

Ursidae (Mammalia, Carnivora) from the Late Oligocene of the “Phosphorites du Quercy” (France) and a reappraisal of the genus *Cephalogale* Geoffroy, 1862

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ABSTRACT

Many karstic fissure fillings from the Quercy (France) constitute fossil bearing localities which give an exceptional open laboratory for the study of evolution of vertebrates and especially mammals from the Eocene to the Early Miocene. A couple of localities from the Late Oligocene (MP 28 = 24.9-24.5 Ma) have yielded, among several taxa, the best sample ever found of a hemicyonine ursid. This sample corresponds to a new species and allows a reappraisal of several other species belonging to lineages attributed to a new tribe (Cephalogalini n. tr.). The latter occupied in Europe along the Oligocene and the lower Miocene some canid-like ecological niches. This tribe was replaced at the end of the Lower Miocene by the Hemicyonini, another tribe of Hemicyoninae (Ursidae).

KEY WORDS

Hemicyoninae,
evolution,
biometry,
ecology,
Late Oligocene,
Quercy,
new tribe,
new genera,
new species.

RÉSUMÉ

Ursidae (Mammalia, Carnivora) de l'Oligocène supérieur des « Phosphorites du Quercy » avec une révision du genre Cephalogale Geoffroy, 1862.

Plusieurs remplissages de fissures karstiques du Quercy (France) sont des sites fossilifères qui constituent un exceptionnel laboratoire à ciel ouvert pour l'étude de l'évolution des vertébrés et particulièrement des mammifères depuis l'Éocène jusqu'au début du Miocène. Deux localités de l'Oligocène supérieur (MP 28 = 24,9-24,5 Ma) ont livré, parmi de nombreux taxons, le meilleur échantillon jamais découvert d'un Ursidae Hemicyoninae. Cet échantillon correspond à une nouvelle espèce et permet une révision de plusieurs autres espèces appartenant à des lignées regroupées dans la nouvelle tribu des Cephalogalini n. tr. Les représentants de celle-ci occupaient en Europe durant l'Oligocène et le début du Miocène des niches écologiques analogues à celles de canidés actuels. Cette tribu fut remplacée à la fin du Miocène inférieur par les Hemicyonini, une autre tribu d'Hemicyoninae (Ursidae).

MOTS CLÉS

Hemicyoninae,
évolution,
biométrie,
écologie,
Oligocène supérieur,
Quercy,
tribu nouvelle,
genres nouveaux,
espèce nouvelle.

INTRODUCTION

Fissure filling localities situated in the Quercy (south western France) have yielded a large number of fossils dated from the Middle Eocene to the Early Miocene although the bulk of the fauna was deposited from the Late Eocene to the Late Oligocene (see Bonis 2011 for a more complete bibliography). The fossils studied in this article come from two Quercy localities, Pech du Fraysse and Pech Desse. A hemicyonine Ursidae, *Adelpharctos ginsburgi* Bonis, 2011, has already been described from Pech du Fraysse (Bonis 2011) but there is, in each locality, another hemicyonine species which belongs to a new hemicyonine genus close to *Cephalogale* Jourdan, 1862. The sum of specimens in these localities constitutes the best sample ever found of a hemicyonine ursid. The Quercy fossiliferous karstic fillings have been dated by the mammalian fauna they contain, especially from the evolutionary degree of rodents. In the case of these localities, the presence of the Theridomyidae Alston, 1876 *Issiodoromys limognensis* Schmidt-Kittler & Vianey-Liaud, 1987, *Archaeomys laurillardii* Gervais, 1848, *Archaeomys helveticus* Vianey-Liaud, 1977 and the Eomyidae Depéret & Douxami, 1902, *Eomys quercyi* Comte et Vianey-Liaud, 1987 and *Eomys gigas* Comte & Vianey-Liaud, 1987 indicates a Late Oligocene age (Remy *et al.* 1987; Biochrom' 97) and more precisely the MP level 28, about 24.9-24.5 Ma (Mertz *et al.* 2007). The studied material had been until now attributed to the genus *Cephalogale* Jourdan, 1862, it is actually stored in the University of Poitiers.

MATERIAL AND METHODS

LOWER DENTITION

Pech du Fraysse: left m1, PF 33; right m1, PF 38; left m1, PF 45; left m2, PF 48; right m3, PF 50; left m2, PF 48; left m3, PF 51; left mandible with p2-p3, m1-m2, PF 420; right mandible with m1-m2, PF 421; right mandible with m2-m3, PF 422; left m3, PF 629; right mandible with fragmentary m1-m2, PF 630; right mandible m1, PF 631.

Pech Desse: right mandible with p2-m1, PD 22; left m1 talonid, PD 57; right mandible with p3, PD 90; right mandible with p4-m3, PD 95; left mandible with p2-p3, PD 124; left m1, PD 156; left m1, PD 157; left m1, PD 156; left m1, PD 160; left m1, PD 179; right p4, PD 232; left mandible with c, p2-m2, PD 273; left mandible with p4, PD 315; left p4, PD 322; left m1, PD 323; right p1, PD 328; left m2, PD 329; left m1, PD 179; left mandible with p3-m3, PD 475; right mandible with p2-m2, PD 476; left mandible with p2-m2, PD 477; left m1, PD 506.

UPPER DENTITION

Pech du Fraysse: left maxilla with P4-M1, alveoli of M2, PF 35; left maxilla with P3-P4, PF 37; right M1, PF 39; left M1, PF 40; left M1, PF 41; right M1, PF 42; left M1, PF 43; right P4, PF 44; right P3, PF 46; left P4, PF 47; left M2, PF 49; left maxilla with M1, PF 50; right maxilla with M1, PF 53; right M1, PF 56; right M2, PF 58; left maxilla with M1-M2, PF 430; left M1, PF 528; left M2 PF 632; left maxilla with P4-M2, PF 633; right maxilla P4-M1, PF 634; right maxilla with M2, PF 636; right maxilla with M1-M2, PF 635; right broken P4, PF 637.

Pech Desse: left maxilla with P4, broken M1, PD 45; left P4, PD 55; left M1, PD 56; right maxilla with P2-M1, PD 130; right M1, PD 135; right M1, PD 137; right maxilla with M1, PD 321; right maxilla with P4-M2, PD 507; left M2, PD 514.

METHODS

The material will be metrically studied to see whether it can be assigned to a single species or not. The measurements of specimens coming from both localities will be compared together by multivariate analysis and with extant species whose dimorphism, generally sexual dimorphism, is known through indices of dimorphism. A principal component analysis tests the degree of difference in size and a factorial correspondence analysis tests the difference in proportions (Bonis & Lebeau 1974) of m1, the lower carnassial, which is the most abundant tooth in the sample. After a definition of a new genus and the description

of the material, the Quercy specimens will be compared to the species of *Cephalogale* Jourdan, 1862, to the closely related genera *Phoberogale* Ginsburg & Morales, 1995 and *Zaragocyon* Ginsburg & Morales, 1995, and to other specimens described as *Cephalogale* to show the differences. A more inclusive examination will then try to find if there are additional lineages and evolutionary trends in the history of these genera, to replace the species in some genera and to look for their relationships with the Middle Miocene Hemicyoninae Frick, 1926.

This study will incorporate also original unpublished specimens from the Quercy and Saint Gérard-le-Puy housed in the Muséum national d'Histoire naturelle, Paris (MNHN) which allow a better understanding of these Oligocene Carnivora and will allow to define a new tribe whose type genus is *Cephalogale*, which is founded on the species *Cephalogale geoffroyi* Jourdan, 1862 which comes from the quarry of Billy (Allier, France) level of Créchy-bas (Berthet *et al.* 2005) near the well known Early Miocene sites of Saint Gérard-le-Puy but containing a Late Oligocene vertebrate fauna of MP 29 about 24.2–24.5 Ma (Mertz *et al.* 2007) thus a little younger than the faunas from Pech du Fraysse and Pech Desse (Biochrom' 97).

SYSTEMATICS

Order CARNIVORA Bowdich, 1821
Family URSIDAE Fischer de Waldheim, 1817
Sub-family HEMICYONINAE Frick, 1926

Tribe CEPHALOGALINI n. tr.

TYPE GENUS. — *Cephalogale* Jourdan, 1862 by present designation.

DIAGNOSIS. — Partially coming from the descriptions of Beaumont (1965), Bonis (1973), Hunt (1998), and Teilhard de Chardin (1915).

Digitigrade Hemicyoninae containing several lineages of small (Early Oligocene) to medium sized (Late Oligocene–Early Miocene) primitive ursids (skull length of about 10–20 cm). Dental formula = I3/2–3, C1/1, P4/4, M2/3. The m2 has a metaconid larger or

equal to the protoconid like in the Amphicyonodontidae Simpson, 1945 but the Cephalogalini n. tr. are distinguished from them by the m1 which is larger relatively to the premolars and whose metaconid is reduced (open trigonid), trigonid is more bladelike and talonid has a robust elongated hypoconid continuing by a low crest which encloses the talonid basin and continues in the lingual side before gently joining the metaconid without any notch; sometimes a very small entoconid is present in the crest; m2 has a reduced or absent paraconid and a talonid similar to that of m1. There is an overall evolutionary trend toward an increasing of size, reduction of metaconid of m1 and correlative increasing distance between m1 paraconid and metaconid, increasing relative length of the m2 talonid. Some lineages may be distinguished by the size and shape of the lower premolars which can be laterally compressed and bladelike to somewhat robust and transversely widened depending on the lineage; p1 elongated and knoblike, posterior accessory cusp often present in p2–3, generally present, although sometimes very small, in p4. No posterior accessory cusps on P1–3. P4 is short relative to the molars with a well developed, more or less posteriorly situated protocone and a short metastyle and sometimes with a very small parastyle. Low cuspidated M1 with post-protocrista joining directly the distal border, except in *Adelpharctos* Bonis, 1971, without any contact with the metacone thus the trigone basin is posteriorly open; there is a trend to a sub-quadrate occlusal outline with inflation of the metaconule; large lingual and variable buccal cingulum; M2 smaller and lower cuspidated than M1 with a variable occlusal outline from triangular to oval, buccal cusps being separated or quite fused; ursid basicranium with Type A bulla (Hunt 1974), well ossified, completely enclosing middle ear, with inflation of medial part of bulla in some species.

GENERA INCLUDED. — *Cephalogale*, *Adelpharctos* Bonis, 1971, *Filholictis* n. gen., *Phoberogale* Ginsburg & Morales, 1995, *Cyonarctos* n. gen.

Cephalogale Jourdan, 1862

DIAGNOSIS. — Medium sized to large Cephalogalini n. tr., relatively short and robust P2–P3 and p2–p4, without pac or pacd or with a reduced pacd in p4.

TYPE SPECIES. — *C. geoffroyi* Jourdan, 1862 by original designation.

OTHER SPECIES. — *C. ginesticus* Kuss, 1962; *C. gergoviensis* Viret, 1929; *C. shareri* (Wang, Hunt, Tedford & Lander, 2009).

