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A new canid *Nurocyon chonokhariensis* gen. et sp. nov. (Canini, Canidae, Mammalia) from the Pliocene of Mongolia

With 2 figs, 2 pls, 2 tabs

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Abstract

A new genus and species of Canidae – *Nurocyon chonokhariensis* – is described from the Lower Pliocene lacustrine deposits of the Khirgisnur Formation of the Chonokhariakh-1 locality (northwestern Mongolia, the Great Lakes Depression). A well-preserved skull of the new canid demonstrates an unusual combination of primitive and derived features that distinguish it from other Pliocene members of the tribe Canini *(Eucyon, Nyctereutes* and *Canis)*. Unlike *Canis* and like *Eucyon* and *Nyctereutes*, it shows primitive characters, such as the fan-shaped supraoccipital shield and limited posterior extension of the frontal sinus. It differs from *Canis* and *Eucyon* in its advanced, nearly hypocarnivorous type of tooth pattern, which it shares with *Nyctereutes*. At the same time, the advanced similarity in the dorsal expansion of the frontal sinus and in the loss of the vulpine groove support its relationship with *Canis* but distinguish it from the other Canini. Thus, the cranial morphology of the studied form does not indicate a close affinity with any known genus of Pliocene Eurasian Canini and supports a full genus-level separation of this Mongolian dog. *"Canis" adoxus* from the Pliocene of Europe is the only fossil species to share similarities with *Nurocyon.* Phylogenetically, *Nurocyon chonokhariensis* probably represents a separate lineage of Canini which emerged during the early radiation and diversification of Eurasian canids at the beginning of the Pliocene.

Key words: Carnivora, Canidae, *Nurocyon chonokhariensis* gen. et sp. nov., Early Pliocene, Mongolia.

Introduction

Originally, the Canidae (Canini) came to Eurasia from America in the Late Miocene. The earliest canid, *Canis cipio* Crusafont Pairó, is first recorded in Europe from Spain in the faunas corresponding to MN 12 (Rook 1993).

The penetration of canids into the Eurasian Carnivora assemblage was associated with a global rearrangement of structural composition of the mammalian community which occurred at the end of the Miocene. The global extinction of many members of the Hyaenidae, especially of their canid-like morphotypes at the Miocene-Pliocene boundary, led to a prominence of dogs in the assemblages (Werdelin & Turner 1996). This resulted in a rapid radiation of canids and in the origin of many new and diverse taxa, which occupied free ecological niches. However, owing to the fragmentary character of Pliocene remains and to the lack of a detailed analysis of the early canids, new genera have not been recognized for a long time and all Eurasian fossil forms have been referred to the recent genera *Canis, Vulpes,* and *Nyctereutes*.

The extensive studies of Canidae conducted recently (Wang 1994, Tedford et al. 1995, Wang et al. 1999) and the revision of Eurasian Canini (Rook 1993) have enabled an evaluation of the available records in a new, revised context of canid systematics, and demonstrate a high diversity of the Old World Caninae.

The new genus *Eucyon* Tedford & Qiu was erected to describe a group of relatively primitive species of Canini with a phylogenetic position close to the base of the *Canis*-group. This genus had a long history in America starting from the middle Late Miocene. It penetrated Eurasia at the end of the Miocene, appearing at the same time in both Europe (Italy, Brisighella) and Asia (Mongolia, Khirgisnur-2, lower level) (Rook 1993, Tedford & Qiu 1996, Vislobokova et al. 2003).

New complete and taxonomically diverse material of Pliocene Asian canids has recently become known from Russia, Tajikistan, Mongolia and China (Sotnikova 1989,

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ROOK 1993, TEDFORD & QIU 1996), suggesting that this area was an important centre of canid radiation. This material includes the remains of a fossil group with a non-identified systematic position. Among them, there is a well-preserved skull of a canid from the Chonokhariakh-1 locality, northwestern Mongolia.

Abbreviations for collections and material compared:

AMNH	American Museum of Natural History, New York (USA)
F: AM	Frick collection of AMNH, New York (USA)
GIN	Geological Institute, Russian Academy of Sciences, Moscow (Russia)

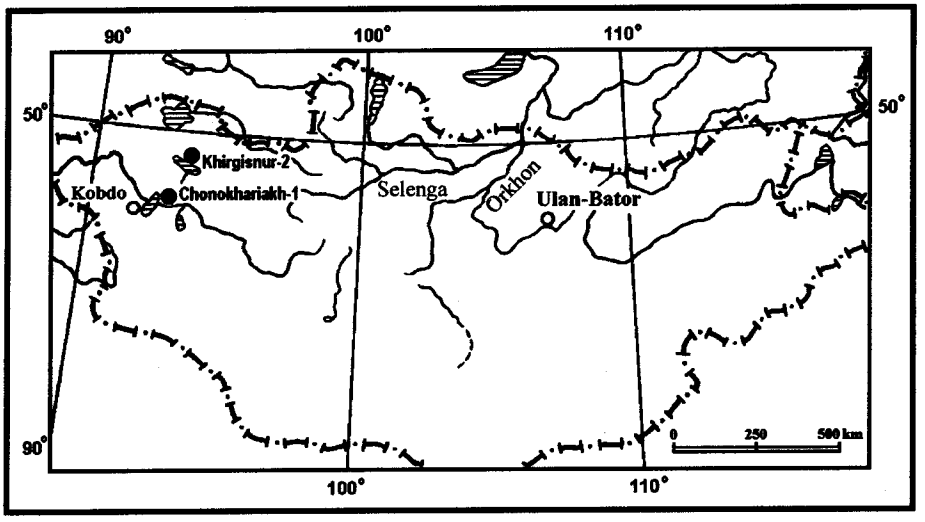

Fig. 1: Territory of Mongolia with the localities of mammalian fauna discussed in the text.

