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Guild structure of the carnivorous mammals (Creodonta, Carnivora) from the Taatsiin Gol area, Lower Oligocene of Central Mongolia

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For the first time, comparative information is given for the paleobiological pattern of the carnivorous mammals from the Oligocene of the Taatsiin Gol area, Mongolia. Creodonts and carnivorans have been described several times from Central and Outer Mongolia since 1924. The fauna of Taatsiin Gol consists of a large and rather unique variety of carnivorous mammals. The faunal list contains four taxa of creodonts. All of them belong to the genus *Hyaenodon*. The carnivorans are more diverse. The Feliformia and Caniformia consist of five taxa. The nimravids are represented by *Nimravus mongoliensis*. The smallest member of this carnivorous guild is the enigmatic *Palaeogale sectoria*. Estimations of body masses, diet classes and locomotor patterns are given. Only three of four diet classes are present. There is no evidence of a non-vertebrate/meat group as there is probably no representative of the 10-30 kg class. Four different locomotor patterns are identified, while arboreal and semiaquatical taxa are lacking. The Oligocene carnivorous guild of Taatsiin Gol shows similarities to the Recent guild of carnivorans from the Serengeti.

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INTRODUCTION

Three parameters are mostly taken to estimate the (paleo-)ecomorphology of a fossil taxon: body mass, diet class, and locomotor pattern. A lot of analyses have been done on single carnivorous taxa for one of these parameters, but studies on complete faunas are sparse for predatory mammals. Instead, carnivorans are often excluded from analyses of fossil faunas (e.g., Legendre 1986). In this paper, we estimate all three parameters for all known creodonts and carnivorans of the fauna from the Lower Oligocene of Taatsiin Gol area, Central Mongolia, to get a first insight into the paleobiology of not only a single taxon, but also the complete guild. Such guild structures based on ecomorphology can then be compared to that of other faunas to demonstrate similarities or dissimilarities irrespective of the taxonomical structure of the fauna. The worth of this approach has been demonstrated by, e.g., Van Valkenburgh (1992), Viranta & Andrews (1995), and Morlo (1999). The fact, that the majority of the specimens described from the Taatsiin Gol area are cranial remains, restricts the methods we can apply. We therefore do not deal with absolute data, but assign the taxa to parameter classes. Such a semi-quantitative approach, especially concerning body mass, follows Dayan & Simberloff (1996) and Morlo (1999).

MATERIAL

Carnivorous mammals are known from the Taatsiin Gol area since the Central Asian Expedition of the American Museum of Natural History (1924, 1925). Many other scientific expeditions took place since then: the Mongolian Paleontological Expedition of the Soviet Academy of Science from 1946 to 1949 (Gromova 1952), the Polish-Mongolian Paleontological Expedition from 1963 to 1964 (Kielan-Jaworowska & Dovchin 1968), and the Austrian-Mongolian Paleontological Expedition from 1996 to 1998 (Daxner-Höck *et al.* 1997, Höck *et al.* 1999, Daxner-Höck 2000). Detailed descriptions of the carnivorous mammals found by this expeditions are on their way (Nagel & Morlo in prep.), but first results are given in Nagel & Morlo (2001). For the ecomorphological analysis given in here we also include the published material from the Polish-Mongolian Paleontological Expedition and from the Central Asian Expedition of the American Museum of Natural History.

We recognise a total of 11 carnivorous taxa found by the different scientific groups in the Taatsiin Gol area (Matthew & Granger 1924, 1925, Dashzeveg 1964, 1985, Gromova 1959, Spassov & Lange-Badré 1995, Hunt 1998, Nagel & Morlo 2001 and in prep.). These are:

Creodonta

Hyaenodon gigas DASHZEVEG, 1985: fig. 12 *H. gigas* was originally described from Khoer-Dzan. Nagel & Morlo (2001) assigned a gigantic third phalanx from Taatsiin Gol as *H.* cf. *gigas* to that species. *Hyaenodon incertus* DASHZEVEG, 1985: fig. 9. *H. incertus* was originally described from the Ergilin Formation of Khoer-Dzan. Nagel & Morlo (2001) reported it from the Taatsiin Gol area. *Hyaenodon pervagus* MATTHEW & GRANGER, 1924. This taxon was described by specimens coming from the Hsanda Gol Formation. Subsequent authors (Lange-Badré & Dashzeveg 1989, Dashzeveg 1985, Nagel & Morlo 2001) confirmed its presence in the Taatsiin Gol area. *Hyaenodon eminus* MATTHEW & GRANGER, 1925: fig. 13. Originally described from the Ergilin Dzo Formation, *H. eminus* was first recorded from Taatsiin Gol by Nagel & Morlo (2001).

