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ON SOME OLIGOCENE CARNIVOROUS MAMMALS
FROM CENTRAL ASIA

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Among the Oligocene mammal-bearing deposits of Central Asia, two are very famous: Ergilin Dzo and Shand Gol Svitas in which terrestrial predaceous mammals are represented by Creodonta and Carnivora. On the basis of isolated teeth and fragmentary jaws, five previously known species of *Hyaenodon* are identified: *H. eminus*, *H. cf. gigas*, *H. incertus*, *H. mongoliensis* and *H. pervagus*, the latter being figured for the first time. Carnivora are poorly represented with two taxa, *Palaeogale sectoria* and *Amphicynodon teilhardi* from the Shand Gol Svita only. The affinities of the different species of these three genera with those from North America and Western Europe are debated. Stratigraphic and palaeogeographic implications are considered from their relationships.

Key words: Mammalia, Creodonta, Carnivora, *Hyaenodon*, *Palaeogale*, *Amphicynodon*, Systematics, Oligocene, Kazakhstan, Mongolia, China.

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INTRODUCTION

Over sixty years ago, the first finds of creodont mammals from Mongolia were collected by the Central Asian Expedition of the American Museum of Natural History. Some specimens were briefly described in preliminary reports by Matthew and Granger (1924, 1925a,b,c), most of them being hitherto unstudied.

Further collecting was made in 1946—1949 by the Mongolian Paleontological Expedition of the Soviet Academy of Sciences. These remains from Oligocene deposits in the Ergilin Dzo and Tatal Gol area (South-eastern and Western Gobi), added to those from sites near Chelkar Teniz (Kazakhstan, USSR) were described by Gromova (1952).

Twenty years later, the Polish-Mongolian Paleontological Expedition (Kielan-Jaworowska *et al.* 1965) also assembled a fine but small series of mammal fossils from the Valley of Lakes Depression, in the neighbourhood of Tatal-Gol.

In these last collections, there were hyaenodonts and also some Carnivora throwing light on the history of these groups in Central Asia.

The recent discovery of new Palaeogene fossiliferous localities (Shunkht, Khoer Dzan) in Mongolia, by one of the authors (D. D) has considerably increased the number of Hyaenodontidae finds. Most of the systematic information regarding this material is reported in Dashzeveg's publication (1985).

The material described in the present article includes teeth and fragmentary jaws up to now unpublished and collected mainly from Mongolia, with a few from China during expeditions mentioned above.

Concerning the ages assigned to the fossiliferous localities, we have adopted the stratigraphic data and the well-argued correlation chart by Russell and Zhai (1987) whose Asiatic biostratigraphic synthesis has seemed to us to represent the most up-to-date available document on this question at the present time .

Abbreviations.—Each specimen is identified by the abbreviation of the Curator-Institution followed by a number. Abbreviations used in this paper are:

AMNH—American Museum of Natural History

BM—British Museum (Natural History) London.

MPE—Mongolian Paleontological Expedition of USSR Academy of Sciences (1946—1948)

PIN—Paleontological Institute, USSR Academy of Sciences, Moscow

PMP—Polish-Mongolian Paleontological Expedition

PSS—Paleontology and Stratigraphy Section of Geological Institute, Mongolian Academy of Sciences, Ulan Bator.

ZPAL—Institute of Paleobiology of the Polish Academy of Sciences, Warsaw.

Measurements were made by means of callipers accurate to 0.1 mm, abbreviations of these and other parameters are:

H—Height

RV—Range of variation

L—Length

SD—Standard deviation

M—Mean

W—Width

N—Number of specimens

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SYSTEMATICS

Infraclass **Eutheria** Gill, 1872

Order **Creodonta** Cope, 1875

Family **Hyaenodontidae** Leidy, 1869

Genus *Hyaenodon* Laizer et Parieu, 1839

Hyaenodon eminus Matthew et Granger, 1925

(pl. 12: 9; table 1)

1925. *Hyaenodon eminus* Matthew et Granger: 2, figs. 1—3.

1964. *Hyaenodon eminus* Matthew et Granger; Dashzeveg 268, pl. 1: 2.

Holotype: Right lower jaw with P₃—M₃ and roots of C, P₂ (AMNH 20362).

Paratypes: Right lower jaw with P₃—M₂ (AMNH 29363); left M² (AMNH 20364).

Type horizon and locality: Ergilin Dzo Formation, member Sevkhul, Lower Oligocene (?Upper Eocene); Ergilin-Dzo, Eastern Gobi, Mongolia.

Material.—Fragment of left mandible ramus with P₃ and P₄ (PSS 27—100), Khoer Dzan, Eastern Gobi.

Description.—P₃ and P₄ from Khoer Dzan are most closely comparable to those of the paratype AMNH 20363: short anterior edge, no accessory anterior cusp but a mesio-lingual thickening; P₃ slightly larger than P₄, both of them low. There is no available comparison with the holotype because P₃ has unfortunately been broken since being figured by Matthew and Granger (1925).

Table 1

Measurements of P₃ and P₄ of *Hyaenodon eminus* (in mm)

	Type	PSS 27—100	AMNH 20363	31*	M	SD
P ₃	L	11.5	9.6	10.0	10.3	0.53
	W	5.3	4.2	4.8	4.7	0.72
P ₄	L	11.0	9.0	9.8	10.0	0.42
	W	5.5	4.7	4.8	5.0	0.09

* after Dashzeveg 1964

Remarks.—Matthew and Granger compared *H. eminus* to the European Ludian species, *H. minor*. Both of them have a single rooted P₁. The measurements of the teeth of *H. eminus* fit well with those of the smallest *H. minor*, except M₂ and M₃ which are shorter. However, *H. eminus* is different from *H. minor* by its lower, thinner and more slender mandible, by the shorter length of the three lower molars, by the shorter talonid of M₁ and M₂, by the lack of the vestigial talonid in M₃ and the larger length ratio of P₃/P₄. In the last three characters, *H. eminus* is more derived than *H. minor*.

Occurrence.—Mongolia: Eastern Gobi, Ergilin Dzo, Khoer Dzan, Ergilin Dzo Formation (Upper Eocene and Lower Oligocene).

Hyaenodon pervagus Matthew et Granger, 1924

(pl. 9: 1—7; pl. 10: 1—8; pl. 11: 1—4; pl. 12: 1—3; table 2, 3)

1924. *Hyaenodon pervagus* Matthew et Granger: 1.
 1952. *Hyaenodon aymardi* Filhol; Gromova: 59, fig. 1—7; pl. 1: 1—10, pl. 2: 1—5, 7, 8.
 1952. *Hyaenodon ambiguus* Martin; Gromova: 64, fig. 8; pl. 2: 6.
 1952. *Hyaenodon dubius* Filhol; Gromova: 66, fig. 10; pl. 2: 3, 4.
 1985. *Hyaenodon* sp. 3; Dashzeveg: 250, fig. 17, 18, 19.

Holotype: Part of left mandible with P₄, M₁, M₂ (AMNH 19005); figured herein: pl. 9: 1.

Paratypes: Right maxilla with P₃, P₄ (AMNH 19006); left mandibular fragment with P₂, dp₃, dp₄M₁ (AMNH 19125), left P₄ and M₁ (AMNH 19015), right lower jaw partially edentulous with M₃ (AMNH 19126); hinds limbs and partial feet (AMNH 19002).

Type horizon and locality: Shand Gol Formation, Middle Oligocene; Tatal Gol (Grand Canyon).

Material.—Mongolia: Shand Gol Formation s. l.: mandible with canines, premolars and M₁, M₂, right premaxillary with incisors, canine and P¹ (AMNH 21367); right M¹ and M², left M², right and left P², left M² and right M₃ (AMNH 21657); right M₃ (AMNH 26069); left P⁴, M¹, M² (AMNH 21643). Shand Gol Formation, Tatal Gol: right P₂ (broken). P₃, P₄, M₁ (ZPAL MgM III 80); left M¹, M² (ZPAL MgM III 81); right M₂ (ZPAL MgM III 82) right M₁ (ZPAL MgM III 83); left M₁ (ZPAL MgM III 84); right P₄ (ZPAL MgM III 85); right P₃ and left P₄ (ZPAL MgM III 86a, b); right P₄, M₁ (broken) (ZPAL MgM III 79); left P¹ (ZPAL MgM III 86c); right P² (ZPAL MgM III 86d); left P³ (ZPAL MgM III 86e); left P₁ (ZPAL MgM III 86f); left P₂ (MgM III 86g); right P₃ (ZPAL MgM III 86h); left P₃ and P₄ (ZPAL MgM III 86i, j); right M₁ and M₂ (ZPAL MgM III 86k, l); right M¹ and M² (ZPAL MgM III 86m, n).

