The wide ranging genus *Eucyon* Tedford & Qiu, 1996 (Mammalia, Carnivora, Canidae, Canini) in the Mio-Pliocene of the Old World

Lorenzo ROOK

Università di Firenze, Dipartimento di Scienze della Terra,
via G. La Pira, I-50121 Firenze (Italy)
lorenzo.rook@unifi.it

ABSTRACT

The occurrence of the Tribe Canini (subfamily Caninae) in the Hemphillian (Mio-Pliocene) of North America has been long known without finding contemporary relatives in the Old World. Although scanty and sometimes problematic, the remains of rare dogs in the Old World fossil record are important because they attest to the occurrence of a more diverse taxonomy within the tribe Canini in the late Miocene and Pliocene of Eurasia and Africa. The occurrence of North American *Eucyon* from eastern Asia to western Europe has been securely documented and finally in the very recent years, multiple new findings in eastern Africa of this same genus attest undoubtedly to its occurrence in the fossil record of this continent. The late Miocene expansion of the genus *Eucyon* from America to Eurasia and Africa is a synchronous event with global significance for the Old World continental carnivore guild composition and turnover. Although the *Eucyon* documentation remains quite fragmentary, the general pattern of the dispersal westwards through the Holarctic from North America to the Old World (Asia, Europe, and Africa) is defined. The important fossil documentation at some sites across these continents allowed the recognition of different *Eucyon* species, although deeper analyses are still needed to understand the full pattern of *Eucyon* relationships and its evolutionary history across North America and the Old World.

KEY WORDS
Mammalia,
Carnivora,
Canidae,
Eucyon,
dispersal events,
Mio-Pliocene,
North America,
Eurasia,
Africa.

RÉSUMÉ

Eucyon *Tedford & Qiu, 1996 (Mammalia, Carnivora, Canidae, Canini), genre à large répartition du Mio-Pliocène de l'Ancien Monde.*

L'apparition de la tribu des Canini (sous-famille Caninae) dans l'Hemphillien (Mio-Pliocène) d'Amérique du Nord était connue depuis longtemps sans équivalent dans l'Ancien Monde. Bien que peu abondants et parfois problématiques, les restes de «chiens» dans le registre fossile de l'Ancien Monde sont cruciaux car ils attestent de l'existence d'une diversité taxonomique plus importante de la tribu des Canini au cours du Miocène supérieur et du Pliocène en Eurasie et en Afrique. Au cours des récentes décennies, l'existence du genre nord-américain *Eucyon* en Asie orientale et en Europe occidentale a été clairement attestée et, au cours des toutes dernières années, plusieurs découvertes en Afrique de l'Est ont prouvé incontestablement son existence dans le registre fossile de ce continent. La dispersion fini-miocène du genre *Eucyon* d'Amérique vers l'Eurasie et l'Afrique est un événement synchrone de portée globale pour la composition et le renouvellement de la guilde des carnivores de l'Ancien Monde. Bien que notre connaissance d'*Eucyon* reste assez fragmentaire, le schéma général de sa dispersion vers l'ouest à partir de l'Amérique du Nord vers les régions paléarctiques de l'Ancien Monde (Asie, Europe et Afrique), est bien défini. L'importance des données fossiles de certains sites de ces continents permet de reconnaître différentes espèces d'*Eucyon*, bien que des analyses plus approfondies soient nécessaires pour comprendre le schéma complet des relations d'*Eucyon* et son histoire évolutive à travers l'Amérique du Nord et l'Ancien Monde.

MOTS CLÉS
Mammalia,
Carnivora,
Canidae,
Eucyon,
événements de dispersion,
Mio-Pliocène,
Amérique du Nord,
Eurasie,
Afrique.

INTRODUCTION

The genus *Eucyon* Tedford & Qiu, 1996 is the earliest advanced member of the tribe Canini Fischer de Waldheim, 1817 (Carnivora, Canidae, Caninae). It first occurs in the Clarendonian (late Miocene; 12-9 Ma) of North America (Tedford & Qiu 1996; Wang & Tedford 2008). Being the size of a jackal, *Eucyon* is clearly distinguished from the Vulpini Hemprich & Ehrenberg, 1932 tribe because of the occurrence, for the first time among the Canini, of developed (although small) frontal sinuses expanding into the base of postorbital processes (Tedford & Qiu 1996). This trait, which produces the absence of typical "vulpine depression" on the dorsal surface of the postorbital process, will be maintained as a distinctive trait of the later members of the tribe (members of the genus *Canis* Linnaeus, 1758) where frontal sinuses are much expanded backwards, inflating the region of the postorbital constriction (Tedford *et al.* 1995).

By the latest Miocene, species of *Eucyon* have appeared in Central Asia (Sotnikova & Rook 2009), Europe (Rook 1992), and Africa (Morales *et al.* 2005; Howell & García 2007). From a biogeographical perspective, the origin of the genus is identified in North America (Tedford & Qiu 1996), suggesting a westward dispersal of this form during the latest Miocene (Fig. 1). This dispersal event is not isolated, as the late Miocene is characterized by a number of taxa migrating between North America and the Old World (Flynn *et al.* 1991; Tedford *et al.* 1991; Pickford *et al.* 1995; Qiu 2003). While *Eucyon* did not survive the late Hemphillian in North America (where it gave rise to the first representative of *Canis*; Wang & Tedford 2007, 2008), the genus reached a relative high diversity in the Pliocene of Eurasia, surviving until the very late Pliocene in China, Tadzhikistan, Kazakhstan, and south eastern Mediterranean regions (Turkey, Morocco) (Spassov & Rook 2007; Sotnikova & Rook 2009).
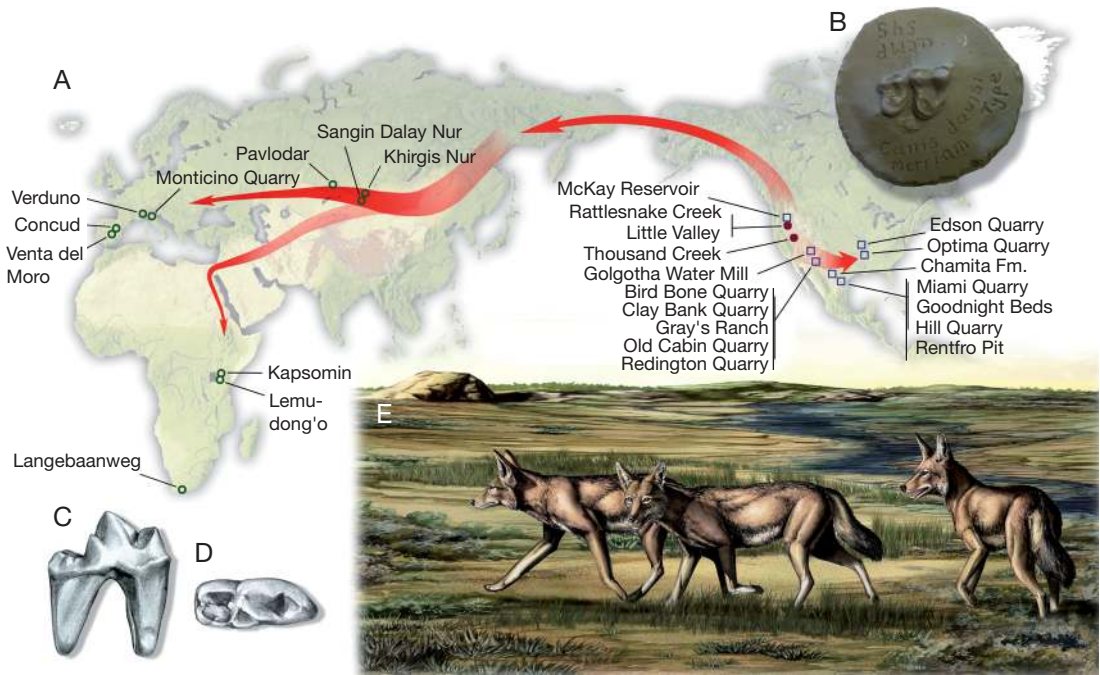
Fig. 1. — The latest Miocene *Eucyon* Tedford & Qiu, 1996 dispersal: **A**, oldest record of *E. davisi* (Merriam, 1911) is from Early Hemphillian localities in the western North America (●). The genus quickly expands its record to east in the central and south eastern North America, where it is a common element in late Hemphillian local faunas (□). The late Miocene (MN 12-13 in the European mammal biochronology; ○ locations correspond to time of transcontinental dispersal of the genus, across the Beringia, towards Asia, Europe, and Africa; **B**, type specimen of *E. davisi*, right M$^{1-2}$ in occlusal view (M^1 length measures about 10 mm) from Rattlesnake creek, early Hemphillian, Oregon (UCMP545; Earth Sciences Dept., University of Florence); **C**, **D**, *E. monticinensis* (Rook, 1992) left M$_1$ in lingual (**C**) and occlusal (**D**) views (M$_1$ length about 17 mm) from Monticino Quarry near Brisighella (BRS27/6; Earth Sciences Dept., University of Florence); **E**, the figure is completed by a reconstructed scene of a group of adult *Eucyon* moving eastward in a late Miocene Central Asia grassland scenario. The artistic scene aims to ideally represent the dispersal of the genus *Eucyon* from North America to the Old World during the latest Miocene.

The genus *Canis* (the most derived clade within the Tribe Canini; Tedford *et al.* 1995) derives from *Eucyon* and has its first occurrence in North America at about 6-5 Ma, close to the Mio-Pliocene transition (Wang & Tedford 2007, 2008), while its record in the Old World is much younger. The dispersal of the wolf-sized members of the genus *Canis* to Asia and Europe is one of the dispersal events that has been identified and used in defining the biochronology of the Late Villafranchian Mammal Age (Azzaroli 1983; Rook & Torre 1996). The dispersal of the genus *Canis* has been diachronous across Eurasia: its first occurrence out of North America is in China from deposits dated approximately 3.4 Ma (Flynn *et al.* 1991; Rook 1993) therefore significantly earlier than in Europe (Azzaroli 1983; Rook & Torre 1996). The dispersal of the wolf-like dogs into Eurasia (the *Canis* event) roughly corresponds to the disappearance of the genus *Eucyon* in Europe (Sotnikova & Rook 2009).

RECOGNIZING THE GENUS *EUCYON*

Until the 1990s, the fossil record of the Canini in the Old World regions was extremely poor and scanty. The very rare fossils of *Canis*-like forms of the Palaearctic region known from the end of the Miocene to Pliocene times were regarded as members of the genus *Canis* "*sensu stricto*" although doubts regarding the real attribution of

late Miocene dogs to the genus *Canis* were raised by the author (Rook *et al.* 1991; Rook 1992; Torre *et al.* 1992).