Carnivora -Feliformia

Asiavorator gracilis (SPASSOV & LANGE-BADRÉ, 1995: fig. 1-4, 6)
This species is a known member of the Taatsiin Gol fauna and was reported after its description by Hunt (1998) and Nagel & Morlo (2001).

Shandgolictis elegans (MATTHEW & GRANGER, 1924: fig. 6A,F)
After being described from Taatsiin Gol, additional specimens of this species were described by Dashzeveg (1996), Hunt (1998), and listed in Nagel & Morlo (2001).

Carnivora -Caniformia

Amphicticeps shakelfordi (MATTHEW & GRANGER, 1924: fig. 4-5)
Besides the holotype, the only other record from Taatsiin Gol came from Nagel & Morlo (2001).

'Amphicynodon' teilhardi (MATTHEW & GRANGER, 1924: fig. 6D)
This species, originally described from the Hsanda Gol Formation of Loh, was reported from Taatsiin Gol by Lange-Badré & Dashzeveg (1989) and Nagel & Morlo (2001). An investigation in progress reveals that this species does not belong to *Amphicynodon* but probably to a new genus (Nagel & Morlo in prep.)

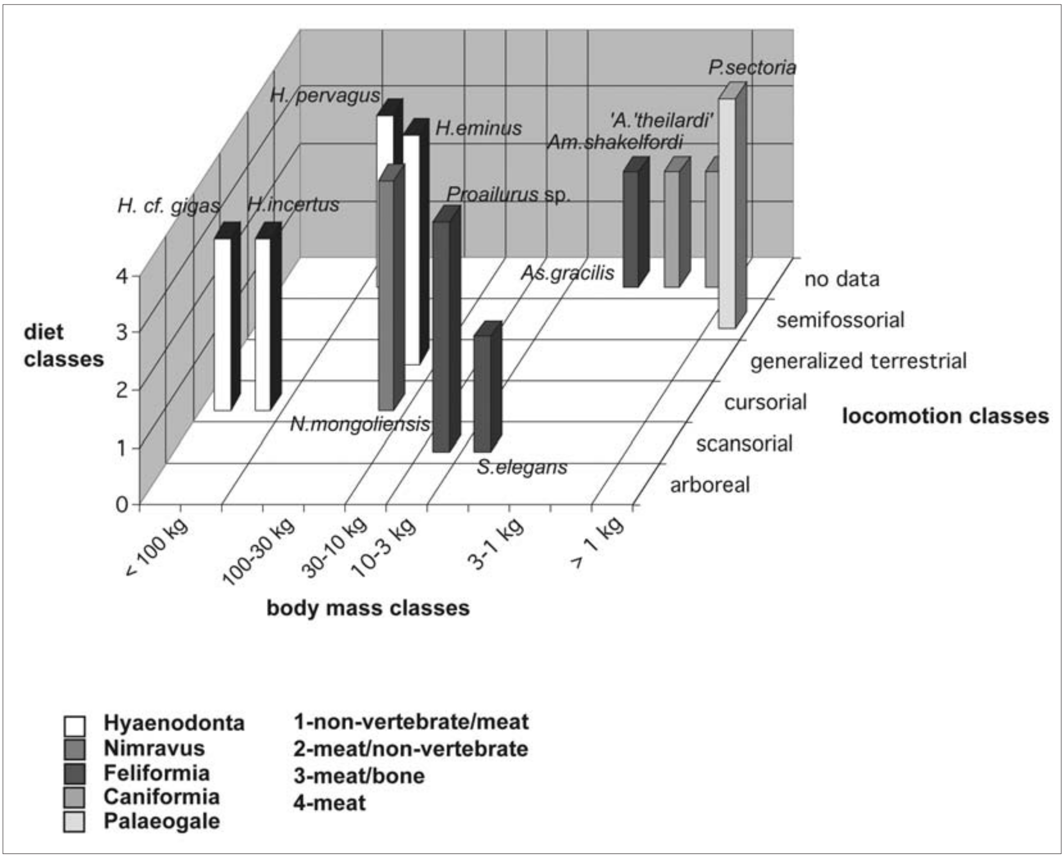

Figure 1 Structure of the carnivorous mammal fauna from Taatsiin Gol, Hsanda Gol Formation, Central Mongolia/Oligocene.

