

LUCJAN SYCH

## LAGOMORPHA FROM THE OLIGOCENE OF MONGOLIA

(Plates LI-LIV)

*Abstract.* — A revision of the Asiatic species of *Desmatolagus* MATTHEW & GRANGER, *Agispelagus* ARGYROPULO and *Procaprolagus* GUREEV has been carried out on the basis of abundant remains collected from seven localities. A model of the dentition of Oligocene lagomorphs, based on four successive ontogenetic age groups distinguished in *Desmatolagus gobiensis*, is presented. Its application has made it possible to synonymize some species with the appropriate developmental stages of *D. gobiensis*.

### INTRODUCTION

More than dozen various species of lagomorphs have been described from the Oligocene of Asia. The remains known so far were collected by the successive American, Soviet and Polish-Mongolian expeditions in Mongolia, China and Kazakhstan. Out of the six Asiatic Oligocene genera — *Gobiolagus*, *Desmatolagus*, *Sinolagomys*, *Ochotonolagus*, *Agispelagus* and *Procaprolagus* — distinguished by different authors, the last three seem to be insatisfactorily defined. The *Desmatolagus* group of genera, marked by both ochotonid and leporid features, needs a special investigation on account of their peculiar tooth anatomy.

Lagomorph remains described in this paper were collected in the following Oligocene localities in Mongolia: Loh (Shand Gol = Hsanda Gol), Tatal Gol, Buylstyeen Khuduk, Ulan Ganga, Khatan Khayrkhan, Boongin Gol and Nareen Bulak. Particular data concerning the situation and geology of these localities are given by GRADZIŃSKI *et al.* (1968) and Kowalski (1973). The lagomorph remains collected from the Hsanda Gol Formation, locality of Loh are relatively abundant, because Loh has been explored several times by the Central Asiatic Expedition of the American Museum of Natural History (1922) and the Polish-Mongolian Expeditions (since 1963). The excavations made in the Tatal Gol region situated close to Loh, during the Palaeontological Expeditions to Mongolia of the USSR Academy of Sciences (1946-1949) and in the course of the Polish-Mongolian explorations mentioned above also gave, among other materials, numerous fairly well preserved lagomorph remains. The excavations in other Asiatic localities — Shargaltein near Taben-Buluk in Kansu, China (BOHLIN, 1942) and Agispe in Khazakhstan (ARGYROPULO, 1940) — provided several species of *Sinolagomys*, *Agispelagus* and *Desmatolagus*, of which some should be revised.

Lack of complete skeletons and, at least, well-preserved skulls and, on the other hand, the abundance of mandibles and maxillae have brought about the adoption of the only possible, special approach to the taxonomy of the fossil Lagomorpha. Since systematics cannot be

neglected in the present paper, it is based here on precise observations of tooth morphology and a detailed examination of the ontogenic changes of teeth. Attention is paid both to the evolutionary significance of various tooth structures and to the details of systematic divisions.

Abbreviations used in this paper:

- AMNH — American Museum of Natural History (New York).  
 PIN — Palaeontological Institute, USSR Academy of Sciences (Moscow).  
 ZPAL — Palaeozoological Institute, Polish Academy of Sciences (Warsaw).

#### ACKNOWLEDGMENTS

The author expresses thanks to Prof. ZOFIA KIELAN-JAWOROWSKA for allowing him the investigation of the lagomorph collection from the Gobi Desert being in the possession of the Palaeozoological Institute, Polish Academy of Sciences. He is also greatly indebted to Dr. MALCOLM C. MCKENNA for the long-term loan of the collection of Oligocene lagomorphs from Mongolia belonging to the American Museum of Natural History in New York.

## SYSTEMATICS AND DESCRIPTIONS

Family OCHOTONIDAE THOMAS, 1897

Genus DESMATOLAGUS MATTHEW & GRANGER, 1923

Syn.: PROCAPROLAGUS GUREEV, 1960

*Desmatolagus gobiensis* MATTHEW & GRANGER, 1923

(Pls LI-LIV)

1923. *Desmatolagus gobiensis* n.g., n.sp.; W. D. MATTHEW & W. GRANGER, p. 8, Text-figs 10.  
 1926. *Desmatolagus gobiensis*; TEILHARD DE CHARDIN, p. 23.  
 1926. *Desmatolagus pusillus* sp.n.; TEILHARD DE CHARDIN, p. 23, Text-fig. 12.  
 1926. *Desmatolagus radcidens* n.sp.; TEILHARD DE CHARDIN, p. 24, Text-fig. 13.  
 1937. *Desmatolagus gobiensis*; B. BOHLIN, pp. 17, 18.  
 1937. ? *Desmatolagus parvidens* sp.n.; B. BOHLIN, pp. 22, 23.  
 1937. *Desmatolagus shargaltensis* sp.n.; B. BOHLIN, pp. 18, 19.  
 1940. *Desmatolagus gobiensis*; A. E. WOOD, p. 345.  
 1941. *Desmatolagus gobiensis*; J. J. BURKE, pp. 14, 15, 16.  
 1942. *Desmatolagus gobiensis*; B. BOHLIN, p. 32.  
 1960. *Procaprolagus mongolicus*; A. A. GUREEV, pp. 18, 19, 20.  
 1960. *Procaprolagus orlovi*; A. A. GUREEV, pp. 20, 21, Text-fig. 8.  
 1960. *Procaprolagus vetustus*; A. A. GUREEV, pp. 17, 18.  
 1960. *Sinolagomys tatalgolicus* sp.n.; A. A. GUREEV, p. 9, Text-fig. 2.  
 1967. *Desmatolagus gobiensis*; M. R. DAWSON, p. 290.

**Material.** — Loh, Hsanda Gol Formation: 32 fragmentary right and left halves of maxillae with teeth partly preserved, 65 fragments of damaged right and left mandibles with teeth partly preserved (ZPAL MgM-III/79). Khatan Khayrkhan: 12 fragmentary right and left maxillae with teeth partly preserved, 22 fragments of right and left mandibles with teeth partly heavily damaged (ZPAL MgM-III/80). Tatal Gol, Hsanda Gol Formation, lower parts: 8 fragmentary right and left maxillae with teeth partly preserved, 14 fragments of right and left mandibles with teeth well preserved (ZPAL MgM-III/81). Tatal Gol, Hsanda Gol Formation, upper parts: 3 damaged halves of right and left maxillae, 5 heavily damaged right and left mandibles (ZPAL MgM-III/82). Boongeen Gol: a fragment of the left mandible with P<sub>3</sub>-M<sub>1</sub> well preserved, a right maxilla heavily damaged with P<sup>2</sup>-M<sup>1</sup> preserved (ZPAL

MgM-III/83). Ulan Ganga: 3 fragmentary mandibles with  $P_4$ - $M_2$  (ZPAL MgM-III/84). Nareen Bulak: 4 fragmentary mandibles without  $P_3$  and  $M_1$  (ZPAL MgM-III/85). Buylstyeen Khuduk: a part of damaged mandible with  $P_4$ - $M_1$  (ZPAL MgM-III/86).

**Description.** — Among the upper cheek teeth of the species of the *Desmatolagus* group  $P^4$ ,  $M^1$  and  $M^2$  are homogeneous in structure, differing in details of the occlusal and lingual surfaces according to the degree of wear. The shape of these teeth is characteristic, because in them the lingual part of the crown is hypsodont and the buccal part brachyodont with two cusps, an anterior and a posterior. The anterior cusp of  $P^4$  is always less prominent than the posterior one, this relation being reversed in  $M^1$  and  $M^2$ . Two roots, corresponding to these cusps, are very short as compared with the length of the rest of the tooth, hidden in the alveolus. The presence of the anterior and posterior cusps on the buccal side of each of these teeth and an enamel fold termed the hypostria, homologous to the hypostria of other lagomorphs, separating the anterior and posterior crown corners on the lingual side, induce the author to adopt the denominations anteroloph and posteroloph for the respective corners and adjoining crown portions. The hypostria is present only in young specimens and extends for hardly one-third of the tooth width. This fold becomes shallower with time and eventually disappears, so that the lingual side of the crown is flat and even gains some convexity. The transverse section of the tooth at this stage of development shows a certain tapering of the outline of the crown on the lingual side. This character has been used as one of the criteria of the division of specimens of this species into age groups. The inner part of the hypostria assumes the form of a thin "pipe", which branches off from the main fold and runs parallel to the margin of the tooth towards the alveolus. The farther inwards, the smaller is the diameter of the pipe, which finally disappears entirely (Pl. LI, Figs 1, 2). In the continually worn surface of the tooth the pipe appears as a rounded islet of enamel beside the shallower and shallower hypostria. The hypostria vanishes earlier than the pipe does, which leads to such a developmental stage of the tooth that its lingual portion of occlusal surface exhibits only the presence of the islet, whereas the hypostria itself is missing and the lingual outline of the tooth, as already mentioned above, bulging (more wedge-shaped).

