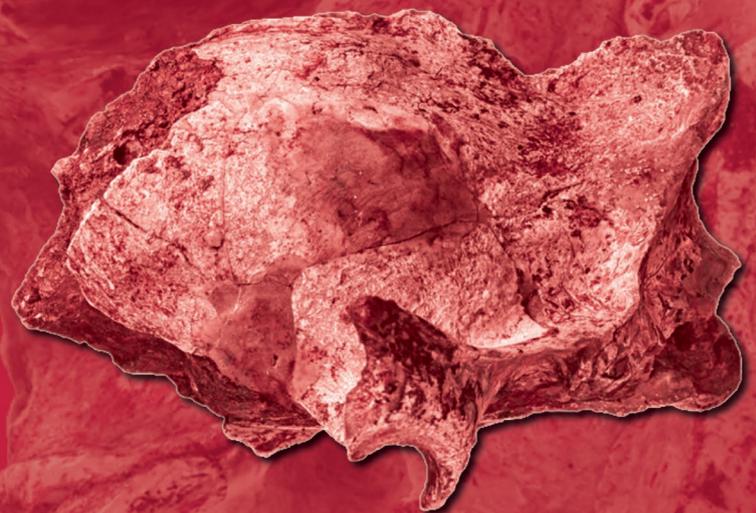


Description of a new species of *Cynodictis*
Bravard & Pomel, 1850 (Carnivora, Mammalia)
from the Quercy Phosphorites with comments
on the use of skull morphology for phylogenetics

Kévin LE VERGER, Floréal SOLÉ & Sandrine LADEVÈZE



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Description of a new species of *Cynodictis* Bravard & Pomel, 1850 (Carnivora, Mammalia) from the Quercy Phosphorites with comments on the use of skull morphology for phylogenetics

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ABSTRACT

Amphicyonidae Trouessart, 1885 are among the oldest known carnivoran groups, with the oldest representatives in Europe belonging to the genus *Cynodictis* Bravard & Pomel, 1850. This genus, discovered in the middle of the 19th century, presents a particularly confusing taxonomic history. Early on it was subject to taxonomic inflation, but now its diversity is reduced to six species. It is therefore interesting to question the relevance of dental characteristics, knowing that these structures have, very often, been the only anatomical elements used for the description of extinct mammalian taxa. Thanks to the several deposits of the Quercy Phosphorites, many crania of *Cynodictis* are available, allowing us to address this issue. In this comparative study, several skulls belonging to this genus are compared. Finally, we describe a new species, *Cynodictis peignei* n. sp., and discuss the relevance of cranial characters in comparison with dental characters and the ecological information from these structures.

KEY WORDS

Caniformia,
Paleogene,
Europe,
cranium,
osteology,
new species.

RÉSUMÉ

Description d'une nouvelle espèce de Cynodictis Bravard & Pomel, 1850 (Carnivora, Mammalia) provenant des Phosphorites du Quercy; réflexion sur l'utilisation de la morphologie du crâne dans les analyses phylogénétiques.

L'un des plus anciens groupes de carnivores connu correspond aux Amphicyonidae Trouessart, 1885, dont le plus ancien représentant en Europe appartient au genre *Cynodictis* Bravard & Pomel, 1850. Ce taxon, découvert au milieu du 19^{ème} siècle, présente une histoire taxonomique particulièrement confuse. D'abord soumis à une inflation taxonomique, sa diversité s'en trouve réduite aujourd'hui à six espèces. Ce constat conduit à questionner la pertinence des caractéristiques dentaires en sachant que ces structures ont, très souvent, été les seuls éléments anatomiques utilisés pour la description des taxons mammaliens fossiles. Avec l'apport de plusieurs gisements des Phosphorites du Quercy, plusieurs crânes de *Cynodictis* sont disponibles, nous permettant d'aborder cette question. Dans le cadre d'une étude comparative, plusieurs crânes appartenant à ce genre sont comparés dans cet article. L'un d'eux appartient à une nouvelle espèce: *Cynodictis peignei* n. sp. Nous discuterons à cette occasion de la pertinence des caractères crâniens en comparaison des caractères dentaires et nous intéresserons aux informations écologiques que ces structures peuvent apporter.

MOTS CLÉS
Caniformia,
Paléogène,
Europe,
crâne,
ostéologie,
espèce nouvelle.

INTRODUCTION

Based on current knowledge, the history of carnivorans in Europe begins at the end of the Eocene (MP18 – MP = Mammal Paleogene reference-levels – Priabonian; BiochroM'97 1997) with the appearance of the first caniformians. In 1850, a mandible (see Gervais 1852) was discovered in fossiliferous sediments from the vicinity of La Débruge (Vaucluse, France) and was assigned to a new carnivoran genus: *Cynodictis* Bravard & Pomel, 1850. Unfortunately, these paleontologists never had the chance to extensively describe the species. Subsequently, Gervais (1852) described a new species based on this specimen, *Cynodictis lacustris* (type species), while Pomel (1853) referred a new species, *C. parisiensis* (based on the work of Cuvier 1821) to *Cynodictis*. Alternatively regarded as a canid, as a 'miacid' (Teilhard de Chardin 1915; Piveteau 1961; Petter 1966; Ginsburg 1966; Bonis 1966, 1969; Springhorn 1977) or as a carnivorous mammal without clear systematic position (Kotsakis 1980), *Cynodictis* is now considered to be the sister genus of all other amphicyonids based on recent phylogenetic studies (Hunt 1996; Tomiya & Tseng 2016), a hypothesis that was previously proposed by Beaumont (1973) and Savage (1977).

Shortly after the discovery of *Cynodictis lacustris*, a gigantic karst system was discovered by mining in the southwestern France. During the second half of the 19th century, phosphate exploitation unearthed many fossiliferous localities, which correspond to pockets of richly fossiliferous phosphates named the "Phosphorites du Quercy" (Cavaillé 1974). A true death trap for Paleogene faunas, this geological formation was – and still is – a windfall for paleontologists. For nearly 150 years, the abundance and quality of fossils, as well as the presence of specimens of all sizes (thus showing little taphonomic bias) have allowed various studies, such as population evolution (Remy *et al.* 1987), systematics (Bonis 1978), and functional anatomy (Martinez & Sudre 1995). The quantity of specimens collected is such that since 1965 more than 92

new species have been described (Legendre *et al.* 1997). In addition, preservation can be described as exceptional: complete skeletons (Bonis 1995) and skulls of small and rarely found mammals (Vianey-Liaud 1974) have been discovered.

The "Phosphorites du Quercy" are crucial to better document and understand the history of *Cynodictis*, especially thanks to the discovery of a very large number of mandibles. Filhol (1876, 1882) described more than twenty species, causing the genus *Cynodictis* to undergo "une véritable inflation taxonomique" ['a real taxonomic inflation'] (Bonis 1978: 303). Schlosser (1902) also described new species referred to this genus, as did Teilhard de Chardin (1915) shortly thereafter. Surprisingly, the specific diversity of *Cynodictis* was not questioned or studied until the work of Bonis (1978). His drastic and necessary taxonomic revision helped to reduce the diversity of the genus from more than twenty species to four valid species – *Cynodictis lacustris* Gervais, 1852; *C. intermedius* Filhol, 1876; *C. longirostris* Filhol, 1872; and *C. exilis* Teilhard de Chardin, 1915. Two years later, Kotsakis (1980) also performed a taxonomic revision of the genus and modified the diversity of the group. *Cynodictis intermedius* was invalidated and subsumed under *C. lacustris*, as already envisaged by Bonis (1978). The genus is currently composed of six species: *C. lacustris*, *C. longirostris*, *C. exilis*, *C. ferox* Filhol, 1876, *C. crassus* Teilhard de Chardin, 1915, and *C. cayluxensis* Filhol, 1876. It is noteworthy that these species are only recognized from the morphology of the mandible. Teilhard de Chardin (1915: 120), however, mentioned that "Le crâne complet d'un *Cynodictis* n'a jamais encore été décrit à ma connaissance. Il en existe pourtant plusieurs dans les collections, bien déterminables grâce aux dents conservées." ["To my knowledge, no complete cranium of a *Cynodictis* has yet been described. Nevertheless, several that are readily identifiable based on their preserved dentitions exist in collections."] The Muséum national d'Histoire naturelle (MNHN) houses several skulls from the Quercy Phosphorites, which allow for a more detailed description of each species and, therefore, a

TABLE 1. — Specimens of each species of *Cynodictis* Bravard & Pomel, 1850 measured for the lower dentition.

Species	Specimen	Preserved teeth	Reference
<i>C. cayluxensis</i> Filhol, 1876	MNHN.F.Qu unnumbered (holotype)	p3-m3 (vestigial m3)	direct observation
<i>C. crassus</i> Teilhard de Chardin, 1915	MNHN.F.Qu8921 (holotype)	p2-m3 (vestigial m3)	direct observation
<i>C. exilis</i> Teilhard de Chardin, 1915	MNHN.F.Qu8993 (holotype)	p2-m2	direct observation
<i>C. ferox</i> Filhol, 1876	Java collections of the MNHN	p4-m1	Filhol 1876
<i>C. lacustris</i> Gervais, 1852	MNHN.F.Qu unnumbered (genoholotype – holotype)	p4-m1	Bonis 1978
<i>C. longirostris</i> Filhol, 1872	MNHN.F.Qu8933 (holotype)	p2-m2	direct observation
<i>C. peignei</i> n. sp.	–	no mandible	–

better delimitation of the diversity within this genus. This is the main goal of the present comparative study, which also aims to describe a new species of *Cynodictis*, as well as discussing the pertinence of cranial characters compared to dental characters in systematics.

MATERIAL AND METHODS

STUDIED SPECIMENS

The specimens studied here are all from the Quercy Phosphorites. The specimen that is the subject of the detailed anatomical description is an incomplete *Cynodictis* cranium in two parts: MNHN.F.Qu9007 (snout) and MNHN.F.Qu9008 (neurocranium), labelled as *C. intermedius*. Comparative specimens are: a subcomplete cranium of *Cynodictis lacustris* (MNHN.F.Qu17502) – curated as *C. intermedius* –, which preserves the premaxillary including the right P1-M1 and left P1-M2 (left P4 and M1 incomplete), whereas the zygomatic arches and part of the sagittal crest are missing; an incomplete cranium of *Cynodictis lacustris* (MNHN.F.Qu1903-20) – curated as *C. intermedius* –, which is complete except for the anterior part of the orbital constriction, and only the M1 (incomplete) and the right M2 are present; an incomplete cranium of *Cynodictis exilis* (MNHN.F.Qu unnumbered) with the zygomatic arches and front of the snout missing, but right P2-P4 and left P3-M1 present (only the stylar plate is missing on M1). The rest of the data are from the literature (references below). For body mass and diet estimations, dental measurements were either taken from specimens housed in the collection of the MNHN or from the literature (Table 1).