This skull was found in the locality situated in the northern Great Lakes Depression between the Khara-Us-Nur and Khara-Nur lakes, on the right bank of the Chonokhariakh Creek, northwestern Mongolia (fig. 1) The bone bed bearing the bird, fish, and mammal fauna is associated with the lacustrine and alluvial sediments of the Khirgisnur Formation (DEVIATKIN 1970). The Khirgisnur-2 section, where the Upper Miocene (late Turolian) and Lower Pliocene (Ruscinian) horizons were distinguished from their mammal fauna content, is the stratotype of the formation (PEVZNER et al. 1982). According to the geological records, the bone bed of Chonokhariakh-1 is correlated with the Pliocene part of the sediments in the Khirgisnur-2 reference locality (DEVIATKIN 1981).

At present, only assemblages of fishes and birds from Chonokhariakh-1 have been described (SYTCHEVSKAYA 1989, KUROCHKIN 1985). The mammalian fauna is up to now known mainly from a preliminary faunal list (presented by DEVIATKIN 1981: 68). A detailed description of the rich mammalian fauna from the locality, except for the postcranial remains of a hipparion, has never been published, although the investigation of some mammalian groups is in progress. Recently ZAZHIGIN & LOPATIN (2001) described a new dipodid rodent *Stylodipus perfectus* from Chonokhariakh-1 and suggested a Ruscinian age (MN 14–15) for this mammalian assemblage according to the Microtinae data.

This paper presents a description of a new genus and species of fossil canid from the Chonokhariakh-1 site of Mongolia.

IGF	Geological and Paleontological Museum of Florence State University, Florence (Italy)
OSM	Palaeontological Museum of Odessa State University, Odessa (Ukraine)
PIN	Palaeontological Institute, Russian Academy of Sciences, Moscow (Russia)
ZM MSU	Zoological Museum of Moscow State University, Moscow (Russia)

All studied specimens are derived from the collections of fossils of the Paleontological and Geological Institutes, Russian Academy of Sciences, Moscow. The following cranial material was used for comparison: type of *Eucyon zhoui*, cast of AMNH: V12181 (THP 10199); *Eucyon davisi*, F: AM 97056 and cast of AMNH: 12182 (THP 22818); type of "*Vulpes*" *odessana*, OSM 3220, and collection of dental and cranial remains PIN 390; type of "*Canis*" *adoxus*, cast of IGF: RSS 45; type of "*Canis*" *cipio*, cast of IGF; type of *Canis lepophagus*, cast of AMNH: 104783 (WT-881); *Nyctereutes sinensis*, GIN 482/250 (undescribed) and *N. sinensis*, F: AM 96759. The skulls of living canids from the AMNH and ZM MSU were also used for this study. All measured data are in millimeters.

Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Family Canidae Fischer von Waldheim, 1817
Subfamily Caninae Fischer von Waldheim, 1817
Tribe Canini Fischer von Waldheim, 1817
Genus ***Nurocyon*** gen. nov.

Type species: *Nurocyon chonokhariensis* sp. nov.

Included species: Type species only.

Age and distribution: Only known from the Early Pliocene (MN 14–15) of Mongolia.

Etymology: Mongolian: *Nur* – lake, Greek: *cyon* – dog, as the type skull was found in lacustrine deposits of the Chonokhariakh section in the Great Lakes Depression, northwestern Mongolia.

Diagnosis: Medium-sized canid close in size to female specimens of living and fossil coyotes. It is characterized by the following advanced characters: deep skull with frontals lacking a vulpine depression, dorsally inflated frontal sinus which penetrates the postorbital processes almost to their tips, high sagittal crest, enlarged mastoid process, tubular auditory meatus, and relatively shortened upper carnassial and canine. These derived characters are combined with primitive features such as the presence of a fan-shaped supraoccipital shield, rounded inion, small and slightly inflated bulla, and transversely elongated first upper molar with a well-developed parastyle.

Differential diagnosis: *Nurocyon* differs from *Nyctereutes* in its larger size, more developed frontal sinus, transversely elongated M1–2 and in having postorbital processes without any evidence of vulpine depression. *Nurocyon* differs from *Eucyon* in having a deep skull, high sagittal crest, tubular auditory meatus, robust upper carnassial, and inflated frontals without vulpine depression. *Nurocyon* differs from the known Pliocene species of *Canis* in having a less arched skull, shorter snout, lesser posterior extension of the nuchal crest, fan-shaped supraoccipital shield, and hypocarnivorous type of teeth pattern. The narrow and extremely elongated temporal region and the bulla with almost flat ventral surface are additional characters that differentiate the new canid from other Canini.

Nurocyon chonokhariensis sp. nov.
(pl. 1, figs. 1–2, pl. 2, figs. 1–3)

Holotype: A nearly complete skull (PIN 2737–257) with right M1 and M2, posterior portion of P4 and P2. The remaining teeth are crushed. Nasals and palate are compressed along the midline of the skull. Premaxillary is slightly broken anteriorly.

The type skull was collected by E. Deviatkin in 1970.

Type locality: Chonokhariakh-1, Great Lakes Depression, northwestern Mongolia. The lower part of the Pliocene lacustrine section, level 0–9, ferruginous sands.