Another structure which undergoes a modification on the occlusal surface is the so-called crescent (WOOD, 1940), positioned centrally on it (Pl. LI, Figs 1, 2). Its shape, like that of all other structures, has been restored on the basis of observations covering many stages of wear of the crown. The crescent is a paraboloidal structure, extending deep inwards, with its horns pointing in the direction of the buccal cusps on the occlusal surface. Its lingual rounded portion forms a ridge protruding above this surface. The crescent is surrounded with enamel and its inside is filled with dentine. As the crown wears, the anterior arm of the crescent disappears earlier than its posterior arm does, this being so especially on  $M^1$  and  $M^2$ . These teeth often show only the posterior part of the crescent, considerably narrowed, in the form of a long islet of enamel. On the molars the crescent disappears together with the islet of the pipe, while on  $P^4$  it persists longer. This is connected with the relatively early wear of the molars, which worked together with the deciduous premolars. The structure which interferes with the crescent in the course of wear are thin irregular enamel ridges, formed on the occlusal surface in the close vicinity of the buccal cusps. The cusps of the occlusal surface in this region of the teeth are covered with a thick layer of enamel in youth; this surface is somewhat wavy and, consequently, the wear of its enamel ridges results in the formation of characteristic grooves. Their shape is, however, of no taxonomic importance.

The growth rates of the lingual and buccal portions of  $P^4$ ,  $M^1$  and  $M^2$  are unequal. The buccal cusps, which have a limited power of growing but, on the other hand, are never exposed

to heavy abrasion, may have persisted unchanged for a long part of life. On the contrary, the lingual portion of each tooth grew continuously, especially as regards its height. The permanent growth of the lingual portion accompanied by its wear maintained the height of the crown constant. However, very old individuals, in which the balance of growth and abrasion was disturbed, had the lingual portions of these teeth distinctly lowered. Figuring to oneself the internal and external structures of  $P^4$ ,  $M^1$  and  $M^2$  described above, one should keep in mind that the model (Pl. LI, Fig. 1) illustrating their spatial relations represents not only the tooth at a juvenile stage of development, for such young tooth is considerably shorter than it might be judged from the figure. The model shows the mutual relations of the structures in such a manner, as if the growth of the tooth continued and the wear of the crown never existed. This sort of reconstruction of growth not only conveys an idea of the distribution of morphological details, but also makes it possible to compare them in different species and to divide specimens into age groups.

$P^2$  is clavate in shape and a part of its root projects remarkably above the alveolus, the root being open. The crown consists of three lobes, unequal in size, separated from each other only partly by two enamel folds, which squeeze in from the anterior side. The buccal lobe is smaller than the other ones (Pl. LIV, Fig. 3). Young  $P^3$ , with its crown unworn, is also trilobate in shape. Its wear, however, uncovers a tortuous fold of enamel, pressed in from the front towards the back and turning buccal (Pl. IVL, Fig. 3). The postero-buccal region of the crown has a cuspidal bulge, corresponding to the posterior cusp of  $P^4$ ,  $M^1$  and  $M^2$ , but no small buccal root under it, the tooth being hypsodont in this part. The only root of  $P^3$ , thin and long, grows out of the crown on the anterobuccal side, where there is a fold corresponding to the crescent of the other upper cheek teeth. Very few specimens of  $M^3$  preserved complete are fine and clubshaped, with an elliptic occlusal surface and one open root.

The above-mentioned division of specimens of *Desmatolagus gobiensis* with their upper dentition preserved into relative age groups has been based on the following criteria:

group I — hypostria present at least on  $M^2$ , sometimes also on  $M^1$ ,

group II — hypostria absent from  $M^1$  and  $M^2$ , instead there is an indentation of the upper portion of the lingual wall of these teeth,

group III — the lingual portion of the wall of  $M^2$  and  $M^1$  and sometimes also of  $P^4$  is distinctly bulged lingual, having a wedgeshaped outline in its transverse section and on the occlusal surface (Pl. LI, Fig. 2), and

group IV — the morphological details of the occlusal surface of  $M^1$  and  $M^2$  are destroyed, the lingual portion of this surface being worn nearly to the border of the alveolus.

Although the teeth of the lower row:  $P_4$ ,  $M_1$  and  $M_2$  seem to be utterly hypsodont, they consist of a crown part and a root part. The crown is very high, composed of a trigonid and a talonid, the junction of which into a whole is hidden in the alveolus on the buccal side in young specimens. As the time passes the junction emerges from the alveolus. In old specimens the place of separation of the roots appears above the alveolus (Pl. LIII, Fig. 3). Each of these teeth has two roots, of which the anterior is the extension of the trigonid and the posterior the extension of the talonid. The two roots do not lie exactly in the same plane, their free ends diverge somewhat. The trigonid is higher than the talonid. On the posterior wall of the trigonid of  $P_4$ , just close to the occlusal surface, there is a small bulge of enamel turned backwards, towards the talonid. It is less distinct on  $M_1$  and only vestigial or missing completely on  $M_2$ . This bulge, so far unnamed, occurs in the form of a vestige in very many species of fossil lagomorphs. It is a remnant of a structure, the discovery of which in its original unreduced form would throw more light on the evolution of the dentition of this group. The

talonid of young specimens has an enamel fold filled with cement on the postero-lingual side (Pl. LII, Fig. 1). This fold extends from the occlusal surface, where it is widest, sometimes as far as halfway down the part of the tooth projecting above the alveolus. As the tooth wears, the fold becomes shallower and shallower and eventually disappears. The disappearance occurs almost simultaneously in all the three teeth, sporadically a trace of the fold can be observed only on  $M_2$ .

In the mandible  $P_4$ ,  $M_1$ ,  $M_2$  and partly also  $M_3$  show great similarity in structure, just as in the maxilla  $P^4$ ,  $M^1$  and  $M^2$  are characterized by its great homogeneity. The crown of  $M_3$  also divides into the trigonid and the talonid, but their surfaces of wear lie in nearly the same plane. The division of this tooth into the crown and root is much more distinct, because the junction of the talonid and trigonid is nearly always situated high above the alveolus. There are exceptional specimens (e.g. ZPAL MgM-III/79/43), in which the talonid is markedly lowered and, owing to atypical occlusion, unworn. The upper portion of the root of  $M_3$  protrudes partly beyond the alveolus in occasional specimens (Pl. LIII, Fig. 1).

The first tooth of the row,  $P_3$ , differs in shape and size from the other ones. Buccally its crown is partly divided by a fold of enamel, which runs from the occlusal surface downwards and disappears halfway down the tooth. The occlusal surface is generally in the form of a triangle with its corners rounded, which shape is, however, rather variable. The alveolus of  $P_3$  is much lowered on the diastema side so that a large part of the anterior wall of this tooth is uncovered (Pl. LII, Fig. 3). About 30 per cent of the  $P_3$  specimens observed have an additional small enamel fold, which begins about halfway up this wall, above the alveolus. As the tooth grows, the fold comes nearer the occlusal surface.

The division of the mandibles into four age groups has been based on the following characters of  $P_4$ ,  $M_1$  and  $M_2$ :

group I — the posterior fold of the talonid well hidden and the junction of the talonid and trigonid concealed in the alveolus;

group II — the posterior fold of the talonid missing or at the most in the form of a trace on  $M_2$  and the junction of the talonid and trigonid visible at the border of the alveolus;

group III — the junction of the trigonid and talonid well seen above the alveolus, the roots completely hidden in it;

group IV — the junction of the trigonid and talonid close to the occlusal surface, the outline of the upper portion of the roots visible above the alveolus.

The lower incisors are massive and chisel-shaped, their posterior end reaching the anterior border of the roots of  $M_2$  in adult specimens. There are no extant upper incisors in the material under description.

Parts of the palatines are preserved only in some of the specimens. In the specimen MgM-III/79/83 the arch of the choanal opening turns between  $M^1$  and  $M^2$ . The size of this opening, nowhere preserved whole, can be estimated on the basis of the details of the specimen MgM-III/79/85. It was comparatively narrow, in general outlines resembling somewhat the corresponding opening in modern *Oryctolagus cuniculus*. The maxillae are heavily fenestrated and, in addition, there is a fairly deep foramen of nondescript homology. Other two small maxillopalatine openings are situated at the height of  $P^4$ . A third small opening lies medially to  $P^3$ , being sometimes displaced backward or forward. The zygomatic arch is fine in structure, its anterior base, seen from the palatal side, is placed between  $P^3$  and  $P^4$ . The incisive foramen is heart-shaped and extends backward to the posterior border of  $P^3$ .

