

First record of immigrant *Phoberogale* (Mammalia, Ursidae, Carnivora) from Southern California

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ABSTRACT

Phoberogale Ginsburg & Morales, 1995, is a primitive ursid named to separate hypercarnivorous species from a rather heterogeneous group formerly included in the genus *Cephalogale* Jourdan, 1862. The presence of *Cephalogale* (*s.l.*) in the Great Plains of the United States has been documented since the late 1980s, often in the context of immigrant taxa and Neogene biochronology. However, no formal description or illustration of the respective specimens was published. Recently, an

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associated skull and left dentary were recovered from an early Miocene terrestrial deposit in southern California. We take this opportunity to describe the California specimen, which represents a new species, *Phoberogale shareri* n. sp. This new species belongs to the *Phoberogale-Phoberocyon* lineage and is distinguished from species of *Cephalogale* (*s.s.*) by its larger size, less-reduced pre-carnassial premolars, and less-elongated M2. Within the genus *Phoberogale*, *P. shareri* n. sp. is more derived than European species (*P. bonali*, *P. depereti*, *P. ginesticus*) as indicated by its larger size and more differentially enlarged p4 compared to the p3. It differs from Pakistani *P. bugtiensis* in having a less prominent notch between the anterior base of the P4 paracone and protocone, a more distinct anterior ridge on the P4 paracone, and more mediolaterally shortened M1-2. *Phoberogale shareri* n. sp. represents the first known Pacific Coast occurrence of this lineage and has important zoogeographic and biochronologic implications.

RÉSUMÉ

Première trace de l'immigrant *Phoberogale* (Mammalia, Ursidae, Carnivora) en Californie du sud.

Phoberogale Ginsburg & Morales, 1995 est un genre d'ursidés primitifs créé pour distinguer les espèces hypercarnivores d'un groupe assez hétérogène intégré auparavant dans le genre *Cephalogale* Jourdan, 1862. La présence de *Cephalogale* (*s.l.*) dans les Grandes Plaines des États-Unis a été documentée dès la fin des années 80, souvent à propos de taxons immigrants et de la biochronologie du Néogène, mais aucune description formelle ou illustration des spécimens n'a été publiée. Depuis, un crâne associé à un dentaire gauche a été découvert dans des dépôts continentaux du Miocène inférieur de Californie méridionale. Nous profitons de cette opportunité pour présenter les spécimens de Californie, qui représentent une nouvelle espèce, *Phoberogale shareri* n. sp. Cette nouvelle espèce appartient à la lignée *Phoberogale-Phoberocyon* et se distingue des espèces de *Cephalogale* (*s.s.*) par une plus grande taille, des prémolaires pré-carnassières moins réduites et une M2 moins allongée. Au sein du genre *Phoberogale*, *P. shareri* n. sp. est plus dérivé que les espèces européennes (*P. bonali*, *P. depereti*, *P. ginesticus*) comme le montrent sa plus grande taille et une différence de taille plus nette entre p4 et p3. Elle diffère de *P. bugtiensis* du Pakistan par une encoche moins proéminente entre les bases antérieures du paracône et du protocône de P4, une crête antérieure du paracône de P4 plus distincte et des M1-2 moins élargies médiolatralement. *Phoberogale shareri* n. sp. représente la première apparition connue de cette lignée sur la Côte pacifique, ce qui a des implications zoogéographiques et biochronologiques importantes.

MOTS CLÉS

Mammalia,
Carnivora,
Ursidae,
système,atique,
zoogéographie,
Miocène,
Californie,
espèce nouvelle.

INTRODUCTION

The genus *Cephalogale* Jourdan, 1862 *s.l.*, (including *Phoberogale* Ginsburg & Morales, 1995), is a medium- to large-sized arctoid carnivore generally regarded as an early member of the Family Ursi-

dae. It is characterized by its cursorial adaptations, such as digitigrade posture, and hypercarnivorous dentition, in contrast to extant ursids that are all plantigrade and possess the most hypocarnivorous teeth known in the Order Carnivora (Hunt 1998a; Ginsburg 1999). Such a tendency toward curso-

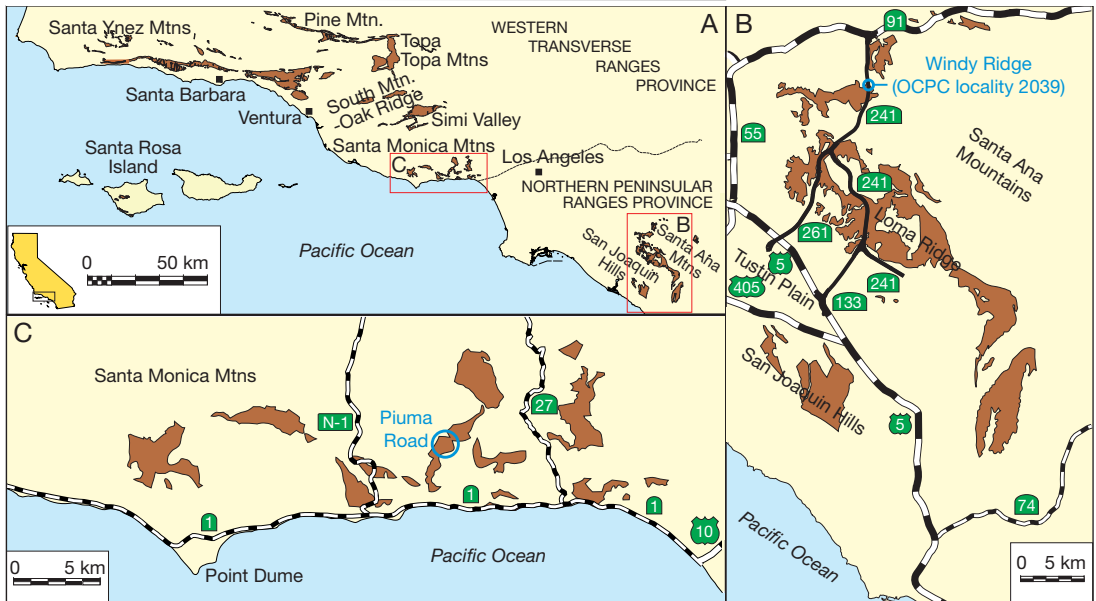


Fig. 1. — Location of ETC Windy Ridge (OCPC 2039) and Piuma Road localities, and exposures of Sespe Formation (shaded) in southern California. Modified from Calvano *et al.* (2008).

rial locomotion in *Cephalogale* might be linked to its widespread geographic distribution. Indeed, beyond its original discovery in Europe, where up to 10 species have been described in the Oligocene through early Miocene (Bonis 1973), an early Miocene species is also known from Pakistan (Forster-Cooper 1923). More recently, hints of its existence in Oligocene strata of Georgia, Mongolia, and China also have begun to surface (Gabuniya 1964, 1966; Wang & Qiu 2003; Wang *et al.* 2005), suggesting a pan-Eurasian distribution. As better records become available from Asia, additional discoveries will likely follow.

Despite its wide distribution, *Cephalogale* had not been reported in North America until quite recently. It is perhaps not surprising, even logical in hindsight, that Tedford *et al.* (1987) announced the existence of *Cephalogale* in the New World and used its first appearance as an immigration event to define the late Arikareean North American Land Mammal Age (NALMA) (Ar3 of Tedford *et al.* 2004: fig. 6.3). Its New World presence was further documented by Hunt (1998a) in his summary of North American fossil ursids (see also Hunt 2004).

Based on dental dimensions, yet providing no detailed description, Hunt (1998a) noted that there are possibly three species from the late Arikareean and early Hemingfordian of Nebraska, Wyoming, and New Mexico in the United States, based on specimens in the Frick Collection at the American Museum of Natural History (F:AM) and in the University of Nebraska State Museum (UNSM), and that some North American forms are larger than the European species.

So far, no record of *Cephalogale* is known west of the Continental Divide, despite its apparently widespread presence east of the Rocky Mountains. It is thus significant that an agency-mandated paleontologic mitigation program in the Santa Ana Mountains of Southern California (Fig. 1) resulted in the recovery of a well-preserved skull and left dentary of *Phoberogale* Ginsburg & Morales, 1995, a genus recently erected to encompass hypercarnivorous species formerly included in the rather heterogeneous *Cephalogale*. The associated skull and ramus from Southern California represent the only such specimen of its kind in North America and, therefore, are appropriate as the holotype of a