TOOTH AND SKULL NOMENCLATURE

The anatomical description of the skull of *C. peignei* n. sp. is a revision of the brief descriptions provided by previous authors (Filhol 1876; Teilhard de Chardin 1915; Bonis 1978; Kotsakis 1980). The cranial nomenclature is based on the detailed description of the cranial osteology of *Nandimia binotata* Gray, 1830 (African palm civet) by Wible & Spaulding (2013). Biological interpretations are inferred from the study of *Canis lupus* Linnaeus, 1758 by Evans (1993). For the description of the molariform dentition, Szalay's (1969) dental nomenclature was used. The dental nomenclature of premolars follows Ginsburg (1999). To simplify the reading, upper teeth are in capital letters (e.g., first premolar: P1) and lower teeth are in lower case (e.g., p1).

MEASUREMENTS, BODY MASS AND DIET DIVERSITY

Paleoecological reconstruction is generally based on three parameters, body mass, locomotion and diet, which make it possible to estimate the trophic position as well as the ecological niche of an organism. These estimates are often based on cranial and dental measurements.

In this study, the cranial measurements have been adapted to the completeness of the material (Fig. 1). For two incomplete specimens, part of the snout was missing and the total lengths of the snout and cranium were therefore roughly estimated by size comparisons with the entire sample.

Body masses of *Cynodictis* were estimated based on incomplete cranial material. Methods established by Van Valkenburgh (1990) for Carnivoramorpha have been used. Body mass (BM) in kg is calculated in three different ways: 1) from skull length (SKL in mm); 2) from occiput to orbit length (OoL in mm); and 3) from m1 length (m1L in mm). The cranial data was preferred to dental data because they produced smaller standard deviations (Van Valkenburgh 1990). The three formulas based on the length of the skull and m1 are as follows:

- 1) $\text{Log}_{10}(\text{BM}) = [3.13 \times \text{Log}_{10}(\text{SKL})] - 5.59$
- 2) $\text{Log}_{10}(\text{BM}) = [3.44 \times \text{Log}_{10}(\text{OoL})] - 5.74$
- 3) $\text{Log}_{10}(\text{BM}) = [2.97 \times \text{Log}_{10}(\text{m1L})] - 2.27$

Diet was inferred from indices and categories defined by Van Valkenburgh (1988, 2007) in Carnivora. These categories are: 1) hypercarnivore, the organism feeds on more than 70% meat; 2) scavenger, the organism feeds on more than 70% meat and large bones; 3) mesocarnivore, the organism feeds on 50% to 70% meat, with the balance made up of nonvertebrate foods; and 4) hypocarnivore, the organism feeds on more than 70% nonvertebrate foods. Among the five possible indices to infer dietary category, the two most representative categories were selected: RBL (ratio of the length of the trigonid of m1 (BL) to the total length of m1) and RPS (width of the largest lower premolar (PMW) divided by the cube root of weight) (Van Valkenburgh 1988). The value of each index for each species is then compared to Van Valkenburgh's categories (1988: appendix 3) in order to assign them a diet.

COLLECTION ABBREVIATIONS

MNHN.F. fossil collection of the Muséum national d'Histoire naturelle, Paris;
 MNHN.F.Qu fossil collection from the Quercy Phosphorites (MNHN).

TABLE 2. — Measurements (in mm) of skull of *Cynodictis* Bravard & Pomel, 1850 from the sample. Abbreviations: **H**, height; **L**, length; **N**, neurocranium; **OoL**, occiput to orbit length; **S**, snout; **SKL**, skull length; **W**, width. Symbols: *, estimated measurement; ?, missing data.

Specimen	Snout			Neurocranium			Cranium	
	SL	SW	SH	NL	NW	NH	SKL	OoL
<i>C. peignei</i> n. sp.	40	30	19	43	47	33	113*	81*
<i>C. exilis</i> Teilhard de Chardin, 1915 (MNHN.F.Qu unnumbered)	26*	29	12	36	?	27	99*	65
<i>C. lacustris</i> Gervais, 1852 (MNHN.F.Qu17502)	31*	27	21	36	36	30	105*	76
<i>C. lacustris</i> (MNHN.F.Qu1903-20)	?	?	?	38	39	31	?	72

TABLE 3. — Measurements (in mm) of teeth of *Cynodictis* Bravard & Pomel, 1850 from the sample. Abbreviations: **L**, length (anteroposterior); **W**, width (linguolabial). Symbol: ?, missing data.

Specimen	I1		I2		I3		C		P1		P2		P3		P4		M1		M2	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W
<i>C. peignei</i> n. sp.	2.5	1.1	3.0	1.5	4.5	2.0	7.0	4.0	3.0	2.0	5.0	2.0	5.5	3.5	10.0	7.0	7.0	9.5	?	?
<i>C. exilis</i> Teilhard de Chardin, 1915 (MNHN.F.Qu unnumbered)	?	?	?	?	?	?	?	?	?	?	4.5	2.3	6	3.5	9.5	7.0	5.5	?	?	?
<i>C. lacustris</i> Gervais, 1852 (MNHN.F.Qu17502)	?	?	?	?	?	?	?	?	3.0	1.8	5.0	3.0	6.5	3.5	9.3	7.5	7.2	10.5	4.5	6.0
<i>C. lacustris</i> (MNHN.F.Qu1903-20)	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	7.0	9.5	4.0	7.0

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
 Order CARNIVORA Bowdich, 1821
 Family AMPHICYONIDAE Trouessart, 1885
 Subfamily AMPHICYONINAE Trouessart, 1885

Genus *Cynodictis* Bravard & Pomel, 1850

TYPE SPECIES. — *Cynodictis lacustris* Gervais, 1852 by original designation (“*Cynodon lacustre*” in Gervais 1852: 113, pl. 25).

INCLUDED SPECIES. — *Cynodictis longirostris* Filhol, 1872; *C. cayluxensis* Filhol, 1876; *C. ferox* Filhol, 1876; *C. crassus* Teilhard de Chardin, 1915; *C. exilis* Teilhard de Chardin, 1915; *C. peignei* n. sp.

DISTRIBUTION. — The oldest occurrence of *Cynodictis* is in the French sites of La Débruge (MP18), Ste-Neboule (MP18) and Pont d’Assou (MP19), followed by discoveries in the Montmartre deposits (MP19). *Cynodictis* from the southern United Kingdom are probably the same age as the latter. All are referred to the Priabonian. The age of the Frohnstetten (Germany) is considered little younger, from the end of the Eocene (latest Priabonian). The remains from the Quercy Phosphorites are referred partly to the late Eocene, but mostly to the lower Oligocene. The most recent known occurrence corresponds to an unpublished cranium found at Aubrelong 1 (MP21 – Quercy Phosphorites). Although in this locality, the presence of remains attributed to “*Cynodictis palmidens*” was mentioned, the unpublished cranium does not correspond to it and we recognize this specimen as *Cynodictis* (KLV, FS, SL, in prep). The stratigraphic distribution of *Cynodictis* is therefore confined to Western Europe from MP18 to MP21. It should be noted, however, that some authors suggest that *Cynodictis* is present up to MP23 (for more details on this question, see Kotsakis [1980: 268, 269]).

DIAGNOSIS (emended from Teilhard de Chardin 1915 and Tomiya & Tseng 2016). — Differs from other European amphicyonids by: premolars broad, triangular, and bearing strong accessory cusps (the protoconid is well developed and the cingulum extends from the mesial to the distal directions and has a pointed end); m1 markedly larger than the all premolars and very tall; paraconid on m1 generally

as tall as the protoconid on p4; protoconid on m1 much taller than para- and metaconid; trigonid on m1 mesiodistally compressed, but with proto- and paraconid laterally flattened and together forming a nearly longitudinal edge; shallow talonid, delimited by a sharp hypoconid, a sharp entoconid, a small accessory entoconulid, and often by a poorly developed hypoconulid; m2 very similar to the m1, with strong anterolabial edge and without any tendency to a noticeable crushing talonid, or to a lengthening of the talonid; m3 rounded and often vestigial; P4 with sharp and anteriorly placed protocone; M1 with well-developed parastyle and equally developed para-, meta- and protocones, with a symmetrical and crescentic protocone whose branches lead to equal-sized para- and metaconules, and with strong cingulum; M2 similar to M1. Differs from North American amphicyonids by the absence of an upper third molar, the presence of a parastyle on P4 forming a small bulge, and a posteriorly oriented postprotocrista on the M1.

Cynodictis peignei n. sp.
 (Figs 2-4)

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

HOLOTYPE. — Incomplete cranium in two parts: MNHN.F.Qu9007 (snout) and MNHN.F.Qu9008 (neurocranium), with I1-M1 left and I1-P4 right (P4 broken).

TYPE LOCALITY AND HORIZON. — Quercy Phosphorites (old collection), estimated as late Eocene to early Oligocene (see Thenius [1959] and discussion of Kotsakis [1980: 268, 269]). It is noteworthy that the Mouillac deposit is no longer recognized since it is a mixture of phosphate bags, and the associated fauna gives no clue about the relative age of the specific Mouillac site.

