LUCJAN SYCH

MIXODONTIA, A NEW ORDER OF MAMMALS FROM THE PALEOCENE OF MONGOLIA

(Plates XXV-XXVIII)

Abstract. — The remains of *Eurymylus laticeps* MATTHEW & GRANGER from the Paleocene of Naran Bulak are analysed in detail and compared with the remains of this species from Khashaat. Comparisons with the Lagomorpha, Rodentia and Insectivora have induced the author to draw the conclusion that the species under discussion does not belong to any of these three mammalian orders, but to the distinct order Mixodontia, descending from Cretaceous insectivores and extinct in the Paleogene.

INTRODUCTION

The discovery of remains of the Paleocene mammal *Eurymylus laticeps* MATTHEW & GRANGER, 1925 at Naran Bulak in the Gobi Desert during the Polish-Mongolian Palaeontological Expedition in 1964 has given occasion to the resumption of the dicussion on this enigmatic species and its origin. So far its occurence is restricted to two localities: Khashaat (= Gashato) (MATTHEW & GRANGER, 1925), and Naran Bulak, where *Eurymylus* was found by Prof. K. KOWALSKI in 1964 (KIELAN-JAWOROWSKA & DOVCHIN, 1968/69). The geological age of both these finds has been established as the late Paleocene (GRADZIŃSKI *et al.* 1968/69).

In 1925 the first description of *Eurymylus laticeps* was presented by MATTHEW & GRANGER on the basis of a skull fragment with well preserved cheek-teeth found at Khashaat. *Eurymylus* was then included in the family Plesiadapidae of the order Menotyphla. The same authors simultaneously described another species, *Bäenomys ambiguus* MATTHEW & GRANGER, 1925, from a mandibular fragment of the same age and placed it among the Glires. Having found further cranial fragments of both these species, MATTHEW *et al.* (1929) arrived at the conclusion that all the remains found up to that time represented one species, *Eurymylus laticeps*. They erected a new family, the Eurymylidae, for this species and assigned it to the Glires. They emphasized, that *Eurymylus* is neither a lagomorph nor a rodent, though, in their opinion, the characters which it has in common with the primitive Eocene rodents are the most numerous. WOOD (1942) acknowledged *Eurymylus* to be one of the most primitive lagomorphs. Since then, in the eyes of many authors trying to find the ancestors of lagomorphs in other mammalian groups, — such as the insectivore Zalambdalestidae (RUSSELL, 1959), the Leptictidae (VAN VALEN, 1964) or even the primitive ungulate Condylarthra (WOOD, 1957) — *Eurymylus* has become an intermediate link. The material used as the basis for various hypotheses about the origin of the Lagomorpha was, however, incomplete insomuch that it was impossible to recognize *Eurymylus* as lagomorph quite unquestionably. The acquisition of some better-preserved remains only strengthened many of the justified doubts as to the relation of *Eurymylus* to the Lagomorpha. Considerations on the morphology of this species and its possible relations to other groups of mammals are presented in this paper.

Abbreviations used:

A. M. N. H. — American Museum of Natural History, New York.
Z. Pal. — Palaeozoological Institute, Polish Academy of Sciences, Warsaw.
Z. Z. S. — Institute of Systematic and Experimental Zoology, Cracow.

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DESCRIPTIONS

MIXODONTIA, new order

Derivation of the name: Mixodontia referring to the mixed type of dentition.
Geographical and stratigraphical range: Gobi Desert, Mongolian People's Republic, late Paleocene.

The new order is monotypic, the diagnosis is as for the type species of the only genus *Eurymylus*.

Family EURYMYLIDAE MATTHEW, GRANGER & SIMPSON, 1929

Genus EURYMYLUS MATTHEW & GRANGER, 1925

Eurymylus laticeps MATTHEW & GRANGER, 1925

(Pls. XXV-XXVIII)

1925. *Eurymylus laticeps* n. sp.; W. D. MATTHEW & W. GRANGER, Fauna and correlation..., pp. 1, 7, Fig. 7.
1925. *Bäenomys ambiguus* n. sp.; W. D. MATTHEW & W. GRANGER, *Ibid.*, pp. 1, 5-6, Fig. 5.
1929. *Eurymylus laticeps*; W. D. MATTHEW, W. GRANGER & G. G. SIMPSON, Additions to the Fauna..., pp. 6-7, Figs 4-5.
1940. *Eurymylus*; A. E. WOOD, The mammalian fauna..., pp. 357-358.
1942. *Eurymylus laticeps*; A. E. WOOD, Notes on the Paleocene lagomorph Eurymylus, pp. 1-7, Figs 1-7.
1942. *Bäenomys ambiguus*; A. E. WOOD, *Ibid.*, pp. 3, Fig. 7.
1951. *Bäenomys*; BOHLIN, Some mammalian remains..., p. 17.
1964. *Eurymylus laticeps*; L. VAN VALEN, A possible origin for rabbits, pp. 484-490, Figs 1*a*, 3.
1968/69. *Eurymylus*; Z. KIELAN-JAWOROWSKA & N. DOVCHIN, Narrative..., p. 17.
1968/69. *Eurymylus*; A. SULIMSKI, Paleocene genus Pseudictops..., pp. 101.

Type horizon: Upper Paleocene.
Type locality: Khashaat (Gashato), Gobi Desert, Mongolian People's Republic.
Type specimen: A. M. N. H. No. 20422.

Diagnosis. — Mammals with a pair of continually growing incisors in both the mandible and the maxilla. Lower cheek-teeth, 5 in number, of the tuberculo-sectorial type. Upper cheek-teeth, 5 in number (P^3-M^3), of the tuberculous type, transversely elongated, with well-developed lateral cusps and a medial one on the molars inclusive of M^3. Lower incisors extending far to the rear, up to the region of M_3. P_3 smaller than the other cheek-teeth. Angular process of mandible bent medially. Posterior palate with choanal foramina beginning at the line of M^3.

Material. — Nine specimens: lower jaws with dentition and fragments of upper jaws from Naran Bulak.

Description of dentition. — The row of the upper cheek-teeth consists of 5 teeth, from P^3 to M^3. The molars can readily be distinguished from the premolars, as they have two roots on the lateral side, shorter and thinner than the medial root. The premolars have two roots each, the medial root being shorter and slenderer than the corresponding root in the molars. The cheek-teeth are low-crowned and the boundary between the crown and the remaining part of the tooth is very sharp, though no distinct cingulum has been observed. The medial side of the tooth row approximates to a straight line, its lateral side to a semi-circular line. The premolars are less worn than the molars, which is well seen in the best-preserved specimen Z. Pal. No. MgM-II/62. The same is also true of specimen A. M. N. H. No. 20422 and, partly A. M. N. H. No. 21737.

