

PALAEOCENE AND EOCENE MIXODONTIA (MAMMALIA, GLIRES) OF MONGOLIA AND CHINA

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ABSTRACT. Three new mixodont genera and species from the late Palaeocene of Mongolia, *Khaychina elongata*, *Eomylus zhigdenensis*, and *Amar aleator* are described; '*Mimotona borealis*' (late Palaeocene of China) is referred to *Eomylus*. Also described is *Mimotona lii* n. sp. from the middle Palaeocene of China. The dentition of *Gomphos elkema* is more fully documented by new material, as is that of *Rhombomylus* and *Eurymylus*. *Gomphos*, *Rhombomylus*, and '*Matutinia*' are compared and '*M. nitidulus*' referred to *Rhombomylus*. The additional specimens and taxa contribute to our knowledge of a group that could be ancestral to rodents and lagomorphs.

MIXODONTS are frequently cited when the subject of the ancestry of rodents and lagomorphs is discussed (Sych 1971; Li 1977). Although this possibility has not received unanimous acclaim (Butler 1985), it is our belief that when the diversity of mixodonts is better known the transition between them and probably both rodents and lagomorphs will be demonstrable. This paper deals with new material that increases by 50% the number of described taxa in the group.

The description of new mixodonts from the early Palaeogene of Mongolia has necessitated a review of the forms similarly endowed with a gliriform adaptation and with comparable cheek tooth morphology. We have tried to provide here an essentially complete photographic documentation of the Mixodontia, not all of the previously described forms having been adequately illustrated.

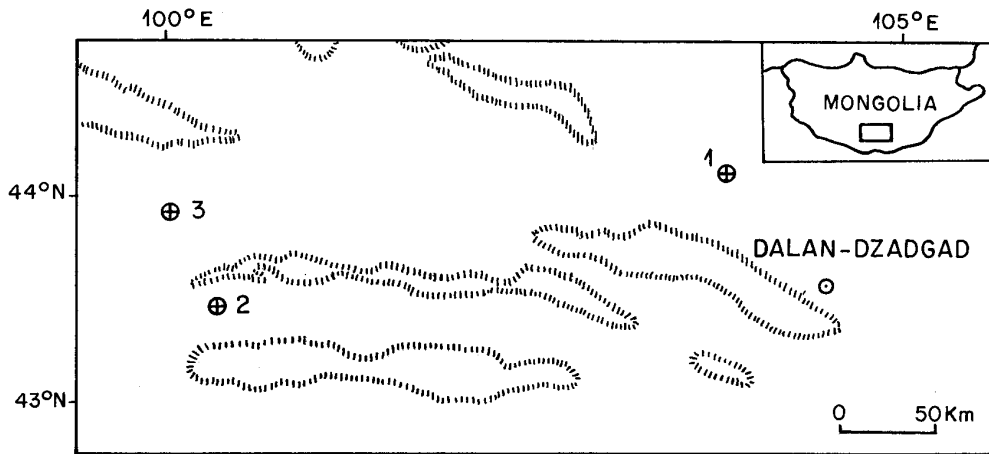
This paper is part of a series dealing with new discoveries in the late Palaeocene and early Eocene of Mongolia. Recent descriptions of the biostratigraphy and new faunal elements were made by Dashzeveg (1982a), Russell and Dashzeveg (1986), and Dashzeveg, Russell, and Flynn (1987).

The Mongolian Mixodontia described in this article come from well-studied beds (see, for example, Badamgarav and Reshetov 1985) in three intermontane depressions in the southern part of the country, the Nemegt Basin, the Ulan-Nur Basin, and the Bugin-Tsav Basin (text-fig. 1).

In the Nemegt Basin mixodonts and other vertebrates were collected from four quarries situated at different stratigraphic levels within the Naran-Bulak Beds, not taking into account surface finds (text-fig. 2).

I. Tsagan-Khushu locality, Quarry 3, Zhigden Member: this new site, discovered (by D. D.) in 1984, is 300 m to the north of the classic Quarry 1. The bone-bearing lens of red sandy clay has a thickness of about 1 m and is situated in the upper part of the Zhigden Member. Jaws and teeth of mixodonts dominate in the assemblage; the new genera and species *Eomylus zhigdenensis* and *Amar aleator* were among these. The notoungulate *Arctostylops macrodon* and the tillodont *Ernanodon* sp. also occur here.

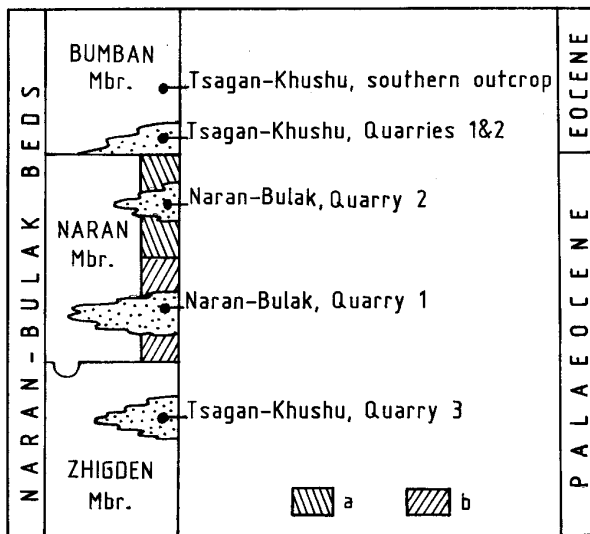
II. Naran-Bulak locality, Quarry 1, Naran Member (alluvial deposits): this site was found near the landmark termed the North Sphinx during the Mongolian Palaeontological Expedition of the Academy of Sciences of the Soviet Union in 1948; its vertebrates are the most studied and its position at the base of the Naran Member is well established. The fossiliferous sediments are white quartz sands with intercalated lenses of gravel. *Prodinoceras*, *Archaeolamda*, and *Pachyaena* are the most important elements (see Flerov 1952, 1957; Kielan-Jaworowska 1968/1969; Dashzeveg 1976, 1982b); a specimen referable to *Eomylus zhigdenensis* n. gen. n. sp. has also been found here.



TEXT-FIG. 1. Sketch map of the south-central part of Mongolia showing the situation of 1, the Ulan-Nur Basin with the Gashato locality; 2, the Nemegt Basin with the localities of Naran-Bulak and Tsagan-Khushu; 3, the Bugin-Tsav Basin with the Khaychin-Ula locality. Modified from Gradzinski *et al.* 1968/1969.

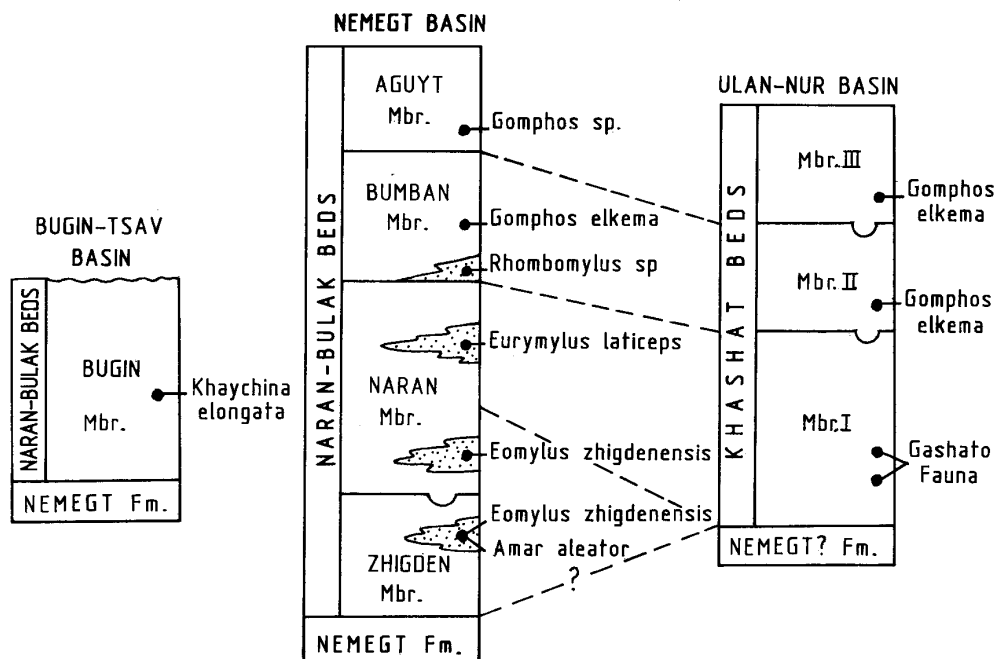
In the upper part of the white sands the sediment becomes more argillaceous and has furnished rare remains of small mammals: *Arctostylops*, *Pseudictops*, and the mixodont *Eurymylus*.

III. Naran-Bulak locality, Quarry 2, Naran Member (lacustrine deposits): this richly fossiliferous site was discovered (by D. D.) during the Polish Palaeontological Expedition of 1964-1965 and is situated about 250 m east of the Naran-Bulak Quarry 1. The white sands and sandstones have yielded abundant remains of Arctostylopidae, Pseudictopidae, and mixodonts. The first author has also collected material referable to *Prionessus*, *Oxyaena*, 'Sinopa', and *Dissacus* (Dashzeveg 1977) and worked by screen-washing.



TEXT-FIG. 2. Composite section of the Naran-Bulak Beds in the Nemegt Basin showing the stratigraphic position of the fossiliferous quarries. a, alluvial deposits. b, lacustrine deposits.

IV. Tsagan-Khushu locality, Quarry 1, Bumban Member: an extensive collection of fossil mammals was obtained here (by D. D.) by screen-washing. The fossils occur in lenses of sandy gravel, above the green clays of the Naran Member, which are 10–30 cm thick and contain numerous remains of small vertebrates. The material, referable to insectivores, primates, condylarths, and perissodactyls, as well as mixodonts, has been discussed in Dashzeveg (1977, 1979a, b), in Dashzeveg and McKenna (1977) and in Russell and Dashzeveg (1986).



TEXT-FIG. 3. Biostratigraphic correlation between the Ulan-Nur Basin, the Nemegt Basin, and the Bugin-Tsav Basin.

V. Tsagan-Khushu locality, Quarry 2, Bumban Member: this site, near the boundary between the Naran and Bumban Members, is 300 m south of Quarry 1. Brown sandstone and gravel lenses, 20 cm to 1 m in thickness, have produced a rich mammalian assemblage very similar to that from Quarry 1. As concerns mixodonts, *Rhombomylus* and *Gomphos* are known from here. *Gomphos* has also been discovered, as a surface find, on the southern side of Tsagan-Khushu.

In the south-eastern part of the Ulan-Nur Basin is situated the important locality of Gashato. Its fauna and stratigraphy have been much discussed. According to the field research of the first author (D. D.) the mixodont *E. laticeps* comes from the red clay of the first member of the Khashat Beds (or Svita, in Soviet and Mongolian usage); it is found together with *Arctostylops macrodon*, *A. iturus*, and *Prionessus lucifer*.

The fauna of the second and third members of the Khashat Beds is not yet known, except for *G. elkema*. Remains of the latter have also been found at the base of the third member. The material of *Gomphos* collected (by D. D. in 1978) from the second member is illustrated here (text-fig. 24).

The known Gashato fauna of the first member is correlated with the lacustrine deposits of the Naran Member of the Naran-Bulak Beds in the Nemegt Basin and is considered to be late Palaeocene in age. Recently, *G. elkema* has been found in the Bumban Member of the Naran-Bulak Beds, which

are otherwise well dated as early Eocene by such forms as *Hyopsodus*, *Homogalax*, and numerous rodents. This implies that the second and third members of the Khashat Beds are approximate age equivalents of the upper part of the Naran-Bulak Beds.

In the Bugin-Tsav Basin Palaeocene and Eocene deposits are exposed along its southern side where they form a series of cliffs extending over a distance of 20 km. The late Palaeocene sediments, named the Bugin Member by the first author, crop out in the region of Khaychin-Ula II (Khaychin I, according to Badamgarav and Reshetov 1985), and consist of light grey or greenish grey deposits of sandstones, clay, and gravelites unconformably overlying the late Cretaceous Nemegt Formation. The mixodont *Khaychina elongata* n. gen., n. sp. was found in the middle part of the Bugin Member, where *Prodinoceras* sp. and *Archaeolambda trofimovi* were also discovered. Based on the presence of the latter two taxa, the Bugin Member can be correlated with the Naran Member of the Naran-Bulak Beds in the Nemegt Basin.

ABBREVIATIONS

IVPP. Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, Chinese People's Republic.

MgM. Prefix referring to collections in the Institute of Palaeobiology, Warsaw, Poland.

PSS. Prefix referring to the collections of the Palaeontology and Stratigraphy Section, Institute of Geology, Academy of Sciences of the Mongolian People's Republic, Ulan Bator.

V. Prefix referring to the collections of the IVPP.

Measurements are in millimetres.

SYSTEMATIC PALAEOLOGY

The Mixodontia were for many years confused with and included in the order Anagalida. We refer to the Mixodontia only those forms characterized by enlarged, apparently ever-growing incisors, a diastema, premolar loss, and a relatively short, deep mandible, in contrast to members of the Anagalida which have small incisors, little or no diastema, unreduced premolars, and an elongate, shallow mandible. This article is essentially a revision of the Mixodontia viewed in this concept.

