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New remains of Hyaenodontidae (Creodonta, Mammalia) from the Oligocene of Central Mongolia

Nouveaux restes de Hyaenodontidae (Creodonta, Mammalia) de l'Oligocène de Mongolie centrale

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Abstract

New specimens of hyaenodontid creodonts are described which were unearthed in Mongolia by the Austrian–Mongolian Paleontological expeditions. Five taxa are identified: *Hyaenodon eminus*, *Hyaenodon pervagus*, *Hyaenodon* cf. *incertus*, *Hyaenodon* cf. *mongoliensis*, and cf. *Hyaenodon gigas*. Hitherto unknown morphological details are reported for most of these species. The implications to systematic of the species and the genus *Hyaenodon* are discussed. These *Hyaenodon* remains suggest a separate evolutionary lineage, with different species in Europe and Asia, even if the genus is also known from contemporary faunas of Europe and North America.

Résumé

De nouveaux spécimens de Créodontes Hyaenodontidae découverts en Mongolie par les expéditions paléontologiques austro-mongoles sont décrits. Cinq taxons sont identifiés : *Hyaenodon eminus*, *Hyaenodon pervagus*, *Hyaenodon* cf. *incertus*, *Hyaenodon* cf. *mongoliensis* et cf. *Hyaenodon gigas*. Des données morphologiques inédites sont rapportées pour la plupart de ces espèces. Les implications sur la systématique des espèces et du genre *Hyaenodon* sont discutées. La faune de *Hyaenodon* fait apparaître unelignée évolutive distincte avec des espèces différentes en Europe et en Asie, bien que le genre soit connu aussi dans des faunes contemporaines d'Europe et d'Amérique du Nord.

1. Introduction

Fossil carnivorous mammals are known from the Taatsiin Gol area since the Central Asian expedition of the American Museum of Natural History (Matthew and Granger, 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 and 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 investigate the creodont specimens found by the Austrian–Mongolian expedition during three field trips 1995–1997 with a focus on their systematics and paleobiogeography. The carnivoran mammals found in those field trips and an analysis of the carnivore paleo-guild from Taatsiin Gol are published elsewhere (Nagel and Morlo, 2003).

2. Geology, material, and methods

The specimens were found in the profiles of Shand Gol (SHG), Ikh Argalatyn Nuruu (IKH), and Shand-Tatal (Fig. 1). The collected fossils from Shand Gol range from biozones A to B, Ikh Argalatyn Nuruu and Shand Tatal are stratified as biozone B (early Lower Oligocene).

We follow the biostratigraphy of Daxner-Höck et al. (1997) and Höck et al. (1999) for the Hsanda Gol and the Loh Formation. A brief summary is given here: the stratigraphy is based on rodent assemblages and 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 (Fig. 2).

Biozone A is only known from below and biozone B from above Basalt layer I in the Hsanda Gol Formation. Therefore A is assigned to the Early Oligocene older than 31.5 Ma and characterized by the presents of *Karakoromys decessus* and the last appearance data (LAD) of *Ardynomys* sp. and *Eucricetodon asiaticus*, and the first appearance data (FAD) of *Cricetops*, *Tsaganomys*, *Cyclomylus*, and *Selenomys*. Biozone B is assigned to the Early Oligocene between 31.5 and 28 Ma. It is characterized by the FAD of *Promeniscomys* sp., *Tatar-*
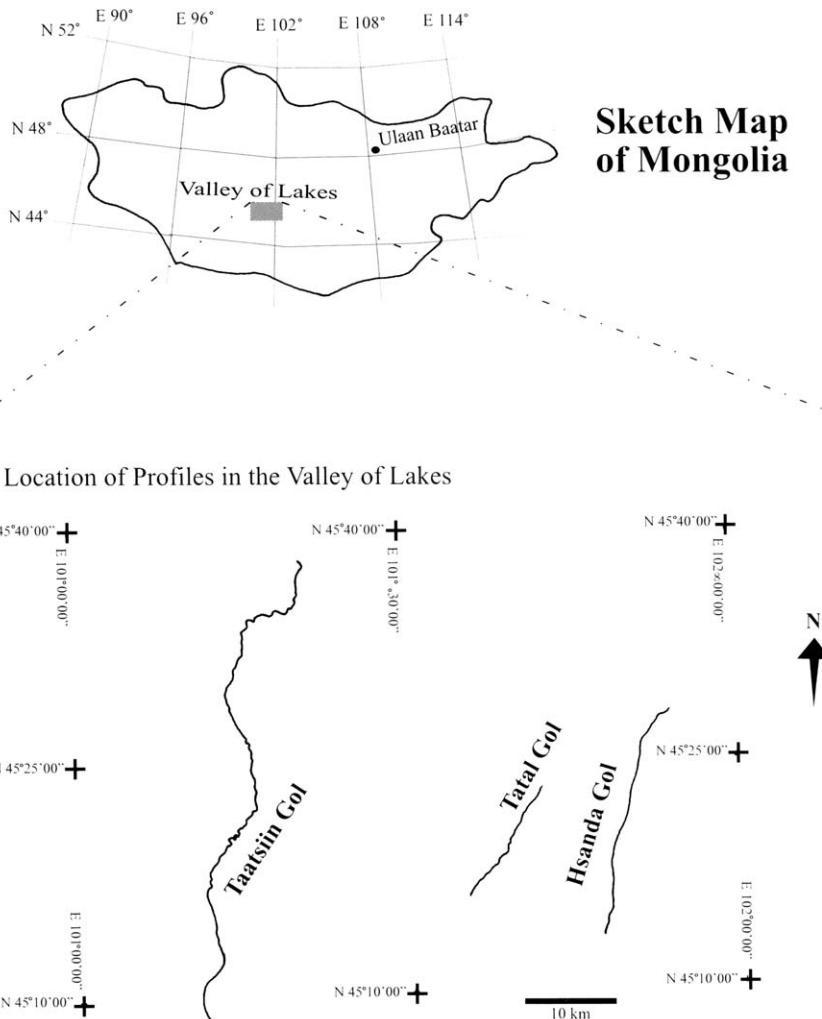
Fig. 1. Geographical distribution of the localities.
Fig. 1. Distribution géographique des localités.

omys minor, *Parasminthus* cf. *asiae-centralis*, and *P. tangingoli* as well as by the LAD of *K. decessus*, *T. minor*, *Selenomys mimicus*, *Cricetops dormitor*, *Eucricetodon caducus*, *E. asiaticus*, and *Heosminthus* sp.

Biozone C is known from the upper levels of the Hsanda Gol Formation as well as from the Loh sediments, below but all above basalt layer II. Age determination: around 28 Ma, which is early Late Oligocene.