Adelpharctos Bonis, 1971

EMENDED DIAGNOSIS. — Cephalogalini n. tr. with a more cutting dentition than the other genera of the sub-family, m1 shorter relative to the premolar row with a less reduced metaconid and a talonid tapering backward. P2-3 with three roots, P4 short and robust, triangular shaped M1 with a metaconule more buccal relatively to the protocone than in other Cephalogalini n. tr. M1, hypometacrista joining the base of the metacone and with a modest linguo-distal cingulum.

TYPE SPECIES. — *A. mirus* Bonis, 1971.

OTHER SPECIES. — *A. ginsburgi* Bonis, 2011.

Filholictis n. gen.

TYPE AND UNIQUE SPECIES. — *Canis filholi* Munier-Chalmas in Filhol, 1877 by original designation.

DERIVATIO NOMINIS. — Dedicated to H. Filhol who published many Quercy fossils.

DIAGNOSIS. — Same as that of the type species.

Filholictis filholi

(Munier-Chalmas in Filhol, 1877)

Canis filholi Munier-Chalmas in Filhol, 1877: 319, figs 123, 124. — Beaumont 1965: 23.

Cephalogale filholi – Schlosser 1888: 103; 1904-1905: 293. — Bonis 1973: 82.

HOLOTYPE. — Mandible figured by Filhol (1877: figs 123, 124); (MNHN.F.nn).

DIAGNOSIS. — Primitive middle sized Cephalogalini n. tr. differing from the Amphicyonodontidae by the large lower carnassial relative to the premolars and from the other Cephalogalini n. tr. by a less reduced metaconid of m1 in contact with the paraconid and closing the central valley of the trigonid. High lower premolars without pacd, p3 as tall as p4 both being higher than the paraconid of m1; m2 relatively short for a Hemicyoninae, paraconid present but metaconid more developed than the protoconid.

TYPE LOCALITY. — Unknown, “Phosphorites du Quercy”.

GEOLOGICAL AGE. — Unknown but probably Oligocene.

Phoberogale

Ginsburg & Morales, 1995

DIAGNOSIS. — Medium sized to large Cephalogalini n. tr., low and elongated P2-P3 and p2-p4, p2-p4 with developed pacd, robust cingula and cingulids in all the cheek teeth.

TYPE SPECIES. — *Cephalogale depereti* Viret, 1929 by original designation.

OTHER SPECIES. — *P. gracile* (Viret, 1929); *P. bonali* (Helbing, 1928); *P. minor* (Filhol, 1877).

Cyonarctos n. gen.

ETYMOLOGY. — From the Greek cyon (dog) and arctos (bear) for an ursid looking like a canid.

TYPE SPECIES. — *Cyonarctos dessei* n. sp. by present designation.

DIAGNOSIS. — That of the type species.

DIFFERENTIAL DIAGNOSIS. — *Adelpharctos* differs by the larger size, the relatively higher trigonid and the short talonid of m1, the three rooted P2-P3 and the more V shaped M1. *Cephalogale* lacks a pacd in p2-p3, p4 is lower than the paraconid of m1, the premolar crowns more massive, diastemas between p2-p3 and p3-p4. *Phoberogale* has lower and more elongated P2-P3 and p2-p4, and robust cingula and cingulids *Filholictis* n. gen. is more primitive with m1 shorter relative to the premolars and with its metaconid in contact with the paraconid, and a short m2.

Cyonarctos dessei n. sp.

Cephalogale cf. *minor* – Bonis 1974: 28. Non *Cephalogale minor* Filhol, 1882.

Cephalogale minor – Remy et al. 1987: 187. — Biochrom' 97: 793.

Cephalogale cadurcensis – Remy et al. 1987: 187. Non *Canis cadurcensis* Filhol, 1877.

Cephalogale sp. – Remy et al. 1987: 187.

HOLOTYPE. — Left hemi-mandible with p2-m2 (PD 477) from Pech Desse.

PARATYPES. — Left hemi-mandible with broken p2, p3-m3 (PD 475), left hemi-mandible with c, p2-m2 (PD 273), fragment of right maxilla with P2-M1, (PD 130), frag-

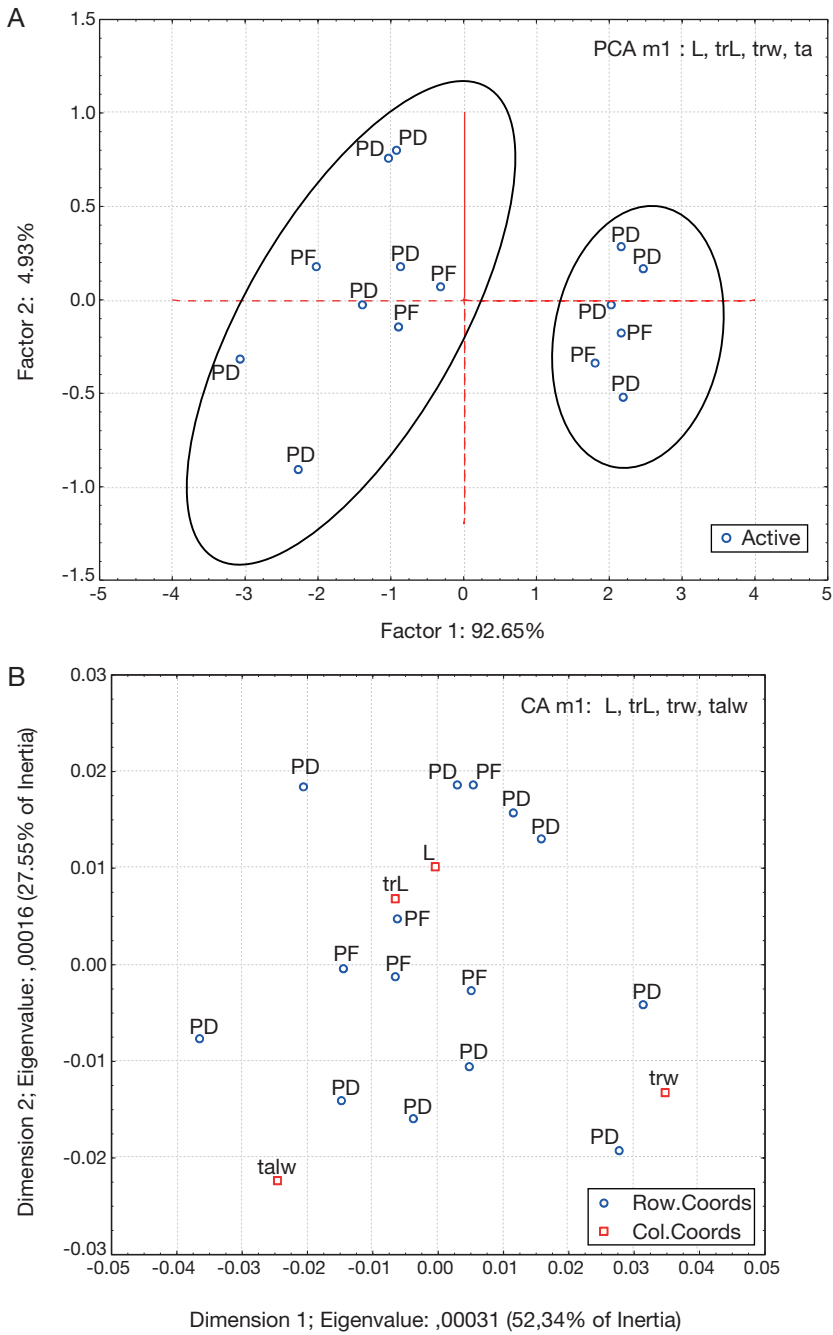


FIG. 1. — *Cyonarctos dessei* n. gen., n. sp. from Pech Desse-Pech-de-Fraysse: **A**, principal component analysis based on four m1 measurements (m1 length, trigonid of m1 length, trigonid of m1 width, talonid of m1 width); plotting in the plane of the two first principal components of specimens from Pech Desse (PD) and Pech du Fraysse (PF); **B**, correspondence analysis based on the same data.

ment of right maxilla with P4-M2 (PD 507), left M2 (PD 514), right M1 (PD 137) and other labelled material from Pech Desse which are identified as the components of the original type series (ICZN: art. 73 D).

LOCALITY. — Pech Desse near Mouillac, Quercy, France.

REFERRED SPECIMENS. — See material from Pech du Fraysse.

DATING. — MP 28 (about 24.9-24.5 Ma).

DISTRIBUTION. — Quercy (South western France).

ETYMOLOGY. — Dedicated to my colleague Jean Desse who gave his name to the locality.

DIAGNOSIS. — Small, (minimum length of m1 = 14.5 mm), to medium-sized (maximum length of m1 = 18.2 mm) *Cephalogalini* n. tr. P2-P3 without posterior accessory cusp (pac); P2 slightly asymmetrical; P3 symmetrical; P2-3 with tall and acute crowns; P4 with moderately distally displaced large protocone, moderate cingulum, very small parastyle, short metastyle blade; triangular M1 with paracone higher than metacone, V shaped protocone of which the anterior arm joins the mesial cingulum while the posterior one turns distally and thus opening the trigone basin; oval M2 with metacone smaller than or similar to the paracone and close to or separated from the paracone; small one-rooted p1; p1-p3 asymmetrical without posterior accessory cuspid (pacd); p4 more symmetrical with a developed pacd; p2 as tall as p3 and p4 taller than the m1 paraconid; m1 with moderately reduced metaconid and a “*Cephalogale* like” talonid; m2 with a small but clear paraconid and a relatively short talonid; small m3 with a clear metaconid and a distinct talonid.

BIOMETRY OF *CYONARCTOS DESSEI* N. GEN., N. SP.

The morphological characters of the material from Pech du Fraysse and Pech Desse correspond to those of the tribe *Cephalogalini* n. tr. It can be divided in each locality in two populations clearly separated by the size but attributed to one species.

Metric analysis of the dental material included within the genus *Cyonarctos* n. gen. in the two studied localities, and especially m1 measurements, is used to decide if the fossils belong to a single species or not. Although the m1 length would be “the poorest predictor of body weight” (Van Valkenburgh 1990), it generally gives a good indication on the sexual dimorphism in extant species of carnivorans. A principal components analysis (PCA) based on m1 dimensions (Fig. 1A) shows a group of small specimens clearly separated from a group

of larger specimens. The morphological characters of these groups are quite similar and the problem is to know if there are two size separated species or only one dimorphic species, generally carnivoran males being larger than females with some exceptions. A correspondence analysis (CA) shows that the two groups are mixed (Fig. 1B). The CA being based on the differences in proportions (Bonis & Lebeau 1974), it indicates that both groups, small and large individuals, have the same proportions. The difference in size between the two groups is tested by comparisons with extant and fossil species.

Metric comparisons with extant or fossil taxa were made from published data (Del Campana 1913; Spahni 1955; Bonifay 1971, 1972; Poplin 1972; Bonifay 1975; Davis 1977; Klein 1986; Berta 1988; Legendre & Roth 1988; Van Valkenburgh 1990; Dayan *et al.* 1992; Kieser & Kroeneveld 1992a, b; Koufos 1992; Fistani & Crégut-Bonhoure 1993; Okarma & Buchalczyk 1993; Argand 1995; Crégut-Bonnoure 1996; Rook & Torre 1996; Baryshnikov 1996, 2012; Gittleman & Van Valkenburg 1997; Szuma 2000; Dayan *et al.* 2002; Palmqvist *et al.* 2002; Abramov & Puzachenko 2005; Baryshnikov & Tsukala 2010; Castel *et al.* 2010; Pérez-Rippol *et al.* 2010; Woldrich 1879) and personal data.