Suborder incertae sedis

Nimravidae

This enigmatic group of sabertoothed carnivores longly was placed into the Felidae, but later was identified as a distinct family. Meanwhile, even its position inside the feliforms was questioned (Flynn & Galiano 1982) and in the moment, its relationships to the other carnivore groups remain unclear (Bryant 1991).

Nimravus mongoliensis (GROMOVA, 1959: fig. 1)

Originally described from Khoer-Dzan, this nimravid was reported from Taatsiin Gol by Nagel & Morlo (2001). *Proailurus* sp. was reported from the Hsanda Gol Formation by Hunt (1998: fig. 22) from a single specimen. The m1, however, very probably represents a small nimravid (Peigné, pers. comm.).

Palaeogale sectoria GERVAIS, 1852

The familial position of *Palaeogale* is still unclear. With some uncertainty, Flynn & Galiano (1982) indicate a relationship to viverravids, a position which was confirmed later by Flynn *et al.* (1988). This species, firstly described from Europe, was mentioned from the Hsanda Gol Formation of Tatal Gol by Matthew & Granger (1924) and reported from Taatsiin Gol by Nagel & Morlo (2001).

Abbrevations of collections

AMNH = American Museum of Natural History, New York. BDAMS = Biological Department, Mongolian Academy of

Sciences, Ulanbataar. PSS = Section of Paleontology and Stratigraphy, Geological Institute, Mongolian Academy of Sciences, Ulanbataar. ZPAL = Institute of Paleobiology, Polish Academy of Sciences, Warsaw

METHODS

Three parameters were used to define ecomorphology: diet, locomotion, and body mass. Since not all necessary data are available in every taxon, the applied methods are listed separately for each taxon.

Estimation of body mass is often regarded as the most important parameter, since it has a major impact for the way of life, e.g., food resources or behaviour, of a predatory mammal (e.g., Wilson 1975, Vézina 1985, McNab 1989, Damuth 1990, McClearn 1992). For creodonts and carnivorans, body mass can be calculated by regressions of metric data of the carnassial length (Thackeray & Kieser 1992, Viranta & Andrews 1995, Legendre & Roth 1988, Van Valkenburgh 1990, Dayan & Simberloff 1996, Morlo 1999). Another approach is estimation by cross-sections of limb bones (Gingerich 1990, Anyonge 1993, Heinrich & Biknevicius 1998, Egi 2001). It has been suggested that body mass estimations based on limb bone parameters are more reliable than calculations based on the length of the lower carnassial (for primates: Rafferty *et al.* 1995, Ruff 1990; for carnivorans: Anyonge 1993, Egi 2001). However, due to the extreme paucity of creodont or carnivoran postcranials in the Taatsiin fauna we have to deal with the dentition as data source. Regressions for body mass coming from metric data of the carnassials were given by Legendre & Roth (1988) for carnivorans and by Morlo (1999) for creodonts. Dayan & Simberloff (1996) introduced a detailed separation of six body mass classes: (1) < 1 kg, (2) 1-3 kg, (3) 3-10 kg, (4) 10-30 kg, (5) 30-100 kg and (6) > 100 kg.

Van Valkenburgh (1988) established methods to define dietary preferences in carnivorans. In that paper she also included two taxa of the creodont genus *Hyaenodon*. Muizon & Lange-Badré (1997) demonstrated the structural similarity of the dentition of all carnivorous mammals. Consequently, Morlo (1999) expanded the estimation of the diet pattern to all groups of creodonts and demonstrated the limitations of such an approach. In this study, we follow Van Valkenburgh (1988) in separating four diet classes based on the measurements of lower teeth: meat, meat/bone, meat/non-vertebrate, and non-vertebrate/meat.

Locomotor pattern is either judged by comparison with recent postcranial elements or by using geometric indices (Barneth & Napier 1953, Carrano 1996, Ginsburg 1961, Janis & Wilhelm 1993, Jenkins & Camazine 1997, Laborde 1987, MacLeod & Rose 1993, Heinrich & Rose 1997, Taylor 1974, 1976, 1989, van Valkenburgh 1985, 1987, 1992, Wang 1993).

In classifying locomotor pattern, we follow MacLeod & Rose (1993) and separate six classes: (1) arboreal, (2) scansorial, (3) cursorial, (4) generalized terrestrial, (5) semifossorial, (6) semiaquatical. In contrast to MacLeod & Rose we solely used qualitative data.