Shunkht: left lower jaw fragment with P₄ (broken), M₁, M₂ (PSS 29-15); left lower jaw fragment with P₄, M₁, M₂ (PSS 29-17); right lower jaw fragment with P₃, P₄, M₁ and M₂ (PSS 29-20); right M¹ (PSS 29-22); left P⁴ (PSS 29-23); left M₂ (PSS 29-24); left P₃ (PSS 29-25); right M¹ (PSS 29-26); right P₃ (PSS 29-27).

Khoer Dzan: right P³ and P⁴ (PIN 27-83).

Ergilin Dzo: left lower jaw fragment with P₂, P₃, P₄, all of them broken referred with reserve to *H. pervagus* (PSS 21-35).

China: Urtyn Obo, East Mesa: right M₃ (AMNH 26069).

Emended diagnosis.—Medium-sized *Hyaenodon*, smaller than *H. incertus*. Length and width of teeth less than *H. incertus*, by about 20—30%. Tooth enamel almost smooth. Premolars with acute shearing edges, lingual cingulum and no mesial cusp. Two-rooted P¹ and P₁. P₂ with very short posterior edge. P₄ with thin, concave, mesial ridge above a cingular thickening. Subquadrate M₂ with a very short talonid and wide valley deeply open to the vestigial lingual cingulum. M₃ with paraconid very thick and strongly lingually concave pre- and postparacristid. P³ with a faint postero-lingual thickening. P⁴ with reduced triangular protocone. In the upper molars, no parastyle; protocone heavily reduced, almost missing in M². The carnassial notch of M² very short and the cutting edge extending up from the apex of the pseudamphicone to the distal tip of the metastylar blade.

Description.—The incompletely fused symphysis reaches the anterior edge or half of P₃. The anterior mental foramen is under the posterior root of P₁ or between P₁ and P₂; the posterior one is beneath the posterior root of P₃.

Table 2
Measurements (in mm) of lower teeth of *Hyaenodon pervagus*

	N	Type	RV	M	SD	
P ₂	L	4	12.5—17.5	14.3	1.92	
	W	4	5.3—8.5	6.3	1.28	
P ₃	L	7	13.4—15.8	14.5	0.92	
	W	7	5.8—7.2	6.2	0.18	
P ₄	L	12	17.3	13.5—17.3	15.1	1.37
	W	10	8.4	6.2—8.4	7.3	0.64
M ₁	L	13	11.7	8.8—13.7	10.4	2.39
	W	12	6.1	4.9—7.2	5.7	0.45
M ₂	L	11	16.5	12.4—16.5	14.1	1.84
	W	10	7.8	6.0—7.8	6.8	0.39
M ₃	L	4		17.3—21.0	19.1	
	W	3		6.3—8.5	7.4	0.89

P₁ is a low-crowned tooth with a very reduced anterior root. The two roots are heavily sloped backwards. The mesial edge of the cusp is short, the distal one, long.

P₂ is a high-crowned and stout tooth, shaped like a crook. There is no mesial cusp, only a tiny antero-lingual cingular point from which arises the shearing ridge of the main cusp. The anterior and posterior edges are steeply sloped. In some specimens, a small distal point is present.

P₃ and P₄ are higher-crowned than in other species of similar size. They lack a mesial cusp too. P₃ is a little longer than P₄. Morphologically, they look like P₂, with the sharp ridges and the mesio-lingual thickening of the cingulum. The mesial edge is strongly concave, above the cingulum. In some specimens from Ergilin-Dzo and Shunkht, there is a faint anterior cusp, but never in ones from Tatal Gol. There is a small posterior cusp, conical in P₃, tall and short-bladed in P₄. The lingual cingulum is often well-developed. The posterior alveolus of P₃ is very large as on the holotype and the first three premolars are closely crowded.

M₁ is small. It makes up less than 50% of the length of M₃ and 75% of M₂ on AMNH 21367, 71% on the holotype. The talonid diverges and is cut deeply from the protoconid. In some specimens, M₁ is erupted obliquely as if there were not enough space for it.

M₂ makes up 61% of the length of M₃. This tooth is characterized by the square shape of the trigonid, because of its subequal length and height. The paraconid and the protoconid are of the same length. The lingual valley is widely and deeply open

to the cingulum, between them. The talonid is very short and stands parallel to the protoconid. The hypoflexid is not deep and the buccal base of the protoconid, scarcely protrudes. The design of the lingual enamel above the roots is subrectilinear or gently sloped up above the interradicular space.

M₃ has a very thick paraconid from the apex of which descends lingually an enamel fold. The protoconid makes up 68% of the tooth length. The preparacristid is not lined up with the postparacristid. Consequently, the lingual face of the tooth is strongly concave in its middle part, near the carnassial notch and the lingual valley is deep. The sharp tip of the protoconid extends beyond the base of the crown. One specimen (AMNH 26029) possesses a small cuspule at the distal edge of the protoconid, representing the vestigial talonid.

On all of the three molars, the ectocingulum buttress is faint; the mesial face is wide and flat, with the mesio-lingual edge thin and prominent at the base. The channel to serve as a guide for the previous tooth is present only on the anterior root. Similarly, the lingual cingulum is well-developed on each molar. As in the premolars, the three unworn molars have shearing, slender edges.

No upper tooth of *H. pervagus* has been figured although two premolars, P³ and P⁴, are present in the paratype. On the basis of size and occlusal relationships, these premolars can be assigned to *H. pervagus* and a few new specimens can be attributed too on the same criteria.

P¹ is a very small, short and low-crowned tooth, with two roots.

P² is short and high with short mesial and distal edges.

P³ is longer than high. It is implanted obliquely in comparison to P² and P⁴. There is a posterior conical cuspule. It has only two roots, the distal one is stout because of a lingual thickening of the crown.

P⁴ is shorter than P³ (table 3). The protocone tends to be reduced: it is a small, low, triangular cusp bordered by a large cingulum and situated near base of the main buccal cusp. The distal cusp is tall and very thick. The parastyle is reduced to an anterior cingular thickening.

Table 3
Measurements (in mm) of upper teeth of *Hyaenodon pervagus*

	N	RV	M	SD	
P ³	L	2	15.5—15.8	15.6	0.15
	W	2	7.6—8.6	8.1	0.50
P ⁴	L	3	13.1—16.8	14.3	1.72
	W	2	10.4—10.7	10.6	0.15
M ¹	L	4	14.2—17.3	15.2	1.57
	W	2	8.1—10.0	9.1	0.95
M ²	L	3	18.8—23.7	21.1	2.01
	W	1	8.5	8.5	

In M^1 and M^2 , the paracone and the metacone are fused. In an unworn M^1 , the top of the paracone is observed at two-thirds of the distance along the mesio-buccal ridge. There is no parastyle. In M^1 , the protocone is a small conspicuous cuspule; in M^2 it is lacking, only the lingual root persisting. M^1 has a long projecting metastyle not lined up with the postmetacrista. The metastylar blade of M^2 is buccally deflected. The carnassial notch is hardly indented and the shearing post-metacrista is extended up to the metastyle. The buccal face of the pseudamphicone is flat.

Remarks.—Until now it has been very difficult to identify *H. pervagus* because Matthew and Granger did not illustrate this species and did not give any specific morphological or biometrical character. In the present state of our knowledge, no character distinguishes specimens from Shunkht and Shand Gol Formations from the type designated by Matthew and Granger. Hence all the new mentioned material is referred to *H. pervagus*.

This little collection as a whole is as yet fragmentary and insufficient to estimate biometrically the intraspecific variation. The means and the ratios are not really significant because of the small size of samples. Nevertheless, they provide a mean comparing *H. pervagus* with the other Asiatic species of *Hyaenodon*. *H. pervagus* is less specialized than *H. incertus* and *H. mongoliensis*, with incompletely fused symphysis, two-rooted P_1 and the M_2 and M_3 with deep valleys. It is distinguished from the other Asiatic species, by the larger size, the width/length ratio and the sharp-edged premolars. No comparison with *H. yuanchensis* is possible because the holotype of the latter is a juvenile mandible with deciduous teeth.