The age: Early Pliocene (MN 14–15).

Etymology: "*chonokhariensis*", from Chonokhariakh, as the type skull was derived from lacustrine deposits in the Chonokhariakh section (Great Lakes Depression, northwestern Mongolia).

Referred specimens: GIN K3 1978–1, frontal part of a skull with P3–M2, unknown locality, Mongolia, likely Pliocene in age.

Diagnosis: As for the genus.

Description: The skull of *Nurocyon chonokhariensis* is intermediate in size between that of the living coyote *Canis latrans* and the Asian jackal *Canis aureus*. It is close in size to Pliocene canids such as *Eucyon zhoui* and *Canis adoxus* from Eurasia and to *Canis ferox* and *Canis lepophagus* from North America (tab. 1).

In dorsal view the facial and occipital portions of the skull are nearly equal in length. The premaxillary is large and massive; its width in the curve in front of the junction with the nasal bone is 8.7 mm. The frontal process of nasal bone reaches the posterior end of the maxillary. The postorbital processes are relatively short and inflated; their dorsal surface lacks the vulpine depression. The frontal sinus penetrates the postorbital processes but their tips are solid because the cranial bone is very stout. The frontal region behind the postorbital processes is markedly inflated dorsally. The morphology of this region indicates that the frontal sinus is more expanded posteriorly and dorsally than laterally. The inner structure of the frontal region, as seen in the specimen GIN K3 1978–1, shows that the sinus extends posteriorly along the anterodorsal surface of the braincase and ends at nearly 2/3 of the distance between the postorbital processes and the frontoparietal suture. The braincase is slightly inflated, especially anterior to the frontoparietal suture. The type specimen PIN 2737–257 has a strong elongation of the temporal region behind the orbit; the same character can be seen in GIN K3 1978–1. The temporal crests restrict the area of maximum inflation of the frontal bone and are united near the frontoparietal suture. The well-developed sagittal crest reaches its maximum height (11.5 mm) in the interparietal part of the skull. The lateral profile of the parietal part of the sagittal crest is straight, whereas the interparietal part of the crest is slightly arched and directed downward posteriorly.

In lateral view the frontal region arches slightly dorsally while it is straight where the rostrum joins the frontals. The skull is deep, its height at the level of frontoparietal suture is 50 mm. The infraorbital foramen is compressed in

Table 1: Comparison of cranial measurements of *Nurocyon chonokhariensis* and other Pliocene canids.
*Measurements after MILLER & CARRANZA-CASTAÑEDA (1998). All measurements are in millimeters.
Measures are: 1 = Greatest length: Distance from anterior tip of premaxillae to the posterior point of inion; 2 = Condylobasal length: Distance from anterior tip of premaxillae to posterior point of condyles; 3 = Length: Distance from posterior border of canine alveolus to foramen magnum notch; 4 = Facial length: Distance from anterior tip of premaxillae to the middle point between postorbital processes; 5 = Tooth row length: Alveolar length between P1–M2; 6 = Length M2 to bulla: Minimum distance from posterior edge of alveolus of M2 to depression in front of bulla; 7 = Postorbital length: Distance from middle point between postorbital processes to frontoparietal suture along the middle line of the skull; 8 = Zygomatic width: Greatest distance across zygoma; 9 = Width at canines: Maximum width above canines; 10 = Palatal width at P1: Minimum width between inner sides of alveoli; 11 = Frontal shield width: Maximum breads across postorbital processes; 12 = Postorbital constriction width: Least width across frontals behind postorbital process; 13 = Interorbital width: Minimum breadth across dorsal margins of orbit; 14 = Mastoid width: Maximum breadth across mastoid processes; 15 = Braincase width: Maximum breadth across brains; 16 = Facial depth: Minimum distance from outer alveolar margin of M1 to most ventral point of orbit; 17 = Bulla length: Greatest length of bulla; 18. P4 length: Maximum anteroposterior length measured on outer side; 19. M1–2 length: Maximum anteroposterior length measured on outer side.

	Nurocyon chonokhariensis PIN 2737-257	*E. davisi* F: AM 97056	E. zhoui IGF cast V12181	*C. adoxus* AMNH cast Rss-45	C. lepophagus AMNH cast 104783	*C. ferox** IGM 1130
1	187.0 ca	156.0	177.4	179.5	186.0	178.0
2	180.0 ca	141.0	160.0	173.0	177.3	-
3	146.0	123.0	133.1	146.0	145.4	-
4	94.0 ca	87.0	91.2	98.0	103.1	-
5	65.0	55.0	60.8	62.2	67.6	68.5
6	48.0	38.5	42.5	46.7	47.4	42.0
7	39.0	26.7	31.0	32.3	31.8	-
8	103.0	88.0	100.0	86.0 ca	96.3	85.0 ca
9	31.2	28.2	29.5	27.5	26.7	24.6
10	20.0	19.6	20.0	16.3	18.0	18.1
11	44.3	40.8	43.4	42.0	46.8	46.0
12	31.0	30.0	28.1	29.7	31.4	28.1
13	32.4	27.2	36.4	27.4	30.6	-
14	59.2	-	57.5	56.6	53.5	-
15	54.1	54.1	58.7	52.0	52.3	45.6
16	26.5	20.0	20.4	-	25.8	23.2
17	22.0	21.5	22.6	23.2	20.1	-
18	16.7 ca	15.4	15.5	16.1	17.7	16.9
19	20.7	17.8	18.0	19.5	18.8	-

cross section and is situated above the posterior end of P3. The zygomatic arch is deep and robust. The jugal is also relatively large (with a depth of 13.8 mm in front of the postorbital process) suggesting the development of a large masseter muscle. A prominent knot on the anteroventral portion of the zygomatic arch marks the attachment of this muscle in the skull PIN 2737–257. The long and vertically oriented paroccipital process has a free tip which in lateral view is located 4.4 mm below the ventral surface of the auditory bulla and is bent laterally in ventral view. The mastoid process is large and knob-like. The inion does not strongly overhang the occipital condyles.