CLASS DESIGNATIONS PER TAXON

Creodonta

Hyaenodon: There is no living relative of this genus. Furthermore, the characteristic carnassials of carnivorans are lacking, instead all three lower molars formed a cutting blade. Morlo (1999) took this into account and calculated the body mass using the mean length of lower molars. Body mass estimations on long bones were given by Egi (2001). Different interpretations of the locomotor pattern of *Hyaenodon* are given by Mellet (1977) and Janis & Wilhelm (1993). Because the latter authors compared it to modern carnivorans, they assigned a generalized locomotor pattern. If compared to contemporary taxa all investigated species of *Hyaenodon* were interpreted as being cursorial (Mellet

1977, Morlo 1999, Egi 2001).

Hyaenodon gigas: We used the holotype of this species for comparisons (which includes P4-M2) because sufficient material is lacking from Taatsiin Gol. The equation for body mass estimation given by Morlo (1999) cannot be applied because from *H. gigas* neither lower molars nor long bones were found yet. Instead, we took the size relation of the preserved teeth to the well known North American species *H. horridus* to estimate its body mass. Body mass of *H. horridus* was estimated by limb bone data. Due to the unrobustness of this calculation, we enlarged the possible body mass range by adding and substracting 50%. This value was given by Morlo (1999) for correcting body mass estimation for creodonts due to their short and broad limbs relative to carnivores. For diet class, we compared the upper teeth to *H. horridus*. Due to their high morphological resemblance, we assigned *H. gigas* to the same class as *H. horridus* estimated by the equation given by Van Valkenburgh (1988). For locomotor pattern, we grouped the third phalanx from Taatsiin Gol to the ungual outlines investigated by MacLeod & Rose (1993).

Hyaenodon incertus: Estimations for body mass and diet class are possible with PSS 27-37, a fragment of a left mandible with fragment of p4, m1-3 (Dashzeveg 1985: fig. 9). Locomotor pattern is assigned by functional analysis of the proximal radius and ulna, preserved from Taatsiin Gol (Nagel & Morlo in prep.).

Hyaenodon pervagus: Estimations for body mass were calculated by taking the metric data (both published and our own) of the smallest and largest specimens of m1, m2, and m3, respectively, and applying the equation of Morlo (1999). For diet class assignment, we used AMNH 19005, a fragment of a left mandible with p4-m2 (Lange-Badré & Dashzeveg 1989: pl. 9, fig. 1) and two m3 out of the material of Nagel & Morlo (2001, in prep.). Due to the absence of any assigned postcranials, we did not assign a locomotor pattern.

Hyaenodon eminus: Estimations of body mass and diet class were done on AMNH 20362, a fragment of a right mandible with m1-m2 and fragment of m3. For correcting data of m3, we used data and pictures of BDAMS 31 (Dashzeveg 1964: pl. 1, fig. 2). Assignment to a locomotor pattern is solely based on the only known postcranial remain, a glenoid fragment from Taatsiin Gol which shows the typical morphology of *Hyaenodon* (Nagel & Morlo in prep.).

Carnivora - Feliformia

The body masses and diet classes of *Asiavorator* and *Shandgolictis* can be assumed by metric data of m1, taking regressions given by van Valkenburgh (1988) and Legendre & Roth (1988). The locomotor pattern of *Asiavorator* is discussed by Hunt (1998) in his study of the postcranial remains (AMNH 19123 and 82310) from the Hsanda Gol formation. These two specimens presumably belong to one individual. According to Hunt (1998) the species was probably scansorial with some affinity towards a generalised terrestrial pattern. Postcranial elements of *Shandgolictis* are missing so far and we, thus, did not assign it to a locomotor pattern.

Carnivora - Caniformia

The body masses and diet classes of *Amphicticeps* and '*Amphicynodon*' were estimated by the equations on metric data of m1 given by van Valkenburgh (1988) and Legendre & Roth (1988). Due to the lack of postcranials, we did not assign them to a locomotor pattern.

Nimravus mongoliensis No equations have been given for estimating body mass or diet class in nimravids. The lower teeth, especially p4 and m1 are very similar to that of machairodontine cats. Body mass can therefore be estimated by the equations of van Valkenburgh (1988) and Legendre & Roth (1988) based on metric data of m1 of felids. Estimation of diet class additionally uses p4. Locomotor class is inferred by a calcaneum

Table 1 Body mass classes, diet classes, and locomotor patterns of carnivorous mammals from Taatsiin Gol, Hsanda Gol Formation, Central Mongolia/Oligocene.