A sexual dimorphism index (SDI 1) can be computed for m1 by the difference between male and female m1 length means $\times 100$ divided by the sum of both means:

$$\frac{(Lm1a - Lm1b) \times 100}{Lm1a + Lm1b}$$

This ratio gives the difference between male and female specimens relatively to the size of m1. It has been computed for 152 extant populations of carnivorans analysed from data in the literature. The resulting histogram is J shaped (Fig. 2), the lowest values, (similar of slightly different sex sizes), are close to the vertical axis and the highest values (large difference between both sexes) are far from it. Most of the species indices are situated between the values zero to four (116 species or populations). The SDI 1 for the two Quercy localities (7.2) is between four and eight values with 26 extant species, eight species having higher

indices. The largest differences may occur in large species as *Panthera leo* (Linnaeus, 1758), *Panthera tigris* (Linnaeus, 1758) or *Ursus arctos* Linnaeus, 1758 but also in medium sized as *Gulo gulo* Linnaeus, 1758 or *Felis temmincki* Vigors & Horsfield, 1827 and small species as *Mustela erminea* Linnaeus, 1758. Indices can vary within a same genus and even within the same species depending on the origin of the sample (0.16 to 4.8 for *Canis latrans* Say, 1823, 2 to 10 for *Ursus arctos*, 3.25 to 10.4 for *Panthera leo*, 1.5 to 5.8 for *Nasua nasua* Linnaeus, 1766 and 0.3 to 5.1 for *Vulpes vulpes* (Linnaeus, 1758)). The SDI 1 of the Pech Desse-Pech du Fraysse sample is compatible with a single species hypothesis.

The observed range of the m1 length within a group of specimens corresponds to another index of sexual dimorphism (SDI 2): “(Lm1 of the smallest specimen/Lm1 of the largest specimen) × 100”. Here we compare the group of small specimens (females?) and the group of large specimens (males?) of the Fig. 1. In a sample of m1, if the difference in length between the two extreme specimens is low, the ratio will be close to 100, but if the difference is significant, the ratio will be lower. When the ratio of the difference in size of the m1s is computed in extant carnivorans whose sexes are known, we observe that this index, computed in large populations, is higher for each sex than when the two morphs are mixed, indicating the sexual dimorphism (Table 3). For example, in *Meles meles* Linnaeus, 1758 from Transcaucasia, the index is 76 for the males, 88 for the females but only 75 when the two sexes are mixed. That index reaches 96 for the group of small specimens (14.49/15.05) and 90 for the group of large specimens (16.46/18.22) of Pech Desse and Pech du Fraysse. It reaches only 79.5 when the two groups are mixed (14.49/18.22). The last value is close to those which are generally found in extant and fossil carnivorans when both sexes are mixed. Even if this index is partially depending on the number of specimens, it gives a quite good idea on the sex difference in a sample of extant or fossil carnivorans. In the case of the studied fossils, we conclude that the numbers are compatible with a single species hypothesis.

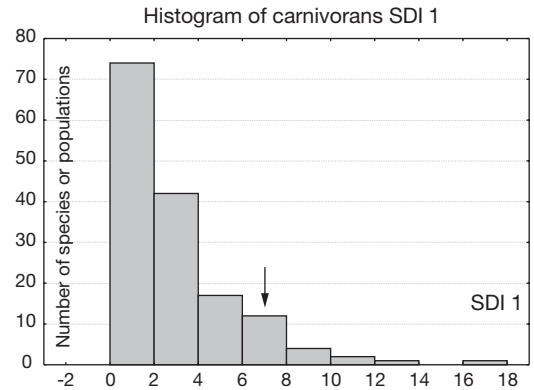


FIG. 2. — Distribution of the SDI 1 (ratios of smallest individual m1 length/largest individual m1 length) among several species or populations of carnivorans. The arrow indicates the position of the Pech Desse and Pech-du-Fraysse material.

Thus each index within both groups, small and large, of the Quercy material seems to be too high to belong to two different species but they are convenient with a sexual dimorphism. Thus, on these criteria, the whole material from Pech Desse and Pech du Fraysse seems to be within the range of a single species.

DESCRIPTION OF *CYONARCTOS DESSEI* N. GEN., N. SP. *Mandible*

There are four quite complete mandibles from Pech Desse, one from Pech du Fraysse (Fig. 3) and several fragments from Pech Desse and Pech du Fraysse. The corpus is quite robust (PD 273) or more slender (PD 475, 476, 477, PF 420) but it is always anteriorly tapering. The ventral border is gently convex in all specimens and the maximum height of the mandible is under m1. There is one mental foramen beneath the mesial root of p2 and another one beneath p3. The coronoid process is high with a large masseteric fossa. The condyle, moderately extended laterally, is situated at the level of the apex of m1. The symphyseal plate has a defined area of smooth bone above the rugose portion (Figs 3B, 4B). It is interpreted as corresponding to the presence of a fibrocartilage pad as in the wolf and allowing a quite flexible mandible symphysis and acting as a cushion during the displacements of the two branches of the mandible during chew-

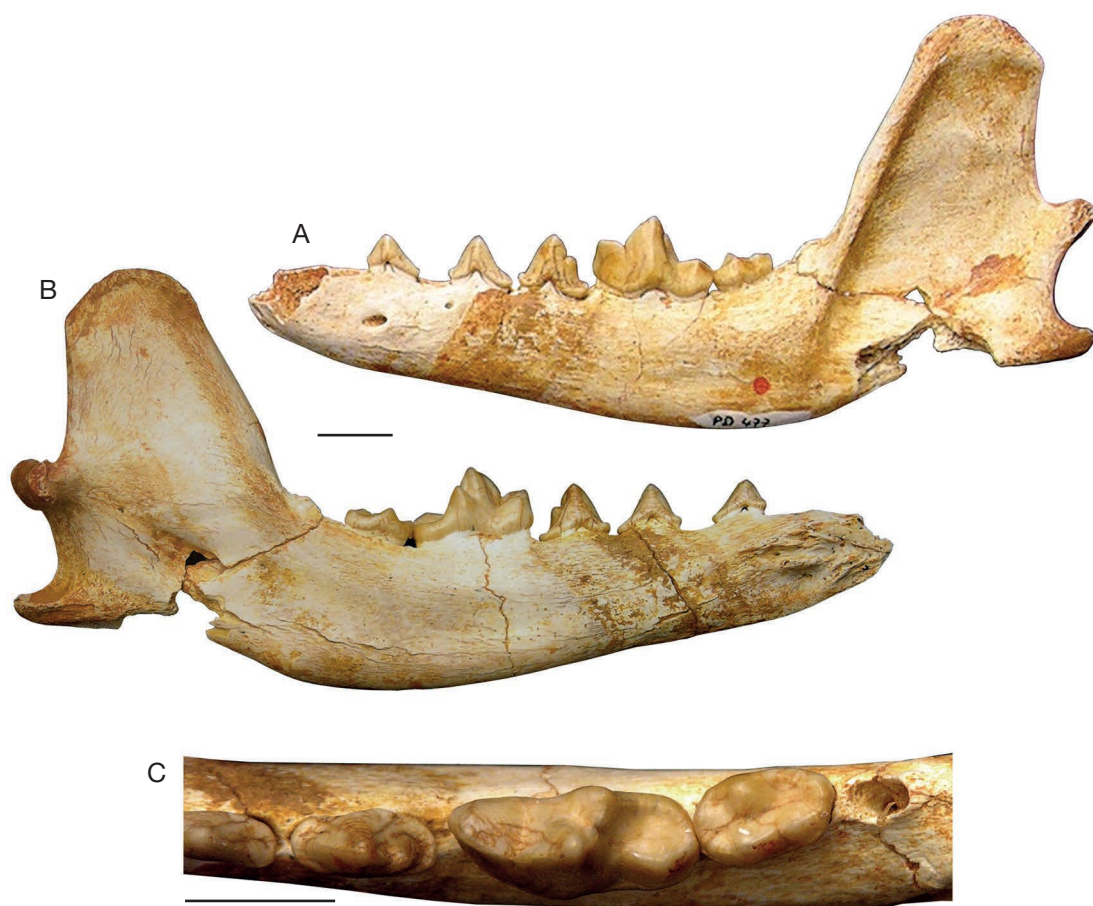


FIG. 3. — *Cyonarctos dessei* n. gen., n. sp.: left hemi-mandible PD 477, holotype: **A**, buccal view; **B**, lingual view; **C**, occlusal view. Scale bars: 1 cm.

ing (Scapino 1965, 1981; Hunt 2009). Below the smooth plate, there are bony rugosities forming quite horizontal ridges converging forward. Two small foramina are ventrally situated beneath the canine for entry of nerves and blood vessels into this area (Scapino 1965: fig. 12). The smooth surface of the symphyseal plate is a horizontal rectangle in the large mandible PD 273 and a smaller elongated oblique oval in PD 477.

Lower dentition (Table 1; Figs 3-6)

The incisors are missing in all the specimens but two very small alveoli, corresponding to i2 and i3 are present in PD 315 and PD 477 mesio-buccally

of the canine; the former is mesio-distally elongated and narrow, the latter is rounded and just a little enlarged. There is no place for a first incisor alveolus. The canine, whose crown is partially broken in PD 273, has a robust root but must have been quite low. The single rooted p1 is lacking in all the specimens. The other premolars increase in size from p2 to p4. The former is low, slightly elongated, without any accessory cusp and with a distal half longer than the mesial one and a faint distal crest from apex to the base. Separated by a short diastema (1 to 4 mm), p3 is quite similar to p2 but the difference in length between mesial and distal halves of the crown is lesser and there



FIG. 4. — *Cyonarctos dessei* n. gen., n. sp.: left hemi-mandible PD 273: **A**, buccal view; **B**, lingual view; **C**, occlusal view. Scale bars: 1 cm.

is possibly a very minute posterior accessory cuspid (pacd) and a mesial basal cuspid (PD 273); a slight crest runs distally from the apex to the base. The crown of p4 is more symmetrical, with both mesial and distal basal cuspids and with a well developed posterior accessory cuspid in the distal crest. The premolars are quite tall, p3 being as tall as the paraconid of m1 and p4 being taller than it. In m1, the protoconid is taller than the paraconid; the metaconid is reduced and posteriorly displaced, clearly separated from the paraconid. The talonid has an elongated and dominant hypoconid prolonged by a crest which encloses the narrow talonid basin and joins the metaconid without any notch. The metaconid of m2 is the taller cuspid of this tooth; the paraconid is present and a small mesio-buccal crest encloses the small trigonid basin; the talonid is similar in shape to that of m1. The m3 is oval,

the metaconid higher than the protoconid and the paraconid is very small, a small hypoconid is present in the buccal crest. The cingulids are present but weak in premolars and molars.