On consultation with R. H. Tedford (New York), who had already resolved this issue in an unpublished manuscript (Tedford & Taylor 1978, unpublished), in my Ph.D. dissertation (Rook 1993) I informally used the generic name "*Eucyon* Tedford & Qiu, in press" to refer to the late Miocene and earliest Pliocene *Canis*-like forms of North America and the Old World. In the mid 1990's the new genus *Eucyon* was finally described by Tedford & Qiu (1996), referring it to the most primitive *Canis*-like forms of the tribe Canini.

Although the fossil record of the genus still is relatively scanty, much more information is currently available thanks to the description of new fossils and to the re-study of old collections.

In the evolutionary scenario of late Miocene-early Pliocene fossil dogs, the taxonomic positions of a few fossils still remain unresolved. "*Canis*" *michauxi* Martin, 1973 (early Pliocene; MN15) still has an uncertain status. The remains of this form are too few for reliable generic determination and comparison. "*Canis*" *michauxi* is an enigmatic, very large form described from Perpignan (southern France) and the type specimen of this species is no longer available for study. The catalogue number reported in Martin (1973) probably refers to collections in the Perpignan "Collège scientifique universitaire" but it is no longer possible to locate them (J. Michaux pers. comm. in Rook 1993).

Large-sized dogs are documented also in the fossil record in the late Hemphillian of North America (late Miocene to early Pliocene; Tedford *et al.* 2009), and in the Pliocene of Eurasia at (in addition to Perpignan) Csarnota-1 in Hungary (Kormos 1933; Rook 1993) and Chono-Kariakh in Transbaikalia (MN 14). The latter specimen has recently been described as a new species in a new genus: *Nurocyon chonokariensis* Sotnikova, 2006. Although scanty and problematic, these remains are important because they demonstrate the occurrence of a diverse taxonomy within the tribe Canini in the Pliocene of Holarctica and Africa.

AN OVERVIEW OF THE GENUS *EUCYON*

Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Family CANIDAE Fischer de Waldheim, 1817
Subfamily CANINAE Fischer de Waldheim, 1817
Tribe CANINI Fischer de Waldheim, 1817

Genus *Eucyon* Tedford & Qiu, 1996

Tedford & Qiu (1996) named the new genus *Eucyon* for some primitive *Canis*-like forms from the late Hemphillian of North America and from the Pliocene of China. The taxon matches closely with the accumulated data on the zoogeography and morphology of the late Miocene and early Pliocene *s.l. Canis*-like dogs, and for the moment represents a convenient and logical taxonomic allocation for Pliocene dog evolutionary history (Wang *et al.* 2004a, b; Wang & Tedford 2007, 2008).

According to the diagnosis published by Tedford & Qiu (1996), the genus *Eucyon* is distinguished from the fossil and living Vulpini by possession of three synapomorphies also possessed by all other members of the Canini: 1) a frontal sinus that invades the base of the postorbital process usually removing the "vulpine depression" on the dorsal surface of the process; 2) a paroccipital process that is expanded posteriorly and usually has a salient tip; and 3) a mastoid process that is enlarged into a knob or ridge-like prominence.

Furthermore, *Eucyon* lacks a feature characteristic of all other Canini, namely development of a transverse cristid connecting the hypoconid and entoconid of the M_1 talonid. Much attention has been given in the literature to the "simple" talonid structure in the lower carnassial as a feature characteristic of *Eucyon*. In their phylogenetic analysis of the living Canini, Tedford *et al.* (1995) clearly demonstrated that within the Caninae, a morphological trend in the M_1 talonid is the increasing dimensions of the entoconid, the base of which may become large enough to coalesce with that of the hypoconid blocking the talonid basin and splitting it into two basins separated by a cristid connecting the two cuspids. The occurrence of this transverse cristid is the final step in the morphocline leading

to the carnassial talonid structure typical of living Canini. As a matter of fact, although considered a derived feature of the Canini, most Vulpini have also achieved the same condition and populations of *Vulpes* Frisch, 1775 and *Urocyon* Baird, 1857 species may include a sizable proportion of individuals in which the entoconid and hypoconid are joined by cristids from these cusps to form a transverse crest (Tedford *et al.* 1995). Thus, it would not be an exception of the possibility to find in *Eucyon* population, morphotypes with lower carnassial talonid showing the occurrence of a transverse cristid connecting hypoconid and entoconid. In addition to the above traits, *Eucyon* species have, as an autapomorphy, a second posterior cusplet on the P_4 possessed only by the wolf group among the Canini (Tedford & Qiu 1996). Further characteristics of the genus are, in the mandible an attenuated (primitive, cf. Gaspard 1964; Tedford *et al.* 1995) angular process, with insertion for the inferior ramus of the median pterygoid muscle (inferior fossa) not expanded, and in general body proportions, the relative lengthening of the limb bones, especially in the front limbs, with a radius/tibia ratio usually greater than 80%.

A number of species are nowadays recognised in the literature to be included in the genus *Eucyon*, with a zoogeographic range across North America, Asia, Europe and Africa. An overview of the species described for the genus is offered herein.

NORTH AMERICA

Eucyon davisi (Merriam, 1911)

TYPE LOCALITY. — Rattlesnake Creek, early Hemphillian, Oregon.

AGE. — Hemphillian (late Miocene to earliest Pliocene).

GEOGRAPHIC RANGE. — United States; Eastern and Central Asia (see below).

This is a widely distributed species, first appearing in the Early Hemphillian (middle late Miocene) of western United States (Oregon, Nevada) and widely distributed in the late Hemphillian (latest Miocene to earliest Pliocene) through most of United States (Oregon, Nevada, Arizona, New Mexico, Kansas, Oklahoma, Texas) (Harrison 1983; Rook 1993; Tedford *et al.* 2009) (Fig. 1). The intraspecific variability of this taxon, which has a very large temporal range, is considerable (cf. Rook 1993). *Eucyon* did not survive the late Hemphillian in North America (Wang & Tedford 2007, 2008).

A typical Canini trait that first occurs within North American species is the enlargement of the frontal sinuses that expand backwards with the tendency to extend at the level of the post-orbital constriction (Tedford *et al.* 1995; Wang & Tedford 2008). This is coupled with a more derived morphology (in respect to basal Caninae *Leptocyon* Matthew, 1918), in the external brain anatomy characterised by longer cruciate sulci, more expanded sigmoid gyri (although still relatively small) and by the presence of postcruciate and ansate sulci (Lyras & van der Geer 2003).

In living Canini, the expansion of frontal sinuses is linked to the increase of nasals cavity and the noticeable development of turbinate processes and thus to the olfactory system (Tedford *et al.* 1995). The complex maxilloturbinates, with their increase action of breath and moisture exchange, has been a key for canid success in both cold and arid environmental conditions (Wang & Tedford 2008). Such anatomical trait could be also used as an indirect, speculative, inference social behavioural of the genus. Social behaviour is usually not preserved in the fossil record and the typical canid pack hunting social behaviour can only be approached in an indirect way (Andersson 1991; Van Valkenburg & Koepli 1993; Van Valkenburg *et al.* 2003). Nowadays, social hunting in the Caninae is mostly confined to the *Canis* clade (*Canis* and *Lycaon* Brookes, 1827; Macdonald *et al.* 2004) and probably began to develop within this early member of the tribe Canini. The genus *Eucyon*, with its developing expanded turbinates/frontal sinuses, was probably one of the first members of the tribe to possibly use the developed olfactory system as a capability for developing social behaviour (pack hunting). The dramatic change in environmental scenario by the late Miocene was responsible of the replacement of forests and woodlands of the North American mid-continent by extensive grasslands (Cerling *et*

al. 1997; Janis *et al.* 2002). This environmental shift coincided with the Hemphillian faunal turnover, which severely affected the diversity of mammals both in the ungulate and carnivore faunas (Van Valkenburg 1988; Webb & Opdyke 1995; Janis *et al.* 2002; Hunt 2004). A scene in which "the canine's ultimate triumph in the world" (Wang & Tedford 2008: 131) is recorded, and in which the evolution of a behaviour common in living Canini, but very difficult to be detected in the fossil record, more probably emerged as well.

ASIA

Eucyon sp.

LOCALITY. — Khirgis Nur (Mongolia).

CHRONOLOGIC RANGE. — Latest Miocene.

Until recently, the oldest documentation of the genus *Eucyon* in Asia was dated to the early Pliocene (Tedford & Qiu 1996). The *Eucyon* absence from latest Miocene documentation was representing a sort of "*E. vacuum*" in Asia (Wang & Tedford 2008: 145), given the latest Miocene occurrence of the genus in North America, Europe (Rook 1992) and Africa (Morales *et al.* 2005; Howell & García 2007).

The occurrence of *Eucyon* has now been recorded from the latest Miocene of Central Asia, in Mongolia, at Khirgis Nur (Sotnikova & Rook 2009). The previous claimed occurrence of the genus in China from the Upper Baodean (late Miocene) beds in the Yushe basin reported by Deng (2006: 156) is invalid (X. Wang pers. comm.). Given the outstanding record of the late Miocene of China and especially the Yushe Basin, it may well be that eventually late Miocene records of *Eucyon* will be found in China, but such an evidence is not available yet.

The new data from Mongolia reveal that the earliest occurrence of the genus in Asia coincides with that in Europe and Africa, suggesting that the disperal of *Eucyon* from America to the Old World was synchronous. This "*Eucyon* datum" had a profound significance for the Old World continental carnivore guild composition and turnover (Fig. 1).

Eucyon davisi (Merriam, 1911)

TYPE LOCALITY. — See above.

GEOGRAPHIC RANGE IN ASIA. — China, Mongolia, Kazakhstan.

CHRONOLOGIC RANGE. — Latest Miocene to early Pliocene.

Canini not distinct at the specific level from the typical North American species *E. davisi*, have been reported in the early Pliocene fossil record of China by Tedford & Qiu (1996). These authors report the occurrence of *E. davisi* in China along with that of another species (*E. zhoui* Tedford & Qiu, 1996, see later) that has no New World counterpart, suggesting later Miocene differentiation in the genus prior to its appearance in the Asian record (Tedford & Qiu 1996). Chinese specimens attributed to this species include complete skulls (while the North American record does not include complete good skulls). The Chinese material has been used by Tedford & Qiu (1996) to characterize cranial morphology of the species.