P^3 has one unworn pronounced cusp, which in position corresponds to the paracone (terminology after Wood, 1940). This cusp is well seen both in Z. Pal. No. MgM-II/62 and in A. M. N. H. No. 20422. This last specimen shows a trace of another cusp, the lateral one, in the form of a small enamel fold, poorly seen in Z. Pal. No. MgM-II/62. In all the specimens the enamel is worn off more heavily on the medial side. In No. MgM-II/63, which belonged to a juvenile, P^3, situated right under its deciduous tally, DM^3, has been preserved unworn. The grinding surface of an unworn P^3 shows the presence of two cusps, a lateral in the paracone position and a medioanterior in the protocone position, separated by a valley. The crown--surrounding enamel forms a sharp ridge markedly raised above the dentine all round the tooth. Thus, even at this early stage of growth of the tooth the enamel forms sharp ridges so that an erupting tooth is similar to its more worn future form. When wear has begun, the medioanterior cusp disappears.

P^4, like P^3, has one unworn cusp in the paracone position with a concave surface on the lateral side. In A. M. N. H. No. 20422 and A. M. N. H. No. 21737 the wear of the enamel of this cusp is more advanced and consequently it forms an elongate fold.

On the lateral side M^1, M^2 and M^3 have two conspicuous cusps each, of which the anterior corresponds in position to the paracone and the posterior to the metacone. The tops of these cusps are not worn in any of the specimens from Naran Bulak. Nevertheless, Z. Pal. No. MgM-II/62 and Z. Pal. No. MgM-II/64 differ from each other in degree of wear. In Z. Pal. No. MgM-II/64 not only have all the molars their lateral cusps perfectly well preserved, but also the medioanterior cusp, which corresponds in position to the protocone, is partly preserved in them. It is well seen on M^3, the least worn of the molars. The metacone and protocone in Z. Pal. No. MgM-II/64 are connected by an obliquely running crest of enamel, preserved whole on M^3, partly worn on M^2, and still more worn on M^1. The wear of the medial portion of this crest is accompanied by the disappearance of the eminence of the protocone. The molars of Z. Pal. No. MgM-II/62 show a more advanced stage of wear, only the lateral cusps are preserved on them. The posterior of these cusps still bears some remnants of the worn enamel crest directed towards the place occupied previously by the protocone, now completely worn away. Traces of this crest are visible in the form of a small enamel fold in A. M. N. H. No. 21737 and A. M. N. H. No. 20422. Thus, in respect of individual age the specimens under discussion may be arranged in the following sequence: Z. Pal. No. MgM-II/63, Z. Pal. No. MgM-II/64, Z. Pal. No. MgM-II/62, A. M. N. H. No. 20422 and A. M. N. H. No. 21737.

Table 1

Measurements of *Eurymylus laticeps* teeth (in mm)

Specimen Z. Pal. No.	MgM-II/58		MgM-II/59		MgM-II/60		MgM-II/61		MgM-II/62		MgM-II/63		MgM-II/64		MgM-II/65		MgM-II/66	
	left	right	left	right	left	right	left	right	left	right	left	right	left	right	left	right	left	
P^3 ant.-post.									1.47	1.33								
P^3 width ant.																		
P^3 width post.																		
P^4 ant.-post.									1.64	1.63								
P^4 width ant.																		
P^4 width post.																		
M^1 ant.-post.									1.97	1.93			1.85					
M^1 width ant.									3.19	3.07			2.32					
M^1 width post.									2.97	2.87			2.47					
M^2 ant.-post.									1.77				1.82					
M^2 width ant.									2.90				2.30					
M^2 width post.									2.37				2.03					
M^3 ant.-post.									1.37				1.73					
M^3 width ant.									2.60				2.20					
M^3 width post.									2.21				2.00					
P_3 ant.-post.		1.30		1.40	1.13													
P_3 width max.		0.97		1.27	1.03													
P_4 ant.-post.		2.08		1.85	1.87			1.67										
P_4 width trig.		1.83		1.70	1.70			1.82										
P_4 width tal.		1.43		1.37	1.43			1.41										
M_1 ant.-post.		2.09			1.93			2.00							2.20			
M_1 width trig.		1.95		1.81	1.73			2.01							2.07			
M_1 width tal.		2.03			1.95			2.13							2.03			
M_2 ant.-post.		2.21		2.07	2.03			2.20							2.24			
M_2 width trig.		1.93		1.97	1.90			2.19							2.25			
M_2 width tal.		2.08		2.15	1.95			1.98							2.03			
M_3 ant.-post.		2.60		2.53	2.51			2.61										
M_3 width trig.		1.87		2.10	1.99			2.12										
M_3 width tal.		2.30		2.27	1.97			1.95										
I^3 width									1.97	1.95	1.72	1.75					2.00	
I^3 thickness									1.72	1.77	1.55	1.83					1.77	
I_1 width				1.55				1.93										
I_1 thickness				1.67				1.75										

The presence of two milk-teeth in Z. Pal. No. MgM-II/63 is instructive. The first of them (anterior) is DM^2, the other — DM^3. This last tooth resembles the molars of Z. Pal. No. MgM-II/62 in shape. The two lateral cusps of DM^3 are unworn, whereas the medial side is already partly worn and, as a result, has lost its cusp. The only other detail preserved is the above-mentioned enamel crest running medially from the posterolateral cusp. DM^3 has three roots, two of which, the lateral ones, growing out just at the base of the cusps, are fine and widely disposed, and the medial one is stouter, longer and directed towards the palate. DM^2 differs from the other teeth in shape. It is considerably smaller and its grinding surface has the shape of a triangle, the long side of which rests against the anterior wall of DM^3. One of the two cusps present on the surface of DM^2 protrudes at the anterior vertex of this triangle of the crown, the other one at its buccal side. Both of them bear traces of slight wear, owing to which the enamel forms rounded islets on their tops (Pl. XXVIII, Fig. 1*a-b*, 3). DM^2, like its neighbour, has three roots.