Upper dentition (Table 2; Fig. 7)

A piece of maxilla with P3 and part of the mesial alveoli of P4 (PF 46), another one with P3-P4 (PF 37) and a third with P2-M1 (PD 130) are the witnesses of ante-carnassial premolars; their crowns are simple, acute, without accessory cusp, slightly elongated, lower than the paracone of P4 and the mesial portion is shorter than the distal one, especially in P3; there are two small crests, a mesial one from the apex to the mesio-lingual corner and a distal one from the apex to the distal border; a weak cingulum surrounds the base of the crown of P3. The carnassial is short relatively to

TABLE 1. — Measurements of lower teeth of *Cyonarctos dessei* n. gen., n. sp. Abbreviations: **PF**, Pech-du-Fraysse; **PD**, Pech Desse; **m**, mean; **min**, minimum; **max**, maximum; **n**, number of specimens; **L**, length; **w**, width; **trL**, trigonid length; **trw**, trigonid width; **talw**, talonid width.

	c		p2		p3		p4		m1				m2			m3	
	L	w	L	w	L	w	L	w	L	trL	trw	talw	L	trw	talw	L	w
PD																	
n	1	1	5	5	6	6	9	9	10	10	10	10	6	6	6	2	2
m	9.84	7.03	7.35	3.03	8.5	3.71	10.62	4.92	16.25	11.2	6.87	6.63	8.84	5.84	4.77	5.35	4
min			6.88	2.6	7.6	3.15	8.95	3.73	14.5	10	5.75	5.6	7.5	5.15	3.51	5.34	3.7
max			8.44	3.5	11.1	5.76	13.4	6.53	18.2	12.8	7.6	7.9	11	7.1	6.15	5.35	4.3
PF																	
n			1	1	1	1			6	6	6	6	5	5	5	4	4
m			7	3	8.2	3.6			16.35	11.05	6.67	6.45	8.68	5.69	5.09	5.04	3.95
min									14.6	10.1	6	5.8	7.5	5	4.75	4.5	3.45
max									18.1	11.7	7.5	7.3	9.7	6.2	5.4	5.6	4.8
PD-PF																	
n	1	1	6	6	7	7	9	9	16	16	16	16	11	11	11	6	6
m	9.84	7.03	7.29	3.03	8.4	4.05	10.62	4.92	16.29	11.14	6.79	6.96	8.77	5.76	4.91	5.14	3.96
min			6.88	2.6	7.6	3.15	8.95	3.73	14.5	10	5.75	5.6	7.5	5	3.51	4.5	3.45
max			8.44	3.5	11.1	5.76	13.4	6.53	18.2	12.8	7.6	7.9	11	7.1	6.15	5.6	4.8

the molars with a relatively short and quite robust metastyle; the protocone is a large semi-circular basined platform surrounded by a moderate cingulum and situated quite anteriorly for a hemicyonine; the moderate cingulum is surrounding the whole crown; a mesial crest runs from the apex of the paracone to the cingulum which is turning up as a very small parastyle and separated from the protocone by a shallow notch. In M1, the V shaped protocone is anteriorly prolonged by the preprotocrista to the base of the mesial surface of the paracone and posteriorly by a very tiny, quite indistinct metaconule, the large trigone basin being distally open; the paracone is larger and taller than the metacone and its mesial width is larger than its distal one; a distinct cingulum surrounds the buccal face ending mesially by a small bump corresponding to a tiny parastyle. The lingual cingulum is developed around the protocone but more distolingually. M2 has an oval occlusal outline; the paracone generally is larger and slightly taller than the metacone; the other characters are similar to those of M1 although the V is more open, its distal crest being almost parallel to the sagittal plane, and the cingulum better spread around the protocone although posteriorly thicker.

COMPARISONS

Most of the features observed in this material correspond to those of species allocated until now to the genera *Cephalogale* Jourdan, 1862, *Phoberogale* Ginsburg & Morales, 1995 and *Zaragocyon* Ginsburg & Morales, 1995. The species *geoffroyi*, *ginesticus*, *ursinus*, *brevirostris*, *gergoviensis*, *shareri* will be placed in *Cephalogale*, and *depereti*, *gracile*, *bonali*, *minor* in *Phoberogale* following the discussion. The species *bugtiensis* in an undetermined genus and *meschethense* is not a *Cephalogalini* n. tr. Nevertheless, in the comparisons, the generic name used in the literature will be conserved into brackets insofar the comparison being made species after species, it will be easier to find these species in the different publications.

Cephalogale geoffroyi, type species of the genus, is known from a specimen, fragments of skull and mandible, from the base of the quarry of Billy (Allier, France) dated to Late Oligocene (MN 29) (Huguency *et al.* 2003; Berthet *et al.* 2005), thus a little younger than *Cyonarctos dessei* n. gen., n. sp. In *C. geoffroyi*, the lower premolars lack a pacd, p4 is lower than the paraconid of



FIG. 5. — *Cyonarctos dessei* n. gen., n. sp., left hemi-mandible PD 475: **A**, buccal view; **B**, lingual view, right hemi-mandible PD 33; **C**, occlusal view. Scale bars: 1 cm.

m1, especially when we take into account the heavy wear of the latter whereas there is only a slight wear in the apex of p4; there are larger diastemas between p2-p3 and p3-p4; m2 is worn out and it is quite impossible to distinguish its morphological features.

Cephalogale ginsticus Kuss, 1963 may be in the same lineage as *C. geoffroyi* (Bonis 1973). Notwithstanding the larger size, it differs from the studied material by the less tall lower premolars separated by larger diastemas and without pacd, more symmetrical p4, more reduced m1 metaconid, absence of paraconid and longer talonid of m2, rounded m3, shorter and wider P3, more distally situated protocone of P4, distinct metaconule of M1, less transversally extended M2.

Cephalogale ursinus Bonis, 1973 from Paulhiac (MN 1) differs in the same characters and in m2 without paraconid and with a longer talonid relative to the trigonid.

Cephalogale brevirostris (Croizet *in* Blainville, 1845-1864 *nec* Filhol, 1879) was described through a mandible coming from Cournon (France) in the level MP 28-29 close to that of Pech Desse and Pech du Fraysse (Huguency 1997). It differs from *Cyonarctos dessei* n. gen., n. sp. in the shape of the premolars, without any pacd and quite reduced with long diastemas between them, and p4 lower than the paraconid of m1.

Cephalogale gergoviensis Viret, 1929 is a medium sized species known from a single specimen, a left mandible with part of the canine and p2-

TABLE 2. — Measurements of upper teeth of *Cyonarctos dessei* n. gen., n. sp. Abbreviations: see Table 1; **msL**, metastyle length; **mw**, mesial width; **dw**, distal width.

	P2		P3		P4				M1			M2	
	L	w	L	w	L	w	msL	msw	L	mw	dw	L	w
PD													
n	1	1	1	1	3	4	4	4	5	5	5	2	2
m	7.28	2.39	8.1	3.09	12.6	7.88	4.89	4.67	10	13.2	11.25	6.31	9.52
min					12.39	7.29	4.7	4.11	8.75	12.3	10.82	5.66	9.59
max					12.72	8.72	5.12	5.23	12	15.6	12.54	6.97	9.66
PF													
n			1	1	6	7	6	6	13	13	13	7	7
m			8.05	3.66	14.4	9.53	5.51	5.33	10.5	13.6	11.8	6.84	10.7
min					12.8	8.44	4.75	4.7	9.05	11.63	10.13	5.1	8.85
max					15.9	10.1	6.4	5.73	13	16.45	14.1	8.03	12.5
PF-PD													
n	1	1	2	2	9	10	10	10	18	18	18	9	9
m	7.28	2.39	8.07	3.37	13.8	8.93	5.92	5.6	10.4	13.5	11.65	7.19	9.61
min			8.05	3.09	12.4	7.29	4.7	4.11	8.75	11.63	10.13	5.1	8.85
max			8.1	3.66	15.9	10.1	6.4	5.73	13	16.45	14.2	9	12.52

m2, coming from Romagnat (Limagne, France) which is dated to MP 28-29 (Hugueney 1997). The premolars are closer together, their buccal faces are regularly swollen whereas the lingual ones are expanded in the middle part but hollow mesially and distally, there are two crests, mesial and distal; there is a very discrete buccal cingulid; p4 is slightly taller than the m1 paraconid with a tiny pacd. The m1 has a protoconid clearly taller than the paraconid; reduced and posteriorly displaced metaconid (visible in buccal view) and a talonid with a high hypoconid and a crest closing the talonid and contacting the base of the metaconid without any notch. The m2 is long with metaconid higher but less extended than protoconid, a low mesial ridge closes the trigonid basin and a minute cuspid may correspond to a vestigial paraconid; the talonid is similar to that of m1 but more reduced.

Phoberogale depereti (Viret, 1929) from the Early Miocene of Montaigu le Blin, Saint Gérard-le-Puy Basin, Allier, France (MN 2a) displays a larger size (m1 = 19 to 23 mm), low (lower than the paraconid of m1) and elongated lower premolars with a very well developed buccal cingulid, posterior accessory cuspids in p3, p4 and sometimes p2; the m1 metaconid is more reduced and more posteriorly situated; the paraconid is lacking in

m2 whose talonid is elongated relative to the reduced trigonid. These features greatly differ from those of the Pech Desse and Pech du Fraysse material. It is the same for the slightly smaller species *Phoberogale bonali* (Helbing, 1928) of which morphological characters are close to those of *P. depereti* with the same low, cuspidated and elongated lower premolars, robust cingulids and reduced trigonid and elongated talonid of m2 but a less reduced m1 metaconid (Helbing 1928). *Phoberogale bonali* comes from the locality of La Milloque (MP 29) and thus is younger than the Pech Desse and Pech-du-Fraysse fossils and older than the fossils from Saint Gérard-le-Puy.

"*Cephalogale*" *gracile* (Pomel, 1847) corresponds to specimens from St Gérard-le-Puy (MN 2a) published as *Cephalogale minor*, *C. breviostris* and *?Amphicyon* by Filhol (1879), the three being synonymous of the Pomel's species and especially "*C. breviostris*" does not correspond to the species from Cournon. Viret (1929) gave the following diagnosis: "size between those of *C. geoffroyi* and *C. minor*, P4 with a slightly posteriorly situated, well marked protocone, M1 width equal to length with a well developed postero-internal metaconule, thin lower premolars" (author's translation). The overall size (m1 = about 15-16 mm) is in the range of that of our material but the mandibular pre-



FIG. 6. — *Cyonarctos dessei* n. gen. n. sp., left hemi-mandible PF 420: **A**, buccal view; **B**, lingual view; **C**, occlusal view. Scale bars: 1 cm.

molars are lower and more elongated; they have a well developed buccal cingulid and p3, like p4, has a distinct pacd. The m1 has an elongated trigonid with a reduced metaconid and m2 has an elongated talonid relatively to the trigonid which has no paraconid. M1 has a more developed metaconule and a trend to a subquadrate occlusal outline. Despite the smaller size, these morphological features fit quite well with those of *Phoberogale depereti*.

