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EUCYON MARINAE SP. NOV. (MAMMALIA, CARNIVORA), A NEW CANID SPECIES FROM THE PLIOCENE OF MONGOLIA, WITH A REVIEW OF FORMS REFERABLE TO THE GENUS

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Abstract. A new canid species from the genus *Eucyon* - *Eucyon marinae* sp. nov. is described from the Late Ruscinian or the Early Villafranchian of Mongolia. The species is characterised by very specific large but narrow premolars and slender mandible. The paper also provide a discussion on the ecology of the species as well as a review of Late Miocene and Early Pliocene fossil canids from North America, Eurasia and Africa referable to the genus *Eucyon*. Problems related to the taxonomy of *Eucyon* and other *Canis*-like forms are discussed.

Riassunto. Viene descritta una nuova specie di canide del genere *Eucyon* (*Eucyon marinae* sp. nov.) su reperti provenienti da depositi pliocenici (Rusciniano superiore / Villafranchiano inferiore) della Mongolia. La nuova specie è caratterizzata da premolari allungati e da corpo mandibolare snello. Vengono inoltre discussi aspetti legati alla ecologia di questa nuova specie. Completa il lavoro una revisione dei canidi fossili del Miocene Superiore e Pliocene Inferiore di Nord America, Eurasia ed Africa riferibili al genere *Eucyon*, con una discussione sui problemi ancora aperti riguardo la tassonomia del genere *Eucyon*.

Introduction

Until relatively recently, the fossil *Canis*-like forms of the Holarctic region known from the late Miocene to Pliocene time were regarded as members of the genus *Canis* "sensu stricto". Doubts regarding the real attribution of Late Miocene dogs to the genus *Canis* were raised by Rook et al. (1991) and Rook (1992, 1993) on consultation with R.H. Tedford (New York) who had already resolved this issue in an unpublished manuscript (Tedford & Taylor, MS unpublished). In 1996 the new genus *Eucyon* was finally described by Tedford & Qiu (1996), referring to it the most of the primitive *Canis*-like forms. Although the history of the genus is as yet poorly known, it is clear that the eastern and central Asian region was an important area for this group origin and dispersion. As a contribution to the knowledge of the evolutionary history of the genus *Eucyon*, we report here the description of a new representative from the Pliocene of Mongolia.

We report on two mandibular fragments and a lower canine that were collected in the beginning of the 80s in the region of field activities of Bulgarian geologists from the BULGARGEOMIN company. The fossils were found by Dr. P. Bakalov (Mining-Geological Institute, Sofia). The right hemimandible and canine were taken to the senior author (NS) by the collector, while the other remains were given to Dr. M.V. Sotnikova (Institute of Geology, Moscow) by the intermediary of Dr. E. Deviatkin (Institute of Geology, Moscow). The latter specimen was kindly returned by Dr. M.V. Sotnikova to NS.

Systematic Paleontology

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

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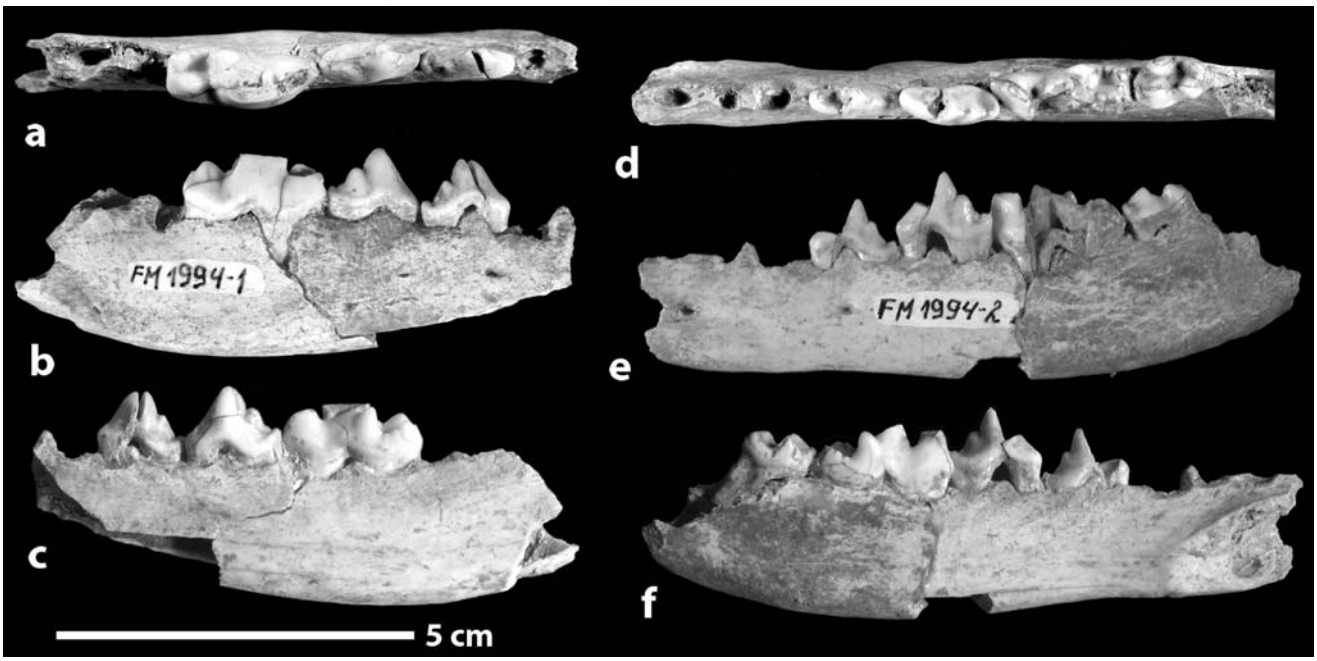

Fig. 1 - *Eucyon marinae* sp. nov. Holotype: right hemimandible (FM 1994-1) in occlusal (a), buccal (b) and lingual (c) views; left hemimandible (FM 1994-2) in occlusal (d), buccal (e) and lingual (f) views.