The masseteric fossa stands out against the remaining lateral surface of the mandible. The anterior border of this fossa lies in the region of the middle of  $M_2$  or somewhat to the

front. Anteriorly the fossa ends in a tuberosity (Pl. LII, Fig. 3), which in some specimens is quite conspicuous (e.g. MgM-III/81/11, MgM-III/81/17, MgM-III/79/95 and MgM-III/79/86). The mental foramen is generally situated just in front of P<sub>3</sub>, in the lateral aspect of the mandible. In some specimens (e.g. MgM-III/82/8) it lies closer to the border of the diastema.

The division of the portion of material of *D. gobiensis* in which I distinguish age groups (I-IV) on the basis of the criteria given above is as follows:

### Loh

maxillae:	mandibles:
I — ZPAL MgM-III/79: 1, 2, 4, 9, 33, 38, 98;	I — ZPAL MgM-III/79: 21, 22, 25, 31, 32, 43, 54, 55, 59, 64, 75, 77, 79, 86, 88, 99;
II — ZPAL MgM-III/79: 14, 15, 30, 51, 62, 72, 83, 84, 85;	II — ZPAL MgM-III/79: 23, 24, 27, 40, 60, 61, 87, 94, 95, 96, 102;
III — ZPAL MgM-III/79: 6, 10, 12, 41, 48, 56, 81, 82, 100;	III — ZPAL MgM-III/79: 26, 28, 29, 34, 37, 39, 42, 45, 46, 49, 63, 65, 68, 69, 70, 73, 74, 76, 80, 91, 92, 93, 97, 101;
IV — ZPAL MgM-III/79: 13, 78.	IV — ZPAL MgM-III/79: 36, 44, 50, 57, 67.

### Khatan Khayrkhan

maxillae:	mandibles:
I — ZPAL MgM-III/80: 10;	I — ZPAL MgM-III/80: 19, 20, 23, 35;
II — ZPAL MgM-III/80: 8, 11, 12, 16;	II — ZPAL MgM-III/80: 1, 2, 4, 5, 6, 7, 21, 25, 30, 36, 37;
III — ZPAL MgM-III/80: 14, 15, 38;	III — ZPAL MgM-III/80: 27, 29, 33, 39;
IV — no specimens.	IV — ZPAL MgM-III/80: 3.

### Tatal Gol (lower beds)

maxillae:	mandibles:
I — ZPAL MgM-III/81: 12;	I — ZPAL MgM-III/81: 3, 11, 20;
II — ZPAL MgM-III/81: 8;	II — ZPAL MgM-III/81: 1, 4, 16, 17, 18;
III — no specimens;	III — ZPAL MgM-III/81: 5, 9, 14, 15, 21;
IV — no specimens.	IV — ZPAL MgM-III/81: 2.

### Tatal Gol (upper beds)

maxillae:	mandibles:
I — no specimens;	I, II — no specimens;
II — ZPAL MgM-III/82: 3;	III — ZPAL MgM-III/82: 4, 6, 7, 8;
III — ZPAL MgM-III/82: 2;	IV — no specimens.
IV — no specimens.	

### Boongeen Gol

maxillae:	mandibles:
I — no specimens;	I — ZPAL MgM-III/83: 1;
II — ZPAL MgM-III/83: 2;	II, III, IV — no specimens.
III, IV — no specimens.	

### Ulan Ganga

maxillae — no specimens;
mandibles:
I — no specimens;
II — ZPAL MgM-III/84: 1, 2;
III, IV — no specimens.

### Nareen Bulak

maxillae — no specimens;
mandibles:
I — no specimens;
II — ZPAL MgM-III/85: 2, 3;
III — ZPAL MgM-III/85: 4, 7;
IV — no specimens.

**Buylstyeen Khuduk**

maxillae:

- I — no specimens;  
 II — ZPAL MgM-III/86: 3;  
 III, IV — no specimens.

The measurements of the teeth of *D. gobiensis* in particular age groups and their fundamental statistical analysis are given in Tables 1 and 2. The measuring points were treated as extremes. It was impracticable to measure other parts of the skull than teeth because of the fragmentary state and variation of the material (see Discussion, p. 75). It is, besides, difficult to draw comparisons between the skull measurements now obtained and the data published by other writers, since their definitions of the measuring points are unsatisfactory. The tooth-row lengths compared by different authors caused many classificatory misunderstandings in the group *Desmatolagus*, which shows a large amount of variation in size. Some species of the genus *Desmatolagus* were described only on the basis of the lengths of the tooth-row and lower diastema, which, however, change with age.

***Desmatolagus robustus* MATTHEW & GRANGER, 1923**

(Pls LIII, LIV)

1923. *Desmatolagus robustus* sp.n.; W. D. MATTHEW & W. GRANGER, p. 10, Text-figs 11, 12.  
 1926. *Desmatolagus robustus*; TEILHARD DE CHARDIN, p. 23.  
 1937. *Desmatolagus ? robustus*, ? *Desmatolagus robustus*; B. BOHLIN, pp. 63, 64.  
 1941. *Desmatolagus robustus*; J. J. BURKE, pp. 16-22.  
 1942. *Desmatolagus robustus*; B. BOHLIN, p. 70.  
 1960. *Agispelagus youngi* sp.n.; A. A. GUREEV, p. 27, Text-fig. 11.  
 1960. *Procaprolagus maximus* sp.n.; A. A. GUREEV, p. 22.  
 1960. *Desmatolagus robustus*; A. A. GUREEV, p. 14, Text-figs 5a, b, w, g.  
 1967. *Desmatolagus robustus*; M. R. DAWSON, p. 290.

**Material.** — Loh, Hsanda Gol Formation: 7 heavily damaged fragmentary mandibles with some teeth preserved (ZPAL MgM-III/87:1, 3, 4, 6, 7, 8, 9), 2 fragmentary maxillae with partial dentition (ZPAL MgM-III/87:2 and 5).

**Description.** — The paucity of material did not permit the distinction of different developmental stages of the dentition, which was possible in the case of *D. gobiensis*. The specimen ZPAL MgM-III/87/2 has P<sup>3</sup>, P<sup>4</sup> and M<sup>1</sup> preserved. The enamel pattern on the occlusal surface of all the three teeth is worn away to a very great degree, so that not only the hypostria has disappeared from M<sup>1</sup> and P<sup>4</sup> but, what is more, the outline in its place on the lingual side on both these teeth tapers characteristically. Traces of the crescents appear in the form of thin elongate ridges of enamel, which are besides very hard to distinguish from the surrounding dentine. Neither are there any traces left by the pipe. The buccal cusps are reduced by wear to less than half their height. The presence of the buccal roots corresponding to the buccal cusps is characteristic. The anterior base of the zygomatic arch being damaged, the anterior buccal root of P<sup>4</sup> is particularly well seen. The lingual parts of P<sup>3</sup>-M<sup>1</sup> possess a thick root of hypsodont type. The specimens under description belonged to a very old individual, in which the degree of wear probably corresponded to that in group IV of *D. gobiensis*, very advanced in age. The lingual portions of the occlusal surfaces are much more worn than they are in the most heavily worn specimens of the previous species (Pl. LIV, Fig. 2). Owing to

Table 1

Measurements of upper teeth of *Desmatolagus gobiensis* (in mm)

		I			II			III		
		M	N	s	M	N	s	M	N	s
P <sup>1</sup>	1. Length	1.03±0.24	6	0.60±0.17	1.21±0.24	13	0.89±0.17	1.26±0.18	13	0.66±0.12
	2. Width	1.93±0.45	6	1.11±0.32	2.48±0.31	13	1.13±0.22	2.96±0.42	13	1.55±0.30
P <sup>4</sup>	1. Length	1.68±0.18	8	0.52±0.13	1.75±0.12	13	0.44±0.08	1.77±0.09	13	0.34±0.06
	3. Anteroloph width	2.76±0.24	8	0.69±0.17	3.38±0.31	13	1.13±0.22	3.72±0.40	12	1.41±0.28
	4. Posteroloph width	2.73±0.21	8	0.60±0.15	3.34±0.29	13	1.07±0.20	3.56±0.55	12	1.91±0.38
	5. Minimal width	2.51±0.28	8	0.81±0.20	3.17±0.34	13	1.24±0.24	3.49±0.42	12	1.48±0.30
M <sup>1</sup>	1. Length	1.49±0.13	8	0.37±0.09	1.52±0.13	13	0.48±0.09	1.54±0.08	13	0.30±0.50
	3. Anteroloph width	2.89±0.30	8	0.85±0.21	3.41±0.39	12	1.37±0.27	3.60±0.38	12	1.32±0.26
	4. Posteroloph width	2.50±0.17	8	0.50±0.12	2.97±0.33	12	1.17±0.23	3.23±0.34	12	1.20±0.24
	5. Minimal width	2.34±0.28	8	0.82±0.20	3.05±0.41	12	1.43±0.29	3.31±0.40	12	1.39±0.28
M <sup>2</sup>	1. Length	1.35±0.06	6	0.17±0.04	1.39±0.12	10	0.39±0.08	1.38±0.07	10	0.25±0.05
	3. Anteroloph width	2.58±0.28	6	0.71±0.20	2.95±0.22	10	0.72±0.16	3.10±0.33	10	1.07±0.23
	4. Posteroloph width	2.10±0.20	6	0.51±0.14	2.48±0.29	10	0.93±0.20	2.55±0.32	9	1.02±0.22
	5. Minimal width	1.67±0.17	6	0.43±0.12	2.50±0.33	10	1.06±0.23	2.72±0.39	10	1.25±0.27