“*Cephalogale*” *minor* Filhol, 1882 (nec Filhol 1879) is the most commonly cited species of the genus, particularly through dozens of hemi-mandibles unearthed from the “Phosphorites du Quercy”. The species name had been created by Filhol for

a fossil from Saint Gérard-le-Puy belonging to “*Cephalogale*” *gracile* (see above), thus, because the synonymy, the term remained valid for another species, and from the publication (Filhol 1882) it has been used for the Quercy specimens. There is a large size variation between all the specimens attributed to this species (Beaumont 1965) and, taking into account the time range of the Quercy deposits (several million years), there are probably several species in the material coming from the old collections. The size of the specimens figured by Filhol (1882, pl. 5) is lesser (m1 = 13 to 14 mm) than those measured in the Pech Desse and Pech-du-Fraysse sample. The size of the lectotype (MNHN.F.QU9316) corresponds to that

TABLE 3. — Sexual Dimorphism Index 2 Length of the smaller m1/length of the larger m1 in *Cyonarctos dessei* n. gen., n. sp. and some other extant or fossil carnivoran populations. Abbreviations: **1**, Abramov & Puzachenko 2005; **2**, Argand 1995; **3**, Baryshnikov 1996, 2012; **4**, Baryshnikov & Tsukala 2010; **5**, Berta 1988; **6**, Bonifay 1971; **7**, Bonifay 1972; **8**, Bonifay 1975; **9**, Castel *et al.* 2010; **10**, Crégut-Bonhoure 1996; **11**, Dayan *et al.* 1992; **12**, Dayan *et al.* 2002; **13**, Del Campana 1913; **14**, Fistani & Crégut-Bonhoure 1993; **15**, Koufos 1992; **16**, Okarma & Buchalczyk 1993; **17**, Pérez-Rippol *et al.* 2010; **18**, pers. obs.; **19**, Poplin 1972; **20**, Rook & Torre 1996; **21**, Spahni 1955; **22**, Szuma 2000; **23**, Woldrich 1879; **24**, Kieser & Groeneweld 1992a, b.

Species	Origin	M	F	M+F	Ref.
<i>Meles meles</i> Linnaeus, 1758	Europe	78	78	74	1
<i>Meles meles</i>	Transcaucasie	76	88	75	1
<i>Meles leucurus</i> (Hodgson, 1847)	Siberie	76	81	75	1
<i>Meles leucurus</i>	Far East	83	86	80	1
<i>Meles anakuma</i> Temminck, 1844	Japan	90	91	89	1
<i>Canis lupus</i> Linnaeus, 1758	Middle East Wurm - extant			70	11, 12
<i>Canis lupus</i>	Europe-Wurm - extant			79 to 89	3, 10, 18, 23
<i>Canis lupus</i>	Poland	91	97	87	16
<i>Canis etruscus</i> Major, 1877	Europe			84 to 86	6, 14, 16, 21
<i>Canis arvensis</i> Linnaeus, 1758	Europe			83 to 91	14, 16, 20
<i>Canis aureus</i> Linnaeus, 1758	Israel	78	86	78	12
<i>Canis dirus</i> Leidy, 1868	S. America			78	5
<i>Cuon alpinus</i> (Pallas, 1811)	Europe-Asia			75 to 89	3, 18, 23
<i>Canis adustus</i> Sundeval, 1847	Afrique	95	98	89	24
<i>Canis mesomelas</i> Schreber, 1775	Afrique	99	99	94	24
<i>Lycaon pictus</i> Temminck, 1820	Afrique	79	78	74	24
<i>Vulpes chama</i> (A. Smith, 1833)	Afrique	68	66	66	24
<i>Vulpes vulpes</i> (Linnaeus, 1758)	Poland			72	22
<i>Vulpes vulpes</i>	France			81	19
<i>Alopex lagopus</i> (Linnaeus, 1758)	unknown			81	18, 19
<i>Protocyon orcesi</i> Hoffstetter, 1952	S. America			85	5
<i>Protocyon troglodytes</i> (Lund, 1838)	S. America			84	5
<i>Ursus arctos</i> Linnaeus, 1758	different localities	83	89	80 to 85	6, 7, 18, 21
<i>Ursus etruscus</i> Cuvier, 1823	different localities			80 to 86	2, 6
<i>Ursus deningeri</i> Reichenau, 1906	different localities			78 to 85	2, 6
<i>Ursus spelaeus</i> Rosenmüller, 1794	different localities			71 to 86	2, 18, 21
<i>Selenarctos thibetanus</i> (Cuvier, 1823)	Asia			75 to 86	10, 14, 21
<i>Melursus ursinus</i> (Shaw, 1791)	Asia			81	21
<i>Thalarctos maritimus</i> (Phipps, 1774)	unknown			84	21
<i>Cyonarctos dessei</i> n. gen., n. sp.	France	90	96	79,5	
<i>C. ginsticus</i> - <i>C. "ursinus"</i>	France			75	
<i>P. depereti</i> - <i>P. gracile</i>	France			62	

of the smaller specimens of Pech Desse and Pech-du-Fraysse (p2: 6.3×3.2, p3: 7.3×3.6, p4: 9×4.2, m1: 14.2×6, m2: 7.7×5.3, m3: 4.8×4.9) but the premolars are the premolars and bear a more robust cingulum like the premolars of *Phoberogale*. The generic status of the other Filhol' specimens is uncertain.

"*Canis*" *filholi* (Munier-Chalmas in Filhol, 1877) is known by a hemi-mandible from the phosphorites of Quercy (Filhol 1877: figs 123, 124). This is not a *Cynodictis* or a synonym of *C. minor* as advanced by Beaumont (1965: 24). The premolars are simple without any posterior accessory cuspid, m1 is shorter relatively to the premolars than in

Cyonarctos dessei n. gen., n. sp. as is m2, while m3 is relatively larger. The most striking difference with *Cyonarctos dessei* n. gen., n. sp. is the larger metaconid of the carnassials, which mesially joins the paraconid, a unique occurrence within the numerous observed mandibles of *Cephalogalini* n. tr. This character, already observed by Filhol (1877: 319), is a very plesiomorphic feature that recalls the morphology of the genera *Amphicynodon* and *Pachycynodon*, and might justify a separate genus for this specimen.

I did not find the specimen, a fragment of mandible from the "Phosphorites du Quercy"

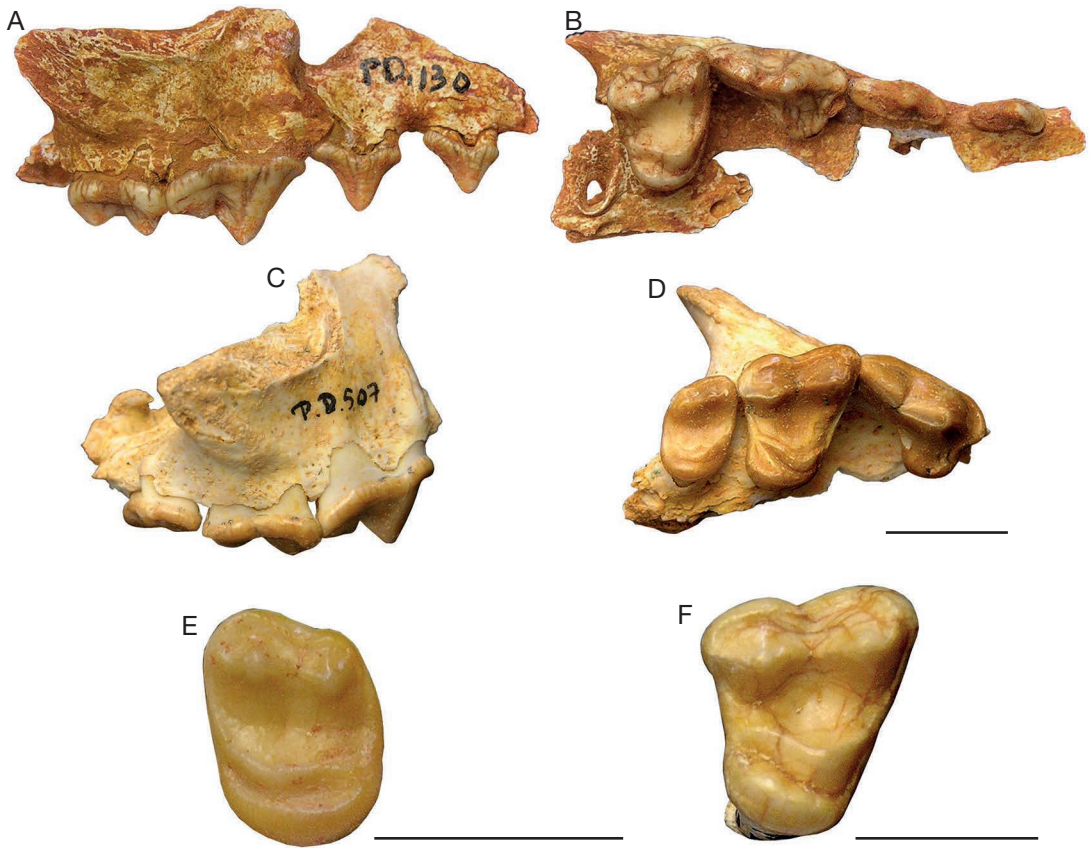


FIG. 7. — *Cyonarctos dessei* n. gen., n. sp. right maxilla PD 130: **A**, buccal view; **B**, occlusal view, right maxilla PD 507; **C**, buccal view; **D**, occlusal view, left M2 PD 514; **E**, occlusal view; right M1 PD 137; **F**, occlusal view. Compare to Figures 9 and 10. Scale bars: 1 cm.

with m1-m2, that Filhol (1877: figs 44, 45) figured as *Canis cadurcensis* Filhol, 1877. It looks like the genus *Cephalogale* (Schlosser 1888: 103; Beaumont 1965: 14). From the figure, m1 has a reduced metaconid, as noted by Filhol, and m2 has a well distinct paraconid. The size, not given by Filhol, can be estimated from the drawings (m1 length = 15.2 mm; m2 length = 8 mm). These characters may fit those of large specimens of Pech Desse. Beaumont (1965) identified a fragment of mandible from the “Phosphorites du Quercy” in the Vienna Museum with m1-m2 as *C. cadurcensis* (Beaumont 1965: 14, fig. 17) with m1 = 17.9 mm and m2 = 10.8 mm and a fragment of mandible with m2 whose length is 11.6 mm. But, insofar the type specimen is lost

and the locality is unknown, *C. cadurcensis* must be considered as *nomen nudum*.

All these species have been described from specimens coming from Europe and especially France where *Cephalogalini* n. tr. are quite common in Late Oligocene and Early Miocene layers. Nevertheless the genus *Cephalogale* has been recorded in Asia and North America.

“*Cephalogale*” *meschethense* Gabunia, 1964 from the Oligocene of the republic of Georgia does not belong to this genus. The m1 (Gabunia 1964: pl. 1, fig. 4; Gabunia 1966: fig. 4a) with a massive metaconid, long talonid and crenulated entocoid crest looks more like a derived *Amphicynodon* or *Pachycynodon* and probably belongs to a new genus of amphicynodontid.