Eucyon marinae sp. nov.

Fig. 1

Holotype. Two mandible fragments, right and left, of the same individual (Coll. No. FM 1994, National Museum of Natural History, Sofia) with almost unworn teeth. The right hemimandible (FM 1994-1) bears p3-p4 and damaged m1 (the mandibular ascending ramus is missing). The left hemimandible (FM 1994-2) bears p3-m2 (p3 -m1 damaged and the ascending mandibular ramus is missing). Isolated from the right mandibular fragment is also a right lower canine (FM 1994-3) with damaged crown.

Etymology. From the name of our colleague Marina V. Sotnikova (Moscow) in recognition of her contributions to Central Asia carnivore evolution.

Material referred. All the material described belongs to the holotype.

Repository. National Museum of Natural History, Sofia, Bulgaria.

Diagnosis: A species of *Eucyon* having a large but slender and graceful mandible with elongate rostral portion and very long premolar row. Lower third and fourth premolars particularly elongated, very high and narrow, with strong main posterior cusp.

Locality and biochronologic position. The fossil mandible fragments were found at a locality called Muhor-Erig, in the basin of the Uldzitu-hol River in Central Mongolia. They come from a drill-hole made in relation to geological investigations in reddish-brown clay sands of the middle of the three alluvial Neogene sedimentary layers represented in the region between South Hangay and the Valley of Lakes (Fig. 2). The reddish sands were present in the upper part of the drill-hole section (P. Bakalov pers. comm.; E. Deviatkin in litt.). Some indeterminate rhinocerotid tooth fragments and several isolated *Hipparion* teeth were found with the *Eucyon* mandible. Based on their small dimensions and brachyodonty, the *Hipparion* teeth are referred to the latest stages of the *Hipparion* ex gr. *gracile* evolutionary lineage (V. Zhegallo pers. comm.). This would suggest a Late Ruscinian age for all the fossils, although, on the grounds of the vertical extension of the sedimentary succession, an early Villafranchian age cannot be rouled out. Similar red sands exist in the upper part of the section of the early Villafranchian locality of Shamar in Northern Mongolia (E. Deviatkin pers. comm.; M. Sotnikova, pers. comm.).

Description

Mandible. The mandibular fragments and tooth rows show relatively large dimensions (Tab. 1), comparable in size to a recent coyote, and larger than most *Eucyon* spp. The mandible is elongated and the distance between the two *foramina mentale* great. This character has varying taxonomic value amongst the Carnivora: in the genus *Martes,* for example, the noted distance could be a feature of specific significance (Novikov 1956), while it shows significant individual variability in several canids. Nevertheless, such great distance as in the case of mandible FM 1994-2 is an indication of an elongation of the anterior portion of the mandible, a condition clearly demonstrated in the same specimen also by the length of the premolars (see below). Thus the long distance between the mental foramina is in this case probably of some significance. The mandibular corpus is rather high under the molars, but relatively narrow: the low mandibular width under m1 (the area of maximum pressure on the mandibular corpus) compared to the relatively long tooth-row (Tab. 1), illustrates the relative gracility of the mandible.

Canine. The lower canine is relatively large in comparison to the other *Eucyon* species and the other Early-Middle Pliocene canids of Eurasia (Tab. 1).

*Premolars***.** The premolar row is very long with considerable gaps between p1-p2 and p2-p3. Judging by the alveolar mesio-distal dimensions p1 and p2 are large. The p3 and p4 are very large and similar in shape:

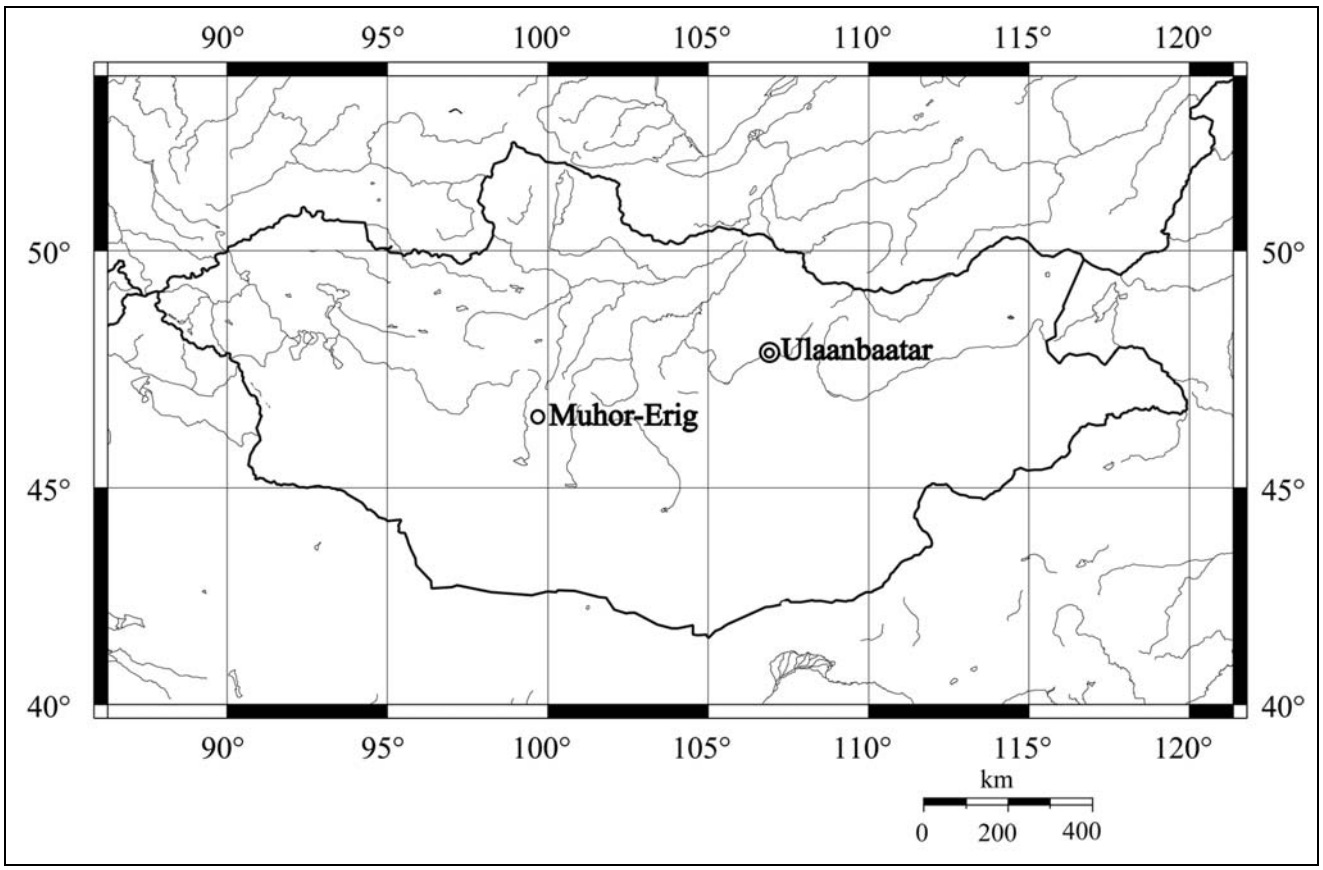

Fig. 2 - Geographic map of Mongolia with location of Muhor-Erig (Uldzitu-hol river basin), type locality for *Eucyon marinae* sp. nov.

	Eucyon marinae		*E. davisi*		*E. minor*	*E. zhoui*	*Canis latrans**
	FM1994-1	FM1994-2	UO-26742	UO-3241	97048 (cast) Am. Mus.Nat.Hist	10199	No 65229, female Berlin Nat. Hist. Museum
p1-m2	-	74.4 (alveolar)	64,8	61,5	58,2	65,5	74.4 (alveolar)
p1-p4	-	46.3 (alveolar)	38,9	37	35,5	37,7	43.8 (alveolar)
m1-m2	-	29(alveolar)	25,2	25	25,5	27,4	30,8
p3-p4	25,3	25,4	22,1	22,1	21	-	25,5
p4 length	13,3	13,4	11,2	11,2	-	11,2	12,4
p4width	5,5	5,4	5,3	4,5	-	5	5,3
p4 height (lateral)	9,8	10	9,2	8,9	-	-	9,2
p3 length	12,1	12	10,3	10	-	10,7	11,6
p3 width	4,4	4,4	4,6	3,9	-	4,5	4,3
p3 height	8,6	8,7	8,1	-	-	-	7,8
m1 length	19,3	19,2	17,7	17,5	16,4	18,4	21,8
m1width	7,3	-	-	7,2	6,7	7,7	8,7
m1talonid length	-	6,1	5,1	5,7	5	-	-
m2 length	-	9,9	8,6	8,5	8	9,2	13,4
m2 width	-	6,8	-	5,9	5,6	6,7	6,3
mandibular width at m1	8	7,9	8,6	8,1	8,2	9,1	8,9
mand. height (lateral) at m1	19,5	18,5	18,2	19,1	15	-	20,5
c1width	-	5,9	4,8	5,7	-	-	5,9
inter-foraminal distance	-	20,4	-	-	-	14,5	14,3

Tab. 1 - Comparative mandibular and lower teeth dimensions of *E. marinae* sp. nov. (* standard for ratio diagrams in Figs. 3, 7 and 8).

very long and tall (absolute size) but narrow (Tab. 1; Fig. 3a-c). They show a lingually curved tooth apex and well marked posterior cingulum. The main posterior cuspids are very stout: large in p4 and somewhat smaller but also well marked in p3. A second posterior cusplet is formed in front of the p4 posterior cingulum. This cusplet is well developed and clearly separated from the cingulum. The crown length of these teeth is visibly greater than the height. The length of the mesial edge in p3 is somewhat smaller, but close in size to the length of the distal edge in p3, and the mesial edge length in p4 is practically equal to the distal edge in p4. The p3 is only slightly lower in height than p4. Its mesial width is practically equal to the distal width. The distal width of