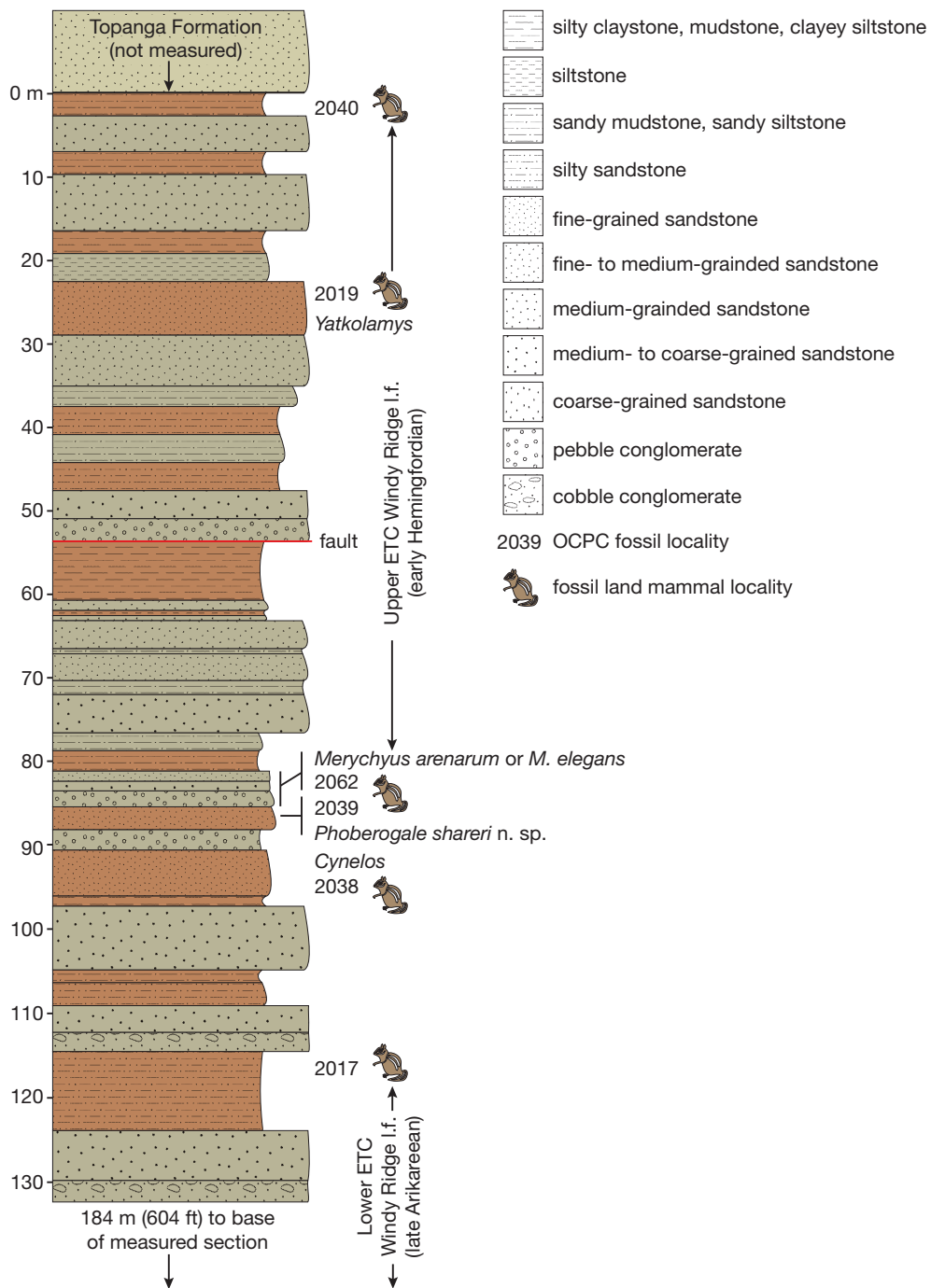


FIG. 2. — Stratigraphic column of ETC Windy Ridge section. After Lander (2003: pl. 10). Colors are simplified approximations of the original colors observed in outcrops of the formation.

new species, *P. shareri* n. sp. We dedicate this paper to a festschrift volume in honor of Professeur Louis de Bonis, a long-time colleague and a preeminent expert on fossil carnivores, including *Cephalogale*.

MATERIAL AND METHODS

In this paper, we provide a detailed description of the unique Southern California specimen of *Phoberogale*. Although we make occasional reference to other North American specimens from east of the Continental Divide, those specimens, much more numerous in the F:AM and the UNSM collections, will be described elsewhere. For comparative purposes, we examined selected examples of *Cephalogale* and *Phoberogale* from the classic collections of the Quercy district housed in the Naturhistorisches Museum Basel, the British Museum of Natural History, and the Muséum national d'Histoire naturelle in Paris, as well as the more recent, stratigraphically controlled collections in the Université de Poitiers. For Asian specimens, we examined the holotype of *Phoberogale bugtiensis* Cooper, 1923 and had access to an unpublished manuscript on new specimens of *Cephalogale* from the Hsanda Gol Formation of Mongolia.

ABBREVIATIONS

BMNH	British Museum of Natural History, London;
ETC	Eastern Transportation Corridor, California;
F:AM	Frick Collection, American Museum of Natural History, New York;
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing;
l.f.	local fauna;
MAE	Collections of the joint Mongolian Academy of Sciences – American Museum of Natural History Paleontological Expeditions, currently housed in American Museum of Natural History, New York;
MN	European Neogene mammal zone/unit;
MP	European Paleogene mammal zone/unit;
NALMA	North American Land mammal Age;
OCPC	Orange County Paleontological Collection, County of Orange, Resources and Development Management Department, Santa Ana, California;
SR	State Route;
UNSM	University of Nebraska State Museum, Lincoln, Nebraska.

SYSTEMATICS

Order CARNIVORA Bowdich, 1821
 Infraorder ARCTOIDEA Flower, 1869
 Parvorder URSIDA Tedford, 1976
 Superfamily URSOIDEA
 Fischer de Waldheim, 1817
 Family HEMICYONINAE Frick, 1926
 Subfamily PHOBEROCYONINAE
 Ginsburg & Morales, 1995
 Genus *Phoberogale* Ginsburg & Morales, 1995

Phoberogale shareri n. sp.
 (Figs 3-5; Tables 1; 2)

Cephalogale sp. – Whistler & Lander 2003: 256.

HOLOTYPE. — OCPC 21794 and 21795, rostral part of skull missing tip of inion and much of basicranial region, but with complete upper dentition except right P1, and nearly complete left dentary with c-m2 and m3 alveolus; field number BMM111396.1; collected by Brett M. Malas, Raytheon Infrastructure Services, Inc., December 29, 1995. Although the skull (21794) and dentary (21795) were catalogued with separate numbers, they belong to the same individual, based on their recovery at the same locality and the similar size relationships and stages of wear of their teeth.

ETYMOLOGY. — In honor of Mr Kevin W. Sharer for his leadership as Chairman of the Board of Trustees at the Natural History Museum of Los Angeles County.

TYPE LOCALITY. — OCPC 21794-5 were collected as a result of mitigation activities conducted in support of grading for the Eastern Transportation Corridor (ETC) highway construction project (Lander 2003). The type locality, OCPC locality 2039, is in the northern (ETC Windy Ridge) segment of SR 241, about 8.2 km south of its intersection with State Route 91 (Riverside Freeway) and north of its intersection with SR 261 in sec. 23 T.4S. R.8W. (33°49'34"N/117°42'52"W) in the northern Santa Ana Mountains of Orange County, coastal southern California (Fig. 1).

DIAGNOSIS. — *Phoberogale shareri* n. sp. is easily distinguished from "*Cephalogale*" *minor* Filhol, 1879 [Filhol 1879] by its much larger size, enlarged P4 and m1, posteriorly located P4 protocone, and differentially enlarged p4 relative to p3. It differs from species of *Cephalogale* (*C. geoffroyi* Jourdan, 1862, *C. ursinus* Bonis, 1973, *C. brevirostris* (Croizet, 1836) [Croizet 1836]) in its larger size and primitively less reduced pre-carnassial premolars and less elongated M2. Within the

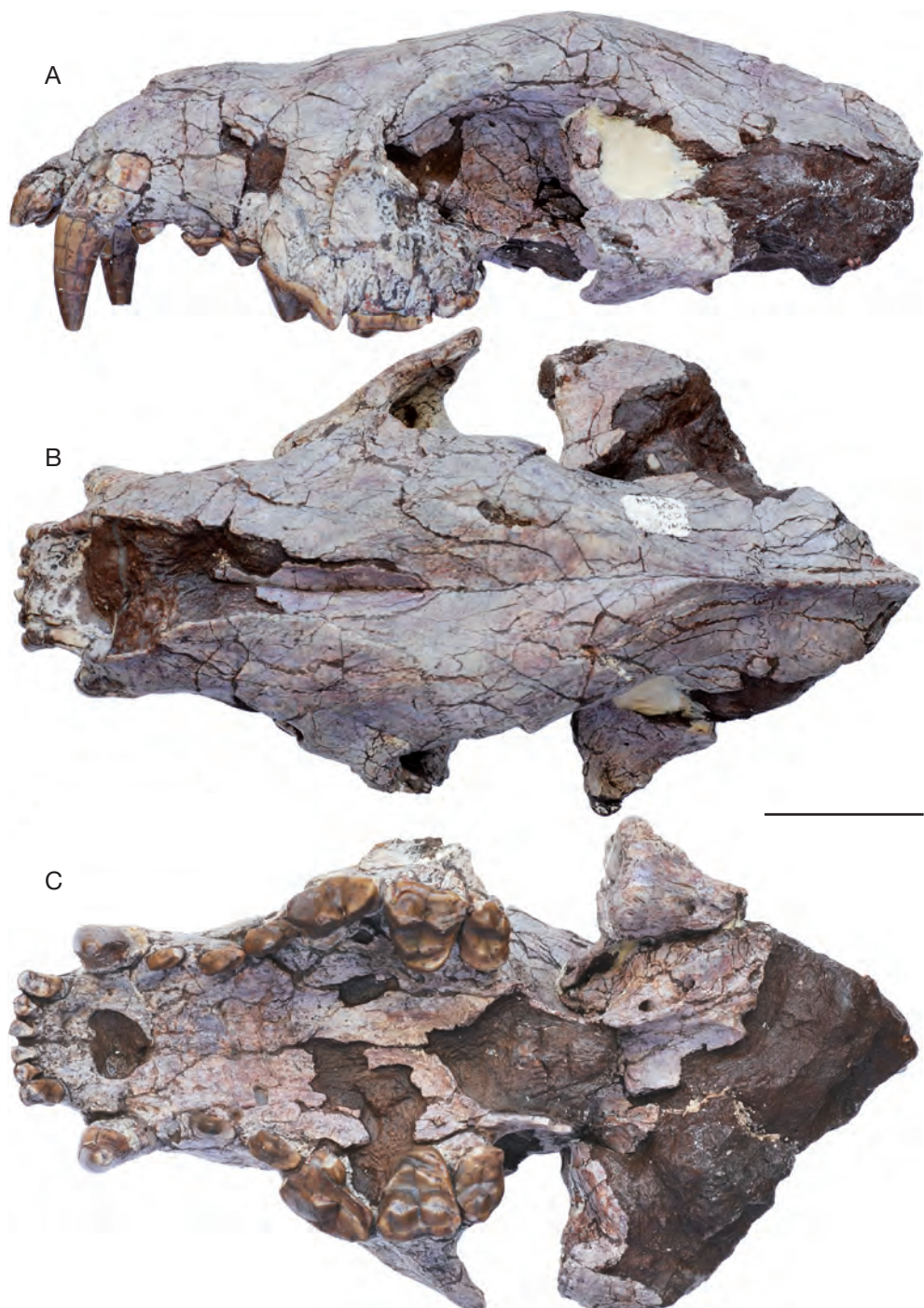


FIG. 3. — *Phoberogale shareri* n. sp., OCPC 21794, holotype (associated with OCPC 21795) from ETC Windy Ridge locality, Orange County, California; lateral (A), dorsal (B), and ventral (C) views of partial skull. Scale bar: 30 mm.