In ventral view the incisive foramen extends posteriorly to the level of the middle part of the canine alveolus and reaches anteriorly to the level of I3. The palate extends to the end of the tooth row. The posterior inner end of the maxilla has a sharp process behind the lingual root of M2. The bulla has a flattened medial surface and moderately developed meatal tube. The anterior border of the bulla reaches the postglenoid process. The strongly arched zygoma, large occipital condyles and fan-shaped supraoccipital shield are also present.

Dentition: upper incisors and first three premolars are represented by alveoli, the anterior part of the crown of P4 is broken, M1 is worn (PIN 2737–257), whereas P3 and M1–2 are complete (GIN K3 1978–1). Both upper canines are also missing but their extremely shallow alveoli indicate the presence of very short crowns. Judging from the size and position of the remaining alveoli, I3 is enlarged with respect to I1–I2, P1 is large and single-rooted, and the premolars are separated by a short diastemata. The second premolar lacks a posterior cusp (PIN 2737–257) but a minute cusp occurs on the posterolabial cingulum of P3 (GIN K3 1978–1). The upper carnassial is relatively short

and robust, its length is 82.1–83.7% the length of M1–2. This carnassial has a slightly notched anterior border of the crown and a well-developed lingual cingulum. Its paracone is surrounded by a weak anterobuccal cingulum, its protocone is large, high, and is situated medial to the paracone. Upper molars are lower crowned than the premolars, elongated transversely and lengthened anteroposteriorly. Their paracone is slightly larger than the metacone. The M1 has a well-developed buccal cingulum with a prominent parastyle, small paraconule, large metaconule, and anteroposteriorly extended hypocone with a slightly bifurcate dorsal outline (measurements in tab. 2).

Nurocyon is differentiated from the Vulpini by the following derived characters: the frontal sinus is developed and penetrates the postorbital processes, the vulpine groove (depression) is absent and the paroccipital process is expanded posteriorly. The skull from Chonokhariakh-1 is undoubtedly to be referred to the Canini because of all the synapomorphies it shares with other members of the tribe: the orbital part of the zygomatic arch lacks a lateral flare, the paroccipital process expands posteriorly and bears a large free tip, the mastoid process is enlarged and the frontal sinus is developed.

Nowadays, the tribe Canini is divided into three groups.

Table 2: Comparison of dental measurements of *Nurocyon chonokhariensis* and other Miocene and Pliocene canids. Abbreviations: L – length; W – width; * – alveolar length. All measurements are in millimeters.

	LC-M2*	LP1-P4*	LP1	LP2	LP3	LP4	WP4	LM1	WM1	LM2	WM2
Nurocyon PIN 2737/257	76.5	46.9	5.5*	10.5*	12.2	16.7*	-	13.3	16.6	7.9	11.2
Nurocyon GIN KZ/1978-1	-	49.0	5.2*	9.4*	10.2*	18.0	9.3	13.2	16.3	7.4	12.2
E. davisi F: AM 97056	67.7	42.1	5.2	8.3	9.8	16.3	8.1	11.7	15.0	7.3	9.8
E. zhoui cast AMNH V12181	74.0	44.9	5.0	9.1	10.4	16.1*	8.9	11.3	15.3	6.0	9.4
E. odessana PIN 390-158	70.0	44.9	5.7	9.7	10.4	17.0	7.5	10.9	13.2	5.9	9.3
C. adoxus cast IGF Rss-45	72.4	45.8	5.0	8.5	9.1	17.1	9.2	12.2	14.1	7.4	10.9
C. lepophagus cast AMNH 104783	81.3	51.9	5.2	9.5	11.7	19.1	8.2	10.9	16.1	8.3	11.4
C. cipio cast IGF	-	-	-	-	13.0	21.6	9.8	13.1	15.8	7.3	11.0
N. sinensis F: AM 96769	61.1	37.5	-	-	-	14.7	6.5	9.9	12.2	6.9	9.4
N. sinensis GIN 482-250	67.1	39.5	4.3	7.2	8.0	14.3	7.5	10.4	13.7	6.7	9.9

Comparison and discussion

The study of morphological characters of *N. chonokhariensis* and the determination of its phylogenetic relationships are based on the results of the analysis of Canidae summarized in publications by BERTA (1988), WANG (1994), TEDFORD et al. (1995) and WANG et al. (1999). All recent studies on the phylogeny of living Caninae acknowledge the existence of two tribes in this subfamily: Vulpini and Canini.

The first one includes the South American canids and *Nyctereutes,* the second combines *Canis*-like dogs, and the third one is represented by the fossil genus *Eucyon* (TEDFORD et al. 1995, TEDFORD & QIU 1996). Since the new canid demonstrates an unusual combination of primitive and advanced cranial and dental features, a detailed comparison with species of all known Pliocene genera (*Eucyon, Nyctereutes* and *Canis*) is needed for the determination of its phylogenetic position within the Canini.