Explanations of symbols: M — arithmetic mean  
s — standard deviation  
N — number of specimens  
I, II, III — age groups

Table 2

Measurements of lower teeth of *Desmatolagus gobiensis* (in mm)

		I			II			III			IV		
		M	N	s	M	N	s	M	N	s	M	N	s
P <sub>4</sub>	1. Length	0.92±0.20	12	0.70±0.14	1.09±0.09	14	0.35±0.06	1.17±0.17	18	0.75±0.12	1.23±0.13	5	0.30±0.09
	2. Width	1.25±0.24	12	0.85±0.17	1.42±0.12	14	0.48±0.09	1.48±0.12	18	0.54±0.09	1.31±0.16	5	0.38±0.12
P <sub>4</sub>	1. Length	1.83±0.17	21	0.79±0.12	1.99±0.14	28	0.78±0.10	2.04±0.12	31	0.69±0.08	2.03±0.10	6	0.25±0.07
	2. Trigonid width	1.89±0.19	20	0.89±0.14	2.10±0.13	28	0.71±0.09	2.16±0.20	30	1.15±0.14	2.37±0.17	6	0.42±0.12
	3. Talonid width	1.34±0.13	21	0.61±0.09	1.36±0.10	28	0.55±0.07	1.35±0.11	31	0.66±0.08	1.33±0.05	5	0.13±0.04
M <sub>1</sub>	1. Length	1.84±0.17	21	0.80±0.12	1.90±0.11	31	0.62±0.07	1.91±0.16	31	0.90±0.11	1.88±0.10	5	0.24±0.07
	2. Trigonid width	1.99±0.16	21	0.75±0.11	2.13±0.16	26	0.83±0.11	2.11±0.14	27	0.75±0.10	2.22±0.15	5	0.34±0.10
	3. Talonid width	1.40±0.12	21	0.59±0.09	1.37±0.10	28	0.56±0.07	1.38±0.12	29	0.68±0.08	1.39±0.15	4	0.30±0.10
M <sub>2</sub>	1. Length	1.91±0.15	18	0.65±0.10	1.93±0.12	25	0.60±0.08	1.98±0.15	31	0.87±0.11	1.85±0.07	4	0.14±0.04
	2. Trigonid width	1.93±0.22	18	0.94±0.15	2.14±0.12	21	0.57±0.08	2.15±0.16	27	0.87±0.11	2.30±0.11	4	0.22±0.07
	3. Talonid width	1.37±0.09	17	0.38±0.06	1.34±0.07	24	0.37±0.05	1.37±0.09	31	0.54±0.06	1.29±0.13	4	0.26±0.09
M <sub>3</sub>	1. Length				0.80±0.12	7	0.33±0.08	0.87±0.08	12	0.31±0.06			
	2. Trigonid width				0.95±0.13	6	0.34±0.09	1.09±0.20	13	0.73±0.14			
	3. Talonid width							0.71±0.07	7	0.19±0.05			

Explanations of symbols: M — arithmetic mean  
s — standard deviation  
N — number of specimens  
I, II, III, IV — age groups

the constant growth of the lingual parts of the teeth (presumably lifelong) and strenuous attrition exercised by the lower P and M, mainly in their lingual regions, the occlusal surfaces of P<sup>4</sup> and M<sup>1</sup> are very strongly elongated transversely, which gives these teeth a shape unseen in other species.

The specimen ZPAL MgM-III/87/5, in which the only extant teeth are P<sup>3</sup> and P<sup>4</sup>, provides a somewhat different picture. Although the buccal cusp is here damaged, the crescent is very distinct. A small indentation of enamel can be seen instead of the hypostria on the lingual side. Damaged P<sup>3</sup>, as can be easily pointed out, was a broad tooth. Its preserved anterior fold of enamel is very deep. The relative individual age of this specimen seems to correspond to age group III of *D. gobiensis*. P<sup>2</sup> of the specimen ZPAL MgM-III/87/10 has its crown part three-lobed, and its root, already partly visible above the border of the alveolus, is single, hypsodont, open at the end (Pl. LV, Fig. 1). P<sup>3</sup> of this specimen, considerably worn, has the small antero-buccal root somewhat uncovered. The anterobuccal cusp is, as that in *D. gobiensis*, reduced.

The lower teeth of the P<sub>4</sub>-M<sub>2</sub> group distinguish themselves by the lack of the posterior fold on the talonid (Pl. LIII, Fig. 2). It may well be that this fold existed in a reduced form in very young individuals, for among the above-mentioned specimens of *D. robustus* there were no specimens of developmental stages corresponding to groups I and II of *D. gobiensis*. The junction of the trigonid and talonid in the specimens ZPAL MgM-III/87/6, 7, 8 and 9 is usually situated high above the alveolus. The bulging of the posterior wall of the trigonid is very distinct on P<sub>4</sub> (specimens ZPAL MgM-III/87/1, 3, 4, 6, 7 and 8), on the other teeth it is quite missing. In the specimen ZPAL MgM-III/87/7 the upper portions of the roots of P<sub>4</sub> and M<sub>1</sub> are visible above the borders of the alveoli, which permits the determination of the age of this specimen in the approximation as corresponding to the transition between groups III and IV of *D. gobiensis*.

P<sub>3</sub> of the specimens ZPAL MgM-III/87/3, 6 and 9 has a very high triangular crown with rounded corners and a shallow buccal fold characteristic of all P<sub>3</sub> of the group *Desmatolagus* (Pl. LIII, Fig. 2). Here, too, the root part can be seen above the alveolus. M<sub>3</sub>, well-preserved in the specimen ZPAL MgM-III/87/9, has a crown in which the occlusal surfaces of the talonid and trigonid lie in the same plane. A high degree of wear of this tooth is manifested by the effacement of the boundary between the trigonid and talonid on the occlusal surface and the presence of only a small indentation of enamel marking the division of the crown into two parts. The single root of M<sub>3</sub> is seen to about the middle of its length above the alveolus and shows a bend towards the back of the mandible.

Table 3

Measurements of upper teeth of *Desmatolagus robustus* (in mm)

	Specimens: 87/10		87/2		87/2	
P <sup>1</sup>	1. Length	0.84		M <sup>1</sup>	1. Length	1.89
	2. Width	1.44			3. Anteroloph width	6.61
P <sup>3</sup>	1. Length	1.94	2.38		4. Posteroloph width	6.16
	2. Width	5.00	5.40		5. Minimal width	6.30
P <sup>4</sup>	1. Length	2.45	2.57			
	3. Anteroloph width	7.50				
	4. Posteroloph width	7.64				
	5. Minimal width	7.30				

Table 4

Measurements of lower teeth of *Desmatolagus robustus* (in mm)

		Specimens:	88/1	87/3	87/4	87/6	87/7	87/8	87/9
P <sub>3</sub>	1. Length			1.82		1.53			1.43
	2. Width			2.28		2.06			1.70
P <sub>4</sub>	1. Length		2.94	2.99	3.00	3.00	2.67	3.14	2.70
	2. Trigonid width		2.63	3.20	2.97	3.05	3.04	3.30	2.90
	3. Talonid width		1.62	1.94	1.62	1.82	1.91	1.96	1.76
M <sub>1</sub>	1. Length		2.66	2.61			2.42	2.64	2.47
	2. Trigonid width			3.10			2.78	3.02	2.68
	3. Talonid width		1.64	1.68			1.80	1.73	1.74
M <sub>2</sub>	1. Length						2.56		2.72
	2. Trigonid width						2.83		2.80
	3. Talonid width						1.75		1.66
M <sub>3</sub>	1. Length								0.97
	2. Trigonid width								1.15
	3. Talonid width								

The anterior border of the masseteric fossa lies in the region of M<sub>2</sub> (Pl. LIV, Fig. 3), the fossa is deep but lacks a tuberosity which is well developed and closes it from in front in *D. gobiensis*. The mental foramen lies in the region of P<sub>4</sub>, less than halfway up the lateral wall of the mandible.