TABLE 1. — Dental measurements (in mm) of *Phoberogale* species. Those for *P. bonali* Helbing, 1928 are from Helbing (1928); those for *P. depereti* Viret, 1929 from Beaumont (1965); those for *P. ginesticus* Kuss, 1962 from Kuss (1962).

	<i>P. shareri</i> n. sp.	<i>P. bugtiensis</i>	<i>P. bonali</i>	<i>P. depereti</i>	<i>P. ginesticus</i>
C1 length	10.2				
C1 width	8.8				
P1 length	7.1				
P1 width	3.7				
P2 length	8.8				
P2 width	4.4				
P3 length	10.3				
P3 width	5.6	4.9			
P4 length	20.3	21.1			
W4 width	12.9	12.7			
M1 length	15.8	15.5		15.0	
M1 width	17.4	18.2		16.5	
M2 length	10.1	9.4			
M2 width	13.1	14.5			
c1 length	10.9				
c1 width	7.6				
p1 length	6.5				
p1 width	3.3				
p2 length	8.3		9.0		
p2 width	5.1		5.0		
p3 length	10.0		10.0		
p3 width	5.5		5.5		
p4 length	13.4		12.7	13.0	11.5
p4 width	7.5		7.0		6.5
m1 length	24.6		19.2	19.8	22.0
m1 width	10.6		8.0	9.2	9.2
m1 trigonid length	17.4				
m2 length	13.5		10.8	12.1	12.5
m2 width	9.7		7.2	7.9	8.0

genus *Phoberogale*, *P. shareri* n. sp. is distinguished from European species (*P. bonali* Helbing, 1928, *P. depereti* Viret, 1929, *P. ginesticus* Kuss, 1962) by its larger size, and more differentially enlarged p4 over p3. It differs from Pakistani *P. bugtiensis* in its less prominent notch between anterior base of P4 paracone and protocone, more distinct anterior ridge on P4 paracone, and more mediolaterally shortened M1-2. Species of *Phoberogale* are distinguished from more-derived *Phoberocyon* by their smaller size, absence of a premasseteric fossa, and lack of a distinct m2 paraconid.

DESCRIPTION

The type and only specimen of *Phoberogale shareri* n. sp. is preserved in deep purplish mudstones, and suffers from minor to modest distortions and cracks. Its teeth are nearly perfectly preserved. Although the basicranial region in OCPC 21794-5 is missing, it is the only associated skull and dentary in North American *Phoberogale* materials, and is thus well suited as a holotype. The skull (OCPC 21794)

and left dentary (OCPC 21795) are catalogued as separate specimens. Similarities in wear stage on the upper and lower teeth and the preservation of bones suggest that they belong to the same individual.

OCPC 21794-5 belongs to a young adult with permanent dentition fully erupted but showing minimal wear. The skull (Fig. 3) is missing the posterior half of the braincase and the basicranial region, but the remaining parts are more or less intact. Overall, the skull is slightly dorsoventrally crushed resulting in a shallower depth, with the most deformation sustained at the orbital region and the glenoid fossa region.

The nasals sag slightly along the mid line such that the left and right nasals meet each other at almost a right angle. The anterior tips of the nasals are missing and the posterior margins extend back behind the anterior rim of the orbit, situated at the same level as the frontal-maxillary suture.



FIG. 4. — *Phoberogale shareri* n. sp., OCPC 21795, holotype (associated with OCPC 21794) from ETC Windy Ridge locality, Orange County, California; lingual (A) and labial (B) views of left dentary. Scale bar: 30 mm.

The frontal is very broad (widest distance between dorsal rims of the orbits is 59 mm and distance between postorbital processes of the frontals is 55 mm). The frontal is slightly elevated behind the postorbital process, indicating a modest development of frontal sinuses. The temporal crests behind the postorbital process are not sharply delineated and they converge to a single sagittal crest about 10 mm anterior to the frontal-parietal suture. About 40 mm of the anterior sagittal crest is preserved and it is quite low (~4 mm in height).

In lateral view, the infraorbital foramen is at the level of the anterior border of the P4 and the infraorbital canal is relatively long. In anterior view, the foramen is a narrow oval with the long axis oriented vertically. The zygomatic arch is mostly missing on both sides, with only the anterior segment preserved on the right side. The remaining zygomatic arch is quite deep, 25 mm at its anterior base and 14 mm at the broken tip. Bones in the orbital region suffer from extensive damage and the lacrimal area is poorly preserved on both sides. Even on the relatively better preserved left

side, individual bones in the orbital mosaic are difficult to make out.

In ventral view, the palate is not broadened as in other North American *Phoberogale* (see Comparison below), with 66.4 mm the maximum distance between the left and right P4s. The incisive foramina are markedly widened and they form a circular opening 12.4 mm in greatest diameter. Part of the palatines, particularly that on the right side near the P4-M1, is missing, and the exact position of the posterior margin is not clear. Judging from the remainder, however, the posterior palatine border seems to stop at a level anterior to the posterior edge of the M2s. The basicranium is largely missing, except the left basisphenoid area. An alisphenoid canal is present. The postglenoid fossae have been forced forward by at least 6 mm, resulting in a shortened orbital region, especially on the right side.

The left dentary is largely intact except the tip of the ascending ramus and angular process (Fig. 4). The horizontal ramus gently tapers toward the anterior end, with the depths and widths below p2, p4, and m2 being 22.2 × 11.8 mm, 22.7 × 11.2 mm, 25.9 × 9.7 mm, respectively. Although the bony surface on the labial side below the m2 is somewhat damaged in an area about 15 mm in width, the remaining bone surrounding this damaged area shows no sign of a premasseteric fossa. The bone between the ventral rim of the masseteric fossa and ventral edge of the horizontal ramus is narrow, measuring 8.2 mm in width. Despite the loss of the tip of the ascending ramus, the overall height of the ascending ramus is estimated to be ~52 mm. The tip of the angular process is missing.

With the exception of the lower incisors, the entire upper and lower dentition is well preserved; only modest wear ensures that the cusp morphology can be described. The dental formula is 3142/3143. Upper incisors form a relatively straight dental arcade and they are procumbent. Wear on the tips of the I1-2 obscures their cusp morphology, but they appear to be unicuspid. The size increase from I1 to I3 is relatively modest and the I3 is not exceptionally enlarged as seen in some large, hypercarnivorous caniforms. The I3 has a medial and lateral ridge, and the medial ridge wraps around lingually to

form a basal cingulum. The upper canine is conical, oval in cross section, curving backward slightly, and has a total length of ~24 mm. An indistinct anterolingual and posterior crest is present along the length of the tooth.

P1-3 are simple, single cusped teeth, and gradually increase in size posteriorly (Figs 3; 5). All have an anterolingual and a posterior crest. A very indistinct cingulum surrounds the entire P3, and that on the P2 is even more indistinct. P4 is large and robust but not to the extent seen in the large phoberocyonine species from the Nebraska Hemingfordian. The paracone has an anterior ridge but lacks a parastyle. The protocone is not advanced but is retracted along the lingual face of the P4, hence is posterior to the anterior edge of the paracone, and a slight notch is present between these cusps. The protocone is low and rather flat anteriorly but includes a small sharp, ridge-like cusp toward the posterior end. A very weak cingulum is present on the anterior and labial margin, and that along the lingual margin is more distinct. A distinct carnassial notch is present.

M1 is subquadrate in occlusal outline. The labial cingulum and parastyle are poorly developed. The paracone is taller crowned than the metacone, although wear on these cusps does not allow a more precise description. The protocone is a low, slightly enlarged cusp situated at the lingual termination of the preprotocrista. The metaconule forms a low ridge posterior to the protocone, and separated from it by a notch. It is anteriorly expanded at the expense of the postprotocrista. The posteriorly directed metaconule ridge adopts a slight labial turn, ending at the posterior margin of the tooth rather than at the base of the metacone. A posterolingual cingulum (hypocone) is moderately developed and wraps anteriorly around the protocone. M2 has an oval outline. Its paracone is much larger than the metacone, and as in M1, the labial cingulum is weak. The protocone-metaconule ridge is low and indistinct. The lingual cingulum (hypocone) is expanded at its posterolingual corner.

The lower incisors are missing. The lower canine is more posteriorly curved than its upper counterpart. The p1-3 are single cusped with an indistinct anterior and posterior ridge (Figs 4; 5).



FIG. 5. — *Phoberogale shareri* n. sp., OCPG 21794–5, holotype from ETC Windy Ridge locality, Orange County, California; occlusal stereo views of lower (A) and upper teeth (B). Scale bar: 30 mm.