Nyctereutes appeared abruptly in Eurasia at the beginning of the Pliocene and was widely dispersed in the Palaearctic region. The Pliocene raccoon dogs are represented by *N. donnezani* (DEPERET) and *N. megamastoides* (POMEL) in Europe, and by *N. tingii* TEDFORD & QIU and *N. sinensis* (SCHLOSSER) in Asia. Among the Pliocene forms the primitive taxa *N. donnezani* and *N. tingii* resemble the more derived *N. megamastoides* and *N. sinensis* in the structure and proportions of the skull, although *N. donnezani* and *N. tingii* had a considerably less pronounced subangular lobe in the mandible and relatively larger and more quadrangular molars. Compared with their living relatives the fossil forms had a larger size and a more hypocarnivorous type of teeth, namely, large and widened molars and a relatively short upper carnassial (CZYZEWSKA 1969, TEDFORD & QIU 1991).

Although *N. chonokhariensis* is significantly larger than the fossil specimens of *Nyctereutes* and reaches the size and proportions of the earliest *Canis* members, it is close to the Pliocene raccoon dogs in most dental characters. Both *N. chonokhariensis* and the Pliocene *Nyctereutes* possess the following features: short upper canine, relatively short and robust carnassial with developed lingual and anterobuccal cingulum, and broad and large M1 with strongly developed conules. All shared dental characters are commonly associated with the hypocarnivorous adaptations of canids. In the canid systematic they are usually considered to be derived characters (BERTA 1988: 34, WANG et al. 1999: 316–320). A relatively short facial portion, stout cranial bones and a slightly rugose surface of the parietal bone, which are also shared by both *Nurocyon* and the Pliocene *Nyctereutes*, are likely associated with the hypocarnivorous adaptations as well. Remarkably enough in general cranial characters *Nurocyon* demonstrates *Canis*-like derived features, namely, a large size, strongly arched zygoma, high sagittal crest, and inflated frontals lacking the vulpine depression. It retains, however, the primitive, fan-shaped form of the occipital shield, unlike *Canis*.

This analysis shows that the most important derived features of *Nurocyon* are shared with the *Canis* group of canids. Its similarity with *Nyctereutes* apparently can be interpreted as an independent tendency of *Nurocyon* to evolve hypocarnivorous adaptations.

The genus *Eucyon* was established by TEDFORD & QIU (1996) on the abundant materials of early Canini from the Late Miocene of North America and from the terminal Miocene – Pliocene of Eurasia. It was proposed for the array of relatively primitive species within the Canini. The studied form shares with *Eucyon* all the cranial synapomorphies that were proposed by TEDFORD & QIU (1996: 36) for distinguishing their new genus from Vulpini. *Nurocyon* is also similar to *Eucyon* in retaining a primitive, fan-shaped form of the supraoccipital bone, but differs from it in having a relatively large and more developed frontal sinus (a synapomorphy which it shares with *Canis*).

At present the following species are included in the genus *Eucyon*: *E. davisi* (MERRIAM), *E. zhoui* TEDFORD & QIU, *E. minor* (TEILHARD & PIVETEAU), *E. odessana* (ODINTZOV), and *E. monticinensis* (ROOK) (TEDFORD & QIU 1996). All these species but *E. minor* and *E. monticinensis,* which are excluded from further comparison, were described on cranial material.

BERTA (1988) considered *E. davisi* as a stem taxon for both the South American Canini and the advanced forms of the *Canis* group of canids. However, according to the latest phylogenetic analysis, the species of the genus *Eucyon* are more closely related to the *Canis* group of Canini than to the South American canids (R. H. TEDFORD, personal communication, 2001). The earliest and most primitive *E. davisi*, which ranges from the middle Late to the latest Miocene in North America and which occurs in the Early Pliocene in Asia, is closely related to the late Turolian European *E. monticinensis* (ROOK 1992, TEDFORD & QIU 1996). Well-preserved cranial material of *E. davisi* is known from different Pliocene sites in China. Measurements of the skull of *E. davisi*, compared with those of *Nurocyon*, are reported here (fig. 2). Except for a clearly larger size, the log-ratio diagram shows significant differences between the Mongolian dog and *E. davisi* in most proportions, especially in the length of the temporal fossa, the length of the area of postorbital constriction and in the braincase width. A significant difference in size and proportions of the teeth is also observed (fig. 2, tab. 2).

The other Pliocene Eurasian eucyons – *E. odessana* and *E. zhoui* – possess several advanced features that make them approach the *Canis* group (IVANOFF 1996, TEDFORD & QIU 1996). "*Vulpes" odessana* was established by ODINTZOV (1967) on the basis of abundant cranial and dental remains of a small-sized canid from the Pliocene (latest Ruscinian) fauna of Odessa Catacombs in Ukraine. ROOK (1993) referred it to the group of primitive Eurasian Canini. This group was later included by TEDFORD & QIU (1996) in the new genus *Eucyon*. The Odessan form resembles *E. davisi* in size and proportions of the skull and in some dental characters, but it is more derived than *E. davisi* in having significantly larger incisors and bullae. Preliminary data (by IVANOFF 1996: 38) shows that in the Odessan dog the cranial frontal sinus expands into the postorbital processes and to the frontoparietal suture, which completely coincides with this character observed in the wolf-like canids. Consequently, the Odessan canid differs from *N. chonokhariensis* and from all cranially known species of *Eucyon* in its highly derived structure of the frontal region.

