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Oligocene-Miocene Vertebrates from the Valley of Lakes (Central Mongolia): Morphology, phylogenetic and stratigraphic implications

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7. The carnivore guild of the Taatsiin Gol area: Hyaenodontidae (Creodonta), Carnivora, and Didymoconida from the Oligocene of Central Mongolia

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(With 2 figures)

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Abstract

New specimens of hyaenodontid creodonts, carnivorans, and didymoconids were unearthed in Mongolia by the Austrian-Mongolian Paleontological Expeditions. They are important additions to the faunal list from the Taatsiin Gol area and provide insight into the distribution, migration and paleobiology of hyaenodontids, carnivorans and didymoconids in the Oligocene of Asia. Five species of the genus *Hyaenodon* were identified. The Mongolian members of that genus are well separated from European and North American species. The Carnivora are represented by eight taxa, two of which are new. With the exception of the species *Palaeogale sectoria*, carnivorans differ even more than the hyaenodontids from their respective European and North American relatives and thus are mostly separated at the generic level. Didymoconida is the most endemic order of the three. It is only known from Asia and was totally absent in other continents. Three didymoconid taxa were found by the Austrian-Mongolian Expeditions.

Among the three orders Creodonta, Carnivora, and Didymoconida, most taxa are known from Central Asia only, which is why the carnivore fauna is interpreted to have been highly endemic. Its guild structure resembles those found in savannah-like environments today.

Keywords: Hyaenodon, Carnivora, Didymoconida, Paleobiogeography, Paleobiology, Oligocene, Asia

Introduction

The first investigation on fossil carnivorous mammals from the Taatsiin Gol area was conducted by the Central Asian expedition of the American Museum of Natural History (MATTHEW & GRANGER 1924, 1925). Many other scientific expeditions followed: the Mongolian Paleontological expedition of the Soviet Academy of Science from 1946 to

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1949 (Gromova 1952), the Polish-Mongolian Paleontological expedition from 1963 to 1964 (Kielan-Jaworowska & Dovchin 1968), ongoing work of the AMNH, and the Austrian-Mongolian Paleontological expedition from 1996 to 1998 (Daxner-Höck et al. 1997, Höck et al. 1999).

In this paper we provide an overview of the hyaenodontid, carnivoran, and didymoconid specimens found by the Austrian-Mongolian Expedition during three field trips from 1995–1997. Since then, additional specimens were collected during re-evaluation of the stratigraphic context by Daxner-Höck & Badamgarav (2007). Here, we summarize the new results with a focus on their implications on carnivore guild structure and paleobiogeography. The taxonomic and systematic results obtained by evaluating the carnivorous mammals found on those field trips are published elsewhere (Morlo & Nagel 2002, Morlo & Nagel 2006, Nagel & Morlo in prep.), as is a first analysis of the carnivore paleo-guild from Taatsiin Gol (Nagel & Morlo 2003). Because collection specimen numbers were not available for all specimens in those publications, they are provided here for the first time (especially for the creodonts of Morlo & Nagel 2006).

Geology, material, and methods

The specimens were found in the profiles of Shand Gol (SHG), Ikh Argalatyn Nuruu (IKH), and Shand-Tatal. The collected fossils from Shand Tatal yielded only fossils from Biozone A, Shand Gol ranges from biozones A to B, and Ikh Argalatyn Nuruu is stratified as biozone B (early Lower Oligocene).

The stratigraphy is based on rodent assemblages. Seven biozones were identified, with a clear lithostratigraphic position within the sediments and age information through $^{40}Ar/^{39}Ar$ dating of three interlayered basalts. For a detailed biostratigraphy see Daxner-Höck & Badamgarav (2007). All measurements are made with calipers to the nearest 0.1 mm. Tooth measurements given are max. length to max. breadth (L:B). Tooth morphology nomenclature follows Van Valen (1994). "P4" refers to the upper, "p4" to the lower tooth. Those tooth positions verified by alveoli only are referred to in brackets. The specimens are all housed in the collection of the Vienna Museum. Specimen collection numbers contain information on year of collection, location, and the specimen number itself. They are listed in the figure captions together with the field numbers for stratigraphic information.