The lower row of cheek-teeth of *Eurymylus* consists of five teeth, from P_3 to M_3. All of them have markedly elongated roots and a relatively low crown, sharply demarcated from the rest of the tooth, there being no cingulum. It is characteristic that the grinding surface is the widest on M_3 and M_2 and tapers towards the front. The premolars are small and only slightly worn. The crown of the smallest of them, P_3, consists of two parts, of which the higher anterior part may correspond to the trigonid and the lower posterior one to the talonid. The anterior part of P_3 is a single cusp preserved whole in Z. Pal. No. MgM-II/58 and Z. Pal. No. MgM-II/60 and somewhat worn in Z. Pal. No. MgM-II/59, A. M. N. H. No. 21738 and A. M. N. H. No. 21735. In Z. Pal. Nos. MgM-II/58, 59, 60, 61, A. M. N. H. Nos. 21735 and 21738 P_4 is well preserved. This tooth shows only slight traces of wear in Z. Pal. Nos. MgM-II/58 and 60. The P_4 teeth of the specimens housed in the American Museum of Natural History are more worn and show a pattern of several small folds and islets of enamel. The unworn crown of this tooth has two cusps, a higher medial and a lower lateral, in the anterior part, which corresponds to the trigonid. The first of them may correspond in position to the paraconid, the other one to the protoconid. The two cusps are separated from each other by a deep groove, which cuts into the crown for about one-third of its height. As the tooth wears away, the groove becomes more and more shallow to disappear in the end so that Z. Pal. No. MgM-II/61 is already devoid of it. At an early stage of wear the posterior part of P_4, corresponding in position to the talonid, is only an eminence, in which the distinction of the hypo- and entoconid is not possible. M_1 and M_2 have a bifid structure; their anterior part, corresponding to the trigonid, is elevated and the posterior part, which forms the talonid, is lowered. The arrangement of M_1 and M_2 is such that the talonid of M_1 and the trigonid of M_2 form one grinding surface, and so do the talonid of M_2 and the trigonid of M_3. In width the talonids of M_1 and M_2 equal or exceed the trigonids of these teeth. M_3, the largest of all the cheek-teeth, differs from them in structure. Its part corresponding to the talonid is bifid and consists of an anterior lobe and a posterior one. The anterior lobe, which at a low degree of wear is as wide as the trigonid (Z. Pal. No. MgM-II/58), has the shape of a transverse crest ending in 2 cusps, a larger cusp on the lateral side and a smaller one on the medial side. The posterior lobe, broken away in Z. Pal. No. MgM-II/58, was probably a single unworn conspicuous cusp, which in Z. Pal.Nos. MgM-II/59, 60, and 61 has left a semicircular loops of enamel connected with the enamel of the anterior lobe in the front. No M_3 teeth have been found in the specimens housed in the Amer. Museum of Natural History.

The incisors are relatively well preserved in Z. Pal. Nos. MgM-II/62 and 63 (upper) and Z. Pal. Nos. MgM-II/59 and 61 (lower). They are continually growing parallelepipedal teeth. Their transverse sections show triangles with rounded vertices. They chisel-like at ends. The upper incisors are curved to a greater extent than the lower ones, the radii of their external curvatures being, respectively, about 11,0 and 13,5 mm. Enamel covers the labial side of the upper and lower incisors. In the polarisationsmicroscope the lower incisor appears to have a two-layered structure, the difference between the layers being indicated by the different directions of arrangement of the prisms.

The most striking characteristic of the studied specimens of *Eurymylus* is the lack of another posterior pair of upper incisors, which pair is typical of the Lagomorpha. The incompleteness of the remains described so far from Khashaat did not allow the determination of the number and kind of incisors in *Eurymylus*. The alveoli of the upper incisors are situated so close to the incisive foramina in the anterior palate that there is no room for the alveoli of the posterior pair. The position of the incisors in relation to the cheek-teeth differs between the upper and lower jaws. The lower incisor reaches to the rear as far as M_3, the upper one ends in the region of P^3 (Pl. XXV, Fig. 3).

It is not quite certain whether the left ramus of the maxilla of Z. Pal. No. MgM-II/60 and the mandible of No. MgM-II/62 belonged to one specimen. None the less, the occlusion is very exact for the whole length of the two rows of cheek-teeth. The trigonid of P_3 projects remarkably to the front, its posterior portion sliding along the anterior wall of P^3. Further to the rear arrangement of the upper and lower teeth in relation to one another is such that the anterolateral part of each anteroloph, as a rule, wears off the talonid. At the same time this arrangement causes the trigonid to grind off the anterior margin of each upper tooth obliquely. Thus, the upper cheek-teeth are worn in two planes, a horizontal and an obliquely frontal. The anterior margins ground off in this way in the upper cheek-teeth are well seen in Pl. XXVIII, Fig. 3*a*. P^3 is the least worn. It seems to have played a far lesser role in grinding food than the other cheek-teeth. The grinding surfaces of the upper tooth row are oriented transversely, those of the lower row longitudinally. In *Eurymylus* the main grinding movements of the mandible must have been done in a transverse direction in relation to the maxilla.

Skull. The toothless edge of the maxilla is about 7.5 mm long in Z. Pal. No. MgM-II/62, the same measurement in the mandibles being approximately half this length. The upper and lower edges of the mandible are sub-parallel, and there are two mental foramina between M_3 and P_3 in the anterior part of the mandible; the anterior of the foramina lies under P_3 and the posterior one between P_4 and M_1. Two distinct crests which limit the masseteric fossa anteriorly meet at a point lying on a vertical plane passing through the anterior lobe of M_3. A striking character of the mandible of *Eurymylus* is the medial bend of the angular process, which is well seen in Z. Pal. Nos. MgM-II/61 and 59. Although the fragile angular process is not preserved whole in either specimen, the twisting of its basal portion is evident (Pl. XXVII, Fig. 4). The mandibular symphyse is short and the suture itself does not reach 4 mm in length. It runs obliquely downwards and to the rear from the labial margin of the mandible.

The intermaxilla borders upon the maxilla so that the suture between them crosses the diastema at about one-third of its length measured from the rear. The Khashaat specimens show the presence of some foramina in the lateral surface of the maxilla, denominated by Wood (1942) as fenestration. In the anterior palate there are two large incisive foramina, which extend forwards near the alveoli of the upper incisors and backwards to the line of the anterior borders of the alveoli of P^3. The palatine of Z. Pal. No. MgM-II/62 is partly broken away. Its preserved part shows that the palatal bridge occupied a very large part of the space between the tooth rows. The anterior border of the choanal opening is not visible, but the arrangement of the palatal bones indicates that it lies far to the rear, at nearest in line with the middle of P^3. The maxilla of Z. Pal. No. MgM-II/63 has a small opening on its lateral side, near the anterior margin of the orbit. There are no visible openings in this place in Z. Pal. No. MgM-II/62.

