — Études sur quelques mammifères des Phosphorites du Quercy. I. Le genre *Stenoplesictis. Annales de Paléontologie* 30: 63-72.

Piveteau J. 1962. — L'encéphale de *Viverravus angustidens*, Miacidé des Phosphorites du Quercy. *Annales de Paléontologie* 48: 165-175.

Rage J.-C. 2006. — The lower vertebrates from the Eocene and Oligocene of the phosphorites du Quercy (France) an overview, *Strata,* série 1, 13: 161-173.

Rémy J. A., Crochet J.-Y., Sigé B., Sudre J., Bonis L. de, Vianey-Liaud M., Godinot M., Hartenberger J.-L., Lange-Badré B. & Comte B. 1987. — Biochronologie des phosphorites du Quercy : mise à jour des listes fauniques et nouveaux gisements de mammifères fossiles. *Münchner Geowissenschaftliche Abhandlungen* A (10): 169-188.

Ringeade M. & Michel P. 1994a. — Une nouvelle sous-espèce de Nimravidae (*Eusmilus bidentatus ringeadei*) de l'Oligocène inférieur du Lot et Garonne (Soumailles, France) : étude préliminaire. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences* 318: 691-696. https://gallica.bnf.fr/ark:/12148/bpt6k65095354/f89.item

Ringeade M. & Michel P. 1994b. — À propos de l'*Eusmilus* (*Eusmilus bidentatus ringeadei* Ringeade et Michel 1994) de Soumailles, canton de Duras (Lot et Garonne, France) : étude descriptive. *Paleo* 6: 5-37.

Schlosser M. 1888. — Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europäischen Tertiärs und deren Beziehungen zu ihren lebenden und fossilen aussereuropäischen Verwandten. *Beiträge zur Paläontologie Österreich Ungarns und des Orients* I. Theil 6: 1-224. II Theil 7: 1-162.

Schlosser M. 1899. — Ueber die Bären und bärenänlichen Formen des europäischen Tertiärs. *Palaeontographica* 46 (4) : 95-148.

Sigé B., Aguilar J. P. & Marandat B. 1991. — Extension au Miocène inférieur des remplissages phosphatés du Quercy, la faune de vertébrés de Crémat (Lot, France). *Geobios* 23 (4): 497-502. https://doi.org/10.1016/S0016-6995(06)80251-2

Springhorn R. 1877. — Revision fer alttertiären europäischen Amphicyonidae (Carnivora, Mammalia). *Palaeontographica* A 158 : 26-113.

Teilhard de Chardin P. 1915. — Les carnassiers des phosphorites du Quercy. *Annales de Paléontologie* 9: 103-190.

Toohey L. 1959. — The species of *Nimravus* (Carnivora, Felidae). *Bulletin of the American Museum Natural History* 118: 71-112. http://hdl.handle.net/2246/1972

Trouessart E. 1904. — *Catalogus mammalium tam viventium quam fossium quinquinale supplementum.* Vol. 1. R. Friedländer & Sohn, Berlin: 1-546, 224. https://doi.org/10.5962/bhl.title.61437

Turner A. 1984. — Dental sex dimorphism in European Lions (*Panthera leo* L.) of the Upper Pleistocene: palaeoecological and palaeoethological implications. *Annales Zoologici Fennici* 21: 1-8. https://www.jstor.org/stable/23734092

Vianey-Liaud M. & Legendre S. 1986. — Les faunes des phosphorites du Quercy : principes méthodologiques en paléontologie des mammifères; homogénéité chronologique des gisements de mammifères fossiles. *Eclogae geologicae Helvetiae* 79 (3): 917-944. http://doi.org/10.5169/seals-165856

Viret J. 1929 — Les faunes de mammifères de l'Oligocène supérieur de la Limagne bourbonnaise. *Mémoires de l'Université de Lyon* 47: 1-305.

Wang B. & Qiu Z. 2003. — Notes on Early Oligocene Ursids (Carnivora, Mammalia) from Saint Jacques, Nei Mongol, China. *Bulletin of the American Museum of Natural History* 279: 116-124. https://doi.org/10.1206/0003-0090(2003)279<0163:C>2.0.CO;2

Wolsan M. & Lange-Badré B. 1996. — An arctomorph carnivoran skull from the Phosphorites du Quercy and the origin of procyonids. *Acta Palaeontologica Polonica* 41 (3): 277-298.