Abbreviations

AMNH	American Museum of Natural History, New York, USA.
BDMAS	Biological Department, Mongolian Academy of Sciences, Ulanbataar, Mongolia.
BM	British Museum for Natural History Museum, London, UK.
NHMW	Naturhistorisches Museum, Wien, Austria.
PSS	Section of Paleontology and Stratigraphy, Geological Institute, Mongolian Academy of Sciences, Ulanbataar, Mongolia.
ZPAL	Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.
*	first taxon description

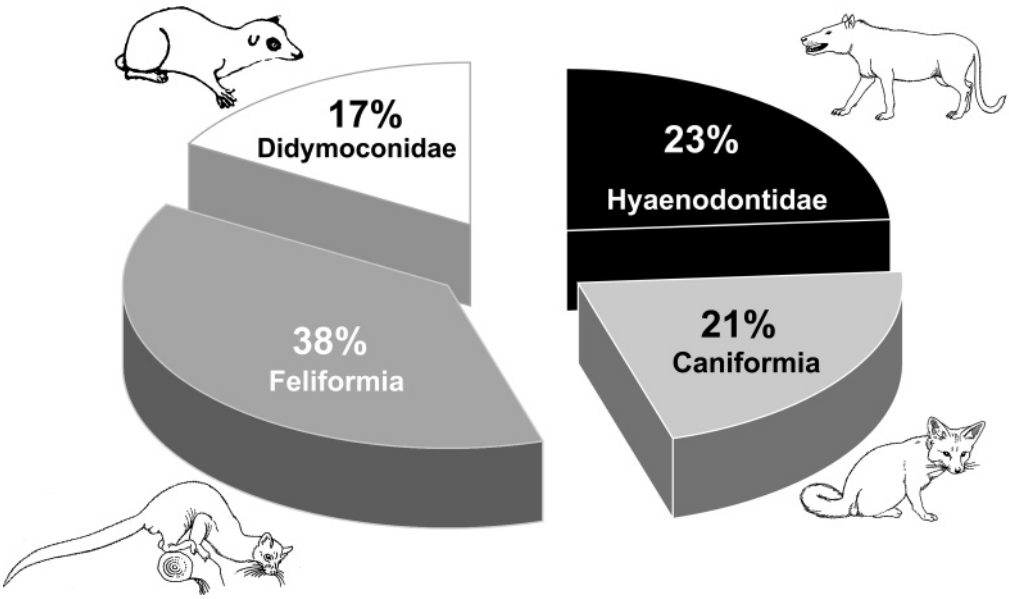


Fig. 1: Percentage of the main groups of carnivorous mammals found by the Austrian-Mongolian expedition from Taatsiin Gol, Hsanda Gol Formation (Lower Oligocene).

Systematic Paleontology

A total of twenty carnivore taxa are known from the Lower Oligocene of the Taatsiin Gol area – five hyaenodontids, twelve carnivorans, and three didymoconids. We were able to confirm fourteen of these taxa in the material found by the Austrian-Mongolian expedition. Additionally, two new taxa are identified.

The hyaenodontids played an important role in the faunal composition. *Hyaenodon gigas, H. mongoliensis*, *H. incertus*, *H. pervagus*, and *H. eminus* were identified in the present material, but are all first described from Khoer-Dzan (MATTHEW & GRANGER 1924, DASHZEVEG 1964, 1985, LANGE-BADRÉ & DASHZEVEG 1989, LAVROV 1999, NAGEL & MORLO 2006).

Among the carnivorans, three arctoid taxa are present in the new material. Hitherto, six species of arctoids were described. From three already erected *Ampicticeps* species (MATTHEW & GRANGER 1924, WANG et al. 2005a), only *A. shackelfordi* could be identified. The new specimens belonging to this species are slightly smaller than previously found individuals. The larger species, *A. makhchinus* and *A. dorog*, were not present, but a possibly new, very small taxon of *Amphicticeps* is recorded for the first time. *Amphicynodon teilhardi* (MATTHEW & GRANGER 1924, CIROT & BONIS 1992, WANG et al. 2005a) is still the only Mongolian member of this genus and a constant member of the carnivorous mammals from the Taatsin area. *Cephalogale* sp. (WANG et al. 2005a) and *Pyctis inamatus* (BABBITT, 1999) were not found among the present material.