For the first described mixodont, *Eurymylus*, the family name Eurymylidae was proposed (Matthew *et al.* 1929). Nearly fifty years later, discoveries in China produced taxa that Li (1977) placed in the new family Mimotonidae. At the time he remarked that the family was tentatively established for the new forms, a fact that was noted by Bleefeld and McKenna (1985); the latter, basing their opinion on article 15 of the International Code of Zoological Nomenclature, declared the name not available. Since the name has been widely used for the past ten years, taxonomic stability is not particularly well served by this decision. Also, Dr Li (in Li & Ting 1985, p. 44) has referred to 'the new family Mimotonidae' that he created in 1977, obviously eliminating the tentativeness that was previously expressed. To date, the Eurymylidae and the Mimotonidae are the only recognized mixodont families.

Cohort GLIRES Linnaeus, 1758

Order MIXODONTIA Sych 1971

Family EURYMYLIDAE Matthew, Granger and Simpson, 1929

Subfamily EURYMYLINAE new

Eomylus n. gen.

Type species. *Eomylus zhigdenensis* n. sp.

Referred species. *E. borealis* (Chow & Qi 1978).

Age and distribution. Late Palaeocene, Mongolian People's Republic and Chinese People's Republic.

Diagnosis. Dental formula: ?-0-2-3/1?-0-2-3. Differs from *Rhombomylus*, *Matutinia*, *Mimotona*, *Heomys*, *Eurymylus*, *Amar* (n. gen.), and *Gomphos* by its short (anteroposteriorly), transversely

elongate upper molars and by the lack of expansion of the hypoconal shelf, and from all but *Mimotona* and *Amar* by the position of the hypocone lingual with respect to the protocone. Differs from *Rhombomylus*, *Matutinia*, *Mimotona*, and *Heomys* by the absence of a lingual groove extending vertically between the protocone and hypocone. Differs from *Heomys* by a greater degree of unilateral hypsodonty (enamel of crown low on one side of a tooth and higher on the other) and from *Gomphos* and *Amar* by the absence of a parastyle. Differs from *Heomys* and *Eurymylus* by the absence of a dorsoanteriorly oriented flange on the anterior facial surface of the jugal arch (but is similar to the condition in *Mimotona*; unknown in *Rhombomylus*, *Gomphos*, *Amar*, and *Matutinia*).

It should be noted that the hypocone here is lingual only in the unworn condition. With considerable wear the protocone would become the more lingual. Also, concerning transverse elongation, since the upper molars in several of the enumerated genera tend to be pyramidal and to wear rapidly, the teeth in an older individual have an aspect of greater transverse elongation than do little or unworn teeth. This is well illustrated in *Eurymylus* where the specimens figured by Sych (1971) look anteroposteriorly short and wide transversely, but in the unworn specimen, PSS 20-162, figured here (text-fig. 5) the occlusal surface is subquadrate or even elongate anteroposteriorly.

Etymology. *Eos* (Gk.), dawn; *mylos* (Gk.), grinder, and by extension, molar.

Eomylus zhigdenensis n. sp.

Text-figs. 4, 6, 7

Holotype. PSS 20-139, right maxillary fragment with M1/-M2/.

Referred specimens. PSS 20-137, mandibular fragment with left M/1-M/3; PSS 20-138, right mandibular fragment with M/1-M/2.

Locality and stratigraphic distribution. Tsagan-Khushu locality, Nemegt Basin, southern MPR; Zhigden Member of the Naran-Bulak Beds; late Palaeocene.

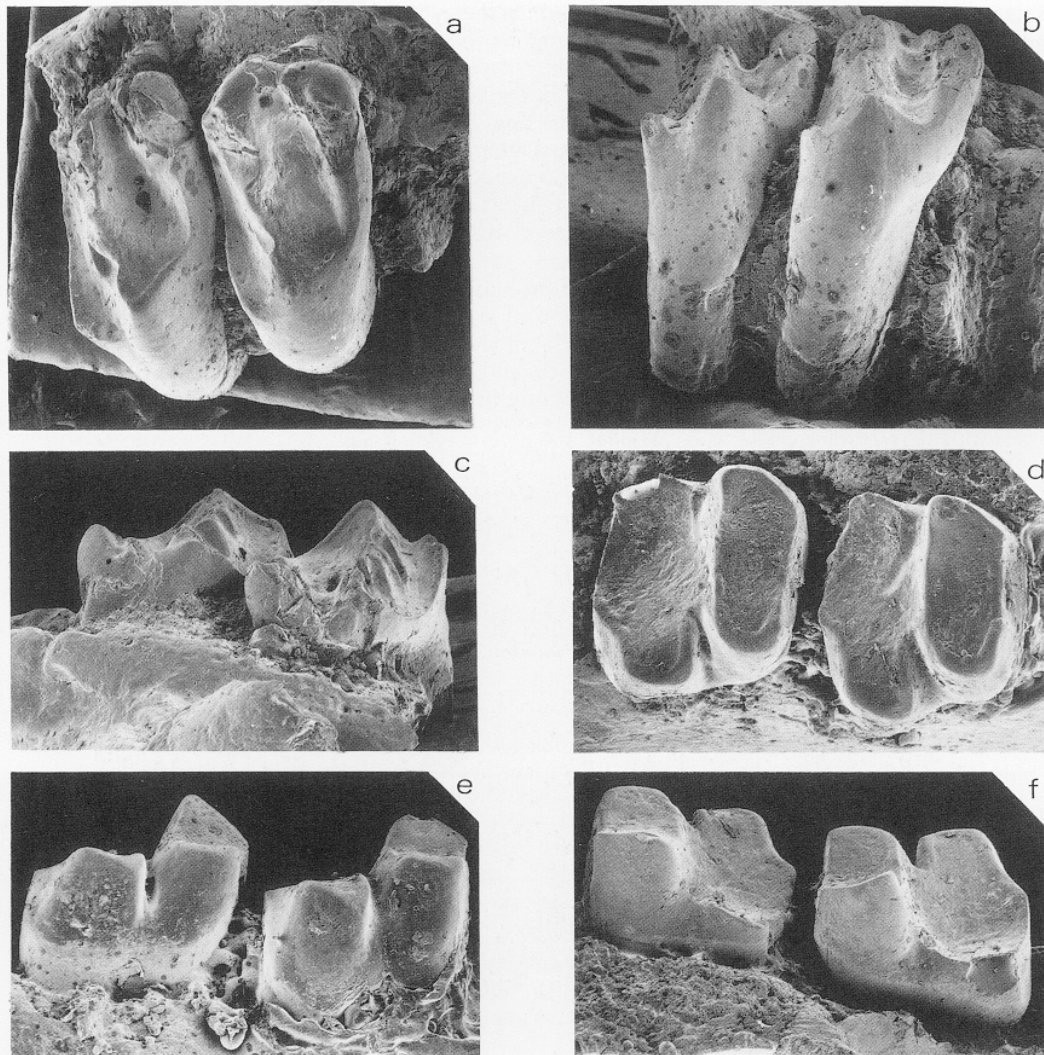
Questionably referred specimen. PSS 20-133, left mandible with P/4-M/3, from the Naran-Bulak locality, Nemegt Basin, MPR; Naran Member of the Naran-Bulak Beds; late Palaeocene. All specimens are from the collections of the Department of Stratigraphy and Palaeontology, Institute of Geology, Academy of Sciences of the MPR, Ulan Bator.

Diagnosis. As for genus, only species.

Etymology. *Zhigden* (Mong.), gooseberry; from the name of the geologic member in which the type and referred specimens were found.

Description. The type specimen, PSS 20-139 (text-fig. 4a-c), is a maxillary fragment retaining only M1/ and M2/, but the teeth are well preserved and very little worn. Remnants of anterior alveoli indicate that P4/ and P3/ were present, as was M3/. The molar teeth are notably narrow and transversely elongate. In posterior view, the protocone is of subequal height to the two labial cusps, but the hypoconal shelf, or posterior cingulum, is situated well below the summit of the protocone; no hypocone is present and the shelf is narrow. The pre- and postprotocristae form sharp crests extending between the protocone and the bases of the paracone and metacone; the preprotocrista is low just anterior to the protocone, forming an opening to the trigon basin, but the postprotocrista is high and strong throughout its length. Transverse chewing movements obviously followed the axis of this crest. A weak paraconule is present close to the lingual base of the paracone; the metaconule is more strongly developed and is winged, with an anterior crest curving to the lingual base of the metacone and a posterior crest extending to the posterior base of this cusp. There are no styler cusps and no anterior cingulum. Labially, the crown height is very low, while lingually it is at least three times as high, thus manifesting unilateral hypsodonty. The lingual base of the molar teeth extends far beyond the level of the protocone, situating the latter at about 1/3 of the tooth's width from its lingual border. Despite a marked curvature (in occlusal view) of the maxillary bordering the alveoli the molar teeth appear to have been aligned in a rather straight row and to have been all about the same size; the premolars are situated more lingually.

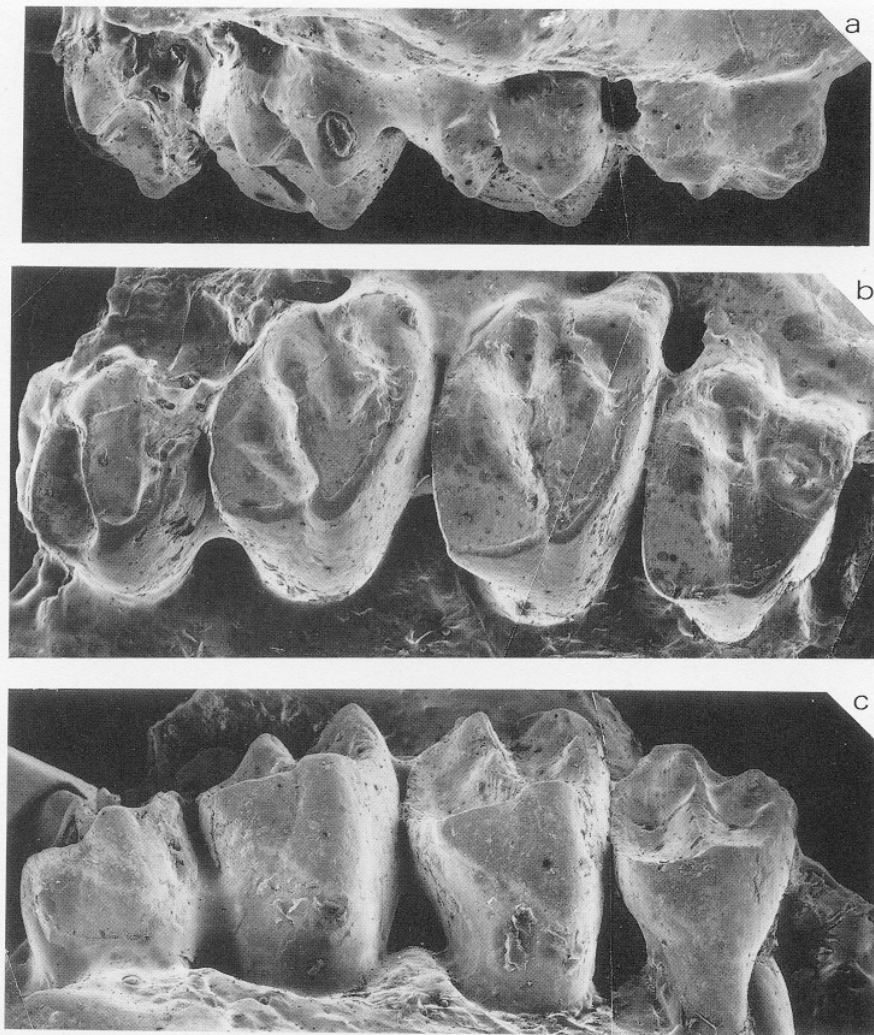
On the basis of accordance in size and identical provenance, two partial mandibles are referred to this species, PSS 20-137, with the left M/1-M/3 (text-fig. 6) and PSS 20-138, with the right M/1-M/2 (text-fig. 4d-f). Occlusion between the unworn right maxillary and the heavily worn right mandible does not give very satisfactory results,



TEXT-FIG. 4. *Eomylus zhigdenensis* n. gen., n. sp. *a-c*, PSS 20-139, holotype, right maxillary with M1-M2/. *a*, occlusal view; *b*, lingual view; *c*, labial view. *d-f*, PSS 20-138, right mandibular fragment with M1-M2/. *d*, occlusal view; *e*, labial view; *f*, lingual view. All views $\times 15$; both specimens from the Zhigden Member of the Naran-Bulak Beds at Quarry III, Tsagan-Khushu, Mongolia; late Palaeocene.

but does not entirely negate the possibility of their being conspecific. Most of the features of PSS 20-138 have been eliminated to the point of the two molars being represented only by the elongate oval surface of the trigonid and the larger (and wider) surface of the talonid. The posterior wall of the trigonid remains, however, and indicates the absence of propalinal movement. The incisor is preserved, extending posteriorly to below M/3; it is not known if a second incisor was present. From the curvature of the remaining part of the incisor and the position of the premolar alveoli it would seem that the diastema was very short.