DIFFERENTIAL DIAGNOSIS. — The new species of *C. peignei* n. sp. is exclusively known by its cranium and its comparison to other *Cynodictis* species (diagnosed on the basis of lower teeth characters) is consequently

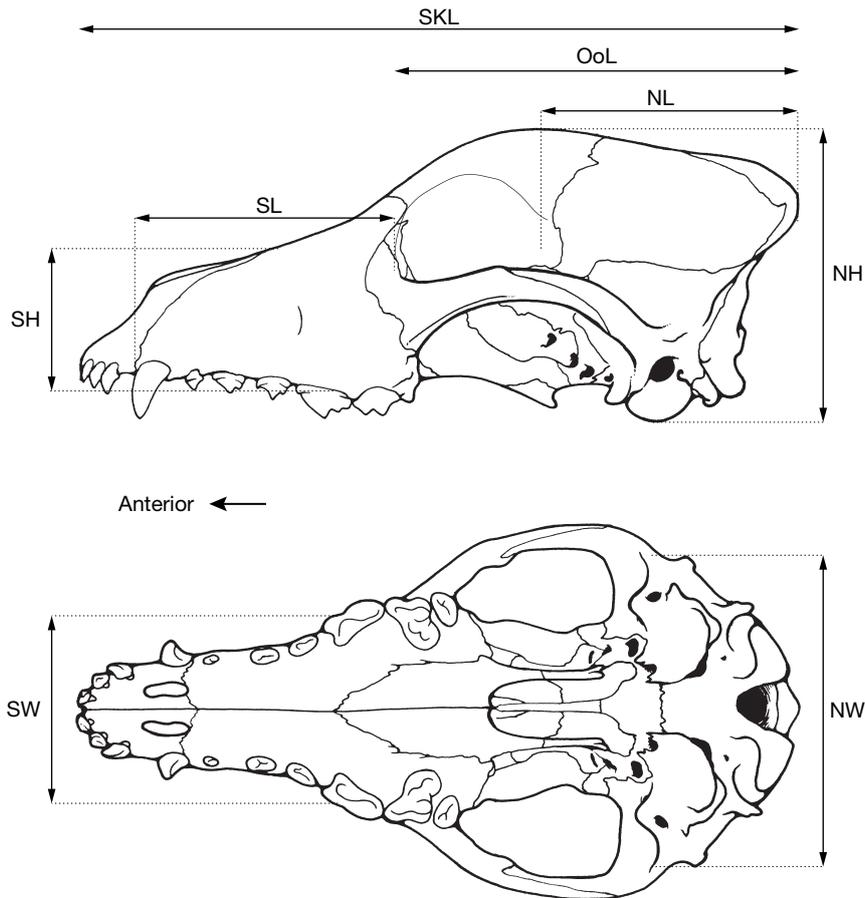


FIG. 1. — Schematic representation of cranial measurements on the dog cranium (*Canis lupus*, modified from Evans 1993) in lateral (**top**) and ventral (**bottom**) views. These measurements were taken on the cranium of each specimen of *Cynodictis* Bravard & Pomel, 1850 studied here. The length of the snout is measured from the anterior edge of the orbit to the anterior of the canine. The width is measured from the anterior edge of one P4 to the other. The height is measured from the frontal-nasal junction on the midline to the palatine. The length of the neurocranium is measured from the inner-most edge of the temporal fossa to the maximum posterior point in strict lateral view. The width is measured between the supramastoid crista processes. The height is measured from the dorsal-most point to the ventral-most point. The total length of the cranium, as well as the length from the occiput to the orbit are also measured. Abbreviations: **H**, height; **L**, length; **N**, neurocranium; **OoL**, occiput to orbit length; **S**, snout; **SKL**, skull length; **W**, width.

limited to those known by cranial remains. Only two crania have been assigned to mandibular remains, belonging to two species: *C. lacustris* (MNHN.F.Qu17502) (Teilhard de Chardin 1915: pl. II – former *C. intermedius*), and *C. exilis* (MNHN.F.Qu unnumbered).

C. peignei n. sp. cannot be compared to most of the existing other species of *Cynodictis* because they are not known by cranial remains: *C. cayluxensis*, *C. ferox*, *C. crassus*, *C. longirostris*. For the latter, Teilhard de Chardin (1915) illustrated in occlusal view a piece of a right maxilla bearing P2-M1, stored at the Montauban Museum, which he recognized as *Cynodictis* (?) *longirostris*. Even though this determination is not certain, *C. peignei* n. sp. differs from this specimen by: a larger diastema between P2 and P3; P2 and P3 longer; P3 with a very strongly defined cingulum behind the accessory cusp; P4 very similar but with a smaller width at the base of the protocone; M1 with a straight styler shelf on the labial edge of the tooth in occlusal view (central curvature on this same edge because of the development of the paracone and metacone in the Montauban Museum specimen); cingulum of M1 on the lingual edge forming a well-marked fossa between the latter and the protocone.

C. peignei n. sp. differs from *C. exilis* by: its much larger and stronger cranium; contact between the posterodorsal process of premaxillary and the lateral edges of the nasal more posterior (at the level of the canine in *C. exilis*); infra-orbital foramen at the level of P3 (posterior margin of P3 in *C. exilis*); weaker transverse elongation of the zygo-

matic arches; lacrimal foramen twice the size; post-tympanic process of squamosal less anteroventrally oriented; paroccipital processes proportionally taller and exoccipital wider; tensor tympani fossa larger; roof of the external acoustic meatus much deeper; nuchal crests almost vertical; braincase proportionally larger (despite the size difference); foramina for the ramus temporalis much smaller and closer to the sagittal crest; P3 much higher than P2 (P2 and P3 almost the same height in *C. exilis*); accessory cusp of P3 much larger; P4 with a narrower protocone area; metastyle of P4 shorter.

C. peignei n. sp. differs from *C. lacustris* by: a less transverse elongation of zygomatics arches; post-tympanic process of squamosal less vertically oriented; larger exoccipital despite a similar paroccipital process; larger tensor tympani fossa (although *C. lacustris* has a larger tensor tympani fossa than *C. exilis*); roof of the external acoustic meatus larger and deeper (it is the narrowest and shallowest in *C. lacustris* compared to *C. peignei* n. sp. and *C. exilis*); nuchal crests more vertically oriented (the nuchal crest of *C. lacustris* even hides the occipital condyles); much larger braincase; foramen for ramus temporalis closer to the sagittal crest (even closer in *C. lacustris* than in *C. exilis*); protocone area of P4 narrower; P4 metastyle shorter; M1 with a more rectangular shape; styler shelf of M1 narrower, shorter and less posteriorly oriented; M1 metaconule more prominent; M1 protocone less prominent and M1 metacone higher than the paracone.

MEASUREMENTS. — See Table 2 and Table 3.

DESCRIPTION

Cynodictis peignei n. sp. is about twice as large as other species of the genus. Although broken at the level of postorbital constriction, the cranium is taller, wider and longer than other crania referred to *Cynodictis*. For instance, the braincase of the holotype is twice as large as that of *C. lacustris*. This large size recalls *C. longirostris* (Filhol 1876; Teilhard de Chardin 1915; Bonis 1978), which is considered a large species of *Cynodictis* and notably characterized by the lengthening of the dentary. *Cynodictis peignei* n. sp. is, however, larger than this species. The specimen has lost most of the zygomatic arches, and parts of the neurocranium and of the inner wall of the orbit are missing. The right I1-P4 (incomplete P4) and the left I1-M1 (incomplete M1) are present. The skull has many fused bones. Very few sutures are clearly visible. The clearest sutures correspond to the following junctions: premaxillary-maxillary; premaxillary-nasal; maxillary-nasal; maxillary-palatine; maxillary-frontal; nasal-frontal; exoccipital-petrosal; squamosal-petrosal; basioccipital-basisphenoid. The lacrimal-maxillary and exoccipital-supraoccipital contacts can also be faintly distinguished. In addition, the teeth are all permanent and show significant wear. From all these observations, we consider this specimen to be an adult individual (Thomé & Geiger 1997; Rager *et al.* 2013).

Dorsal view (Fig. 2A)

The cranium of *Cynodictis peignei* n. sp. is composed of three parts: the snout, the orbito-temporal region and the braincase. The snout has parallel edges, which gives it a rectangular shape. The premaxillary is high and extends well beyond the anterior part of the nasal. Its posterodorsal process reaches as far caudal as the level of the P2. The maxillary extends onto the orbit. It shows slight lateral bulges in its anterior part, corresponding to the root of the canine. The infraorbital foramen, located at the level of the P3, is very wide and transversely extended. The nasal bones extend from the distal end of the snout (at the anterior border of the canine) to the frontal bones, where they are U-shaped. The frontal is not complete but seems large in *C. peignei* n. sp. A very small depression is visible on its midline. The maxillary process of the frontal is strongly developed anteriorly, reaching the anterior level of the P3. The post-orbital constriction is not preserved and cannot be described. The orbito-temporal region is very poorly preserved. The zygomatic arches, including the jugal and the zygomatic process of the squamosal, are not preserved. The base of the squamosal zygomatic process in the posterior portion of the temporal fossa is perpendicular to the anteroposterior axis of the skull. The zygomatic arch ends at the contact of the squamosal with the alisphenoid and parietal bones; its posterolateral end shows a marked supramastoid crista and is curved posteriorly. The supramastoid crista joins the post-tympanic process of the squamosal, the latter extending posteriorly to the nuchal crest. These crests have an oblique orientation with respect to the dorsoventral and anteroposterior axes. The sagittal crest is incomplete. It originates at the level of the connection between the two temporal ridges and joins the contact between the two

nuchal crests corresponding to the occipital protuberance. The nuchal and sagittal crests are well developed in *C. peignei* n. sp. The bulge of the parietal reflects the size of the lyre-shaped endocranium. On the parietal, close to the occipital protuberance, there is a well-marked foramen, on both sides of the sagittal crest, which corresponds to the passage of the ramus temporalis of the facial nerve.

Lateral view and internal wall of the orbit (Fig. 2B)

In this view, the skull appears more elongated than high. The height of the skull increases only slightly from front to back. The maxillary is broad and slightly domed under the orbit. The lacrimal, preserved on the left side of the cranium, is in contact with the frontal, maxillary, palatine, and jugal. The lacrimal is a small bone with slightly visible wavy sutures, and which has a relatively large lacrimal foramen, filled on the left by sediment, but visible on the right side. More or less circular, it is located on the medial edge of the jugal above the maxillary foramen (the internal orifice of the infra-orbital foramen). The maxillary foramen is about three times larger than the lacrimal foramen. The post-orbital process, which is located posterodorsally to the lacrimal and frontal and represents the posterodorsal limit of the orbit, forms a prominent point on the left side. The maxillary tuberosity is rather weak. The palatine, in its most anterior part (i.e., at the junction with the lacrimal and the maxillary), has only one foramen. The quality of preservation does not make it possible to know exactly whether it is the caudal palatine foramen or the sphenopalatine foramen (not illustrated here). The rest of the inner wall of the temporal fenestra is not preserved. On the posteroventral part of what is preserved of the zygomatic arch, the post-glenoid process is well marked. It is very slightly curved forward and thus forms the floor of the glenoid fossa. Posterior to the post-glenoid process and just posterior to the external acoustic meatus, the squamosal presents a very slightly developed post-tympanic process, which is very strongly anteroventrally oriented. It is joined by the mastoid process of the petrosal, which is half as small and points ventrally. Posterior to the mastoid process is the paroccipital process (jugular process of Evans 1993 = paracondylar process of the exoccipital of Wible & Spaulding 2013). This process is well developed and posteroventrally oriented. The exoccipital forms a ventral condyloid pit between the paroccipital process and the occipital condyle. The latter is rather broad and oriented in the same way as the paroccipital process. The two occipital condyles form the foramen magnum, which is wider than high. In lateral view, the connection between the nuchal and sagittal crests provides a very wide area for insertion of the temporal and nuchal muscles.