The feliform carnivorans are represented by five taxa in the new material, one of which is new. Six valid species were previously described from the Oligocene of Mongolia. *Asiavorator altidens*, *Asiavorator* new species, *Shandgolictis elegans,* and *Shandgolictis simplex* are known from this area only (Dashzeveg 1996, Hunt 1998, Nagel & Morlo 2003, Nagel & Morlo in prep.). *Nimravus mongoliensis* (Gromova, 1959) was first described from Khoer-Dzan, while *Palaeogale sectoria* (Matthew & Granger 1924, Nagel & Morlo 2003) is known from Europe as well as North America. It is the only species of the Taatsiin Gol guild with a larger distribution area. The elusive felid *Proailurus* sp. (Hunt 1998) was not present among the new specimens, but the only previously assigned specimen may belong to Nimravidae instead of *Proailurus* (pers. comm. S. Peigné).

Among Didymoconidae, only two Oligocene species have previously been recorded from the Oligocene of Mongolia: *Didymoconus colgatei* and *D. berkeyi* (Matthew & Granger 1924, Lopatin 1997, 2006). Both are also present in the new material. Additionally, a more plesiomorphic taxon was found. The single isolated lower molar was assigned to cf. *Ergilictis* (Morlo & Nagel 2002).

The carnivorous mammals of the Taatsiin Gol area are mainly composed of small to medium-sized animals such as *Hyaenodon eminus, Amphicticeps shackelfordi, Amphicticeps* small species*, Asiavorator altidens*, *Asiavorator* new species, *Shandgolictis elegans*, *Palaeogale sectoria*, and the three didymoconid taxa. With *H. pervagus*, one large carnivore is well abundant, whereas the other large species *H. incertus*, *H. mongoliensis*, and *Nimravus intermedius* occur only rarely. Very rare are remains of the giant *Hyaenodon gigas*, which was known based solely on a few isolated teeth. Now, an ungual is added to this record.

Tab. 1: Minimum individual number (MIN) of carnivorous taxa found by the Austrian-Mongolian Paleontological Expedition in Taatsiin Gol area.

Species	MIN
Hyaenodon eminus	1
Hyaenodon pervagus	5
Hyaenodon cf. *incertus*	2
Hyaenodon mongoliensis	1
Hyaenodon gigas	1
Amphicynodon teilhardi	4

Species	MIN
Amphicticeps shackelfordi	5
Amphicticpes small species	1
Shandgolictis elegans	3
Asiavorator altidens	2
Asiavorator n. sp.	1
Nimravus mongoliensis	1

Species	MIN
Palaeogale sectoria	9
cf. *Ergilictis*	1
Didymoconus colgatei	5
Didymoconus berkeyi	1

Faunal List

Order Creodonta Cope, 1875

Family Hyaenodontidae Leidy, 1869

Subfamily Hyaenodontinae Leidy, 1869

Genus *Hyaenodon* Laizier & Parieu, 1838

Hyaenodon eminus MATTHEW & GRANGER, 1925
(MORLO & NAGEL 2006: figs. 3–4)

M a t e r i a l : NHMW 2005z0223/0001, field no. SHG-S/2, fragment of right mandible with p4-m1. NHMW 2005z0223/0002, field no. Mo97 SHG-S/3, glenoid fossa of a scapula fragment.

Hyaenodon pervagus MATTHEW & GRANGER, 1924
(MORLO & NAGEL 2006: figs. 5–16)

M a t e r i a l : NHMW 2005z0224/0001, field no. SHG-AB/5/4, isolated fragment of left P4. NHMW 2005z0224/0002, field no. SHG-AB/5/11, isolated fragment of right P4. NHMW 2005z0225/0001, field no. SHG/O/1, isolated tooth crown of left M2. NHMW 2005z0226/0001, field no. SHG-C/1, fragment of right mandible with (p4-m2), m3. NHMW 2005z0224/0003, field no. SHG-AB/5/3, isolated left p2. NHMW 2005z0224/0004, field no. SHG-AB/5/9, isolated fragment of right p2. NHMW 2005z0224/0005, field no. SHG-AB/5/5, isolated right p4. NHMW 2005z0224/0006, field no. SHG-AB/5/2, isolated left p4. NHMW 2005z0224/0007, field no. SHG-AB/5/7, isolated right p4 fragment. NHMW 2005z0227/0001, field no. IKH-A/24, isolated right p4, paraconid of right m3, and undeterminable root fragments. NHMW 2005z0224/0008, field no. SHG-AB/5/6, isolated right m1. NHMW 2005z0224/0009, field no. SHG-AB/5/10, isolated fragment of right m1. NHMW 2007z0017/0001, field no. SHG, isolated (?) p2 fragment. NHMW 2007z0018/0001, field no. DEL WP31, isolated left Cinf and left p2.