There probably is a bias between biozone B and C because of a significant difference in the rodent assemblages. *Tachyoryctoides obrutschewi*, *Tataromys parvus*, and *Tataromys sigmodon* appear only in Biozone C. *Parasminthus parvulus* is present in Biozone C and for the last time in C1. Biozone C1 fossils are known from the Hsanda Gol and the Loh formation and are stra-
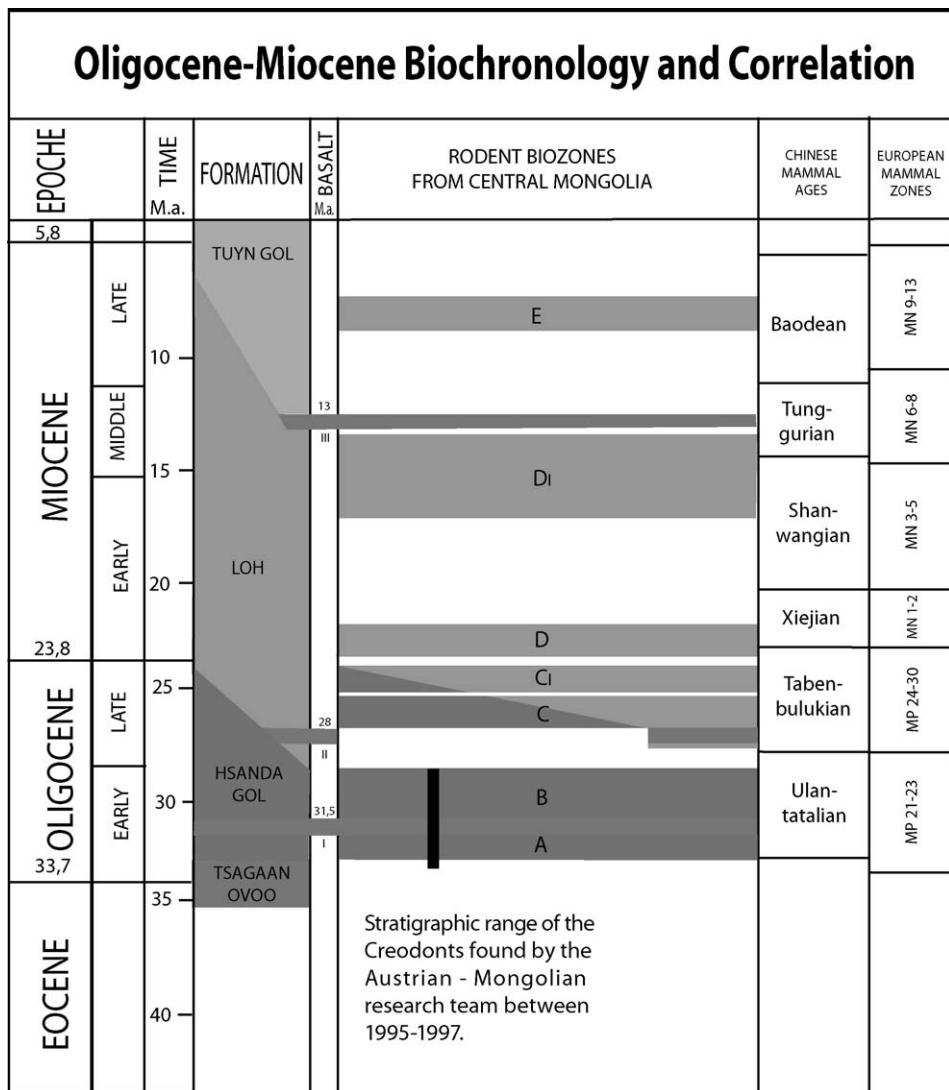
Fig. 2. Stratigraphical distribution of the localities.
Fig. 2. Distribution stratigraphique des localités.

tified as Late Oligocene. The best and most abundant markers are *Yindirtemys deflexus* and *Yindirtemys gobiensis*, only known from this Biozone (C1).

Biozone D is characterized by *Tachyoryctoides kokonorensis*, also known from the Chinese Xiejian. Daxner-Höck et al. (1999) follows Li and Qiu (1980) who claimed the beginning of the Miocene with this characteristic rodent. Furthermore the solemn appearance of *Prodistylomys* and *Distylomys* was noted. Biozone D1 is situated below basalt layer III (13 Ma) and large mammals such as *Gomphotherium* and *Anchitherium* were found there. This indicates an Early to Middle Miocene age, together with Megacricedtodon and Heterosminthus. Fossils from Biozone E were recovered from above basalt layer III. There are major differences in the

fauna. First appearance of *Paralactaga*, *Lophocricetus* and *Prosiphnaeus* indicate a Late Miocene age.

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. Tooth positions verified by alveoli only are referred to by brackets. The specimens are all housed in the collection of the Vienna Museum. Specimen collection numbers content information on year of collection, location, and the specimen number itself. To simplify citations in the descriptions and discussions, we mention only the specimen field numbers.

3. Systematic paleontology

CREODONTA Cope, 1875

HYAENODONTIDAE Leidy, 1869

HYAENODONTINAE Leidy, 1869

Hyaenodon Laizier and Parieu, 1838

Hyaenodon today contents at least 20 species from the Oligocene of Asia, Europe, and North America (see Lange-Badré, 1979 for an older species list). Eight hyaenodontine species have been described from the Oligocene of Mongolia and China, not all of them assigned to *Hyaenodon*: *Hyaenodon pervagus* Matthew and Granger, 1924, *Hyaenodon eminus* Matthew and Granger, 1925, "*Pterodon*" *exploratus* Dashzeveg, 1964, "*Megalopterodon*" *mongoliensis* Dashzeveg, 1964, *Hyaenodon gigas* Dashzeveg, 1964, *Hyaenodon chunkhtiensis* Dashzeveg, 1985, *Hyaenodon incertus* Dashzeveg, 1985, "*Macropterodon zelenovi*" Lavrov, 1999, *Hyaenodon neimongoliensis* Huang and Zhu, 2002, and *Hyaenodon weilini* Wang et al., 2005. Additionally, Lavrov (1999) used the genus names *Hyaenodon* (for *H. eminus*) and *Neohyaenodon* Thorpe, 1922 (for *H. incertus* and *H. gigas*) while Lavrov and Emry (1998) regard them as subgenera. Originally, *Protohyaenodon* Stock, 1933 and *Neohyaenodon* were created for the North American species *P.* "*exiguus*" (= *P. venturae*) and *N. horridus*, respectively. Mellett (1977: 14) used these names on subgenus level only to separate the two divergent lineages of North American *Hyaenodon* "that arose from *Hyaenodon* [*Neohyaenodon*] *vetus* and *Hyaenodon* [*Protohyaenodon*] *venturae*". Consequently, Mellett (1977) did not consider the existence of a subgenus *Hyaenodon*. Using *Neohyaenodon* and *Hyaenodon* as genus (or subgenus) names, but not *Protohyaenodon*, as Lavrov and Emry (1998) and Lavrov (1999) did for the Asian taxa, thus changes the systematic concept Mellett invented for North American *Hyaenodon* only. It also implies a migration of North American *Neohyaenodon* species into Asia, because *H.* (*Neohyaenodon*) *vetus* is stratigraphically older than the supposed *Neohyaenodon* species *N. mongoliensis* and *N. gigas*. Unfortunately, neither Lavrov and Emry (1998) nor Lavrov (1999) provided evidence for this systematical approach or discussed its paleobiogeographic implications. Separation of Eurasian *Hyaenodon* on genus or subgenus level and their possible relationship to the North American taxa awaits a revision of all belonging taxa and is far beyond the scope of this paper. We therefore restrict the subgenera *Protohyaenodon* and *Neohyaenodon* to the North American species in the original sense of Mellett (1977) and sustain use of the genus name *Hyaenodon* for the Asian species without regarding any subgenera (thereby following Lange-Badré, 1979; Lange-Badré and Dashzeveg, 1989).