In addition to the material from the Yushe Basin (China), a few other findings referable to *E. davisi* have been recently reported from earliest Pliocene in Mongolia (Khirgis Nur, upper levels, and Sangin Dalay Nur) and Kazakhstan (Pavlodar) (Sotnikova & Rook 2009) (Fig. 2).

The occurrence of *E. davisi* in Pliocene sediments in China and Mongolia extends the geographic and geologic range of this taxon (surviving here until the mid Pliocene, perhaps around 2.5 Ma), with an enormous temporal range of more than 6 Ma, from about 9 to 2.5 Ma (Tedford & Qiu 1996).

Eucyon zhoui Tedford & Qiu, 1996

TYPE LOCALITY. — Yushe Basin (China).

AGE. — Early to Middle Pliocene.

This species is known from the early to middle Pliocene of China only from the Yushe Basin. The inferred magnetostratigraphic correlation of the associated deposits which yielded specimens of the species ranges from the late Gilbert to early
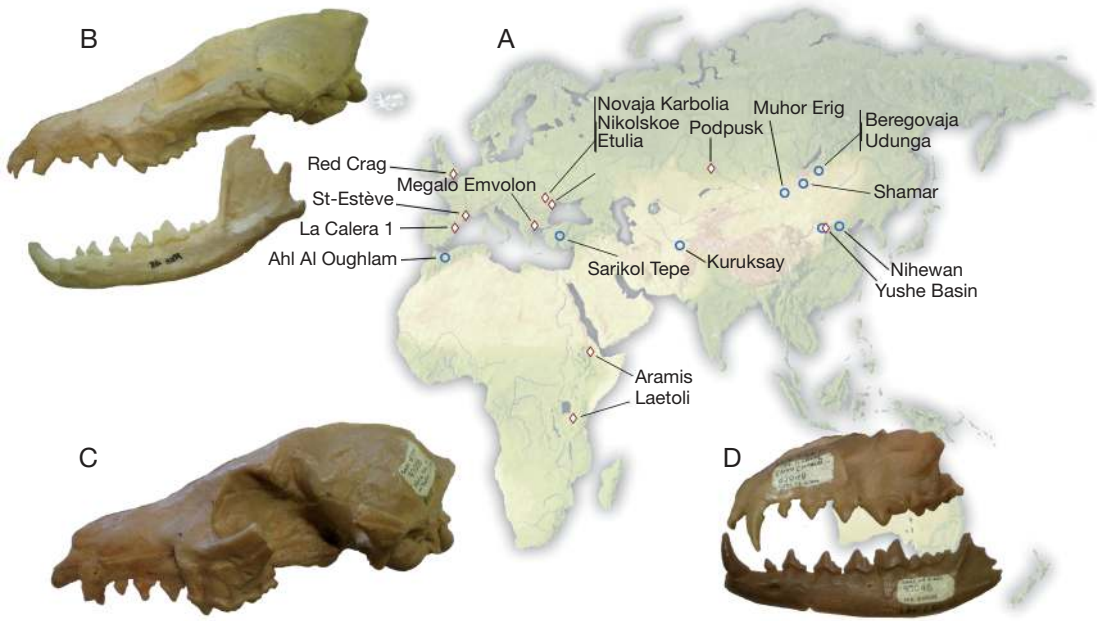
FIG. 2. — The early and mid-Pliocene *Eucyon* Tedford & Qiu, 1996 distribution: **A**, during early and mid-Pliocene times (◇) the genus *Eucyon* had a wide distribution across Eurasia. The very late record of the genus (○, late Pliocene/middle Villafranchian) seems to be limited to central Asia and to the more arid areas of eastern Eurasia (Turkey, North Africa); **B**, the typical Pliocene species from Europe *E. adoxus* (Martin, 1973) from St-Estève (near Perpignan, France; MN 15), cast of skull (approximate length 18 cm) and mandible (reversed) RSS-45 (Basel Naturhistorisches Museum); **C**, *E. davisi* (Merriam, 1911) from Hsia Kou (Yushe basin, China; Pliocene), cast of skull (approximate length 15 cm) F:AM-97056 (American Museum of Natural History, New York); **D**, *E. zhoui* Tedford & Qiu, 1996 from Chao Chuang (Yushe basin, China; Pliocene), cast of skull (reversed) and mandibular ramus (approximate length of mandibular ramus 10 cm) F:AM-97048 (American Museum of Natural History, New York).

Gauss chrons (latest Ruscinian and early Villafranchian, MN15-16; Tedford & Qiu 1996; Deng 2006). The species *E. zhoui* is larger in size than *E. davisi*, and differs from the North American species because of peculiar cranial proportions and because it shows more derived traits both in mandible and teeth morphology. According to Tedford & Qiu (1996), *E. zhoui* could be more closely related to the *Canis*-group than to *E. davisi*.

Eucyon minor
(Teilhard de Chardin & Piveteau, 1930)

Canis chihliensis var. *minor* Teilhard de Chardin & Piveteau, 1939; see Rook 1993; Tedford & Qiu 1996.

TYPE LOCALITY. — Nihewan (China).

AGE. — Late Pliocene; Haiyan Fm. correlative, early Matuyama.

GEOGRAPHIC RANGE. — China, Mongolia, Transbaikalia.

This is a relatively late *Eucyon* species known from the "Villafranchian" (Nihewanian) of China (the deposits from Nihewan of Teilhard de Chardin & Piveteau (1930) are correlative with the Haiyan Fm. of the Yushe Basin, dated by magnetostratigraphy to the early Matuyama; Flynn *et al.* 1991; R. H. Tedford pers. comm. in Rook 1993). Other specimens of *E.* cf. *minor* from the late Pliocene of Mongolia (Rook 1993) are kept within the collections of the Institute of Geology in Moscow (GIN), from three Pliocene sites (MN 16, early Villafranchian; Pevzner *et al.* 1982; Vislobokova *et al.* 2001): Shamar, Beregovaja and Udunga (Fig. 2).

The specimen from Udunga has been described by Sotnikova & Kalmykov (1991) as *Canis* sp. The samples from Shamar and Beregovaja have been listed by Kurtén (1974) as coyote-like dogs. The lower carnassial morphology of the Shamar and Beregovaja specimens have the typical characteristics of the genus *Eucyon*. Rook (1993), on the basis of dental morphology and the similarities with *E. minor* from China, attributed this material to *E.* cf. *minor*. More recently, Sotnikova (2004) proposed the same taxonomic placement for the larger of the two Shamar mandibles, but suggested an attribution to a new species for the smaller one. An attribution of the Shamar and Beregovaja specimens to *E.* cf. *minor* has been also suggested by R. H. Tedford (pers. comm. in Spassov & Rook 2007).

Eucyon marinae Spassov & Rook, 2007

TYPE LOCALITY. — Muhor-Erig (Mongolia).

AGE. — Late Pliocene.

This species of *Eucyon* has been described from a geological context in Central Mongolia suggesting a late Ruscinian age, although, an early Villafranchian age cannot be ruled out (Spassov & Rook 2007). *Eucyon marinae* is a relatively large species, comparable in size with *E. davisi* (Merriam, 1911) and *E. monticinensis* (Rook, 1992) but with slender and gracile mandible with elongate rostral portion and very long premolar row.

EUROPE

Eucyon cipio (Crusafont Pairó, 1950)

TYPE LOCALITY. — Concud (Spain).

AGE. — Late Miocene (Turolian; MN 12).

GEOGRAPHIC RANGE. — Teruel basin (Spain).

The species was the first canine to be documented in the fossil record of the Old World (Crusafont Pairó 1950). Known from the late Turolian (MN 12) of Spain, it has been regarded for long time as a member of the genus *Canis* "*sensu stricto*"

(Crusafont Pairó 1950; Pons Moyá & Crusafont Pairó 1978; Alcalá Martínez 1994) but an attribution to the genus *Canis* was later questioned by Rook *et al.* (1991) Torre *et al.* (1992) and Rook (1992, 1993).

Eucyon cipio is represented by the type specimen (a right maxillary bone bearing P^3-M^2) from Concud (Crusafont Pairó 1950; Pons Moyá & Crusafont Pairó 1978) and by an isolated right lower carnassial (M_1) from Los Mansuetos (Alcalá Martínez 1994).

The dental morphology for both upper dentition (P^4 with a small protocone, anteriolingually oriented and extended; lingual cingulum in M^1 ending at the level of metacone; M^2 relatively large) and lower tooth (M_1 talonid lacking a transverse cristid between hypoconid and entoconid), is primitive and suggestive of a taxon at an early stage of evolution before the differentiation of the genus *Canis*. As a matter of fact *E. cipio* predates the first occurrence of the true genus *Canis* in North America and is roughly contemporary to the *Eucyon* first occurrence in North America (Wang & Tedford 2007, 2008).

Eucyon monticinensis (Rook, 1992)

TYPE LOCALITY. — Monticino gypsum quarry (Brisighella; Italy).

AGE. — Latest Miocene (Turolian; MN 13).

GEOGRAPHIC RANGE. — Latest Miocene of Italy and Spain.

Described from late Messinian (MN 13) of Italy, *E. monticinensis* is, together with *E. davisi* and *E. intrepidus* Morales, Pikford & Soria, 2005, one of the earliest representatives of the genus (Rook 1992). The small dog from the Monticino gypsum quarry was first described as "*Canis*" sp. by Rook *et al.* (1991) and later referred to the new species by Rook (1992). The species has been recently identified at Verduno, a new Messinian (MN 13) vertebrate bearing site in north western Italy (Sardella 2008).