Hyaenodon cf. *incertus* DASHZEVEG, 1985
(MORLO & NAGEL 2006: figs. 17–21)

M a t e r i a l : NHMW 2005z0228/0001, field no. Mo95TAT-D, isolated fragment of right P2. NHMW 2005z0229/0001, field no. SHG AB/5/1, fragment of left m3. NHMW 2005z0229/0002, field no. SHG-AB/5/O/1, isolated left m3 with some mandibular fragments remaining. NHMW 2005z0230/0001 and NHMW 2005z0230/0002, field no. IKH-B/a/0, proximal fragments of right ulna and radius.

Hyaenodon cf. *mongoliensis* (DASHZEVEG, 1964)
(MORLO & NAGEL 2006: Fig. 22)

M a t e r i a l : NHMW 2005z0299/0001, field no. Mo97 SHG-C/1, isolated fragment of left p4.

cf. *Hyaenodon gigas* DASHZEVEG, 1985
(MORLO & NAGEL 2006: Fig. 23)

M a t e r i a l : NHMW 2005z0300/0001, field no. Mo95 IKH-A-Mix/O, right ungual.

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1945

Infraorder Arctoidea Flower, 1869

Family indet.

R e m a r k : The higher-rank taxonomic position of *Amphicynodon* and similar genera such as *Amphicticeps*, *Pachycynodon* and *Cynodictis* is still under discussion (see Wang et al. 2005a, Nagel & Morlo, in prep.).

Genus *Amphicynodon* Filhol, 1881

***Amphicynodon teilhardi* (Matthew & Granger, 1924)**
(Nagel & Morlo in prep.)

M a t e r i a l : NHMW 2007z0021/0001, field no. Mo95 IKH A1/2/2, left mandible with broken p2, p3-m1. NHMW 2007z0021/0002, field no. Mo95 IKH B/a, right mandible with p2-m1. NHMW 2007z0022/0001, field no. Mo97 SHG AB above 13-16, left mandible fragment with m1. NHMW 2007z0023/0002, field no. Mo95 TAT/3, left mandible with broken p4 and m1.

aff. *Amphicynodon sp.*

M a t e r i a l : NHMW 2007z0021/0003, field no. Mo95 IKH A2-4, fragment of left mandible with p2-4 and m1-trigonid. NHMW 2007z0023/0001, field no. Mo95 TAT-D/4/2, maxillar fragment with M1.

***Amphicynodon* sp. (Matthew & Granger 1924)**
(Nagel & Morlo in prep.)

M a t e r i a l : NHMW 2007z0024/0001, field no. SHG, left mandible fragment with p3 to (m1). NHMW 2007z0024/0002, field no. SHG AB, right p3. NHMW 2007z0025/0001, field no. TGR-C, right p4.

Genus *Amphicticeps* Matthew & Granger, 1924

***Amphicticeps shackelfordi* Matthew & Granger, 1924**
(Nagel & Morlo in prep.)

M a t e r i a l : NHMW 2007z00260001, field no. Mo95 Shand-Tatal/1, right maxilla with P3-4 and broken M1. NHMW 2007z0026/0002, field no. Mo95 Shand-Tatal/4, isolated right m1. NHMW 2007z0026/0003, field no. Mo95 Shand Tatal/2 surface, right mandible with alveoli of c-p2, p3-4. NHMW 2007z0027/0001, field no. Mo 01 TGL B/1, left mandible with alveoli of p3, p4-m1. NHMW 2007z0027/0002, field no. Mo 01 TGL B/2, right mandible with m1-m2, alveolus for m3. NHMW 2007z0028/0001, field no. DEL B/12 m1-talonid, m2-3.

cf. *Amphicticeps* small species
(MORLO & NAGEL in prep.)

M a t e r i a l : NHMW 2007z0029/0001, field no. Mo95 IKH-A/1/2/1, right mandible with p4, m1-talonid, and m2-3.

Suborder Feliformia KRETZOI, 1945

Family Stenoplesictidae SCHLOSSER, 1923

Genus *Shandgolictis* HUNT, 1998

***Shandgolictis elegans* HUNT, 1998**
(NAGEL & MORLO in prep.)

M a t e r i a l : NHMW 2007z0030/0001, field no. SHG AB/0, fragment of right maxilla with P4-M2. NHMW 2007z0030/0002, field no. SHG 6 AB, fragment of right mandible with alveoli of p3, p4-m1, alveoli of m2. NHMW 2007z0031/0001, field no. TGR C/2, fragment of right mandible with alveoli for p1-p3, p4-m1, alveoli for m2. NHMW 2007z0032/0001, field no. UNCH 3+4 mix, proto- and paraconid of m1. NHMW 2007z0030/0003, field no. Mo95 SHG, left mandible with p4, p3 broken, alveolus for p2 and p1.