Matthew and Granger have compared *H. pervagus* with *H. cruentus* and *H. heberti*. *H. cruentus*, a North-American species has been synonymized by Mellett (1977) with *H. horridus*. *H. pervagus* differs from *H. horridus* in its smaller size, in having reduced protocone on P^4 and the upper molars, in the more fused paracone and metacone (= pseudamphicone) of M^1 and M^2 and in the different ratios of M_1 and M_2 versus M_3 . In fact, *H. pervagus* fits better with *H. montanus*, another North-American Middle Chadronian species, by the same character mentioned above. It is not easy to compare *H. pervagus* with the French species *H. heberti* because the latter is poorly known. *H. heberti* is quite different from *H. pervagus* in its stronger size, in having a diastema between P_2 and P_3 , in its non-shearing premolars with a long mesial edge.

On the other hand, some teeth from Ergilin Dzo and Tatal Gol Formations, referred by Gromova (1952) to *H. dubius* and *H. aymardi*, another European species, have been misidentified and they should be assigned to *H. pervagus* as should the mandible fragment in Gromova (1952: 67, fig. 10) considered to belong to *H. incertus* by Dashzeveg (1985).

Occurrence.—Mongolia: Ergilin Dzo Formation-Shand Gol Formation (Lower—Middle Oligocene); Tatal Gol and Shand Gol (upper layers of the basal lava); Valley of Lakes Depression, Ergilin Dzo, Khoer Dzan, Shunkht. USSR: Chelkar Teniz (Middle Oligocene). China: Lower Urtyn Obo Formation East Mesa (Lower Oligocene).

Hyaenodon incertus Dashzeveg, 1985

(pl. 13: 1; table 4, 5)

1985. *Hyaenodon incertus* Dashzeveg: 241, figs. 9—11.

1985. *Hyaenodon* sp. 2: Dashzeveg: 250, fig. 16.

Holotype: Fragment of left mandibular ramus with P_4 (broken) and the three molars (PSS 27-37).

Type horizon and locality: Lower lacustrine beds, Ergilin Dzo Formation, Lower Oligocene; Khoer Dzan, Mongolia.

Material.—Khoer Dzan: fragment of right dentary with fused symphysis, P₄ and M₁ (PSS 27-75); P₄ (PIN 27-77b). Urtyn Obo: right symphysis and mandibular fragment with heavily eroded C, P₃, P₄, M₂, M₃ (broken) (AMNH 26068); Camp Margetts: incomplete left fragmentary mandible with eroded P₂, P₃, P₄, M₁, M₂ (AMNH 95778).

Description.—The two new teeth are very similar in size and in morphology to those figured by Dashzeveg (1985: fig. 9, 10).

P₄ is fairly sloped backwards. There is no mesial basal cusp. The talonid is high and narrow. The two roots are joined a few millimeters from the crown. Size is slightly larger than that of the holotype but nothing is known about the intraspecific variation.

M₁ is badly damaged. The mesio-buccal part of the crown is heavily abraded and the occlusal wear facet is at the same angle as on the type. The proportions and the morphology of the talonid appear to conform more closely with those of the holotype.

A short diastema (3.5 mm) extends between P₂ and P₃. P₂ has two roots almost equally developed. P₁ is lacking but this may be accidental because the bone here has a pathological osteoporous aspect from C to P₃ alveoli.

The narrow and fused symphysis extends to half the length of P₃. There is no pit for genioglossal muscles (one of the differences from the genus *Pterodon*). The anterior part of the dentary is low (32, 5 mm between P₄ and M₁) and not very thick (17 mm at the same locus). A large single mental foramen is situated below the P₂ anterior alveolus.

Table 4
Measurements (in mm) of teeth of *H. incertus*

	Type	PSS 3110—43	PIN 21—42	PSS 27—75	AMNH 26068	M
P ₃	L	14.0			16.7	15.3
	W	9.0			7.5	8.3
P ₄	L	17.0		17.7	16.7	17.3
	W	11.0		10.5	8.5	10.0
M ₁	L	13.0	12.0	11.0	13.5	12.4
	W	7.5	8.0	7.7		7.7
M ₂	L	16.0	14.0	16.0		15.4
	W	9.0	9.0	8.5		8.7
M ₃	L	26.0	25.0	23.0		24.7
	W	11.0	11.0	10.0	9.0	10.3

Remarks.—Some new specimens show the morphology of the anterior part of the mandible which was previously unknown. The short diastema between the anterior premolars characterizes a long-faced *Hyaenodon*.

Although the intraspecific variation has not been adequately sampled, it seems that the fragmentary right mandible figured by Dashzeveg (1985: fig. 16) might be referred to *H. incertus*.

Two lower jaws (AMNH 26066, 26067) from Ulan Gochu, with deciduous dentition are assigned with high probability to *H. incertus* too. P_1 is single-rooted with a very steep slope backwards. M_1 presents a lighter coloration like the North-American *H. horridus* milk teeth. The measurements of M_1 and M_2 fit well with those of the holotype. On the other hand, these two juvenile mandibles resemble *H. yuanchensis* Young 1937. The latter is a juvenile specimen too, from Yuanchu, South Shansi, with single-rooted P_1 . The teeth are close in size to the two specimens from Ulan Gochu (table 5). It is always unsafe to make an immature specimen the holotype of a new species. It is possible that *H. incertus* and *H. yuanchensis* are conspecific but it would be premature to synonymize them without more data about the latter.

From the phylogenetic point of view, *H. incertus* could be related to *H. mongoliensis*. Both belong to the same broad type with long fused symphysis,

Table 5
Measurements (in mm) of lower teeth referred to *H. incertus* and compared to *H. yuanchensis*

	<i>Hyaenodon yuanchensis</i>	<i>Hyaenodon incertus</i>	
		AMNH 26066	AMNH 26067
L d P_1 W		11.8 6.0	11.3; 11.5 6.5; 6.7
L d P_2 W	14.5 8.5	10.4 4.1	11.8 4.5
L d P_3 W		11.8; 12.0 4.9; 5.8	13.8 6.3
L d P_4 W	14.0 7.3	13.5; 13.0 5.8; 6.0	14.3 6.6
L M_1 W		14.0; 15.0 7.0; 7.0	14.0 7.4
L M_2 W			18.5

small diastema between P_2 and P_3 , premolars without mesio-basal cusp, strongly backwardly sloped P_3 and P_4 . *H. incertus* could be either a morphocline or the female of *H. mongoliensis*. More material is needed before choosing between these two interpretations.

Occurrence.—Mongolia: Khoer Dzan and Bayan Tsav; lower lacustrine beds, Ergilin Dzo Formation; China: Urtyn Obo, Houldjin Formation and Baron Sog Formation, Lower Oligocene.

Hyaenodon mongoliensis (Dashzeveg, 1964)

(pl. 13: 2, 3; table 6)

1964. *Megalopteron mongoliensis* Dashzeveg: 265, pl. 1: 1ab.

1967. *Pterodon mongoliensis* (Dashzeveg); Van Valen: 267.

1977. *Hyaenodon mongoliensis* (Dashzeveg); Mellett: 124.

1979. *Hyaenodon mongoliensis* (Dashzeveg); Lange-Badré: 136.

Holotype: Incomplete lower jaws with left C, P_2 — M_2 and right I_2 , P_2 — M_2 (BD 21); figured in Dashzeveg 1964: pl. 1: 1ab.

Type horizon and locality: Ergilin Dzo Formation; Bayan Tsav, Mongolia.

Material.—Khoer Dzan: left symphysis and mandibular fragment with P_2 and P_3 (PSS 27-76); right mandibular fragment with P_4 (PSS 27-77).

Near Baron Sog Lamasery: right M_2 (AMNH 26269).

Description.—The two new fragments of mandible fit well with the holotype. They are noteworthy for the thickness of the dentary: 25.5 mm and 25.3 mm, halfway beneath P_4 and 26 mm in the type. The upper part of the lingual face of the dentary is strongly inflated and could be related to the stout development of the roots of the premolars or to the strengthened insertion of the mylohyoid muscles. Dashzeveg did not mention this feature in his diagnosis but it is possible to explain it functionally. *H. mongoliensis* has a fused large symphysis that required more force to open its jaws and to chew its food.