The lower diastema is proportionally longer than in *D. gobiensis*. It is approximately as long as the tooth-row measured over the occlusal surface. The specimen ZPAL MgM-III/87/10 has the anterior margin of the palatal bridge on the right side partly preserved. Thus, the posterior edge of the incisive foramen is here visible. It extends to the middle of P<sup>2</sup>. The measurements of the dentition of *D. robustus* are given in Tables 3 and 4. The measuring points are treated as extremes.

## DISCUSSION

In the light of the present knowledge of the Oligocene forms of the Lagomorpha from Asia the following two problems seem to be worth while considering here: 1. the systematic relation of the species here described to the other forms of the same period in Asia and 2. the morphological variation of the group *Desmatolagus* and its relation to the Ochotonidae and Leporidae.

The model of a constantly growing and unworn tooth, such as the "synthetic PM" is, reconstructed from different developmental stages of middle premolars and molars, applies, somewhat modified, to all the Oligocene and Miocene lagomorph species. Its evolutionary significance will be dealt with in a separate paper. Only these characters will be discussed here which permit comparisons of the species and genera named below.

*Relationships of D. gobiensis and D. robustus to other species of this genus.* — The genus *Desmatolagus* MATTHEW & GRANGER 1923 has hitherto contained the following species: *D. robustus* MATTHEW & GRANGER 1923, *D. gobiensis* MATTHEW & GRANGER 1923 (localities

are mentioned at the beginning of this paper), *D. pusillus* TEILHARD DE CHARDIN 1926 (Saint Jacques, San-too-ho region, China), *D. radicens* TEILHARD DE CHARDIN 1926 (same locality, China), *D. vetustus* BURKE 1941 (Ulan Gochu, Mongolia), *D. ardynense* BURKE 1941 (Ardyn Obo, Mongolia), *D. shargaltensis* BOHLIN 1937 (Shargaltein, Kansu), ?*Desmatolagus parvidens* BOHLIN 1937 (same locality), and two species from North America: *D. dicei* BURKE 1936 and *D. gazini* BURKE 1936, whose systematic membership in the genus *Desmatolagus* was often called in question (among others, WOOD, 1941; DAWSON, 1967). Investigators did not generally give attention to the ontogenetic changes in the permanent teeth of the Lagomorpha, the descriptions and considerations on deciduous teeth excepting. A closer analysis of the dentition of the species here described has shown that it is expedient to synonymize some of the species of the genus *Desmatolagus*.

Thus, according to the description of *D. radicens* given by TEILHARD DE CHARDIN (1926) the characters in which this species differs from the other ones are its somewhat larger measurements ( $P_4$ - $M_2$  length is about 6 mm), the presence of two coalesced roots and lack of the posterior fold on the talonid in  $M_3$ , and on account of the presence of roots the impermanence of the growth of the cheek teeth. A comparison with the corresponding characters of *D. gobiensis* has revealed that the  $P_4$ - $M_2$  length lies well within the limits of the length of this section of the tooth-row in groups III and IV of *D. gobiensis* (5.91 mm). The lack of the posterior fold on the talonid characterizes groups III and IV of this last species and the presence of the roots emerging above the alveolus in a later period of life (groups III and IV) is a typical character of all lagomorphs of the Oligocene. The uniformity of the two species in respect of the characters mentioned justifies the recognition of *D. radicens* as synonymous with *D. gobiensis*.

*D. parvidens* BOHLIN 1937 has been described from Shargaltein, Kansu (type Sh. 723), on the basis of a fragmentary right maxilla with  $DP^4$ ,  $P^4$  and  $M^1$ . The occlusal surface of  $P^4$  has been uncovered. The permanent teeth have characteristic short roots corresponding to the buccal cusps. As can be seen from an illustration (BOHLIN, 1937, p. 23, Text-fig. 22), the tip of the main root of  $M^1$  appears on the opposite surface of the maxillary just as it does in *D. gobiensis*. The occlusal surface of  $P^4$  of *D. parvidens* has the same morphological details as those in the specimens of *D. gobiensis* of age group I, they differ only in the degree of wear. The author did not give the measurements of *D. parvidens*, confining himself to the statement that  $P^4$  of his species is considerably smaller than it is in *D. gobiensis* and *D. shargaltensis*. The measurements of the upper premolars change markedly in particular age groups of *D. gobiensis*. As will be seen from the description of *D. gobiensis* given by BOHLIN, the specimens of this species may be included in groups II and III adopted by me. It seems natural that *D. parvidens*, having the smallest measurements of the three possibilities discussed, may be regarded as a young stage of *D. gobiensis*.

*D. shargaltensis* BOHLIN 1937 has been described on the basis of the specimen Sh. 771, which is a fragmentary maxilla with  $P^4$ - $M^2$ . As its illustration (BOHLIN, 1937, p. 18, Text-fig. 15) shows, it has a dentition the wear of which corresponds to the developmental stage of group I of *D. gobiensis* or still younger one, for the hypostria exists both on  $M^2$ ,  $M^1$  and, in a vestigial form, on  $P^4$ , the crescent is very distinct on  $P^4$  and  $M^1$ , and the buccal cusps are partly preserved. Moreover, the author writes that this specimen is much smaller than the specimens of *D. gobiensis* known to him. The uncovered buccal roots of the teeth in specimen No. 771 have the same shape as the roots of *D. gobiensis*. As there are no other characters differentiating the specimen of *D. shargaltensis* from *D. gobiensis*, it should be regarded as a young developmental stage of this last species and the name *D. shargaltensis* as a synonym of *D. gobiensis*.

The remaining Asiatic species of the genus *Desmatolagus*, *D. ardynense*, *D. vetustus* and *D. pusillus*, whose descriptions compared with those of the species here presented comprise actual characters in which they differ from the other species, must be recognized as species distinct from *D. gobiensis*.

*Relationships of D. gobiensis and D. robustus to other genera.* — In 1940 ARGYROPULO described a new lagomorph species, *Agispelagus simplex*, from the layers of the Lower Miocene (regarded as the Upper Oligocene by GUREEV) at Agispe in Kazakhstan. In the genus *Agispelagus* GUREEV (1960) included nine specimens of lagomorphs from the Oligocene of Tatal Gol (designated as the series PIN 475-1974) and described the species *Agispelagus youngi* GUREEV 1961. If the diagnostic characters of the genus and species *A. simplex* seem to differentiate this form fairly well from the other Oligocene and Miocene lagomorphs, the reality of GUREEV'S species may be questioned because of the striking agreement of its characters with the corresponding characters of *D. robustus*. Thus the talonids of  $P_4-M_2$  have no posterior fold at all both in GUREEV'S species and in *D. robustus*. Its lack is not caused by their individual age, for the type specimens, illustrated by GUREEV, belonged to relatively young specimens. This is well seen from PIN 475-1974 (GUREEV, 1960, p. 28, Fig. 11b, w), in which the trigonid-talonid junctions in  $P_4-M_2$  are visible at the border of the alveoli. The specimen PIN-1973, whose upper teeth  $P^3-M^2$  are shown in Fig. 11a (l. c.), has the crescent preserved on  $P^4-M^2$  and the hypostria on  $M^2$  and  $M^1$ , which would indicate its relatively little advanced age. The morphological details of the crowns of  $P^3$ ,  $P^4$  and  $M^1$  in these specimens well agree with the details in *D. robustus* (ZPAL MgM-III/87/2 and 5). The mandible height at  $M_3$  is 10.4 mm and 11.6 mm in GUREEV'S specimens and 10.9 mm in ZPAL MgM-III/87/9. The length of the lower tooth-row in the specimens of *A. simplex* is 12.2 and 12.8 mm and in ZPAL MgM-III/87/9 — 11.9 mm. The coincidence of the measurements and characters of the specimens under comparison leads to the inference that *Agispelagus youngi* is a synonym of *D. robustus*.

A similar situation emerged, when the species *Sinolagomys tatalgolicus* GUREEV 1960 has been described on the basis of five fragmentary mandibles from the Oligocene layers at Tatal Gol. I acknowledge this species included in the genus *Sinolagomys* BOHLIN 1937, comprising three other Late Oligocene species, *Sinolagomys kansuensis* BOHLIN 1937, *Sinolagomys major* BOHLIN 1937 and *Sinolagomys gracilis* BOHLIN 1942, known from the material from Kansu, as a synonym of *Desmatolagus gobiensis* for the following reasons: 1. the concurrence of measurements (the mandible height at  $M_3$  ranges in age groups III and IV of *D. gobiensis* from 7.3 to 8.5 mm and in *S. tatalgolicus* from 7.6 to 8.6 mm, and their alveolar lengths of the lower toothrow differ by 0.4 mm), 2. the agreement of the structural details and wear of crowns in the lower teeth of *D. gobiensis* from age groups III and IV with the corresponding characters of *S. tatalgolicus*, and 3. the complete want of knowledge of the upper dentition of *S. tatalgolicus*, which would be essential to the assertion of the unquestionable membership of GUREEV'S species in the genus *Sinolagomys*. The remaining species of *Sinolagomys* are readily distinguishable from the other Oligocene forms from Asia.