Genus Asiavorator SPASSOV & LANGE-BADRÉ, 1995

***Asiavorator altidens* SPASSOV & LANGE-BADRÉ, 1995**
(NAGEL & MORLO in prep.)

M a t e r i a l : NHMW 2007z0034/0001, field no. TGL A/12 , isolated right P4. NHMW 2007z0034/0002, field no. TGL A/11 right mandible fragment with alveoli of p1, p2-3, anterior cusp of p4. NHMW 2007z0034/0003, field no. TGL A/13, fragment of right mandible with talonid of m1, alveoli for m2. NHMW 2007z0035/0001, field no. Mo01 TGW-D, right mandible with p4, anterior root of p3, p2 and alveolus for p1.

cf. *Asiavorator* sp.

M a t e r i a l : NHMW 2007z0036/0001, Mo95 TAT6, left P4 fragment. NHMW 2007z0037/0001, Mo95 TGR C/2/2, left P4 fragment.

***Asiavorator* nov. spec.**
(NAGEL & MORLO in prep.)

M a t e r i a l : NHMW 2007z0038/0001, Mo03 TGR-ZO, right mandible fragment with p3 – m2.

Carnivora inc. sed.

Family Nimravidae Cope, 1881 *sensu* Morlo et al. 2004

Genus *Nimravus* Cope, 1879

***Nimravus mongoliensis* (Gromova, 1959)**
(Nagel & Morlo in prep.)

M a t e r i a l : NHMW 2007z0039/0001, field no. IKH-A/4, root of left upper canine crown only partly preserved. NHMW 2007z0040/0003, field no. Mo01 SHG, cusp of Csup. NHMW 2007z0040/0001, field no. SHG-A/18-20, collected on the surface, isolated fragment of left P3. NHMW 2007z0042/0001, field no. Mo95 BUK-A/12, right I3. NHMW 2007z0041/0001, field no. UNCH 3+4, right calcaneum. NHMW 2007z0040/0002, field no. Mo97SHG, Gala, right ungual.

cf. Viverravidae

Genus *Palaeogale* Meyer, 1846

***Palaeogale sectoria* (Gervais, 1852)**
(Nagel & Morlo in prep.)

M a t e r i a l : NHMW 2007z0045/0010, field no. IKH-A/T95, isolated left P4 with the metastyle damaged. NHMW 2007z0043/0001, field no. TGR AB/22, fragment of left maxilla with P3-P4 NHMW 2007z0044/0001, field no. Mo01 SHG-AB, fragment of right maxilla with P3-M1. NHMW 2007z0045/0010, field no. IKH-A1/T95, right P4. NHMW 2007z0045/0005, field no. IKH A/1/1, fragment of right mandible with (p4), m1-m2. NHMW 2007z0045/0008, field no. IKH-A/1/2, fragment of right mandible with (c-p2), posterior root of p3, p4. NHMW 2007z0045/0006, field no. IKH-A-mix, fragment of left mandible with (p2-p3), p4, talonid of m1. NHMW 2007z0045/0002, field no. IKH-B/a/1, fragment of right mandible with (c-p3), p4-m1. NHMW 2007z0045/0001, field no. IKH-B/a/2, fragment of left mandible with (m1), m2. NHMW 2007z0045/0004, field no. IKH-B/a/3, fragment of right mandible with posterior part of p4, m1, and the roots of m2. NHMW 2007z0044/0002, field no. SHG/1, fragment of left mandible with p4-m1, (m2). NHMW 2007z0045/0003, field no. IKH-A 2-4, fragment of left mandible with posterior root of p3, p4-m1, (m2). NHMW 2007z0044/0007, field no. SHG/2, fragment of right mandible with broken roots of p3-m1, m2; NHMW 2007z0044/0006, field no. SHG/3, fragment of left mandible with p1-p3. NHMW 2007z0044/0005, field no. SHG/4, fragment of right mandible with roots of lower canine and p1-p3, p4. NHMW 2007z0044/0004, field no. SHG 1, fragment of left mandible with (p1-p2), p3-p4. NHMW 2007z0044/0003, field no. SHG 2, fragment of left mandible with (p2-p3), roots of p4, m1-m2. NHMW 2007z0043/0003, field no. TGR-AB21, fragment of left mandible with (c-p3), p4-m1. NHMW 2007z0043/0005, field no. TGR-AB22/2, fragment of right mandible with m1 and roots of m2. NHMW