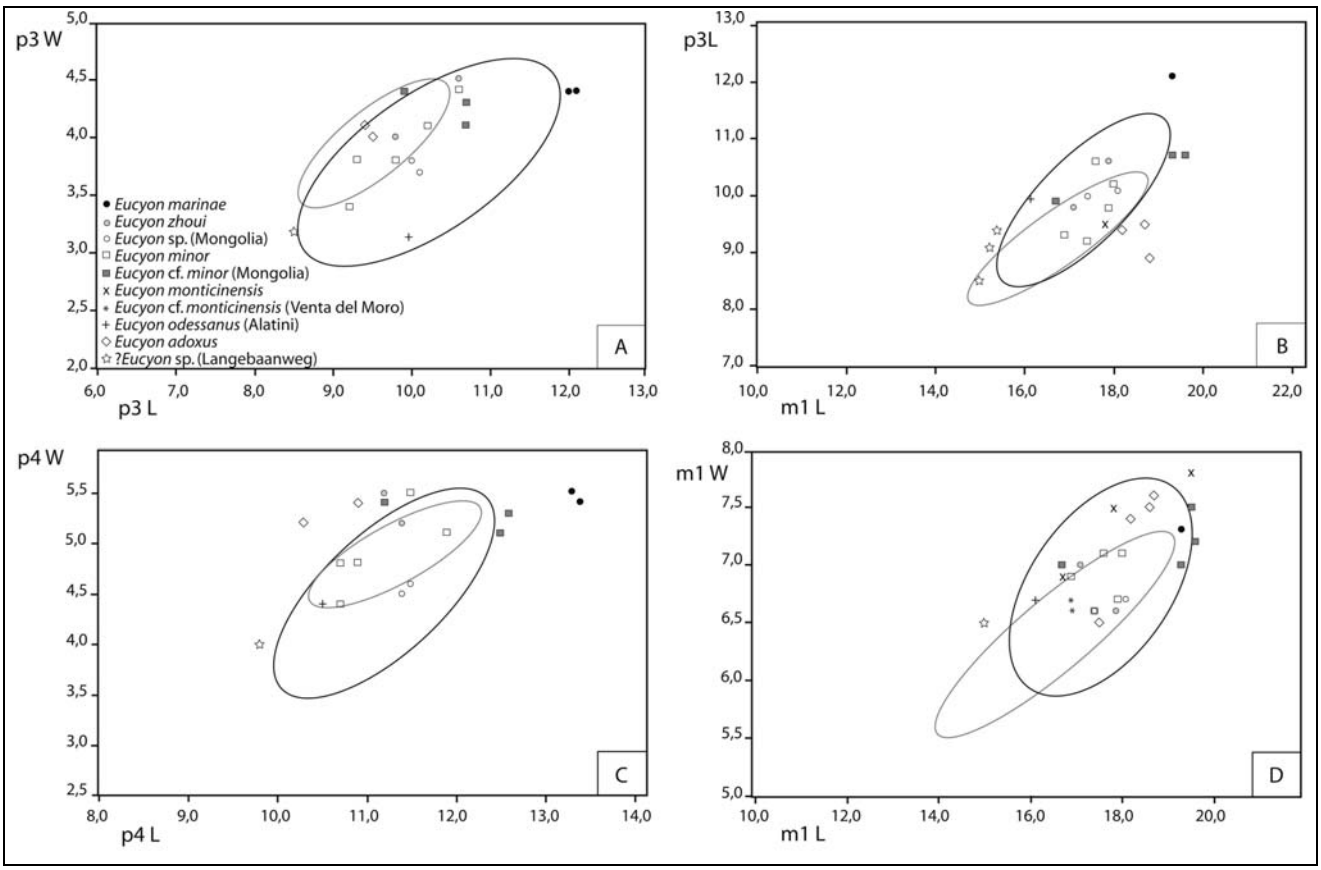

Fig. 3 - Bivariate plot of lower premolars and carnassial length/width for *Eucyon marinae* and comparative sample. Black line represents the range of *Eucyon davisi* sample; gray line represents the range of *Eucyon odessanus* sample (data from Rook 1993).

p4 is only slightly greater than the mesial one, which is rare in both *Eucyon* and *Canis.*

Molars. The molar rows (m1-m2) are large in their absolute dimensions (in comparison with other *Eucyon* forms), but relatively short in comparison to the premolar rows (Tab. 1; Fig. 3a-b). The lower carnassial tooth (m1) is large in absolute dimensions, with several progressive features: short and narrow talonid (Tab. 1), considerably slanting anterior edge of the paraconid. The direction of the anterior edge of the paraconid in canids can show some individual variation, but generally it is a significant feature with taxonomic value at the specific and even generic levels. In *Canis* the slanting of the edge is an apomorphy of the evolved forms. At the same time, the metaconid is well developed, with slightly inclined backward tip, and the talonid is characterized by a complex relief: an additional very small cusplet is positioned distal to the protoconid and two additional cusplets (post-metaconid and pre-entoconid) exist in both left and right m1, between the metaconid and the entoconid. In addition, a small hypoconulid is distinctly seen at the distal border of the m1 talonid between the entoconid and the hypoconid. The main cuspids of the talonid (the hypoconid and the entoconid) are well preserved on m1 of the right hemimandible (FM 1994-1). They are not connected by transverse cristids (Fig. 4). The hypoconid is large. Its ridges are positioned mesio-distally from the tip. The entoconid is much smaller, positioned on the lingual periphery of the talonid and its ridges are somewhat oblique to the tooth axial direction. The hypoconulid basin between this cusplet and the entoconid is narrow. A deep talonid basin is formed in front of the entoconid. The apex of the m1 paraconid is broken but seems to be clearly lower (lower positioned in the mandible) than the p4 apex.

The second molar is large and elongated, with a broad mesial part and a slightly concave lingual border. The anterior cuspids are well developed, the labial one (the protoconid) somewhat larger than the metaconid. The protoconid apex is slightly more mesially positioned than that of the metaconid (the noted morphology of the main mesial cuspids of m2 is an apomorphy in the closely related and more evolved genus *Canis*). The hypoconid is strong, but the entoconid is not developed and there is a cingulum on the distolingual border of the tooth.

Comparison and Discussion

Tedford and Qiu (1996) named the new genus *Eucyon* for some primitive *Canis*-like forms. The new taxon compares closely with the accumulated data on the zoogegraphy and morphology of the Late Miocene

Fig. 4 - *Eucyon marinae* sp. nov. FM 1994-1, lower carnassial in occlusal view. Please note the structure of the talonid basin (see text for discussion). Bar scale 1 cm.

and Early Pliocene s.l. *Canis*-like dogs, and for the moment represents a convenient and logical taxonomic decision regarding Pliocene dog evolutionary history. At least three (but most probably no less than five) species can at present be included in this clade: *Eucyon davisi* (Merriam, 1911); *Eucyon monticinensis* (Rook, 1992); *Eucyon minor* (Teilhard & Piveteau, 1930) (= *Canis chihliensis minor*); *Eucyon zhoui* Tedford & Qiu, 1996 (which might be a primitive member of *Canis*) and most probably also *Eucyon odessanus* (Odintzov, 1967), very similar in size and morphology to *Eucyon davisi* (see Tedford & Qiu 1996; Rook 1993).

