



## NEW GENUS OF AMPHICYONID CARNIVORAN (MAMMALIA, CARNIVORA, AMPHICYONIDAE) FROM THE PHOSPHORITES OF QUERCY (FRANCE)

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Bonis, L. de (2020): New genus of amphicyonid carnivoran (Mammalia, Carnivora, Amphicyonidae) from the phosphorites of Quercy (France). – Fossil Imprint, 76(1): 201–208, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

**Abstract:** An isolated mandible of Carnivora (Mammalia) from the phosphorites of Quercy (France) is described as a new genus. It is compared with the amphicyonid genus *Cynodictis*, some primitive North American amphicyonids, and with European and North American Eocene carnivoraforms. I conclude that it is a primitive amphicyonid which may be dated to the middle or late Eocene.

**Key words:** Eocene, Europe, North America, Carnivoraformes

Received: March 11, 2019 | Accepted: March 21, 2020 | Issued: November 9, 2020

### Introduction

There is a large Jurassic limestone plateau in the French departments of Lot, Aveyron, and Tarn and Garonne. It emerged during the Cenozoic. During the middle of the Cenozoic it included a karstic system with a net of fissures, caves, and galleries that were filled by red clays containing a phosphatic sediment, the phosphorite. Discovered around 1866 by the chemist J. A. Pommarède, the phosphatic clays were worked in the last third of the 19<sup>th</sup> century for the phosphorite which was used as fertiliser for fields. However, in the clays there were also thousands of fossils, especially the teeth and bones of vertebrates, which were collected by scientists and amateurs without taking into account the precise localities of the specimens. Thus, all the fossils were mixed up and it was impossible to date any bones, despite the great number of specimens scattered in private collections or in museums. Different studies (Gervais 1872, Filhol 1872a, b, 1873, 1874, 1876, 1877, 1882, Schlosser 1887, 1888, 1899, Gaillard 1908, Piveteau 1931, 1943, 1962, Ginsburg 1966, 1979, Bonis 1971, Springhorn 1977) concluded that the sediments were deposited over a large period of time from the middle Eocene to the late Oligocene.

Nevertheless, more recent studies showed that each site has a homogeneous fossil fauna which can be used to date the different localities (Gèze 1938a, b, Vianey-Liaud and Legendre 1986, Rémy et al. 1987, Biochrom'97 1997, Bonis et al. 1973, Bonis 1974, 1981, 2011, 2013) and the dating was extended from the late middle Eocene (Astruc et al. 2000) to the early Miocene (Sigé et al. 1991).

The order Carnivora is present among the fauna recorded in the phosphorites of Quercy (Filhol 1872a, b, 1873, 1874, 1876, 1877, 1882, Schlosser 1887, 1888, 1899, Teilhard de Chardin 1915, Piveteau 1931, 1943, 1962, Ginsburg 1966, 1979, Bonis 1966, 1971, 1974, 1978, 2011, 2019, Springhorn 1977) and there have been many publications on their species. Some of these carnivorans were revised by Teilhard de Chardin (1915). Among the new material described by Teilhard de Chardin, there was a small mandible which was considered as the holotype of a new species that he named *Cynodon miacinus*. Teilhard de Chardin was confused about the systematic position of the specimen. He noted that it displayed contradictory, primitive or derived, characters, but he finally linked it to the genus *Cynodon* AYMARD, 1846, today *Amphicyonodon* FILHOL, 1881 insofar as the name of Aymard (1846) was preoccupied by *Cynodon* SPIX, 1829, a fish genus. Nevertheless, there are many differences between *Amphicyonodon* and the studied mandible. I decided to examine the specimen and to find a more precise systematic position.

### Material and methods

The only referred material is a mandible housed in the MNHN, Paris, MNHN 1903-20, holotype (by monotypy) of the species “*Cynodon*” *miacinus* TEILHARD DE CHARDIN, 1915.

The measurements were made by digital callipers to the nearest 0.01 mm and presented to the nearest 0.1 mm. The material was compared with the old collections of Quercy which contain most of the types of specimens and with the

fossils from other localities. The photographs were taken with a Nikon Coolpix 750 camera and processed with Adobe Photoshop.