The infraorbital foramen is situated somewhat anteriorly to the line connecting the P^3 teeth. The middle of the zygomatic process of the maxilla seen below also lies close to this line. On the lateral side of the anterior part of the zygomatic arch there is a depression, which extends up to the anterior end of the arch.

DISCUSSION

Comparison of a single species represented by nine fossil fragments, with groups of the rank of order, each of which contains numerous and greatly differentiated species, is difficult. The objective of this discussion is to confront the opinions on the relation of *Eurymylus* to other mammalian groups and to point out the rightness of its removal from the Lagomorpha.

A comparison of the specimens from Naran Bulak with the specimens from Khashaat collected by the American Expeditions shows that they belong to the same species *Eurymylus laticeps*. Slight differences between particular specimens result from their different individual age and individual variation. The specimens from Khashaat and Naran Bulak complement one another. Twenty one characters have been selected for further considerations. They are divided into two groups according to their evolutionary importance and taxonomic value. The first group includes characters of particular systematic value, the other ones are either qualities correlated with the characters of the first group or those used for further, more detailed comparisons with other groups of mammals.

Group I

1. A pair of continually growing upper incisors
2. Upper row composed of 5 cheek-teeth; lack of P^2
3. Upper molars transversely elongated with 2 or 3 cusps and a crest of enamel
4. M^3 like other upper molars
5. Lower incisors extend far backwards in mandible, up to under M_3
6. P_3 and P_4 smaller than other lower cheek-teeth
7. M_3 trilobed and largest of all lower cheek-teeth
8. Angular process of mandible bent madially
9. Choanal opening situated far backwards, near M^2 or M^3; palatal bridge very wide

Group II

1. Presence of deciduous P^2 (DM^2)
2. All lower cheek-teeth with roots, upper cheek-teeth showing weak hypsodonty on medial side
3. Two-layered enamel of lower incisors
4. Posterior part of rows of cheek-teeth showing largest contact-surface at occlusion
5. Unworn lower molars of tuberculo-sectorial type
6. Transverse direction of fundamental movements of mandible
7. Two mental foramina in mandible
8. Strongly elongated shape of incisive foramine in palate
9. Maxilla fenestrated
10. Anterior root of zygomatic arch with a pronounced depression, which extends up to the anterior end of the arch
11. Infraorbital foramen situated further forward than tooth row
12. Cheek-teeth of low-crowded type

RELATION TO THE LAGOMORPHA

Wood (1942) made an attempt at conclusive estimation of the relations between *Eurymylus* and the Lagomorpha and summarized his results in a table comprising 4 distinguishing characters and 14 similarities. It seems useful to compare Wood's opinions on the classificatory value of the characters selected by him with those adopted in the present study.

The most striking similarity of *Eurymylus* to the Tertiary lagomorphs is the bipartite structure of the lower cheek-teeth (M_1, M_2 and, partly, P_4). This is the only character from among those included in group I. The talonids and trigonids of these teeth in *Eurymylus* and lagomorphs seem to be homologous. Besides, the relation between these teeth, as has already been described (p. 149), is such that the talonid of one tooth and the trigonid of the next one form a common wearing surface. This fact is connected with occlusion, with the presence of two lateral cusps on the upper molars and with the horizontal transversal movements of the mandible in relation to the maxilla. These characters are undoubtedly common at least to all lagomorphs and the specimens from Khashaat and Naran Bulak. Another similarity which brings *Eurymylus* closer to the Lagomorpha is the presence of the large elongate incisive foramina in the anterior palate. These characters were also distinguished by WOOD, who in addition to them mentioned a number of other ones, in my opinion, of no actual importance to the affinity between the specimens discussed and the Lagomorpha. Some of these characters are connected with the presence and position of small apertures in the skull and mandible. Thus, WOOD writes of the „fenestration of maxilla incipient in *Eurymylus* as pitting". The use of the term „fenestration" for a group of several small openings in the maxillare seems to suggest the occurrence of real fenestration typical of the Lagomorpha, which in *Eurymylus* is lacking. All these openings but one are almost invisible in the specimens from Naran Bulak. This character seems to have been poorly fixed and it is rather unimportant to our comparisons. This is also true of the mental foramina, which are 3 in specimens from Khashaat and 2 in the specimens from Naran Bulak. The situation of these apertures and also the positions of the infraorbital foramen and the other foramina serving to innervate and vascularize the skull are to a various degree subordinated to the general structural and functional arrangements of the skull bones in different mammalian groups. It seems therefore that the taxonomic value of such characters as the position of foramina of this type and small differences in their numbers ought not to be overestimated. Here these characters have been placed in the group II.