Ventral view (Fig. 2C)

Laterally, the premaxillary ends in front of the canines, while its posterior extension forms a point ending posterior to the canines. The premaxillary has two incisive foramina and one interincisive foramen. The former have a teardrop shape, while the latter is much smaller. The palatine is partially damaged, but the maxillary-palatine contact is distinguishable, it starts at

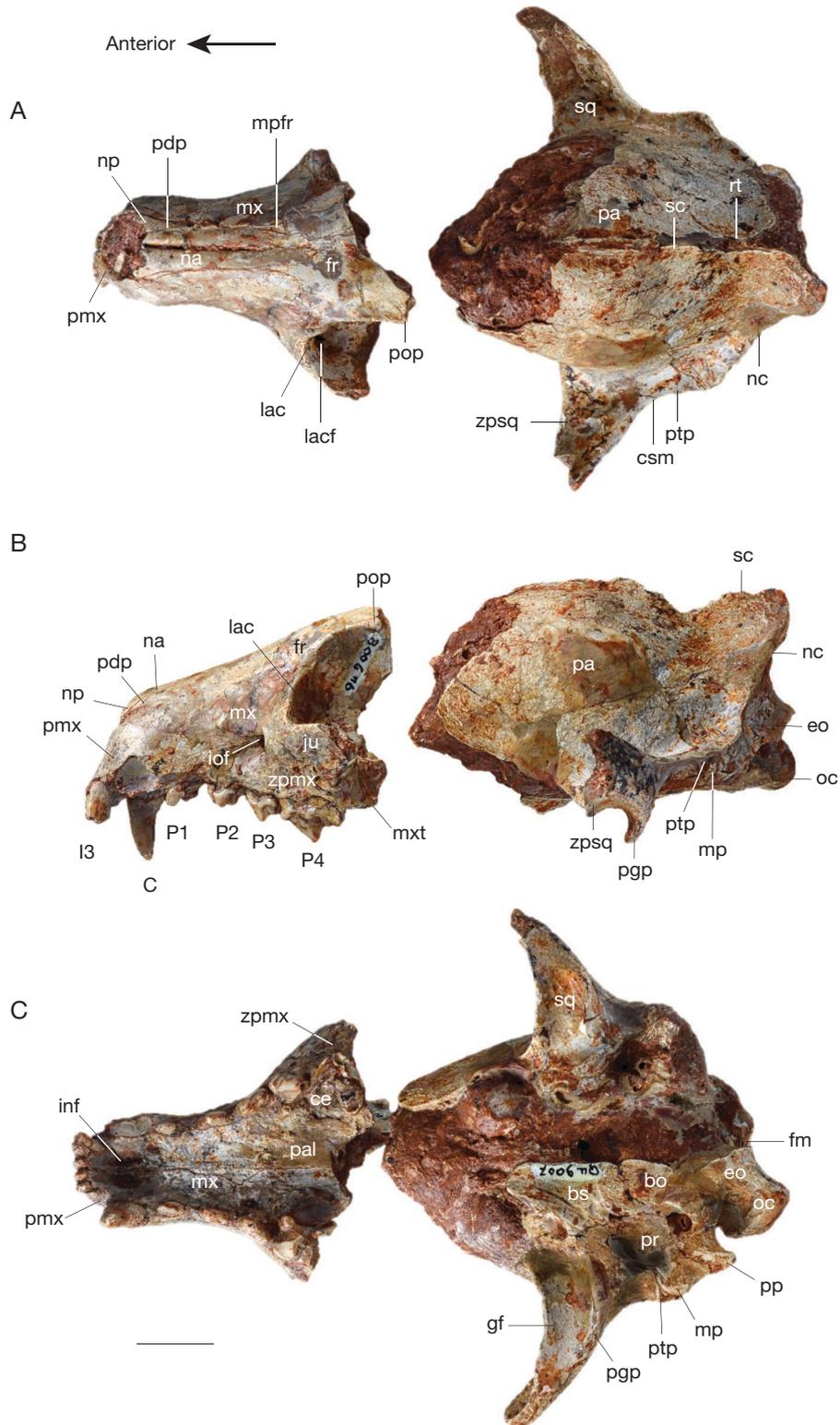


FIG. 2. — Cranium of *Cynodontictis peignei* n. sp. (snout - MNHN.F.Qu9007; neurocranium - MNHN.F.Qu9008) in dorsal view (A), lateral view (B) and ventral view (C). Abbreviations: **bo**, basioccipital; **bs**, basisphenoid; **C**, upper canine; **ce**, carnassial embrasure pit; **csm**, crista supramastoideus; **eo**, exoccipital; **fm**, foramen magnum; **fr**, frontal; **gf**, glenoid fossa; **I3**, upper third incisor; **inf**, incisive foramen; **iof**, infraorbital foramen; **ju**, jugal; **lac**, lacrimal; **lacf**, lacrimal foramen; **mp**, mastoid process; **mpfr**, maxillary process of frontal; **mx**, maxillary; **mxt**, maxillary tuberosity; **na**, nasal; **nc**, nuchal crest; **np**, nasal process of nasal; **oc**, occipital condyle; **P1**, upper first premolar; **P2**, upper second premolar; **P3**, upper third premolar; **P4**, upper ultimate premolar; **pa**, parietal; **pal**, palatine; **pdp**, postero-dorsal process of premaxillary; **pgp**, postglenoid process; **pmx**, premaxillary; **pop**, postorbital process of frontal; **pp**, paroccipital process; **pr**, promontorium of petrosal; **ptp**, posttympanic process of squamosal; **rt**, foramen for ramus temporalis; **sc**, sagittal crest; **sq**, squamosal; **zpmx**, zygomatic process of maxillary; **zpsq**, zygomatic process of squamosal. Scale bar: 10 mm.

TABLE 4. — Measurements (in mm) and estimation of body mass (in kg) and diet for each species of *Cynodontis* Bravard & Pomel, 1850 (see the Material and methods part for measured specimens and equations used). Age range is given only as an indication because most species are only known in the old Quercy collections (upper Eocene to lower Oligocene). Abbreviations: **BL**, blade length; **BM**, body mass; **Hyp.**, Hypercarnivory; **m1L**, m1 length; **Mes.**, Mesocarnivory; **OoL**, occiput to orbit length; **PMW**, premolar max width; **RBL**, relative blade length; **RPS**, relative premolar size; **SKL**, skull length. Symbol: ?, missing data.

Species	Age range	SKL	Bodymass					Diet				Category	
			BM	OoL	BM	m1L	BM	BL	PMW	RPS	RBL		
<i>C. cayluxensis</i> Filhol, 1876	MP19?-21?	?	?	?	?	13.6	12.5	11	?	?	0.81	Hyp.	
<i>C. crassus</i> Teilhard de Chardin, 1915	MP19?-21?	?	?	?	?	13	10.9	10	4.2	1.89	0.77	Hyp.	
<i>C. exilis</i> Teilhard de Chardin, 1915	MP19-21?	99	4.53	65	?	3.14	8.9	3.5	6.25	2.9	1.90	0.70	Mes.
<i>C. ferox</i> Filhol, 1876	MP19?-21?	?	?	?	?	12.5	9.7	?	4	1.87	?	Mes.	
<i>C. lacustris</i> Gervais, 1852	MP18-21?	105	5.45	74	?	4.9	11	6.7	7.6	3.6	1.91	0.69	Mes.
<i>C. longirostris</i> Filhol, 1872	MP19?-21?	?	?	?	?	12.4	9.5	9	4.3	2.03	0.73	Hyp.	
<i>C. peignei</i> n. sp.	MP19?-21?	113	6.86	81	?	6.69	?	?	?	?	?	?	

the anterior edge of the P4. The palatine, anteriorly rounded, forms a shelf delimited laterally by the P4 and M1. The major palatine foramina are no longer distinguishable. The posterior portion of the palatine, the presphenoid, the pterygoid and the anterior part of the basicranium are not preserved. Two foramina of great size, and in the same depression at the base of the alisphenoid, are visible laterally on the right side of the skull. The anterior-most foramen corresponds to the caudal opening of the alisphenoid canal. The posterior-most one corresponds to the foramen ovale. It is oriented obliquely and is opposite to the glenoid fossa. Laterally to these foramina, the squamosal bears the glenoid fossa, which is very elongated transversely. The condylar process of the mandible articulates in this pit. The basisphenoid and basioccipital are altered and barely distinguishable. The tubercle bordering them, where the longus capitis muscle attached, is not preserved.

Auditory region (Fig. 3)

At the posterior part of the post-glenoid process and close to the lateral edge of the skull is the post-glenoid foramen of the squamosal. Posterior to it and posteromedially located in the tympanic cavity, a deep and narrow depression corresponds to the petrotympanic fissure (from which emerges the chorda tympani). Medially to the latter and bordering the (incomplete) tegmen tympani of the petrosal, a wide anteroposteriorly stretched depression is probably a facet for the insertion of the spine of the rostral process of the malleus (as described and illustrated in *Nandinia* Gray, 1830 by Wible & Spaulding 2013). Laterally to the petrotympanic fissure, a smaller but deeper depression, just posterior to the post-glenoid foramen, likely received the anterior crus of the ectotympanic, the external element of the auditory bulla. Near its external edge, a large and broad bony shelf formed by the squamosal corresponds to the roof of the external acoustic meatus. It is bordered anterolaterally by the post-tympanic process of the squamosal, on which there is a facet for the insertion of the posterior crus of the ectotympanic, which is attached posteriorly to the mastoid process of the petrosal. The petrosal is characterized in ventral view by an anterior bean-shaped part that is stretched anteriorly, the promontorium, and a posterior tongue-like part, the mastoid. The promontorium is slightly rough on its lateral and central surfaces. Its anterior extension is elongated and rounded. It has a transverse groove for the passage of the internal carotid artery.

The promontorium of *C. peignei* n. sp. is pierced at its posterior base by two foramina: the opening of the cochlear fossula, which contains the fenestra cochleae, and, anterodorsally to the lateral rim at the cochlear fossula, the vestibular fossula (fenestra vestibuli), more dorsal and rounded, which housed the footplate of the stapes. The opening of the cochlear fossula is directed towards the mastoid plate of the petrosal. The cochlear fossula is anteriorly overlapped by a bulge of the promontorium resulting from the first turn of the underlying cochlea (= tympanic ramp). The latter is connected to the tympanic cavity by the secondary tympanic membrane, housed in the cochlear fossula. The posterior extension of the cochlear fossula forms a broad depression stretched transversely and laterally bordered by a short process, interpreted here as the medial section of the caudal tympanic process (*sensu* MacPhee 1981). The vestibular fossula, which connects the ossicular chain to the vestibular ramp of the cochlea, is located anterior to the probable level of the tympanohyal (not preserved here) and opens towards the roof of the external acoustic meatus. These two openings are separated by the crista interfenestralis. The mastoid part of the petrosal is delimited anterolaterally by the mastoid process, which forms a narrow transversely and ventrodorsally elongated shelf. Posterior to the mastoid process, a bean-shaped osseus plate is delimited medially by a broad shelf of the mastoid that is very slightly concave, almost flat, and smooth. This plate corresponds to the mastoid exposure. The shelf continues medially to the exoccipital and participates in the prominent paroccipital process of the exoccipital.