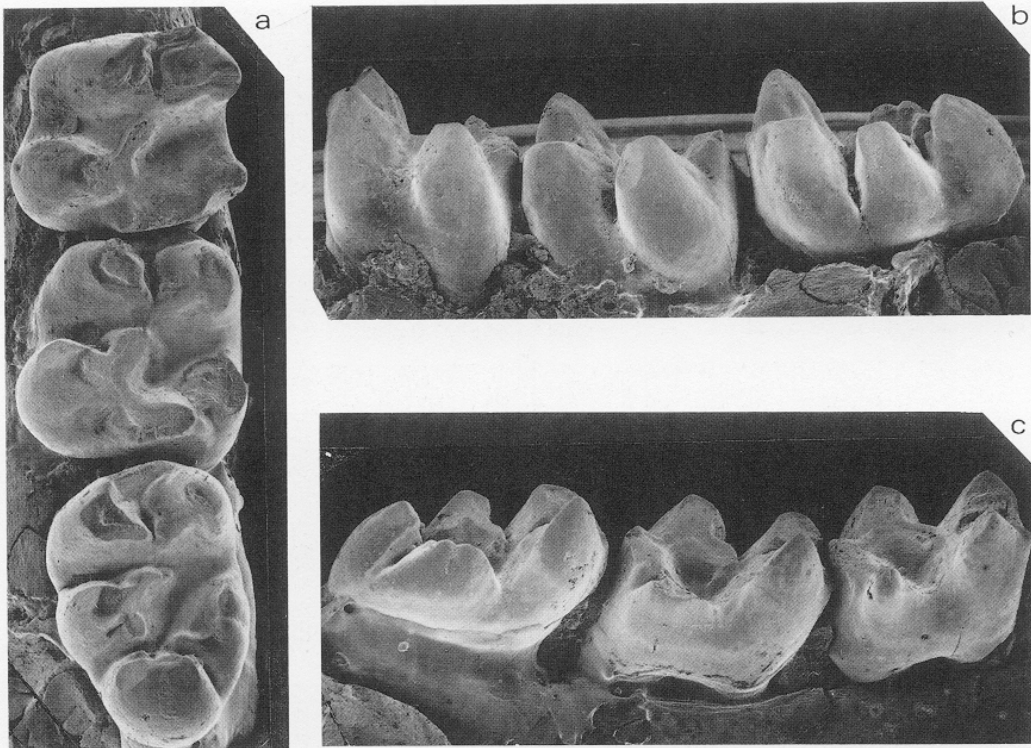
If PSS 20-138 is truly referable to *Eomylus zhigdenensis* it lends credence to the attribution of the latter to the



TEXT-FIG. 5. *Eurymylus laticeps* Matthew and Granger, 1925. *a-c*, PSS 20-162, right maxillary with DP4/-M3/. *a*, labial view; *b*, occlusal view; *c*, lingual view; note the definitive P4/ erupting below the DP4/. All views $\times 15$. Specimen from the Naran Member of the Naran-Bulak Beds at Naran-Bulak locality, Mongolia; late Palaeocene.

Mixodontia by the posterior extension of the incisor and by the apparent shortness of the mandible measured between P/3 and the anterior extension of this incisor.

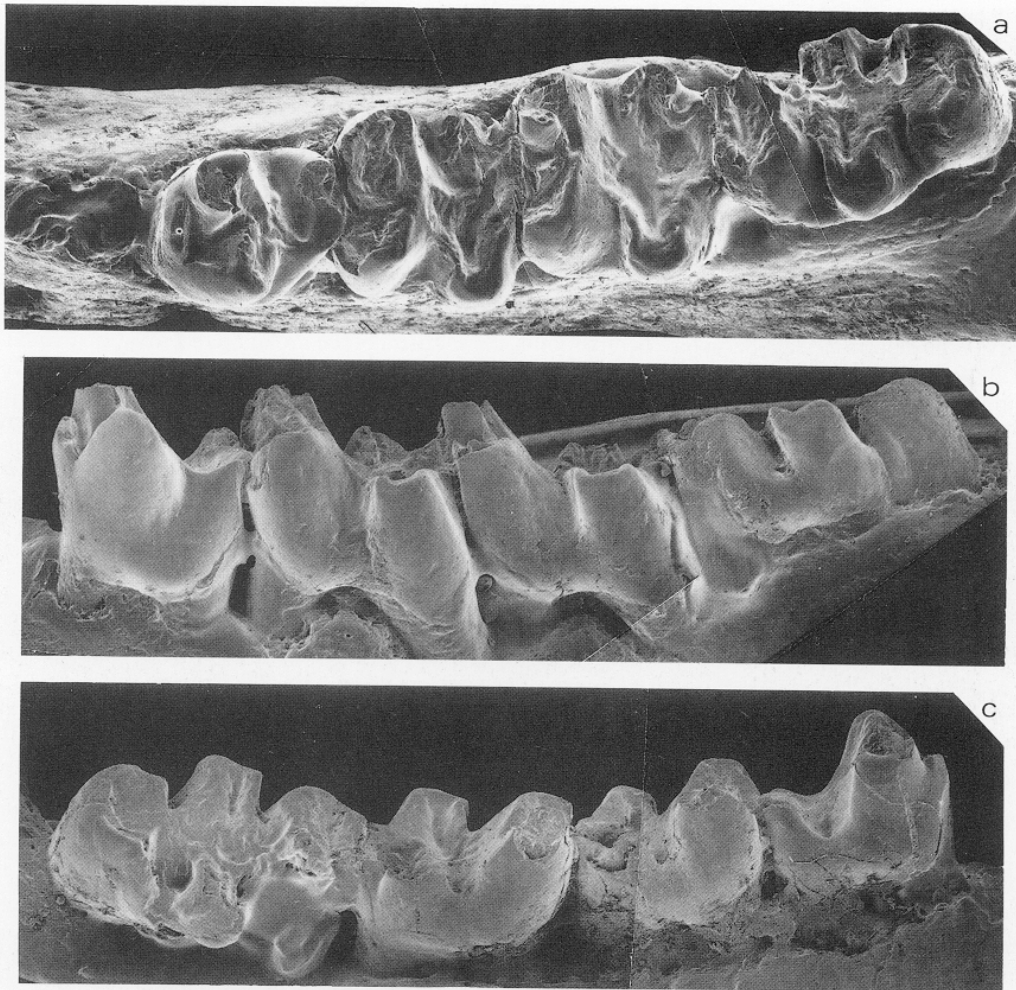
If PSS 20-138 and 20-137 can be considered as representative of *E. zhigdenensis* the latter differs (in its lower dentition) from *Rhombomylus*, *Matutinia*, *Eurymylus*, *Gomphos*, and *Hypsimylus* by the wider talonid on M/1 and M/2; from *Mimotona* (*M. wana*, *M. robusta*, and *M. lii* n. sp.), *Gomphos*, and *Hypsimylus* by having less unilateral hypsodonty; from *Mimotona* (*M. wana*, *M. robusta*, and *M. lii* n. sp.) and *Gomphos* by the greater separation of the protoconid and hypoconid; from '*M. borealis*' by the absence of a deep groove between the hypoconulid and entoconid and by smaller size; from the mandible referred to *Heomys* (V 4322) by the M/1 and M/2



TEXT-FIG. 6. *Eomylys zhigdenensis* n. gen., n. sp. PSS 20-137, left mandible with M/1-M/3. a, occlusal view; b, labial view; c, lingual view. All views $\times 15$. Specimen from the Zhigden Member of the Naran-Bulak Beds at Quarry III, Tsagan-Khushu, Mongolia; late Palaeocene.

more subquadrate and the M/3 more elongate; and from *Zagmys* Dashzeveg *et al.* (1987) by a reduced paraconid.

The three molars of PSS 20-137 (text-fig. 6) are very well preserved and have undergone but little wear. There is no anterior cingulum; the paraconid is absent or perhaps barely indicated and crestiform on M/1. The protoconid, though the first to be reduced by wear (with the hypoconid), was probably nearly as high as the metaconid; a weak anterior crest extends from the protoconid to the anterior side of the metaconid and a posterior median crest of the protoconid is separated from a similar crest of the metaconid by a sharp, deep notch. The metaconid is the dominant cusp and is emphasized by a posterolingual crest extending vertically from its summit to its base. Difference in height of the trigonid with respect to the talonid is not great. On a fresh, unworn tooth the talonid basin is deep, with a groove in the bottom oriented obliquely, passing through the notch between the entoconid and the base of the metaconid and extending towards a notch between the hypoconid and the hypoconulid. With considerable wear, as in PSS 20-138, this obliquity becomes less apparent and the tooth takes the aspect of having undergone, principally, transverse wear. The cristid obliqua is inflated by a more or less crestiform mesoconid and attains the posterior surface of the trigonid below the protoconid-metaconid notch. In little or unworn condition the cristid obliqua is separated from the trigonid by a transverse groove. The hypoconid has a pinched (anteroposteriorly) aspect and extends notably beyond the protoconid in width; in M/3 it is subequal to the latter in width. In M/1 and M/2 the hypoconid is apparently connected by a low crest to the hypoconulid, but in M/3 the two cusps are separate. The hypoconulid is large, centrally located, and transversely elongate; it is possible that a small cuspule existed at its labial extremity (by which a connection was made with the hypoconid in M/1 and M/2), but it is largely removed by wear in the available material. The entoconid is high and situated close to the hypoconulid, to which it is connected by a high crest. In labial view the protoconid and



TEXT-FIG. 7. *Eomylus zhigdenensis* n. gen., n. sp. nov. *a-c*, PSS 20-133, left mandible with P/4-M/3. *a*, occlusal view; *b*, labial view; *c*, lingual view. All views $\times 15$. Specimen from the Naran Member of the Naran-Bulak Beds at Quarry I, Naran-Bulak, Mongolia; late Palaeocene.

hypoconid are rather widely separated and there is little or no evidence of unilateral hypsodonty. M/3 is the longest of the molars and also the narrowest.

The mandible from the Naran Member of the Naran-Bulak Beds, PSS 20-133 (text-fig. 7), closely resembles those from the Zhigden Member; it is more complete but the teeth are considerably more worn than those of PSS 20-137. Its principal differences from the Zhigden specimens appear to be in the proportions of the molar teeth; M/1 and M/2 are slightly smaller and M/3 is notably longer with the talonid exceeding the width of the trigonid as in M/1 and M/2. It is quite possible that these small differences reflect only intraspecific variation, although with a larger sample distinction of a form common to the Naran Member might be demonstrable. If the specimen is referable to *Eomylus zhigdenensis* (and in any case, it is closely related), it provides interesting details lacking in the Zhigden Member mandibles. For one thing, only a single incisor is present. The latter is separated from P/3 (represented only by the roots) by a short, sharply crested diastema. P/4 is well preserved and presents a

well-developed protoconid and metaconid with the latter being the higher. No paraconid is present but a strong paralophid closes a small trigonid basin anteriorly. The talonid is well basined (but open lingually) and much narrower than the trigonid. Two subequal cusps, aligned transversely, are situated centrally at the posterior extremity of the talonid. From what remains of the coronoid process it can be seen to arise well behind the M/3.

Measurements.

	L	W		L	W		L	W		L	W	
PSS 20-139			M1/	1.4	3.2	M2/	1.5	3.3				
PSS 20-137			M/1	1.8	2.1	M/2	2.2	2.2	M/3	2.6	1.8	
PSS 20-138				1.9	2.1		2.1	2.1				
PSS 20-133	P/4	1.8	1.5		1.6	2.0		2.0	2.0		2.8	2.0

Discussion. Even though none of the Zhigden specimens display the gliriform character of the anterior part of the dentition that characterizes mixodonts, comparison of the molar teeth provides adequate evidence to ensure referral to this group. Supplementary data from the Naran mandible (PSS 20-133) supports this attribution. The maxillary PSS 20-139 was chosen as type specimen because many of the taxa that have been referred to the Mixodontia are based on type material of the same nature (*Eurymylus*, *Matutinia*, *Rhombomylus*, *Mimotona*, and *Heomys*). The relationships of *Eomylus zhigdenensis* are considered in detail below.

Eomylus borealis (Chow and Qi, 1978) new combination

Text-fig. 8

Synonym. *Mimotona borealis* Chow and Qi, 1978.

Holotype. V 5531, right mandibular fragment with P/4-M/2; IVPP, Beijing, China.

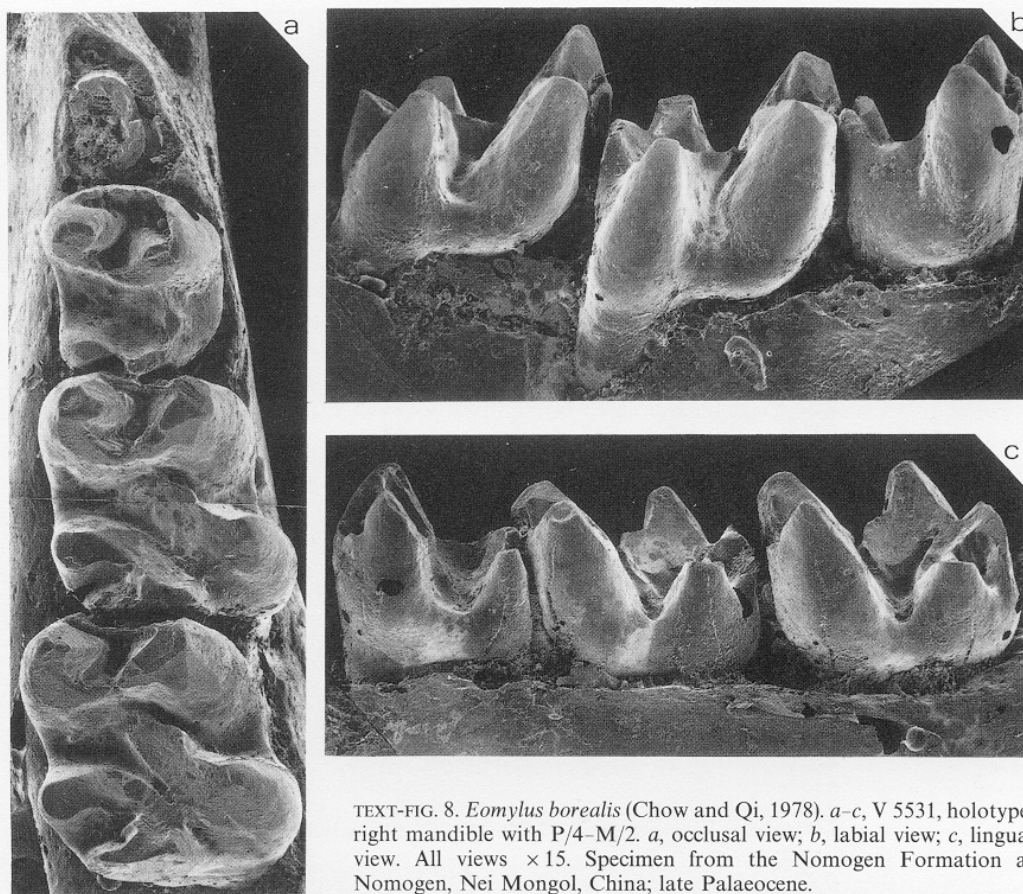
Referred material. This species is cited at Bayn Ulan, Nei Mongol (Zhai, pers. comm. 1981), but the material is undescribed.