Taxon	Body mass class	Diet class	Locomotor pattern
Hyaenodon cf. *gigas*	> 100kg	bone/meat	cursorial
Hyaenodon incertus	> 100 kg	bone/meat	cursorial
Hyaenodon pervagus	30-100 kg	meat	no data
Hyaenodon eminus	30-100 kg	meat	cursorial
Asiavorator gracilis	1-3 kg	meat/non-vertebrate	no data
Shandgolictis elegans	1-3 kg	meat/non-vertebrate	scansorial
Nimravidae sp.	3-10 kg	meat	no data
Amphicticeps shakelfordi	1-3 kg	meat/non-vertebrate	no data
'Amphicynodon' teilhardi	1-3 kg	meat/non-vertebrate	no data
Nimravus mongoliensis	30-100 kg	meat	generalised terrestrial
Palaeogale sectoria	<1 kg	meat	semifossorial

and an ungual (Nagel & Morlo in prep.). Due to the very scarce remain of a small nimravid (=*Proailurus* in Hunt 1998) from the Hsanda Gol Formation, we use the similar sized *Eofelis* (Peigné 2000) from the European Oligocene for comparisons.

Palaeogale sectoria Estimation of body mass was done by equations of van Valkenburgh (1988) and Legendre & Roth (1988) based on metric data of m1, that of diet class on equations based on p4, m1, and m2, respectively. No postcranials are known from Mongolia. However, the species is also reported from Europe and North America (for the last review see Morlo 1996). Recently, Martin & Lim (2001) considered the taxon to be fossorial. In our view it should be better assigned to a semifossorial pattern, because it is less adapted to fossoriality than other carnivorans, e.g., *Meles* (Morlo, own data).

RESULTS

The guild of carnivorous mammals from Taatsin Gol contains 11 taxa representing at least six different ecomorphs. Concerning body mass, the guild structure is equivalent to modern guilds of carnivores e.g. the Serengeti, in having the largest species, *H*. cf. *gigas*, larger than *Panthera leo* while the smallest species, *Palaeogale sectoria*, is about the size of a small weasel like *Mustela erminea*. From four defined diet classes, only three are present. A hypocarnivore (non-vertebrate/meat) is lacking. Four different locomotor patterns are developed. However, the pattern could not be identified for five taxa, due to lack of material. Present are cursorial, generalised terrestrial, scansorial, and semifossorial taxa, while arboreal and semiaquatical taxa are lacking.

DISCUSSION

The presence of all body mass classes in the guild implies that the 11 taxa are well separated by size. This becomes even clearer if having a closer look to the large and very large taxa. *Hyaenodon* cf. *gigas* is larger than a tiger, while *H. incertus* is about the size of a small lion. Both are bone/meat eater. *H. pervagus* reaches the size of a leopard. Size therefore would be the only ecomorphological difference between these three, if *H. pervagus* can be considered to be cursorial as all investigated species of *Hyaenodon*. *H. eminus*, the smallest species of that genus present, is about the size of the striped hyaena and differs additionally in being a hypercarnivore and not a bone-crusher. About the size of *H. pervagus* is the largest Carnivora of the sample, *Nimravus mongoliensis*. This taxon differs from *Hyaenodon* in being generalized

Table 2 Body mass classes, diet classes, and locomotor patterns of carnivorous mammals from the Serengeti, Africa (according to Anyonge 1993, Van Valkenburgh 1987, 1988, Nowak & Paradiso 1983, Grzimek 1987 and own unpublished data).

Taxon	Body mass class	Diet class	Locomotor pattern
Panthera leo	> 100kg	meat	scansorial
Panthera pardus	30 - 100 kg	meat	scansorial
Acinonyx jubatus	30 - 100 kg	meat	cursorial
Caracal caracal	10 - 30 kg	meat	scansorial
Felis serval	10 - 30 kg	meat	scansorial
Lycaon pictus	10 - 30 kg	meat/non-vertebrate	cursorial
Canis mesomelas	10 - 30 kg	meat/non-vertebrate	cursorial
Canis aureus	3 - 10 kg	meat/non-vertebrate	cursorial
Canis adustus	10 - 30 kg	meat/non-vertebrate	cursorial
Otocyon megalotis	3 - 10 kg	meat/non-vertebrate	generalised terrestrial
Crocuta crocuta	30 - 100 kg	meat/bone	generalised terrestrial
Hyaena hyaena	30 - 100 kg	meat/bone	generalised terrestrial
Mellivora capensis	3 - 10 kg	meat/non-vertebrate	semifossorial
Civettictis civetta	10 - 30 kg	non-vertebrate/meat	semifossorial
various Viverridae	1 - 3 kg	non-vertebrate/meat	semifossorial