Posteroventrally, the paroccipital process of *C. peignei* n. sp. is hollowed out on its anterolaterally oriented inner face. It bears two ridges: the most mesial extends from the apex of the process to the cochlear fossula; the most lateral (more altered) extends from the same apex to the mastoid process, with a slight curve. The medial margin of the mastoid shelf forms a thin bony process surmounted by a bulge in front of the cochlear fossula. It corresponds to the lateral section of the caudal tympanic process (*sensu* MacPhee 1981). If the tympanohyal was present it would form, with the caudal tympanic process, a very rounded notch, the stylomastoid foramen (not preserved here). More dorsally, the stapedius fossa is deep, more or less oval and its anterior wall is formed by the gyrus (a cerebral convolution) of the underlying semi-circular lateral canal. It indicates the location of the stapes

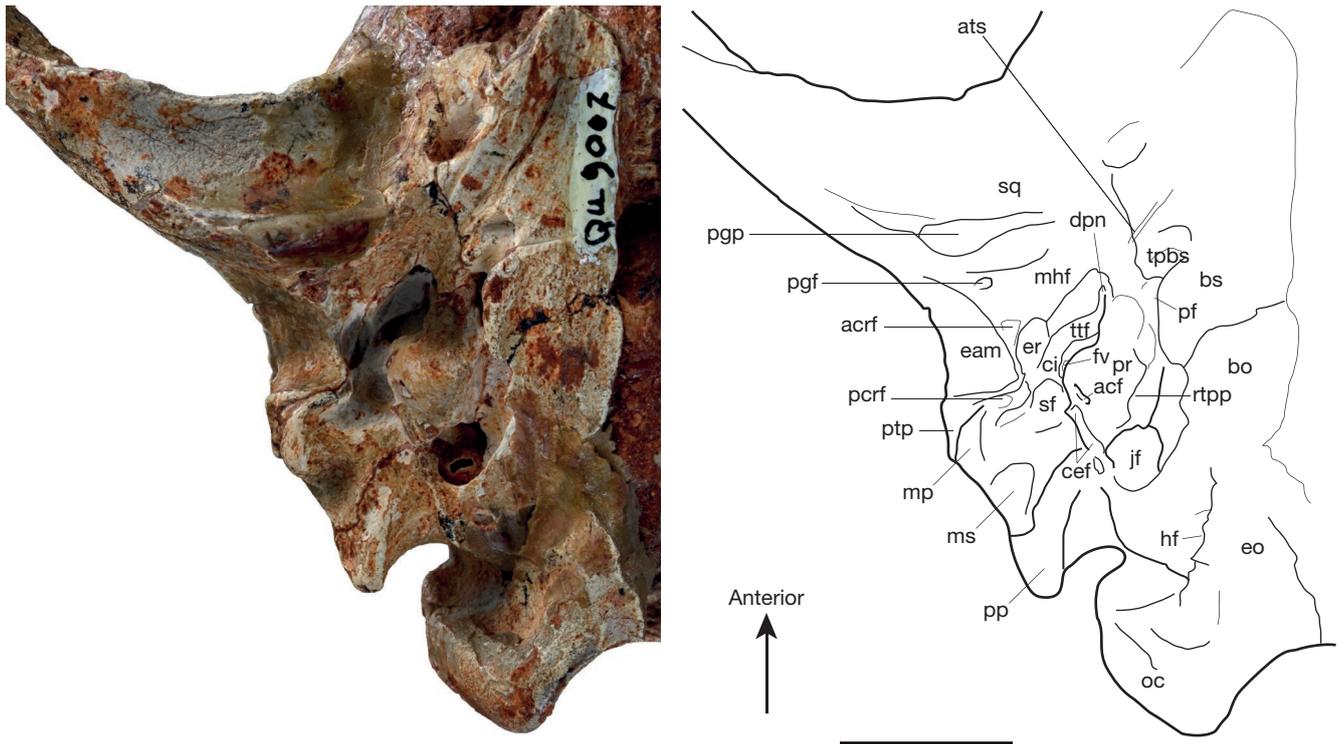


FIG. 3. — Right basicranium of *Cynodontictis peignei* n. sp., MNHN.F.Qu9008, in ventral view. Abbreviations: **acf**, aperture of cochlear fossula; **acrf**, facet for anterior crus of ectotympanic; **ats**, sulcus for auditory tube; **bo**, basioccipital; **bs**, basisphenoid; **cef**, facet for caudal entotympanic; **ci**, crista interfenestralis; **dpn**, foramen for deep petrosal nerve; **eam**, roof of external acoustic meatus; **eo**, exoccipital; **er**, epitympanic recess; **fv**, fenestra vestibuli; **hf**, hypoglossal foramen; **jf**, jugular foramen; **mhf**, facet for mallear hook of rostral process; **mp**, mastoid process; **ms**, mastoid shelf; **oc**, occipital condyle; **pcrf**, facet for posterior crus of ectotympanic; **pf**, piriform fenestra; **pgf**, postglenoid foramen; **pgp**, postglenoid process; **pp**, paroccipital process; **pr**, promontorium; **ptp**, posttymppanic process of squamosal; **rtp**, rostral tympanic process of petrosal; **sf**, stapedius fossa; **sq**, squamosal; **tpbs**, tympanic process of basisphenoid; **tff**, tensor tympani fossa. Scale bar: 10 mm.

and stapedial muscle. Anterolaterally and medially delimited by the promontorium, is a wide and deep depression, slightly deteriorated. The bony roof of this depression consists partly of an epitympanic wing of the petrosal (particularly altered here) anteriorly, and an epitympanic wing of the squamosal and tegmen tympani posteriorly. The anterior-most cavity, which is oriented transversely, is the pit for the tensor tympani muscle, attached to the tympanic membrane and whose function is to dampen the sounds and houses the “nape” of the malleus. The tensor tympani fossa is separated from a more posterior and rounded depression by a small bony wall. This depression is hollowed out by two fossae. The most anterior one, which is also the widest, is the epitympanic recess. Essential in the proper functioning of the ossicular chain, the epitympanic recess housed the malleus-incus articulation. The most posterior pit, the fossa incudis, is half the size but deeper than the epitympanic recess. It housed the short process of the incus. It is located anteriorly to the stapedius fossa and is separated from it by the crista parotica, which forms a thick bone barrier.

Medial to the epitympanic recess and the fossa incudis is the damaged facial canal. This canal runs along the medial edge of the promontorium. It opens between the epitympanic recess and the vestibular fossula. On the medial edge of the promontorium and on the most medial part of the posterior bulge of the cochlear fossula are two very distinct facets that receive the caudal entotympanic (an element of the auditory

bullae). The most anterior and longest facet is on the rostral tympanic process of the petrosal. The bony margin marking the posterior border of the cochlear fossula is attached to two marked tubercles of the exoccipital. These two tubercles delimit two grooves, of which the most posterior probably marks the passage of the vagus nerve (X).

Anteromedially to these two tubercles there is a large foramen corresponding to the jugular foramen. The jugular foramen is included in a long fissure – enlarged in the specimen because of a taphonomic deformation –, which extends between the promontory and the basioccipital. The hypoglossal foramen pierces the exoccipital, and is located posteromedially in the jugular foramen. The promontorium apex is medially separated from the basioccipital by a very large hole, which may correspond either to the piriform fenestra (*sensu* MacPhee 1981), or to the foramen lacerum of Evans (1993) (see the discussion concerning this structure in Wible & Spaulding 2013). This orifice contains the foramen for the internal carotid artery. At the front of this large hole, the tympanic process of the basisphenoid forms a large bone pocket. The basioccipital is too altered to observe an excavation as in other *Cynodontictis* skulls (KLV pers. obs.). Located between the tympanic process of the basisphenoid and the sulcus for the auditory bulla, a well-marked groove begins at the level of a foramen just anterior to the apex of the promontorium. This foramen probably marks the passage of the deep petrosal nerve.

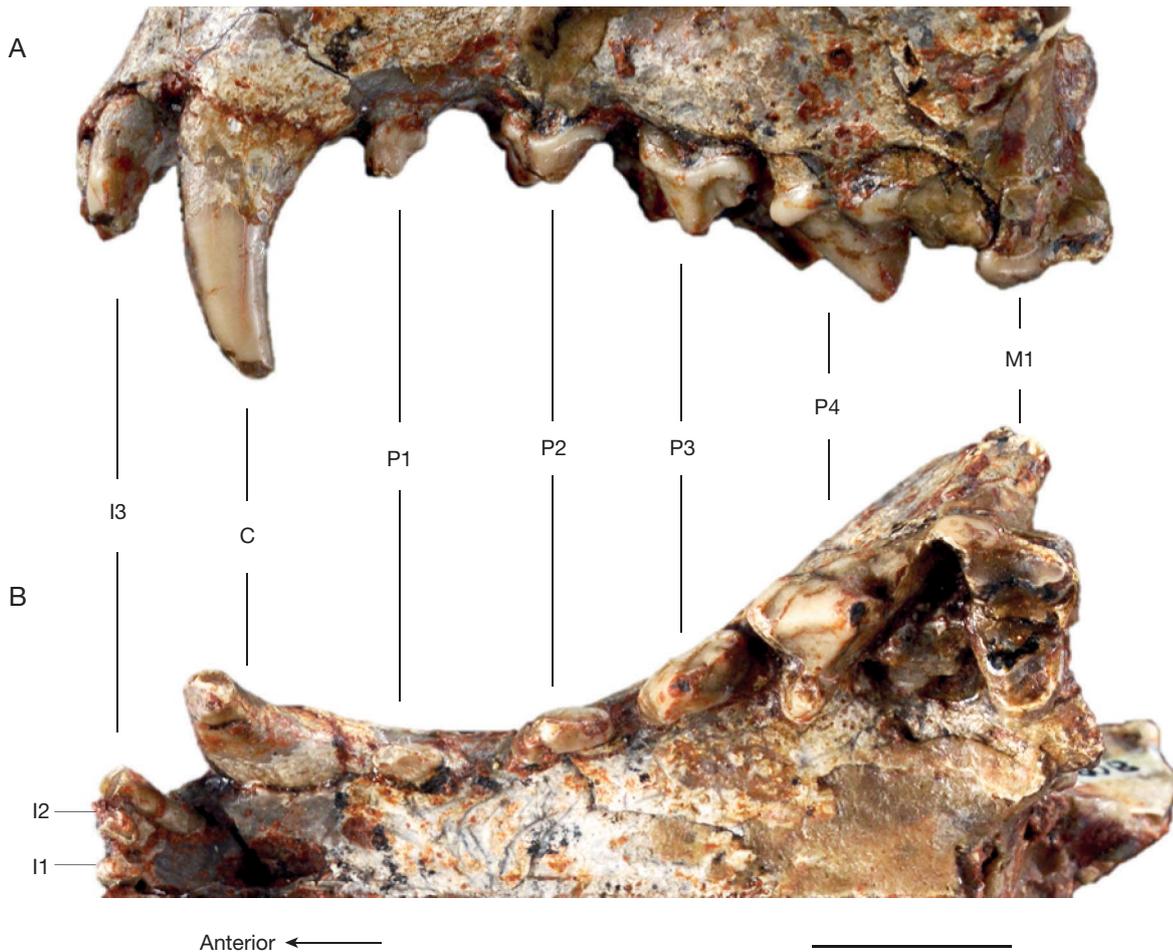


FIG. 4. — Upper left dentition of *Cynodictis peignei* n. sp. (MNHN.F.Qu9007): **A**, I3-M1 in labial view; **B**, I1-M1 in occlusal view. Abbreviations: **C**, canine; **I1**, first incisor; **I2**, second incisor; **I3**, third incisor; **M1**, first molar; **P1**, upper first premolar; **P2**, upper second premolar; **P3**, upper third premolar; **P4**, upper ultimate premolar. Scale bar: 10 mm.