In the original description of the species, Rook (1992) referred to *E.* cf. *monticinensis* also the
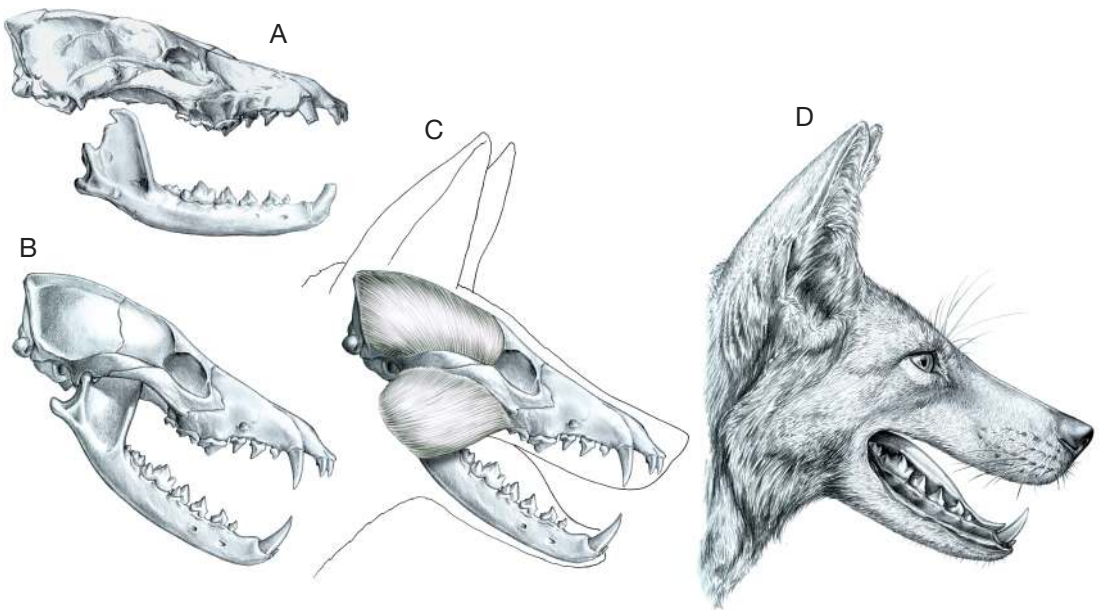
FIG. 3. — *Eucyon adoxus* (Martin, 1973) from St-Estève (near Perpignan, France; MN 15): **A**, type specimen RSS 45, approximate length of the skull 18 cm; **B**, skull and mandible reconstruction based on type specimen RSS 45; **C**, reconstruction of principal jaw-abductor muscles positioned on the reconstructed skull; **D**, life appearance of the head.

material from the late Miocene Spanish site of Venta del Moro, previously described as *Nyctereutes* Temminck, 1839, *Canis*, and *Vulpes* (Morales & Aguirre 1976; Morales 1984). Noteworthy is that in recent years the site of Venta del Moro yielded a number of new *Eucyon* specimens. A revision of the old and new material allowed Montoya *et al.* (2009, this volume) to erect a new specific name for the Spanish latest Miocene Canini, *E. debonisi* Montoya, Morales & Abella, 2009.

Eucyon odessanus (Odintzov, 1967)

TYPE LOCALITY. — Odessa Catacombs (Ukraine).

AGE. — early Pliocene (Ruscinian; MN 15).

GEOGRAPHIC RANGE. — Moldova, Ukraine, Greece, Turkey.

A very large sample from the Odessa catacombs (MN15; Ukraine) has been described as *Vulpes odessana* by Odintzov (1967). Rook (1993) considered this material, as well as the unpublished skull from the early Pliocene of Etulia in Moldova (kept in the collections of the Institute of Geology in Moscow) as belonging to the genus *Eucyon*. The dentition of *E. odessanus* is similar in dimensions to *E. davisi* but it shows some differences in premolars proportions (Tedford & Qiu 1996; Spassov & Rook 2007).

Two hemimandibles from Alatini (now Megalo Emvolon; early Pliocene of Greece; Koufos *et al.* 1991) were described as *Nyctereutes donnezani* (Depéret, 1890) by Sickenberg (1972). Doubts regarding the generic attribution of this material were expressed by Soria & Aguirre (1976) and referral to *Eucyon* has been suggested by Rook (1993). Koufos (1997) re-described one of the mandibles as *E. davisi*, although stressing some similarities with the species *E. odessanus*. In the writer opinion, *E. odessanus* is to be considered a species distinct from *E. davisi* and the Megalo Emvolon specimens are better attributable to the Odessa species. *Eucyon* cf. *odessanus* is also reported from a middle Villafranchian site of Turkey (Sarikol Tepe; Kostopoulos & Sen 1999).

Eucyon adoxus (Martin, 1973)

Type locality. — St-Estève, near Perpignan (France).

Age. — Early Pliocene (Ruscinian; MN 15).

Geographic range. — France, Spain.

This is a relatively large Pliocene dog from MN15 of St-Estève, near Perpignan, in southern France (Fig. 2). *Eucyon adoxus* is characterized by an elongate rostrum and mandible and is clearly not a vulpine (as is claimed by some authors, e.g., Pons Moyá & Crusafont Pairó 1978), because it does not have the typical vulpine depression in the region of postorbital constriction of the frontal bones (Rook 1992, 1993). Although the mandibles of the Perpignan dog show features typical of *Eucyon*, Tedford & Qiu (1996) note that some of the derived features they display (mainly in the dentition) are synapomorphies for other canine lineages and therefore they could represent a taxon different from *Eucyon*. As discussed in Rook (1993) and then supported by Wang & Tedford (2008), it is maintained here the opinion that the Perpignan dog is one of the latest representatives of the evolutionary differentiation of the genus *Eucyon* in Europe (Fig. 2). A number of contemporary findings occur in Europe (La Calera I, Spain: Alcalá Martínez 1994; Red Crag, UK: Lydekker 1885; Rook 1992, 1993).

The record of this species includes a magnificently preserved type skull and mandibles (specimen RSS 45; Fig. 3A, B). The material is good enough for allowing a reconstruction of the life appearance of the head of this species (Fig. 3D), herein joined with the reconstruction of principal jaw-abductor muscles (Fig. 3C).

?*Eucyon* sp.

Canis ex gr. *lepophagus* from Kuruksay – Sotnikova 1989.

Locality. — Kuruksay (Kazakhstan).

Age. — Late Pliocene (MN17).

Two mandibular fragments from Kuruksay (Kazakhstan; MN17) were described by Sotnikova (1989) as *Canis* ex gr. *lepophagus*. The material was excavated from the type locality of "*Canis*" *kuruksaensis* Sotnikova, 1989. This led Rook (1993) to suggest the inclusion of these mandibles in the latter species. The relationships of these mandibles to the skull of "*Canis*" *kuruksaensis* (a dog that should be included in the genus *Eucyon* according to R. H. Tedford [pers. comm. in Spassov & Rook 2007]) are not yet clarified. In the original description (Sotnikova 1989; description published well before the naming of the genus *Eucyon*) the mandibular diagnostic features separating *Canis* from the later described *Eucyon* are not discussed. In any case, the material is in a very bad state of preservation and a definite decision regarding their taxonomic status will be a difficult task (Spassov & Rook 2007).

Africa

Recognition of the occurrence of the genus *Eucyon* in the fossil record of the African continent has been fully acknowledged only in very recent years. Rook (1993) reported that the occurrence of different *Eucyon* species was possibly identifiable also in one latest Miocene and one early Pliocene site in Africa: 1) the latest Miocene of E Quarry at Langebaanweg (South Africa; Fig. 1), from where Hendey (1974, 1978, 1981) described some remains (among which an almost complete cranium and mandibles) as *Vulpes* sp. and as "gen. et sp. not det. (?aff. *Canis brevirostris*)"; 2) various sites at Laetoli (early Pliocene, Tanzania; Fig. 2), from where Barry (1987) referred to as "new genus?, aff. *Canis brevirostris*" a number of fragmentary remains.

Rook (1993) revised the material and hypothesized that both Langebaanweg and Laetoli fossil canids could represent the occurrence of the genus *Eucyon* in Africa (the Langebaanweg form being very primitive). An opinion that was supported by Werdelin & Lewis (2000), at least for the material from Laetoli referred by Barry (1987) to "new genus?, aff. *Canis brevirostris*". As a matter of fact however, a proper taxonomic identification of these fossils needs further work.

A further occurrence of *Eucyon* in Africa is at the late Pliocene site of Ahl Al Oughlam in Morocco. There Geraads (1997) described a few remains of *Canis* n. sp., aff. *C. aureus* Linnaeus, 1758. The material, whose morphology resembles *Eucyon*, was recently maintained within the genus *Canis* by Geraads (2008).

It is only in very recent years that new material has been described from fossil sites in the latest Miocene of Kenya (Kapsomin and Lemudong'o) and early Pliocene of Ethiopia (Aramis).

Eucyon intrepidus
Morales, Pikford & Soria, 2005

Type locality. — Kapsomin (Tugen Hills, Kenya).

Age. — Latest Miocene.

Geographic range. — Kenya.

This species is the earliest known Canini in Africa. First described for material from the latest Miocene of Kapsomin (Tugen Hills, Lukeino Fm.; Morales *et al.* 2005), it has been identified also from the latest Miocene site of Lemudong'o (Howell & García 2007). Both the occurrences are in Kenya (Fig. 1). This species (like the second African one ?*E. wokari* García, 2008; see below) differs from the typical contemporary North American and European species (*E. davisi* and *E. monticinensis* respectively) by its smaller size and the greater relative heights of the trigonid cusps. This African species is described as characterized by a shorter talonid in respect to European and North American *Eucyon*. The sample from Kapsomin (Morales *et al.* 2005) does not include a lower carnassial, but this tooth has been recovered from Lemudong'o (Howell & García 2007). According to Howell & García (2007), M_1 talonid has an open occlusal basin without a cristid linking hypoconid and entoconid, one of the diagnostic features for the genus *Eucyon*.

?*Eucyon wokari* García, 2008

Type locality. — Aramis (Ethiopia).

Age. — Early Pliocene.

The remains from Aramis represent the most recently described species of the genus, although the occurrence of an upper M^3 in the maxilla (García 2008: 586; Fig. 3) cast doubts even on the tribe attribution of this taxon. Comparable in size with the late Miocene African species *E. intrepidus*, the detail morphology of ?*Eucyon wokari* lower molars is peculiar, especially for the talonid structure in the lower carnassial. The latter is described as highly derived being hypoconid and entoconid "connected by a tiny cristid" (García 2008: 588). This character (see above, the discussion on *Eucyon* distinctive features), is usually absent in all the *Eucyon* species, but present in all the other Canini (Tedford & Qiu 1996), and may occur also in living Vulpini populations (Tedford *et al.* 1995).

According to García (2008) ?*Eucyon wokari* might represent a new eastern African chronospecies of this canid lineage that inhabited eastern Africa during the Pliocene and, as it is the case of the very derived *E. zhoui* from China (Tedford & Qiu 1996), ?*Eucyon wokari*, could be eventually more closely related to the *Canis*-group than to *Eucyon*.

CONCLUSIONS

The dispersal event of Canini into Old World Carnivora guild was associated with a global re-arrangement of structural composition of mammalian communities at the end of the Miocene. The long-term effect of this dispersal has been the disappearance of many taxa of the Hyaenidae family (especially the canid-like morphotypes) and the expansion of Canini into the Pliocene and Pleistocene carnivore guilds (Werdelin & Turner 1996).