Among the most advanced *Eucyon* species the studied dog is closest in size to *E. zhoui.* The latter is a more derived relative of *E. davisi* in certain dental and mandibular characters and existed in Asia (China) in the Early Pliocene (TEDFORD & QIU 1996).

The characters uniting *N. chonokhariensis* with *E. zhoui* are the fan-shaped supraoccipital shield with a rounded convex apex, a large interparietal bone with a well-developed occipital area, vertically oriented paroc-

cipital process with free tips, relatively small bullae, P3 lacking posterior cusplets, a relatively short upper carnassial with a strong protocone and nearly subquadrate form of anterolabial border, and upper molars with a well-developed buccal cingulum. The derived characters that distinguish *N. chonokhariensis* from *E. zhoui* are a larger size, markedly inflated frontals, which lack a vulpine depression on the dorsal surface of the postorbital processes, and the more dorsally and posteriorly extended frontal sinus. The Mongolian skull is deeper in the frontal and occipital region. It has a more prominent and higher sagittal crest and a deeper jugal and zygoma with stouter orbital part of the latter. Its glenoid fossa and occipital condyle are larger whereas the auditory meatus is smaller relative to the skull length. Additional differences are also seen in the stronger mastoid process, tubular bulla, enlarged I3 and robust P4 and M1–2 of *Nurocyon chonokhariensis*.

Almost all derived characters of *N. chonokhariensis* listed above are synapomorphies with the *Canis* group. Within this group the Mongolian dog reaches the size of the living jackals and coyotes, but it is proportionally closer to the fossil coyote-like dogs because of their more elongated and narrow postorbital area.

In North America the earliest coyote-like Pliocene canids are known from the late Hemphilian of Central Mexico as *Canis ferox* (Miller & Carranza-Castañeda 1998) and from numerous Blancan localities as *C. lepophagus* Johnston (Nowak 1979). In Europe fossil coyotes did not occur prior to the beginning of the Pleistocene (Late Villafranchian) and are represented by *Canis arnensis* Del Campana (Kurtén 1974, Torre 1979). In Asia this group of canids likely appeared somewhat earlier than in Europe (Rook & Azzaroli Puccetti 1996).

Miller & Carranza-Castañeda (1998) described the new species *Canis ferox* and regarded it as an ancestral form of *C. lepophagus*. Owing to the highly fractured state of this skull its resemblance to the Mongolian dog is hard to establish, although their cranial size seems to coincide fully (tab. 1). In addition they share a long and narrow area of postorbital constriction, small alveoli of the upper canine and a bifurcated hypocone of M1. On the other hand, a distinct triangular outline of the supraoccipital shield with a sharp and pointed apex distinguishes *C. ferox* from *N. chonokhariensis* and allows its identification as a true member of the *Canis* group.

Johnston (1938) originally described and considered *C. lepophagus* the "forerunner" of the living coyote. *C. lepophagus* differs from *C. latrans* in primitive characters, i.e. a smaller size, narrower braincase, a narrow area of the postorbital constriction, and less inflated bullae. *C. lepophagus* also shares all these listed primitive features with *N. chonokhariensis*. Comparison of the Mongolian skull with the type specimen of *Canis lepophagus* from Cita Canyon (W.T. 881, AMNH 104783, cast) also showed their similarity in measurements and proportions (tab. 1). However, *Canis lepophagus* possesses some features of the *Canis* group which are missing in Mongolian form, namely, an elongated facial part of the skull, nearly triangular form of the supraoccipital shield and a relatively narrow and long P4 (tab. 2).

Three canid species approximately the size of *N. chonokhariensis* with an unclear generic definition are known from the Pliocene of Eurasia. *"Canis" michauxi* was described by Martin (1973) only on a single mandible and thus cannot be discussed further. *"Canis" cipio* by Crusafont Pairó (1950) is known from the Late Miocene (MN 12) localities in Spain. This form differs from *Eucyon* species in the upper teeth proportions, the structure of M1, and in its larger size (Rook 1992). *"Canis" cipio* is sometimes considered as ancestor of *Canis etruscus* (Pons Moya & Crusafont Pairó 1978b, Torre 1979), although its systematic position and phylogenetic relationships are still topics for discussion. For instance, Rook (1992) believes that *"C." cipio* is close to some canids from the late Hemphilian of North America.