Locality and stratigraphic distribution (of the type). Nomogen locality, Nei Mongol, CPR; Nomogen Formation; late Palaeocene.

Distinctive characters. Differs from *E. zhigdenensis* by its greater size and by the presence of a deep groove in the lower molars between the hypoconid and the hypoconulid.

Discussion. *E. borealis* was first referred to the genus *Mimotona*, but it is immediately distinguished from the two other species, *M. wana* Li, 1977 and *M. robusta* Li, 1977, by the presence of only a single incisor. Further comparison shows that it differs fundamentally from these species also in the morphology of its molars. For example, in *M. wana* the protoconid and hypoconid in labial view form parallel columns that are close together and nearly vertical; in *E. borealis* these columns are considerably further apart and are oblique. Molar crown height in *M. wana* is moderate lingually but notably greater labially, representing a degree of unilateral hypsodonty; both sides of the molar crowns in *E. borealis* are of about the same height. In occlusal view the hypoconulid and entoconid in *M. wana* are strongly linked, while they are separated by a deep groove in *E. borealis*. In *M. wana* the P/3 has a strong protoconid and metaconid and even a rudimentary paraconid; a well-developed (for a P/3) talonid is also present. Of the P/3 in *E. borealis* only the root is preserved, but it appears too small to have supported the complicated sort of crown seen in *M. wana*.

The teeth of the single specimen of *M. robusta* are rather heavily worn, but the labial columns formed by the protoconid and hypoconid appear to be more similar to those of *M. wana* than to those of *E. borealis*, that is to say, close together and nearly vertical. Like *M. wana*, *M. robusta* possesses two (lower, at least) incisors. Probably hypoconulid-entoconid relationships are also as in *M. wana* (strongly linked), reinforcing the affinity between it and *M. wana* and distinguishing the species from *E. borealis*. One can mention in passing that *M. robusta* differs principally from *M. wana* by a considerably greater size and by the proportions of P/4. To conclude, the observations enumerated above lead us to propose that the species *borealis* is better referred to *Eomylus* than it is to *Mimotona*.



TEXT-FIG. 8. *Eomylus borealis* (Chow and Qi, 1978). *a-c*, V 5531, holotype, right mandible with P/4-M/2. *a*, occlusal view; *b*, labial view; *c*, lingual view. All views $\times 15$. Specimen from the Nomogen Formation at Nomogen, Nei Mongol, China; late Palaeocene.

Amar n. gen.

Type species. *Amar aleator* n. sp.

Age and distribution. Late Palaeocene, MPR.

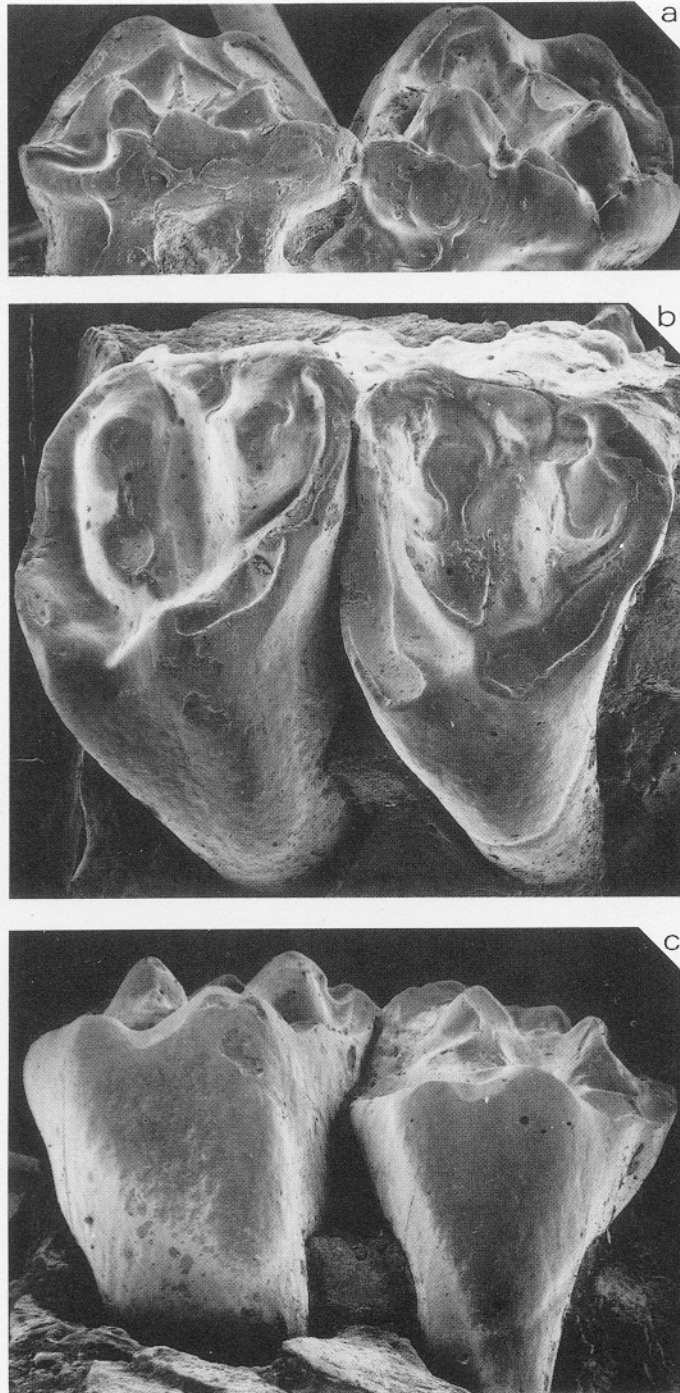
Diagnosis. Differs from *Eurymylus*, *Rhombomylus*, *Eomylus*, *Heomys*, and *Mimotona* by the presence of a labial cingulum and a strong mesostyle on the upper molars, and by the absence of a vertical lingual groove between the protocone and hypocone; differs from *Eomylus*, *Gomphos*, and *Mimotona* by upper molars that are longer and less transversely elongate; differs from *Gomphos* by a stronger mesostyle and labial cingulum and (also from *Mimotona*) by less lingual hypsodonty; differs from *Rhombomylus*, *Eurymylus*, *Gomphos*, and *Heomys* by the position of the hypocone lingual with respect to the protocone.

Etymology. *Amar* (Mong.), peace.

Amar aleator n. sp.

Holotype. PSS 20-161, right maxillary fragment with M1-/M2/.

Locality and stratigraphic distribution. Tsagan-Khushu locality, Quarry 3, Nemegt Basin, southern MPR; Zhigden Member of the Naran-Bulak Beds; late Palaeocene.



TEXT-FIG. 9. *Amar aleator* n. gen., n. sp. *a-c*, PSS 20-161, holotype, right maxillary with M1/-M2/. *a*, labial view; *b*, occlusal view; *c*, lingual view. All views $\times 15$. Specimen from the Zhigden Member of the Naran-Bulak Beds at Quarry III, Tsagan-Khushu, Mongolia; late Palaeocene.

Diagnosis. As for genus, only species.

Etymology. *Aleator* (L.), dice-player, referring to the uncertainty over its taxonomic position.

Description. Only M1/ and M2/ are preserved in PSS 20-161, but the presence of at least P4/ is indicated by alveoli, and of M3/ by a wear facet on the posterior side of M2/ and a partial alveolus. The two molars are notably subquadrate in their present state and even with wear would never become exaggeratedly transversely elongate. The strong preprotocrista (in which the presence of a paracone is suggested by a widening of the crest) is continuous with the labial cingulum that itself joins the posterior cingulum. In M2/ the labial cingulum is weak or briefly interrupted opposite the paracone and metacone. A prominent mesostyle is formed between the two cusps; the paracone is the larger of the two; a suggestion of a parastyle is present. A metaconule that is subequal in size to the metacone occurs immediately lingual to the latter. The protocone is as high as the labial cusps and even higher in M2/. The hypocone is situated only slightly below the summit of the protocone and is as far lingual as the latter in M1/ and even further lingually in M2/. The hypoconal shelf is wide; there is no anterior cingulum. Lingual hypsodonty is well developed.

Measurements.

		L	W		L	W
PSS 20-161	M1/	3.0	4.0	M2/	3.3	4.5

Discussion. In the morphology of the labial region (cingulum, mesostyle) of its upper molars *Amar* resembles *Gomphos*, although in occlusal view the M1/-M2/ of the latter, with a labially protruding paracone, differ considerably. In lingual hypsodonty the upper molars of *Amar* do not equal that in *Gomphos* and little exceed, if any, the condition in *Eomylyus*, *Rhombomylyus*, and *Eurymylyus*. The lingual slope of the molars is steeper than in *Gomphos*, but more sloping than in *Mimotona* and *Heomys*; it is about the same as in *Rhombomylyus*, *Eurymylyus* and *Eomylyus*.

In the upper teeth of *Amar* we find no characters, not duplicated in the Eurymylidae, that indicate a particular relationship to lagomorphs, such as have been postulated for *Mimotona* and *Gomphos*. The similarity to *Gomphos* in the presence of a labial cingulum and a mesostyle is striking and could suggest affinity, but the upper molars otherwise differ markedly in the position of the hypocone, in the slope and inflation of the lingual part of the teeth, and in degree of hypsodonty. Pending discovery of more complete material, and referable lower jaws, we will consider *Amar* to be a member of the Eurymylidae and not a mimotonid.

No contemporary taxa, known only from the lower dentition, possess teeth that could be compatible with the upper dentition that represents *Amar*.

Family EURYMYLIDAE?
Subfamily KHAYCHININAE new
Khaychina n. gen.

Type species. *Khaychina elongata* n. sp.

Age and distribution. Late Palaeocene, MPR.

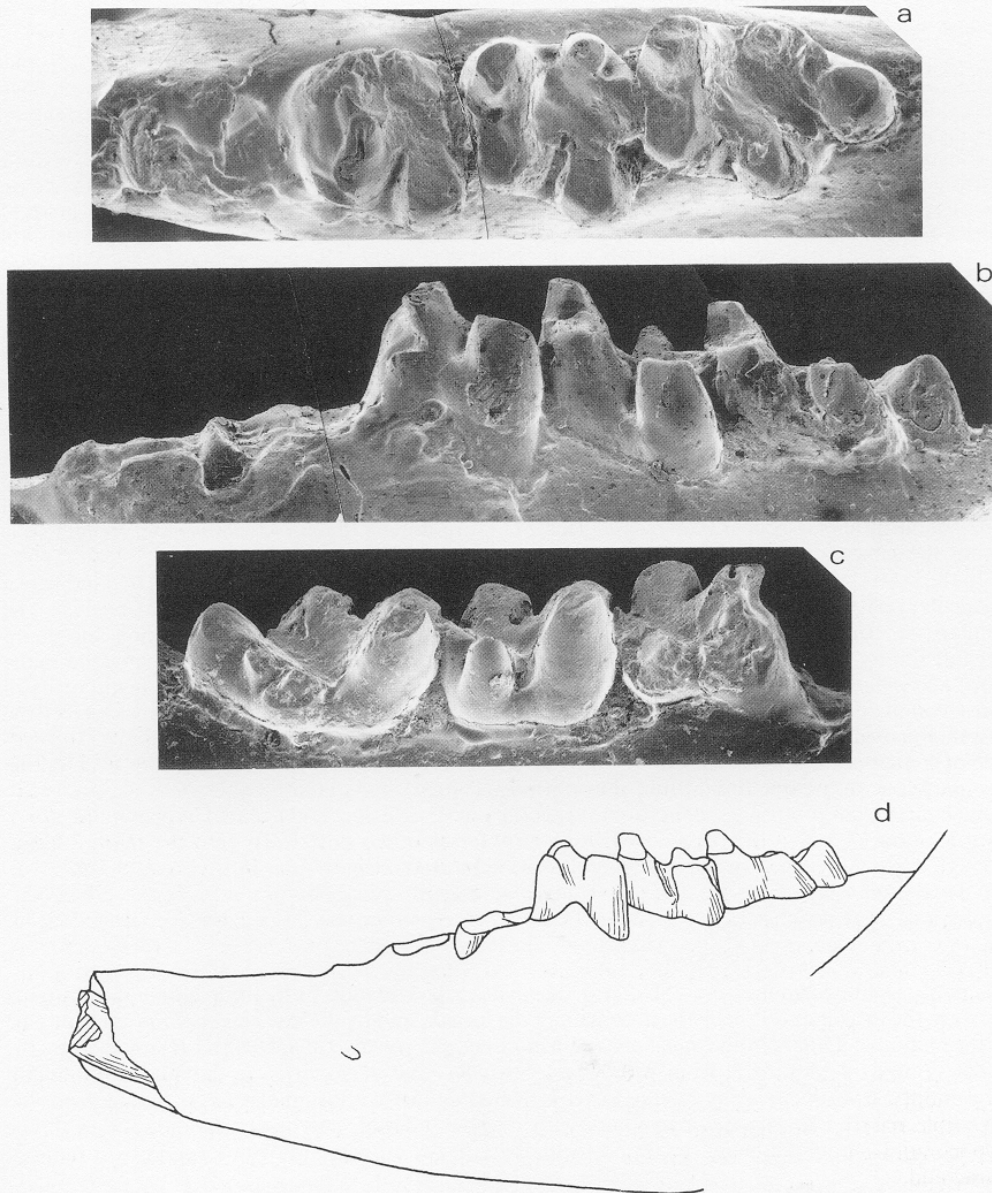
Diagnosis. Dental formula 1-0-2-3. Differs from all described mixodonts by the length of the diastema between the incisor and P/3, by the proclivity of the incisor, and by the low height of the anterior part of the mandible. Differs from *Rhombomylyus*, *Matutinia*, *Eurymylyus*, *Gomphos*, and *Hypsomylyus* by the wider talonid of M/1-M/3; from *Mimotona*, *Gomphos*, and *Hypsomylyus* by having no unilateral hypsodonty; from *Eomylyus* by having lower crowned molars with a smaller hypoconulid; from the mandible referred to *Heomys* by molars with a wider talonid, narrower trigonid, and with the hypoconulid-entoconid being separated to the base of the crown; and from *Zagmys* by a reduced paraconid.