On PSS 27-76, there is a very large, single alveolus for P_4 , behind which extends a diastema of about 8.3 mm. It is probably an accidental, individual variation because the superficial bone is not altered and the mandibular spongiosa does not show any pathological osseous tissue.

P_2 , P_3 , P_4 have no anterior basal cusp, only a small mesio-lingual thickness of cingulum. P_2 is very asymmetrical with a large posterior edge. P_3 has a posterior, very high and short talonid. P_4 looks like P_3 but it is larger, with an anterior edge more strongly sloped.

M_2 is like those of the holotype with the talonid well-cut from the protoconid.

Remarks.—The new specimens are morphologically very close to the holotype of *H. mongoliensis* previously described by Dashzeveg (1964) under the name *Megalopteron mongoliensis*. Only the dimensions are slightly different: smaller for the premolars and longer for M_2 . However, these differences should not be emphasized because all the specimens including the type do not come from the same locality, nor from the same stratigraphic level. Moreover, the intraspecific variation and sexual dimorphism are not adequately sampled yet with 4 fragments. Consequently, all these factors might be enough to explain the variability in size that is within the limits defined by Mellett (1977) for the North American species of *Hyaenodon*.

Occurrence.—Mongolia: Khoer Dzan and Bayan Tsav; lower and upper alluvial beds of Ergilin Dzo Formation. China: Ulan Gochu Formation (or maybe Baron Sog Formation, Russell and Zhai 1987); Lower Oligocene.

Table 6
Measurements (in mm) of cheek teeth and lower jaw of *H. mongoliensis*

	Type*	P ₂ PSS 27—76	P ₃		P ₄		M ₂	
			Type*	PSS 27—76	Type*	PSS 27—77	Type*	AMNH 26269
Length	25	17	25	19.2	26	21.5	21	23.7
Width	10	10	15	12.5	16	13.5	13	10
Height between P ₄ and M ₁	41	40.3						
Thickness at the same level	26	25.5				25.3		

* after Dashzeveg 1964

Hyaenodon cf. *gigas*

(pl. 12: 4, 5, 6; table 7)

Material.—Left P³ and right P₃ (PSS 27-78). Left P₂ (PIN 27-85); Khoer Dzan, Lower Oligocene.

Description.—These three very large-sized teeth are somewhat damaged and poorly preserved. Therefore their dimensions given (table 7) are underestimated.

P² larger than high carries a small distal basal cusp on a high position. The posterior edge is short. P³ has a distal strongly bulging cusp. On the lingual face it is part of a low prominence bordering the distal cusp. There is no separate lingual root and the entocingulum is well-developed.

No tooth has a mesial cusp: the anterior part is short and steeply sloped, with a more and less acute crest terminated by a triangular cingular thickening.

Remarks.—According to their morphology, these three teeth pertain certainly to *Hyaenodon*. Three large species of *Hyaenodon* have been collected in the Ergilin Dzo Formation: *H. gigas* Dashzeveg, 1985, *H. mongoliensis* Dashzeveg, 1964 and *H. incertus* Dashzeveg, 1985. The specimens described above compare closely in size with *H. gigas* only, the two latter are clearly smaller. But, the holotype of *H. gigas* is a maxilla with P⁴ and two molars and there is no other material. Consequently, an accurate determination is not possible and in the absence of more complete material it is better to assign these three isolated teeth to *H. cf. gigas*.

Table 7
Measurements (in mm) of teeth of *H. cf. gigas*

	P ²	P ³	P ₃
L	26.4	26.9	25.9
W	13.9		16.5

Hyaenodon sp.

(pl. 12: 8)

Material.—Right M_3 (PSS 27-79) damaged and PSS 27-80: $L \times W = 30.2 \times 13.3$; Khoer Dzan, Lower Oligocene.

Description.—These two molars are most similar in size and morphology. The width is about 23% of the length. The preparacristid is more sloping than those of European *Hyaenodon* species. The postparacristid is twice as long as the preparacristid. The high buccomesial buttress extends up to the carnassial notch.

Both possess a small pointed cuspule posteriorly at the base of the protoconid; it represents a vestigial talonid.

Remarks.—These two M_3 's are too fragmentary for specific determination. They might be referred to the one of the three large-sized species collected from the same or similar stratigraphical level: *H. incertus*, *H. mongoliensis* and *H. gigas*. The two new M_3 's are larger than those of *H. incertus* and probably too short to be assigned to *H. gigas*, although M_3 of this species is unknown. M_3 is also lacking on the holotype of *H. mongoliensis*. In any case, according to Mellett (1977), the most intraspecifically variable in size teeth in *Hyaenodon* are the carnassials, by about 30% because they are the last to erupt and are situated at the end of the tooth row. Therefore, we do not intend to identify specifically, these M_3 .

Order Carnivora Bodwich, 1821
 Infraorder Feliformia Kretzoi, 1945
 Family uncertain
 Genus *Palaeogale* Meyer, 1846
Palaeogale sectoria Gervais, 1852
 (pl. 14: 1–4; table 8)

1852. *Palaeogale sectoria* Gervais: t. II., explanation of Pl. 28, p. 10.

1924. *Bunaelurus parvulus* Matthew et Granger: 8, fig. 6B.

1924. *Bunaelurus ulysses* Matthew et Granger: 8, fig. 6C.

1946. *Palaeogale parvula* (Matthew et Granger); Simpson: 9.

1946. *Palaeogale ulysses* (Matthew et Granger); Simpson: 12, fig. 4.

1968. *Palaeogale ulysses* (Matthew et Granger); Mellett: 11.

1968. *Palaeogale parvula* (Matthew et Granger); Mellett: 11.

1981. *Palaeogale lagophaga* Cope 1873; de Bonis: 14, fig. 14.

1981. *Palaeogale inflexis* Matthew 1873; de Bonis: 15.

Holotype: Left lower jaw with C, P_2 , P_3 , P_4 , M_1 , M_2 . BM 27816

Type horizon and locality: Garouillas level (Brunet and Vianey—Liaud 1987), Middle Stampian, Middle Oligocene; Antoingt (Auvergne, France).

Material.—Shand Gol Formation, Tatal Gol: right mandibular fragments with M_1 , M_2 (ZPAL MgM III/88 and 90); left mandibular fragment with P_4 , M_1 (ZPAL MgM III/89); left fragmentary lower jaw with P_4 , M_1 , M_2 (ZPAL MgM III/91); right lower jaw fragments with P_1 , P_2 , P_4 (ZPAL MgM III/92), with P_2 , P_3 , P_4 (ZPAL MgM III/93 and 94); right P_4 (ZPAL MgM III/95).

Description.—All the undamaged specimens show alveoli for four premolars. On the whole, the teeth are similar to those of *P. sectoria* described by de Bonis (1981). P_1 unknown up to now, is a tiny, bucco-lingually compressed pinshaped

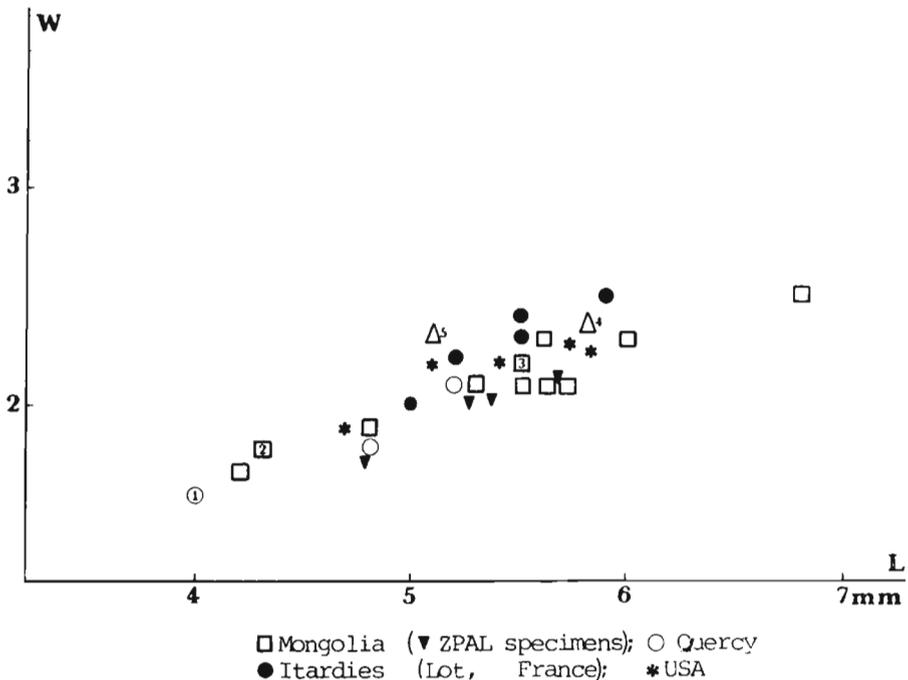


Fig. 1. Diagram of variation of width versus length of M_1 in *Palaeogale sectoria* (from de Bonis 1981, modified): 1—*P. felina* (lectotype), 2—*P. parvulus* (holotype), 3—*P. ulysses* (holotype), 4—*P. lagophaga* (holotype), 5—*P. infelix* (holotype). All are synonyms of *P. sectoria*.