I begin the discussion of the differences distinguishing *Eurymylus* from the Lagomorpha at the characters which were unknown before the latest finds because of the incompleteness of the material. As has already been mentioned, *Eurymylus* has only one-anterior-pair of incisors; it lacks the posterior pair typical of the Lagomorpha. There is even no room for these teeth between the incisive foramen, elongated towards the front, and the anterior pair of incisors. All the fossil and recent lagomorphs so far known have this other, posterior pair of incisors. The structure of the anterior portion of the intermaxilla and the lack of room for an additional pair of teeth allow the supposition that the specimens under study are not cases of an anomaly consisting in the stoppage of development of the second pair of incisors. Anomalies in the growth of dentition were dealt with in many studies, e.g. those by M'INTOSH (1929), who gave much attention to the rabbit, and VAN VALEN (1966), who described a case of the abnormal rat that lacked some incisors. Naturally, the lack of this character did not exclude the rat from the Rodentia just as the lack of the posterior pair of upper incisors would not necessarily have to cause the exclusion of *Eurymylus* from among the Lagomorpha. In comparisons of this sort it is indispensable to analyse the characters complexly. The lack of the posterior incisors in *Eurymylus* is only one of the set of characters that distinguish it from the Lagomorpha. Another character is the very long palatal bridge, which is accompanied by a shifting of the choanal opening far to the rear, as in rodents or insectivores. The quality of the mandible unknown from the fossil and contemporary lagomorphs is a medial bend in its angular process (Pl. XXVII, Fig. 4). A similar bend is observed in some rodents and it is also one of the constant characters of marsupials. Further, one of the significant differences between *Eurymylus* and the Lagomorpha, which was emphasized by Wood (1942), is the lack of P^2, existing in lagomorphs. In the Mongolian species the upper row is therefore composed of 5 teeth. To be sure, in the lagomorph family Ochotonidae the upper row consists also of 5 teeth, always including P^2 but without M^3, which in other lagomorph groups is small and cylindrical. Thus, the occurrence of 5 teeth in the upper row in *Eurymylus* cannot result from the homology of its first premolar with P^2 of the Ochotonidae and, what is more, specimen Z. Pal. No. MgM-II/64 has 2 extant milk teeth, of which one is DM^2. The lack of P^2 in the permanent dentition and the presence of its equivalent in the deciduous dentition seem to indicate that *Eurymylus* presented an intermediate or final stage of reduction of this tooth within an unknown evolutionary line which it represented. This opinion seems to agree also with the general evolutionary trend in mammals towards the reduction of the number of teeth with the progress in their specialization. It is particularly instructive to compare the upper molars of fossil lagomorphs with the corresponding teeth in *Eurymylus*. The crown structure of the tricuspid teeth with a crest of enamel connecting the metacone well seen in specimen Z. Pal. No. MgM-II/64, Pl. XXVI, Figs 3, 3*a*, little resembles the upper molars of the primitive Oligocene Palaeolaginae from Asia and North America. Fig. 4 in Pl. XXVII shows the upper cheek-teeth characteristic of the genus *Palaeolagus*, a typical member of the group mentioned, juxtaposed with the corresponding teeth of *Eurymylus*. It is scarcely possible to admit the existence of an evolutionary process which would have led to the transformation of 3 nearly uniformly structured cuspid molars of *Eurymylus*, more advanced in specialization than the teeth of the much younger Lagomorpha, into 3 molars with an internal fold of enamel (hypostria). In particular, the development of the last tricuspid M^3 of *Eurymylus* into a simple cylindrical M^3 of lagomorphs seems hardly probable. The difference between the upper molars of *Eurymylus* and those of lagomorphs must therefore be recognized as one of the fundamental differences.

The lower dentition of *Eurymylus* appears no less interesting. A large incisor extending posteriorly up to under M_3 is not typical of the Lagomorpha. Its length and position do not differ from the pattern peculiar to rodents. The enamel covering the labial side of the incisors shows a differentiation into two layers. The microscopic structure of enamel was frequently considered to be one of the distinctive characters in some groups of mammals (Korvenkontio, 1934; Bohlin, 1951; Wahlert, 1968). In the Lagomorpha there is, as a rule, one layer (Wood, 1967), which may sometimes be differentiated weakly in respect of its structure as in the fossil species of unknown age, *Mimolagus rodens* Bohlin, 1951, from western Kansu. The structure of enamel in *Eurymylus* more resembles the enamel of rodents, especially the so-called pauciserial type described by Wahlert (1968) in the Eocene rodents, than the enamel of the Lagomorpha, even that of *Mimolagus*. According to Wahlert (1968), the microstructure of the enamel of the incisors may rather be analysed as an additional character useful to determine the systematic position of higher taxonomic units of rodents. It seems that the differences found in the structure of enamel of the incisors between *Eurymylus* and both rodents and lagomorphs should also be treated as an additional quality, which only complements the analysis of the morphology of this species (cf. group II of characters).

Mimolagus rodens Bohlin, 1951 has been acknowledged to be the most primitive of the fossil Lagomorpha in the evolutionary sense. It has been placed (Dawson, 1967; Van Valen, 1964) beside *Eurymylus* in the family Eurymylidae. Considering the possible affinities of *Mimolagus*, Bohlin (1951) mentioned rodents and lagomorphs, especially *Desmatolagus*, *Mytononolagus* and *Bäenomys* (= *Eurymylus*), to which, according to him, *Mimolagus* was most closely related. He writes: „Only the lower dentition of *Bäenomys* has been described. Its teeth have very low crowns and *Bäenomys* therefore is the form which in this respect resembles *Mimolagus* most". It does not seem quite understandable why BOHLIN emphasizes the resemblance in respect of the dentition of the mandible, while the mandible of *Mimolagus rodens* has not been found and described among the remains of this species. A comparison of the remains of *Mimolagus* known to me on the basis of Bohlin's description and illustration with the specimens of *Eurymylus* showed that despite some similarities in shape of the middle teeth of the upper row, which are besides heavily worn in *Mimolagus*, the two species differ remarkably from each other. Unlike *Eurymylus*, *Mimolagus* may be recognized as a primitive lagomorph on account of the presence of the posterior pair of the upper incisors (the perfectly well preserved alveoli of these teeth can be seen in the illustrations given by BOHLIN), the presence of P^2 and the structure of enamel which resembles that in the Lagomorpha.

The foregoing considerations suggest that *Eurymylus* was a species evolutionary advanced in a different direction from that of any group of the Lagomorpha. In particular, the central point of the evolution of dentition in *Eurymylus* seems to have been shifted towards the rear of the mandible and maxilla. This is indicated by both the upper and lower molars, which are of large size, lack of P^2, small P_3, and the lower incisor moved far backwards. The theory of morphogenetic fields introduced by BUTLER (1939) for the dentition of mammals and widely used and developed since then (MILES, 1968) elucidates these trends in evolution. According to this theory, in the course of ontogenetic development the growth of particular portions of the organism is controlled within the so-called morphogenetic fields, i.e. the zones of activity of the biochemical factors activating growth processes and leading to the rise of structures which are always similar in a given zone. The dentition develops as a series of units-teeth inside its own morphogenetic fields, each of these units developing in an individual manner proper to its position in the field. The morphogenetic field of dentition is said to have a longitudinal anteroposterior axis with different morphogenetic properties at its ends (MILES, 1968). The field is differentiated so as to form regions corresponding to each, the incisors, canines and molars, particular regions having always a certain degree of evolutionary independence, e.g. the reduction of the canines need not always be associated with a parallel decrease in the size of molars. The evolutionary differentiation of the morphogenetic field of dentition seems to have assumed two different directions in *Eurymylus* and in the Tertiary Lagomorpha; it led to the above-described more marked development of the teeth at the back of the mandible and maxilla in the former and, on the contrary, to an increase in the size of P_3, the thrusting of the incisors far to the front and the reduction of back molars in the latter. Summing up these considerations, I must state that the separation of *Eurymylus* from the order Lagomorpha seems to be well grounded.