Size increase from p1-p3 is gradual and slight. The p4 is substantially larger and more robust than p3, and in addition to anterior and posterior ridges, a small posterior accessory cusp is present. The p4 also has a more pronounced cingulum, particularly along the lingual border. The lower carnassial (m1) is long, with a well-defined shearing blade formed by the labial facet of paraconid and protoconid. The protoconid is much taller than the paraconid. The metaconid is low and slightly offset from the protoconid (positioned at the posterolingual aspect of the protoconid). A dominant hypoconid occupies more than two thirds the width of the talonid. A lower entoconid ridge, with less than one third the width of the talonid, encloses a shallow basin. The entoconid crest is not divided into smaller cusps. The m2 protoconid is larger than the metaconid in occlusal view. Wear on these cusps prevents an estimate of their relative height, but it is likely that the protoconid is taller than the metaconid, based on comparisons with other North American *Phoberogale* specimens. A paraconid is absent, and in its place is a triangular platform enclosed between protoconid and metaconid. As in the m1, the m2 hypoconid is much larger and higher than the entoconid, which is a low crest. An m3 is indicated by a single-rooted alveolus.

GEOLOGY, ASSOCIATED FAUNA, AND AGE

Surficial geologic mapping of the northern Santa Ana Mountains is provided by Morton & Miller (1981) and Schoellhamer *et al.* (1981). Grading for the northern segment of SR 241 north of Irvine Lake cut through one of the thickest sections of the undifferentiated continental Sespe and marine Vaqueros formations (Fig. 2). In the northern Santa Ana Mountains, these formations interfinger extensively (Schoellhamer *et al.* 1981) and are not easily distinguished or mapped separately. The upper or dominantly marine "Vaqueros" lithofacies consists of interbedded reddish, buff, and gray to white sandstones and greenish-gray to white sandstones and siltstones, whereas interbedded reddish, buff, and gray to white sandstones and claystones constitute the lower or continental "Sespe" lithofacies (Lander 2003; Whistler & Lander 2003). The formations have a combined maximum thickness of roughly 900 m

(2955 ft) (Schoellhamer *et al.* 1981). Locally in the ETC Windy Ridge section of SR 41, the exposed, upper portion of the sequence is 317 m (1039 ft) thick and is cut by at least three minor unmapped faults. The magnitude and sense of offset along these faults are undocumented. Consequently, the amount of section that has been removed or repeated by faulting is undetermined. The base of the section was not exposed by grading. Whistler & Lander (2003) considered the Sespe/Vaqueros Formation in the ETC Windy Ridge section to range in age from late Uintan to early Hemingfordian. The entire section is composed of the "Sespe" lithofacies, which is disconformably overlain by the marine, late Hemingfordian Topanga Formation (Calvano *et al.* 2003).

The *Phoberogale shareri* n. sp. type locality (OCPC locality 2039) was in a 2.7 m (9 ft) thick, fine-grained red sandstone 307 m (1006 ft) above the base of the ETC Windy Ridge section, and a greater, but undetermined, distance above the base of the formation (Fig. 2). This locality is approximately 85 m (280 ft) below the disconformably overlying, marine Topanga Formation of late Hemingfordian age, but the intervening section is cut by the upper of the three documented faults. The holotype (OCPC 21794-5) is preserved in a deep purplish claystone and is the only specimen collected from the site. Stratigraphically correlative sections (ETC Jamboree Road section, Bolero Lookout, Laguna Hills) yielded magnetostratigraphic records variously correlated with C5Cr-C5Er (16.73-19.05 Ma) (Prothero & Donohoo 2001; Calvano *et al.* 2008). However, Whistler & Lander (2003) revised the land mammal age assignment for two assemblages in the ETC Jamboree Road section and, consequently, changed the chron assignments to C5Cn-6r (17.28-20.52 Ma).

The upper part of the ETC Windy Ridge section, which contains late Arikareean and early Hemingfordian land mammal assemblages, is above an intraformational unconformity that lies at the base of a conglomeratic interval and separates this part of the section from the lower part (Calvano *et al.* 2003). The lower part of the section yielded a late Uintan land mammal assemblage at OCPC locality 2020 (Calvano *et al.* 2003; Whistler & Lander 2003).

Whistler & Lander (2003) divided the land mammal assemblages from the upper part of the ETC Windy Ridge section into the upper and lower ETC Windy Ridge local faunas (l.f.s). The early Hemingfordian, upper ETC Windy Ridge l.f. is represented by taxa from OCPC localities 2019 and 2040, whereas the late Arikareean, lower ETC Windy Ridge l.f. spans the “290 m of section below locality OCPC 2019” and includes OCPC localities 2016-2018 (Whistler & Lander 2003). Taxa from the upper ETC Windy Ridge l.f. include *Cynelos* sp., *Cymarctoides whistleri* Wang & Tedford, 2008, *Phlaocyon taylora* Hayes, 2000, *Cuyamalagus dawsoni* Hutchison in Hutchison & Lindsay, 1974, *Nototamias* spp., *Miospermophilus* spp., *Yatkolamys* sp., and *Merychyus elegans* Leidy, 1859, while the lower ETC Windy Ridge l.f. contains Heterosoricidae, *Cuyamalagus dawsoni* Hutchison in Hutchison & Lindsay 1974, *Gripholagomys?* sp. *Nototamias* spp., *Miospermophilus* sp., *Schizodontomys* sp., *Leidymys nematodon* (Cope, 1879), *Merychyus?* sp., *?Tanymyktter* sp., *?Machaeromeryx tragulus* Matthew, 1926, and *?Pseudoblastomeryx advena* Matthew, 1907 (Whistler & Lander 2003: table 2; Wang & Tedford 2008). In particular, the murid rodent *Yatkolamys* sp. from OCPC locality 2019 and the oreodontid artiodactyl *Merychyus arenarum* or *M. elegans* from OCPC locality 2062 (Fig. 2) were considered typical of the early Hemingfordian NALMA and played a key role in separating the upper ETC Windy Ridge l.f. from the lower. Whistler & Lander (2003: 256, fig. 11.4) assigned the *Phoberogale shareri* n. sp. holotype (OCPC 21794-5) from OCPC locality 2039 to *Cephalogale* sp., which at that time they regarded as a member of the upper ETC Windy Ridge l.f. (Fig. 2).

The *Phoberogale shareri* n. sp. type locality (OCPC locality 2039) is approximately 56-66 m (185-215 ft) below OCPC locality 2019, which yielded dominantly early Hemingfordian *Yatkolamys* sp. and the lowest assemblage assigned to the upper ETC Windy Ridge l.f. by Whistler & Lander (2003), but about 27-39 m (87-127 ft) above OCPC locality 2017 and the highest assemblage referred to the lower ETC Windy Ridge l.f. (Fig. 2). On the other hand, an undetermined species of *Merychyus* occurs at OCPC locality 2062, no more than 7.0 m (23 ft) above OCPC locality 2039 (Lander 2003).

Yatkolamys and *M. elegans* are reported in the early Hemingfordian Runningwater Formation of northwestern Nebraska (Martin & Corner 1980; Lander 1998: locality CP106). Partly on the basis of the latter two taxa, Whistler & Lander (2003: fig. 11.5) correlated the upper ETC Windy Ridge l.f. and correlative assemblages (including Santiago Canyon Landfill l.f.) in the “Sespe” lithofacies with taxonomically similar assemblages in the Runningwater Formation. In contrast, latest Arikareean *Merychyus arenarum*, but neither *M. elegans* nor *Yatkolamys*, occurs in the Anderson Ranch Formation, which immediately underlies the Runningwater Formation. Found at least 52 m (171 ft) below *Yatkolamys*, the crushed *Merychyus* skull (OCPC 22097) from OCPC locality 2062 (Fig. 2) cannot be assigned confidently to either species. Consequently, the *Phoberogale shareri* n. sp. holotype from no more than 7 m (23 ft) lower in the section (Fig. 2) does not occur in association with an age-diagnostic species of this oreodont. Another age-diagnostic taxon in the upper ETC Windy Ridge l.f. is *Cynelos* sp., which is based on a partial skull and postcranial skeleton from OCPC locality 2038, no more than 11 m (35 ft) below the *Phoberogale shareri* n. sp. type locality, OCPC locality 2039 (Fig. 2). This medium-sized amphicyonid carnivore, presumably an immigrant from Eurasia, is first recorded in North America by a single isolated lower carnassial from the late Arikareean Agate Spring l.f. of northwestern Nebraska, and did not become well represented in the North American fossil record until the early Hemingfordian NALMA of the Great Plains (Hunt 1972; Tedford & Frailey 1976; Hunt 1998b). This skull, based on its proportions and dentition, suggests a latest Arikareean age. Unfortunately, other age-diagnostic taxa, such as the latest Arikareean oreodont *Merycochoerus matthewi* and early Hemingfordian *M. magnus* and *M. proprius*, are not recorded from the undifferentiated Sespe and Vaqueros formations.

Radiometric data from the Sespe Formation support a latest Arikareean age for *Phoberogale shareri*. n. sp. Along Piuma Road in the central Santa Monica Mountains of Los Angeles County (Fig. 1), *Leidymys nematodon* occurs in the lower part of the Piuma Member of the Sespe Formation,

TABLE 2. — Craniodontal dimensions (in mm) of *Phoberogale shareri* n. sp. from California, and *Phoberogale* sp. (F:AM 54464) from the *Cephalogale* Jourdan, 1862 Ash locality, Dawes Co., Nebraska.