The taxonomic position of *"Vulpes" odessana* Odintzov, 1967 is still debated (see Ivanoff 1996), as well as that of another European Pliocene form: *"Canis" adoxus* Martin, 1973. Rook (1993) included this taxon within the genus *Eucyon*, while Tedford & Qiu (1996) note some derived features in "*C.*" *adoxus* and believe that the species should not be assigned to *Eucyon*.

Another probable representative of the genus *Eucyon* is *"Canis kuruksaensis"* Sotnikova, 1989 from the Pliocene of Kazakhstan (R.H.Tedford & M.V. Sotnikova in litt.).

Different *Eucyon* species possibly are represented also in the latest Miocene and early Pliocene in Africa. From the latest Miocene of E Quarry at Langebaanweg (South Africa) Hendey (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*). From various sites at Laetoli (Early Pliocene, Tanzania), 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). As a matter of fact the taxonomic attribution of these fossils needs further work.

In the evolutionary scenario of Late Miocene-Early Pliocene fossil dogs, the taxonomic positions of "*Canis*" *cipio* Crusafont, 1950 (Late Miocene; MN12) and "*Canis*" *michauxi* Martin, 1973 (Early Pliocene; MNQ15) are still unclear. The remains of these forms one are too few for reliable generic determination and comparison. Large dogs comparable in size to the latter two species are documented in the fossil record of the North American Late Hemphillian (Late Miocene; Tedford & Taylor MS unpublished), in the Pliocene of Eurasia, at Csarnota-1 in Hungary (Kormos 1933; Rook 1993) and from Chono-Kariakh in Transbaikalia (MN 14; unpublished material from GIN, Moscow; Rook 1993). Discussion of the taxonomic position of such forms is beyond the scope of the present paper.

The teeth of the Muhor-Erig mandible possess all the diagnostic features of *Eucyon*: lack of the transversal cristids connecting the hypoconid and entoconid and presence of a second posterior cuspid (cusplet) on the p4.

The generic features of *Eucyon* seen in the mandible are rather evident. Their manifestation (for example the presence or absence of the cristids on the hypo- and entoconid) in other canids does not have the same taxonomic importance. The same cristids have only specific-level value in *Nyctereutes* species such as *N. donnezani* and *N. tingi*. The lack of cristids can be seen (as individual variation) in representatives of highly derived