RELATION TO THE RODENTIA

The presence of the continually growing incisors and the long palatal bridge are characters which *Eurymylus* has in common with rodents. They are of a high taxonomic rank and placed in the first group of characters but, which must be emphasized, practically the only ones that these animals share with each other, for the medial bend of the angular process of the mandible occurs only in some of the rodents. Instead, a comparison of the upper cheek-teeth of *Eurymylus* with the corresponding row in the Paleocene rodents from the genus *Paramys* LEIDY, 1871 (see MCKENNA, 1961), leads to the conclusion that the paramyid multicuspid molars, far advanced in evolution, have no characters homologous with the characters of the tricuspid molars of *Eurymylus*. In view of the great differences distingushing these types of teeth and the lack of any intermediate forms the attempts at finding a homology between them are for the time being fated to fail. It cannot be ruled out that such intermediate forms will be found in Asia, though as yet the most ancient primitive rodents are known from the New World. Thus, the recognition of *Eurymylus* as a member of the order Rodentia would have still poorer grounds than its inclusion in the Lagomorpha.

RELATION TO THE INSECTIVORA

So far the considerations on the relationships of *Eurymylus* to the Insectivora have practically been carried out in the bearing of researches aiming at the finding of the ancestors of the Lagomorpha. One of the first hypotheses about the relationships between the Lagomorpha and Insectivora was RUSSELL'S (1959) idea concerning the possibility of seeking the ancestors of lagomorphs in the insectivore Zalambdalestidae. The considerations in this respect hardly seem to be constructive, since, firstly, the relationships of the Lagomorpha need not be studied through the genus *Eurymylus* and, secondly, the differences in the structure of the skull and dentition between *Eurymylus* and *Zalambdalestes* are too great to compare these two forms without investigating the intermediate stages of their evolution and these have not been discovered as yet. Refuting Russell's hypothesis about the possibility of close relationships between lagomorphs and the Zalambdalestidae, VAN VALEN (1964) compares *Eurymylus laticeps* with the Paleocene genus *Pseudictops* MATTHEW *et al.*, 1929 from Mongolia. The upper cheek-teeth are, in my opinion, the only structures with which the corresponding teeth of *Eurymylus* might really be compared directly. The similarity of these teeth consists in the elongation of their grinding surfaces in a transverse direction in both species and in the presence of 2 lateral cusps and a medial cusp on the upper molars. However, their homology is not quite clear. The similarity in respect of the lower dentition boils down to the bicuspid structure of the molars. The differences in the structure of the anterior parts of the mandible and maxilla and in the number and specialization of the incisors and canines are enormous. SULIMSKI (1968) also lays stress on these differences, which the abundance of his materials makes quite convincing. It is true that in view of the lack of other forms having more characters in common with *Eurymylus*, *Pseudictops* shows the greatest resemblance to it. This resemblance and, the more so, affinity are, however, very remote. Thus, we arrive at the conclusion that the contemporaneous *Eurymylus* and *Pseudictops*, were members of separately evolving groups, which probably had their common ancestors only among very remote Cretaceous primitive mammals.

PHYLOGENETIC POSITION OF *EURYMYLUS*

On the basis of the foregoing considerations *Eurymylus* seems to belong to a group which originated from the Cretaceous Insectivora, fairly close to the group *Pseudictops*, but representing a completely different line of evolution. *Eurymylus* was therefore probably an issueless evolutionary line which became extinct before the Eocene and deserves to be distinguished as a separate order.

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Kraków, May 1970

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PLATES

L. SYCH: MIXODONTIA, A NEW ORDER OF MAMMALS

PLATE XXV

(see also Plates XXVI, XXVII, XXVIII)

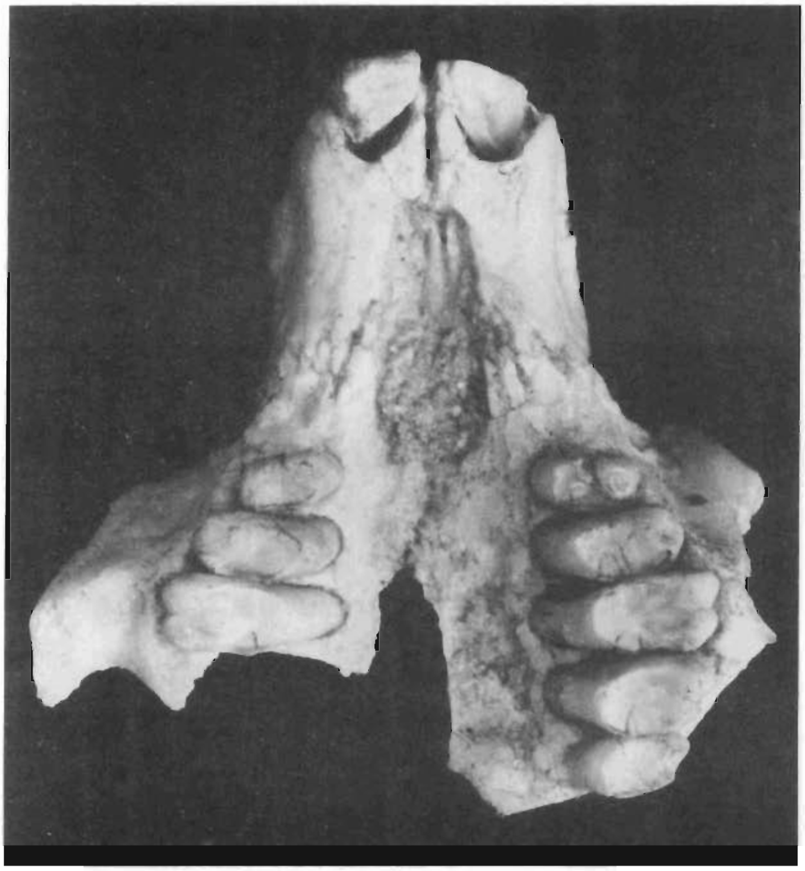
Upper Paleocene, Naran Bulak, Nemegt Basin, Gobi Desert, Mongolia.

Fig. 1. Anterior part of the snout in palatal view (Z. Pal. No. MgM-II/62); ×5.6.

Fig. 2. Frontal section of the lower incisor. Only the enamel layer consisting of two parts of enamel prism bounds is visible; ×4.2.

Fig. 3. The rentgenogram of the lower jaw showing the position of the lower incisor and tooth roots (Z. Pal. No. MgM-II/61); ×9.8.