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

### Abbreviations

MNHN Muséum national d'Histoire naturelle, Paris, France  
pacd posterior accessory cuspid

## Systematic palaeontology

**Superorder Carnivoraformes FLYNN, FINARELLI  
et SPAULDING, 2010**

**Order Carnivora BOWDICH, 1821**

**Suborder Caniformia KRETZOI, 1943**

**Family Amphicyonidae TROUËSSART, 1885**

***Storchictis* n. gen.**

**Type species.** *Cynodon miacinus* TEILHARD DE CHARDIN, 1915.

**Origin of the name.** Dedicated to Gerhard Storch for his numerous works on fossil vertebrates.

**Diagnosis.** See that of the type species.

***Storchictis miacinus* (TEILHARD DE CHARDIN, 1915)**

1915 *Cynodon miacinus*; Teilhard de Chardin, pp. 17–18, 53, pl. 1, fig. 8.

1965 « *Amphicyonodon* » *miacinus*; Beaumont, p. 28.

**Holotype.** Hemimandible MNHN 1903-20 with p2, p4–m2 (Text-fig. 1).

**Emended diagnosis.** Smallest known European Amphicyonidae; gracile mandible, one mental foramen, top of ascending ramus semi-circular with an acute distally directed process, elongate angular process, p2 and p4 higher than the paraconid of m1 with a small basined talonid, large height difference between m1 protoconid and paraconid, the former relatively short, metaconid of m1 is well developed and higher than paraconid, deep V-shaped talonid valley of m1 with entoconid slightly higher than hypoconid, complete and relatively high trigonid of m2 with talonid similar to that of m1.

**Differential diagnosis.** *Amphicyonodon* differs greatly from *Storchictis* by the presence of two mental foramina on the mandible, the rounded ascending ramus top, the thicker and low lower premolars, the thicker m1 with a lower trigonid with a smaller difference in height between the protoconid and paraconid and a basined talonid; in m2, the trigonid is low, the protoconid is equal to or smaller than the metaconid and the talonid is shallow and basined.

*Cynodictis* differs from *Storchictis* by the presence of two mental foramina on the mandible, the axe-shaped ascending ramus, the relatively lower p2 and p4, the longer mesio-distally protoconid of m1, the smaller difference in height between the protoconid and paraconid of m1, the slightly lower trigonid of m2.

**Type locality.** Precise locality unknown, Quercy phosphorites, France.

**Geological age.** Unknown, possibly middle or late Eocene.

**Description.** All the teeth are unworn except a small wear on the top of the paraconid of m1 which does not take on the height of the cuspid. The enamel has small pits due to weathering in the fossilisation process.