Etymology. *Khaychina*, in allusion to the region that produced the type specimen, Khaychin-Ula, MPR.

Khaychina elongata n. sp.

Text-fig. 10

Holotype. PSS 30-3, left mandible with the incisor and M/1-M/3.



TEXT-FIG. 10. *Khaychina elongata* n. gen., n. sp. *a-d*, PSS 30-3, holotype, left mandible with incisor and M/1-M/3. *a*, occlusal view of molars; *b*, labial view; *c*, lingual view. *a-c*, $\times 15$; *d*, labial view of mandible, $\times 7.5$. Specimen from the Naran Member of the Naran-Bulak Beds at Khaychin-Ula I, Mongolia; late Palaeocene.

Locality and stratigraphic distribution. Khaychin-Ula I region, Bugin-Tsav Basin, southern MPR; Naran Member of the Naran-Bulak Beds; late Palaeocene.

Diagnosis. As for genus, only species.

Etymology. *Elongata* (L.), elongate, with reference to the length of the diastema between the incisor and the P/3 of the type specimen.

Description. As noted above, one of the most striking characters of PSS 30-3 is the length of the diastema between the single, procumbent incisor and the P/3; it is slightly more than the length of the molar series. A common proportion in mixodonts is about half this length. Only the roots of P/3 and P/4 remain; they indicate that the P/3 was narrow (apparently about half the width of P/4) and supported by a single root. P/4 was probably submolariform and nearly as big as M/1, although with a narrower talonid. The three molars increase in length from the first to the last; M/1 is subquadrate except for the bulge of the hypoconid. In all three the hypoconid extends very markedly labially. The trigonid is slightly damaged in M/1, but probably there was no paraconid developed; it is absent in the other molars. An anterior loph extends from the protoconid to the anterior side of the metaconid. The latter is the dominant cusp. The protoconid and hypoconid are rather close together but in labial view do not form the sort of columns seen in *Mimotona* or *Gomphos*. A large mesoconid exists on the cristid obliqua and extends well up on the posterior wall of the trigonid. The latter is strongly sloping but much of the inclination is due to wear. An oblique groove crosses the talonid basin from the notch between the metaconid and entoconid to another notch between the hypoconid and the hypoconulid. The latter is well separated from both the entoconid and the hypoconid and on M/3 forms a distinct third lobe. The teeth are low crowned, lower than those of any other described mixodont, including those of the mandible referred to *Heomys*. The jaw is low and elongate, particularly anteriorly; the coronoid process rises well behind M/3.

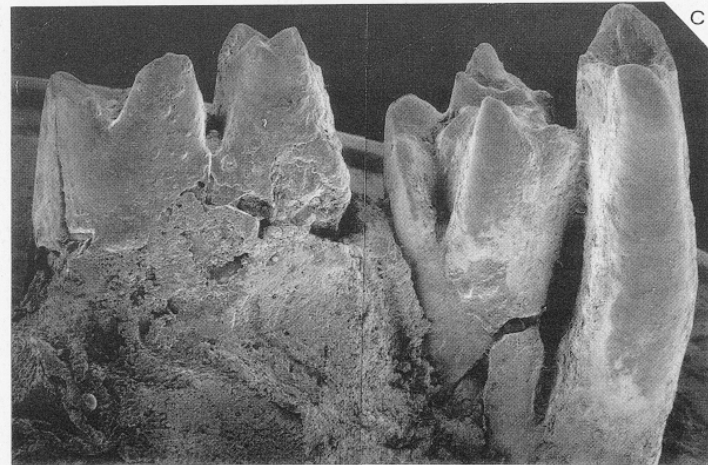
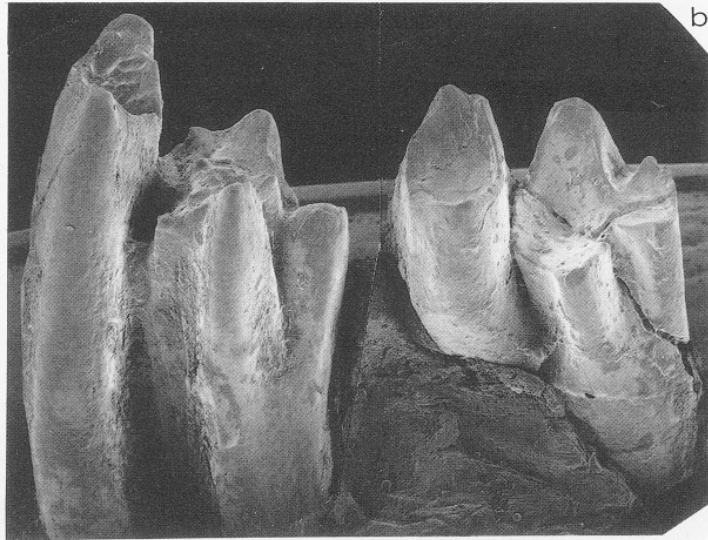
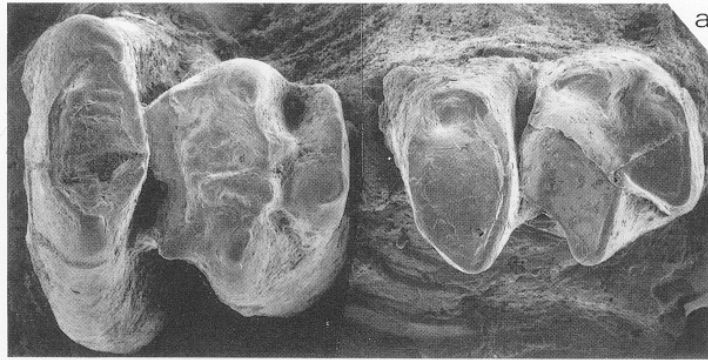
Measurements.

		L	W		L	W		L	W
PSS 30-3	M/1	1.6	1.8	M/2	1.7	1.9	M/3	2.5	1.8

Discussion. *K. elongata* is a form characterized by extremes: it exceeds all other mixodonts in length of diastema, in incisor proclivity, and in relative width of M/1 and M/2. Its molars are very low crowned and lack unilateral hypsodonty. Attribution to any of the existing anagalidan or mixodont families would considerably expand the limits of that family. The question of reference to the Rodentia could even be raised, but primitive rodents do not generally have a distinct and isolated hypoconulid, nor a third lobe on M/3, and the trigonid basin of early forms opens posteriorly into the talonid basin through a notch between the protoconid and metaconid; the trigonid basin is closed in PSS 30-3. What we have here is a species that strongly diverges from all known mixodonts. Given the distinctions upon which some early rodent families have been proposed (for example, Yuomyidae as separate from Cocomyidae, in Dawson *et al.* 1984), it would be relatively easy to define a 'Khaychinidae'. For the moment, we shall resist the temptation, knowing that many more mixodonts await discovery, among which might be morphological intermediates linking *Khaychina* more closely to the Eurymylidae.

Hypsomylyus beijingensis is known from a single specimen (text-fig. 11) comprised only of two lower teeth. One of the two has been identified by Zhai (1977) as DP/4 and shows extreme hypsodonty. The following tooth is considered to be M/1 and is much less hypsodont, exhibiting a condition only slightly more than that seen in *Eurymylyus* or *Eomylyus borealis* and comparable to that in *Rhombomylyus*. Concerning the identification of the anterior tooth, in the opinion of P. M. Butler (pers. comm., 1986), 'to have a milk molar more hypsodont than the permanent molar would be most unusual, almost unique'. We will regard it as P/4.

Apart from the hypsodonty (which is bilateral) of the P/4, there are no significant characters indicating a relationship to the Mimotonidae. Until further evidence indicates differently, we will place it in the Eurymylidae, in a new subfamily Hypsimylyinae, but its affinities are obscure.



TEXT-FIG. 11. *Hypsimylus beijingensis* Zhai, 1977. *a-c*, V 5242, holotype, left P/4-M/1. *a*, occlusal view; *b*, labial view; *c*, lingual view. All views $\times 15$. Specimen from the Changxindian Formation at Changxindian, Beijing, China; late Eocene.

Family MIMOTONIDAE Li, 1977

Mimotona lii n. sp.

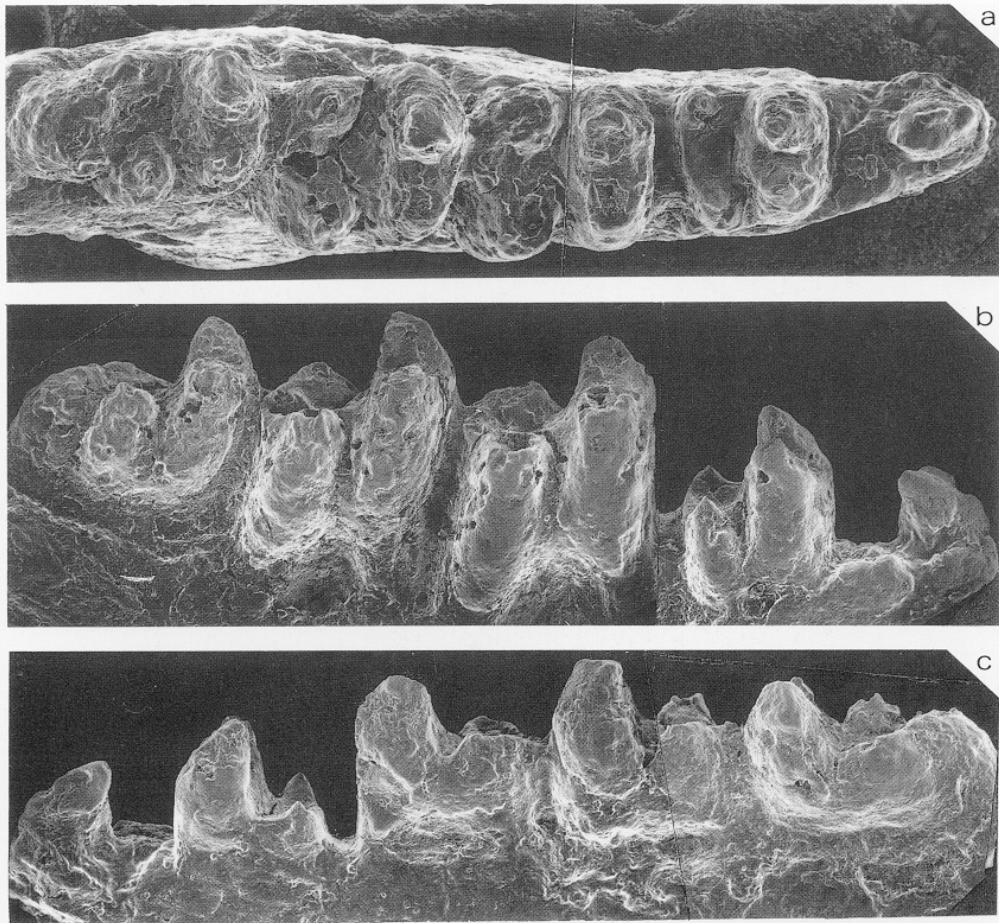
Text-fig. 12

Synonym. *Mimotona* n. sp., in Li 1977.