3.1. H. eminus *Matthew et Granger, 1925 (Figs. 3 and 4)*

    * 1925. *H. eminus* - Matthew and Granger, 2, Figs. 2 and 3.

    1964. *H. eminus* - Dashzeveg, 268, Pl. 1, Fig. 2.

    1989. *H. eminus* - Lange-Badré and Dashzeveg, 127, Pl. 12, Figs. 8 and 9.

    ?1993. *Hyaenodon* sp. 2 - Huang, 301.

    1999. *H. eminus* - Lavrov, 328.

Holotype: AMNH 20362, fragment of right mandible with fragment of p2 (missing in Mellett's description), p3, fragment of p4, m1 and fragments of m2-3 (Matthew and Granger, 1925: Fig. 1) from the Lower Oligocene Ergilin Dzo Formation, member Sevkuhl, Ergilin-Dzo, Eastern Gobi, Mongolia (after Lange-Badré and Dashzeveg, 1989).

Paratypes: AMNH 20363, fragment of right mandible with p3-4, m1-2 (Matthew and Granger, 1925: Fig. 2) and AMNH 20364, fragment of right maxilla with M2 (Matthew and Granger, 1925: Fig. 3), both from the same site as the holotype.

Related specimens: BDMAS 31, fragment of left mandible with alveoli of c and p1, fragment of p2, and p3-m3 (Dashzeveg, 1964: Pl. 1, Fig. 2) from the Ergilin-Dzo Formation of Khetsoo Tsav, Ergilin-Dzo, Eastern Gobi, Mongolia. PSS 27-100, fragment of left mandible with p3-4 (Lange-Badré and Dashzeveg, 1989: Pl. 12, Fig. 9) from the Lower Oligocene Houldjin Formation of Khoer Dzan, Eastern Gobi, Mongolia.

Age and distribution: Previously known from the middle and late Lower Oligocene of Mongolia only.

New specimens: Field number SHG-S/2, fragment of right mandible with p4-m1 (Fig. 3). Field number Mo97 SHG-S/3, right scapula fragment with right glenoid fossa (Fig. 4).

3.1.1. Description

The p4 (7.5:4.3) is a strong and high tooth with rugose enamel. It lacks an anterior basal cusp, but a small labial swelling is developed instead. Its protoconid is abrased at the tip and the postprotocristid is slightly damaged. Posteriorly, a blade-like talonid is present. The m1 (5.6:3.4) is much smaller than p4 and highly abrased, especially at the postparacristid and the blade-like talonid which reaches a sixth of the overall tooth length (Fig. 3).

The scapula fragment (Fig. 4) shows typical characters of *Hyaenodon*: the glenoid fossa is shallow and its outline is very oval with the acromion ending far distally from the glenoid. These characters are typical for cursoriality (e.g. Ginsburg, 1961; Taylor, 1974; Mellett, 1977). According to its size, *H. eminus* is the only possible *Hyaenodon* species this postcranial fragment can belong to.

3.1.2. Comparisons and remarks

Morphology as well as sizes of the described fragments fit well to *H. eminus*. There is no other Mongolian *Hyaenodon* described of this size. *H. chunkhtiensis* Dashzeveg, 1985 is about 25% smaller and has a reduced talonid on m1. The m1 of the holotype of *H. chunkhtiensis* is however very abrased. Additionally, it is unclear how both species differ among m2. We, thus, cannot completely exclude that SHG-S/2 represents a very large *H. chunkhtiensis*, but by only one specimen known of this species, it seems to be very unlikely. *H. pervagus* Matthew and Granger, 1924 is much larger and has smooth enamel (Lange-Badré and Dashzeveg, 1989). Huang (1993) assigned an isolated m1 from the Lower Oligocene of the Ulantatal Formation to "*Hyaenodon* sp. 2". The tooth is slightly larger than *H. eminus* (8.0:3.5 mm), but does not

reach the size of *H. pervagus*. Because it resembles *H. eminus* in size and morphology, we provisionally assign it to that species, as well. Gromova (1952) interpreted an isolated M2 from Tatal Gol as M1 of the European species *H. exiguus* (Gervais, 1873), but Lange-Badré (1979) recognized the specimen as a M2 and assigned it to *H. filholi* Schlosser, 1887. According to its size, it may belong to *H. eminus*, but without being able to restudy it, this can only be guessed. *H. eminus* thus was present in Mongolia at least throughout the complete Lower Oligocene.

3.2. H. pervagus *Matthew et Granger, 1924 (Figs. 5–16)*

*1924. *H. pervagus* - Matthew and Granger, 1.

1952. *Hyaenodon aymardi* Filhol - Gromova, 59, Figs. 1–7, Pl. 1, Figs. 1–10, Pl. 2, Figs. 1–5 and 7–8.

1964. *H. pervagus* - Dashzeveg, 268, Pl. 1, Fig. 2.

1979. *Hyaenodon dubius* - Lange-Badré, 151, 153.

1989. *H. pervagus* - Lange-Badré and Dashzeveg, 127, Pl. 12, Figs. 8 and 9.

Holotype: AMNH 19005, fragment of left mandible with p4-m2 (Lange-Badré and Dashzeveg, 1989: Pl. 9, Fig. 1) from the Middle Oligocene, Loh, Hsanda Gol Formation.

Paratypes: AMNH 19006, right maxilla with p3, p4. AMNH 19125, left mandibular fragment with p2, dp3, dp4, m1. AMNH 19015, left p4 and m1. AMNH 19126, right lower jaw partially edentulous with m3. AMNH 19002, hind limbs and partial feet.

Related specimens: Despite the holotype and the specimens cited with it in Matthew and Granger (1924), Lange-Badré and Dashzeveg (1989) described 25 specimens from the Hsanda Gol Formation housed in the AMNH and ZPAL, nine specimens from Shunkht, housed in the PSS, and either one specimen from Khoer Dzan (Ergilin Dzo Formation) housed in the PIN, from the Chinese Urtyn Obo, housed in the AMNH, and, with some doubts remaining, from Ergilin Dzo itself, housed in the PSS.

Age and distribution: Early to late Oligocene of Mongolia, China, and Kazakhstan.