	<i>P. shareri</i>	F:M 54464
Length of rostrum	91.6	95.2
Palatal breadth across P4s	66.4	76.5
Breadth across zygomatic arches	<110	158
Width across upper canines	43.2	57.0
Minimum breadth between dorsal orbital rims	55.5	62.7
Width across postorbital constriction	36.6	42.8
Maximum diameter of upper canine	10.2	14.6
Distance between posterior border of M2 and foramen rotundum	35.5	59.1

whereas *Yatkolamys* sp. occurs near the top of the upper part of the member (Fig. 1; Fisk *et al.* 2001; Lander *et al.* 2001a; Lander *et al.* 2001b; Lander 2003; Calvano *et al.* 2008: fig. 10). The two taxa are widely separated stratigraphically, as in the Santa Ana Mountains. The Upper Saddle Peak Tuff lies near the base of the upper part of the Piuma Member, roughly 255 m (835 ft) below the *Yatkolamys* record, and has been determined to be 21.1 ± 0.2 Ma old (Lander *et al.* 2003; Calvano *et al.* 2008: fig. 10). The level that produced the *Phoberogale* skull probably correlates with one between the tuff and the level that produced *Yatkolamys* sp.

COMPARISON WITH NORTH AMERICAN FORMS

Mainly through intensive collecting by the F:AM and UNSM, such relatively rare carnivorans as *Phoberogale* were accumulated over time. Although the specimens were collected many decades ago, their existence was announced quite recently and only in the context of North American biochronology, i.e. *Cephalogale* (now *Phoberogale*), along with other immigrants, was used to define the late Arikareean NALMA (Tedford *et al.* 1987; 2004). In his summary of North American ursids, Hunt (1998a) briefly discussed the nature of North American *Cephalogale*. He listed three unnamed species from eight localities: “*Cephalogale* new species I” from Standing Rock Quarry, Zia Sand Formation (late Arikareean), Sandoval County, New Mexico; “*Cephalogale* new species II” from University Quarry, Upper Harrison Beds (late Arikareean), Sioux County, Nebraska and 16 Mile District, Upper Harrison Beds, Goshen County, Wyoming; and “*Cephalogale* new species

III” from five different localities in the overlying Runningwater Formation or equivalent beds (early Hemingfordian), Morrill, Sheridan, Dawes, and Box Butte counties, Nebraska. Dental, postcranial and rare cranial fossils constitute the North American material, with the largest sample coming from the early Hemingfordian Bridgeport Quarries.

A comprehensive description of these materials is beyond the scope of this study. Instead, we provide a brief comparison, leaving a full treatment of the remaining North American material for future studies. A decade ago, Hunt (1998a) noted that the largest North American form of *Cephalogale* (*s.l.*), his early Hemingfordian species III, exceeded in lower carnassial size (m1 length ~23-31 mm) all of the known Eurasian forms (~12-23 mm). Hunt’s *Cephalogale* new species I-II were smaller, poorly represented late Arikareean ursids, known by fragmentary teeth only, whereas the larger, early Hemingfordian species III was represented by numerous specimens from the Bridgeport Quarries.

Phoberogale shareri n. sp. is closest in size to Hunt’s (1998b) species II from the late Arikareean of Wyoming (a partial maxilla with M2), as well as small individuals from the Bridgeport Quarries. Compared to the Bridgeport Quarries form, OCPC 21794-95 lacks a parastyle on P4 and consequently lacks a distinct notch between the anterior border of the paracone and the protocone. The California species has a metaconule ridge on M1 closer to the metacone, i.e. directed more labially, in contrast to the more anteroposterior orientation of the ridge in the Bridgeport Quarries species. This feature also results in a more developed M1 hypocone (from

the posterolingual cingulum) at the expense of the metaconule in the California species as opposed to equal development of metaconule and hypocone in the Bridgeport Quarries carnivore. In addition, the Bridgeport hypodigm displays a distinct paraconule lacking in *P. shareri* n. sp.

Of the F:AM material, the best preserved specimen is a nearly complete skull and partial skeleton (F:AM 54464) from the “Cephalogale Ash” locality 1 mile west of the post office at Marsland, Dawes County, Nebraska. This skull shows a rostrum 4% longer than *P. shareri* n. sp. and a palate 15% broader. This contrast in width is even more pronounced across the zygomatic arches where F:AM 54464 exceeds *P. shareri* n. sp. by 44%. Similarly, the forehead is broader in F:AM 54464 and the upper canines are more widely spaced (Table 2). Although the glenoid fossae of OCPC 21794 have been anteriorly displaced, the left alisphenoid canal and area of the orbital fissure are relatively intact. Here the distance between the posterior margin of M2 and the foramen rotundum in F:AM 54464 is 66% greater than in *P. shareri* n. sp. and this distinction cannot be explained away by mere preservational effects. It is uncertain whether these proportional differences are due to sexual dimorphism, as F:AM 54464 is likely a male with a large upper canine (maximum diameter of 14.6 mm vs. 10.2 mm for OCPC 21794), a large I3 relative to I1-2, and a high sagittal crest.

Other than the above proportional differences between the California and Nebraska skulls, additional characters indicate that they belong to different species. The lateral profile of the sagittal crest in F:AM 54464 is essentially horizontal with a gentle downward curvature near the frontal-parietal suture – the crest is prolonged posteriorly where it forms an overhanging inion. This profile displays a gradual increase in crest depth to the point where the surface of the braincase bends downward. Here the maximum depth of the crest near the inion is ~29 mm. The crest profile for OCPC 21794, on the other hand, slopes downward in the posterior direction. The posterior terminus of the sagittal crest is broken at the point where the braincase surface begins to slope ventrally. Up to this point the sagittal crest shows no sign of increasing depth, which is no

greater than 4 mm throughout its preserved length. Hence, a less pronounced inion seems probable in OCPC 21794 and suggests a subtle difference in overall proportions of the temporal muscles and posterior cranium in the two carnivores.

DISCUSSION

Despite over a century and a half of study, records for *Cephalogale/Phoberogale* and related forms are still quite poor, and the majority of published specimens are fragmentary maxillaries and dentaries, with only one previously figured skull of “*C.*” *minor* (Beaumont 1965: fig. 14) and a partial skull of *C. gracile* (Viret 1929: pl. IX, fig. 4a). Bonis’ (1973) systematic synthesis is still the most comprehensive compared to other recent treatments (Beaumont 1965; Ginsburg & Morales 1995), even though he did not attempt to treat every species. We did not personally examine most of the European specimens. Consequently, our systematic determination relies on published descriptions, figures, and measurements, while acknowledging the limitations in not studying these specimens firsthand.

TAXONOMY OF *CEPHALOGALE* (*PHOBEROGALE*) SPECIES

Since the first recognition of *Cephalogale* (Jourdan 1862), more than a dozen species have been referred to the genus at one time or another. Beaumont (1965) was first to attempt a systematic revision of the genus, and he recognized eight European and one Asian species: *C. gracile* (Pomel, 1846) [Pomel 1846] from Saint-Gérard-le-Puy (Allier, MN2a), *C. geoffroyi* from Billy (Allier, MP30), *C. cadurcensis* (Filhol, 1877) from an unspecified locality in the Quercy district, *C. minor* from Saint-Gérard-le-Puy, *C. brevirostris* from Gergovie (Puy-de-Dôme), *C. bonali* Helbing, 1928 (see also Helbing 1922) from La Milloque (Lot-et-Garonne, MP29), *C. depereti* Viret, 1929 from Montaigne-le-Blin in St-Gérard-le-Puy (MN2a), *C. gergoviensis* Viret, 1929 from plateau de Gergovie (Puy-de-Dôme), and *C. bugtiensis* Cooper, 1923 from the early Miocene Dera Bugti fauna of Baluchistan. Since Beaumont’s revision, three additional spe-

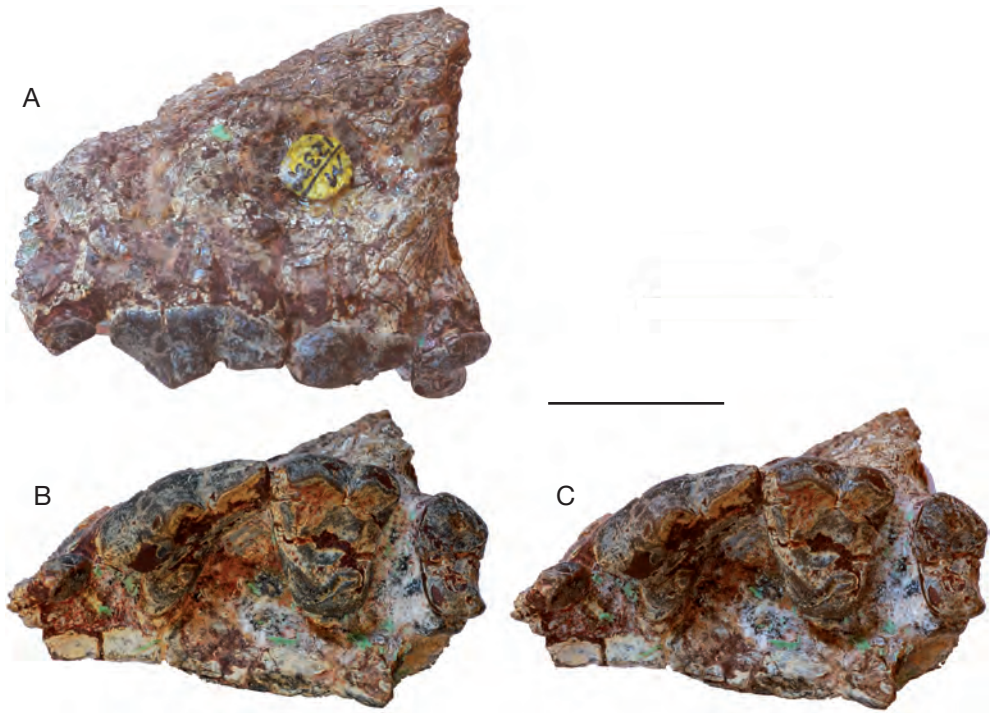


FIG. 6. — *Phoberogale bugtiensis* Forster-Cooper, 1923, BMNH M12338, holotype from Dera Bugti, Baluchistan, Pakistan; lateral (A) and occlusal stereo (B, C) views of left maxillary. Scale bar: 20 mm.

cies have been added: *C. ginesticus* Kuss, 1962 from Ginestous (MN1) in the Toulouse region in southwestern France, *C. meschethense* Gabuniya, 1964 from the late Oligocene upper Pestrotsvet Svita of Georgia, and *C. ursinus* from the early Miocene of Paulhiac (Lot-et-Garonne, MN1). More recently, in his biometric analysis of *Cephalogale*, Bonis (1973) brought in an additional species, *C. filholi* (Munier-Chalmas, 1893) [Munier-Chalmas 1893]), but excluded *C. cadurcensis*.