The occurrence of the tribe Canini (subfamily Caninae) since the late Miocene of North America has been well known for a long time. Their occurrence in North America has been then confirmed by a large number of findings in the Hemphillian (Mio-Pliocene), with virtually no finding of contemporary relatives in the Old World until few decades ago.

In recent decades, the occurrence of North American *Eucyon* from eastern Asia to western Europe has been securely documented and finally in the last few years, multiple new findings in Eastern Africa of this same genus attest undoubtedly its occurrence also in the fossil record of this continent. Even if scanty and problematic, the remains of rare larger dogs (among which those of "*Canis*" *michauxi*) are also important because they attest the occurrence of a more diverse taxonomy within the tribe in the Pliocene of Holoarctic regions.

Although the *Eucyon* documentation remains quite fragmentary, the general pattern of the dispersal westwards through the Palaearctic from North America to the Old World (Asia, Europe and Africa) can be now outlined (Figs 1; 2). The important fossil documentation at some sites across these continents allowed the recognition of different *Eucyon* species, although deeper analyses are still needed to understand the full pattern of *Eucyon* relationships and its evolutionary history across North America and the Old World.

REFERENCES

ALCALÁ MARTÍNEZ L. 1994. — *Macromamíferos neógenos de la fosa de Alfambra-Teruel*. Teruel Instituto de Estudios Turolenses, Museo Nacional de Ciencias Naturales, Madrid, 554 p.

ANDERSSON K. 2005. — Were there pack-hunting canids in the Tertiary, and how can we know? *Paleobiology* 31: 56-72.

AZZAROLI A. 1983. — Quaternary mammals and the "End-Villafranchian" dispersal Event. A turning point in the history of Eurasia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 44: 117-139.

BARRY J. C. 1987. — Larger Carnivores (Canidae, Hyaenidae, Felidae) from Laetoli, *in* LEAKEY M. D. & HARRIS J. M. (eds), *Laetoli: a Pliocene Site in Tanzania*. Clarendon Press, Oxford: 235-258.

CERLING T. E., HARRIS J. M., MACFADDEN B. J., LEAKEY M. G., QUADE J., EISENMANN V. & EHLERINGER J. R. 1997. — Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389: 153-158.

CRUSAFONT PAIRÓ M. 1950. — El primer representante del género *Canis* en el Pontiense Eurasiatico (*Canis cipio* nova sp). *Boletin de la Real Sociedad Española de Historia Natural*, Madrid, 48: 43-56.

DENG T. 2006. — Chinese Neogene Mammal Biochronology. *Vertebrata PalAsiatica* 44: 143-163.

FLYNN J. J., TEDFORD R. H. & QIU Z. 1991. — Enrichment and stability in the Pliocene mammal faunas of North China. *Paleobiology* 17: 246-265.

GARCÍA N. 2008. — New *Eucyon* remains from the Pliocene Aramis Member (Sagantole Formation), Middle Awash Valley (Ethiopia). *Comptes rendus Palevol* 7: 583-590

GASPARD M. 1964. — La région de l'angle mandibulaire chez les Canidae. *Mammalia* 28: 249-329.

GERAADS D. 1997. — Carnivores du Pliocène terminal de Ahl Al Ougham (Casablanca, Maroc). *Geobios* 30: 127-164.

GERAADS D. 2008. — Plio-Pleistocene Carnivora of northwestern Africa: a short review. *Comptes rendus Palevol* 7: 581-599

HARRISON J. A. 1983. — The Carnivora of the Edson Local Fauna (late Hemphillian), Kansas. *Smithsonian Contributions to Paleobiology* 54: 1-42.

HENDEY Q. B. 1974. — The Late Cenozoic Carnivora of the southwestern Cape Province. *Annals of the South African Museum* 63: 1-369.

HENDEY Q. B. 1978. — Late Tertiary Mustelidae (Mammalia, Carnivora) from Langebaanweg, South Africa. *Annals of the South African Museum* 79: 329-357.

HENDEY Q. B. 1981. — Paleoecology of the late Tertiary fossil occurrences in "E" Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. *Annals of the South African Museum* 84: 1-104.

HOWELL F. C. & GARCÍA N. 2007. — Carnivora (Mammalia) from Lemudong'o (late Miocene: Narok District, Kenya). *Kirtlandia* 46: 121-139.

HUNT R. M. JR 2004. — Global climate and the evolution of large mammalian carnivores duringlater Cenozoic in North America. *Bulletin of the American Museum of Natural History* 285: 139-156.

JANIS C. M., DAMUTH J. & THEODOR J. M. 2002. — The origin and evolution of the North American grassland biome: The story from hoofed mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 177: 183-189.

KORMOS T. 1933. — Die Wölfe des ungarischen Oberpliozäns. *Folia Zoologica et Hydrobiologica* 5: 13-35.

KOSTOPOULOS D. & SEN S. 1999. — Late Pliocene (Villafranchian) mammals from Sirakol Tepe, Ankara, Turkey. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 39: 165-202.

KOUFOS G. D. 1997. — The canids *Eucyon* and *Nyctereutes* from the Ruscinian of Macedonia, Greece. *Paleontologia i Evolució* 30-31: 39-48.

KOUFOS G. D., SYRIDES S. & KOLIADIMOU K. K. 1991. — A Pliocene primate from Macedonia (Greece). *Journal of Human Evolution* 21: 289-204.

KURTÉN B. 1974. — A history of coyote-like dogs in North America (Canidae, Mammalia). *Acta Zoologica Fennica* 140: 1-38.

LYDEKKER R. B. 1885. — *Catalogue of the Fossil Mammalia in the British Museum. Part I: Primates, Chiroptera, Insectivora, Carnivora.* British Museum (Natural History), London, 263 p.

LYRAS G. & VAN DER GEER A. 2003. — External brain anatomy in relation to the phylogeny of Caninae (Carnivora: Canidae). *Zoological Journal of the Linnean Society* 138: 505-522.

MACDONALD D. W., CREEL S. & MILLS M. G. L. 2004. — Canid society, *in* MACDONALD D. W. & SILLERO ZUBIRI C. (eds), *The Biology and Conservation of Wild Canids*. Oxford University Press, Oxford: 85-106.

MARTIN R. 1973. — Trois nouvelles espèces de caninae (Canidae, Carnivora) des gisements Plio-Villafranchiens d'Europe. *Documents du Laboratoire de Géologie de la Faculté de Sciences de Lyon* 57: 87-96.

MERRIAM J. C. 1911. — Tertiary mammal beds of Virgin Valley and Thousand Creek in North-western Nevada. Part II: vertebrate faunas. *University of California Publications in Geology* 11: 199-304.

MONTOYA P., MORALES J. & ABELLA J. 2009. — *Eucyon debonisi* n. sp., a new Canidae (Mammalia, Carnivora) from the latest Miocene of Venta del Moro (Valencia, Spain). *Geodiversitas* 31 (4): 709-722.

MORALES J. 1984. — *Venta del Moro: su macrofauna de mamíferos, y biostratigrafía continental del Mioceno terminal mediterráneo.* Tesis Doctoral 15/84 Editorial de la Universidad Complutense de Madrid, Spain, 313 p.

MORALES J. & AGUIRRE E. 1976. — Carnívoros de Venta del Moro (Valencia). *Trabajos sobre Neógeno-Cuaternario* 5: 31-74.

MORALES J., PICKFORD M. & SORIA D. 2005. — Carnivores from the late Miocene and basal Pliocene of the Tugen Hills, Kenya. *Revista de la Sociedad Geologica Española* 18: 39-61.

ODINTZOV I. A. 1967. — New species of Pliocene Carnivora, *Vulpes odessana* sp. nov. from the Karst Cave of Odessa. *Paleontologicheskyi Sbornik*, L'vov University, 4: 130-137 (in Russian).

PEVZNER M. A., VANGENGEIM E. A., ZHEGALLO V. I., ZAZHIGIN B. S. & LISKUN I. G. 1982. — Correlation of the upper Neogene sediments of Central Asia and Europe on the basis of paleomagnetic and biostratigraphic data. *International Geology Review* 25: 1075-1085.

PICKFORD M., MORALES J. & SORIA D. 1995. — Fossil camels from the Upper Miocene of Europe: implications for biogeography and faunal change. *Geobios* 28: 641-650.

PONS MOYÁ J. & CRUSAFONT PAIRÓ M. 1978. — El *Canis cipio* Crusafont (1950), comparacion con los canidos del Plioceno y Pleistoceno europeo. *Acta Geologica Hispanica* 13:133-136.

QIU Z. 2003. — Dispersals of Neogene carnivorans between Asia and North America. *Bulletin of the American Museum of Natural History* 279: 18-31.

ROOK L. 1992. — "*Canis*" *monticinensis* sp. nov., a new Canidae (Carnivora, Mammalia) from the late Messinian of Italy. *Bollettino della Società Paleontologica Italiana* 31: 151-156.

ROOK L. 1993. — *I cani dell'Eurasia dal Miocene Superiore al Pleistocene Medio.* Ph.D. Dissertation, Modena, Bologna, Firenze and Roma "La Sapienza" Universities, Italy, 153 p., 29 plates.

ROOK L. & TORRE D. 1996. — The "Wolf-event" in Western Europe and the beginning of the Late Villafranchian. *Neues Jahrbuch für Geologie und Päläontologie-Monatshefte* 8: 495-501.

ROOK L., FICCARELLI G. & TORRE D. 1991. — Messinian carnivores from Italy. *Bollettino della Società Paleontologica Italiana* 30: 7-22.

SARDELLA R. 2008. — Remarks on the Messinian carnivores (Mammalia) of Italy. *Bollettino della Società Paleontologica Italiana* 47: 195-202.

SICKENBERG O. 1972. — Ein unterkiefer des Caniden *Nyctereutes donnezani* (Dep.) aus der umgebung von Saloniki (Griech. Mazedonien) und seine biostratigraphische bedeutung. *Annales Naturhistorisches Museum Wien* 76: 499-513.

SHOTWELL J. A. 1956. — Hemphillian mammalian assemblage from north-eastern Oregon. *Bulletin of the Geological Society of America* 67: 717-738.

SHOTWELL J. A. 1970. — Pliocene mammals of south-western Oregon and adjacent Idaho. *Bulletin of the University of Oregon Museum of Natural History* 17: 1-103.

Soria D. & Aguirre E. 1976. — El canido de Layna: revision de los *Nyctereutes* fosiles. *Trabayos sobre Neogeno-Cuaternario* 5: 83-115.