The mandible is small (p2–m2 = 23 mm; Teilhard de Chardin gives 39 mm for i3–m3) and bears p2, p4–m2 and alveoli of the canine, p1, p3, and m3, the latter being very small. The corpus is shallow, elongate, the lower border being convex from the cranial extremity to the level of the ascending ramus where it goes up and is slightly concave. There is only one mental foramen below the root of p1. The ascending ramus is high with a semi-rounded top and an acute distally pointed process. The masseter fossa is wide, extending cranially to m3, but not so deep; it is reinforced by a strong rim along the cranial border. The articular condyle is broad (8.7 mm) and below there is a well-developed angular caudal process which constitutes a good lever for the muscle pterigoideus medialis. The anterior part of the dentary tapers off and the symphysis is very oblique. The alveolus for p1 is oval and separated from the canine alveolus by about 2.6 mm. After a small diastema (1.4 mm), p2 is higher than the paraconid of m1, sharp and bucco-lingually compressed; the crown is asymmetrical, the distal part being longer than the mesial one; there is a thin cristid along the mesial face and another one along the distal one; a cingulid surrounds the base and, distally, gives rise to a small talonid with a shallow minute basin. The p4, less asymmetrical than p2, is also higher than the paraconid of m1, pointed, and bucco-lingually compressed; there are also mesial and distal cristids, the latter with a trenchant, although step-like, posterior accessory cuspid. The step-like accessory cuspid is considered to be a derived amphicyonid feature (Tomiya and Tseng 2016). Here the cingulid forms a small mesial styloid and, distally, a slightly hollow talonid. The carnassial m1 is characterised by a great height difference between the protoconid and paraconid. The former displays a relatively short buccal face and an almost triangular basal section; the paraconid is far lower and moderately oblique relative to the sagittal plane. The metaconid is slightly higher than the paraconid and is nearly pyramidal with its almost flat buccal and distal faces while the lingual one is convex; it is not much reduced and it is not distally displaced, it does not appear in buccal view of the tooth and it closes the trigonid valley. The talonid is shaped by an entocristid that is slightly higher than the hypoconid, the latter being thicker with a cristid obliqua joining the middle of the base of the protoconid, and a V-shaped large valley; there is no trace of the hypoconulid and the valley is distally open. A cingulid surrounds the crown. The second molar is almost rectangular, although the talonid is slightly narrower than the trigonid (Tab. 1); the latter is complete and high relative to the talonid. The protoconid is higher, while the paraconid and metaconid are lower but well-developed, the former being a low ridge without pointed apex. The talonid is similar to that of m1 except for the cristid obliqua which is parallel to the sagittal plane. There is an oval alveolus for m3.



Text-fig. 1. *Storchictis* n. gen. *miacinus* (TEILHARD DE CHARDIN, 1915). Left hemimandible. a – buccal view, b – lingual view, c – occlusal view. Scale bar = 10 mm.

## Comparisons

### Comparisons with *Amphicynodon*

The generic name “*Cynodon*” (= *Amphicynodon* FILHOL, 1881) was used by Teilhard de Chardin (1915) and before him by Filhol who wrote “*C. gracilis*” on that mandible (see Text-fig. 1a and Teilhard de Chardin 1915: 117). However, the studied mandible is completely different from those of Amphicynodontidae. *Amphicynodon gracilis* for instance is a little larger, it has a relatively lower m1 trigonid with more inflated cuspids, simple and more inflated premolars

with a more marked cingulid, p4 without pacd. The m2 is characterised by a low trigonid in which the metaconid is larger than the protoconid. Most of these characters are shared by all the Amphicynodontidae. Consequently, *Storchictis* n. gen. cannot be placed in this family. The affinities of *Storchictis* must be sought in the primitive amphicyonid genus *Cynodictis* BRAVARD et POMEL, 1850, or in the primitive Carnivoraformes.