Upper teeth (Fig. 4)

The specimen described here was found with two hemimandibles (MNHN.F.Qu9009 and MNHN.F.Qu9010). However, the lower and upper teeth do not occlude properly. This implies that they do not belong to the same specimen (Crompton & Hiiemäe 1969). The right I3, M1, and M2, and the left M2 are not preserved. Moreover, the left M1 and the right P4 are badly damaged. The I1 and I2, separated by a very slight diastema, are smaller than the I3, which is twice as large. The three incisors are conical, rectangular and single-rooted. A very small diastema separates them from the canines. The canines are conical and very slightly curved towards the back. A diastema of about the same length as the one that separates the incisors from the canines is present between the canine and the P1. The latter is single-rooted and has a posterior accessory cusp. The largest diastema separates the P1 from the P2. In lateral view, the teeth are two-rooted, taller, and longer from P2 to P4. The P2 is conical and has a single prominent cusp, the paracone. Its cingulum is very thin, but almost complete. It has a very weak cusp mesially and a stronger one distally. The P3, higher than the P2, has the same morphology as the P2 but differs by having acces-

sory cusps that are more developed and individualized. The first one, which is rounded, is located posterior to the main cusp (= paracone). This accessory cusp and the paracone are connected by a short but well-developed ridge. The second accessory cusp is much smaller and is located anterior to the main cusp. The P4, whose anterior root forms a bulge on the maxillary, has a large oblique cingulum at its anterior base. The paracone is, by far, the tallest cusp of all the premolars. It points backwards and exhibit a posterior ridge as well as an anterior crest. The posterior crest reaches the (incomplete) metastyle, which is long, protruding, and shows a very slight concave curvature at its center. Its contact with the paracone is lingual relative to the middle of the tooth, orienting the metastyle towards the posterior part of the skull. The carnassial notch is present between the paracone and metastyle. The P4 has a fairly large lingual shelf, which carries a well-developed protocone. The M1 is rectangular in shape and partially worn. The cingulum is well developed on the lingual part of the talon, where it forms a very strong bulge that is narrow mesiodistally. The styler shelf, much smaller than the protocone, is oblique orientated outward with respect to the anteroposterior axis. The styler shelf includes three cusps. The

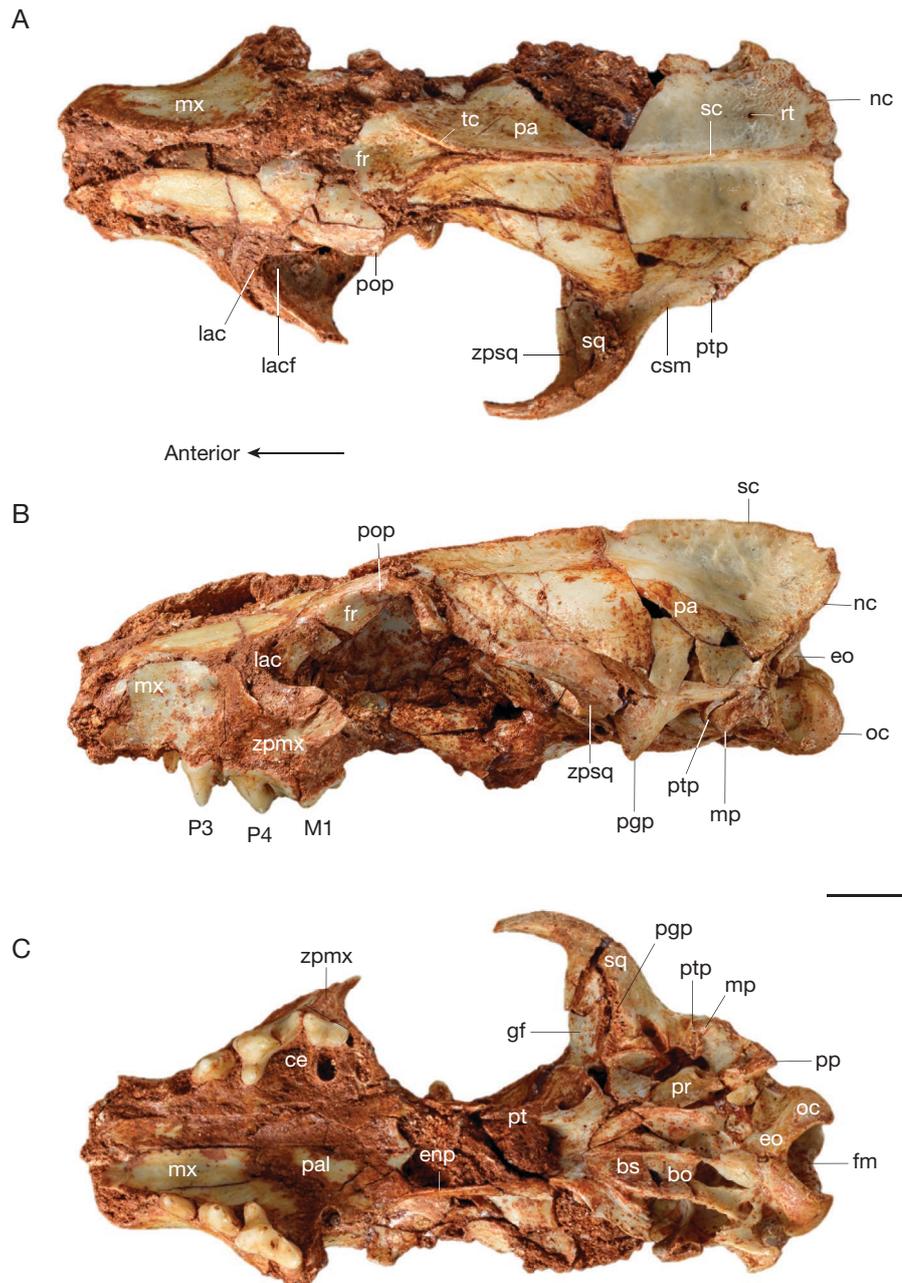


FIG. 5. — Cranium of *Cynodontictis exilis* Teilhard de Chardin, 1915 (MNHN.F.Qu unnumbered) in dorsal view (A), lateral view (B) and ventral view (C). Abbreviations: **bo**, basioccipital; **bs**, basisphenoid; **ce**, carnassial embrasure pit; **csm**, crista supramastoideus; **enp**, entopterygoid process; **eo**, exoccipital; **fm**, foramen magnum; **fr**, frontal; **gf**, glenoid fossa; **lac**, lacrimal; **lacf**, lacrimal foramen; **M1**, upper first molar; **mp**, mastoid process; **mx**, maxillary; **nc**, nuchal crest; **oc**, occipital condyle; **P3**, upper third premolar; **P4**, upper ultimate premolar; **pa**, parietal; **pal**, palatine; **pgp**, postglenoid process; **pop**, postorbital process of frontal; **pp**, paroccipital process; **pr**, promontorium of petrosal; **pt**, pterygoid; **ptp**, posttympanic process of squamosal; **rt**, foramen for ramus temporalis; **sc**, sagittal crest; **sq**, squamosal; **tc**, temporal crest; **zpmx**, zygomatic process of maxillary; **zpsq**, zygomatic process of squamosal. Scale bar: 10 mm.

metastyle is poorly developed, unlike the parastyle that forms a prominent and strongly rounded cusp. Both the metacone and paracone are prominent and sharp, the metacone being the tallest. The centrocrista and the paracrista are more salient than the metacrista. The talon is very broad and points towards the buccal part of the oral cavity (but also with a slight posterior inclination). The protocone is very strong, eroded and is mesially shifted. Close to the protocone, there is a metaconule, but no protoconule is visible (absent or worn

down). The preprotocrista is more marked than the postprotocrista and reaches the parastyle. Two very thin cingulae are visible on the lingual base of the metacone and the paracone.