2007z0043/0002, field no. TGR-AB22/14, fragment of right mandible with single-rooted (p1), p2 broken, p3-4, talonid of m1, (m2). NHMW 2007z0043/0004, field no. TGR-C/1/1, fragment of right mandible with (p2) p3-m2. NHMW 2007z0045/0007, field no. IKH-B/a/4, fragment of left mandible with m1 talonid and m2.

Order Didymoconida KRETZOI, 1943 (sensu LOPATIN 2006)

Family Didymoconidae KRETZOI, 1943

Subfamily Didymoconinae LOPATIN 1997

Genus *Ergilictis* LOPATIN, 1997

cf. *Ergilictis* LOPATIN, 1997
(MORLO & NAGEL 2002: Fig. 1)

M a t e r i a l : NHMW 2000z0055/0037, field no. TGR-AB/22, biozone B, late early Oligocene, isolated right P/4.

Genus Didymoconus MATTHEW & GRANGER, 1924

***Didymoconus colgatei* MATTHEW & GRANGER, 1924**
(MORLO & NAGEL 2002: Fig. 3–7)

M a t e r i a l : NHMW 2000z0056/0026, field no. SHG, left mandibular fragment with P/3, P/4, M/1. NHMW 2000z0056/0040, field no. TGR-C/2, left mandibular fragment with P/3 and P/4. NHMW 2000z0056/0030, field no. TAT-D/1,right mandibular fragment with erupting C, alveoli of P/2, erupting P/3 and trigonid of erupting P/4. NHMW 2000z0057/0039, field no. TGR-C2, two left mandibular fragments: NHMW 2000z0057/0039a, alveolus of I/2, root of I/3, C, P/2, alveolus of P/3, fragment of P/4, and anterior alveolus of M/1; NHMW 2000z0057/0039b with alveoli of C, P/2, and P/3, complete P/4, and anterior alveolus of M/1.

***Didymoconus berkeyi* MATTHEW & GRANGER, 1924**
(MORLO & NAGEL 2002: Fig. 8–10)

M a t e r i a l : NHMW 2000z0058/0025, field no. LOH-C/1/O, fragment of left mandible with P/3. NHMW 2000z0058/0020, field no. RHN-A/7, isolated right P/4. NHMW 2000z0058/0046 field no. UNCH 3+4mix, left humerus fragment. NHMW 2007z00190001, field no. LOH-O, left distal humerus fragment.

***Didymoconus* sp. MATTHEW & GRANGER, 1924**

M a t e r i a l : NHMW 2007z0020/0001, field no. TAT-A, right M1.