### Comparisons with *Cynodictis*

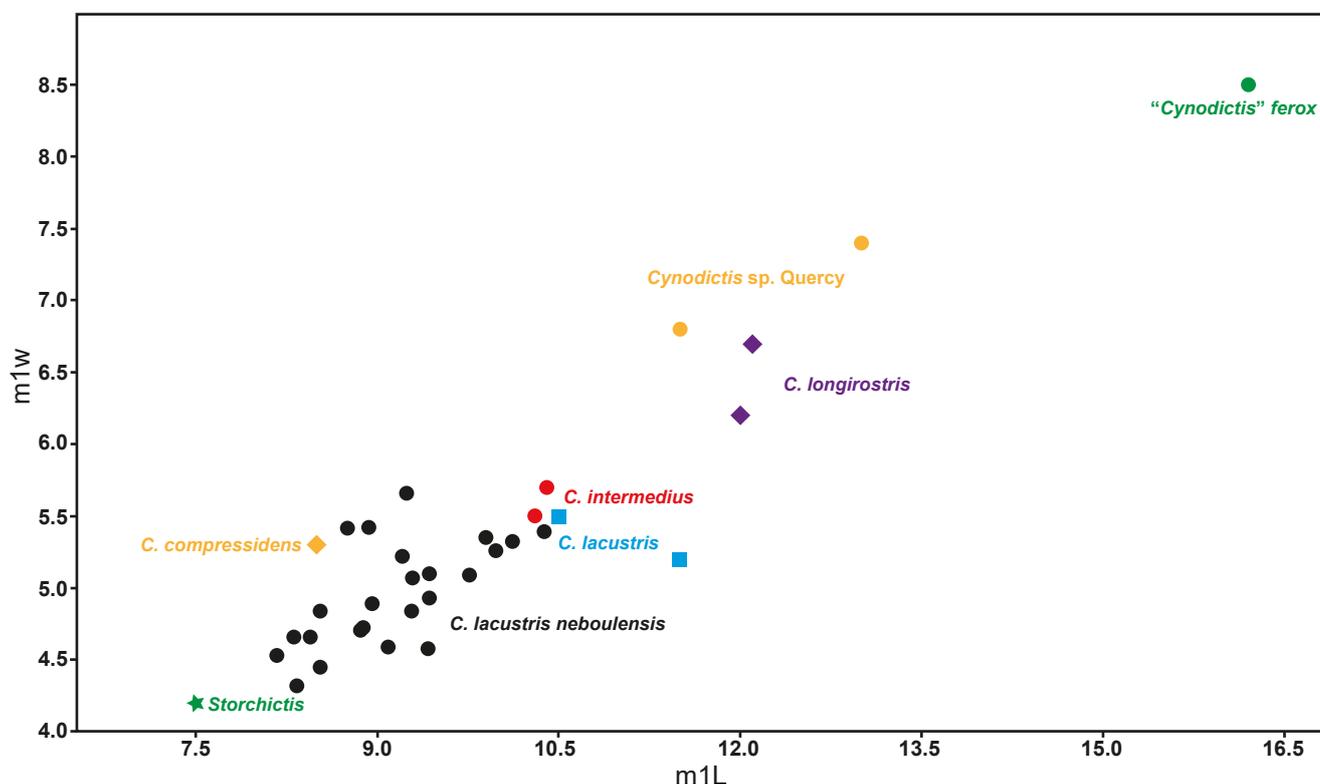
The type species, *C. lacustris* comes from the late Eocene locality La Débruge (Vaucluse, France). It was described by

**Table 1.** Measurements of *Storchictis miacinus* compared to some *Cynodictis* species. L – length, w – width, tr – trigonid, tl – talonid, n – number of specimens, m – mean, s – standard deviation.

Taxon		p2 L	p2 w	p3 L	p3 w	p4 L	p4 w	m1 L	m1 trL	m1 wtr	m1 wtl	m2 L	m2 wtr	m2 wtl
<i>S. miacinus</i>	n	1	1	1	1	1	1	1	1	1	1	1	1	1
	m	3.9	1.9	–	–	5.9	2.5	7.5	4.25	4.2	3.4	4.4	2.8	2.5
<i>C. lacustris nebulensis</i>	n	3	3	7	7	15	15	24	24	24	24	29	29	14
	m	4.1	2.4	5.9	2.7	6.9	3	9.2	5.96	4.6	4.98	5.0	3.5	3.1
	s	–	–	–	–	0.43	0.14	0.52	0.49	0.29	0.42	0.33	0.22	0.37
<i>C. longirostris</i>	n	2	2	1	1	2	2	2	2	2	2	2	2	2
	m	5.6	3.5	7.9	3.8	8.7	4.6	12.1	8.3	6.45	5.85	7.2	5.3	4.25
<i>C. compressidens</i>	n	1	1	1	1	2	2	2	2	1	2	2	2	2
	m	3.7	2.6	5.3	3.5	7.2	3.8	9.8	6.4	5.3	4.55	5.35	3.75	3.6
<i>C. lacustris lacustris</i>	n	–	–	–	–	1	1	2	2	2	2	1	1	1
	m	–	–	–	–	8.8	3.6	11	7.85	5.35	4.4	5.8	4.2	3.6
<i>C. ferox</i>	n	–	–	1	1	1	1	1	1	1	1	1	1	1
	m	–	–	7.5	4.2	11.2	5.7	16.8	11.0	8.2	6.3	9.1	6.0	5.8

Bravard and Pomel (1850) and published again by Gervais (1848–1852). Other species were described from the fossils coming from the phosphorites of Quercy and all are based on isolated mandibles insofar as the old collections were made without any precise locations. Until now, except for a few specimens from La Débruge, the sole population of the genus is that of *Cynodictis lacustris nebulensis* (Bonis 1978) from the Quercynian locality Sainte Néboule (MP 19). Its study was the opportunity of a short revision of the different species of *Cynodictis* by Bonis (1978) and then Kotsakis (1980) which was based on copies of the drawings.