New specimens: Field number SHG-AB/5/4 (Fig. 5), isolated fragment of left P4 (14.3: -). Field number SHG-AB/5/11 (Fig. 6), isolated fragment of right P4 (14.2: -). Field number SHG-O/1 (Fig. 7), isolated tooth crown of left M2 (18.9: -). Field number SHG-C/1 (Fig. 8), fragment of right mandible with (p4-m2), m3 (19.75:6.45). Field number SHG-AB/5/3 (Fig. 9), isolated left p2 (14.0:6.0). Field number SHG-AB/5/9 (Fig. 10), isolated fragment of right p2 (- :6.2). Field number SHG-AB/5/5 (Fig. 11), isolated right p4 (- :7.5). Field number SHG-AB/5/2 (Fig. 12), isolated left p4 (14.5:7.2). Field number SHG-AB/5/7 (Fig. 13), isolated right p4 fragment. Field number IKH-A/24 (Fig. 14), isolated right p4 (15.7:7.8), paraconid of right m3, and undeterminable root fragments. Field number SHG-AB/5/6 (Fig. 15), isolated right m1 (10.4:5.8). Field number SHG-AB/5/10 (Fig. 15), isolated fragment of right m1 (- :6.8).

3.2.1. Descriptions and comparisons

From the upper premolars, only P4 is preserved in our material (Figs. 5 and 6). It is a stout tooth with a well developed, anteriorly oriented parastyle with a wear facet on its lingual side, a well developed protocone, broken in SHG-AB/5/11 (Fig. 6), and a short and high metastyle which is separated from the paracone by a deep notch. The enamel is slightly wrinkled.
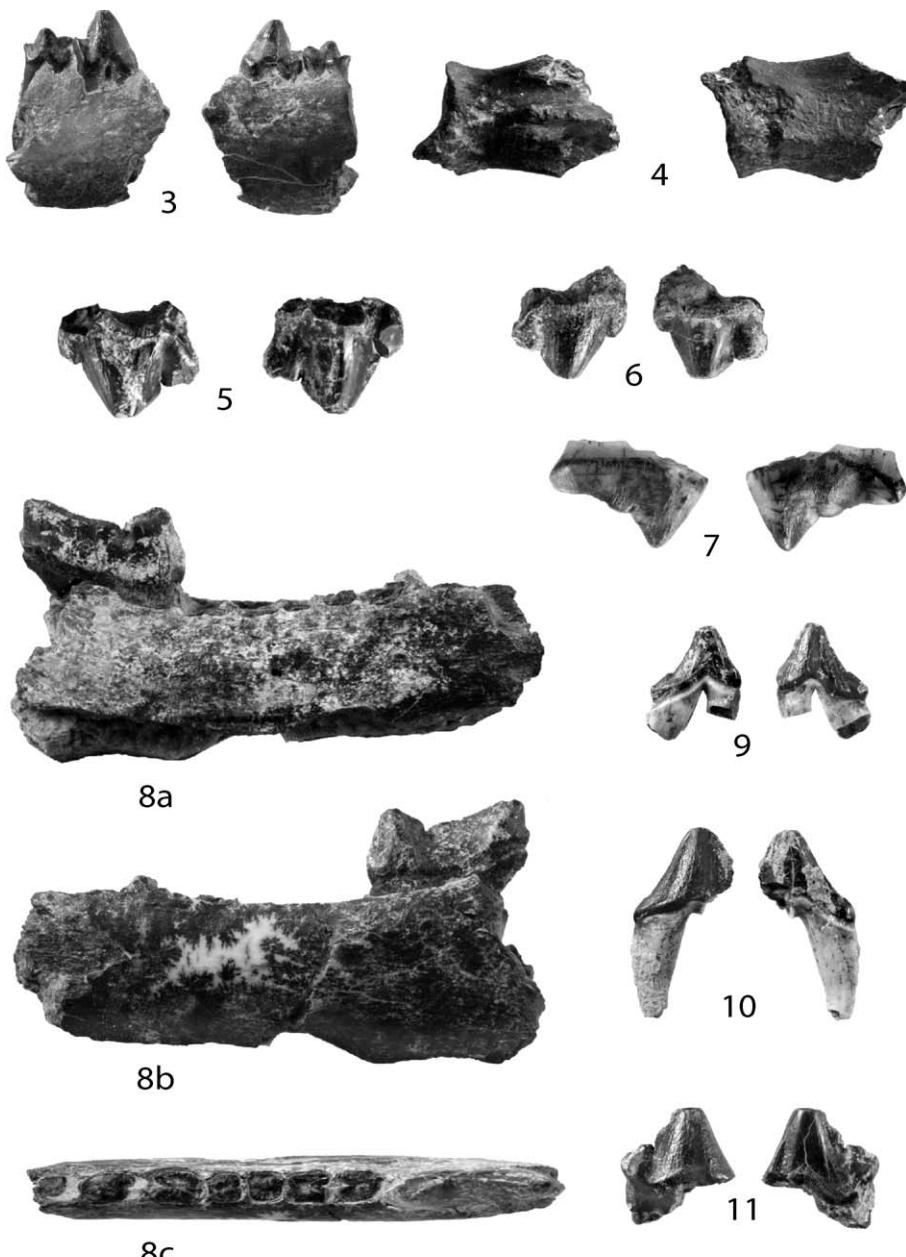
The M2 SHG/O/1 (Fig. 7) is broken where a protocone could have been, but a third root was clearly developed here. The metastylar blade is deflecting strongly labially in its second half. No M2 of *H. pervagus* is known from the old AMNH collections, but both characters were given by Lange-Badré and Dashzeveg (1989) for specimens found by the Polish–Mongolian expeditions.

The symphysis of the robust mandible (Fig. 8) reaches under the anterior part of p3 like in *H. pervagus* but not further, like in *H. incertus* or *H. eminus*.

Among the lower premolars, p2 and p4 are preserved. The p2 (Figs. 9 and 10) is a simple tooth without any accessory cusps. The protoconid is anteriorly placed with the preprotocristid running slightly lingually. The posterior part is elongated to posterior, with the posterior cingulid slightly enlarged where the postprotocristid ends. The enamel is slightly wrinkled.

The four preserved p4 (Figs. 11–14) are of classical *Hyaenodon* shape and morphologically identical to the holotype in the well developed and baso-lingually placed parastylid, the backward sloping massive protoconid, and the high posterior heel. They are, however, in average smaller. SHG-AB/5/2 (Fig. 12), e.g. reaches only 80% of the length of the p4 of the holotype. Closer in size to the holotype is the p4 IKH-A/24 (Fig. 14), the morphology of which only slightly differs in having almost no anterior basal cuspid and the protoconid being higher.