Photo: L. Sych



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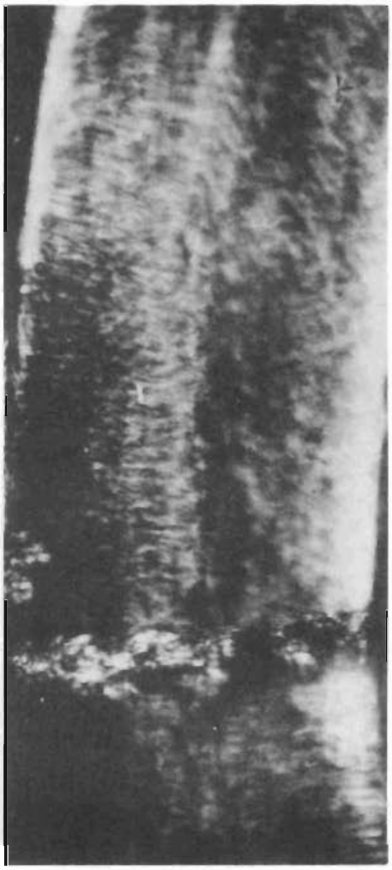

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L. SYCH: MIXODONTIA, A NEW ORDER OF MAMMALS

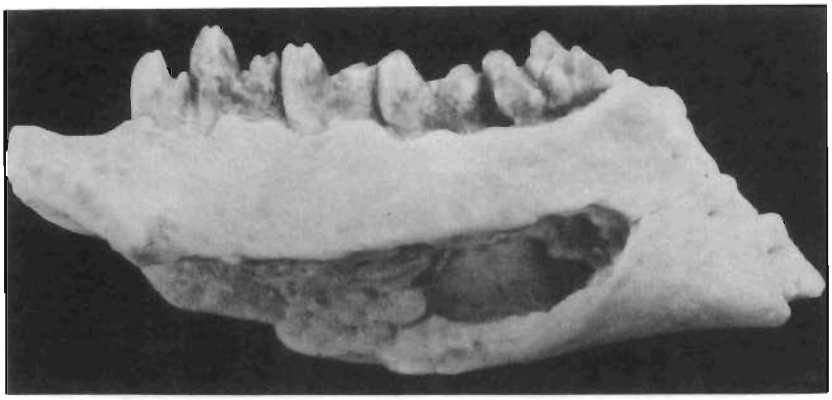
PLATE XXVI

(see also Plates XXV, XXVII, XXVIII)

Upper Paleocene, Naran Bulak, Nemegt Basin, Gobi Desert, Mongolia

Fig. 1*a-b*. Lower jaw in inner and outer views (Z. Pal. No. MgM-II/58); ×6.
Fig. 2*a-b*. Lower jaw in inner and outer views (Z. Pal. No. MgM-II/60); ×6.
Fig. 3*a-b*. Fragment of maxilla in outer and inner views (Z. Pal. No. MgM-II/64); ×9.5.
Fig. 4. Fragment of the lower jaw in inner view (Z. Pal. No. MgM-II/65); ×7.

Photo: L. Sych



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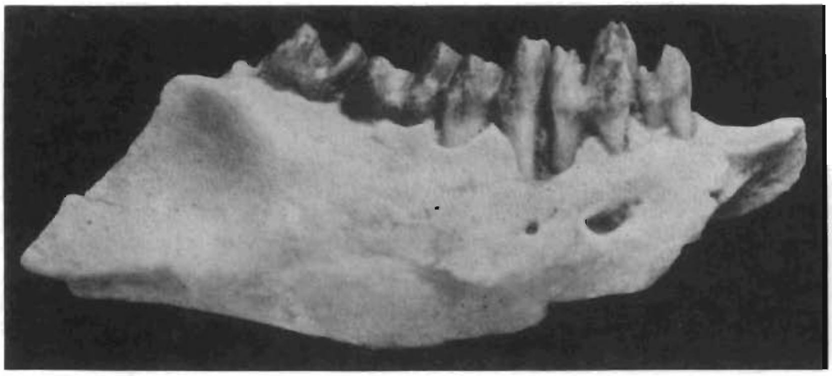

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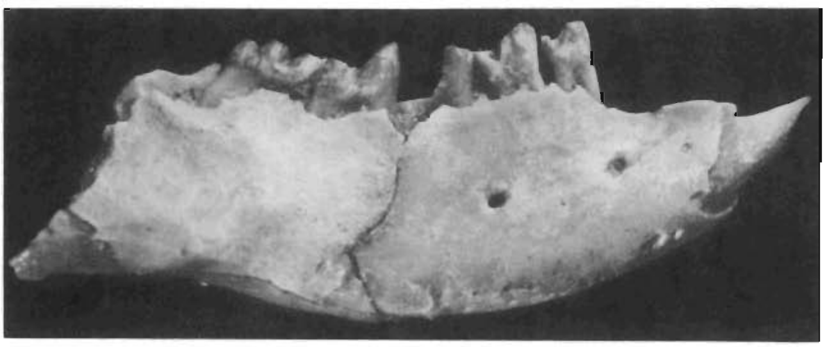
2b



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L. SYCH: MIXODONTIA, A NEW ORDER OF MAMMALS

PLATE XXVII

Page

Eurymylus platiceps MATTHEW & GRANGER 148

(see also Plates XXV, XXVI, XXVIII)

Upper Paleocene, Naran Bulak, Nemegt Basin, Gobi Desert, Mongolia

Fig. 1*a-b*. Lower jaw in inner and outer views; ×5.3.
Fig. 1*c*. The tooth row of the same specimen in occlusal view; ×5.3.
Fig. 2. Lower jaw with dentition in occlusal view, showing the angular process bending medially (Z. Pal. No. MgM-II/61); ×5.6.
Fig. 3. Upper tooth row, (Z. Pal. No. MgM-II/62); ×9.4.

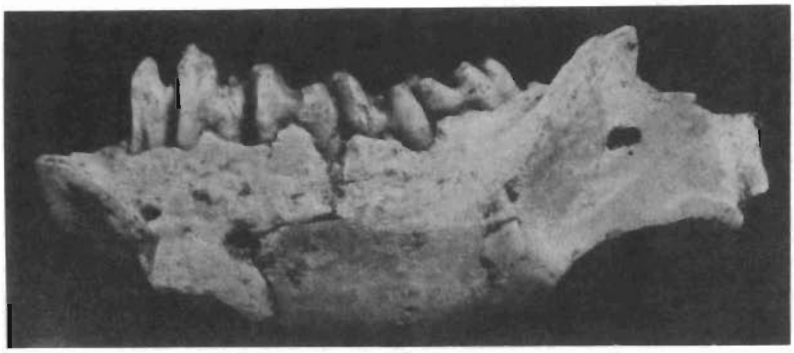
Palaeolagus haydeni LEIDY 155

Oligocene, Orellan Formation, Harrison, Nebraska, U. S. A.