Here, I shall only use the small or medium species which really belong to *Cynodictis*, whilst the others, particularly the largest forms, belong to other genera. *Cynodictis lacustris* (Bravard and Pomel 1850) has a thicker cingulid in p4. The p4 is lower relative to m1, and the height difference between the protoconid and paraconid of m1 is smaller. The trigonid valley between the paraconid and metaconid is more open, and the metaconid is slightly more distal and appears in buccal view. *Cynodictis intermedius* FILHOL, 1876, is close to *C. l. lacustris* and differs from *Storchictis miacinus* by the same characters and by the narrower talonid of m2. The same



**Text-fig. 2.** Scatterplot of the m1 length versus m1 width in *Storchictis* compared to *Cynodictis lacustris nebulensis* (black dots) and other species of *Cynodictis*.

can be said for *C. intermedius viverroides* and there is a lack of m3 as well. The *Cynodictis longirostris* FILHOL, 1872, and *C. longirostris crassa* TEILHARD DE CHARDIN, 1915, are larger than the preceding species and differ from *S. miacinus* by the same characters and also due to the relatively lower p2, the small entoconid of m1 and, especially for *C. l. crassa*, the long m2. *Cynodictis compressidens* FILHOL, 1872, of which type specimen was lost, was used by Teilhard de Chardin (1915) for a mandible that is very close to that of *C. intermedius* and different from the mandible shown by Filhol (1872b: pl. 16, figs 28–30). Nevertheless, Teilhard de Chardin figured other mandibles such as *C. compressidens exilis* which seem similar to the Filhol's specimen. I proposed (Bonis 1978) the mandible MNHN QU 8889 can be considered as the type specimen of *Cynodictis exilis* TEILHARD DE CHARDIN, 1915. The latter, small species of *Cynodictis*, differs from *Storchictis* n. gen. due to its a larger size, more robust p4 and m1, a smaller height difference between the protoconid and paraconid of m1, the paraconid is more oblique relative to the sagittal plane and low entoconid of m1, m2 without a clear paraconid, and a narrow talonid without a clear entoconid. A glimpse at the *C. lacustris nebulensis* sample, the best-known of the genus, shows the same result. The subspecies differs from *Storchictis* due to its larger size (Text-fig. 2), the lower premolars that are not as high, the presence of a small posterior accessory cuspid on p2, the smaller difference in height between the paraconid and protoconid of m1, and the slightly more elongate protoconid of m1, both of the last characters being derived; m2 has a slightly lower protoconid. In conclusion, *Storchictis* cannot belong to *Cynodictis*, due to some of its characters being more primitive such as the tall premolars, the large height difference between the paraconid and protoconid of m1, the latter of which has a narrower mesio-distal diameter, the more developed metaconid, and the well-developed and pointed paraconid of m2.

### Comparisons with the “Miacidae”

The name “*miacinus*” that was given by Teilhard de Chardin to that species indicates that he thought that the mandible had affinities with the family “Miacidae”, which at the time was considered to be a stem group of Carnivora (Piveteau 1961) but nowadays is considered polyphyletic. That family was built around the genus *Miacis* COPE, 1872 (Cope 1880) which was recorded in North America and in Eurasia (*M. sylvestris* MARSH, 1872, *M. vulpinus* SCOTT et OSBORN, 1887, *M. uitensis* OSBORN, 1895 in North America; *M. invictus* MATTHEWS et GRANGER, 1925, *M. thailandicus* DUCROCQ et al., 1992 in Asia; *M. rundlei* HOOKER, 2010 and *Miacis exilis* FILHOL, 1877 in Europe).