The m1 SHG-AB/5/6 (Fig. 15) is highly abrased, but still shows two parallelly running preparacristids antero-labially and antero-lingually. Paraconid and protoconid are of equal length and breadth with the paraconid angled only very little to lingual. The talonid is clearly developed and consists of the hypoconid crest which runs straight in posterior direction at about the middle of the tooth. From its most posterior point the crestid curves first lingually and then down to the tooth base. This is much better seen in SHG-AB/5/10 (Fig. 16), an m1-fragment

Planche 1. **Fig. 3.** *H. eminus* Matthew and Granger, 1924. Field number SHG-S/2, fragment of right mandible with p4-m1. Left: labial, right: lingual view. **Fig. 4.** *H. eminus* Matthew and Granger, 1924. Field number Mo97 SHG-S/3, fragment of glenoid fossa of the right humerus. Left: distal, right: lateral view. Note shallow and oval fossa and short acromion. **Fig. 5.** *H. pervagus* Matthew and Granger, 1924. Field number SHG-AB/5/4, isolated fragment of left P4. Left: labial, right: lingual view. **Fig. 6.** *H. pervagus* Matthew and Granger, 1924. Field number SHG-AB/5/11, isolated fragment of right P4. Left: lingual, right: labial view. **Fig. 7.** *H. pervagus* Matthew and Granger, 1924. Field number SHG/O/1, tooth crown of left M2. Left: labial, right: lingual view. Notice presence of third root and labially deflecting metastylar blade. **Fig. 8.** *H. pervagus* Matthew and Granger, 1924. Field number SHG-C/1, right mandibular fragment with m3. **8a**: labial, **8b**: lingual, **8c**: occlusal view. Notice posterior placement of labial preparacristid and placement of paraconid above lingual preparacristid. **Fig. 9.** *H. pervagus* Matthew and Granger, 1924. Field number SHG-AB/5/3, isolated left p2. Left: labial, right: lingual view. **Fig. 10.** *H. pervagus* Matthew and Granger, 1924. Field number SHG-AB/5/9, isolated right p2. Left: labial, right: lingual view. **Fig. 11.** *H. pervagus* Matthew and Granger, 1924. Field number SHG-AB/5/5, isolated right p4. Left: labial, right: lingual view.

Plate 1. **Fig. 3.** *H. eminus* Matthew et Granger, 1924. Numéro de terrain SHG-S/2, fragment de mandibule droite avec p4-m1. Vue labiale à gauche ; vue linguale à droite. **Fig. 4.** *H. eminus* Matthew et Granger, 1924. Numéro de terrain Mo97 SHG-S/3, fragment de fosse glénoïde d'un humérus droit. Vue distale à gauche ; vue latérale à droite. Noter la fosse ovale et le court acromion. **Fig. 5.** *H. pervagus* Matthew et Granger, 1924. Numéro de terrain SHG-AB/5/4, fragment de p4 gauche isolée. Vue labiale à gauche ; vue linguale à droite. **Fig. 6.** *H. pervagus* Matthew et Granger, 1924. SHG-AB/5/11, fragment de P4 droite isolée. Vue linguale à gauche ; vue labiale à droite. **Fig. 7.** *H. pervagus* Matthew et Granger, 1924. Numéro de terrain SHG/O/1, couronne de M2 left. Vue labiale à gauche ; vue linguale à droite. Noter la présence d'une troisième racine et d'une lame métastylaire déversée labialement. **Fig. 8.** *H. pervagus* Matthew et Granger, 1924. Numéro de terrain SHG-C/1, fragment de mandibule droite avec m3. **8a** : vue labiale, **8b** : vue linguale, **8c** : vue occlusale. Noter la position postérieure de la préparacristide labiale et celle du paraconide au-dessus de la préparacristide linguale. **Fig. 9.** *H. pervagus* Matthew et Granger, 1924. Numéro de terrain SHG-AB/5/3, p2 gauche isolée. Vue labiale à gauche ; vue linguale à droite. **Fig. 10.** *H. pervagus* Matthew et Granger, 1924. Numéro de terrain SHG-AB/5/9, p2 droite isolée. Vue labiale à gauche ; vue linguale à droite. **Fig. 11.** *H. pervagus* Matthew et Granger, 1924. Numéro de terrain SHG-AB/5/5, p4 droite isolée. Vue labiale à gauche ; vue linguale à droite.

12

13

14

15

16

17

18

19

20

22

23

21a

21b

0   1   2   3 cm

21c
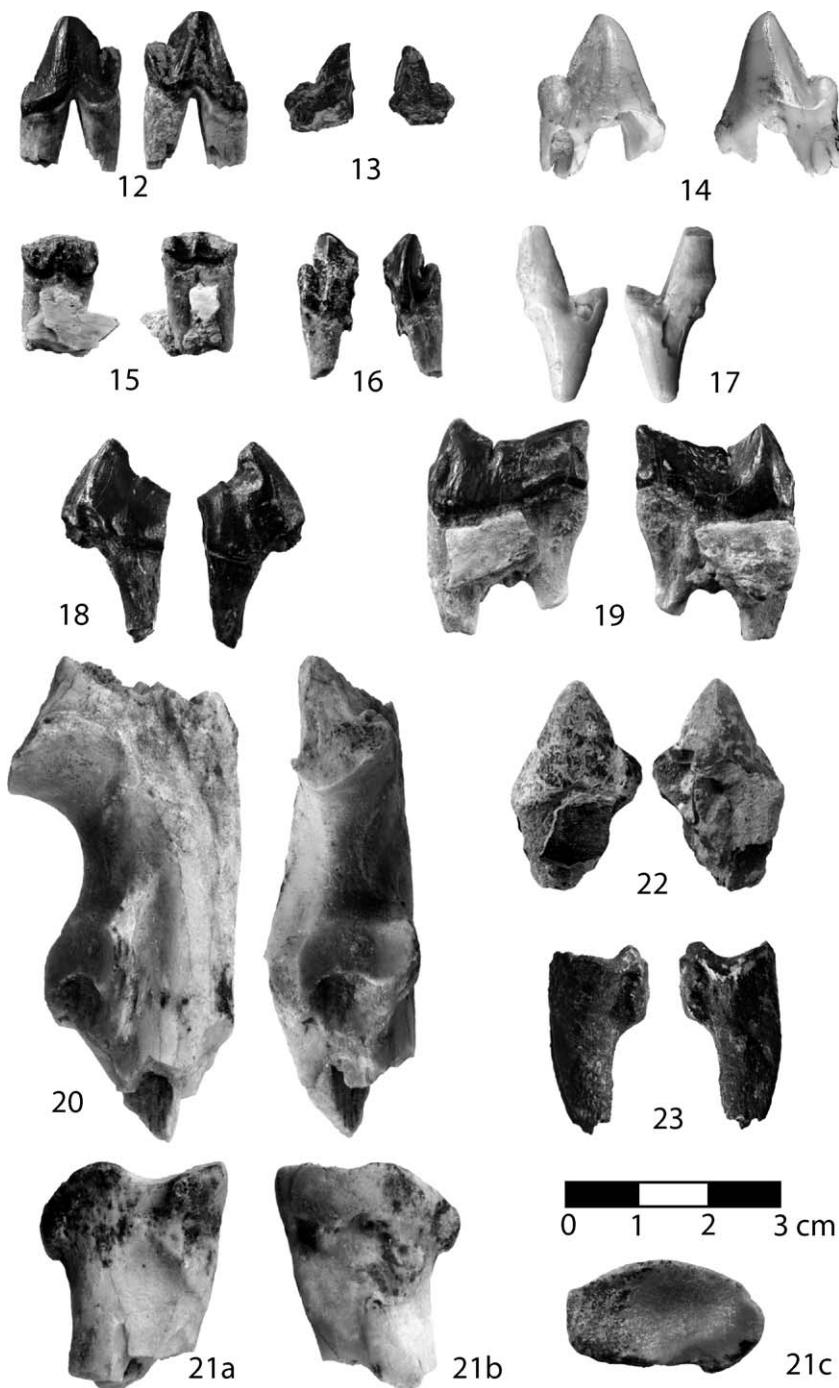
that consists of the protoconid and the talonid only. The tooth fragment is, though morphologically identical, clearly larger than SHG-AB/5/6. A week lingual cingulid is developed.