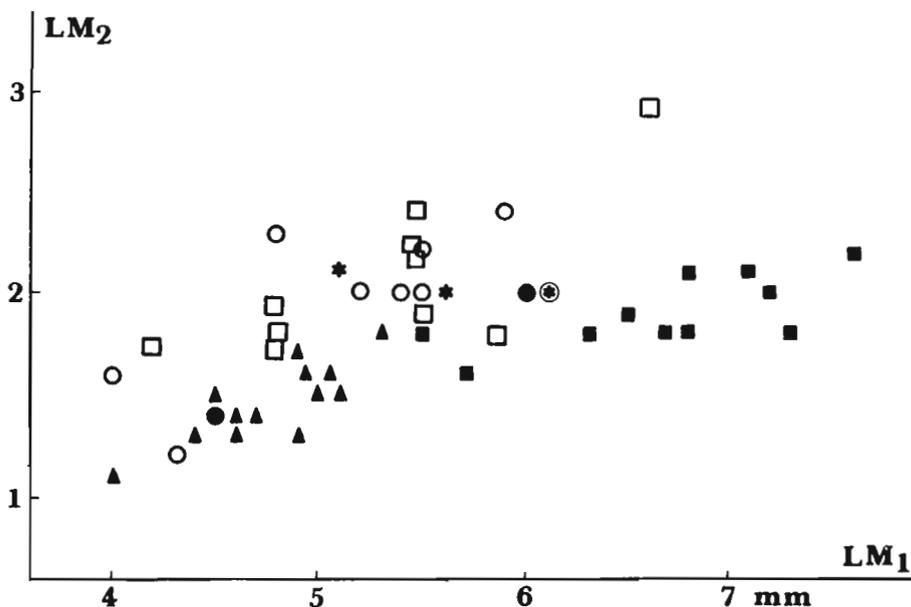
tooth, with a single root. P_4 has always a small anterior accessory cingular cusp. The M_1 protoconid, twice as tall as the paraconid, is not higher than the main cusp. The M_2 trigonid is either narrow, long and overlapped buccally by the M_1 talonid or wide and short.

Remarks.—Matthew and Granger (1924) described two *Bunaelurus* species from Mongolia, *B. parvulus* and *B. ulysses*, both referred to the genus *Palaeogale* by Simpson (1946). The holotype of *P. ulysses* is slightly different in morphology and in size from the holotype of *P. parvula*. In fact, the species name *ulysses* is applied to specimens with P_4 and M_1 longer and broader than those of *P. parvula*. Moreover, the M_1 talonid is longer with respect to the trigonid, because of the well-defined hypoconulid. M_2 of *P. ulysses* differs from M_2 of *P. parvula* by being longer and narrower, by the paracristid very long and by the talonid being usually as broad as the trigonid. These two configurations have been observed in the French material from the Quercy Phosphorites by de Bonis (1981).

The scatter diagram of length versus width of M_1 (fig. 1) demonstrates that the new Mongolian specimens fall within the range of variation of the European species *Palaeogale sectoria* and are especially close to those from Itardies locality. However, if the length of M_1 is the same, its width is slowly smaller in the specimens from Tatal Gol. These same specimens compared with the holotypes of *P. parvula* (AMNH 19013) and *P. ulysses* (AMNH 19004), both synonymised by de Bonis with *P. sectoria* (*op. cit.*) show some differences which are probably the result of intraspecific variation (fig. 1). For instance, the number and the positions of the mental foramina are different. Two mental foramina are usually present, one beneath the anterior root of P_2 , another below P_3 . In ZPAL MgM

Table 8
 Measurements (in mm) of lower teeth of *P. sectoria*.
 Sample includes AMNH specimens

	N	RV	M	SD	
P ₂	L	2	2.1—2.5	2.3	0.2
	W	2	0.8—1.0	0.9	0.1
P ₃	L	3	3.0—4.0	3.5	0.4
	W	3	1.2—1.8	1.4	0.3
P ₄	L	13	2.9—4.7	3.9	0.4
	W	13	1.2—1.8	1.5	0.9
M ₁	L	14	4.2—6.6	5.8	0.7
	W	14	1.6—2.5	2.1	0.2
M ₂	L	6	1.6—2.9	2.3	0.5
	W	6	1.0—1.5	1.3	0.2



P. sectoria : Stampian Europe ○ ; Early Oligocene Mongolia □ ;
 Orellan USA *

P. minuta: Agenian Europe ▲○ ; *P. hyaenoides*: Orleanian Europe ■
P. cf. minuta: Hemingfordian USA ⊙

III/92, there are four foramina, two below P_3 , one below P_2 and one between P_1 and P_2 ; in ZPAL MgM III/88 and 93, there are three mental foramina below P_1 , P_2 and the posterior root of P_4 . These differences are not very important and all the specimens represent in fact the same species, *P. sectoria*.

New material from Tatal Gol (fig. 2) shows some evolutionary trends outlined (size and morphology) toward a species separation leading to *P. minuta* from Agenian localities of St Gérard le Puy and Laugnac (France) and to *P. hyaenoides* from Orleanian Wintershof West (West Germany). It is strange that none of these two species have still been discovered in Asiatic localities.

However, from these data, we can conclude that *P. sectoria* is obviously the ancestor of *P. minuta* and *P. hyaenoides*, and both being issued from a speciation process occurred in Mongolia during the middle part of Oligocene. Therefore, we can consider these species as Asiatic immigrants.

Occurrence.—France: Quercy Phosphorites, Auvergne, Lower and Middle Stampian, Lower-Middle Oligocene. Mongolia: Tatal Gol, Shand Gol Formation, Middle Oligocene. USA: South Dakota, Chadronian Orellan, Lower and Middle Oligocene.

Infraorder Caniformia Kretzoi, 1945

Family Ursidae Gray, 1825

Genus *Amphicynodon* Filhol, 1882

Amphicynodon teilhardi (Matthew et Granger, 1924)

(pl. 14: 5, 6; table 9)

1924. *Cynodon teilhardi* Matthew et Granger: 8, fig. 6B.

1968. *Amphicynodon teilhardi* (Matthew et Granger); Mellett: 11.

1970. *Cynodictis mongoliensis* Janovskaya: 74, 75, fig. 3, 4.

Holotype: Lower jaw fragment with M_1 , M_2 and alveolus of M_3 . (AMNH 19007).

Type horizon and locality: Shand Gol Formation, Middle Oligocene, Loh.

Material.—Lower right jaw fragment with half of P_3 , P_4 , M_1 , M_2 and the alveolus of M_3 (ZPAL MgM III/96); left lower jaw fragment with P_3 talonid, P_4 , M_1 (ZPAL MgM III/97). Tatal Gol, Shand Gol Formation; Middle Oligocene.

Description.—The holotype is badly preserved but the new specimens that are in a better condition, fortunately complement it.

P_3 of which the distal half is present, possesses a very short low talonid. There is no posterior accessory cusp.

P_4 is longer than high. The anterior accessory cusp is lacking but a wide rim encircles the base of the main cusp. The buccal cingulum is wide. The posterior accessory cusp is positioned very high on the buccal flank of the main cusp from which it is separated by a short but distinct carnassial notch. The talonid is short, moderately wide and formed by a strong cingulum that emphasizes the presence of a tiny cusp connected to the accessory cusp by a thin ridge. It lacks a significant basin, bearing only a faint hollow at the base of the lingual side of the posterior accessory cusp. The lingual cingulum is continuous, except below the main cusp where it is interrupted.