Of the above, the most basal species appears to be *C. minor* based on numerous specimens from the classic Quercy fissure fills. A clear understanding of the systematics of this species, however, is hampered by a lack of stratigraphic data for the majority of material that was collected more than a century ago. A sample of several dozen specimens examined by Beaumont encompasses a large size range. For example, Beaumont measured 50 dentaries where m1 length ranges from 12-18 mm. Such a large range

almost certainly includes a stratigraphic component, as well as sexual dimorphism, but lacking detailed documentation for most of the classic European collections, one cannot be certain. We can turn to the Bridgeport sample, however, where m1 length ranges from 23.4 to 30.7 mm (N=16), with a mean of 28 mm, an SD of 2.16, and a coefficient of variation of 7.7. These data support the assumption that 12-18 mm may well be a conceivable range for a single species.

CEPHALOGALE AND *PHOBEROGALE* RECORDS IN ASIA
Five nominal records of *Cephalogale* or *Phoberogale* have been reported from Asia, most of which are fragmentary. The earliest recognized species is *Cephalogale bugtiensis* Forster-Cooper, 1923 from “the early Miocene deposits of Dera Bugti” of Baluchistan. The holotype of *C. bugtiensis*, BMNH M12338, is a fragment of left maxilla with a partial P3 and complete P4-M2 (Fig. 6). The poor state of

preservation and advanced wear on the teeth do not allow confident interpretation of its morphology, particularly the well worn M2. Beaumont (1965) even questioned its membership in *Cephalogale*, and commented that most of its characters are more primitive than the European *C. minor*. The size of *C. bugtiensis* is nearly identical to OCPC 21794. *Cephalogale bugtiensis* mainly differs from *P. shareri* n. sp. in a more pronounced notch between the base of the P4 paracone and protocone, less prominent anterior ridge on P4 paracone, and more mediolaterally broad M1-2. Upper molars in the Bugti specimen, therefore, have an anteroposteriorly narrow appearance, especially the M2. The internal cingulum (hypocone) of M1 is also more thickened at the posterolingual corner. *Cephalogale bugtiensis* also appears to have a lower-crowned P4 protocone compared to the California specimen. Both in size and overall morphology *P. shareri* n. sp. is closest to *C. bugtiensis*, and it is likely that the Bugti form should be referred to *Phoberogale*.

The second record is *Cephalogale meschethense* Gabuniya, 1964 from the late Oligocene upper Pestrotsvet Svita of Georgia (see also Gabuniya 1966). Known from one m1, two canines, and a fragmentary humerus, *C. meschethense* cannot be easily compared with other Asian records and thus has received little attention after its original description. However, from Gabuniya's figure (1966: fig. 4a), *C. meschethense* does appear to have a posteriorly offset metaconid (relative to the protoconid) on m1, a character of basal ursids.

Tang & Qiu (1979) listed *Cephalogale* in the late Eocene Nadu Formation in Guangxi Province, China. Unfortunately, no description was given for the material, which was subsequently missing (Qiu & Li 2003; Wang & Qiu 2003), and the authors only commented that "judging from the carnassial, the specimen from Nadu Formation is more primitive than those from Europe and accordingly its age may be earlier than Oligocene" (Tang & Qiu 1979: 409). In revisiting the issue, the junior author of the original report could not confirm their initial identification (Qiu 2003: 21). Zhai *et al.* (2003), however, recently described a new amphicyonid species, *Guangxicyon sinoamericanus*, from the Nadu Formation with no mention of the

Cephalogale record. The status of the Nadu record thus remains to be confirmed.

Wang and Qiu (2003) reported the occurrence of *Cephalogale* sp., based on a single left M2 (IVPP V12429), from the late early Oligocene Saint-Jacques region in the Wulanbulage Formation, Inner Mongolia, China. The authors remarked that the Chinese material is closest to *C. minor* in size. However, at a length and width of 7.7 × 5.0 mm, IVPP V12429 would be among the smallest individuals of *Cephalogale* because M2s in European *C. minor* range from 6.1-7.4 mm in length and 8.0-10.0 mm in width (Beaumont 1965). The Inner Mongolian specimen does have a posteriorly oriented postprotocrista-metaconule ridge that ends at the posterior border of the tooth, an important character for early ursids (Beaumont 1982). The M2 alone is insufficient to establish its generic identity, and Wang *et al.* (2005: 42) concluded that IVPP V12429 may be possibly conspecific with *Pachycynodon tedfordi* Wang and Qiu, 2003.

Most recently, Wang *et al.* (2005: fig. 15a-c) referred to "*?Cephalogale* sp." a left mandibular fragment with m2 (MAE SG.97.5396) from the early Oligocene Hsanda Gol Formation, eastern Valley of Lakes, central Mongolian People's Republic. However, as conceded by Wang *et al.*, too little was preserved to be certain of its precise taxonomy.

PHYLOGENETIC COMMENTS

Since its initial recognition, *Cephalogale* Jourdan, 1862 has been variously included in canids, amphicyonids, procyonids, amphicyonodontines, and simocyonines (e.g., Schlosser 1888; Teilhard de Chardin 1915; Simpson 1945; Hough 1948). In the last 50 years, however, it has become increasingly clear that the genus occupies a basal position in the Family Ursidae (Beaumont 1965; Bonis 1973; Beaumont 1982; Ginsburg & Morales 1995, 1998; McKenna & Bell 1997; Hunt 1998a).

Of the 11 or so species recognized by Bonis (1973), early workers have long recognized certain morphologic patterns that might indicate discrete lineages within the genus. Viret (1929: 140) divided *Cephalogale* into two species groups: those with complex and trenchant premolars (including *C. minor*, *C. brevirostris*, *C. gracile*, *C. bonali*, and *C. depereti*)

and those with large, simple premolars (including *C. gergoviensis* and *C. geoffroyi*). Beaumont (1965) arrived, less explicitly, at a similar conclusion regarding some of Viret's taxonomic arrangements. Bonis (1973), and also Bonis & Guinot (1987), on the other hand, attempted to delineate three lineages of *Cephalogale* based on proportional relationships of p4, m1, and m2. He recognized a *bonali-depereti* lineage that has a relatively long p4 and low m2/p4 ratio. At the other extreme is a *brevirostris-gracile-ursinus* lineage that features a relatively short p4 and high m2/p4 ratio. Somewhat in between is a *geoffroyi-gergoviensis-ginesticus* lineage that has intermediate values for the above measurements and ratios. However, Bonis (1973) refrained from giving generic status to these lineages, even though he did recognize that certain *Cephalogale* lineages are antecedent to more advanced hemicyonines.

In their studies of a new early Miocene Spanish genus and species, Ginsburg & Morales (1995) formally recognized three lineages within what had been traditionally regarded as a heterogeneous *Cephalogale* (*s. l.*) (see also Ginsburg 1999). A basal "*C. minor*" (genus undefined) group gave rise to two clades: subfamilies Phoberocyoninae and Hemicyoninae. At the base of their newly recognized phoberocyonines (Phoberocyonini of Kordikova *et al.* 2000) is a new genus *Phoberogale* Ginsburg & Morales, 1995, which includes three species previously placed in *Cephalogale*: *P. bonali* (Helbing 1928), *P. deprereti* (Viret 1929), and *P. ginesticus* (Kuss 1962). *Phoberogale* in turn gave rise to the more derived *Phoberocyon* and *Plithocyon*. *Phoberocyon* is characterized by well-developed posterior accessory cusps on p3-4, elongated m1, distinct paraconid on m2, and m2 protoconid higher than metaconid (Ginsburg 1955; Tedford & Frailey 1976; Qiu *et al.* 1986), characters that are further elaborations from those in *Phoberogale*.

The redefined Hemicyoninae of Ginsburg & Morales (1995: fig. 10), a sister clade to Phoberocyoninae, now includes the type species *Cephalogale geoffroyi* plus two related species, *C. ursinus* and *C. brevisrostris*, at the base of the hemicyonine clade, followed by more derived forms such as *Zaragocyon*, *Hemicyon*, and *Dinocyon*. The hemicyonines have strong tuberculate molars at the expense of the car-

nassials, in contrast to the phoberocyonines with more hypercarnivorous dentitions. This phylogenetic theme was further elaborated by Ginsburg (1999) with slight modifications (such as adding *C. gracile* to the hemicyonine lineage). Ginsburg (1999: 120) diagnosed the Hemicyoninae as "Ursids with carnassials lower than in Phoberocyoninae, and elongated upper molars," and "the premolars (P4 excepted) reduced and the upper molars elongated, wider, with a tendency to become inscribed in a square by the increase of the postero-lingual cingulum."