The m3 is not preserved in the holotype, but is complete in AMNH 19126 and SHG-C/Pr1/S (Fig. 7). Both specimens share their differences to *H. incertus*: the labial preparacristid runs much more posteriorly than the lingual one does and the paraconid is placed directly above the lingual preparacristid instead of between those two edges like in *H. incertus*.

3.2.2. Remarks

H. pervagus is by far the most abundant hyaenodontid in the Mongolian Lower Oligocene fauna. The species was described in detail by Lange-Badré and Dashzeveg (1989) who also reported it from Ergilin Dzo, Khoer Dzan (contra Lavrov, 1999), and Urtyn Obo. According to Lange-Badré and Dashzeveg (1989), *H. pervagus* is comparable with the North American *H. (Protohyaenodon) montanus* due to its size and plesiomorphic characters like a double-rooted p1. Also the posteriorly placed labial preparacristid is present in *H. montanus*. However, this character is found in small members of *H. (Neohyaenodon) horridus*, too, while the labially deflecting metastyle in M2 is present in *H. horridus* as well as in the more plesio-

Planche 2. **Fig. 12.** *H. pervagus* Matthew and Granger, 1924. Field number SHG-AB/5/2, isolated left p4. Left: labial, right: lingual view. The strong and lingually placed parastylid, the backward sloping protoconid, and the high posterior heel verify assignment. **Fig. 13.** *H. pervagus* Matthew and Granger, 1924. Field number SHG-AB/5/7, isolated left p4 fragment. Left: labial, right: lingual view. **Fig. 14.** *H. pervagus* Matthew and Granger, 1924. Field number IKH-A/24, isolated right p4. Left: labial, right: lingual view. **Fig. 15.** *H. pervagus* Matthew and Granger, 1924. Field number SHG-AB/5/6, isolated right m1. Left: labial, right: lingual view. **Fig. 16.** *H. pervagus* Matthew and Granger, 1924. Field number SHG-AB/5/10, isolated fragment of right m1. Left: labial, right: lingual view. **Fig. 17.** *H.* cf. *incertus* Dashzeveg, 1985. Field number Mo95 Shand Tatal, isolated fragment of right P2. Left: labial, right: lingual view. **Fig. 18.** *H.* cf. *incertus* Dashzeveg, 1985. Field number SHG AB/5/1, isolated left m3 fragment. Left: labial, right: lingual view. **Fig. 19.** *H.* cf. *incertus* Dashzeveg, 1985. Field number SHG-AB/5/O/1, isolated left m3. Left: labial, right: lingual view. Notice anteriorly placed labial preparacristid and placement of the paraconid. **Fig. 20.** *H.* cf. *incertus* Dashzeveg, 1985. Field number IKH-B/a/0, proximal fragments of right ulna. Left: lateral and right: anterior view. Notice restricted lateral humerus facet. **Fig. 21.** *H.* cf. *incertus* Dashzeveg, 1985. Field number IKH-B/a/0, proximal fragments of right radius. **21a**: anterior, **21b**: posterior and **21c**: proximal view. Notice uneven and narrow radial head and high capitular eminence. **Fig. 22.** *H.* cf. *mongoliensis* Dashzeveg, 1964. Field number SHG/c, isolated fragment of p4. Left: labial, right: lingual view. **Fig. 23.** cf. *H. gigas* Dashzeveg, 1985. Field number Mo95 IKH-A-Mix/O, presumed right ungula. Left: lateral, right: medial view. Notice size and deep fissure.

Fig. 12. *H. pervagus* Matthew et Granger, 1924. Numéro de terrain SHG-AB/5/2, p4 gauche isolée. Vue labiale à gauche ; vue linguale à droite. Cette attribution s'appuie sur la présence d'un fort parastylide en position linguale, d'un protoconide incliné vers l'arrière et d'un talonide haut. **Fig. 13.** *H. pervagus* Matthew et Granger, 1924. Numéro de terrain SHG-AB/5/7, fragment de p4 gauche isolée. Vue labiale à gauche ; vue linguale à droite. **Fig. 14.** *H. pervagus* Matthew et Granger, 1924. Numéro de terrain IKH-A/24, p4 droite isolée. Vue labiale à gauche ; vue linguale à droite. **Fig. 15.** *H. pervagus* Matthew et Granger, 1924. Numéro de terrain SHG-AB/5/6, m1 droite isolée. Vue labiale à gauche ; vue linguale à droite. **Fig. 16.** *H. pervagus* Matthew et Granger, 1924. Numéro de terrain SHG-AB/5/10, fragment de m1 droite isolée. Vue labiale à gauche ; vue linguale à droite. **Fig. 17.** *H.* cf. *incertus* Dashzeveg, 1985. Numéro de terrain Mo95 Shand Tatal, fragment de P2 droite isolée. Vue labiale à gauche ; vue linguale à droite. **Fig. 18.** *H.* cf. *incertus* Dashzeveg, 1985. Numéro de terrain SHG AB/5/1, fragment de m3 gauche isolée. Vue labiale à gauche ; vue linguale à droite. **Fig. 19.** *H.* cf. *incertus* Dashzeveg, 1985. Numéro de terrain SHG AB/5/O/1, m3 gauche isolée. Vue labiale à gauche ; vue linguale à droite. Noter la position antérieure de la préparacristide labiale et celle du paraconide. **Fig. 20.** *H.* cf. *incertus* Dashzeveg, 1985. Numéro de terrain IKH-B/a/0, fragment proximal d'ulna droite. Vue latérale à gauche ; vue antérieure à droite. Noter la réduction de la facette humérale latérale. **Fig. 21.** *H.* cf. *incertus* Dashzeveg, 1985. Numéro de terrain IKH-B/a/0, fragment proximal de radius droit. **21a** : vue antérieure, **21b** : vue postérieure et **21c** : vue proximale. Noter la tête irrégulière et étroite du radius et la tubérosité capitulaire haute. **Fig. 22.** *H.* cf. *mongoliensis* Dashzeveg, 1964. Numéro de terrain SHG/c, fragment de p4 gauche isolée. Vue labiale à gauche ; vue linguale à droite. **Fig. 23.** cf. *H. gigas* Dashzeveg, 1985. Numéro de terrain Mo95 IKH-A-Mix/O, probable phalange terminale. Vue latérale à gauche ; vue médiale à droite. Noter la taille et la profondeur de la fissure.

morphic *H.* (*Protohyaenodon*) *crucians*. Earlier, Gromova (1952) had placed related Mongolian specimens into the European *H. aymardi*, which was followed by Meng and McKenna (1998), still. The species, meanwhile included into *H. dubius* by Lange-Badré (1979), differs, however, significantly from *H. pervagus* in having a diastema at least between p2 and p3 but p1 single-rooted, p4/m3-ratio smaller, and the labial preparacristid more anterior. In the latter two characters it is much more similar to the nevertheless much larger European *H. heberti* and Mongolian *H. incertus*. It therefore is neither possible yet to assign *H. pervagus* to one of the two North American subgenera, if it belongs to one at all, nor to relate it to any European *Hyaenodon* species.