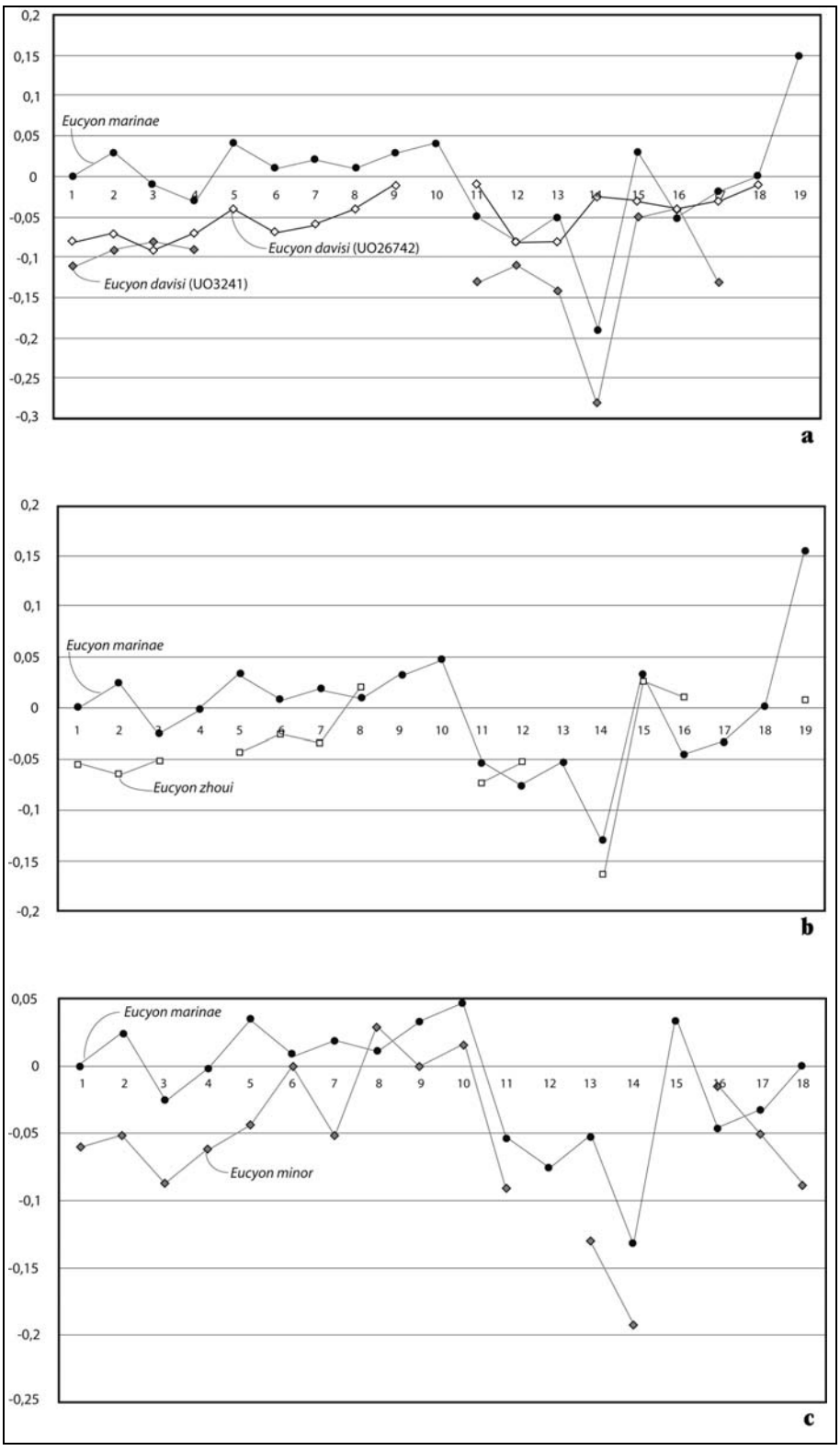

Fig. 5 - Ratio diagram (standard *Canis latrans*) comparing mandibular measurements (see Table 1) of: *Eucyon marinae* sp. nov. and *Eucyon davisi* (a); *Eucyon marinae* sp. nov. and *Eucyon zhoui* (b); *Eucyon marinae* sp. nov. and *Eucyon minor* (c).

forms of *Canis*, such as *C. lupus* (a specimen from the coll. of the N.M.N.H. - Sofia). The early and relatively small *Canis*, however, can be reliably separated on the basis of these characters from *Eucyon*. In the case of Muhor-Erig, the combination of the two typical *Eucyon* mandibular characters unequivocally place the find in *Eucyon*.

Eucyon marinae sp. nov. and North American and Central Asian record of the genus *Eucyon*

Eucyon davisi (Merriam, 1911) - This is a widely distributed species, with several finds from the Late Hemphillian (latest Miocene) of North America, but also from the Pliocene of China (Tedford & Qiu

1996). The intraspecific variability of this taxon, which has a very large temporal range, is considerable (cf. Rook 1993). The differences from the new species *Eucyon marinae* are clear: *E. marinae* has a larger tooth-row (Fig. 5a). In comparison with a large tooth sample of *E. davisi,* is the length of the premolars (p3 and p4; Fig. 3a-c), as well as the height of these teeth, are especially great in the new species. On the other hand, the premolars are relatively more slender than those of *E. davisi* (Fig. 3a,c). At the same time, the molars of the Muhor-Erig mandible are relatively shorter (in proportion to the pm; Fig. 3b,d).

Eucyon zhoui Tedford & Qiu, 1996 - This species is known from the Early to Middle Pliocene of China only. The inferred magnetostratigraphic position of the deposits which yielded specimens of the species ranges from the late Gilbert to early Gauss chrons (Tedford & Qiu 1996). Compared to *Eucyon zhoui, E. marinae* has a clearly larger tooth row, especially the premolar row (Fig. 5b). The premolars (p3-p4) of the Muhor-Erig mandible are much longer, but relatively more slender (Fig. 3a,c). The carnassial, as well the mandible ramus, also seem to be more slender and the rostral part of the mandible more elongated, as testified to by the greater distance between the mandibular foramina (Fig. 5b).

Eucyon minor (Teilhard de Chardin & Piveteau, 1930) (= *Canis chihliensis* var. *minor* Teilhard de Chardin & Piveteau; see Rook 1993; Tedford & Qiu 1996) - 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 Hayan Fm. of the Yushe basin, dated by magnetostratigraphy to the early Matuyama; Flynn et al. 1991; R.H. Tedford pers. comm. in Rook 1993). *E. marinae* differs from *E. minor* in its larger tooth row, longer (absolutely as well as relative to molar length) and clearly taller and more slender premolars (p3-p4; Fig. 3a-b) and mandibular corpus (Figs. 5c, 6a-c). The Muhor-Erig m2 is longer and has an apomorphic morphology with a larger mesiolabial cuspid (paraconid) in relation to the mesiolingual one, while the main posterior cuspids of the premolars are more prominent.

Other specimens of *Eucyon* cf. *minor* from the Late Pliocene of Mongolia (Rook 1993) - In the collections of the Institute of Geology in Moscow (GIN) are kept canid mandibles from three Pliocene sites (MN 16; "early Villafranchian"; Vislobokova et al. 2001): Shamar, Beregovaja and Udunga. The specimen from Udunga, an edentulous mandibular ramus, has been described by Sotnikova & Kalmykov (1991) as *Canis* sp., although at present, M.V. Sotnikova (pers. comm. to NS), rather attributes it to the genus *Nyctereutes.* The samples from Shamar and Beregovaja have been listed by Kurtén (1974) as coyote-like dogs. The lower carnassial mor-