M_1 has the low trigonid characteristic of all species of *Amphicynodon*, with

Fig. 2. Scatter diagram of M_1 length against M_2 length of *Palaeogale* (from de Bonis 1981, modified).

the paraconid located mesio-lingually and the apex of the protoconid tipped backwards. The paralophid is short and separated from the protoconid by a tall, deep carnassial notch. On the lingual side, an open valley isolates the paraconid from the protoconid which is fused to the base of the metaconid. The protoconid is slightly taller than the metaconid. The buccal side of the protoconid base is as long as the paraconid. Observed lingually, the protoconid base appears between the paraconid and the metaconid. The metaconid is as well-developed as the paraconid. Its lingual base is enlarged but does not join the paraconid. It is positioned postero-laterally to the protoconid and projects backwards. Its distal edge forms an obtuse angle with the talonid.

The talonid is very long and low. It is approximately as wide as the trigonid or slightly narrower. In the holotype, the enamel is strongly wrinkled although on ZPAL MgM III/96, the wrinkles are less obvious. The hypoconulid is lacking. The hypoconid is low, thick and poorly individualized; it partially fills the talonid which consequently is not hollowed out, except near the metaconid. The entoconid is missing on the holotype. A posterior crest from the hypoconid encircles the talonid and disappears near the metaconid. On ZPAL MgM III/96, there is a very small entoconid which protrudes from this crest. The lingual side of the talonid is flat and rectilinear. The cristid obliqua is approximately parallel to the antero-posterior axis of the tooth.

M₂ is reduced in size (table 9) but remains functional. This tooth has a short, oval or rounded outline. Its height is similar to that of the talonid of M₁. The talonid is longer than the trigonid. Here too, the enamel is wrinkled. The paraconid is absent. The stoutest metaconid is higher than the protoconid and slightly anterior to the same cusp. Smooth ridges slope down from the top of the two cusps without joining in the basin. Together with the mesial cingulum, they delimit a shallow mesial basin. The hypoconid is lower and thicker than the protoconid. The hypoconulid and the entoconid are absent. A low crest joins the hypoconid to the metaconid and encloses a very small lingual basin.

M₃. No specimen has been found containing M₃. According to the alveolus, however, M₃ is smaller than M₂ and longer than it is wide, with two closely approximated roots.

Remarks.—Matthew and Granger (1924) referred the holotype of *Cynodon teilhardi* only provisionally to the genus *Cynodon* until additional specimens

Table 9

Measurements (in mm) of lower teeth of *Amphicydon teilhardi*

	N		Type	ZPAL MgM III/96	97	98	M
P ₄	3	L		5.5	5.5	5.5	5.5
		W		2.6	2.5	2.9	2.7
M ₁	2	L	7.6	7.7			
		W	3.7	3.8			
M ₂	2	L	3.0	2.8			
		W	2.8	2.6			

became available. They suggested also that *C. teilhardi* fitted better in the subgenus *Pachycynodon* and was not typical of the genus *Amphicynodon* according to Teilhard de Chardin's key (1915). It has been possible to compare *Cynodon teilhardi* with two species of *Pachycynodon* (*P. tenuis* and *P. filholi*) and with three species of *Amphicynodon* (*A. typicus*, *A. leptorhynchus* and *A. gracilis*). *Pachycynodon* has a low trigonid on M_1 as has *Amphicynodon*, but we disagree with Matthew and Granger's interpretation. *C. teilhardi* belongs unquestionably to the genus *Amphicynodon*. It differs from *Pachycynodon* in the situation of the metaconid on M_1 , in the open basin, in the wrinkled enamel, in the reduced paraconid and entoconid in M_2 and in the ratios of the talonid and trigonid on M_2 . All these characters are shared with typical *Amphicynodon* species.

Amphicynodon teilhardi seems to be a closer relative of *A. leptorhynchus* or *A. typicus* than it is of *A. gracilis*. The first three species share the wrinkled enamel and more reduced paraconid on M_2 . *Amphicynodon gracilis* differs principally in the shorter talonid on M_1 and M_2 .

Janovskaya (1970) described *Cynodictis mongoliensis* from the Shand Gol Formation, Tatal Gol. There are no significant morphological or biometrical differences between *C. mongoliensis* and *A. teilhardi* and those that exist represent no more than intraspecific variation. The entoconid is lacking on M_1 . The whole mesial part of M_2 is reduced and the distal basin is very wide, which produces a square outline. M_3 is square, encircled by a strong cingulum; the paraconid and the protoconid are indistinct and the existence of a metaconid is doubtful. Consequently, *Cynodictis mongoliensis* is a junior synonym of *Amphicynodon teilhardi* and must be synonymized with it. However, the M_1 (PIN 475 1390) figured by Janovskaya cannot be assigned to *A. teilhardi* without reserve, because, if the illustration is accurate, the junction between the paraconid and the metaconid is unusual for this genus.

Amphicynodon teilhardi is restricted to the Middle Oligocene level from Tatal Gol and Khatan Khayrkhak (Russel and Zhai 1987). However the genus occurred in Western Europe during the Early Oligocene. A systematic revision is needed in order to establish the relationships between different species described in the two regions.

Occurrence. — Tatal Gol, Shand Gol Formation; Middle Oligocene.

CONCLUSIONS

Despite new discoveries of Palaeogene mammal faunas in Central Asia, our knowledge on the carnivores and the creodonts from this area is still incomplete. On the whole, both are rare and of low diversity, belonging to genera widespread in the holarctic region of the time. The material described up to now is very fragmentary; the samples are not sufficient to indicate significant intraspecific variation and more specimens are obviously necessary to determine evolutionary polarities and chronoclines.

From the nine carnivorous species described by Matthew and Granger from the Shand Gol area, four were refound by PMP expeditions in the later years, at Tatal Gol locality: *Amphicynodon teilhardi*, *Palaeogale sectoria*, *Hyaenodon eminus* and *H. pervagus*.

Amphicynodon teilhardi would be an endemic taxon though the genus is reported from the Lower Oligocene of Western Europe.

Palaeogale sectoria is a well-dated stratigraphic marker. Considerable precision concerning the age of the fossil mammal-bearing level at Tatal Gol has been obtained by radiometric dating of the underlying basaltic beds: 32—32,8 Ma (Evernden *et al.* 1964, corrected from Harland *et al.* 1982). The faunal assemblage from Tatal Gol is therefore correlated with the Chadronian Orellan boundary (Emry 1987), in North America.

In Western Europe, the first occurrence of *P. sectoria* is recorded from two localities of Quercy Phosphorites: La Plante 2 and Mas de Got which are usually attributed to the late Early Oligocene (M. P. 22, Villebramar level) about 35.5 Ma or 34.5 Ma according to Leveque (1987) for Mas de Got. The biostratigraphic range of *P. sectoria* is documented up into the Garouillas level or M. P. 24 which is approximately from 30.6 Ma.

The radiometric age of Tatal Gol is just midway between the lower and upper boundaries of the European range of *P. sectoria*. Moreover, the evolutionary level of the Tatal Gol specimens fits well with those from the locality of Itardies. Therefore, the fauna of Tatal Gol can be correlated with the Itardies level or M. P. 23 of the European Paleogene Mammal chronology.

Concerning the genus *Hyaenodon*, its earliest occurrence, if the taxonomic determination is accurate, is reported from the Lushi Formation by Chow (1973), and from the Lishigou Formation by Gao (1976).