TABLE 4. — Relative proportions of the lower teeth of some Hemicyoninae: *Cyonarctos dessei* n. gen., n. sp., *Cephalogale brevirostris* (Croizet in Blainville, 1845-1864 nec Filhol, 1879), *C. gergoviensis* Viret, 1929, *C. geoffroyi* Jourdan, 1862, *C. depereti* Viret, 1929, *C. bonali* Helbing, 1928, *C. gracile* (Pomel, 1847), *C. ursinus* Bonis, 1973, *C. ginesticus* Kuss, 1962, *C. shareri* (Wang, Hunt, Tedford & Lander, 2009) and *Zaragocyon daamsi* Ginsburg & Morales, 1995. Abbreviations: see Table 1.

Ratio × 100	p3w/p3L			p4w/p4L			p3L/p4L		
	n	range	m	n	range	m	n	range	m
Cephalogalini n. tr.		38-67	52		40-65			70-93	
<i>Cyonarctos dessei</i> n. gen., n. sp.	7	39-52	43.3	9	40-50	46.3	5	86-91	88
Quercy, old collections	25	38-52	46	29	41-55	48	17	77-93	85
<i>Cephalogale brevirostris</i> , holotype	1	59	59	1	57	57	1	75	75
<i>Cephalogale gergoviensis</i> , holotype	1	61	61	1	53	53	1	70	70
<i>Cephalogale geoffroyi</i> , holotype	1	52	52	1	55	55	1	87	87
<i>Phoberogale depereti</i>	1	46	46	3	44-48	45.7	1	75	75
<i>Phoberogale bonali</i>	2	48-52	50	2	47-53	50	2	77-82	79
<i>Phoberogale gracile</i>	3	44-51	47	7	48-55	50	3	80-97	86
<i>Cephalogale ursinus</i>	2	59-67	63	2	54-61	57.5	2	83-83	83
<i>Cephalogale ginesticus</i>	3	56-58	57	4	56-58	57	2	75-81	78
<i>Cephalogale shareri</i> , holotype	1	55	55	1	57	57	1	75	75
<i>Zaragocyon daamsi</i> , holotype	1	44	44	1	47	47	1	79	79
Ratio × 100	p4L/m1L			m2L/m1L			p4L/m2L		
	n	range	m	n	range	m	n	range	m
Cephalogalini n. tr.		51-74			50-71			91-134	
<i>Cyonarctos dessei</i> n. gen., n. sp.	6	59-67	62	5	50-60	55	5	108-123	114
Quercy, old collections	68	52-74	65	42	51-61	55	31	104-134	122
<i>Cephalogale brevirostris</i> , holotype	1	60	60	1	59	59	1	102	102
<i>Cephalogale gergoviensis</i> , holotype	1	69	69	1	70	70	1	99	99
<i>Cephalogale geoffroyi</i> , holotype cast	1	56	56	1	53	53	1	110	110
<i>Phoberogale depereti</i>	8	63-66	64	4	52-59	57	2	112-114	113
<i>Phoberogale bonali</i>	2	65-67	66	1	57	57	1	117	117
<i>Phoberogale gracile</i>	6	56-64	61	5	52-71	59	3	91-117	105
<i>Cephalogale ursinus</i>	2	51-54	52.5	2	52-56	54	2	97	97
<i>Cephalogale ginesticus</i>	4	52-55	54	5	53-59	55.6	4	92-103	96
<i>Cephalogale shareri</i> , holotype	1	55	55	1	55	55	1	99	99
<i>Zaragocyon daamsi</i> holotype	1	58	58	1	61	61	1	95	95

Cephalogale bugtiensis Forster-Cooper, 1923 was recorded from a badly preserved piece of maxilla in the Bugti beds of Pakistan dated to Oligocene and Early Miocene (Welcomme & Ginsburg 1997; Welcomme *et al.* 1997, 1999, 2001). It is larger than the Pech Desse and Pech du Fraysse specimens and has been considered as belonging to *Phoberogale* because its quite large size (Wang *et al.* 2009) but it is difficult to discuss its morphological characters and thus it could be referred to Cephalogalini n. tr., gen. indet.

The genus *Cephalogale* has been reported from several localities in North America (Hunt 1998; Qiu 2003) where a species was recently described

(Wang *et al.* 2009) as "*Phoberogale*" *shareri*. It differs from the studied Quercy ursids by its larger size, the less tall lower p4, reduced p3 relative to p4, more distally situated m1 metaconid, absence of a paraconid in m2, more posteriorly located P4 protocone, and large metaconule of M1.

Adelpharctos Bonis, 1971 does exist in the Quercy (Bonis 1971; 2011) but, by their larger size and their morphology, the two species allocated to that genus are clearly different.

Thus, the Pech Desse and Pech du Fraysse material may be distinguished from other species of *Cephalogale* or *Phoberogale* and belongs to a new species.

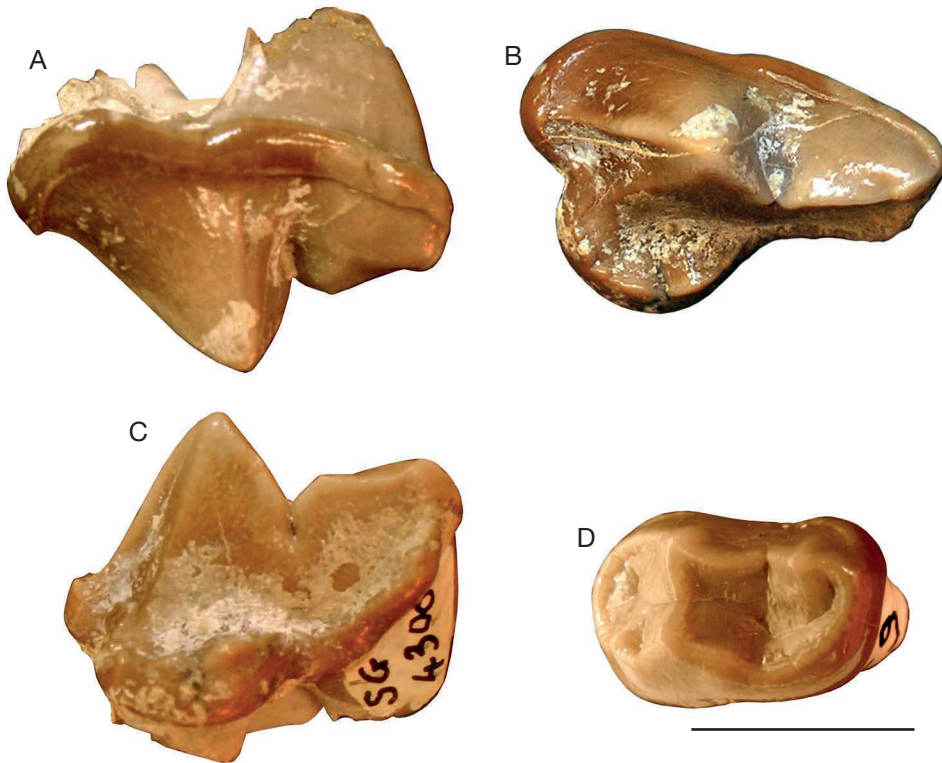


FIG. 8. — *Phoberogale depereti* (Viret, 1929), left P4 (MNHN.F.SG4300): **A**, buccal view; **B**, occlusal view; **C**, lingual view; right m2 (MNHN.F.SG13319); **D**, occlusal view. Scale bar: 1 cm.

DISCUSSION

PUBLISHED SPECIMENS

Considered first as *Canis* (Croizet in Blainville 1845-64; Gervais 1859) or *Amphicyon* (Pomel 1847), the genus *Cephalogale* was erected by Jourdan (1862). Numerous specimens were later unearthed from the “Phosphorites du Quercy” under different names but unhappily without any stratigraphic indication. Other species were described from Oligocene and Early Miocene layers. An overall view was attempted (Beaumont 1965) especially from the Quercy material and another one (Bonis 1973) distinguished different lineages in Oligocene and Early Miocene specimens. The latter “however refrained from giving generic status to these lineages, even though he did recognize that certain *Cephalogale* lineages are antecedent to more advanced hemicyonines” (Wang

et al. 2009: 769). However, Ginsburg & Morales (1995: 813) separated from the Hemicyoninae a sub-family Phoberocyoninae including *Phoberocyon*, *Plithocyon* Ginsburg, 1955 and their new genus *Phoberogale* with the following diagnosis “Ursidae with greatly developed carnassials, P4 and m1, (hypercarnivory trend) and posteriorly situated P4 protocone” (author’s translation). This diagnosis was confirmed by Ginsburg (1999) “Primitive Ursidae with large carnassials (P4, m1). The Phoberocyoninae is a small branch of the ursids showing a tendency to hypercarnivory, with enlargement of the carnassials”. The new genus, *Phoberogale* Ginsburg & Morales, 1995 was included in the Phoberocyoninae with “*Cephalogale*” *depereti* Viret, 1929 as the type species and the following diagnosis “Phoberocyoninae close to *Phoberocyon* and *Plithocyon* by the large size of the carnassials, but more primitive by the m1

structure (with a high and large hypoconid, while the lingual crest of the talonid is simple, with a low and weak entoconid)". Other species were included in the same genus: "*Cephalogale bonali* Helbing, 1928, and *Cephalogale ginesticus* Kuss, 1962. Nevertheless, the species included within the genus *Phoberogale* by Ginsburg & Morales (1995) belong to two different lineages. The type species *P. depereti* (Early Miocene, MN 2a) corresponds to a lineage including *P. bonali* (see Viret 1929; Bonis 1973). This lineage is characterised by low (lower than the m1 paraconid), elongated and quite trenchant crowns of lower premolars (see Viret 1929: 130) although very well developed cingulids amplify the width of the base of the crowns; there are developed posterior accessory cuspids in p3, p4 and sometimes p2. In fact the range of the ratio in % of the length of p4 relatively to that of m1 is 63 to 67, which is in the range of the ratios calculated for Pech Desse and Pech du Fraysse specimens and that calculated for mandibles coming from the old Quercy collections (Table 4). Thus the carnassial is large insofar the overall size is large and I consider these ratios are primitive proportions for the Hemicyoninae. The enlargement of the carnassials correlates with increase in overall size and maintains the same proportions relative to the other teeth. On the other hand, only one upper carnassial allocated to "*Cephalogale depereti*" is published (Viret 1929: pl. VII, fig. 7) and its size, like that of m1, is not impressive relatively to those of the lower premolars or that of m2; the protocone is posteriorly situated after a large notch. Thus I consider that *Phoberogale* is closer to *Cephalogale* and *Cyonarctos* n. gen. than to the Middle Miocene Hemicyonini. Moreover, *Phoberocyon aurelianensis* (Mayet, 1908), type species of the genus *Phoberocyon* (see Mayet 1908: pl. IX, fig. 3 and Ginsburg & Morales 1998: figs 26, 27), differs from *Cephalogale*, *Cyonarctos* n. gen. and *Phoberogale* by its larger size (length m1 = 34.1 to 35.8) and, in m1, by the larger height difference between paraconid and protoconid, more reduced metaconid, a larger hypoconid that reduces the size of the talonid valley and, in m2, presence of a paraconid as well as a protoconid larger than the metaconid and thus *Phoberogale depereti* is clearly different from the phoberocyonines.