The next systematic question calling for an explanation is the relationship of the species of the genus *Procaprolagus* GUREEV 1960 to *D. gobiensis* and *D. robustus*. The genus *Procaprolagus* has been described on the basis of the species *Desmatolagus vetustus* BURKE 1941, found in the Oligocene formations of Ulan Gochu in Mongolia (type specimen: AMNH 26089). In the genus *Procaprolagus* its author placed also three other species, *Procaprolagus mongolicus* GUREEV 1960, *Procaprolagus orlovi* GUREEV 1960 and *Procaprolagus maximus* GUREEV 1960. According to the data given by this author (1960), the difference between the first two species

would concern their size: in his opinion, *P. orlovi* has its mandible more massive, the bend in the diastema smaller and the diastema length greater than the respective details in *P. mongolicus*. The illustrations presenting the lateral aspect of the mandibles in the type specimens of these species (GUREEV, 1960, Figs 7w and 8w) deny this statement, for they show that anyhow the curvature of the diastema is greater in *P. orlovi* than in *P. mongolicus* and the length of the diastema, after both drawings have been reduced to the same scale, is practically the same size or even smaller in *P. orlovi*. In *P. mongolicus* the lower tooth-row of the type specimen (PIN 475-3138), in Fig. 7b (GUREEV, 1960) magnified five times, is larger than the lower tooth-row of the type specimen of *P. orlovi* (PIN 475-3134) drawn to the same scale in Fig. 8d (*l. c.*). Omitting details concerning the measurements of these teeth, we ought to pay special attention to the fact that the  $M_3$  teeth of the type specimens in the illustrations (*l. c.*, Figs 7b and 8b) differ considerably in the shape of talonid, which fact is not mentioned in the text. The shape of  $P_3$  in *P. mongolicus* is probably still another example of the great variability of this tooth observed in specimens of the species belonging to *Desmatolagus* in the collections of both ZPAL and AMNH. Thus, there are no evident reasons for treating *P. mongolicus* and *P. orlovi* as separate species. Furthermore, their comparison with the specimens of groups III and IV of *D. gobiensis* shows that neither the hypostria nor the indentation of the lingual walls of  $P^4-M^2$  exists on the specimens from PIN and that the crescent has disappeared from  $M^2$  and left merely a trace  $P^4$ . Such stage of wear would correspond to an intermediate age between groups III and IV of *D. gobiensis*. The talonids of lower  $P_4-M_2$  lack posterior folds and the junctions of trigonids and talonids on these teeth and on  $P_3$  occur well above the borders of the alveoli. The presentation of the junctions of trigonids with talonids in illustration 8b (GUREEV, 1960) is probably a fault in illustration and observation, because the specimens of the series PIN 475-3134 recognized as *P. orlovi*, known to me from autopsy, have not such junctions, very much besides, like *P. mongolicus* presented in BURKE's illustration of *D. vetustus* (BURKE, 1941, Pl. 16, Fig. 8). The alveolar lengths of the lower tooth-rows of *P. mongolicus* and *P. orlovi* practically do not differ from each other according to GUREEV's data (they are respectively 9.3-10.4 mm and 9.1-10.2 mm) and are larger than the corresponding measurements in *D. gobiensis* from groups III and IV on the average by only 0.68 mm. The foregoing comparisons encourage me to synonymize *P. orlovi* and *P. mongolicus* with *D. gobiensis*.

On the basis of the following characters of *Procaprolagus maximus* GUREEV 1960 from Tatal Gol I synonymize it with *D. robustus*: 1. lack of the posterior folds of the talonids on  $P_4-M_2$  in spite of the relatively unadvanced age of the individual, evidenced by the concealment of the root portions of these teeth in the alveoli; 2. lack of the tuberosity which closes the masseteric fossa. To be sure, the length of the lower tooth-row of *P. maximus* is 1.1 mm greater than that of *D. robustus*, which is a fairly marked difference. It may be explained by the very great individual variation of the species of the group *Desmatolagus*. The very small total number of the specimens collected makes it difficult to estimate the range of variation of this species.

The existence of the genus *Ochotonolagus* GUREEV 1960 with its single species *Ochotonolagus argyropuloi* 1960, described on the basis of a fragment of right and left mandibles from the Oligocene of Tatal Gol (PIN 475-480), as the only material the author had at his disposal, seems to be rather doubtful. Its systematic position remains an open question.

*Relationships of Desmatolagus to the Ochotonidae and Leporidae.* — Writing that *Desmatolagus* "is placed in Leporidae provisionally upon the formal distinction of the number of

cheek teeth", MATTHEW and GRANGER (1923) emphasized that this "genus is undoubtedly related to Ochotonidae". For the genus *Desmatolagus* BURKE erected the monogeneric subfamily Desmatolaginae BURKE 1941 in addition to parallel subfamilies for other genera. At the end of his discussion on the membership of *Desmatolagus* in one of the two families of the Lagomorpha BOHLIN (1942) concludes that *Desmatolagus* was an unquestionable ochotonid. SCHREUDER (1936) and TEILHARD DE CHARDIN (1926) are of the same opinion. DAWSON (1967) states that "species now included in *Desmatolagus* may prove referable to both the Ochotonidae and the Leporidae, as suggested by the somewhat arbitrary and tentatively given familial references below". The occurrence of such characters in *Desmatolagus* as the shape of the occlusal surface of the lower premolars and molars, resembling that in the modern Leporidae to an exceptional extent, the two-lobed structure of the crown of  $M_3$ , the number of the upper and lower teeth (6 and 5, respectively) relates it to the Leporidae, but the characters of the upper dentition, including all the structures that vanish in the course of life and have been described in *Desmatolagus* and partly in *Sinolagomys*, are undoubtedly properties of the primitive Ochotonidae. The erection of a separate taxonomic unit, i.e. a subfamily, for *Desmatolagus* does not, however, solve the systematic problems thoroughly. Such a subfamily, included in the Ochotonidae, would not comprise other primitive and different from *Desmatolagus* forms from the Oligocene and Miocene, the knowledge of which is not, as yet, satisfactory after all. A much more important problem seems to be not a formal division but the detection of structures of evolutionary significance in dentition. In the light of what is known about *Desmatolagus* and the later Miocene lagomorph forms it may be asserted that the morphological structures which are of great importance to considerations on evolution within the whole order are the hypostria, the crescent, the buccal cusps on upper molars and the posterior fold of talonids, and thus characters which nobody has treated synthetically so far. Their significance will be dealt with at large in another paper. The great morphological variability of the species of *Desmatolagus* is very significant; it manifests itself in the unstable position of the mental foramen and the maxillary openings in the palate, the variation in length of the diastema along with the shifting of the lower incisor in relation to the tooth-row, the variation of the buccal roots of the upper molars, and finally the great lability of the shape of the extreme teeth in both rows, especially that of  $P_3$ , accompanied by variation in size. During the Oligocene the *Desmatolagus* group underwent fairly rapid evolutionary changes, drawn from its indubitably copious pool of variation. Changes occur even between *D. gobiensis* and *D. robustus* and they may certainly be defined as the formation of progressiveness of the species *Desmatolagus robustus* in relation to *D. gobiensis*. This is evidenced not only by an increase in measurements but also by the acceleration, in course of life, of the disappearance of primitive characters, like the posterior fold of talonid and the crescent. A separate problem that remains to investigate is the rate of change of brachydonty into complete hypsodonty, characteristic of the Lagomorpha. It is perhaps an indication of the increase in the body measurements in the course of the evolution of this group.