Conclusion

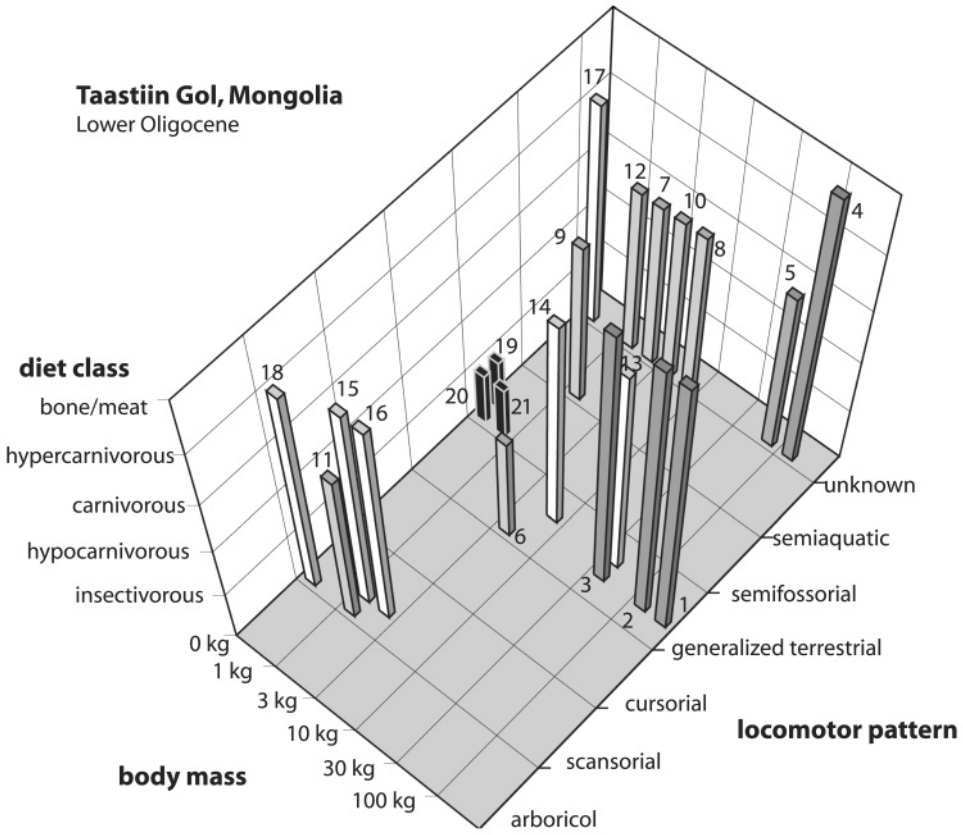
Guild structure

The Didymoconida were the first members of the carnivore guild to be published out of the material found by the Austrian-Mongolian expedition (Morlo & Nagel 2002) from the Taatsiin Gol area. Thereafter, a tentative analysis of the guild structure of Creodonta and Carnivora excluding didymoconids was provided by Nagel & Morlo (2003). In the present contribution, we evaluate all known taxa, including Didymoconida. Three parameters are used to define the carnivore guild: food preference (diet class), locomotor pattern, and body mass. Five classes of dietary preferences are distinguished: bone/meat, hypercarnivorous, carnivorous, hypocarnivorous, and insectivorous diet. This is based on previous studies by Van Valkenburgh (1990), Muizon & Lange-Badré (1997), Morlo (1999), and Nagel & Morlo (2003). The locomotory pattern classes follow MacLeod & Rose (1993) and Morlo (1999). We differentiate between arboreal, scansorial, cursorial, generalized terrestrial, semifossorial, and semiaquatic taxa. Most data are taken from Morlo (1999) and Nagel & Morlo (2003). In other studies, the body mass of carnivores was calculated by indices based on measurements of either the carnassials (Thackeray & Kieser 1992, Viranta & Andrews 1995, Legendre & Roth 1988, Van Valkenburgh 1990, Morlo 1999) or the limb bones (Gingerich 1990, Anyonge 1993, Heinrich & Biknevicius 1998, Egi 2001). Herein, we used the carnassial size(s) to estimate body mass because postcranial elements are only rarely preserved in most Mongolian species and absent among the new taxa. To scope the possible variability of absolute body mass data due to these methodological reasons, we use body mass classes instead of absolute body masses. Didymoconid body mass class was determined using the regression that Morlo (1999) developed for creodonts. Body mass classes are: 0–1 kg, 1–3 kg, 3–10 kg, 10–30 kg, 30–100 kg, >100 kg.

The predator guild from the Taatsiin Gol area (Lower Oligocene) consists of approximately 65 % of very small to small animals (0–10 kg). The gap in the 10–30 kg-class is probably caused by insufficient knowledge of the body mass variation in these animals. Only 6 % of the taxa clearly show hypocarnivorous tendency; most are either hypocarnivorous (35 %) or carnivorous (35 %). This is not uncommon in a carnivorous association, which underwent changes in composition, as did the Mongolian guild at the Eocene/Oligocene boundary (Meng & McKenna 1998). Twenty-four percent of the taxa are bone/meat feeders, which is a higher percentage than in any known association today (Van Valkenburg 1988, 1992, Nagel & Morlo 2003). Unfortunately, nothing is known about the locomotion in seven taxa and therefore the interpretation lacks sufficient information on this important factor.

Stratigraphy and Paleobiogeography

The hyaenodontid fauna of the Taatsiin Gol area, Central Mongolia, is nearly identical to that of contemporary Kasakhstan and China, whereas didymoconids of these areas share the genus *Didymoconus*, but no species. As is also shown by the carnivorans (e.g., Lange-Badré & Dashzeveg 1989, Huang 1993, Huang & Zhu 2003, Wang et al.