Nowadays, the data challenge that point of view, and “*Miacis* represents perhaps one of the most confused genera in the classification of early carnivoraforms, with at least 19 species having been assigned to the genus” (Tomiya and Tseng 2016). In recent attempts to reconstruct carnivoraform phylogeny, the “*Miacis*” species are scattered in different branches of the cladograms (Wesley-Hunt and Flynn 2005, Flynn et al. 2010, Spaulding et al. 2010, Solé 2014, Solé et al. 2014).

I shall examine some European species first and then some North American ones. *Quercygale angustidens*

(FILHOL, 1872) was first considered to be a miacid. A review of its relationships (Wesley-Hunt and Werdelin 2005) led to the conclusion that it was the sister group of the clade consisting of Nimravidae and Carnivora. However, in any case, it is very different from *Storchictis* n. gen. not only due to its larger size but especially due to the shape of the symphysis angle that is close to 90° (Teilhard de Chardin 1915: pl. I, fig. 12), the marked flange, the relatively lower p4, the smaller height difference between the paraconid and protoconid of m1, the shorter protoconid, the shorter and trenchant talonid, and the absence of m3. Most of the *Quercygale* specimens come from the old phosphorites of the Quercy collections but others were recorded elsewhere in late Eocene layers. Another species, *Quercygale smithi* SOLÉ, 2014 was recorded in European early Eocene layers.

*Miacis* was also described in Europe from remains from the old Quercy collections under the name *Cynodictis exilis* FILHOL, 1876 but later under *Miacis exilis* (Teilhard de Chardin 1915, Guth 1964) and, after revision, *Paramiacis exilis* (FILHOL, 1876) by Mathis (1985, 1987). The latter also described another Quercynian species, *Paramiacis teilhardi* MATHIS, 1987. Both species were also recorded and dated in the stratigraphy and in the Quercy fissure fillings of the new Quercynian excavations (Matthis 1985, 1987). These species are smaller and differ from *Storchictis* by the simple premolars (p4 without posterior accessory cuspid) with robust cingulids, the trigonid of m1 with more closely positioned cuspids, a higher and shorter paraconid, a higher contact between the paraconid and metaconid, a more robust hypoconid, and a higher trigonid of m2. These characters may be considered as plesiomorphic features that are present in most of the Eocene carnivoraforms and sometimes are more clearly expressed, see for instance *Gracilocyon solei* SMITH et SMITH, 2009, from the earliest Eocene (Smith and Smith 2009).

It is known that there is a diverse array of early carnivoraforms in North America. The genus *Miacis* was split into several species. The type-species *Miacis parvivorus* COPE, 1872, differs from *Storchictis* due to the simple premolars, particularly p4 which is lacking posterior accessory cuspid, a case which seems to be common in “miacids” where the p4 posterior accessory cuspid is absent or small and lowly situated (Matthew 1909: 347), the very high trigonid with closely positioned cuspids, the height of the closure of the trigonid valley by the contact of paraconid-metaconid, the very high m2 trigonid, and the clear cuspids of m3. *Miacis* was reported from the early Chadronian (early Oligocene) of Texas (Gustafson 1986) with a couple of “miacid” species *Miacis cognitus* GUSTAFSON, 1986, and *M. australis* GUSTAFSON, 1986. However, recently another study of the fossils led to a different result (Tomiya and Tseng 2016). The fossils were dated by radiochronology to about 38 Ma, late Middle Eocene (equivalent of European Bartonian). A cladistics analysis situated the two species in a clade with the European genus *Cynodictis*, thus as two amphicyonid representatives and both species were considered to be type-species of new genera: *Gustafsonia cognita* (GUSTAFSON, 1986) and *Angelarctocyon australis* (GUSTAFSON, 1986). The mandible of the former is unknown but that of the latter is known (Gustafson 1986: fig. 29, Tomiya and Tseng 2016: fig. 4). *A. australis*, whose size

is very close to that of *Storchictis* (both  $m1L = 7.5$  mm), differs from the Quercynian fossil by two mental foramina, p4 without mesial stylid and a shorter talonid, m1 with a smaller height difference between the protoconid and paraconid, a more open trigonid, the metaconid appearing slightly in buccal view (Gustafson 1986: fig. 29, Tomiya and Tseng 2016: fig. 4), and a slightly more elongate protoconid, derived characters, while both m2 seem to be similar but the paraconid of *A. australis* is more pointed and the trigonid is more closed, a plesiomorphic character.