Comparison (Figs 5-7)

The posterodorsal process of the premaxillary of *C. peignei* n. sp. contacts the lateral edges of the nasal further back than in other *Cynodontictis* species. The premaxillary ends laterally at the posterior level of the canine, whereas it ends at the anterior third

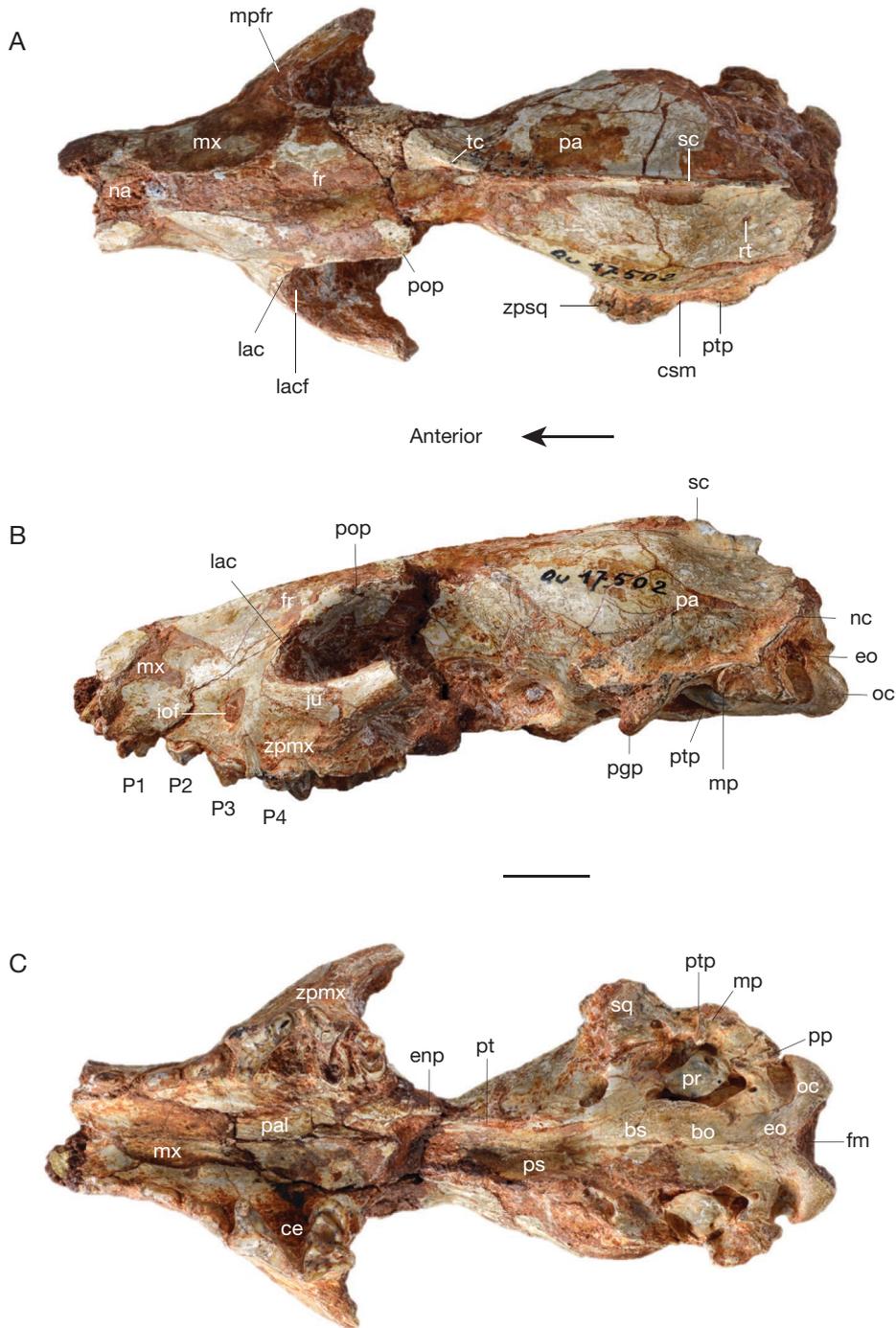


FIG. 6. — Cranium of *Cynodontis lacustris* Gervais, 1852 (MNHN.F.Qu17502) in dorsal view (A), lateral view (B) and ventral view (C). Abbreviations: **bo**, basioccipital; **bs**, basisphenoid; **ce**, carnassial embrasure pit; **csm**, crista supramastoideus; **enp**, entopterygoid process; **eo**, exoccipital; **fm**, foramen magnum; **fr**, frontal; **ioof**, infraorbital foramen; **ju**, jugal; **lac**, lacrimal; **lacf**, lacrimal foramen; **mpfr**, maxillary process of frontal; **mp**, mastoid process; **mx**, maxillary; **na**, nasal; **nc**, nuchal crest; **oc**, occipital condyle; **P1**, upper first premolar; **P2**, upper second premolar; **P3**, upper third premolar; **P4**, upper ultimate premolar; **pa**, parietal; **pal**, palatine; **pgp**, postglenoid process; **pop**, postorbital process of frontal; **pp**, paroccipital process; **pr**, promontorium of petrosal; **ps**, presphenoid; **pt**, pterygoid; **ptp**, posttymppanic process of squamosal; **rt**, foramen for ramus temporalis; **sc**, sagittal crest; **sq**, squamosal; **tc**, temporal crest; **zpmx**, zygomatic process of maxillary; **zpsq**, zygomatic process of squamosal. Scale bar: 10 mm.

of the canine in the other *Cynodontis* species. The infra-orbital foramen of other *Cynodontis* species is located at the anterior edge of the P4. In *C. lacustris*, the posterior part of the nasal bones is V-shaped rather than U-shape as seen in *C. peignei* n. sp. The maxillary process of the frontal also differentiates these two species: its tip stops at the infra-orbital foramen in

C. lacustris. The snout of *C. lacustris* is more tapered than in the other species. In *C. lacustris*, the face abruptly increases in transverse width. This transverse elongation occurs at the level of the infra-orbital foramen and is due to the separation of the zygomatic processes. This transverse elongation is weaker in *C. peignei* n. sp. The snout of *C. peignei* n. sp. is higher than

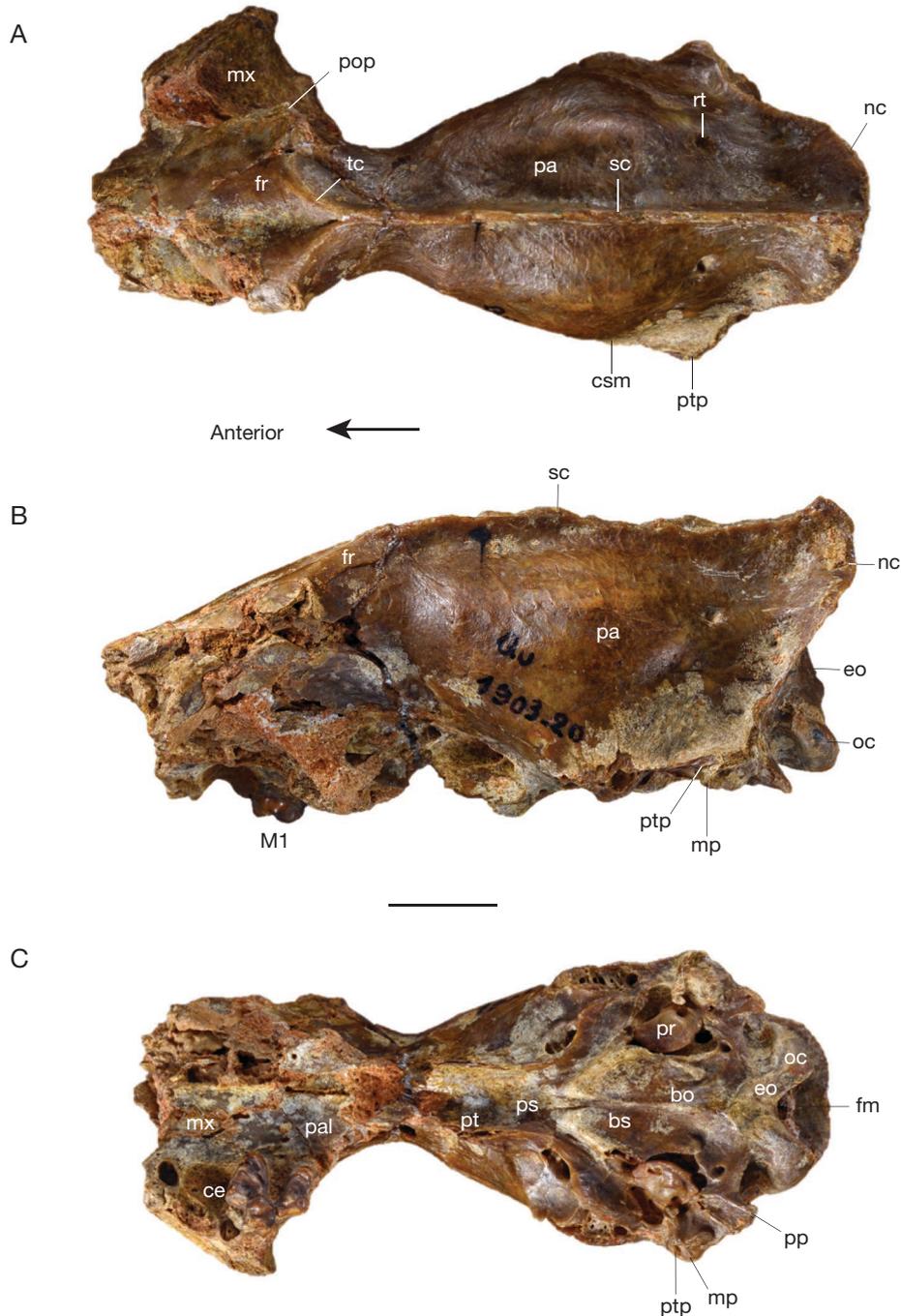


FIG. 7. — Cranium of *Cynodontis lacustris* Gervais, 1852 (MNHN.F.Qu1903-20) in dorsal view (A), lateral view (B) and ventral view (C). Abbreviations: **bo**, basioccipital; **bs**, basisphenoid; **ce**, carnassial embrasure pit; **csm**, crista supramastoideus; **eo**, exoccipital; **fm**, foramen magnum; **fr**, frontal; **M1**, upper first molar; **mp**, mastoid process; **mx**, maxillary; **nc**, nuchal crest; **oc**, occipital condyle; **pa**, parietal; **pal**, palatine; **pop**, postorbital process of frontal; **pp**, paroccipital process; **pr**, promontorium of petrosal; **ps**, presphenoid; **pt**, pterygoid; **ptp**, posttympanic process of squamosal; **rt**, foramen for ramus temporalis; **sc**, sagittal crest; **tc**, temporal crest. Scale bar: 10 mm.

in *C. lacustris*, but, surprisingly, it is not longer. The lacrimal foramen of *C. peignei* n. sp. is larger than in other *Cynodontis* species. The base of the zygomatic process of the squamosal (in the posterior portion of the temporal fossa) forms a forward curvature in all *Cynodontis* species. In *C. lacustris* and *C. exilis*, the post-glenoid process is more forwardly curved; *C. lacustris* has the greatest curvature, pointing almost 30° anteroventrally. In *C. exilis*, the supramastoid crista is flatter,

more pronounced and concave, than in *C. peignei* n. sp. The post-tympanic process of the squamosal is more vertically oriented in *C. peignei* n. sp. than in *C. lacustris* and *C. exilis*. The mastoid process is more rounded and points more laterally. The paroccipital processes of *C. peignei* n. sp. are shorter and the exoccipital is thicker than in other *Cynodontis* species. The promontorium is relatively similar in size but is more massive and less triangular than in *C. exilis* and *C. lacustris*.