The other species allocated to *Phoberogale* by Ginsburg and Morales is *Cephalogale ginesticus* Kuss, 1962 from the Early Miocene (MN 1) localities of Ginestous and Paulhiac (Kuss 1962; Bonis 1973). However, this species belongs to another lineage different from that which likely ends with *Phoberogale depereti*. It is characterized by quite low but short and simple lower premolars separated by large diastemas. The size of m1 is large relative to p4 but not relative to m2 (Table 4). *C. ginesticus* is close, concerning its morphology and proportions, to *Cephalogale geoffroyi*, type species of the genus and I propose to include both species in the genus *Cephalogale*. *C. ursinus* from Paulhiac and *C. brevirostris* from Cournon have the same pattern of premolars and quite the same proportions; the former is more derived by the reduced metaconid of m1 and the m2 without paraconid and with a long talonid, exactly as the larger *C. ginesticus*. *Cephalogale gergoviensis* Viret, 1939 has also robust premolars like the other species of *Cephalogale* but without diastema and with a relatively longer m2; nevertheless it seems closer to *Cephalogale* than to other Cephalogalini n. tr.

The genera *Cephalogale*, *Cyonarctos* n. gen. and *Phoberogale* occurred in a time slice ranging from MP 21 (about 34-33 Ma) to MN 2a (about 22-20.5 Ma), in other words the whole Oligocene and beginning of the lower Miocene. The specimens from the "Phosphorites du Quercy" are certainly heterogeneous. On one hand, they group several lineages and, on the other hand, the representatives of these lineages have probably been modified through time. But nonetheless, the set of fossils coming from the Quercy contains old and primitive specimens together with more derived ones yet, as a whole, it may approximately indicate the primitive features and proportions of the Cephalogalini n. tr. Shape and proportions of the teeth (Tables 4, 5) play a significant role in biting and feeding in Carnivora and allow us to establish precise relationships between the species. Taking into account the lower premolars, we see that the p3 from the Quercy specimens, old and new collections, of which geologic age extends from MP 21 to MP 28, are quite thin with a ratio width/length ranging from 38 to 52. Similar values are found in the group *P. depereti*,



FIG. 9. — *Phoberogale gracile* (Pomel, 1847), Maxilla (MNHN.F.SG355); **A**, occlusal view; **B**, occlusal view; **C**, buccal view. Scale bar: 1 cm.

P. bonali and *P. gracile*. More robust p3s are found in *C. brevirostris*, *C. ginesticus*, *C. ursinus*, “*Phoberogale*” *shareri* and especially *C. gergoviensis*, *C. geoffroyi* being at the limit. The same results are found for p4 but *C. gergoviensis* and *C. geoffroyi* are closer to the first group but we must take into account the robust cingulids in *Phoberogale* which amplify the breadth of the crowns while the upper parts of the crowns are quite thin. For the ratio p3 length/p4 length, the set which probably includes the primitive ratios (77 to 93) is found in the Quercy samples while some species have a reduced p3 length relative to p4, especially *C. gergoviensis*, *P. depereti* and “*Phoberogale*” *shareri*. The m1 length compared to that of p4 indicates quite long premolars in the

Quercy samples with a large range of variation; the same values are found in *P. depereti*, *P. bonali* and, in a lesser extent, *Phoberogale gracile*, *C. gergoviensis* having the larger p4 relatively to m1. The p4 is shorter relatively to m1 in *C. ginesticus*, *C. ursinus* and “*Phoberogale*” *shareri*. The ratio concerning m2 relative to m1 is quite similar (50 to 60) in all the species except *C. gergoviensis* which is characterized by a very long m2. If we compare p4 to m2, we note that the Quercy specimens have a p4 longer than m2 (ratio = 104 to 134). Quite long p4s relative to m2 do exist in *P. depereti*, *P. bonali*, *P. gracile* and *C. geoffroyi* while other species have shorter p4 relative to m2. Nevertheless the three former species have a similar p4 shape (low crowns with

TABLE 5. — Relative proportions of the upper teeth of some Hemicyoninae: *Cyonarctos dessei* n. gen., n. sp., *Cephalogale brevirostris* (Croizet in Blainville, 1845-1864 nec Filhol, 1879), *C. geoffroyi* Jourdan, 1862, *P. depereti* (Viret, 1929), *P. gracile* (Pomel, 1847), *C. "ursinus"* Bonis, 1973, *C. ginesticus* Kuss, 1962, "*C.*" *bugtiensis* Forster-Cooper, 1923, *C. shareri* (Wang, Hunt, Tedford & Lander, 2009) and *Zaragocyon daamsi* Ginsburg & Morales, 1995 and. Abbreviations: see Table 1.

Ratios × 100	P2w/P2L			P3w/P3L			P4w/P4L			P3L/P4L		
	n	min-max	mean	n	min-max	mean	n	min-max	mean	n	min-max	mean
<i>Cyonarctos dessei</i> n. gen., n. sp.	1	33	33	2	38-45	41.5	9	59-73	64	2	63-65	64
Quercy old collections	2	36-43	38.5	3	42-50	46	16	62-71	64.75	3	59-71	66
<i>C. brevirostris</i>							1	65	65			
<i>C. geoffroyi</i> cast	1	54	54	2	53-55	54	1	64	64			
<i>P. depereti</i>							1	63	63			
<i>P. gracile</i>				2	48-50	49	4	56-67	62.5	1	67	67
<i>C. "ursinus"</i>							1	64	64			
<i>C. ginesticus</i>	1	47	47	1	54	54	1	63	63	1	53	53
" <i>C.</i> " <i>bugtiensis</i>							1	64	64			
<i>C. shareri</i>	1	50	50	1	54	54	1	60	60	1	51	51
<i>Zaragocyon daamsi</i>							1	68	68			
Ratios × 100	M1L/P4L			M1dw/M1mw			M1L/M1mw			M2L/M2w		
	n	min-max	mean	n	min-max	mean	n	min-max	mean	n	min-max	mean
<i>Cyonarctos dessei</i> n. gen., n. sp.	4	71-82	77.5	14	80-92	86	18	68-85	77.5	5	58-73	63
Quercy old collections	8	69-81	75	11	83-97	90	12	72-89	82	7	49-72	62
<i>C. brevirostris</i>	1	81	81	1	89	89	1	86	86	2		
<i>C. geoffroyi</i> cast	1	84	84	1	95	95	1	84	84	2	69-80	74.5
<i>P. gracile</i>	2	80-83	81.5	2	93	93	5	86-94	90	2	61-93	77
<i>C. "ursinus"</i>	1	79	79	1	99	99	1	87	87	1	67	67
<i>C. ginesticus</i>	1	68	68	1	94	94	2	88-88	88	1	75	75
" <i>C.</i> " <i>bugtiensis</i>	1	73	73	1	96	96	1	85	85	1	61	61
<i>C. shareri</i>	1	78	78	1			1	91	91	1	77	77
<i>Zaragocyon daamsi</i>	1	89	89	1			1	91	91	1	77	77

a developed pad) and belong to *Phoberogale*. The Californian "*Phoberogale*" *shareri*, despite a small pad in p4, is closer to *C. brevirostris*, *C. gergoviensis*, *C. ginesticus* and *C. ursinus* for p3 proportions, to *C. brevirostris*, *C. ginesticus* and *C. ursinus* for p4 proportions and thus to what I consider as the genus *Cephalogale*, although the type species of the genus, *C. geoffroyi*, has ratios which are at the limit between the two groups.

The upper dentition remains are quite scarce but nevertheless provide an additional perspective from the measurements (Table 5). P2 and P3 are relatively narrow in the Quercy samples and, also for P3 in *P. gracile*, whereas these teeth are robust in *C. geoffroyi*, *C. ginesticus* and *C. shareri*. The proportions of P4 do not differ very much in the studied species which are within the range of the

Quercy material but we note that P3 is shortened relative to P4 in *C. ginesticus* and *C. shareri*. The ratio M1L/P4L varies from 69 to 82 in the Quercy samples and there are the same values for the other specimens, particularly *C. ginesticus* which was put into the genus *Phoberogale* because the so-called preponderant P4. The shape of M1 may be estimated by the index total length/mesial width which ranges from 68 to 89 in the Quercy samples. The upper range of variation in this trait occurs in the Early Miocene species, especially *C. shareri*, indicating a trend to a much longer M1 relatively to its width. Another ratio for M1 could be the ratio between distal width divided by mesial width for which values range from 80 to 97 in the Quercy and from 94 to 99 in the Early Miocene specimens indicating, possibly, another trend toward a more



FIG. 10. — *Phoberogale* cf. *bonali* (Helbing, 1928), left maxilla MNHN.F.QU9290; **A**, occlusal view; **B**, buccal view; **C**, lingual view. Scale bar: 1 cm.

quadratic occlusal outline. Finally, the ratio M2L/M2w varies from 49 to 73 in the Quercy samples and reaches 75 (*C. ginesticus*) and 77 (*C. shareri*) indicating that a high ratio is probably a derived character of these younger species.

In summary *C. brevirostris*, *geoffroyi*, *ursinus* and *ginesticus* comprise a group that constitutes the genus *Cephalogale*. Out of Europe, *C. shareri* seems quite close to this group by most of its characters, justifying its place in *Cephalogale*. *Phoberogale*, with the species *depereti*, *gracile*, *bonali* and *minor*, constitutes another group parallel to the first one.

UNPUBLISHED SPECIMENS

Some new unpublished specimens coming from the collections of the MNHN Paris allow a better knowledge of some lineages. A large (19.7/12.5 mm) upper P4 from Saint Gérard-le-Puy (MNHN.F.SG4300) belongs certainly to *Phoberogale depereti* (Fig. 8A-C). It is characterized by a thick buccal cingulum, large

basined protocone posteriorly situated and separated by a large notch from the mesial surface of the paracone. Its proportions are similar to those of *Cephalogalini* n. tr. species (Table 5). A large (12/8.8 mm) lower m2 (MNHN.F.SG13319) belongs to the same species and is particularly well preserved (Fig. 8D); it shows a reduced trigonid basin without paraconid, a metaconid slightly higher than the protoconid, a blunt crest along the distal surface of the protoconid separated by a narrow notch from a bulbous hypoconid; the same crest, distal to the latter, closes distally the talonid basin, and continues to the distal base of the metaconid.

A maxilla from Saint Gérard-le-Puy with right P3 and M1, left P3-P4 and alveoli of the other cheek teeth (MNHN.F.SG355) corresponds to *Phoberogale gracile* (Fig. 9). P1 is single-rooted, P2 and P3 are double rooted; the latter has a low asymmetric crown encircled by a robust cingulum; there is no pac but a sharp crest runs from the apex to the distal base;

the shape of P3, thin and elongated, fits with that of the lower premolars of *P. gracile* as well as with those of *P. depereti*. The robust P4 (14.4/9.5 mm) is also surrounded by a robust cingulum; the basined protocone is large, set off and separated by a large notch from the mesial base of the paracone without parastyle, the metastyle is not elongated. Morphologically the P4 does not differ from that of *Phoberogale depereti*. M1 is a little worn and eroded by weathering. It is surrounded by a cingulum, thicker in the disto-lingual part; there is a probably present but badly preserved distal metaconule.