As does most p4, also m3 and M2 of our new material represent relatively small individuals according to the size ranges of *H. pervagus* given by Lange-Badré and Dashzeveg (1989). All new specimens, however, fit well to the morphology as given by these authors with the exception of having the enamel of the premolars slightly wrinkled, while it was said to be smooth by Lange-Badré and Dashzeveg. We regard these differences to be minor and nevertheless place all cited specimens into *H. pervagus*, thereby extending its size range to smaller sizes. Whether or not this size variability is affected by sexual dimorphism, as well known from North American *Hyaenodon* species (Mellett, 1977), remains an open question.

The recently erected species *H. neimongoliensis* Huang and Zhu, 2002 from the Early Oligocene of Ulantatal (Inner Mongolia) differs from *H. pervagus* only in having p1 single-rooted, diastemes between the anterior premolars (a character dependent to loss of a p1-root), and lacking a lingual cingulid in the lower teeth. If the erection of *H. neimongoliensis* will be confirmed, the fauna of Ulantatal would be worldwide unique in contenting two *Hyaenodon* species of very similar size and nearly identical morphology.

3.3. *H. cf. incertus Dashzeveg, 1985* (Figs. 17–21)

*1985. *H. incertus* - Dashzeveg, 241, Figs. 9–11.
1985. *P. exploratus* - Dashzeveg, 238, Fig. 7.
1989. *H. incertus* - Lange-Badré and Dashzeveg, 131, Pl. 12, Fig. 7, Pl. 13, Fig. 1.
1999. *N. insertus* - Lavrov, 324.

Holotype: PSS 27-37, fragment of left mandible with fragment of p4, m1-3 (Dashzeveg, 1985: Fig. 9) from the Lower Oligocene of Khoer-Dzan, Ergilin Dzo Formation.

Related specimens: AMNH 26068 (Lange-Badré and Dashzeveg, 1989).

Age and distribution: Lower Oligocene of Mongolia.

New specimens: Field number Mo95TAT-D (Fig. 17), isolated fragment of right P2 (15.3:8.4). Field number IKH-B/a O, fragment of right mandible with anterior alveolus of m1, posterior root of m1, roots of m2, and anterior margin of anterior alveolus of m3. Field number SHG AB/5/0/2 (Fig. 18), fragment of left m3. Field number SHG-AB/5/O/1 (Fig. 19), isolated left m3 (22.1:7.8) with some mandibular fragments remained. Field number IKH-B/a/0, proximal fragments of right ulna (Fig. 20) and radius (Fig. 21).

3.3.1. Description

The fragmental P2 (Fig. 17) is a very high but short tooth consisting only of the lingual curving paracone and a very small posterior cingulum cuspule. Both m3, SHG-AB/5/O/2 (Fig. 18) and SHG AB/5/O/1 (Fig. 19) differ from *H. pervagus* in the more anterior position

of the labial preparacristid and the paraconid being placed not above the lingual preparacristid but just between the edges. Both characters as well as size fit well to m3 of AMNH 26068.

From the ulna IKH-B/a/0 (Fig. 20) only the contact areas to humerus and radius are preserved. The olecranon is broken proximally, but the remaining part shows that it was angled laterally. The lateral humerus facet is clearly restricted by a strong ridge, while such a ridge is lacking for the medial facet. The radius surface is narrow but broad and corresponds to the highly oval outline of the radius head (Fig. 21). The lateral humerus surface is narrow, but high. Despite being extremely narrow, the radius head is highly uneven and possesses a strong capitular eminence.

3.3.2. Comparisons and remarks

The designation of these tooth fragments to *H. incertus* is not fully verified due to their slightly smaller size compared to the hitherto known material (except AMNH 26068). Additionally, after Dashzeveg (1985) the protoconid of m3 is twice as long as its paraconid, equivalent to a relative length of 66% of total m3-length. The relative length of the protoconid of SHG-AB/5/O/1 is only about 58%. On the other hand, both m3 are too large to belong to *H. pervagus* and additionally differ in the morphology of their labial preparacristid from that species. In *H. pervagus*, the largest m3 is about 26% larger than the smallest one (Lange-Badré and Dashzeveg, 1989). Given that 26% size variability and taken SHG-AB/5/O/1 as the smallest specimen, m3 of *H. incertus* could become as large as 27.8 mm. The largest yet known m3, coming from the holotype, is only about 26 mm long, which supports additional evidence that SHG AB/5/0/1 and SHG AB/5/0/2 are close to *H. incertus*. We therefore provisionally refer to them as *H.* cf. *incertus*.

The relationships of *H. incertus* to the similar, but larger *H. mongoliensis* (see below) are debated. Lange-Badré and Dashzeveg (1989) believed them to belong to a single species varying in size by about 25–30% (with AMNH 26068 as the smallest known specimen and thus including our new material). In this case, *H. mongoliensis* (Dashzeveg, 1964) would have nomenclatorical priority. Lavrov (1999), however, stated *H. mongoliensis* to belong to *Macropterodon* Lavrov, 1999 due to a labial thickening of the mandibular body (see Lange-Badré and Dashzeveg, 1989: Pl. 13, Fig. 3b). Such a thickening is lacking in *H. incertus* but is present in *M. zelenovi* Lavrov, 1999 (?= *H. gigas*, see below). If *H. mongoliensis* is placed apart from *Hyaenodon* (as suggested by Lavrov, 1999), the genus name *Megalopterodon* Dashzeveg, 1985, erected for *H. mongoliensis*, would be available. Due to the similarities among the dentition (Lange-Badré and Dashzeveg, 1989) we nevertheless feel a separation on genus level for the taxon not to be necessary. The labial thickening of the mandible body, however, proves *H. incertus* to be specifically separate from *H. mongoliensis*.

Besides being larger, *H. incertus* is very similar to the European *H. heberti* (see Lange-Badré, 1979) in showing a diastema between p2 and p3, having the p4/m3-ratio smaller than in *H. pervagus*, and having the preparacristids of m3 built in the same way.

Judging from the postcranial material, the restricted ability for radial movement following from the shape of the radial head and its ulnar fossa, the narrow lateral fossa for the humerus, and the laterally angled olecranon of the ulna verify that these bone fragments belong to a ground living, generalized to cursorial adapted carnivore. Nimravid ulna and radius clearly differ in having a closed ridge at the lateral end of the radial head, a strong ridge restricting the medial humerus facet, and lacking such a restriction at the lateral humerus facet. Instead, the bone fragments from Mongolia highly resemble the large North American *H. horridus* in size

and morphology. Smaller species, as *H. crucians*, also show similarity but differ in having the proximal lateral flange much larger. Due to their similarity to *Hyaenodon* in morphology and size, the ulna and radius fragments are thus tentatively referred to *H.* cf. *incertus*.