terrestrial and using a specialised killing technique performed by its sabers. Nevertheless, as the largest hypercarnivore, *Nimravus* is clearly larger than *H. eminus.* The small nimravid is the only middle-sized (3-10 kg) member of the guild, while all taxa with a more generalised diet (meat/non-vertebrates) are small. Thus, the feliforms *Asiavorator* and *Shandgolictis* as well as the caniforms *Amphicticeps* and '*Amphicynodon*' fall into this group. Postcranials are only known from *Asiavorator* thus far. Therefore, they all are grouped in the same ecomorphotype as being defined in this study. Some additional information inferred from comparison with the European relatives of the respective taxon can however be given. After that, *Shandgolictis* is quite similar to the European genus *Stenoplesictis* and may represent the same ecomorph in having viverrid affinities. *Stenoplesictis* maybe was scansorial and this is very probably also true for *Shandgolictis*. Concerning the caniforms, the Mongolian taxa seem to represent the same ecomorph as the European *Amphicynodon*. De Bonis (pers. comm.) argues for the European *Amphicynodon*, that forelimb represents very much a scansorial type. *Palaeogale* is the smallest member of the Mongolian guild. The genus was considered to be very weasel-like not only in morphology and sexual dimorphism, but also concerning its ecomorphology (e.g., Morlo 1996).

The composition of the guild of carnivorous mammals from Taatsiin Gol confirms that this fauna lived in an open landscape of savannah-like structure and that is was influenced by the cool and arid climate in the Mongolian Oligocene, proposed by Meng & McKenna (1998). This is especially supported by the cursorial taxa of *Hyaenodon*. It is not contradicted by the presence of scansorial taxa, because all of them are small and need only little arboreal area, probably provided by, even seasonal, rivers and lakes.

The Recent guild of the Serengeti National Park holds 14 taxa, which have a body, weight over 3 kg, and various viverrids with a body weight between 1-3 kg (Grzimek 1987, Nowak & Paradiso 1983). The occurrence of these small carnivores is not fully studied. Therefore, their species names are not listed seperately in Table 2, but it is safe to assume that at least 10 different species are present in the Serengeti today. The assignments to the different diet classes and locomotor pattern generally follow Van Valkenburgh (1987, 1988). In her investigations, however, she included only animals above 7 kg and did not consider a cursorial locomotion pattern. Therefore, the diet class for the viverrids are assigned after Grzimek (1990) and the interpretation of single taxa as cursors follows personal observation.

From the Oligocene of Taatsiin Gol only 11 taxa were found so far. One of the major similarities between the Serengeti carnivore community and the one from Taatsiin Gol is the presence of more than one bone/meat-eating species. Such a pattern is not known from woodland communities. *Hyaenodon gigas* was the top predator and can be seen as an ecomorph to the modern lion, despite of its ossiphagous tendency. *H. incertus* and *H. pervagus* are probably ecomorphs of *Crocuta* and *Hyaena*. *H. incertus* and *Nimravus mongoliensis* cover the class of the meat eaters between 30 and 100kg. Four different forms of the small (1-3kg) meat/non-vertebrate group from Taatsiin Gol belong equally to the Caniformia and the Feliformia whereas their recent counterparts are Viverridae. These however are systematic differences but not ecological ones. More striking dissimilarities are that only one member, the small nimravid, represents the group between 3 and 10 kg and that taxa between 10 to 30 kg body mass are completely missing from Taatsiin Gol. Therefore, we can conclude that either we have not found every carnivorous species yet, or the absence of special predatory ecomorphs is a characteristic of this predatory paleo-community. The locomotor pattern is more difficult to compare than diet and body mass since many data are missing in the Mongolian sample. Still, the similarities outweigh the dissimilarities. Consequently, it is admissible to judge the paleo-guild of predatory mammals from the Oligocene Taatsiin Gol to be similar to the recent Serengeti. The African savannah therefore serves well as a model of the paleoenvironment of the Mongolian site.

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