In *C. lacustris* and *C. peignei* n. sp., the hypoglossal foramen is closer to the petrosal in comparison to the other *Cynodictis* species. The tensor tympani fossa of *C. peignei* n. sp. is larger than in the other *Cynodictis* species. On the other hand, the insertion of the anterior crus of the ectotympanic is relatively smaller in *C. peignei* n. sp. The rostral tympanic process of the petrosal forms a protuberance in *C. peignei* n. sp. The roof of the external acoustic meatus is much deeper in *C. peignei* n. sp. than in other *Cynodictis* species. A major difference should be emphasized: in *C. peignei* n. sp., the nuchal crests are almost vertical and do not mask the condyles, whereas all other *Cynodictis* species, the nuchal crests are very strongly elongated posteriorly to the point at which they completely hide the occipital condyles in dorsal view. The braincase is much larger in *C. peignei* n. sp. The foramina for the ramus temporalis are smaller and closer to the sagittal crest than in other *Cynodictis* species. The condyles are more prominent in *C. peignei* n. sp. than in *C. exilis*. In *C. peignei* n. sp., they are twice as large, resulting in a deeper ventral condyloid fossa. The tubercle lying in the basioccipital and basisphenoid is never complete in our sample, but it should be noted that this structure in *C. lacustris* is much more strongly developed than in *C. peignei* n. sp. and *C. exilis*. There is no particular difference between the P1, P2 and P3 of the *Cynodictis* specimens of the sample, except the presence only in *C. peignei* n. sp. of a P3 higher than the P2, and of a more developed accessory cusp on P3. The P4 has a narrower protocone area, more anteriorly oriented than in other *Cynodictis* species. The metastyle of the P4 of *C. peignei* n. sp. is shorter than in the other species. The M1 of *Cynodictis peignei* n. sp. differs from the other *Cynodictis* species by its less trapezoidal and more rectangular shape. A connection between the stylar shelf and protocone area is absent in the studied specimen. Its stylar shelf is narrower, shorter, and oriented less posteriorly. The metaconule is more prominent, while the protocone is less prominent than in the other *Cynodictis* species. The metacone is taller than the paracone in *C. peignei* n. sp. which is not the case in other species.

RELEVANCE OF CRANIAL CHARACTERS

Among the extinct mammal species described and named so far, a very large number have been defined only based on dental characters. This is illustrated by the diagnoses proposed for almost all mammalian groups (except for Xenarthra and Pholidota because of their reduction of teeth). This is due to the nature of the fossil record: dental elements are abundant because they have been preserved and fossilized due to the mineralization of their tissues. Moreover, dental elements can provide information on the diet, as well as on the body mass of extinct species.

Amphicyonidae are clearly not an exception (see the diagnoses proposed by Springhorn 1977). The characters considered as diagnostic are substantially concentrated on the tooth row and more specifically on the morphology of the m1. However, this type of character has a considerable number of biases because molars have at least three constraints for identification and descriptive studies:

1) Although dental structures are a relevant ontogenetic index – even if it is questionable for some groups (Ciancio *et al.* 2011) –, the patterns of wear and the phenotypic plasticity of the teeth result in morphological variability and may cause problems with fossil species discrimination (Gingerich 1974; Suchentrunk & Flux 1996; Tsoukala 1996; Hillson 2005).

2) Functional constraints on the teeth result in a large number of convergences. This case is well illustrated with the debate on the position of Amphicyonidae. The “bear-dogs”, so named because of their anatomy (dentition and locomotion), which is sometimes similar to that of Canidae, sometimes to that of Ursidae, represent a phylogenetic enigma (Viranta 1996). Historically, they were first considered to be very close to Canidae (Matthew & Granger 1924; Petter 1966), a hypothesis that has been reconsidered recently (Spaulding & Flynn 2012). They have also been considered as the sister group of Ursidae based on many morphological characters (Ginsburg 1966; Hough 1948; Hunt 1977; Wyss & Flynn 1993) or as the sister group of Arctoidea (the group that gathers ursids, pinnipeds, and musteloids; Finarelli 2008; Hunt 1996, 1998). Finally, the most recent studies regard the “bear-dogs” as the sister-group of all Caniformia (Tomiya & Tseng 2016; Wesley-Hunt & Flynn 2005). Other examples are present in the history of the caniforms. For example, the case of Musteloidea, where the whole group presents a wide range of dentition and locomotion, resulting in difficulties for the paleontologists to discriminate the different groups (Law *et al.* 2018).

3) The teeth are subject to serial homology (the similarity of repeated structures within an organism). This calls into question the characterization of a group based on repeated structures. For example, if a group is characterized by the presence of a cingulum on the M1, M2, and M3, then because all these characters are dependent on each other, they should be considered as representing only one characteristic that defines the group, and not as three independent characteristics (Billet & Bardin 2018).

Although these problems seem alarming, we do not aim to question here previous studies because they are based on dental structures: indeed, several dental features used in these publications are not affected by these constraints, and thus are diagnostic (e.g., highly specialized dentition). The goal of the present discussion is to question specific diagnoses based on very weakly defined dental variants, especially when the sampling does not allow study of intraspecific variation.

During more than 150 years, the diversity of the genus varied from six to nearly thirty species (Filhol 1876; Schlosser 1902; Teilhard de Chardin 1915; Bonis 1978; Kotsakis 1980). With the description of *C. peignei* n. sp. herein, seven species are now recognized. The previous overestimation of the taxonomic diversity can be explained by the effect of the constraining dental particularities listed above on the variation within the group.

It is worth remembering that the lower teeth can be morphologically related to the upper teeth in an individual because of the functional links caused by the occlusion (Crompton & Hiiemäe 1969). Dayan *et al.* (2002) showed that dental features within carnivoran populations are more variable than cranial traits. In addition, dental traits are strongly correlated with each other, just

as cranial traits are correlated with each other, but these two sets are not highly correlated with one another (Dayan *et al.* 2002). This implies that teeth and skull may be subject to different selective pressures and constraints (e.g., genetic, development, function) and, therefore, the study of these structures separately might allow for envisaging different scenarios. To conclude, and in ideal cases where most of the skeleton is available for a fossil specimen, paleontologists should try to define in a more comprehensive way the new species they are erecting and should propose detailed and compared diagnoses based on all parts of the skeleton and not teeth (or fragments of teeth) only.

DIVERSITY OF *CYNODICTIS*

During the Paleogene, carnivoran diversity begins with the appearance of Amphicyonidae in Europe, the oldest known representative of which is *Cynodictis*. From the Priabonian (MP18) to today, carnivorans have continued to diversify in Europe and the Amphicyonidae did not depart from this rule until their extinction in the upper Miocene, as evidenced by the more than 19 genera (representing more than 48 species) of this family present in Europe from MP18 to about MN12. This is particularly the case for *Cynodictis*, whose diversity now stands at seven species. This group potentially represents the ecology of the first carnivorans that lived in Europe.

Restricted to Western Europe (France, Germany, United Kingdom), these seven species present a range in estimated body mass of between 4 and 12 kg (Table 4), which is comparable to what is observed in recent foxes (*Vulpes*) (Wilson & Mittermeier 2009). With this relatively small variation, these species probably did not occupy numerous ecological niches and were more likely small predators in the ecosystems of the late Eocene and early Oligocene.

In addition, carnivorans represent an order in which convergence is reflected in the iterative appearance of specialized ecomorphological varieties (Van Valkenburgh 2007). Amphicyonids do not depart from this tendency in that they display ecomorphologies adapted to all niches but seen in other carnivoran groups (Viranta 1996). The early forms of *Cynodictis* are mesocarnivorous and the last forms are more hypercarnivorous (Table 4). The addition of *Cynodictis peignei* n. sp. to the diversity of the group shows a trend towards large forms in comparison to the earliest representatives. Unfortunately, the lack of a precise geological age (late Eocene to early Oligocene) makes it difficult to put this species in this stratigraphic context and its diet cannot be estimated because of missing data (i.e., lack of the lower dentition).

Nevertheless, the trend of diet towards hypercarnivory within the genus suggests that diet specialization could have made this group more vulnerable to extinction (Van Valkenburgh 2007). For example, Holliday & Stepan (2004) showed that this specialization reduces the morphological disparity of jaws and teeth without influencing taxonomic diversity. This may have been the case for the genus *Cynodictis*. However, this implies that hypercarnivorous large or small mammals that are best adapted to environmental conditions during a crisis

will find it more difficult to adapt to environmental change. *Cynodictis* managed to withstand a major faunal turnover, “La Grande Coupure de Stehlin” (Stehlin 1910) – although the phylogenetic affinities between the pre- and post- turnover event species of *Cynodictis* are not known. One potential competitor of *Cynodictis*, *Hyaenodon* Laizer & Parieu, 1838, is also known for having passed the “Grande Coupure”, although the same species are not retrieved before and after the event (Lange-Badré 1979; Solé *et al.* 2018). Among amphicyonids, the genus appearing immediately after the “Grande Coupure” in the fossil record is *Pseudocyonopsis* (MP 21-22), a more robust animal weighing more than 30 kg (Springhorn 1977). Given the major difference in body mass between the two genera, it is not ruled out that the latter is a migrant occupying potentially free ecological niches. Contrary to the general tendency of amphicyonids to diversify, *Cynodictis* saw most of its species disappear sometime after the “Grande Coupure”. This implies that it probably experienced a rapid but deadly renewal. However, this hypothesis can only be explored in the light of a major systematic revision of the many dental specimens that make up the different carnivorans of this period. This revision could be improved by considering the cranial remains, but also the postcranial remains, which are numerous but not yet studied.

CONCLUSION

Alternating between twenty and six species (Filhol 1876, 1882; Schlosser 1902; Teilhard de Chardin 1915; Bonis 1978; Kotsakis 1980), the use of dental characters has resulted in many hypotheses concerning the taxonomy of *Cynodictis* and therefore its evolutionary history. The description of *C. peignei* n. sp. increases the diversity of the genus from 6 to 7 species based on the combination of cranial and dental characters. This leads us to think that a deeper investigation of the oldest carnivorans of Europe would certainly help in a taxonomic revision of all amphicyonids, not only *Cynodictis*. Many skulls of *Cynodictis* are available and have to be extensively studied in order to improve our knowledge of the diversity among this mammalian group, and to provide better specific and generic discrimination. The contribution of cranial characters would allow eliminating misleading variations due to the functional or developmental origins of the teeth, in order to concentrate the descriptions (as well as our scientific attention) on structures whose homology is less doubtful. This would force us to focus on poorly studied anatomical structures, particularly in systematic frameworks.

Other data might help to clarify our knowledge of the amphicyonids. This is the case of the postcranial elements which, for these species, remain very poorly known. In addition to the systematic aspect, focusing our interest on these structures would allow better understanding of the ecology of the first carnivorans and also on the ecological dynamics around the Eocene-Oligocene transition (i.e., *Grande Coupure*). Finally, these data would also allow defining, in the future, the relationships among the European amphicyonids, and thus to better understand their evolution.

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