## Conclusion

The basis of the Carnivora systematics are founded on the structures of the skull, especially those of the ear region (Flower 1869). All the recent reappraisals of the classification essentially used the features derived from the skull. Presently, as is frequent in mammalian palaeontology, there is no a large data set to study the mandible of *Storchictis*. We have to compare our fossil to the taxa of which the skull characters are known and allows us to determine the precise position in relation to their mandibles. *Storchictis*, when compared to *Cynodictis*, may be considered on the one hand as slightly more primitive due to some features, such as the shape of the m1 trigonid and the shape of m2. On the other hand, it is more derived than the non-carnivoran carnivoraforms. In other words, it seems to be closer to the case of taxa such as *Angelarctocyon australis* whose skull anatomy indicates amphicyonid affinities (Tomiya and Tseng 2016). Thus, *Storchictis* displays some features (less “miacid” like trigonid of m1 with less close-positioned cuspids and more elongated paraconid, shorter m2 trigonid) which indicate a trend towards a *Cynodictis*-like anatomy, therefore towards the family Amphicyonidae.

The geologic age of *Storchictis* n. gen. is difficult to estimate. The ages of the phosphorites from Quercy span a large range. Until now the oldest fossils ever found in the phosphorites are dated to middle Eocene (Astruc et al. 2000). The youngest locality is Crémat, dated to early Miocene (Sigé et al. 1991). During that time there were several changes in the European mammal fauna. The most significant is called “Grande Coupure” of the Tertiary (Stehlin 1909) and was considered as the limit between the Eocene and Oligocene. In terms of mammal Paleogene reference-levels (MP), it is between MP 20 and MP 21. Nevertheless, the faunas from the same type of localities are not homogeneous and sometimes taxa could be absent for taphonomic reasons. However, we see that primitive carnivoraforms did not cross the “Grande Coupure”. *Quercygale* is found in MP 16 to MP 17 in the Quercy, such as *Paramiacis* MATHIS, 1985. Likewise, *Cynodictis* is only present in the Quercy in MP 18 and MP 19. Yet, the younger specimens, such as “*Cynodictis*” *palmidens* from Aubrelong 1 (MP 21), which is not a *Cynodictis* (Lange-Badré 2006) have different features. For example, the two specimen holotypes of “*C.* *palmidens*” and “*C.* *palmidens major*” display a drastic reduction of the metaconid of m1 and a shortening of m2, thus indicating a different lineage with a more cutting dentition and the affinities of which have to be determined (Bonis 1978: 308). It has been suggested that other specimens recorded from other sites, notably in Asia,

belong to the genus *Cynodictis*. However, these attributions are probably invalid as has been shown or discussed by several authors (Bonis 1978, Kotsakis 1980, Hunt 1998, Lange-Badré 2006, Egi et al. 2009, Tomiya and Tseng 2016). After the limit of the “Grande Coupure”, it seems that *Cynodictis* and the primitive carnivoraforms were replaced by new migrants such as the fore runner nimravids, Amphicyonodontidae, Cephalogalini, *Palaeogale*, Felidae, and primitive mustelids. Thus, we may speculate that *Storchictis* n. gen. was possibly present in the European middle or late Eocene.

## Acknowledgements

The redaction of that article profited by the staff of PALEVOPRIM University of Poitiers and especially Sabine Riffaut for the work on the figures with Adobe Photoshop. It was made possible by the kindness of Dr. Christine Argot, in charge of the fossil collections in the MNHN. I thank a lot the editors, Floreal Solé and an anonymous reviewer for their comments which greatly improved the manuscript. The English language corrections are due to ProofReading-Service.

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