Another left maxilla with P3-M2 from the "Phosphorites du Quercy" (MNHN.F.QU9290) seems to be a witness of the occurrence of the genus *Phoberogale* in these localities (Fig. 10). P3 is low, elongated with a very well marked cingulum, two acute crests, mesial and distal, run from the apex to the base, the former turning a little lingually. P4 is robust with a well developed cingulum, a thin mesial crest on the mesial face of the paracone, without parastyle, the protocone separated from the mesial paracone by a notch is distally offset but less than in the Saint Gérard-le-Puy specimens. M1 has a clear buccal and a large lingual cingulum; the metaconule is well developed. M2 is ovoid with robust buccal and wide lingual cingula, paracone far larger than metacone, both close together, J shaped protocone, with a long mesial branch joining the mesio-buccal corner and a short distal one ending by a small metaconule. The morphological characters of this specimen fit quite well those of *Phoberogale* and it may be identified as *Phoberogale* cf. *bonali*.

STATUS OF SOME SPECIES

There is also in the MNHN collection, a mandible (MNHN.F.QU9316) which is identified by manuscript notes of R. Lavocat and L. Ginsburg as *Cephalogale* aff. *bonali* which could be also a representative of the genus *Phoberogale* within the Quercy specimens. In fact, the lectotype of "*Cephalogale*" *minor* (MNHN.F.QU9316) is a mandible which also bears characteristics of this genus (Bonis 1973: 83, fig. 22; Filhol 1882: pl. V, figs 1-3) and its name must become *Phoberogale minor* (Filhol, 1882). It differs from other

species of *Phoberogale* by less cuspidated p2-p3, less reduced metaconid of m1 and small paraconid in m2.

Some different described species are separated by the size and shape of teeth, but we note that two species, large *C. gineasticus* and small *C. ursinus* with quite the same morphological characters, are recorded in the Early Miocene (MN 1) locality of Paulhiac and two others, the large *P. depereti* and small *P. gracile*, in the MN 2a locality of Saint Gérard-le-Puy. *P. depereti* and *P. gracile* share a similar premolar morphology (low, elongated, cuspidated thin premolars and robust cingulids and cinguli). Taking into account the large size differences in the samples from Pech Desse and Pech du Fraysse, we may ask if there are really two species in Paulhiac and Saint Gérard-le-Puy. The SDI 1 (Fig. 2) and SDI 2 (Table 3) for the entire sample from Paulhiac are 10 and 75 respectively; the former is similar to that of a population of the extant *Ursus arctos* (2 to 10) and the latter is compatible with a one species hypothesis. Thus I propose to put all the specimens from Paulhiac in the species *C. gineasticus* Kuss, 1962. For Saint Gérard-le-Puy the same values are respectively 14, which is one of the largest value of our comparative sample, just between *Mustela erminea* Linnaeus, 1858 and *Catopuma temmincki* (Vigors & Horsfield, 1827), and 62 which is lower than the lowest value of the comparison sample, *Vulpes chama* (A. Smith, 1833), and does not favour a single species hypothesis. Actually it is probably better to consider that these species are really separated but more material would be necessary to confirm this hypothesis. But in the case of a single species hypothesis, *Phoberogale gracile* (Pomel, 1847) would have priority on *P. depereti* (Viret, 1929).

The place of *Zaragocyon* Ginsburg & Morales, 1995 is quite puzzling. It seems to be in-between Cephalogalini n. tr. and Hemicyonini-Phoberocyonini. It shares with the former the lower premolars similar to those of *Cephalogale*, the same degree of reduction of the m1 metaconid, the same ratio of p4 relative to m2, a quite similar P4 protocone (size and place). It principally shares with the latter long m2 relative to m1, and principally the U-shaped M1 (more triangular in Cephalogalini n. tr.) with a very well developed metaconule and

the M2 elongated and U-shaped. In both molars, elongation involves the lingual part of the teeth.

The mandible with p2-m3 described as *Canis filholi* Munier-Chalmas by Filhol (see above) has been reported to the genus *Cephalogale* (Schlosser 1888; Trouessart 1904-1905; Bonis 1973). I think that this is a representative of a quite primitive hemicyonine different from *Cephalogale* and belonging to a new genus.

CONCLUSIONS

The localities Pech Desse and Pech-du-Fraysse allow for the first time an estimate of the range of the size variation within a species of Cephalogalini n. tr. and complete the morphological description of the tribe. From comparisons with extant species, we see that there is a large range of size within an Oligocene ursid which constitutes a new species, *Cyonarctos dessei* n. gen., n. sp. The relatively abundant material coming from these localities also makes possible a reappraisal of other species coming from other localities. Thus *Cephalogale ursinus* from Paulhiac is considered as a junior synonym of *C. ginesticus* and, probably, *Phoberogale depereti* may be a synonym of *P. gracile*, both species from Saint Gérard-le-Puy.

The Cephalogalini n. tr. are known from MP 21 in Central Europe (Fejfar & Kayser 2005) to MN 2a in Western Europe where they are quite common in strata of the Late Oligocene and first part of the Early Miocene. Nevertheless they are absent in the rich MN 2b locality of Laugnac (Bonis 1973). I think that this absence may indicate a time close to that of the extinction of the tribe in Europe despite the record of *Cephalogale ginesticus* together with *Zaragocyon* in Cetina de Aragon (Early Miocene, MN 2). The appearance of the other Hemicyoninae (Hemicyonini-Phoberocyonini) in Europe did not occur before MN 3 with principally *Phoberocyon* (Wintershof-West, La-Brosse, Chitenay), *Hemicyon* (Wintershof-West, Tuchorice) and *Plithocyon* (Chitenay). *Phoberocyon hispanicus* Ginsburg & Morales, 1998, which would be the oldest and more primitive species of the genus, comes from the locality of Loranca,

Spain, which is dated to MN 2 (Ginsburg & Morales 1998). Nevertheless this hemicyonine is accompanied in Loranca by a mammalian fauna including some species that have been recorded in more recent localities: *Andegameryx laugnacensis* in Espira-du-Conflans (MN 3), *Xenohyus venitor* in Beilleaux, Chitenay, Estrepouy, La Brosse, Pontigné-les-Buissonneaux (MN 3) and Lisboa V (MN 4), *Protaceratherium minutum* in localities dated from MN 1 to MN 4. Moreover, in other Miocene localities, *Leptoplesictis aurelianensis* is found from MN 4-5 (Vieux-Collonges) to MN 7-8 (Anwil), *Pseudaelurus (Styriofelis) turnauensis* is recorded from MN 3 (La Brosse, Mauvière) to MN 10 (Khalifa) through Sansan and Göriach (MN 6), *Brachyodus onoideus* is never recorded before MN 3, its arrival in Europe coinciding with the immigration of the equid *Anchitherium* coming from North America although this latter genus is absent in Loranca which is probably close to the limit MN 2-MN 3 but probably in the earliest MN 3. On the other hand *Zaragocyon* comes from the MN 2 locality of Cetina de Aragon and could be considered as the last derived Cephalogalini n. tr. or the first known Hemicyonini in Europe, a forerunner of the MN 3 migration.

The Hemicyonini are well known from the exhaustive revision of Ginsburg & Morales (1998). They differ from the Cephalogalini n. tr. by their larger size and more derived characters (relatively larger m1 with more reduced metaconid, longer talonid of m2, more distally off-set protocone of P4, longer M1-M2). The polarity of two other characters is less clear. Normally the presence of the paraconid in m2 is primitive but this cuspid is sometimes absent in Cephalogalini n. tr. and Amphicyonodontidae (Ciroit & Bonis 1992) thus its presence in Phoberocyonini (Ginsburg & Morales 1998) might be an ancestral preserved feature (and this group is distinct from all the other ones) or it is a reversion and thus a synapomorphy of the Phoberocyonini. The metaconid of m2 as high or higher than the protoconid is a synapomorphy linking Amphicyonodontidae and Cephalogalini n. tr.; the higher m2 protoconid in Hemicyonini and Phoberocyonini may be a reversion and also a synapomorphy of these tribes.

By their respective sizes and the characteristics of their dentitions, the species of the genera *Cyonarctos* n. gen., *Cephalogale* and *Phoberogale* occupied, in the European Oligocene and earliest Miocene, ecological niches close to those of some extant Canidae from foxes to jackals or coyotes. The jaws display a balance between shearing and chopping teeth like in canids and the symphyseal plate is similar to that of the wolf as we can observe in the Pech Desse material. The material is abundant relatively to other carnivorans in Pech Desse and Pech du Fraysse and may indicate that these Cephalogalini n. tr. were numerous and lived in packs. Nowadays, many canids are pack hunters and possibly it was the same for the Cephalogalini n. tr. which were long-legged “carnivores adapted for open-country predation [...] digitigrade hemicyonine ursids” (Hunt 2009: 4), and the hemicyonines were “[...] long-footed ursids with well adapted running ability and carnivorous dentition [...] hemicyonines paralleled the cursorial predatory canids [...]” (Hunt 1996: 493).

A faunal change occurred in Europe at the limit MN 2-MN 3 when new genera and species arrived from North America and Asia. It seems that the Cephalogalini n. tr. were replaced in their ecological niches which became occupied in the Late Early and Middle Miocene by small amphicyonids (*Pseudarctos* Schlosser, 1888 and *Ictiocyon* Crusafont, Villalta & Truyols, 1955) and small Ursinae (*Ballusia* Ginsburg & Morales, 1998 and *Ursavus* Schlosser, 1888).

In Asia, there are few records of Cephalogalini n. tr. (Qiu 2003). The Early Oligocene Bugti maxilla (Forster-Cooper 1928) seems to belong to a large *Cephalogale* with a quite long P4 relatively to M1, the ratio being the smaller of our samples. Another specimen from the Early Oligocene of Saint Jacques (China), an isolated upper M2, is published as *Cephalogale* sp.; it corresponds by the size and morphology to the smaller M2 from the Quercy (Wang & Qiu 2003). Other *Cephalogale* remains from the Mongolian Hsanda Gol Formation are mentioned in an unpublished manuscript (Wang *et al.* 2009).

Cephalogale has been reported in North America in Late and latest Arikareean and Early Heming-

fordian, 21 and 19 Ma old respectively (Tedford *et al.* 1987; Hunt 1998; Whistler & Lander 2003; Hunt 2004) and, from southern California, a new species was described, *Cephalogale shareri*. This species comes from a level estimated to be latest Arikareean (Wang *et al.* 2009: 764), however of uncertain exact age, possibly occurring within the 20-22 Ma interval. This occurrence may be close to the limit between MN 2/MN 3 in Europe, when the Cephalogalini n. tr. were disappearing. It is approximately also the time when Hemicyonini or Phoberocyonini occurred in Western Europe. In North America the oldest American *Phoberocyon* is recorded around 17-18 Ma (Tedford *et al.* 2004: 186) in the Thomas Farm locality, Florida (White 1947; Tedford & Frailey 1976).

The hemicyonines are unknown before the Oligocene. We don't know any species which could be close to the roots of Hemicyoninae in the New World where the Eocene fauna are quite well known. The sub-family occurred in Europe in the earliest Oligocene together with the Amphicyonodontidae. It is the same for Africa insofar “The order Carnivora has a shorter history in Africa than on any other continent except Australasia and South America” (Werdelin & Peigné 2010: 603). Despite the scarcity of Asiatic data, the hypothesis of an Asiatic origin is highly probable.

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