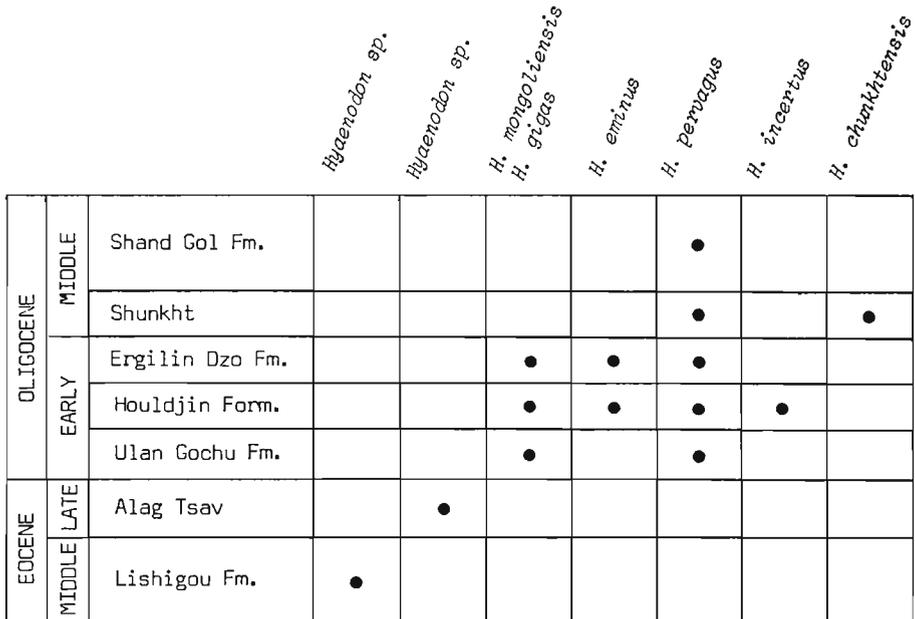


Fig. 3. Stratigraphic distribution of *Hyaenodon* species in Asiatic Paleogene.

These two fossiliferous levels in the Henan Province of China are considered Middle Eocene in age (Russell and Zhai 1987). A large sized *Hyaenodon* sp., only known by a M_3 , was described by Dashzeveg (1985) from the Late Eocene of Alag Tsav, Mongolia. In Europe, *Hyaenodon* occurs at the beginning of Late Eocene and nearly at the same time in North America. Thus, we can conclude to a broad, rapid geographic dispersal during the early Late Eocene (about 42 Ma). Its dispersal from Asia towards North America is better documented than this towards Europe, as it is the case for other mammalian groups.

Five or six valid species of *Hyaenodon* were reported from the interval of Late Eocene—Late Oligocene in Mongolia (fig. 3), *H. gervaisi* and *H. exiguus* mentioned by Gromova (1952) not being taken into account here.

The small *H. eminus*, without any particular affinities to the other Eurasiatic and North American species, might be an endemic form characterizing the Lower Oligocene of Mongolia.

H. pervagus was widespread in time and in space. This species poses the problem of a possible vicariance with *H. montanus* (Middle Chadronian, USA) and *H. dubius* (Stampian, Western Europe) although according to Mellett (1977), *H. montanus* could be related to *H. vetus* (Late Eocene, USA).

On the other hand, it is noteworthy that the highest specific diversity of the genus *Hyaenodon* in Asia (7 species) occurs during the Early and Middle Oligocene exactly at the same time as in Western Europe (6 species) and North America (6 species). The significance of this diversification is not clear. It may have resulted either from the vicariance events in each area since the Late Eocene or from migrations that would be correlated with the general deterioration of climate and with the sea level fall that occurred at the beginning of late Eocene and during the entire Oligocene.

Concerning the contribution of creodonts and carnivores to the biochronology of continental deposits in Mongolia, the assemblage of *H. pervagus*, *P. sectoria* and *A. teilhardi* seems significant for the middle part of Oligocene. However, this faunal characterization should be confirmed by detailed systematic and phylogenetic studies based on a more complete material and by more rigorous stratigraphic data on the Mongolian mammal-bearing deposits.

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BRIGITTE LANGE-BADRE i DEMBERLYIN DASHZEVEG

O PEWNYCH SSAKACH DRAPIEŻNYCH Z OLIGOCENU AZJI CENTRALNEJ

Streszczenie

Opisana fauna ssaków drapieżnych z oligoceńskich stanowisk Gobi składa się z następujących gatunków Creodonta z rodzaju *Hyaenodon*: *H. eminus*, *H. cf. gigas*, *H. incertus*, *H. mongoliensis*, *H. pervagus*, i jednej formy określonej jako *Hyaenodon* sp., oraz dwóch przedstawicieli Carnivora, *Palaeogale sectoria* i *Amphicynodon teilhardi* (pl. 9—14). Faunę tę oznaczono na podstawie fragmentarycznych szczęk i izolowanych zębów. Występowanie wymienionych Carnivora ogranicza się do Svity Shand Gol. Holotyp *Hyaenodon pervagus* został tu zilustrowany po raz pierwszy. Przedyskutowano pokrewieństwa przedstawicieli tej fauny z drapieżnymi Ameryki Płn. i Europy oraz implikacje stratygraficzne i paleogeograficzne tych pokrewieństw.

EXPLANATION OF PLATES 9—14

Plate 9

Hyaenodon pervagus Matthew et Granger
Middle Oligocene, Shand Gol Formation, Loh, Mongolia

1. Holotype. AMNH 19005 (cast): *a* buccal view; *b* lingual view.
2. Right P³ and P⁴. Paratype (AMNH 19006) lingual view.
3. Right M¹ and M² (AMNH 21657): *a* buccal view; *b* lingual view.
4. Right M₃. Paratype (AMNH 19126) buccal view.
5. Left mandible with P₂, dp₃, dp₄, M₁. Paratype (AMNH 19125): buccal view.

6. Left M^1 (AMNH 21657): buccal view.

Early Oligocene, lower Urtyn Obo Formation, East Mesa, China

7. Right M_3 (AMNH 26069): lingual view.

All natural size

Photographs: C. Abrial

Plate 10

Hyaenodon pervagus Matthew et Granger

Middle Oligocene, Shand Gol Formation, Tatal Gol, Mongolia

1. Left P^1 (ZPAL MgM III/86c).
2. Right P^2 (ZPAL MgM III/86d).
3. Left P^3 (ZPAL MgM III/86e).
4. Left P_1 (ZPAL MgM III/86f).
5. Left P_2 (ZPAL MgM III/86g).
6. Right P_3 (ZPAL MgM III/86h).
7. Right P_4 (ZPAL MgM III/86j).
8. Right M_1 (ZPAL MgM III/86k).

a buccal view; b lingual view, $\times 1.5$

Photographs: C. Abrial

Plate 11

Hyaenodon pervagus Matthew et Granger

Middle Oligocene, Shand Gol Formation, Tatal Gol, Mongolia

1. Right P_2 (broken), P_3 , P_4 , M_1 (ZPAL MgM/80).
2. Right M_2 (ZPAL MgM III/86l).
3. Left M^1 (ZPAL MgM III/86m).
4. Left M^2 (ZPAL MgM III/86n).

a buccal view; b lingual view, $\times 1.5$

Photographs: C. Abrial

Plate 12

Hyaenodon pervagus Matthew et Granger

Early Oligocene, Khoer Dzan, Mongolia

1. Right maxillar with P^3 , P^4 (PIN 27-83): buccal view.
2. Right maxillar with P^3 , P^4 (PIN 27-84): occlusal view.

Middle Oligocene, Shunkht, Mongolia

3. Right mandible with P_3 , P_4 , M_1 , M_2 (PSS 29-20): lingual view.

Hyaenodon cf. gigas

Early Oligocene, Khoer Dzan, Mongolia

4. Left P² (PIN 27-85): lingual view.
5. Right P³ (PSS 27-78): a buccal view; b lingual view; c distal view, lingual lobe indicated by an arrow.
6. Right P₃ (PSS 27-78): a buccal view; b lingual view.

Hyaenodon incertus Dashzeveg
Early Oligocene, Khoer Dzan, Mongolia

7. Left P₄ (PIN 27-77b): lingual view.

Hyaenodon sp.
Early Oligocene, Khoer Dzan, Mongolia

8. Right M₃ (PSS 27-80): lingual view.

Hyaenodon eminus Matthew et Granger
Early Oligocene, Khoer Dzan, Mongolia

9. Left P₃, P₄ (PSS 27-100): lingual view.
Natural size except fig. 9×2

Photographs: C. Abrial

Plate 13

Hyaenodon incertus Dashzeveg
Early Oligocene, Khoer Dzan, Mongolia

1. Right mandible with P₄, M₁ (PSS 27-75): buccal view; porous alveolar bone indicated by an arrow.

Hyaenodon mongoliensis (Dashzeveg)
Early Oligocene, Khoer Dzan, Mongolia

2. Right P₄ (PSS 27-77): a buccal view; b lingual view; c distal view; lingual thickening of the dentary indicated by an arrow.
3. Left P₂, P₃ (PSS 27-76): a buccal view; b distal view; lingual thickening of the dentary indicated by an arrow.