Polska Akademia Nauk  
Zakład Zoologii Systematycznej i Doświadczalnej  
31-016 Kraków, Sławkowska 17  
April, 1974

## REFERENCES

- ARGYROPULO, A. J. — see АРГИРОПУЛО, А. И.
- BOHLIN, B. 1937. Oberoligozäne Säugetiere aus dem Shargaltein-Tal (Western Kansu). — *Palaeont. Sin.*, n. s. C, **3**, 1-66, Nanking.
- 1942. The fossil mammals from the tertiary deposit of Taben-buluk, Western Kansu. Part I: Insectivora and Lagomorpha. — *Ibidem*, 8a, 1-113, Nanking.
- BURKE, J. J. 1936. Ardynomys and Desmatolagus in the North American Oligocene. — *Carnegie Mus. Ann.*, **25**, 135-154, Pittsburgh.
- 1941. New fossil Leporidae from Mongolia. — *Amer. Mus. Novit.*, **1117**, 1-23, New York.
- DAWSON, M. R. 1967. Lagomorph history and the stratigraphic record. Essays in Paleont. — *Stratigraphy. Univ. Kansas Dept. Geol. Special Publ.*, **2**, 287-316, Lawrence.
- GRADZIŃSKI, R., KAŻMIERCZAK, J. & LEFELD, J. 1968. Geographical and geological data from the Polish-Mongolian Palaeontological Expeditions. Results Polish-Mongol. Palaeont. Exped. I. — *Palaeont. Pol.*, **19**, 33-82, Warszawa.
- GUREEV, A. A. — see ГУРЕЕВ, А. А.
- KOWALSKI, K. 1974. Middle Oligocene Rodents from Mongolia. Results..., V. — *Palaeont. Pol.*, **30**, 147-178, Warszawa.
- MATTHEW, W. D. & GRANGER, W. 1923. Nine new rodents from the Oligocene of Mongolia. — *Amer. Mus. Novit.*, **102**, 1-10, New York.
- SCHREUDER, A. 1936. Hypolagus from the Tegelen Clay; with a note on recent Nesolagus. — *Arch. Neerland. Zool.*, **2**, 225-239, Leiden.
- TEILHARD DE CHARDIN, P. 1926. Description de mammifères tertiaires de Chine et de Mongolie. — *Ann. Paléont.*, **15**, 1-52, Paris.
- WOOD, A. E. 1940. The mammalian fauna of the White River Oligocene; part III. Lagomorpha. — *Trans. Amer. Philosoph. Soc.*, **28**, 271-362, Philadelphia.
- АРГИРОПУЛО, А. И. 1940. Обзор находок третичных гризунов на территории СССР и смежных областей Азии. — *Природа*, **12**, 74-82, Ленинград.
- ГУРЕЕВ, А. А. 1960. Зайцеобразные олигоцена Монголии и Казахстана. *Труды Палеонтол. Института* **77**, 5-34, Москва.

## EXPLANATION OF PLATES

## PLATE LI

- Fig. 1. Translucent model of the "synthetic PM" in the *Desmatolagus* group. The bucal part of the tooth brachydontic with two small roots, the lingual part, ever-growing and never-worn. *C* — crescent, *Cs* — cusps, *H* — hypostria, *P* — pipe.
- Fig. 2. Five successive stages of the crown wearing drawn at the various growth levels. The teeth of the following specimens of *Desmatolagus gobiensis* MATTHEW & GRANGER 1923 from Loh, Gobi Desert, Mongolia are drawn down from the top respectively: ZPAL MgM-III/79: 2, 10, 72, 72 and 82.

Drawings: J. Świecinski  
L. Sych

## PLATE LII

	Page
<i>Desmatolagus gobiensis</i> MATTHEW & GRANGER . . . . .	184
(see also Plates LI, LIII, LIV)	

Middle Oligocene, Hsanda Gol Formation, Loh, Gobi Desert, Mongolia

- Fig. 1. Lower tooth row  $P_4-M_2$  with the posterior talonid fold visible (ZPAL MgM-III/79/25). Stereopair;  $\times 12.7$ .
- Fig. 2. Lower tooth row  $P_3-M_2$  without the posterior talonid fold (ZPAL MgM-III/79/97). Stereopair;  $\times 9.0$ .
- Fig. 3. Mandible with the lateral tuberosity of masseteric fossa (ZPAL MgM-III/79/70). Stereopair;  $\times 4.4$ .
- Fig. 4. Junction trigonid-talonid visible above the alveoli of  $P_4-M_2$  (ZPAL MgM-III/79/97);  $\times 9.1$ .

Photo: L. Sych

## PLATE LIII

	Page
<i>Desmatolagus gobiensis</i> MATTHEW & GRANGER, 1923 . . . . .	184
(see also Plates LI, LII, LIV)	

Middle Oligocene, Khatan Khayrkhan, Gobi Desert, Mongolia

- Fig. 1. Lower tooth row  $P_3-M_3$  (ZPAL MgM-III/80/37). Stereopair;  $\times 10$ .

	Page
<i>Desmatolagus robustus</i> MATTHEW & GRANGER, 1923 . . . . .	189

Middle Oligocene, Hsanda Gol Formation Loh, Gobi Desert, Mongolia

- Fig. 2. Lower tooth row  $P_3-M_3$  (ZPAL MgM-III/87/9). Stereopair;  $\times 8.7$ .
- Fig. 3. Left mandible, lateral view (ZPAL MgM-III/87/9). Stereopair;  $\times 3.5$ .

Photo: L. Sych

## PLATE LIV

	Page
<i>Desmatolagus robustus</i> MATTHEW & GRANGER, 1923 . . . . .	189
(see also Plate LI, LII, LIII)	

Middle Oligocene Hsanda Gol Formation, Loh, Gobi Desert, Mongolia

Fig. 1. Right maxilla with P<sup>2</sup>-P<sup>4</sup> (ZPAL MgM-III/87/10). Stereopair; × 5.6.

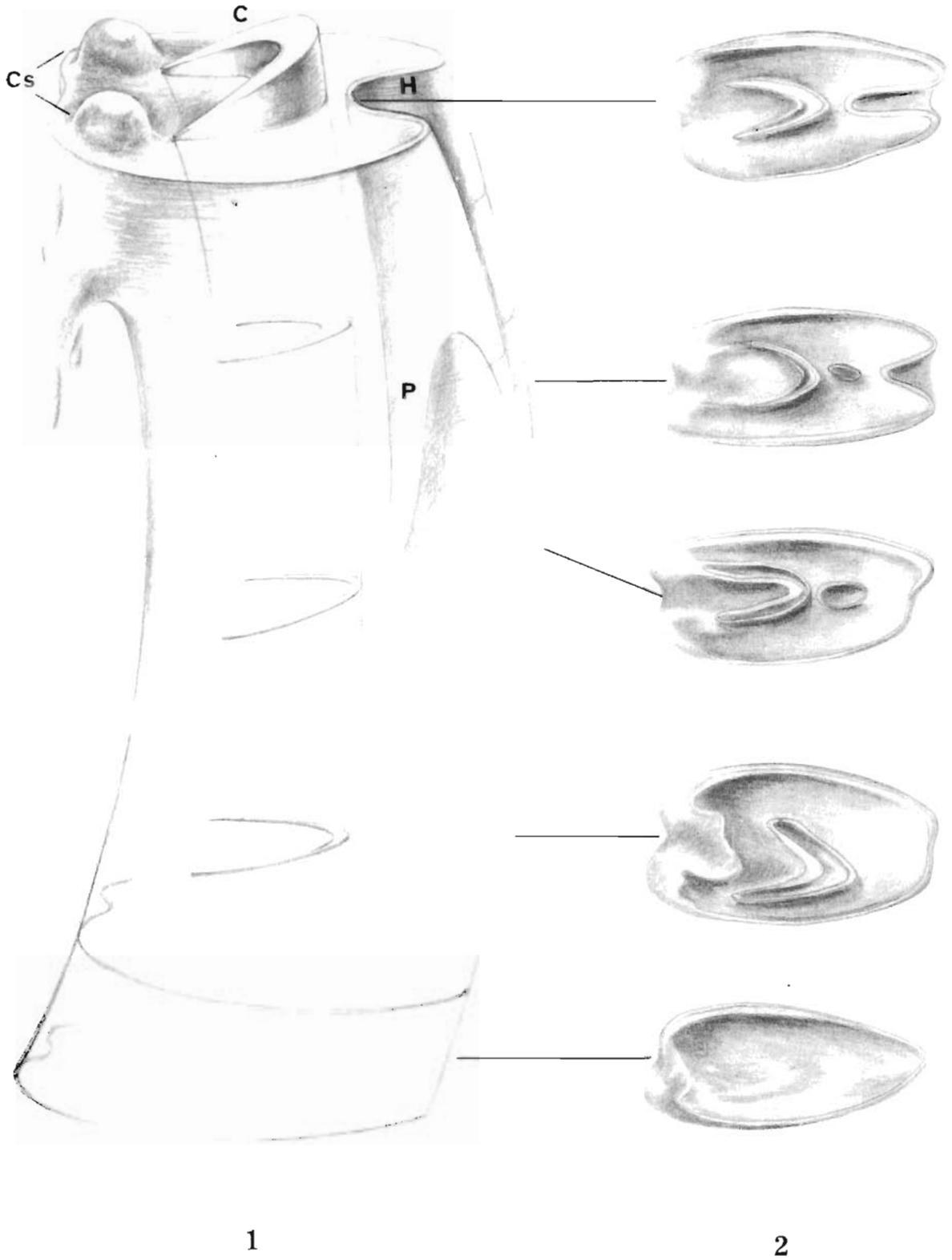
Fig. 2. Left maxilla with P<sup>3</sup>-M<sup>1</sup>, old specimen (ZPAL MgM-III/87/2). Stereopair; × 5.