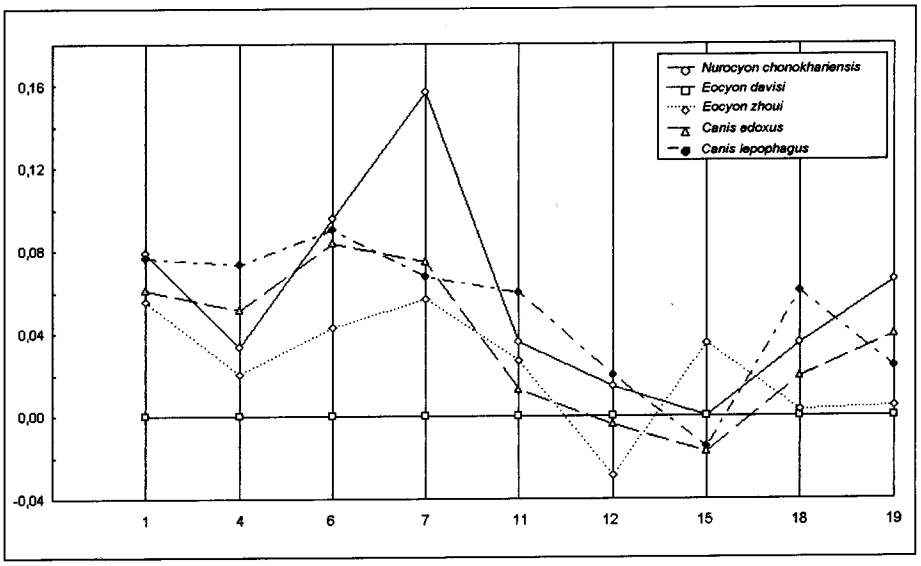

Fig. 2: Log-ratio diagram comparing the cranial proportions of *Nurocyon chonokhariensis* and *Eucyon zhoui*, *"Canis" adoxus*, *Canis lepophagus* with *Eucyon davisi* (standard of comparison) using the following measures: 1 – Greatest length; 4 – Facial length; 6 – Length M2 to bulla; 7 – Postorbital length; 11 – Frontal shield width; 12 – Postorbital constriction; 15 – Braincase width; 18 – P4 length; 19 – M1-2 length. Additional data from table 1

Compared with *Nurocyon*, *"C." cipio* also demonstrates transversally widened upper molars of a size equal to that of the Mongolian form (tab. 2). The upper carnassial of *Nurocyon* is much smaller than in *"C" cipio,* but shares with it such primitive features as a large and robust protocone and a strong and high lingual cingulum. On the other hand, *"C." cipio* strongly resembles the *Canis* group in having an upper carnassial whose length exceeds that of M1+2 together and upper molars with a significant medial constriction.

"Canis" adoxus was described by MARTIN (1973). It was found at Saint-Estève (France) in sediments correlated with the Perpignan faunal level (MN 15). *"C." adoxus* has since been referred to *Canis* (MARTIN 1973, TORRE 1979), to *Vulpes* (PONS MOYA & CRUSAFONT PAIRÓ 1978a), as well as to *Eucyon* (ROOK 1993). Nowadays it is obvious that *"C." adoxus* is neither vulpine nor a true member of the *Canis* group. However, the assignment of *"C." adoxus* to *Eucyon* is also doubtful (TEDFORD & QIU 1996). The major argument advanced by ROOK in favor of the assignment of *"C."adoxus* to *Eucyon* was the lack of the transverse crest on the talonid of m1, whereas the enlarged I3, the well expanded frontal sinus, and the *Canis*-like shape of the supraoccipital shield were arguments for TEDFORD & QIU (1996) against the assignment of this canid to *Eucyon.*

As for the cranial characters, *"C."adoxus* shares most of the Mongolian dog's advanced features, such as a relatively large size, enlarged I3, expansion of the frontal sinus into the postorbital process, elongated postorbital area, high temporal and sagittal crests, and enlarged glenoid cavity. Their similarity in the dental characters demonstrates the slight hypocarnivorous trend in *"C". adoxus* too, an observation of special interest. Like *Nurocyon "C."adoxus* possesses a short upper canine, spaced premolars, an upper first molar elongated anteroposteriorly and bearing a bifurcated hypocone, as well as a relatively short and robust upper carnassial with a large protocone and a paracone surrounded by an anterobuccal cingulum.

Among the Eurasian fossil forms the Mongolian dog is most similar to *"C."adoxus.* However, despite a similar combination of cranial and dental features, the differences between them exclude them as the members of a single lineage of canids. For instance, *"C."adoxus* is more derived in having a *Canis*-like, triangular shape of the supraoccipital shield. It also possesses a very narrow facial portion of the skull and moderately arched zygoma, (tab. 1: 8 and 10), features which are definitely lacking in *Nurocyon.* By contrast, *N. chonokhariensis* differs from *"C."adoxus* in *Canis*-like features such as a strongly arched zygoma and large dorsal inflation of the frontals. Additionally, it has a very long temporal area, unlike other members of Canini (fig. 2, tab. 1: 7). Most likely *N. chonokhariensis* and *"C."adoxus* are sister taxa. The generic identification of *"C."adoxus* remains a subject for discussion and it is not improbable that it should be referred to a new genus.

Conclusion

In summary, a new canid, *Nurocyon chonokhariensis,* from the Early Pliocene of Mongolia displays an unusual combination of primitive and derived features which distinguish it from other Pliocene Eurasian members of the tribe Canini (*Eucyon*, *Nyctereutes* and *Canis*). The studied skull shows three kinds of characters: a group of plesiomorphic features characteristic of the most primitive Canini-like *Eucyon*, a group of apomorphic features of the *Canis* group of Canini, and finally a group of characters that indicate the hypocarnivorous type of the teeth pattern of *Nurocyon.* The latter group of features makes the Mongolian dog resemble the fossil species of *Nyctereutes,* although I interpret this as a convergent similarity.

Accordingly, as the comparative analysis shows, *N. chonokhariensis* is more advanced than the most derived forms of *Eucyon.* It also has a higher number of plesiomorphies than the most primitive members of the *Canis* group, and is thus intermediate between these groups of canids. Phylogenetically it most likely belongs to a separate lineage, which evolved hypocarnivorous adaptations.