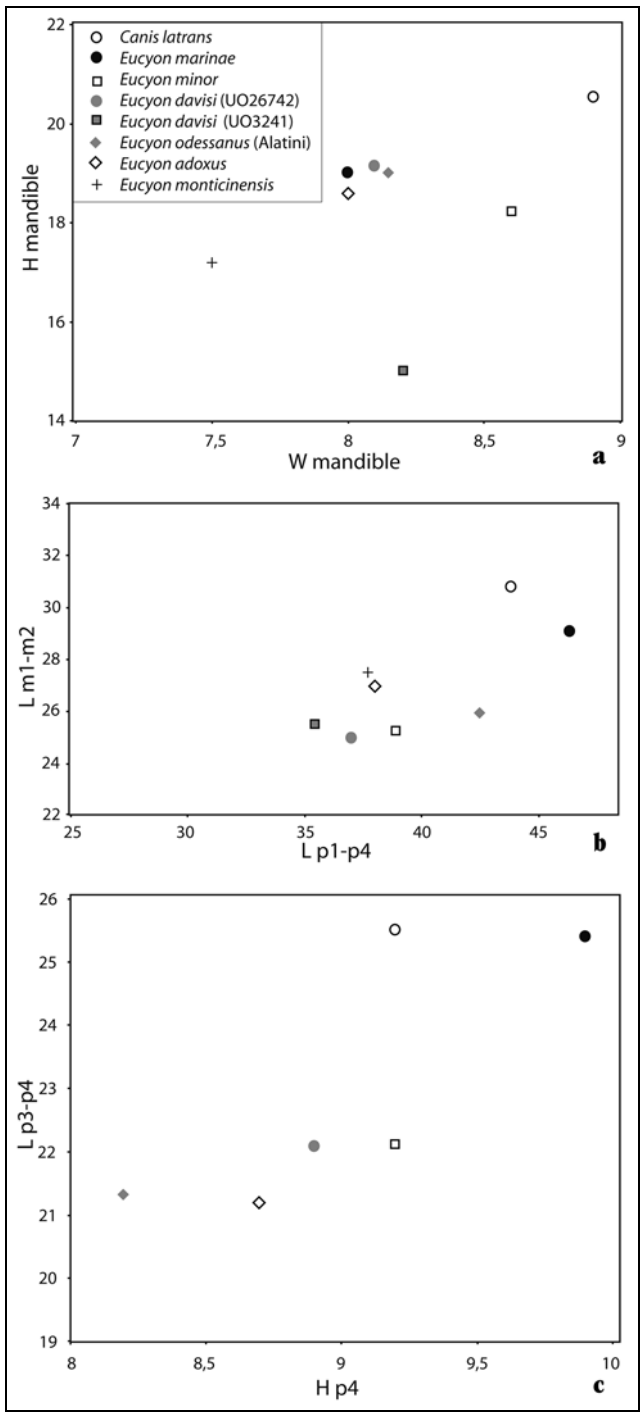

Fig. 6 - Bivariate plot of: mandibular height/width for *Eucyon marinae* and comparative sample (a); m1-m2 length vs. p1-p4 length for *Eucyon marinae* and comparative sample (b); p3-p4 length vs. p4 height for *Eucyon marinae* and comparative sample (c).

phology of the Shamar and Beregovaja specimens have the typical characteristics of the genus *Eucyon* (Rook 1993). Rook (1993), on the grounds of dental morphology and the similarities with *Eucyon minor* from China, attributed this material to *Eucyon* cf. *minor.* A similar opinion has been expressed by R.H. Tedford (pers. comm. to NS). More recently, Sotnikova (2004) proposes the same taxonomic placement for the larger

(more comparable in its dimensions to the Muhor-Erig specimen) of the two Shamar mandibles (GIN 3381-329), but suggests an attribution to a new species for the smaller one (GIN 970-15). In any case, both Shamar mandibles are very different from the Muhor-Erig one. Direct comparison of the *Eucyon marinae* type specimen with a mandible from Shamar (GIN 3381-329), demonstrate that the Shamar fossil has a distinctly shorter premolar row and more conical p4.

Eucyon sp. from the Late Miocene of Mongolia - Unpublished material from latest Miocene localities of Mongolia is kept in the collections of the Institute of Geology (GIN) and of the Institute of Paleontology (PIN) in Moscow. These have been briefly described in Rook (1993). Particularly interesting are two mandibles (PIN3222-57; GIN 2737-275) from Chirgis-Nur-2 (a site at the Mio-Pliocene transition; Pevzner et al. 1982; Tedford et al. 1991) and the sample (several fragmentary specimens without inventory numbers in the GIN collections) from Sangin Dalai Nur (Early Pliocene, correlatable with MN14), of *Eucyon* sp. finds with lower dentitions that have considerably shorter p3-4 than the Muhor-Erig specimen (Fig. 3a-c).

Eucyon marinae sp. nov. and European and African record of the genus *Eucyon*

Eucyon monticinensis (Rook, 1992) - Known from the Late Messinian of Italy, *Eucyon monticinensis* is, together with *E. davisi*, the earliest representative of the genus (Rook 1992, 1993). *Eucyon marinae* differs from the type of *E. monticinensis* in its larger dimensions, including the tooth row, the height of the mandibular corpus, the larger premolars (both absolutely and in proportion to the molars; Figs 3a-c, 6a), the larger m1 metaconid and the longer and taller trigonid. The lower teeth from Venta del Moro (MN13, Spain) identified as *E.* cf. *monticinensis* (Rook 1992; 1993) are also considerably smaller than the Muhor-Erig dentition.

Eucyon odessanus (Odintzov, 1967) - A very large sample from the Odessa catacombs (MN15; Ukraine) has been described as *Vulpes odessana* by Odinzov (1967). Rook (1993) considered this material, as well as the unpublished skull from Etulia (GIN 482-212; Early Pliocene, Moldavia) as belonging to the genus *Eucyon*. *Eucyon odessanus* has teeth that are similar in dimensions to *E. davisi* (and thus smaller than *E. marinae*), but with a somewhat shorter and deeper p3 (Fig 3a-b, d). The premolars (p3-p4) are variable but more conical than in *E. marinae*. The p3 may not have a main posterior cuspid, but if it is present, the cuspid is smaller than in *E. marinae*. Within the sample from the Odessa catacombs, the maximum lower carnassial length may reach the m1 length of the Muhor-Erig mandible, but the average dimension is smaller than in *E. marinae* (Fig. 3b,d). In comparison with the Odessan species, the premolars (p3, p4) of *E. marinae* are proportionally larger in relation to the carnassial length. The dimensions of the premolars of the Muhor-Erig specimen are clearly larger also in absolute size (s. 3c-d).