Spassov N. & Rook L. 2006. — *Eucyon marinae* sp. nov. (Mammalia, Carnivora), a new canid species from the Pliocene of Mongolia, with a review of forms referable to the genus. *Rivista Italiana di Paleontologia e Stratigrafia* 112: 123-133.

Sotnikova M. V. 1989. — [*The Carnivore Mammals from the Pliocene to the Early Pleistocene. Stratigraphic Significance*]. Nauka, Moscow, 122 p. (in Russian).

Sotnikova M. V. 2004. — [The middle Pliocene assemblage of Carnivore from Shamar locality (Northern Mongolia)]. *Abstracts the International Conference on the Paleontology of the Central Asia. Moscow, RAS Paleontological Institute*, 27-28 May, 2004: 54-56 (in Russian).

Sotnikova M. V. 2006. — A new canid *Nurocyon chonokhariensis* gen. et sp. nov. (Canini, Canidae, Mammalia) from the Pliocene of Mongolia. *Courier Forsch-Institut Senckenberg* 256: 11-21.

Sotnikova M. V. & Kalmykov N. P. 1991. — [Pliocene carnivore from Udunga locality, Transbaikal, USSR] *in* Vangengeim I. (ed.), *Pliocene and Anthropogene Paleogeography and Biostratigraphy.* USSR Academy of Sciences, Geological Institute: 146-160 (in Russian).

Sotnikova M. & Rook L. 2009. — Dispersal of the Canini (Mammalia, Canidae: Caninae) across Eurasia during the late Miocene to Early Pleistocene. *Quaternary International* doi:10.1016/j.quaint.2009.06.008.

Tedford R. H. & Qiu Z. 1996. — A new canid genus from the Pliocene of Yushe, Shanxi Province. *Vertebrata PalAsiatica* 34: 27-40.

Tedford R. H. & Taylor B. E. 1978. — *North American Fossil Canidae (Mammalia, Carnivora): the Tribe Canini (Subfamily Caninae).* American Museum of Natural History, unpublished manuscript, New York, 365 p.

Tedford R. H., Taylor B. E. & Wang X. 1995. — Phylogeny of the Caninae (Carnivora: Canidae): The living taxa. *American Museum Novitates* 3146: 1-37.

Tedford R. H., Flynn J. L., Qiu Z., Opdyke N. & Downs W. R. 1991 — Yushe basin, China: Paleomagnetically calibrated mammalian biostratigraphic standard for the late Neogene of Eastern Asia. *Journal of Vertebrate Paleontology* 11: 519-526.

Tedford R. H., Wang X. & Taylor B. E. 2009. — Phylogenetic systematics of the North American fossil Caninae (Carnivora: Canidae). *Bulletin of the American Museum of Natural History* 325: 1-218.

Teilhard de Chardin P. & Piveteau J. 1930. — Les mammifères fossiles de Nihowan (Chine). *Annales de Paléontologie* 19: 1-134.

Torre D., Ficcarelli G., Masini F., Rook L. & Sala B. 1992. — Mammal dispersal events in the early Pleistocene of western Europe. *Courier Forsch-Institut Senckenberg* 153: 51-58.

Van Valkenburg B. 1988. — Trophic diversity in past and present guilds of large predatory mammals. *Paleobiology* 14: 155-173.

Van Valkenburg B. & Koepfli K. P. 1993. — Cranial and dental adaptations to predation in canids, *in* Dunstone N. & Gorman M. L. (eds), *Mammals as Predators. Series Symposia of the Zoological Society of Oxford 65.* Oxford University Press, Oxford: 15-37.

Van Valkenburg B., Sacco T. & Wang X. 2003. — Pack hunting in Miocene Borophagine dogs: evidence from craniodental morphology and body size, *in* Flynn J. L. (ed.), Vertebrate fossils and their context: Contributions in honour of Richard H. Tedford. *Bulletin of the American Museum of Natural History*: 147-162.

Vislobokova I., Sotnikova M. V. & Dodonov A. 2001. — Late Miocene-Pliocene mammalian fauna of Russia and neighbouring countries. Neogene and Quaternary continental stratigraphy and mammalian evolution. *Bollettino della Società Paleontologica Italiana* 40: 307-313.

Wang X. & Tedford R. H. 2007. — Evolutionary history of Canids, *in* Jensen P. (ed.), *The Behavioural Biology of Dogs*. CABI, Wallingford: 3-20.

Wang X. & Tedford R. H. 2008. — Dogs, their fossil relatives and evolutionary history. *Columbia University Press*: 1-219.

Wang X., Tedford R. H., Van Valkenburgh B. & Wayne R. K. 2004a. — Ancestry: evolutionary history, molecular systematics and evolutionary ecology of Canidae, *in* Macdonald D. W. & Sillero Zubiri C. (eds), *The Biology and Conservation of Wild Canids*. Oxford University Press, Oxford: 39-54.

Wang X., Tedford R. H., Van Valkenburgh B. & Wayne R. K. 2004b. — Phylogeny, classification and evolutionary ecology of the Canidae, *in* Sillero Zubiri C., Hoffmann M. & Macdonald D. W. (eds), *Canids: Foxes, Wolves, Jakals and Dogs. Status Survey and Conservation Action Plan*. IUCN/SSC Canid Specialist Group, The World Conservation Union, Gland, Switzerland: 8-20.

Webb S. D. & Opdyke N. D. 1995. — Global climatic influence on Cenozoic land mammal faunas, *in* Kenneth J. P. & Stanley S. M. (eds), *Effects of Post Global Change on Life*. National Academy Press, Washington, DC: 184-208.

Werdelin L. & Lewis M. E. 2000. — Carnivora from the South Turkwell hominid site, northern Kenya. *Journal of Palaeontology* 74: 1173-1180.

Werdelin L. & Turner A. 2000. — Turnover in the guild of larger carnivores in Eurasia across the Miocene/Pliocene boundary. *Acta Zoologica Cracoviensa* 39: 585-592.

APPENDIX 1

List of *Eucyon* Tedford & Qiu, 1996 dentognatic material studied.

The material is listed grouped by continents (North America, Asia, Europe, and Africa). The list of studied specimens is reported, for each species, by locality with the indication of museum/collection repository, catalogue number, anatomic part, and – in case the specimen has been figured – bibliographic reference.

COLLECTION ACRONYMS

AMNH   American Museum of Natural History, New York;
BRS   Museo Civico di Storia Naturale, Faenza;
F:AM   Frick collection, American Museum of Natural History, New York;
FM   National Museum of Natural History, Sofia;
GIN   Geological Institute, Academy of Sciences, Moscow;
ILM   Museo Nacional de Ciencias Naturales, Madrid;
IPS   Institut Catalá de Paleontologia, Sabadell;
KUVP   University of Kansas Museum of Natural History, Lawrence, Kansas;
M   Natural History Museum, London;
NMB   Naturhistorisches Musem, Basel;
PIN   Palaeontological Institute, Academy of Sciences, Moscow;
PQ:L   South African Museum, Cape Town;
UCMP   University of California Museum of Palaeontology, Berkeley, California;
UO   University of Oregon, Museum of Natural History, Eugene;
V [THP] Tianjin Museum (China).

NORTH AMERICA

Eucyon davisi (Merriam, 1911)

Rattlesnake Creek, John Day Valley, Wheeler County (Oregon); late Miocene, early Hemphillian.
  – UCMP 545: fragmentary maxillary bone with right M^1-M^2. Type specimen (figured in Merriam 1911, Rook 1993; Fig. 1A).

Thousand Creek, Humbolt County (Nevada); late Miocene early Hemphillian.
  – UO 12505: right M^1;
  – UO 12543: right M_1 (fragmentary) and left M_2.

Little Valley, Malheur County (Oregon); late Miocene early Hemphillian.
  – U0-26742: fragmentary skull with right pre-maxillary bone bearing I^2-I^3, left maxillary bone bearing P^1-M^2; right and left mandibular rami with I_1-M_3 (figured in Shotwell 1970).

Chamita Fm., Rio Arriba County (New Mexico); late Miocene, early Hemphillian.
  – F:AM 27485: left mandibular ramus with C-M_3;

  – F:AM 49296: left mandibular ramus with P_2-M_2;
  – F:AM 49297: right mandibular ramus with P_3-M_1.

Bird Bone Quarry, Mohave County (Arizona); early Pliocene, late Hemphillian.
  – F:AM 63000: right mandibular ramus with M_1-M_2;
  – F:AM 63001: right mandibular ramus with C-M_2;
  – F:AM 63004: fragmentary cranium with right P^2, P^4-M^2;
  – F:AM 63005: fragmentary cranium with right P^3-M^1;
  – F:AM 63007: fragmentary cranium with left P^3-M^2;
  – F:AM 63015: right and left mandibular rami with P_1-M_1;
  – F:AM 63016a: right mandibular ramus with P_4-M_1;
  – F:AM 63016b: right mandibular ramus with P_3-M_2;
  – F:AM 63019: fragmentary cranium with left P^1-M^2; right and left mandibular rami with P_3-M_3;
  – F:AM 63020: right and left maxillary bones with C, P^4-M^2; right and left mandibular rami with M_1;
  – F:AM 63022: left mandibular ramus with M_1;
  – F:AM 63023: left damaged mandibular ramus with P_4-M_2;
  – F:AM 63025: left mandibular ramus with P_2-M_1;
  – F:AM 63026: left mandibular ramus with P_2-M_2 (figured in Rook 1993);
  – F:AM 63027: right M_1-M_2;
  – F:AM 63028c: left mandibular ramus with P_4-M_2;
  – F:AM 63033: right and left maxillary bones with P^4-M^2;
  – F:AM 63034: right and left maxillary bones with P^1- P^2, P^4-M^2; left mandibular ramus with P_2-P_3;
  – F:AM 63038: palate with right P^2-M^2; right and left mandibular rami with P_2-M_2;
  – F:AM 63039: fragmentary skull with left P^2-M^2;
  – F:AM 63041: left mandibular ramus with P_2-M_2;
  – F:AM 63042: left mandibular ramus with P_1, P_4-M_2;
  – F:AM 63046: right and left mandibular rami with P_3-M_2;
  – F:AM 63051: right and left mandibular rami with M_1 (figured in Rook 1993);
  – F:AM 63056: right and left maxillary bones with P^2, P^4-M^2; right and left mandibular rami with C, P_3-M_2;
  – F:AM 63057: right maxillary bone with P^4-M^2; right and left mandibular rami with M_1;
  – F:AM 63058: right and left maxillary bones with P^2-M^2; right and left mandibular rami with P_2-M_1;
  – F:AM 63063: right maxillary bone with P^4-M^2;
  – F:AM 63199: left M_1;
  – F:AM 72605: right mandibular ramus with P_1-P_4.