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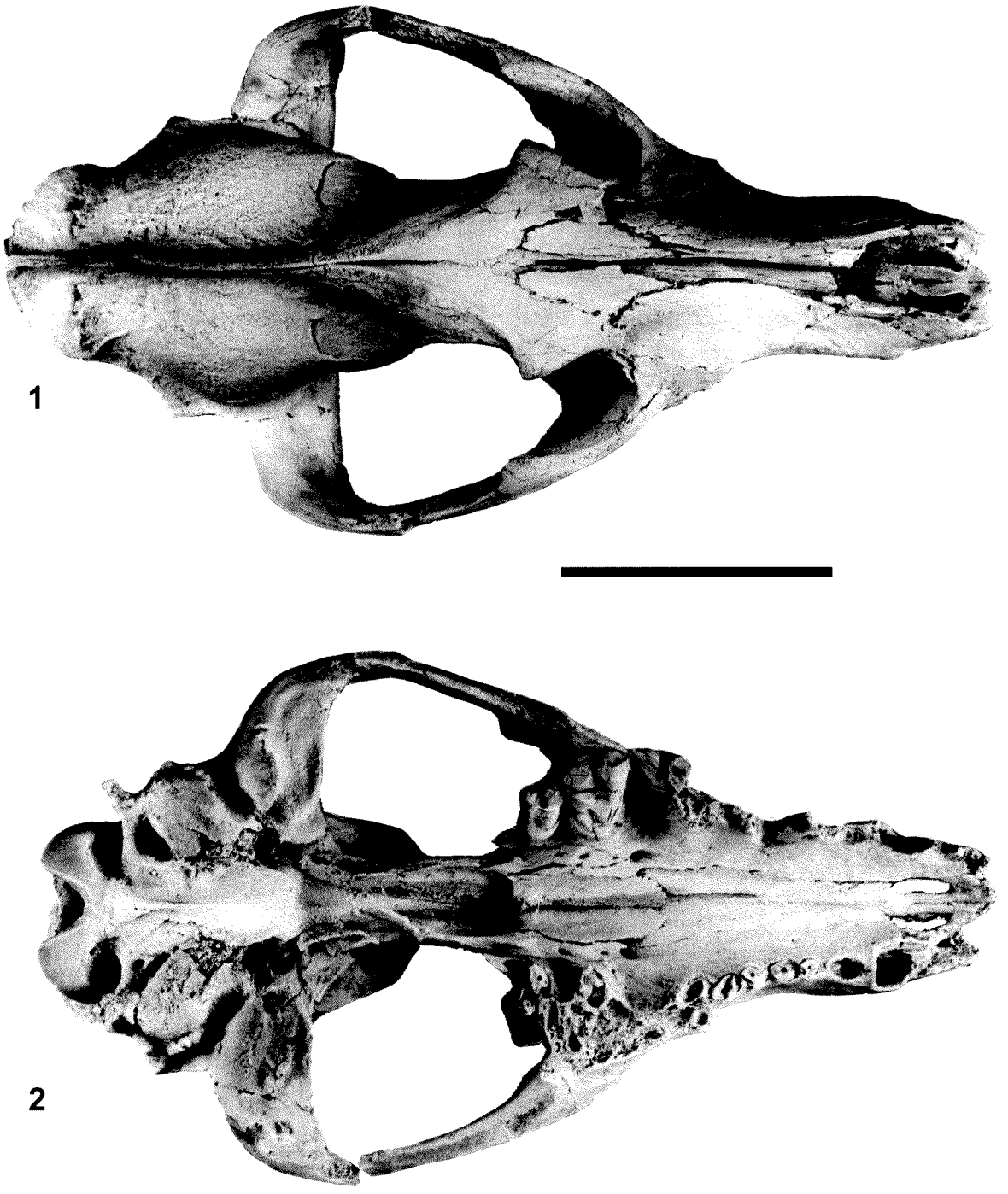
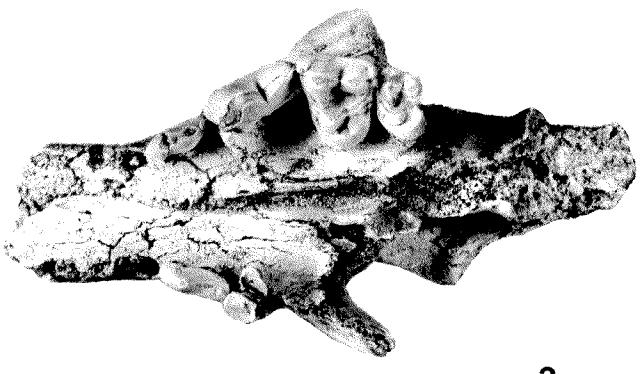


Plate 1

Skull of *Nurocyon chonokhariensis* gen. et sp. nov., PIN 2737-257, holotype

Fig. 1: Dorsal view.

Fig. 2: Ventral view.
Scale bar: 50mm



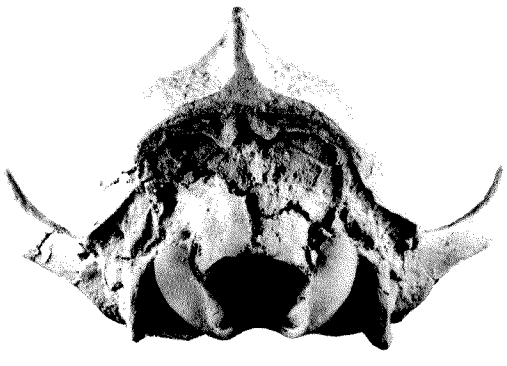


Plate 2

Skull of *Nurocyon chonokhariensis* gen. et sp. nov., PIN 2737-257, holotype.

Fig. 1: Lateral view.

Fig. 2: Occipital view.

Fig. 3: Fragment of the skull of *Nurocyon chonokhariensis* gen. et sp. nov., GIN KZ/1978–1. Occlusal view. Scale bar = 50mm