All natural size

Photographs: C. Abrial

Plate 14

Palaeogale sectoria Gervais
Middle Oligocene, Shand Gol Formation, Tatal Gol, Mongolia

1. Right mandible with P₁, P₂, P₄ (ZPAL MgM III/92).
2. Right mandible with P₂, P₃, P₄ (ZPAL MgM III/93).

3. Right mandible with M₁, M₂ (ZPAL MgM III/90).
4. Left mandible with P₄, M₁ (ZPAL MgM III/89).

Amphicynodon teilhardi (Matthew et Granger)

Middle Oligocene, Shand Gol Formation, Tatal Gol, Mongolia

5. Left P₄ (ZPAL MgM III/97).
6. Right mandible with P₄, M₁, M₂ (ZPAL MgM III/96): a buccal view; b lingual view.

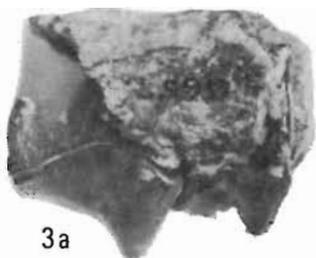
All ×3



2



1a



3a



1b



3b



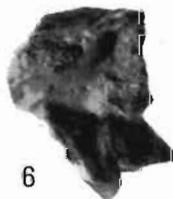
4



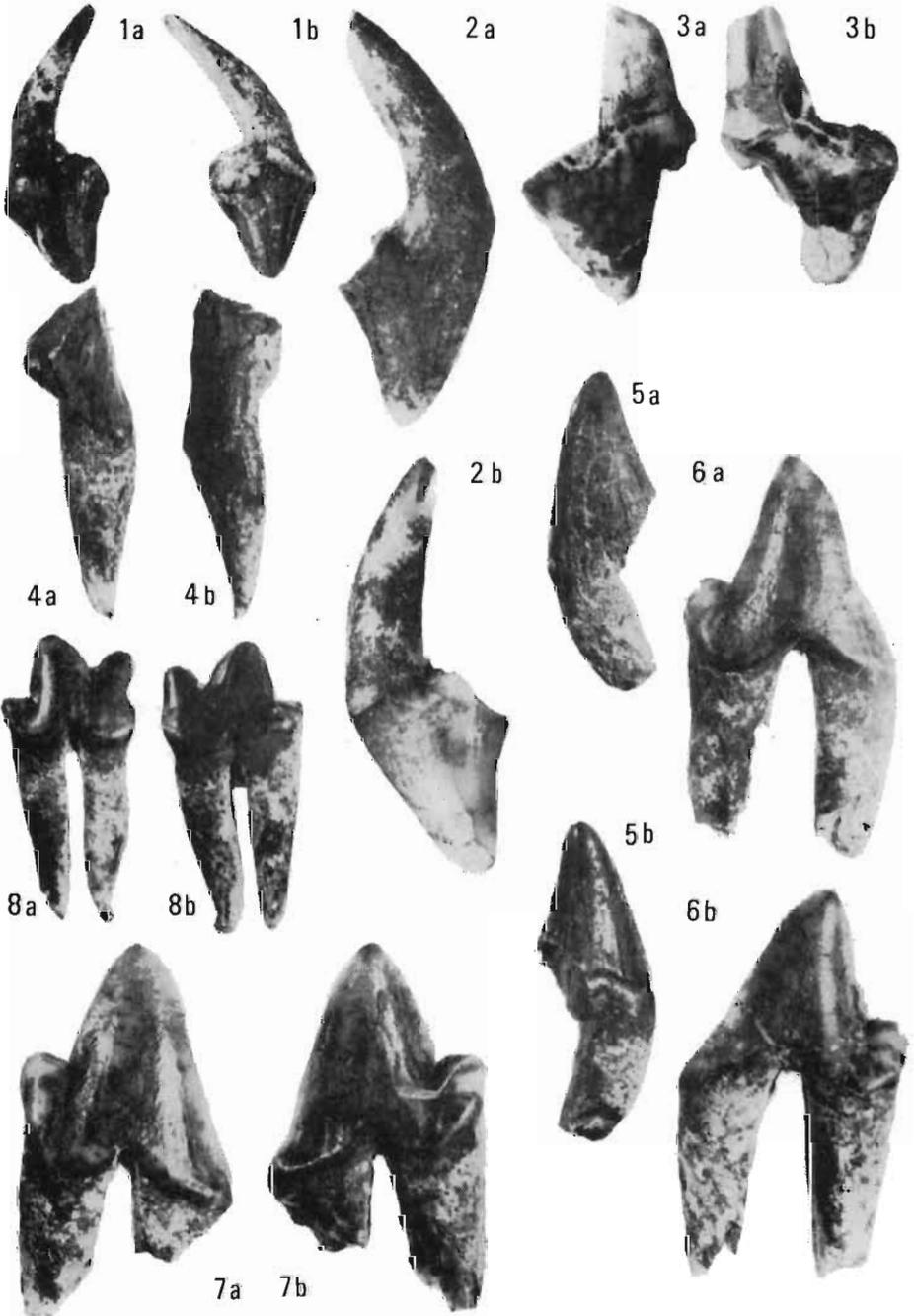
7



5

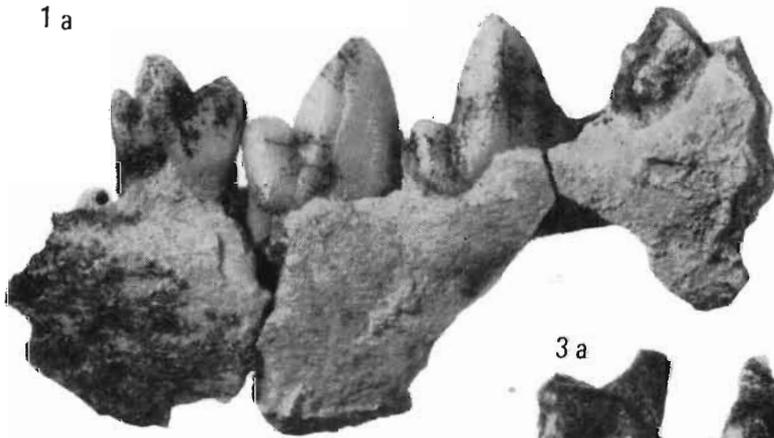


6





1b



1a



3a



4a



2a

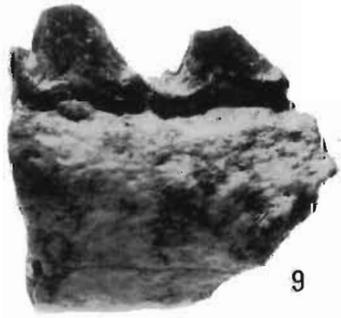
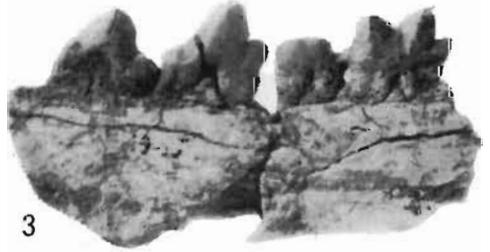
2b



3b



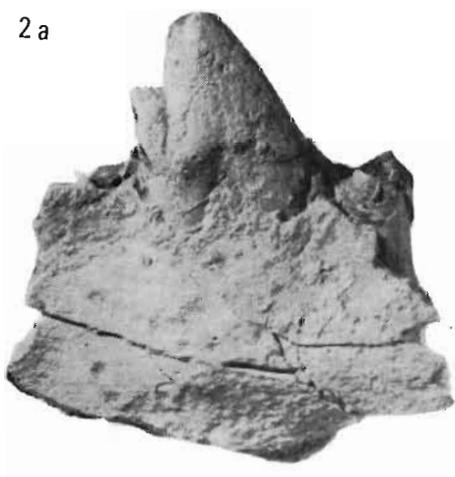
4b



1



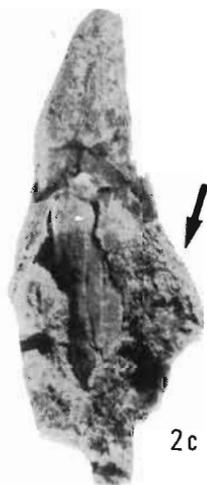
2a



2b



2c



3a



3b