Fig. 4. Upper tooth row (Z. Z. S. No. MF/973/10); ×8.

Photo: L. Sych

1a



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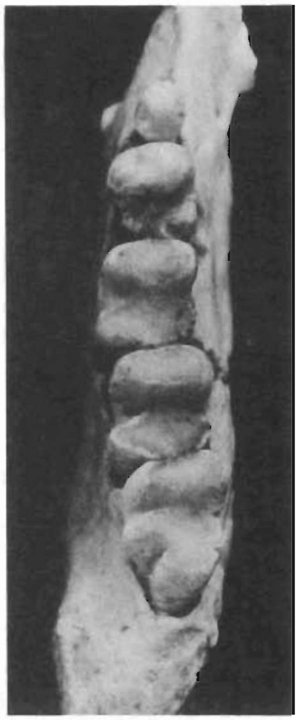

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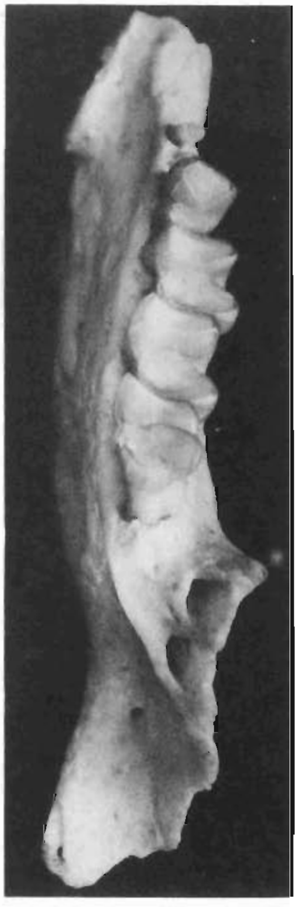

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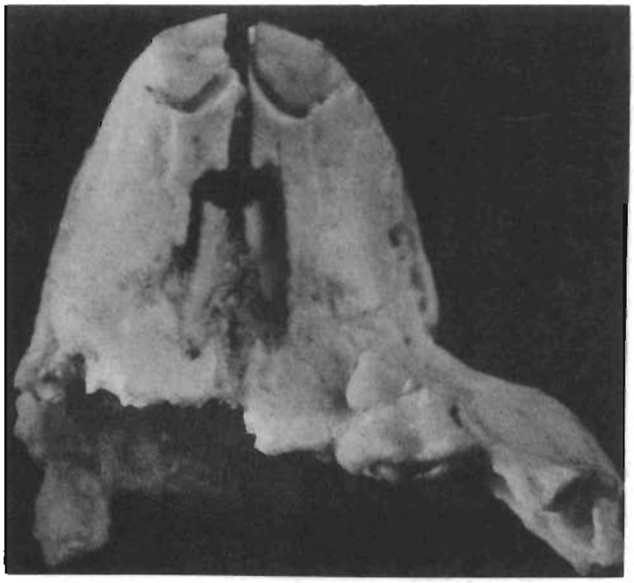
L. SYCH: MIXODONTIA, A NEW ORDER OF MAMMALS

PLATE XXVIII

Upper Paleocene, Naran Bulak, Nemegt Basin, Gobi Desert, Mongolia

Fig. 1*a*. Anterior part of the snout with DM^2 and DM^3 in palatal view (Z. Pal. No. MgM-II/63); ×5.6.
Fig. 1*b*. DM^2 and DM^3 of the same specimen in occlusal view; ×12.
Fig. 2*a-b*. The lower jaw in outer and inner views (Z. Pal. No. MgM-II/61); ×5.6.
Fig. 3. DM^3 and just erupting P^3 in posterior view (Z. Pal. No. MgM-II/63); ×12.
Fig. 4. The upper incisor in lingual view (Z. Pal. No. MgM-II/66); ×6.

Photo: L. Sych



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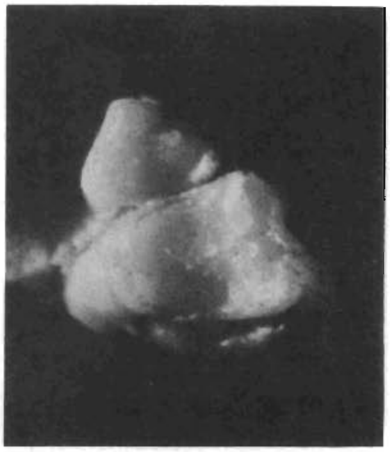

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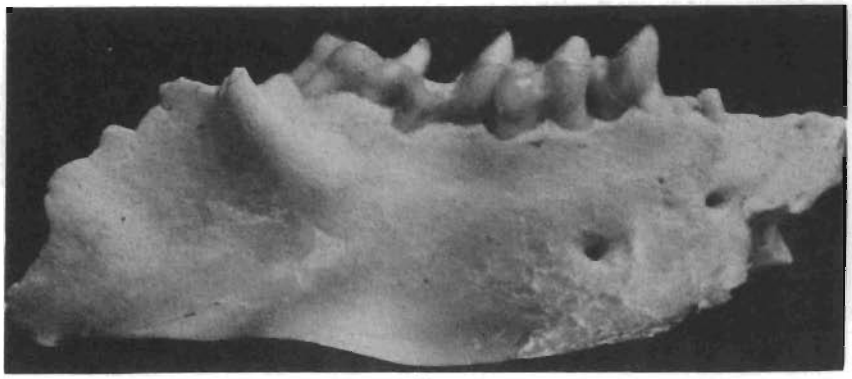

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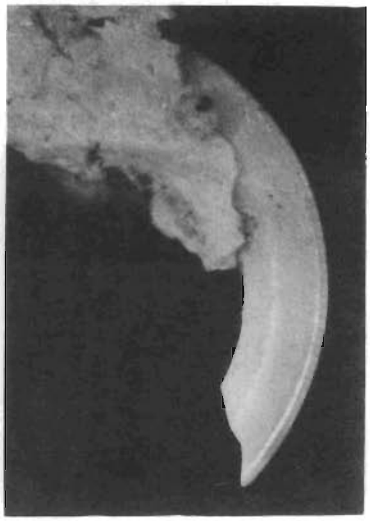

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