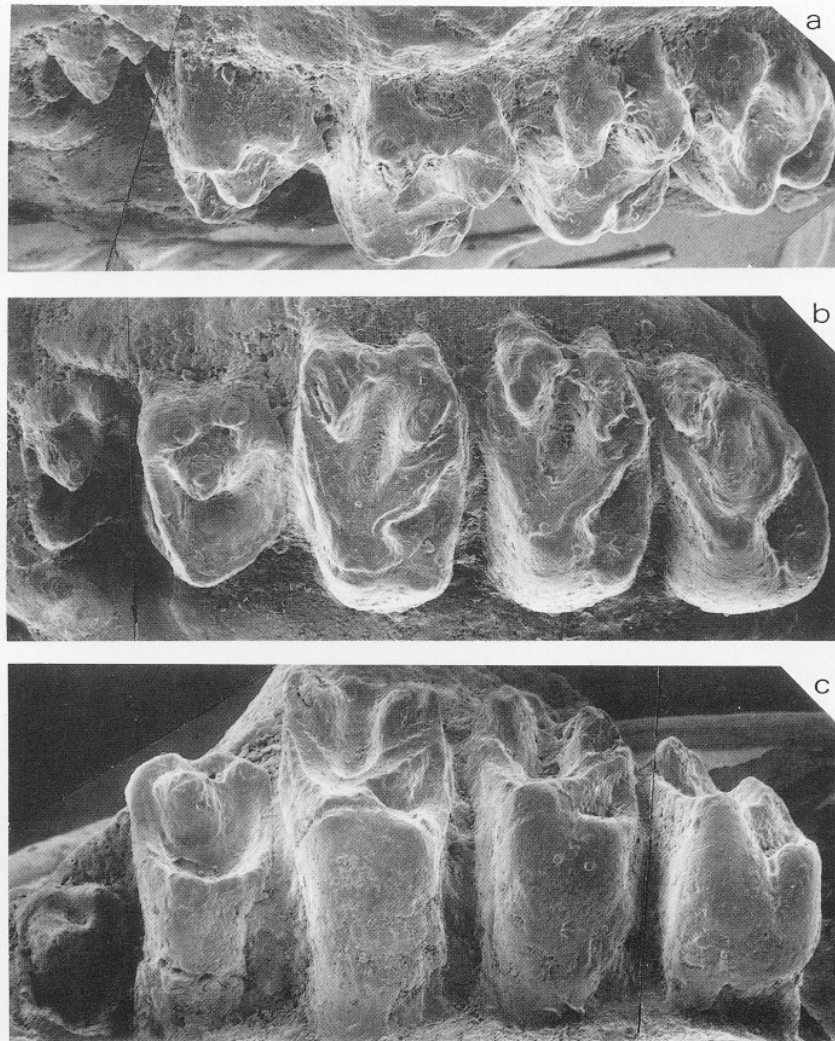
Holotype. V 4327, right mandibular fragment with P/3–M/3; IVPP, Beijing, China.

Locality and stratigraphic distribution. Locality no. 71008, upper part of the Wanghudun Formation, Qianshan Basin, Anhui Province, CPR, middle Palaeocene.

Diagnosis. Differs from *M. wana* by the (apparent) absence of a metaconid on P/3. Differs from both *M. wana* and *M. robusta* by a wider talonid on P/4 and by smaller size. Differs from the mandible referred to *Heomys* (V 4322) by the talonid of P/4 which is wider and (in labial view) of lesser height; by



TEXT-FIG. 12. *Mimotona lii* n. sp. a–c, V 4327, holotype, right mandible with P/3–M/3. a, occlusal view; b, labial view; c, lingual view. All views $\times 15$. Specimen from the Wanghudun Formation, Qianshan Basin, Anhui Province, China; middle Palaeocene.

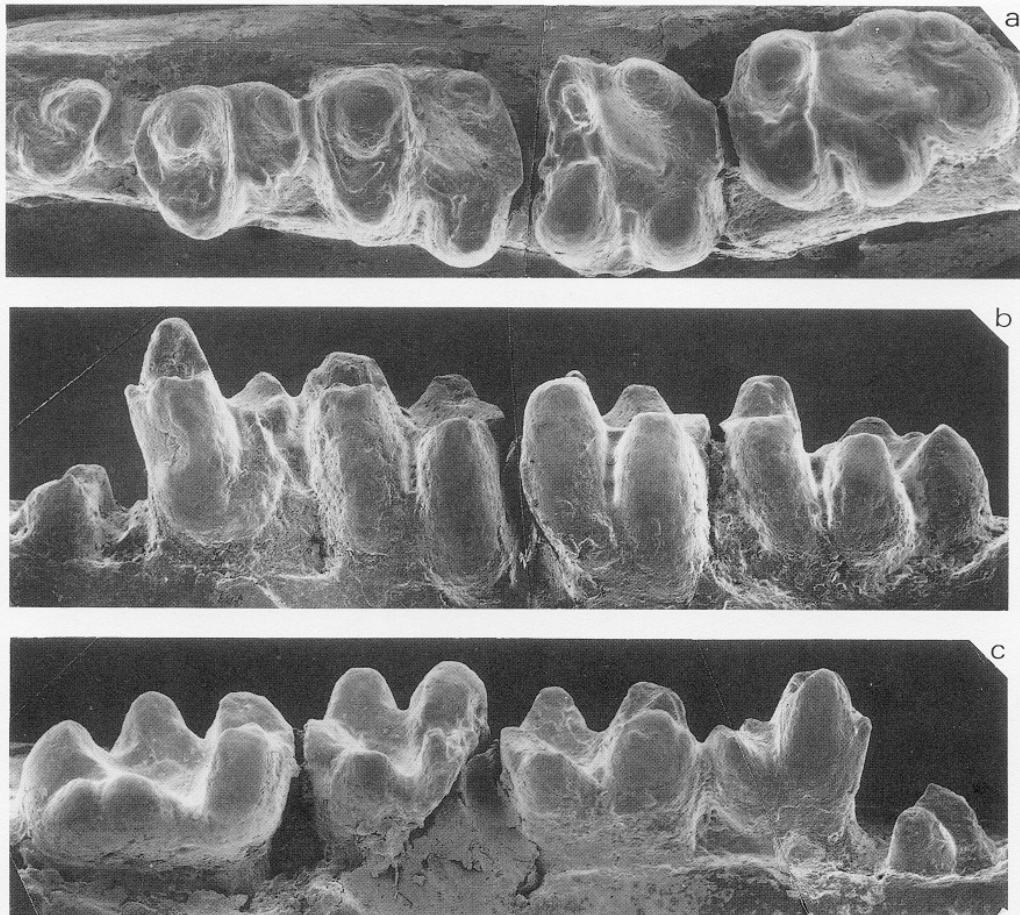


TEXT-FIG. 13. *Mimotona wana* Li, 1977. *a-c*, V 4324, holotype, left maxillary with P3/-M3/. *a*, labial view; *b*, occlusal view; *c*, lingual view. All views $\times 15$. Specimen from the Doumu Formation, Qianshan Basin, Anhui Province, China; late Palaeocene.

the protoconid and hypoconid of the molars which (in labial view) are closer together and form parallel, subequal columns (the hypoconid is the bigger in M/1-M/2 (labial view) of *Heomys*?, V 4322).

Etymology. Named in honour of Dr Li Chuan-kuei, IVPP, Beijing, for his work on the possible ancestors of rodents and lagomorphs.

Description. The P/3 is damaged but seems to have had a single anterior cusp; no details of the posterior part of the tooth are interpretable. P/4 is subquadrate, with the talonid exceeding in width the trigonid. The metaconid is slightly higher than the protoconid but the two are similar in dimensions; a faint cingulum connects them



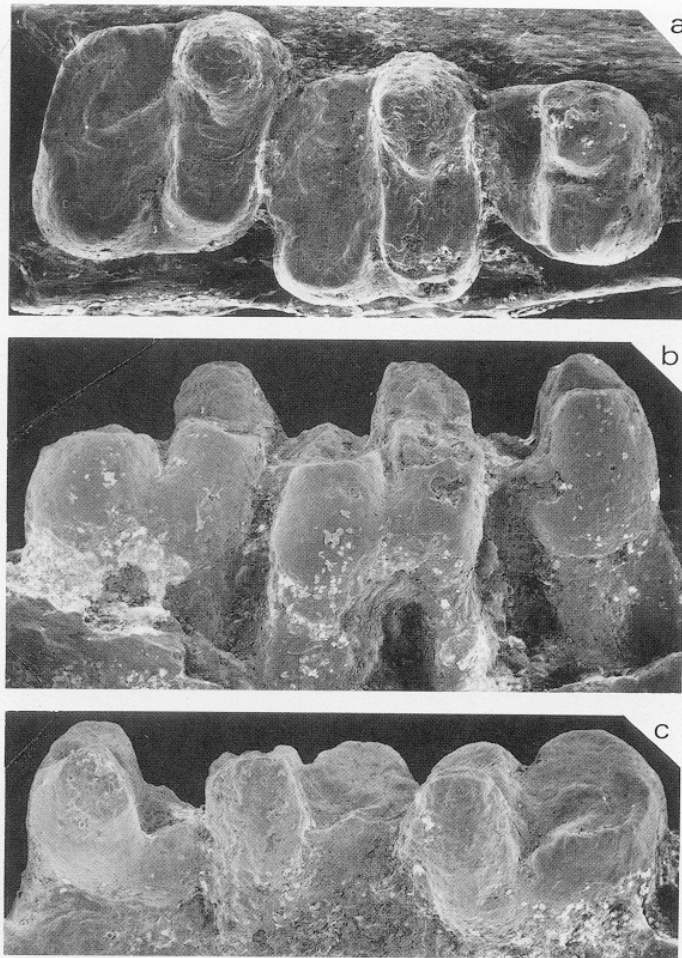
TEXT-FIG. 14. *Mimotona wana* Li, 1977. a-c, V 4325, left mandible with P/3-M/3. a, occlusal view; b, labial view; c, lingual view. All views $\times 15$. Specimen from the Doumu Formation, Qianshan Basin, Anhui Province, China; late Palaeocene.

anteriorly. Although short, the talonid is broadly basined; situated at the posterior corners, the hypoconid and entoconid are of subequal size. If a hypoconulid was present, it was low, small, and crestiform.

Very little distinguishes the molars of *M. lii* from those of *M. wana* (text-figs. 13 and 14) and *M. robusta* (text-fig. 15) except their proportions: M/1 and M/2 are relatively more elongate in *M. lii* and M/3 is less elongate than that of *M. wana* (it is unknown in *M. robusta*).

The mandible of V 4327 is broken just anterior to the P/3. Consequently, the number of incisors is unknown. The enamel of all the teeth has suffered damage by chemical erosion and is pitted.

Discussion. The specimen V 4327 was briefly mentioned by Li (1977), figured, and measured. Following Li, we refer it to *Mimotona*. The principal characters supporting this attribution are: the closeness in labial view of the parallel columns formed by the protoconid and hypoconid and the degree of unilateral hypsodonty seen. *M. lii* differs from the previously described species of *Mimotona*

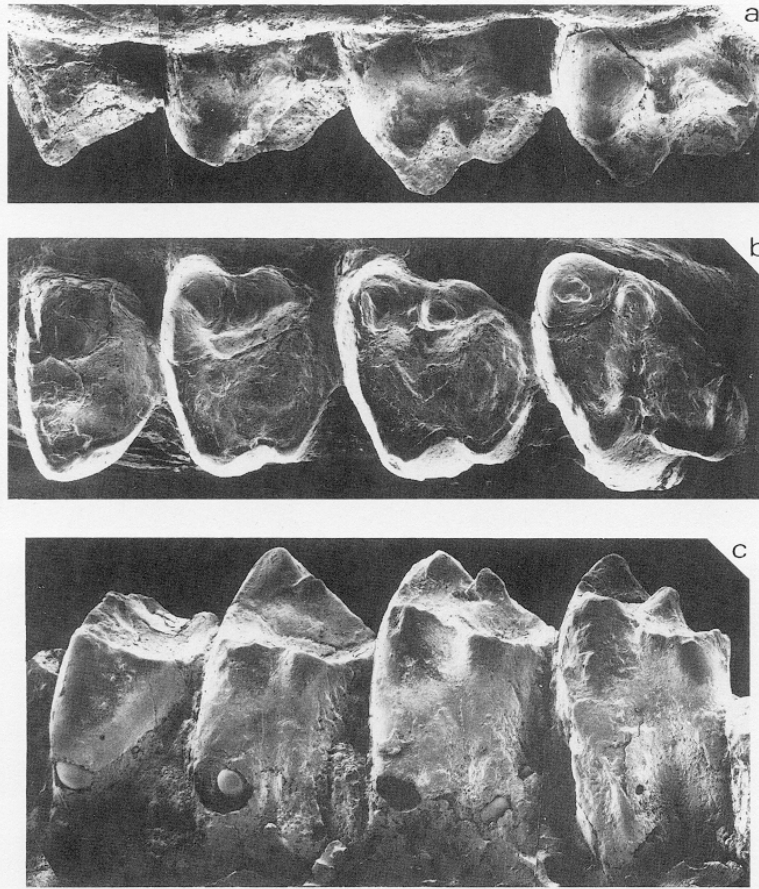


TEXT-FIG. 15. *Mimotona robusta* Li, 1977. *a-c*, V 4329, holotype, right mandible with P/4-M/2. *a*, occlusal view; *b*, labial view; *c*, lingual view. All views $\times 15$. Specimen from the Doumu Formation, Qianshan Basin, Anhui Province, China; late Palaeocene.

essentially in premolar morphology. The proportions of the molars add an additional distinguishing element.