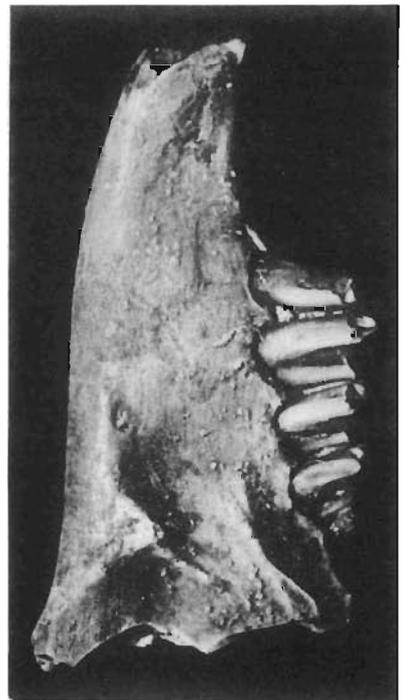
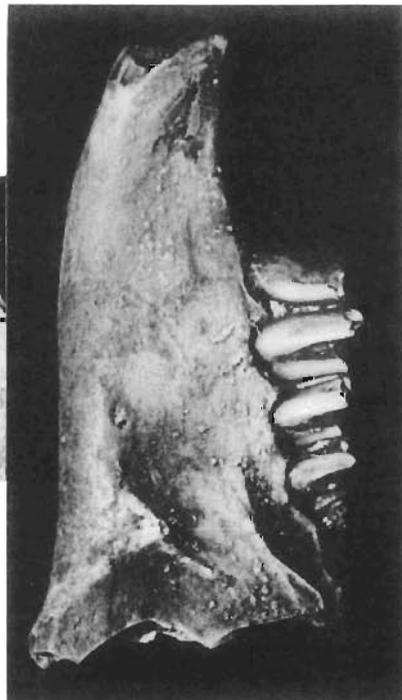
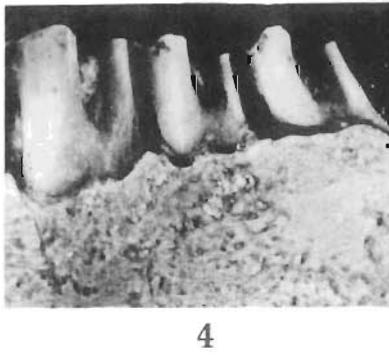
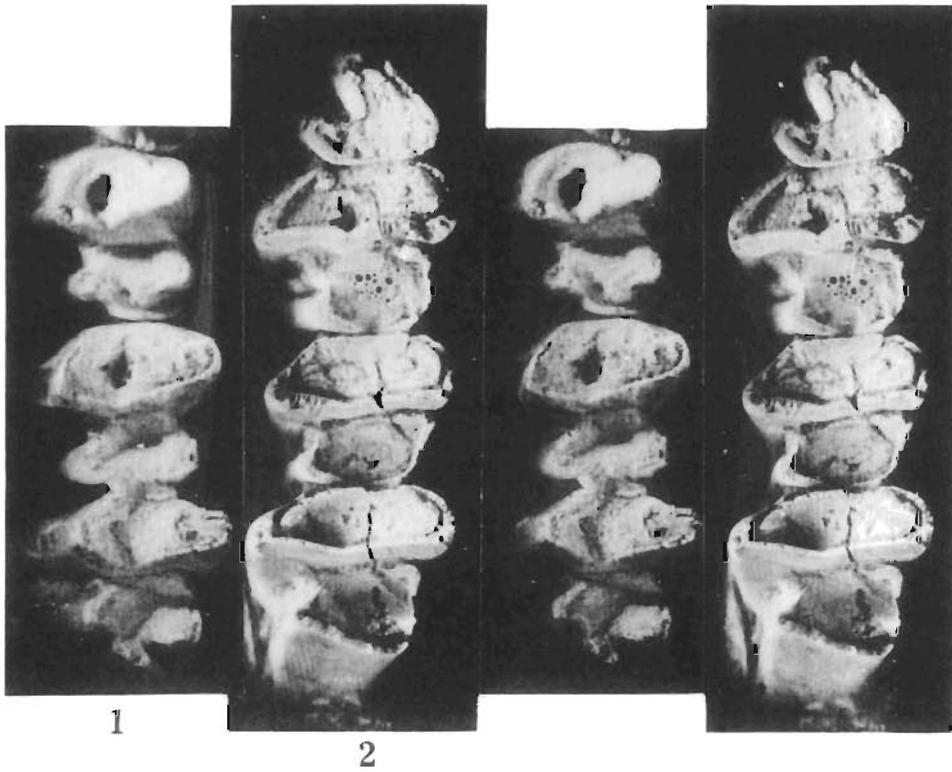
	Page
<i>Desmatolagus gobiensis</i> MATTHEW & GRANGER, 1923 . . . . .	184

Middle Oligocene, Hsanda Gol Formation Loh, Gobi Desert, Mongolia

Fig. 3. Right maxilla with the tooth row P<sup>2</sup>-M<sup>3</sup> (ZPAL MgM-III/79/85). Stereopair; × 6.

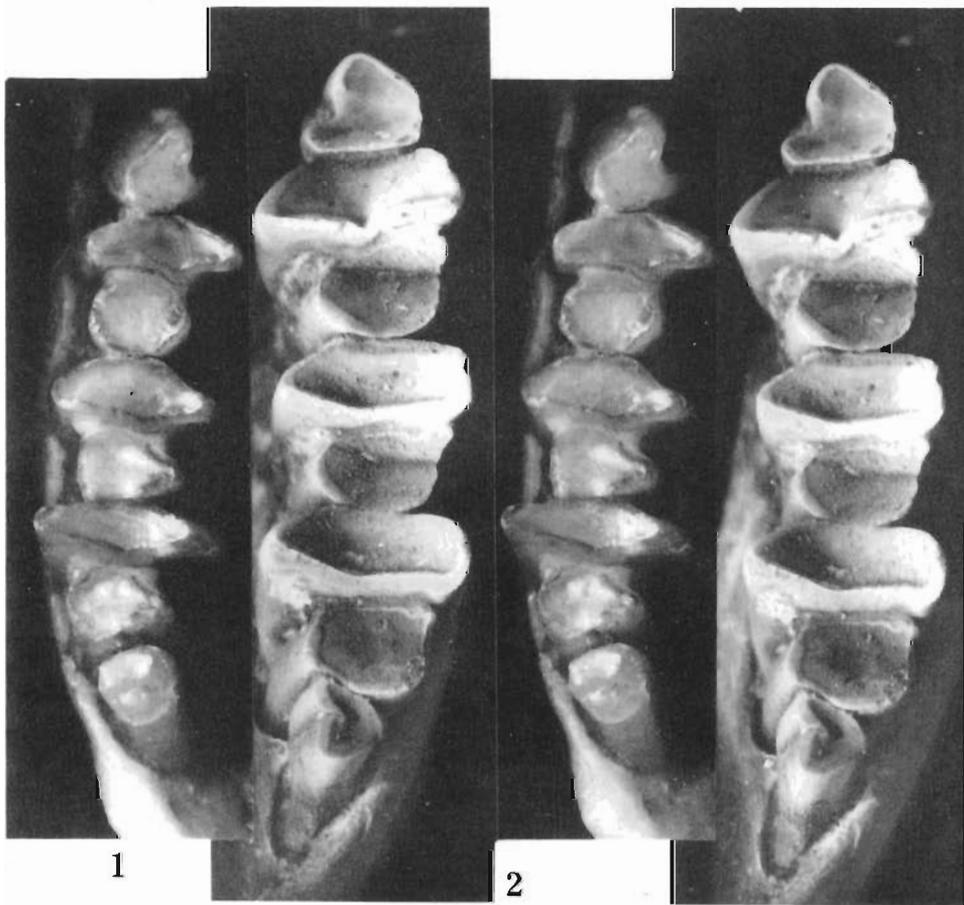
Photo: L. Sych





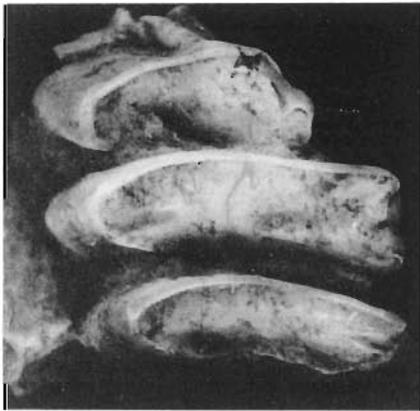


3





1



2



3