Hyaenodontidae: 1- *Hyaenodon* cf. *gigas*, 2- *Hyaenodon incertus*, 3 - *Hyaenodon pervagus*, 4 - *Hyaenodon mongoliensis*, 5 - *Hyaenodon eminus.* Caniformia: 6 - *Cephalogale* sp., 7 - *Amphicticeps makhchinus*, 8 - *Amphicticeps dorog*, 9 - *Amphicticeps shackelfordi*, 10 - *Amphicticpes* small species, 11 - *Amphicynodon teilhardi*, 12 - *Pyctis inamatus.* Feliforme: 13 - *Nimravus mongoliensis*, 14 - *Proailurus* sp., 15 - *Shandgolictis elegans*, 16 - *Asiavorator altidens*, 17 - *Asiavorator* n. sp., 18 - *Palaeogale sectoria.* Didymoconidae: 19 - cf. *Ergilictis*, 20 - *Didymoconus colgatei*, 21 - *Didymoconus berkeyi.*

Fig. 2: Structure of the carnivorous mammal fauna from Taatsiin Gol, Hsanda Gol Formation, Central Mongolia (Lower Oligocene).

2005b), Oligocene Kasakhstan, Mongolia, and China can be interpreted as a single biogeographic region. Together with the known record of most taxa from the Ergilin Dzo and the Khan Dzo Formation, this implies a very large area, which was ecologically stable over a long time. The transgression from the Eocene to the Oligocene is not very marked. Most creodont taxa are already known from the Late Eocene of Asia and survive until the end of the Oligocene. Consequently, MENG & MCKENNA (1998) did not include the carnivorous mammals in their Mongolian Remodelling. This change from a humid climate with a densely forested landscape to an arid climate with a more open landscape is seen only at the species level.

The faunal composition of carnivorous mammals of the Taatsiin Gol area, Central Mongolia, implies a highly endemic character of the fauna with respect to European and North American faunas. Though four out of seven genera are shared with contemporary European and North American faunas (*Hyaenodon*, *Amphicynodon*, *Nimravus*, and *Palaeogale*), the only species also present on the other continents is *Palaeogale sectoria*. This species, however, not only has the most plesiomorphic specimens in Mongolia (verified by, e.g., p1 double-rooted, m2 relatively large, very small overall size), but is also extremely variable in this area (e.g., overall size, number of p1-alveoli, height of m1, size of m2). This implies that it may have originated here and migrated to Europe as well as to North America. The m2 of the endemic arctoids *Amphicynodon teilhardi* and *Ampicticeps* is much more reduced than in comparable European forms. In contrast, the m2 in the endemic feliforms *Shandgolictis* and *Asiavorator* is double-rooted and thus less reduced than in the European *Stenoplesictis* and *Palaeoprionodon*. This verifies that both groups, Mongolian arctoids as well as Mongolian stenoplesictids, represent independent evolutionary lineages relative to their respective European relatives. *Amphicticeps* is discussed as the ancestor of Semantoridae (= Oligobunidae) and, consequently, of pinnipeds (Wolsan 1993, Wang 1999, Sato et al. 2006). *Nimravus* and *Palaeogale* are two genera not only distributed in Asia and North America; moreover, both migrated into Europe after the Grand Coupure. The smallest and most plesiomorphic *Palaeogale* known so far is from the Shand Gol area (smallest in size and sometimes p1 still double-rooted). *Nimravus mongoliensis* was one of the few larger predators from Mongolia and survived the Eocene/Oligocene faunal turnover (Meng & McKenna 1998). Nimravids and Mongolian stenoplesictids disappeared in the late Oligocene, but *Palaeogale* survived until the late early Miocene (MN 4) of Europe (Morlo 1996) and the early Early Miocene of East Asia (Ye et al. 2003). *Nimravus mongoliensis* from Mongolia clearly differs from the European *N. intermedius* in its plesiomorphic, broader m2, m1 with a rudimentary metaconid, and a smaller accessory cusp on p4 (Gromova 1959, Dashzeveg 1996, Peigné 2003). Corresponding to *Palaeogale*, this implies that the more plesiomorphic species lived in Asia.

The Mongolian predator fauna was therefore highly endemic. On the other hand, several taxa (*Amphicticeps*, *Nimravus*, *Palaeogale*) started a successful evolutionary history from this area. This allowed them to migrate into all other northern continents and, in the case of *Amphicticeps* – a possible ancestor of pinnipeds – even to conquer a completely new habitat.

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