DISCUSSION

Our research on the interrelationships of the various forms that enter into the concept of Mixodontia has led us to compare closely *Matutinia* and *Rhombomylus*. The material we used for the latter was principally that referred to *R. turpanensis* (text-figs. 16-18); the maxillary (text-fig. 19) and mandible we had of *R. laianensis* seem to differ very little and the specimens are more worn. Following Zhai (1978) we consider V 4362 (P4/-M3/), V 4363 (I, P/3-M/3), V 4364 (P/4-M/2), and V 4365 (M/3) as representative of *R. turpanensis*. The lesser worn teeth of V 4364 (text-fig. 18)



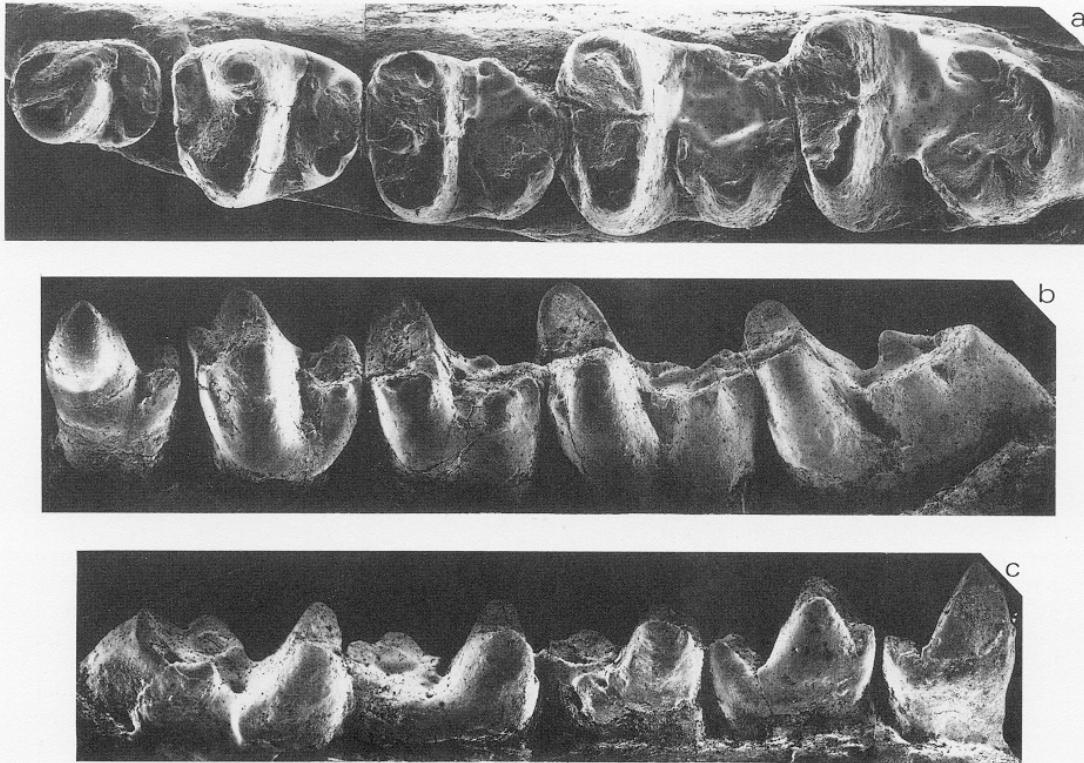
TEXT-FIG. 16. *Rhombomylus turpanensis* Zhai, 1978. *a-c*, V 4362, lectotype, right maxillary with P4/-M3/. *a*, labial view; *b*, occlusal view; *c*, lingual view. All views $\times 10$. Specimen from the Shisanjianfang Formation, Turpan Basin, Xinjiang Uygur Autonomous Region, China; early Eocene.

display differences in morphology from those of V 4363, notably in P/4 (but the P/4 of *R. laianensis* (V 5175) is virtually identical to the P/4 of the latter). The P/4 of *Matutinia nitidulus* (V 5360, the only specimen available with P/4) shows approximately intermediate characters (text-fig. 20). The cheek teeth in this species are slightly lower crowned than those of *R. turpanensis*, although we did not have specimens with identical stages of wear for the two forms. Other than this apparent difference in crown height, no diagnostic distinguishing features of generic value are evident from the lower teeth.

From the single example (V 5359) of the upper dentition of *M. nitidulus* (text-fig. 21) that we were able to compare, a difference in shape of M3/ appears to be the major distinction separating this species from *R. turpanensis*; difference in crown height seems negligible. The teeth in the holotype of the latter are rather heavily worn; the little worn specimen from Tsagan-Khushu (PSS 20-164; text-fig. 22) displays a cheek tooth morphology so similar that its attribution to *Rhombomylus* seems

subject to little doubt, but the M3/ is considerably longer than that of the type. As is commonly the case, the M3 appears to be particularly variable.

We are unable to justify the generic distinction of *Matutinia* from *Rhombomylus*. While we retain the species *nitidulus*, further knowledge of its variability is necessary to ensure its validity. *Rhombomylus* is a highly variable form; Li (pers. comm., 1984) has informed us that there is some doubt concerning the separation of *R. turpanensis* and *R. laianensis*. The problem is under study. Given, then, this variability within *Rhombomylus*, and the numerous points of identity that link *nitidulus* and *turpanensis*, we feel that the former should be placed in the genus *Rhombomylus* (this decision was independently reached by McKenna, pers. comm. 1986).



TEXT-FIG. 17. *Rhombomylus turpanensis* Zhai, 1978. *a-c*, V 4363, left mandible with P/3–M/3. *a*, occlusal view; *b*, labial view; *c*, lingual view. All views $\times 10$. Specimen from the Shisanjianfang Formation, Turpan Basin, Xinjiang Uygur Autonomous Region, China; early Eocene.

No type specimen was designated for *R. turpanensis*. The first specimen mentioned, a skull with an associated mandible (V 4361), is not figured. We shall designate the figured maxillary, V 4362, as the lectotype.

If *R. laianensis* is shown to be conspecific with *R. turpanensis* a supplementary problem arises. *Rhombomylus* was described as a new genus by Zhai (1978) with the type species of *turpanensis*. But the description of *R. laianensis* was published (by Zhai *et al.*) in 1976 and thus has priority if it is truly a senior subjective synonym.

Isolated teeth and incomplete dentitions of *Gomphos* are found sometimes in deposits that contain similarly incomplete remains of *Rhombomylus*. As the teeth are about the same size we will present here a summary of their differences in order to facilitate identifications. The comparisons are based on the material referred to *R. turpanensis* cited above (text-figs. 16-18) and the specimens from Tsagan-Khushu (*R. cf. turpanensis*; text-fig. 22); for *Gomphos* we had (from Tsagan-Khushu) PSS 20-163 (P/4-M/3; text-fig. 23), PSS 20-132 (M/2-M/3), PSS 20-166 (P4/-M1/; text-fig. 25), PSS 20-167 (M1/-M2/; text-fig. 25); and from Gashato (but not from the horizon of the holotype), PSS 33-11 (P/3, M/2-M/3; text-fig. 24).

Upper teeth	P4/	L	W	M1/	L	W	M2/	L	W	M3/	L	W
<i>Rhombomylus turpanensis</i> (V 4362)		2.0	3.5		2.5	3.8		2.8	3.7		2.9	3.5
<i>R. cf. turpanensis</i> (PSS 20-164)		2.0	4.0		2.7	4.4		2.6	3.7		3.3	3.5
' <i>Matutinia</i> ' <i>nitidulus</i> (V 5354)		2.0	3.6		2.5	4.2		2.4	3.4		2.4	
' <i>M.</i> ' <i>nitidulus</i> (V 5359)		2.1	3.6		2.7	3.8		2.8	3.8		2.5	2.7
<i>Gomphos elkema</i> (PSS 20-167)					3.0	5.8		3.0	5.3			
<i>G. elkema</i> (PSS 20-166)		3.1	5.5		2.9	5.7						
Lower teeth	P4/	L	W	M1/	L	W	M2/	L	W	M3/	L	W
<i>R. turpanensis</i> (V 4363)		2.6	2.3		2.7	2.3		3.1	2.7		4.2	3.0
<i>R. turpanensis</i> (V 4364)		2.3	2.2		2.6	2.4		3.2	3.0			
<i>R. turpanensis</i> (V 4365)											4.0	3.0
<i>R. cf. turpanensis</i> (PSS 20-169)		2.8	2.6		3.0	2.8		3.1	3.0		4.0	2.9
<i>R. cf. turpanensis</i> (PSS 20-165)								3.3	3.0		4.3	3.0
' <i>M.</i> ' <i>nitidulus</i> (V 5360)		2.6	2.3		2.9	2.5		3.1	2.7		3.5	2.6
<i>G. elkema</i> (PSS 20-163)		2.7	3.0		2.7	3.1		3.0	3.0		3.5	2.7
<i>G. elkema</i> (PSS 20-132)								3.0	3.0		4.1	3.2
<i>G. elkema</i> (PSS 33-11)	P/3	2.5	1.9					2.9	3.1		3.5	3.0

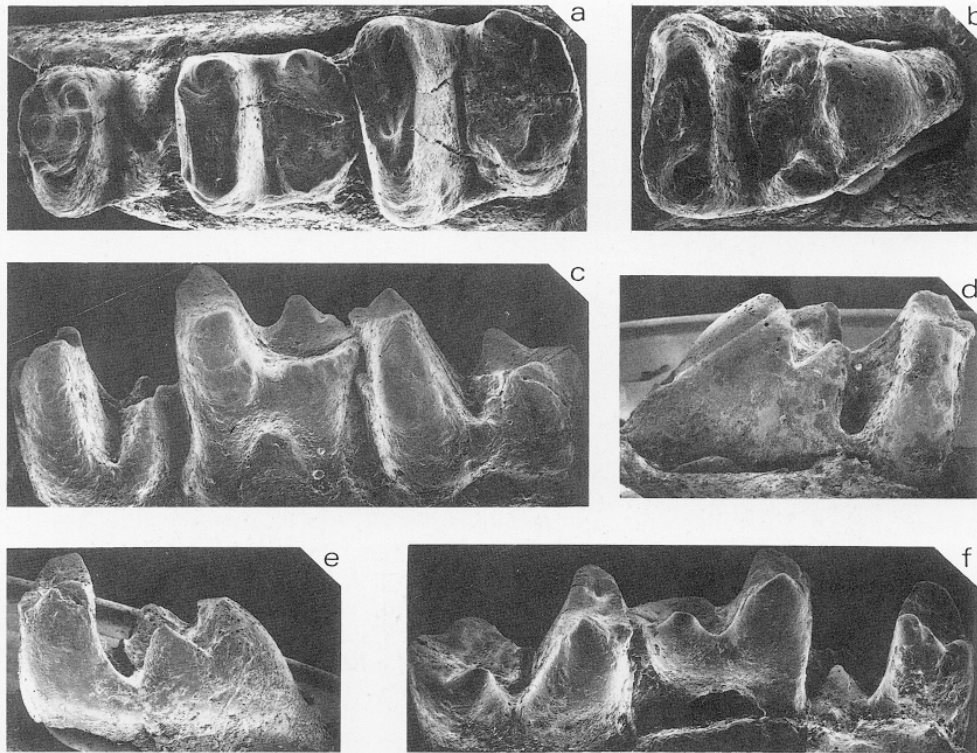
G. elkema differs from *R. turpanensis* by the presence of two lower incisors (seen in PSS 20-134 and PSS 20-98 from Tsagan-Khushu); by an elongate P/3, which is short and small in *Rhombomylus*; by a very molariform P/4 with a much wider talonid; the P/4 in *Rhombomylus* lacks the low situated paraconid; by the lower cheek teeth (P/4-M/2; text-figs. 23 and 24) tending to be subquadrate and the M/3 being shorter with no enlarged third lobe (i.e. the hypoconulid is small); by the columns formed by the protoconid and hypoconid being very close together; and by a greater degree of unilateral hypsodonty.

The upper teeth of *Gomphos* (text-fig. 25) differ from those of *Rhombomylus* by the subcircular contour of P4/ in occlusal view (it is more transverse in *Rhombomylus*); by the presence on P4/ of a single centro-labial cusp (four cusps in *Rhombomylus*); by the P4/-M2/ being greatly inflated lingually and more sloping with considerable unilateral hypsodonty; by the absence of a vertical groove between the protocone and hypocone; by the paracone being circular and cusped, becoming lophlike only with advanced wear, and well separated from the anterior and labial cingula (in *Rhombomylus* there is no labial cingulum and the anterior one is closely appressed to the paracone); by the (apparently) stronger metaconule; and by the presence in the molars of a sort of mesostyle.

None of the specimens available for this study retained all three upper molars. In the maxillary PSS 20-167 (text-fig. 25d), the more posterior of the two teeth preserved has an aspect that could permit its being regarded as M3/; in consequence its companion would be M2/. However, a contact wear facet on its posterior side confirms its identity as an M2/ and thus the tooth preceding it as M1/. An M3/-like aspect for M2/ can also be seen in *Rhombomylus*.