Dashzeveg (1985) described "*P.*" *exploratus* as a new species from the Early Oligocene of Khoer Dzan. The holotype is a mandible fragment clearly containing dp4 and m1 instead of "m1" and "m2" as Dashzeveg stated. Due to the morphological and size resemblance of m1 of "*P.*" *exploratus* to that of *H. incertus*, we refer the holotype of "*P.*" *exploratus* to *H. incertus*. Using Section 24.2.2 of ICZN (Internationale Kommission für Zoologische Nomenklatur, 2000), we thus declare "*P.*" *exploratus* to be a junior subjective synonym of *H. incertus*, both published in Dashzeveg (1985), for that the name *H. incertus* meanwhile is well established and widely used, while "*P.*" *exploratus* is not.

3.4. *H.* cf. *mongoliensis (Dashzeveg, 1964) (Fig. 22)*

*1964. *M. mongoliensis* - Dashzeveg, 265, Pl. 1, Fig. 1.

1989. *H. mongoliensis* - Lange-Badré and Dashzeveg, 134, Pl. 13, Figs. 2 and 3.

pars 1989. *H. incertus* - Lange-Badré and Dashzeveg, 131.

1999. "*Hyaenodon*" *mongolensis* - Lavrov, 325, 328.

1999. "n. gen." *mongolensis* - Lavrov, 328.

Holotype: BDMAS 21, fragments of left and right mandibule with right i3, p2-m2 and left c1, p2-m2 maxilla with P4-M2, from Bayan Tsav, Mongolia, Ergilin-Dzo Formation (Dashzeveg, 1964: Pl. 1, Fig. 1a, b).

Referred material: PSS 27-76, left mandibular fragment with p2-3. PIN 27-77, right mandibular fragment with p4, all from Khoer Dzan. AMNH 26269, isolated right m2. All assigned to *H. mongoliensis* by Lange-Badré and Dashzeveg (1989).

Age and distribution: Lower Oligocene of Mongolia.

New specimen: Field number Mo97 SHG-C/1 (Fig. 22), isolated fragment of left p4 (>20.0: ca.10.0).

3.4.1. Description and comparisons

The isolated premolar (Fig. 22) shows the typical morphology of *Hyaenodon* p4 in having a high protoconid with a lingually curving preprotocristid, which ends in a very small cuspule at the antero-lingual margin of the tooth. A strong posterior heel was present, but is partly broken now. The posterior and lingual margins of the tooth are not preserved. It, however, is clear that it was broadest at the first third of the well-defined postprotocristid.

3.4.2. Remarks

We assign this isolated fragment tentatively to *H. mongoliensis*. The morphology and size of p4 fits perfectly to PSS 27-77, published and depicted by Lange-Badré and Dashzeveg (1989: Pl. 13, Fig. 2). Both specimens are morphologically close, but slightly smaller than p4 of the holotype. For the discussion of the specific identity of *H. mongoliensis* to *H. incertus*, as proposed by Lange-Badré and Dashzeveg (1989), and the different generic names used for the species (Dashzeveg, 1964; Lavrov, 1999) see above remarks to *H. incertus*.

3.5. cf. H. gigas *Dashzeveg, 1985* (Fig. 23)

Holotype: PST 27-10, left maxilla with P4-M2, from the Ergilin-Dzo Formation, Lower Oligocene.

Referred material: PSS 27-78, left P3 and right p3. PIN 27-85, left P2, all from Khoer Dzan (Lange-Badré and Dashzeveg, 1989).

Age and distribution: Lower Oligocene of Mongolia.

New specimen: Field number Mo95 IKH-A-Mix/O (Fig. 23), right ungual.

3.5.1. Description and comparisons

This gigantic ungual shows exactly the morphology known from North American and European members of the genus *Hyaenodon* (see Mellett, 1977, unpublished data MM). It is, however, much larger, e.g. 50% larger than that of *H. horridus*.

3.5.2. Remarks

Two gigantic hyaenodontids of the size of *Hyainailouros* (estimated skull length ca. 60 cm) have been described from the lower Oligocene of Mongolia, *H. gigas* and *M. zelenovi* Lavrov, 1999. Both were mentioned to occur in Khoer Dzan. Lange-Badré and Dashzeveg (1989) referred three isolated premolars (P3, p2, p3) to *H. gigas*, which bases on a maxillar fragment, while Lavrov (1999) created *M. zelenovi* on a single mandibular fragment with p4 and m1. Because the specimens cannot be compared directly due to different tooth positions preserved, their relation to each other is more than unclear. In no other fauna worldwide and in no other age, however, two hyaenodontids of this large size occurred together. In the Early Miocene fauna of Wadi Moghra the gigantic *Megistotherium* is clearly larger than the still very large *Hyainailouros fourtaui* (see Rasmussen et al., 1989). This suggests presence of only one taxon in Mongolia, which shares a labial thickening of the mandible body with *H. mongoliensis* (Lavrov, 1999: 325).

Due to the morphological similarity of the ungual to other *Hyaenodon* species we refer it provisionally to *H. gigas*. This indicates the giant to be present in Mongolia in at least the whole Lower Oligocene.

H. gigas is the possibly ancestor of the Early Miocene Chinese *H. weilini*. Both differ to the other gigantic creodont genus of the Asian Miocene, *Hyainailouros*, in lacking large protocones in the upper molars.

4. Stratigraphy and paleobiogeography

4.1. Stratigraphical distributions

The hyaenodontids found by the Austrian–Mongolian expeditions range stratigraphically throughout the complete Lower and the early Late Oligocene. 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 throughout a long time. Further paleoecological remarks and an analysis of the role the respective *Hyaenodon* species played in the carnivore paleo-guild of the Central Mongolian Oligocene are given in Nagel and Morlo (2003). The transgression from the Eocene to the Oligocene is not very marked. Most creodont genera are known already from the Late Eocene of Asia and survived till the end of the Oligocene. Consequently,

Meng and McKenna (1998) did not include the carnivorous mammals in their Mongolian Re-modeling. The change from a humid climate with a dense forest to an arid climate with a more open landside is seen only on a change on the species level.

4.2. Paleobiogeography

The faunal composition of hyaenodontids of the Taatsiin Gol area, Central Mongolia, is nearly identical to that of the contemporary Kazakhstan and China. Moreover, regional species as *H. chunkhtiensis* or *H. neimongoliensis* are discussed here as possibly junior synonyms of the Mongolian, species *H. eminus* and *H. pervagus*, respectively. As is the shown by the car-nivorans also (e.g. Lange-Badré and Dashzeveg, 1989; Wang et al., 2005), Oligocene Kasakh-stan, Mongolia, and China can be interpreted as a single biogeographic area. Contrastingly, the fauna of this biogeographic area is highly unique compared to that of European and North American faunas: not a single species is shared. However, some taxa resemble European spe-cies largely: *H. eminus* and *H. pervagus* resemble *H. filholi* and *H. dubius*, respectively, at least in size, while *H. incertus* is similar in morphology to *H. heberti* and *H. dubius* but much larger. On the other hand is a giant like *H. gigas* lacking in the European Oligocene while it is present in North America (*Hemipsalodon*). These resemblances are interpreted here as ecomor-phologic instead of phylogenetic, because they mostly reflect similar size instead of similar morphology.

Acknowledgements

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