Eucyon from Alatini (Northern Greece) (Koufos 1997) - Two hemimandibles from Alatini (early Pliocene of Greece) were described as *Nyctereutes donnezani* 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). More recently, Koufos (1997) re-described one of the mandibles as *Eucyon davisi*, although stressing some similarities with the species *E. odessanus*. We think *E. odessanus* is a bona fide species (distinct from *E. davisi*) and that the Alatini specimens are better attributable to the Odessa species, since their size falls within the variability of *Eucyon odessanus* (Fig. 3c-d), although the lower p3 is much narrow (Fig. 3a). As in *E. davisi* and in the Muhor-Erig specimen, the Alatini mandible has a mesio-lingual cuspid of m2 that is smaller (and positioned slightly more distally) than the mesio-labial one. The dentition of the Muhor-Erig specimen is much larger, with p3-p4 that are clearly taller and, in contrast to the Alatini mandible, with well pronounced main posterior cuspids.

Eucyon cf. *odessanus* from Sarikol Tepe (Kostopoulos & Sen 1999) - This find has been recently reported from Sarikol Tepe (MN17, Turkey) by Kostopoulos & Sen (1999). This mandibular fragment with m1-2 has much smaller molars than the Muhor-Erig specimens.

?*Eucyon* sp. from Langebaanweg (Hendey 1978; 1981; Rook 1993) - The lower dentition of the ?*Eucyon* sp. remains (see Rook 1993) from Langebaanweg (South Africa) is considerably smaller than of the Muhor-Erig mandible (Fig. 3a-b, d).

A further occurrence of *Eucyon* in Africa is at the Late Pliocene site of Ahl Al Oughlam in Maroc. Here Geraads (1997) described a few canidae remains as *Canis* nov. sp., aff. *C. aureus*. The material, whose morphology indicate the features of the genus *Eucyon*, is currently under revision (D. Geraads & N. Spassov, in preparation).

Eucyon, Eucyon-like or *Canis*? Discussion on some debated species

Eucyon adoxus (Martin, 1973) - This is a relatively large Pliocene dog from MN15 of St. Estève, Perpignan (France). It 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 1978), since it does not have the typical vulpine depression in the region of zygomatic processes of the frontal bone (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 it displays (mainly in the dentition) are synapomorphies for other canine lineages and it could represent a taxon different from *Eucyon*. It is the conviction of the authors, as discussed in Rook (1993) that the Perpignan dog, as well as the few more or less contemporary findings around Europe (La Calera I, Spain: Alcalá 1994; Megalo Emvolon/Alatini, Greece: Sickenberg 1972, Koufos et al. 1991, Koufos 1997; Red Crag, UK: Lydekker 1885) are late representatives of the evolutionary differentiation of the genus *Eucyon* in Europe.

The size and proportions of the Muhor-Erig mandible are comparable with *Eucyon adoxus.* The premolars diastemas are also similar, as well the relatively derived morphology of m2 (similar positions of the m2 cuspids). The mandible from Muhor-Erig differs from the type of *Eucyon adoxus* mainly in the distinctly larger p3-4 and premolar row in general. The p3 is not so conical and has a more asymmetric contour and stronger main posterior cuspid.

"*Canis*" *michauxi* Martin, 1973 - This is a very large form, poorly known (two fragmentary mandibular fragments) and taxonomically enigmatic, from the Early Pliocene (MN 15) of Perpignan (southern France) described by Martin (1973). The type specimen of this species is not available for study. The specimen numbers reported in the Martin (1973) paper (CSU 35 and CSU 36) probably refer to collections in the Perpignan *"Collège Scientifique Universitaire"* but it has not been possible to locate them (J.Michaux pers. comm. in Rook 1993). Metric comparison is possible with p3. This tooth is, on the basis of data in Martin (1973), somewhat larger and deeper in *"Canis" michauxi* than in the Muhor-Erig material. The premolars of *Eucyon marinae* seem also to be higher-crowned and with less asymmetric mesial and distal ridges, judging from Martin (1973) description and figures.

Canis ex gr. *lepophagus* from Kuruksay (Sotnikova 1989) - Two mandible fragments (PIN3120-616; PIN 3120-356) from the Kuruksay site (Navruho locality; 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, according to R.H. Tedford, pers. comm. to NS, should be included in the genus *Eucyon*) are not yet clarified. In the original description (published in 1989, 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, with the mandibular rami broken and/or deformed, and a definite decision regarding their taxonomic status will be a difficult task. Recently M.V. Sotnikova (pers. comm.) has expressed the opinion that *C. kuruksaensis* is a form very close to *Eucyon*, but possibly different at the generic level.

The Muhor-Erig mandibles show some similarities with the Kuruksay ones, especially in the very large p4. The p3 of the Kuruksay mandibles are shorter and, apparently, lower and more asymmetric in shape due to the long distal edge (a plesiomorphic trait). The main posterior cuspid is not so strong. It is lacking in one of the mandibles and is rudimentary in the other. In spite of the individual variation of such a feature, which may be considerable in canids, the differences in p3 are quite significant. Another difference is the shorter premolar row (p2-p4 = 35 mm.) of the Kuruksay mandibles in comparison with the Muhor-Erig specimens (p2-p4= approx. 39 mm.).

Direct comparison of the Muhor-Erig material with the type skull of "C." *kuruksaensis* shows that the rostrum of the Kuruksay species is short, which can hardly be the case in the Muhor-Erig canid.

Conclusions

The mandible from Muhor-Erig shows all the features of the genus *Eucyon.* Its morphology suggests that it is a distinct species of *Eucyon*. The elongated mandible, with gaps between the very long, tall and slender premolars with strong posterior cuspids is a unique character of this species and suggests an advanced specialization to a specific type of feeding. The size and shape of the premolars suggest a dietary behavior verging on hypercarnivory (Van Valkenburgh 1989). These characters, together with the long premolar row and elongated and relatively graceful mandible suggest a specialization for catching and killing relatively small but mobile and widely distributed prey such as the resident ochotonids. In this way, *Eucyon marinae* sp. nov. may represent a "coyote-like" specialization among the *Eucyon* species.

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