Clay Bank Quarry, Mohave County (Arizona); early Pliocene, late Hemphillian.
  – F:AM 63003: right and left mandibular rami with P_1-M_3;
  – F:AM 63008: fragmentary skull with right and left P^3-M^2; right mandibular ramus with P_4-M_2;
  – F:AM 63008x: left mandibular ramus with P_1-P_4; right mandibular ramus with M_1;
  – F:AM 63008y: fragmentary skull with left P^2, P^4-M^1;
  – F:AM 63009B: fragmentary skull with right and left P^3-M^2 (figured in Rook 1993);

- F:AM 63009a: left mandibular ramus with P_4-M_2 (figured in Rook 1993);
- F:AM 63009b: right mandibular ramus with P_1-M_2;
- F:AM 63011: left maxillary bone with P^2, P^4-M^2;
- F:AM 63014: left mandibular ramus with P_2-M_1;
- F:AM 63016c: left M_1;
- F:AM 63017: left M_1;
- F:AM 63017a: left mandibular ramus with P_2-M_1;
- F:AM 63018: left mandibular ramus with P_2, P_4-M_3;
- F:AM 63024: right mandibular ramus with P_3-P_4 (damaged), M_1-M_2, and damaged M_3;
- F:AM 63028: left M_1;
- F:AM 63028a: left mandibular ramus with P_1-M_2;
- F:AM 63028b: left mandibular ramus with P_2-M_1;
- F:AM 63028e: right mandibular ramus with P_2-M_3;
- F:AM 63028g: left mandibular ramus with P_4-M_1;
- F:AM 63028h: right M_1;
- F:AM 63028j: right mandibular ramus with P_4-M_1;
- F:AM 63028k: right mandibular ramus with M_1;
- F:AM 63029: left mandibular ramus with P_3-M_2;
- F:AM 63031: fragmentary skull with right and left C, P^1-M^2; right and left mandibular rami with P_2-M_2;
- F:AM 63032: right mandibular ramus with M_1-M_2;
- F:AM 63043: right mandibular ramus with P_1-M_1;
- F:AM 63045: right mandibular ramus with P_2-M_2;
- F:AM 63047: right mandibular ramus with P_4-M_2;
- F:AM 63049: left mandibular ramus with M_1;
- F:AM 72591: right mandibular ramus with P_3-M_2;
- F:AM 72592: left mandibular ramus with P_2-M_2;
- F:AM 72596: right mandibular ramus with P_2-M_2;
- F:AM 72602: left mandibular ramus with P_3-M_2;
- F:AM 72604: right mandibular ramus with C, P_1-M_2.

Gray's Ranch Quarry, Mohave County (Arizona); early Pliocene, late Hemphillian.
- F:AM 63040: right mandibular ramus with C, P_1-P_4;
- F:AM 63040a: right maxillary bone with M^1-M^2;
- F:AM 63048: left mandibular ramus with P_3-M_3;
- F:AM 72607: right mandibular ramus with P_2, P_4;
- F:AM 63028i: right mandibular ramus with M_1-M_2.

Edson Quarry (Edson Local Fauna), Sherman County (Kansas); early Pliocene, late Hemphillian.
- KUVP 3608: fragmentary right mandibular ramus with C, P_1-P_4 (figured in Harrison 1983);
- F:AM 49456: right and left mandibular rami with P_1-M_2 (figured in Harrison 1983);
- F:AM 49457: right mandibular ramus with damaged M_1-M_2;
- F:AM 49458: left maxillary bone with P^3-P^4;
- F:AM 49462: left mandibular ramus with C, P_2-M_2;
- F:AM 49463: right mandibular ramus with P_3, M_1-M_2;
- F:AM 49464: partial palate bearing right C, P^1-M^2 (figured in Harrison 1983);
- F:AM 49465: right and left mandibular rami with C, P_1-M_2;
- F:AM 49466: right and left mandibular rami with P_1-M_3.

Optima Quarry (Optima Local Fauna), Texas County (Oklahoma); early Pliocene, late Hemphillian.
- F:AM 62930: left mandibular ramus with P_1, P_3-M_1;
- F:AM 62932: right mandibular ramus with P_3-M_3;

- F:AM 62937: left mandibular ramus with P_2-P_3, M_1;
- F:AM 62939: left mandibular ramus with P_2-M_1;
- F:AM 62951: right mandibular ramus with C, P_1-M_1;
- F:AM 62952: left maxillary bone with P^2-P^3, M^1;
- F:AM 62958: right P^4;
- F:AM 62958a: right P^4;
- F:AM62958b: left P^4;
- F:AM 62958c: right P^4;
- F:AM 62960: right M^1;
- F:AM 62961i: right M_1;
- F:AM 62961o: left M_1;
- F:AM 62961n: left M_1.

Miami Quarry, Hemphill County (Texas); early Pliocene, late Hemphillian.
- F:AM 23353: left mandibular ramus with P_3-M_2;
- F:AM 23373: right maxillary bone with C-I^3, P^2-M^2; right mandibular ramus with P_2-M_1;
- F:AM 23374: left maxillary bone with P^1-P^3, M^1-M^2;
- F:AM 23376c: right M_2;
- F:AM 23376f: right M^1.

Goodnight Beds, Armstrong County (Texas); early Pliocene, late Hemphillian.
- F:AM 49322: right maxillary bone with M^1-M^2.

Hill Quarry, Armstrong County (Texas); early Pliocene, late Hemphillian.
- F:AM 49319: left mandibular ramus with P_3-P_4.

Rentfro pit, Harley County (Texas); early Pliocene, late Hemphillian.
- F:AM 62981: fragmentary skull bearing left P^1-M^2; right mandibular ramus with P_2, P_4-M_2.

McKay reservoir, Malheur County (Oregon); early Pliocene, late Hemphillian.
- UO 3241: left mandibular ramus with C, P_1-P_4 (figured in Shotwell 1956, Rook 1993);
- UO 3253: left M_1 (figured in Shotwell 1956, Rook 1993);
- UO (not numbered): left P^4.

Old Cabin Quarry, Pima County (Arizona); early Pliocene, late Hemphillian.
- F:AM 50605: right M_1;
- F:AM 50681: left mandibular ramus with P_2-P_3, M_1-M_2;
- F:AM 50685: right maxillary bone with P^2-P^4;
- F:AM 50688: right M^1-M^2;
- F:AM 50696: left M_1;
- F:AM 50697: right M_1;
- F:AM 72656: right and left mandibular rami with I_1-I_3, C, P_1-M_2;
- F:AM 72657: left M_1;
- F:AM 72658: left mandibular ramus with P_4-M_1;
- F:AM 72659: right M_1;
- F:AM 72661: fragmentary skull bearing right and left C, P^1-M^2 left mandibular ramus with P_2, damaged P_4-M_3;
- F:AM 72662: fragmentary skull bearing right C, P^1-M^2, and left I^2-I^3, C, P^1-P^3;
- F:AM 75796: fragmentary palate with right P^4 and left M^1-M^2;

– F:AM 75807: right mandibular ramus with P_1-M_1;
– F:AM 75810: right and left mandibular rami with C, P_1-M_3;
– F:AM 75811: right and left mandibular rami with C, P_1-M_2;
– F:AM 75812: right and left mandibular rami with M_1-M_2;
– F:AM 75817: right M_1;
– F:AM 75818: left mandibular ramus with P_3-M_3;
– F:AM 75838: skull bearing right and left P^2-M^2;
– F:AM 75842: left maxillary bone with M^1-M^2.

Redington Quarry, Pima County (Arizona); early Pliocene, late Hemphillian.
– F:AM 63086: right M_1; right mandibular ramus with M_1;
– F:AM 63087: left mandibular ramus with P_1-P_2, M_1;
– F:AM 63088: right M_1.

Golgotha water mill pothole, Lincoln County (Nevada); early Pliocene, late Hemphillian.
– F:AM 49294: right and left mandibular rami with C, P_1-M_2 (figured in Rook 1993).

ASIA

Eucyon sp.

Khirgis Nur Lake (western side), lower part of Khirgis Nur Suite, KhN-2 section, level 5-37 (NW Mongolia); late Miocene, late Turolian, MN 13.
– PIN 2737/275: ventrally damaged left mandibular ramus with alveoli of P_1-M_3 (figured in Sotnikova & Rook 2009).

Olkhon, Baikal Lake, site 520 level B (Transbaikalia); early Pliocene, Ruscinian, MN 14-MN 15.
– GIN (not numbered): left M^2.

Eucyon davisi (Merriam, 1911)

Gusinyi Perelet (Pavlodar 1B), southern West Siberian Plain (Kazakhstan); earliest Pliocene, Ruscinian, MN 14.
– GIN 640/3017: right M^1 (figured in Sotnikova & Rook 2009).

Khirgis Nur Lake (western side), upper part of KhN Suite of KhN-2 section, level 51-55 (NW Mongolia); early Pliocene, Ruscinian, MN 14-MN 15.
– PIN 3222/57: right mandibular ramus with P_3-P_4, M_2 and broken M_1 (figured in Sotnikova & Rook 2009).

Sangin Dalay Nur, Dzabchan basin (NW Mongolia); early Pliocene, Ruscinian, MN 14-MN 15.
– GIN 970-35: right mandibular ramus with M_1-M_2; left mandibular ramus with P_1-P_4, M_2 (figured in Sotnikova & Rook 2009);
– GIN (not numbered): left mandibular fragment with M_2;
– GIN (not numbered): fragmentary P^4.

Liujiagou, Yushe basin, Yuncu Subbasin, SE Shanxi (China); Mazegou Formation, early Pliocene.
– F:AM 97031: left mandibular ramus with C, P_1-M_3.

Xiakou, Liujiagou, Yushe basin, Nihe Subbasin, SE Shanxi (China); Gaozuang Formation (Nanzhuanggou member), early Pliocene (Tedford & Qiu 1996).
– F:AM 97027: nearly complete skull and dentition, right P^2-M^2 and left C, P^2, P^4-M^2;
– F:AM 97028: crushed skull and partial dentition, right P^1-M^1 and left damaged C, P^1-M^2;
– F:AM 97056: complete skull and dentition, right I^2-I^2 and left C, P^1-M^2 (figured in Tedford & Qiu, 1996; Fig. 2C);
– F:AM 97057: nearly complete skull and dentition, right P^1, P^4-M^2 and left P^4-M^2;
– F:AM 97058: broken skull with C, P^1-M^2 and associated right and left mandible with nearly complete dentition (figured in Rook 1993; Tedford & Qiu 1996);
– F:AM 97059: anterior part of skull (crushed) with right I^1, I^3, C, P^1-M^2 and left I^1-I^3, C, P^1-M^2 (figured in Rook 1993);
– F:AM 97061: palate with right C, P^1-P^3 and left I^1-I^3, C, P^1-M^2.