Most recently, in a cladogram of North American fossil ursids, Hunt (1998a: fig. 10.3) included four genera in the New World Hemicyoninae that placed *Cephalogale* (*s. l.*) as a basal taxon, followed by *Phoberocyon*, *Plithocyon*, and an unnamed genus. His hemicyonine clade is defined by elongated paraxonic feet and digitigrade postures, accompanied by key craniodental traits incorporating the Type A ursid auditory bulla and ursid upper molar pattern. The *Phoberocyon-Plithocyon* clade was defined by a premaseteric fossa on the dentary. Hunt in his cladogram described *Cephalogale* as having sectorial carnassials, simple conical premolars, M1 subtriangular to subquadrate, M2 quadrate to subquadrate, a short snout, and auditory bulla somewhat inflated, and presented summary characteristics of the genus in greater detail later in this publication (Hunt 1998a: 180-181). Hunt's cladistic hypothesis is similar to that proposed by Ginsburg & Morales (1995), although he did not treat individual species of *Cephalogale*.

Ginsburg & Morales' (1995) latest attempt at sorting individual species of *Cephalogale* into a cladistic framework helped to focus previous concepts (such as those of Bonis 1973) that have not been taxonomically formalized. In actual practice, their *Phoberogale* and restricted *Cephalogale* are distinguished by size as well as tendencies toward hyper- or hypocarnivorous dentitions (Ginsburg & Morales 1995: fig. 9). The California *Phoberogale shareri* n. sp. appears to fall on the phoberocyonine side of the clade with such hypercarnivorous characters as presence of a posterior accessory cusp on p4, p4 enlarged relative to p3, relatively elongated carnassials at the expense of tuberculate molars, and m2 protoconid taller than metaconid.

ZOOGEOGRAPHIC REMARKS

The majority of North American immigrants used to define or characterize Neogene NALMAs (Tedford *et al.* 1987; 2004) are commonly assumed to come from Asia. However, their actual Asian ancestors mostly remain poorly known (Qiu 2003). The emerging records of Eurasian *Cephalogale* and *Phoberogale* or more accurate calibration of their ages permit additional comments on the immigration of the latter to North America.

Recent field work on the Dera Bugti section by French vertebrate paleontologists indicates that the lower Miocene terrestrial deposits (~250 m) above a sequence of Eocene marine sediments are faunally correlated to the European MN 3-4 units in the range of 17-20 Ma (Welcomme *et al.* 1997). Unfortunately no new material of *Phoberogale bugtiensis* was found and its precise stratigraphic position is thus still in question. Based on rodent faunal considerations, Flynn *et al.* (1986) also speculated that the Bugti fauna is between 18-21 Ma, an estimate roughly equivalent to the North American occurrence of *Phoberogale* spp. Qiu (2003: 21) also deduced that the dispersal of *Cephalogale* (*Phoberogale*) from Europe to North America should have occurred at ~21 Ma. Hunt's (2004) estimate of 23 Ma indicates a somewhat earlier immigration event, based on a radioisotopically calibrated occurrence in the Harrison Formation of Nebraska, as yet undescribed. Despite the poor holotype of *Phoberogale bugtiensis*, size and morphological similarities shared with those of *P. shareri* n. sp. seem to suggest that *P. bugtiensis* is the closest known sister species of the North American clade. If so, it also implies that *Phoberogale shareri* n. sp. predates *P. bugtiensis* and so a much wider geographic distribution for the genus must have existed in the early Miocene. This hitherto unknown record probably existed in much of Eastern Asia, in latitudes higher than its known South Asia location, in order to avail itself of the opportunity to migrate to North America.

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de Bonis, a colleague of the first three authors. His analysis of European *Cephalogale* in 1973 is still the most authoritative treatment and forms a foundation on which this paper is based. It is thus fitting to describe the new North American *Phoberogale* specimen in honor of Louis de Bonis.

Mark A. Roeder of Paleo Environmental Associates, Inc., supervised the recovery of the holotype, which subsequently was prepared and cast by Howell W. Thomas at the Natural History Museum of Los Angeles County.

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REFERENCES

BEAUMONT G. D. 1965. — Contribution à l'étude du genre *Cephalogale* Jourdan (Carnivora). *Schweizerische*

- Paläontologische Abhandlungen* 82: 1-34.
- BEAUMONT G. D. 1982. — Brèves remarques sur la dentition de certains Ursidés (Mammifères). *Archives des Sciences* (Genève) 35: 153-156.
- BONIS L. DE 1973. — Contribution à l'étude des mammifères de l'Aquitainien de l'Agenais, rongeurs-carnivores-perissodactyles. *Mémoires du Muséum national d'Histoire naturelle*, nouvelle série 28: 1-192.
- BONIS L. DE & GUINOT Y. 1987. — Le gisement de vertébrés de Thézels (Lot) et la limite Oligo-Miocène dans les formations continentales du bassin d'Aquitaine. *Münchener Geowissenschaftliche Abhandlungen* 10: 49-58.
- CALVANO G., PROTHERO D. R., LUDTKE J. & LANDER E. B. 2008. — Magnetic stratigraphy of the Eocene to Miocene Sespe and Vaqueros formations, Los Angeles and Orange counties, California, in WANG X. & BARNES L. G. (eds), *Geology and vertebrate Paleontology of western and southern North America*, Contributions in honor of David P. Whistler. *Natural History Museum of Los Angeles County Science Series* 41: 43-61.
- CALVANO G., LANDER E. B., WHISTLER D. P., ROEDER M. A., LUDTKE J., PROTHERO D. R., WALSH S. L. & WAGNER H. M. 2003. — Lithostratigraphic, biostratigraphic, and magnetostratigraphic documentation of a major unconformity in the middle Eocene to early Miocene continental Sespe Formation, northern Santa Ana Mountains, Orange County, southern California, in American Association of Petroleum Geologists Pacific Section Western Regional Meeting Conference Program & Abstracts. *PaleoBios* 23 (1 supplement): 1.
- CROIZET J.-B. 1836. — Indication des fossiles de diverses natures qu'on trouve dans la Montagne de Gergovia. *Bulletin de la Société géologique de France* 7: 104-106.
- FILHOL H. 1879. — Étude des mammifères fossiles de Saint-Gérard-le-Puy (Allier). *Annales des Sciences géologiques* 10: 1-253.
- FISK L. H., LANDER E. B., ALDERSON J. M., ANDERSON E. M., WALKER S. I., ANDERSON C. B. & WHISTLER D. P. 2001. — Late Oligocene and early to middle(?) Miocene land plants, upper Piuma Member, Sespe Formation, and Fernwood Member, Topanga Canyon Formation, central Santa Monica Mountains, Los Angeles County, California. *Geological Society of America Abstracts with Programs* 33: A43.
- FLYNN L. J., JACOBS L. L. & CHEEMA I. U. 1986. — Baluchimyinae, a new tenodactyloid rodent subfamily from the Miocene of Baluchistan. *American Museum Novitates* 2841: 1-58.
- FORSTER-COOPER C. 1923. — Carnivora from the Dera Bugri deposits of Baluchistan. *Annals and Magazine of Natural History* 9: 259-263.
- GABUNIYA L. K. 1964. — *Benaraskaia fauna oligot-senovykh pozvonochnykh*. Tbilisi, Akademiai Nauk Gruzinskoi SSR, Institut Paleobiologii, Izdatel'stvo "Metsniereba", 262 p.
- GABUNIYA L. K. 1966. — Sur les mammifères oligocènes du Caucase. *Bulletin de la Société géologique de France* 8: 857-869.
- GINSBURG L. 1955. — De la subdivision du genre *Hemicyon* Lartet (Carnassier du Miocène). *Bulletin de la Société géologique de France* 5: 85-99.
- GINSBURG L. 1999. — Order Carnivora, in RÖSSNER G. E. & HEISSIG K. (eds), *The Miocene Land Mammals of Europe*. Verlag Dr Friedrich Pfeil, München: 109-148.
- GINSBURG L. & MORALES J. 1995. — *Zaragocyon daamsi* n. gen. sp. nov., Ursidae primitif du Miocène inférieur d'Espagne. *Comptes rendus de l'Académie des Sciences* 321: 811-815.
- GINSBURG L. & MORALES J. 1998. — Les Hemicyoninae (Ursidae, Carnivora, Mammalia) et les formes apparentées du Miocène inférieur et moyen d'Europe occidentale. *Annales de Paléontologie (Vertébrés)* 84: 71-123.
- HELBING H. 1922. — Carnivoren des obern Stampien. *Ecolgae Geologicae Helvetiae* 17: 384-387.
- HELBING H. 1928. — Carnivoren des oberen Stampien. *Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft* 47: 1-82.
- HOUGH J. R. 1948. — A systematic revision of *Daphoenus* and some allied genera. *Journal of Paleontology* 22: 573-600.
- HUNT R. M. JR 1972. — Miocene amphicyonids (Mammalia, Carnivora) from the Agate Spring quarries, Sioux County, Nebraska. *American Museum Novitates* 2506: 1-39.
- HUNT R. M. JR 1998a. — Ursidae, in JANIS C. M., SCOTT K. M. & JACOBS L. L. (eds), *Evolution of Tertiary Mammals of North America*, Volume 1: *Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals*. Cambridge University Press, Cambridge: 174-195.
- HUNT R. M. JR 1998b. — Amphicyonidae, in JANIS C. M., SCOTT K. M. & JACOBS L. L. (eds), *Evolution of Tertiary Mammals of North America*, Volume 1: *Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals*. Cambridge University Press, Cambridge: 196-227.
- HUNT R. M. JR 2004. — Global climate and the evolution of large mammalian carnivores during the later Cenozoic in North America, in GOULD G. C. & BELL S. K. (eds), *Tributes to Malcolm C. McKenna: his students, his legacy*. *Bulletin of the American Museum of Natural History* 285: 139-156.
- JOURDAN M. 1862. — La description de restes fossiles de grands mammifères. Part 2. Les terrains sidérolithiques. *Revue des Sociétés savantes des Départements, publiée sous les auspices du ministre de l'Instruction publique et des cultes* 1: 126-130.
- KORDIKOVA E. G., HEIZMANN E. P. J. & MAVRIN A. V.

2000. — Early Miocene Carnivora of Aktau Mountains, south eastern Kazakhstan. *Paläontologische Zeitschrift* 74: 195-204.
- KUSS S. E. 1962. — Deux nouveaux Canidés (Carnivora) du stampien de Toulouse. *Bulletin de la Société d'Histoire naturelle de Toulouse* 97: 330-344.
- LANDER E. B. 1998. — Oreodontoidea, in JANIS C. M., SCOTT K. M. & JACOBS L. L. (eds), *Evolution of Tertiary Mammals of North America*, Volume I: *Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals*. Cambridge University Press, Cambridge: 402-425.
- LANDER E. B. 2003. — *Eastern Transportation Corridor Paleontologic Resource Impact Mitigation Program Final Technical Report of Results and Findings*. Paleo Environmental Associates, Inc., project nos 94-23 & 99-11. Prepared for Orange County Foothill/Eastern Transportation Corridor Agency and Raytheon Infrastructure Services Incorporated. Paleo Environmental Associates, Inc., Altadena.
- LANDER E. B., WEIGAND P. W., FRITSCHÉ A. E., ALDERSON J. M. & IRIONDO A. 2003. — New 40Ar/39Ar age determinations for two tuffs in the Piuma (Upper) Member of the continental Sespe Formation, central Santa Monica Mountains, California. *American Association of Petroleum Geologists Pacific Section Western Regional Meeting Conference Program & Abstracts*: 76.
- LANDER E. B., WHISTLER D. P., ALDERSON J. M., ANDERSON E. M., WALKER S. I. & ANDERSON C. B. 2001a. — Late Oligocene and early Miocene land mammal biostratigraphy, Piuma Member, Sespe Formation, and Fernwood Member, Topanga Canyon Formation, Saddle Peak area, central Santa Monica Mountains, Los Angeles County, California. *Geological Society of America Abstracts with Programs* 33: A43.
- LANDER E. B., WHISTLER D. P., ALDERSON J. M., FISK L. H., WALKER S. I., ANDERSON E. M. & ANDERSON C. B. 2001b. — Late Oligocene to early or middle Miocene continental vertebrate, marine invertebrate, and land plant biostratigraphy of the Sespe, Vaqueros, and Topanga Canyon Formations, central Santa Monica Mountains, Los Angeles County, California. *PaleoBios* 21 (1 supplement): 6-7.
- MARTIN L. D. & CORNER R. G. 1980. — A new genus of cricetid rodent from the Hemingfordian (Miocene) of Nebraska. *University of Kansas Paleontological Contributions* 103: 1-5.
- MCKENNA M. C. & BELL S. K. 1997. — *Classification of Mammals above the Species Level*. Columbia University Press, New York, 640 p.
- MORTON P. K. & MILLER R. V. 1981. — Geologic Map of Orange County California showing mines and minerals deposits. *California Division of Mines and Geology Bulletin* 204.
- MUNIER-CHALMAS E.-C.-P. 1893. — Sur le Stampien supérieur et sur les grès de Fontainebleau. *Bulletin de la Société géologique de France* 21: 28-30.
- POMEL M. 1846. — Mémoire pour servir à la géologie paléontologique des terrains tertiaires du département de l'Allier. *Bulletin de la Société géologique de France* 3: 353-373.
- PROTHERO D. R. & DONOHOO L. L. 2001. — Magnetic stratigraphy of the lower Miocene (early Hemingfordian) Sespe-Vaqueros Formations, Orange County, California, in PROTHERO D. R. (ed.), *Magnetic Stratigraphy of the Pacific Coast Cenozoic*. Pacific Section Society for Sedimentary Geology 91: 242-252.
- QIU Z.-D. & LI C.-K. 2003. — Rodents from the Chinese Neogene: biogeographic relationships with Europe and North America, in FLYNN L. J. (ed.), *Vertebrate fossils and their context: contributions in honor of Richard H. Tedford*. *Bulletin of the American Museum of Natural History* 279: 586-602.
- QIU Z.-X. 2003. — Dispersals of Neogene carnivores between Asia and North America, in FLYNN L. J. (ed.), *Vertebrate fossils and their context: contributions in honor of Richard H. Tedford*. *Bulletin of the American Museum of Natural History* 279: 18-31.
- QIU Z.-X., YAN D.-F., JIA H. & SUN B. 1986. — The large-sized ursid fossils from Shanwang, Shandong. *Vertebrata Palasiatica* 24: 182-194.
- SCHLOSSER M. 1888. — Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europäischen Tertiärs und deren Beziehungen zu ihren lebenden und fossilen aussereuropäischen Verwandten. II. Theil. Carnivora. *Beiträge zur Paläontologie Österreich-Ungarns* 7: 1-162.
- SCHOELHAMER J. E., VEDDER J. G., YERKES R. F. & KINNEY D. M. 1981. — Geology of the northern Santa Ana Mountains, California, in Geology of the eastern Los Angeles Basin, southern California. U.S. *Geological Survey Professional Paper* 420-D: D1-D109.
- SIMPSON G. G. 1945. — The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 85: 1-350.
- TANG Y.-J. & QIU Z.-D. 1979. — Analysis and discussion of vertebrate fossils from Baise, Guangxi, in INSTITUTE OF VERTEBRATE PALEONTOLOGY AND PALEOANTHROPOLOGY AND NANJING INSTITUTE OF GEOLOGY AND PALEONTOLOGY (ACADEMIA SINICA) (ed.), *Mesozoic and Cenozoic Redbeds of Southern China, Proceedings of the Nanxiong Field Conference of Cretaceous-early Tertiary Redbeds in South China*. Science Press, Beijing: 407-415.
- TEDFORD R. H. & FRAILEY D. 1976. — Review of some Carnivora (Mammalia) from the Thomas Farm local fauna (Hemingfordian: Gilchrist County, Florida). *American Museum Novitates* 2610: 1-9.
- TEDFORD R. H., GALUSHA T., SKINNER M. F., TAYLOR B. E., FIELDS R. W., MACDONALD J. R., RENSBERGER J. M., WEBB S. D. & WHISTLER D. P. 1987. — Faunal succession and biochronology of the Arikarean through Hemphillian interval (late Oligocene through

- earliest Miocene epochs) in North America, in WOODBURN M. O. (ed.), *Cenozoic Mammals of North America, Geochronology and Biostratigraphy*. University of California Press, Berkeley, 153-210.
- TEDFORD R. H., ALBRIGHT L. B. III, BARNOSKY A. D., FERRUSQUÍA-VILLAFRANCA I., HUNT R. M. JR, STORER J. E., SWISHER C. C. III, VOORHIES M. R., WEBB S. D. & WHISTLER D. P. 2004. — Mammalian biochronology of the Arikareean through Hemphillian interval (Late Oligocene through Early Pliocene Epochs), in WOODBURN M. O. (ed.), *Late Cretaceous and Cenozoic Mammals of North America*. Columbia University Press, New York: 169-231.
- TEILHARD DE CHARDIN P. 1915. — Les carnassiers des Phosphorites du Quercy. *Annales de Paléontologie* 9: 101-191.
- VIRET J. 1929. — Les faunes de Mammifères l'Oligocène supérieur de la Limagne Bourbonnaise. *Annales de l'Université de Lyon*, nouvelle série, 47: 1-328.
- WANG B.-Y. & QIU Z.-X. 2003. — Notes on early Oligocene ursids (Carnivora, Mammalia) from Saint Jacques, Nei Mongol, China, in FLYNN L. J. (ed.), *Vertebrate fossils and their context: contributions in honor of Richard H. Tedford*. *Bulletin of the American Museum of Natural History* 279: 116-124.
- WANG X. & TEDFORD R. H. 2008. — Fossil dogs (Carnivora, Canidae) from the Sespe and Vaqueros formations in Southern California, with comments on relationships of *Phlaocyon taylori*, in WANG X. & BARNES L. G. (eds), *Geology and vertebrate Paleontology of Western and Southern North America, contributions in honor of David P. Whistler*. *Natural History Museum of Los Angeles County Science Series* 41: 255-272.
- WANG X., MCKENNA M. C. & DASHZEVEG D. 2005. — *Amphicticeps* and *Amphicyonodon* (Arctoidea, Carnivora) from Hsanda Gol Formation, central Mongolia and phylogeny of basal arctoids with comments on zoogeography. *American Museum Novitates* 3483: 1-57.
- WELCOMME J.-L., ANTOINE P.-O., DURANTHON F., MEIN P. & GINSBURG L. 1997. — Nouvelles découvertes de Vertébrés miocènes dans le synclinal de Dera Bugti (Balouchistan, Pakistan). *Comptes rendus de l'Académie des sciences, Paris, Sciences de la Terre et des Planètes* 325: 531-536.
- WHISTLER D. P. & LANDER E. B. 2003. — New late Uintan to early Hemingfordian land Mammal assemblages from the undifferentiated Sespe and Vaqueros formations, Orange County, and from the Sespe and equivalent Marine formations in Los Angeles, Santa Barbara, and Ventura Counties, southern California, in FLYNN L. J. (ed.), *Vertebrate fossils and their context, contributions in honor of Richard H. Tedford*. *Bulletin of the American Museum of Natural History* 279: 231-268.
- ZHAI R.-J., CIOCHON R. L., TONG Y.-S., SAVAGE D. E., MORLO M., HOLROYD P. A. & GUNNELL G. F. 2003. — An aberrant amphicyonid Mammal from the latest Eocene of the Bose Basin, Guangxi, China. *Acta Palaeontologica Polonica* 48: 293-300.

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