Eucyon zhoui Tedford & Qiu, 1996

Yinjiao village (surroundings), Yushe basin, Nihe Subbasin, SE Shanxi (China); upper Gaozhuang or lower Mazegou formations, early Pliocene (Tedford & Qiu 1996).
– V12181[THP10199]: nearly complete skull and mandible with complete dentition. Type specimen (figured in Tedford & Qiu 1996).

Zhaozuang, Yushe basin, Nihe Subbasin, SE Shanxi (China); upper Gaozhuang or lower Mazegou formations, early Pliocene (Tedford & Qiu 1996).
– F:AM 97048, anterior part of skull with right complete dentition and left I^1-I^3, C, P^1-P^2; associated left mandibular ramus with C, P_1-M_3 (figured in Rook 1993; Fig. 2D).

Eucyon minor (Teilhard de Chardin & Pivetau, 1930)

Hsia Chwang (10 miles south of Shou Yang village), SE Shanxi (China); Haiyan Formation, late Pliocene.
– F:AM 97036: palate with right I^1-I^3, C, P^1-P^3 and left I^1-I^3, C, P^1-P^4;
– F:AM 97051: skull bearing right I^3, C, P^1-P^3, M^1-M^2 and left C, P^1-M^2.

Eucyon cf. *minor*

Shamar (NW Mongolia); late Pliocene, early Villafranchian, MN 16.
– GIN 970-15: left mandibular ramus with C, P_1-M_3 (figured in Rook 1993);
– PIN 3381-329: right mandibular ramus with C, P_1-P_2, P_4-M_3.

Beregovaya (Transbaikalia); late Pliocene, early Villafranchian, MN 16.
– PIN 2975-7: left mandibular ramus with C, P_2-M_2 (figured in Rook 1993);
– GIN 482: fragmentary left mandibular ramus with P_3, damaged P_4, M_1-M_3 (figured in Rook 1993).

Udunga (Transbaikalia); late Pliocene, early Villafranchian, MN 16 (Sotnikova & Kalmiapov 1991).
 – GIN 987: fragmentary left M_2.

Eucyon marinae Spassov & Rook, 2007

Muhor-Erig, Uldzitu-hol river basin (Central Mongolia); Late Pliocene, late Ruscinian or early Villafranchian (Spassov & Rook 2007).
 – FM 1994 (1-2): right mandibular ramus with P_3-P_4, and damaged M_1; left mandibular ramus with P_3-M_2. Type specimen (figured in Spassov & Rook 2007);
 – FM 1004 (3): right lower canine.

EUROPE

Eucyon cipio (Crusafont, 1950)

Concud, Teruel basin (Spain); late Miocene, late Turolian, MN 12.
 – IPS 1988: right maxillary bone with P^3-M^2. Type specimen (figured in Crusafont 1950; Rook 1993).

Los Mansuetos, Teruel basin (Spain); late Miocene, late Turolian, MN 12.
 – IPS (46489): right M_1 (figured in Pons Moyá & Crusafont 1978, Rook 1993).

Eucyon monticinensis (Rook, 1992)

Monticino gypsum quarry, Brisighella, Faenza (Italy); late Miocene (Messinian), late Turolian, MN 13.
 – BRS27-4: right mandibular ramus with P_2 and M_1. Type specimen (figured in Rook *et al.* 1991; Rook 1992, 1993);
 – BRS27-5: right M_2;
 – BRS27-6: right M_1 (Fig. 1C, D);
 – BRS27-7: left P_2;
 – BRS27-8: right upper C;
 – BRS24/12: right M^1 (figured in Rook *et al.* 1991; Rook 1992, 1993);
 – BRS27-21: left M_1 (figured in Rook *et al.* 1991; Rook 1993);
 – BRS27-22: right P_2 (figured in Rook *et al.* 1991);
 – BRS27-23: left damaged M_1;
 – BRS27-24: left M_2 (figured in Rook *et al.* 1991);
 – BRS27-25: right upper C (figured in Rook *et al.* 1991);
 – BRS27-26: right upper C (figured in Rook *et al.* 1991);
 – BRS27-47: right mandibular ramus (juvenile) with DP_2, DP_3 and DP_4 (figured in Rook *et al.* 1991);
 – BRS27-51: right upper C.

Eucyon cf. *monticinensis*

Venta del Moro, Valencia (Spain); late Miocene (Messinian), late Turolian, MN 13.
 – ILM VM-C-1: fragmented right maxillary bone with damaged P^2, P^3;
 – ILM VM-C-2: partial right P^4;
 – ILM VM-C-3: fragmented right maxillary bone with M^1-M^2 (figured in Morales 1984, Rook 1993);
 – ILM VM-C-4: fragmented right mandibular corpus with P_3 and partial M_1 (figured in Morales 1984, Rook 1993);
 – ILM VM-C-5: partial right P^4;
 – ILM VM-C-50: left M_1 (figured in Rook 1993);
 – ILM VM-C-51: left P_2;
 – ILM VM-[11191]: right M_1 (figured in Rook 1993).

Eucyon sp.

Casino basin, Siena (Italy); late Miocene (Messinian), MN 13.
 – M-7156: fragmentary left mandibular corpus with P_3 and roots of P_4.

Eucyon adoxus (Martin, 1973)

St-Estève, near Perpignan, Roussillon (France); early Pliocene, late Ruscinian, MN 15.
 – RSS 45: nearly complete skull with right I^2-I^3, C, P^1-M^2 and left C, P^1-M^2, and associated mandible with right C, P_1-M_2 and left I_2-I_3, C, P_1-M_1. Type specimen (figured in Martin 1973; Rook 1992, 1993; Figs 2B, 3).

La Calera I, Teruel basin (Spain); early Pliocene, early Ruscinian, MN 14.
 – ILM LCA(81)222 [1322]: damaged left M_1;
 – ILM LCA(81)222 [1323]: right M^1-M^2.

Eucyon odessanus (Odinzow, 1967)

Odessa Catacombs, Odessa (Moldova); early Pliocene, late Ruscinian, MN 15.
 – PIN 390-154: fragmentary skull (figured in Rook 1993);
 – PIN 390-155: palate with rigth and left P^3-M^2;
 – PIN 390-156: left maxillary bone with C, P^1-M^1 (figured in Rook 1993);
 – PIN 390-157: left maxillary bone with C, P^1-M^1;
 – PIN 390-158: right maxillary bone with I^1-I^3, C, P^1-M^2;
 – PIN 390-159: right maxillary bone with P^3-M^2;
 – PIN 390-160: right mandibular ramus with C, P_1-M_1 (figured in Rook 1993);
 – PIN 390-161: fragmentary left mandibular ramus with C, P_1-P_4;
 – PIN 390-163: right mandibular ramus with C, P_1, P_4-M_3;
 – PIN 390-164: left mandibular ramus with C, P_1-M_1;
 – PIN 390-165: left mandibular ramus with C, P_1-M_1;
 – PIN 390-166: fragmented right mandibular ramus with P_3-M_3 (figured in Rook 1993);
 – PIN 390-167: fragmented left mandibular ramus with P_4-M_3;
 – PIN 390-168: fragmented left mandibular ramus with P_2-M_3;
 – PIN 390-169: right mandibular ramus with P_3-M_3;
 – PIN 390-170: left mandibular ramus with P_2-P_4, damaged M_1, M_2;
 – PIN 390-171: right mandibular ramus with I_1-I_3, C, P_1-P_3, M_1-M_2;
 – PIN 390-172: right mandibular ramus with I_1-I_3, C, P_2, P_4-M_2;
 – PIN 390-173: left mandibular ramus (juvenile) with

erupting C and P_1, DP_2, DP_3, DP_4, and erupting M_1;
– PIN 390-175: right mandibular ramus (juvenile) with erupting P_3 and P_4;
– PIN 390-177: left mandibular ramus with C, P_1, P_3-M_3;
– PIN 390-178: left mandibular ramus with P_1, P_3-M_1;
– PIN 390-179: left mandibular ramus (juvenile) with P_3 and erupting P_4.

Etulia (Moldova); early Pliocene, Ruscinian, MN 14-MN 15.
– GIN 482-212: fragmentary skull with right C, P^1-M^1 and left P^2-partial P^4, M^2 (figured in Rook 1993).

Nikolskoe (Moldova); early Pliocene, early Ruscinian, MN 14.
– GIN (not numbered): left M^1 (figured in Rook 1993).

Novaja Karbolia (Moldova); early Pliocene, early Ruscinian, MN 14.
– GIN 428-88: edentulous right mandible (figured in Rook 1993);
– GIN (not numbered): left M^1;
– GIN 428-87: left M^1;
– GIN (not numbered): fragmentary left P^4.

?*Eucyon kuruksaensis* (Sotnikova, 1989)
Kuruksay (Kazakhstan); late Pliocene, middle Villafranchian, MN17.

– PIN 3120-251: crushed skull with right and left P^4-M^1. Type specimen (figured in Sotnicova 1989; Rook 1993);
– PIN 3120-257: fragmentary left mandibular ramus with P_1, P_3, M_1-M_2 (figured in Sotnicova 1989; Rook 1993);
– PIN 3120-355: right maxillary bone with P^2-P^3, damaged P^4, broken M^1, and M^2 (figured in Sotnicova 1989; Rook 1993);
– PIN 3120-356: fragmentary left mandibular ramus with P_2-M_2 (figured in Sotnicova 1989; Rook 1993);
– PIN 3120-616: fragmentary left mandibular ramus with P_3-M_1 (figured in Sotnicova 1989; Rook 1993).

AFRICA

Eucyon sp.

Langebaanweg, "E" Quarry, Saldanha, SW Cape province (Sud Africa); Varswater Formation, late Miocene (Messinian) to earliest Pliocene.
– PQ-L 31272: skull with right I^3, C, P^2-M^2 and left I^3, C, P^2-M^1; associated mandibular rami with right C, P_1-M_3 and left C, P_1-M_2 (figured in Rook 1993);
– PQ-L 40041: right mandibular ramus with P_1-M_2 (figured in Rook 1993).