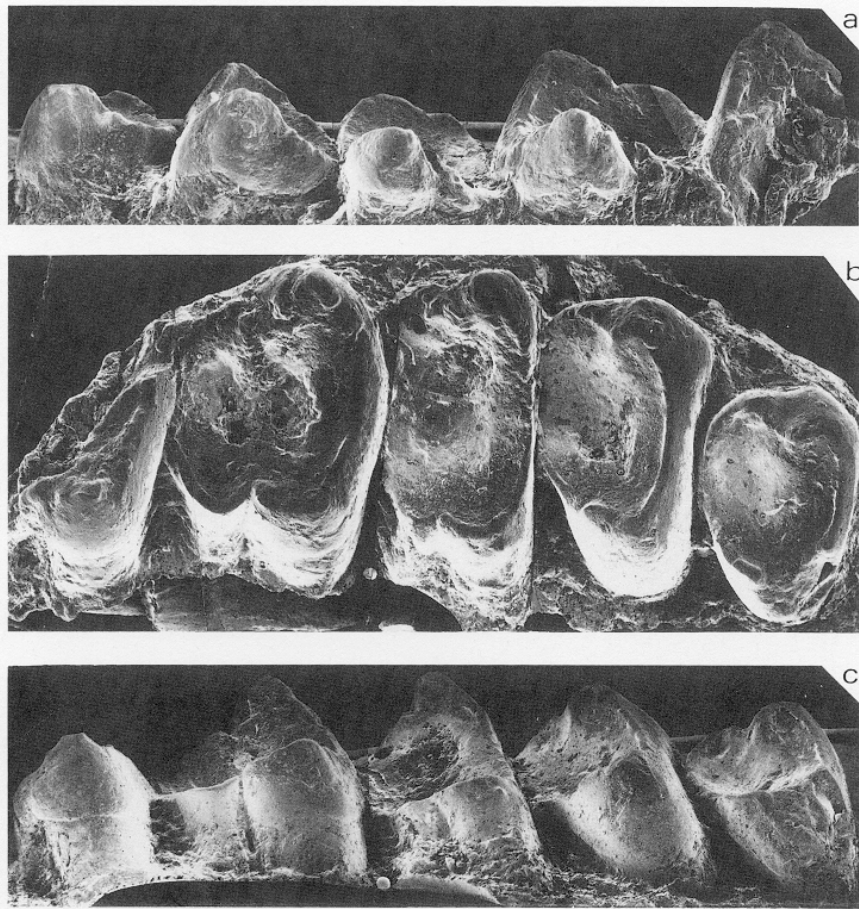
For most of the mixodont taxa very little information is available other than for dentitions, and these are often incomplete. For some of the genera, however, part of the maxillary is preserved which

includes the base of the jugal arch. Examination of this area reveals considerable variety, but in three specimens of *Eurymylus laticeps* a certain uniformity prevails. This suggests that generic differences may be expressed by this morphology as well as by the relationship of the position of the molars with respect to the anterior root of the jugal arch.



TEXT-FIG. 18. *Rhombomylus turpanensis* Zhai, 1978. *a, c, f*, V 4364, left mandible with P/4-M/2. *a*, occlusal view; *c*, labial view; *f*, lingual view. *b, d, e*, V 4365, right M/3. *b*, occlusal view; *d*, labial view; *e*, lingual view. All views $\times 10$. Specimens from the Shisanjianfang Formation, Turpan Basin, Xinjiang Uygur Autonomous Region, China; early Eocene.

As far as can be determined, *Heomys* and (to a lesser degree) *Eurymylus* are distinguished by the presence of a flange, or an abrupt widening of the base of the snout, that slopes in side view anterodorsally, much in the manner of early rodents. Viewed ventrally, the base of the jugal arch in these cases tends to be perpendicular to the tooth row (in *Eurymylus*) or slopes anteriorly with respect to the latter (in *Heomys*). In contrast, there does not seem to be a flange produced on the skulls of *Mimotona*, *Eomylus*, and *Rhombomylus*. The muzzle enlarges progressively toward the rear in what is doubtless a less specialized fashion. Within this general pattern, however, there is diversity; in *Mimotona* the base of the jugal arch is thick and massive, extending from the level of the anterior edge of M1/ to the middle of M2/; in *Eomylus* the base of the arch is much more slender and occupies a position opposite only the posterior half of M1/. It can be noted in passing that the jugal-maxillary

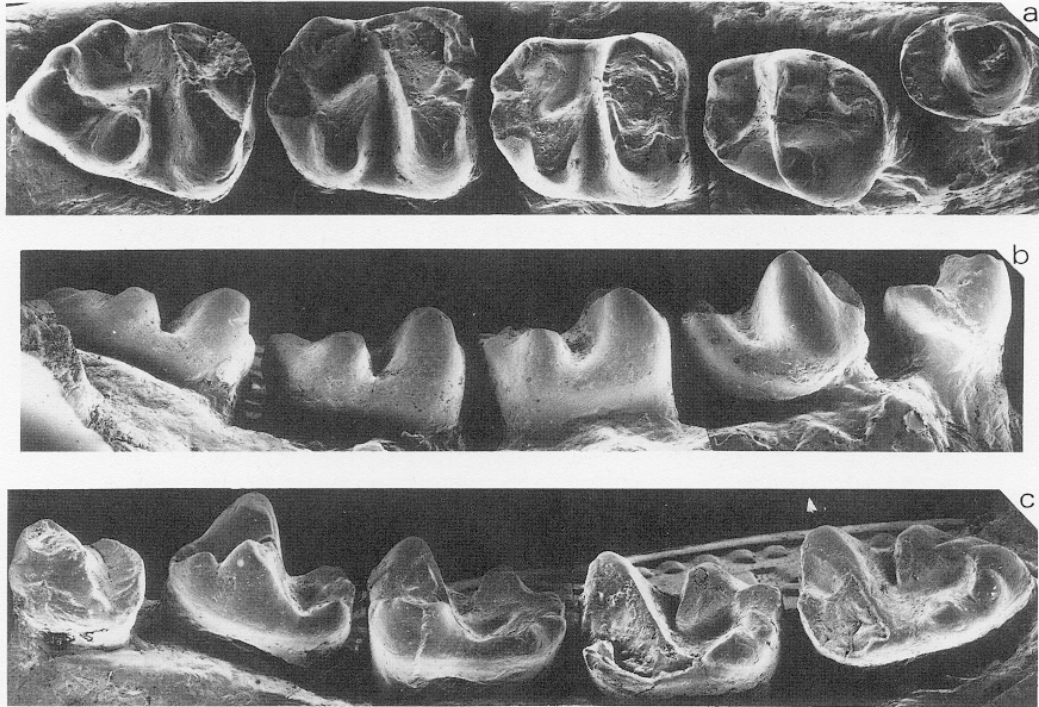


TEXT-FIG. 19. *Rhombomylus laianensis* Zhai *et al.*, 1976. *a-c*, V 5174, holotype, right maxillary with P3/-M3/. *a*, labial view; *b*, occlusal view; *c*, lingual view. All views $\times 10$. Specimen from the Zhangshanji Formation at the Laian locality, Laian District, Anhui Province, China; early Eocene.

suture is clearly preserved in both of these specimens (V 4324, *M. wana*, and PSS 20-139, *E. zhigdenensis*), as well as the ventral orbital rim. From what remains of the latter it appears likely that the orbit extended to the level of the anterior side of P3/ in *Mimotona* and well anterior to this level in *Eomylus*. The orbital situation in *Eurymylus* and *Heomys* seems similar to that in *Eomylus*. Orbital anterior extension in *Rhombomylus* is like that in *Mimotona* and the base of the jugal arch appears to be rather massive, as it is in that genus, but it extends from above P4/ to above M1/, thus being situated more anteriorly.

Summarizing the position of the base of the jugal arch with respect to the tooth row, the most anterior placement is probably that of *Heomys* (above P4/ to above the anterior edge of M2/), which is approximated by that of *Rhombomylus*. *Mimotona* and *Eurymylus* follow (above the anterior side of M1/ to above M2/), and the most posterior condition is that of *Eomylus*.

In early Asian rodents (for example, *Cocomys lingchaensis*, *Tamquammys wilsoni*, and *Petrokozlovia notos*) the anterior edge of the base of the jugal arch falls opposite the level of the posterior side of P3/. In the early lagomorph *Shamolaqus*, the same situation prevails; in *Lushilagus* the jugal arch is slightly more posterior.



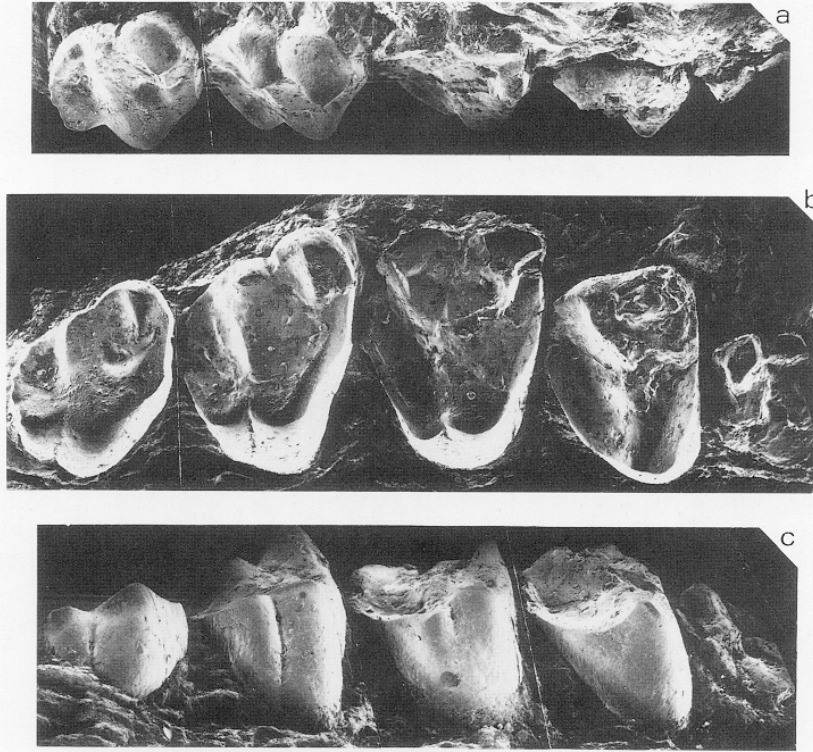
TEXT-FIG. 20. *Rhombomylus nitidulus* (Li *et al.*, 1979). *a-c*, V 5360, right mandible with P/3–M/3. *a*, occlusal view; *b*, labial view; *c*, lingual view. All views $\times 10$. Specimen from the Limuping Formation, at the Lingcha locality, Hengyang Basin, Hunan Province, China; early Eocene.

Continuing research on the structure of the incisor enamel makes it possible to remark that, where it is known in the Mixodontia, it can vary from one layer (as in modern lagomorphs) to a state approximating two (as in modern rodents). The enamel in *Eurymylus* seems to illustrate the weak differentiation of an outer layer and *Heomys* can be said to possess, more or less, two layers. Flynn (in Flynn, Russell and Dashzeveg 1987) noted the presence of only a single layer in *Rhombomylus*, *Gomphos*, and *Zagmys*; a single layer is also cited in *Mimotona* (and *Mimolagus*) by Li and Ting 1985. Given the fact that even early rodents (*Paramys*, for example) do not always display two distinct layers within the enamel of their incisors, the precision of this character for taxonomic purpose is probably not great. It is quite likely that pre-rodents, like pre-lagomorphs, had incisors whose enamel was not differentiated into more than one layer.

We have reviewed these taxa that fall into the category of neither rodents nor lagomorphs but possess the gliriform adaptation. The diversity already recorded and the lack of connecting links, not

only between the taxa in question but between them and their probable rodent and lagomorph descendants, makes it evident that we have barely begun to know the group.

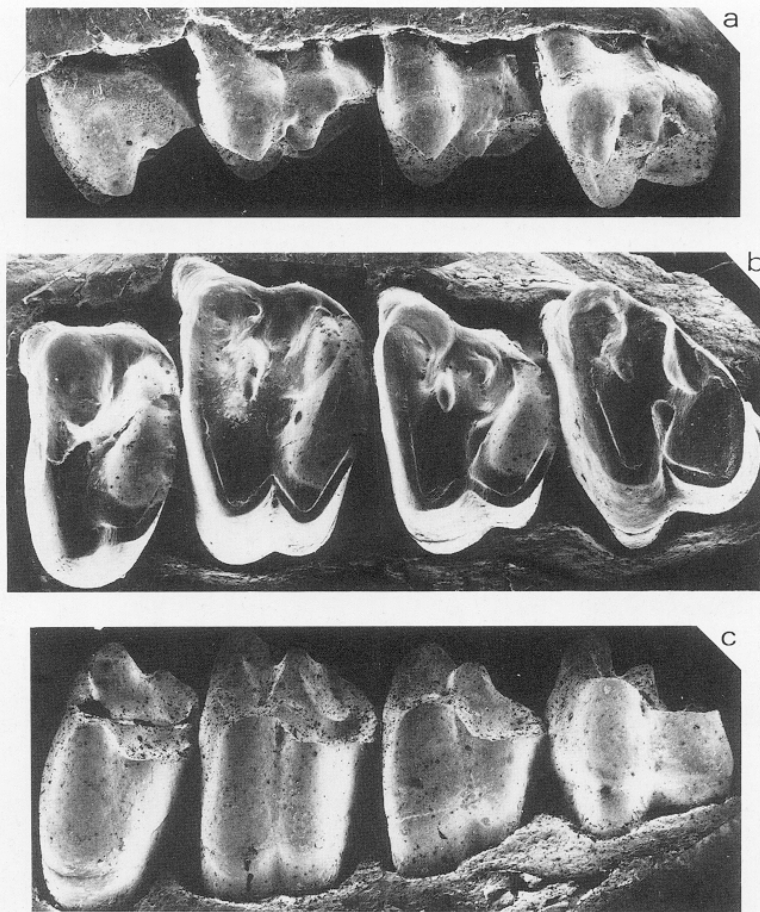
Classifying such an assemblage is challenging. A division can be made based on forms possessing two incisors in each tooth row, coupled with marked unilateral hypsodonty and parallel labial columns in the lower molars produced by the protoconid and hypoconid in close conjunction,



TEXT-FIG. 21. *Rhombomylus nitidulus* (Li *et al.*, 1979). *a-c*, V 5359, right maxillary with P3/-M3/. *a*, labial view; *b*, occlusal view; *c*, lingual view. All views $\times 10$. Specimen from the Limuping Formation at the Lingcha locality, Hengyang Basin, Hunan Province, China; early Eocene.

separated by a shallow groove. While this group, composed of *M. wana*, *M. robusta*, *M. lii*, and *G. elkema*, is rather coherent, an opposing group, united essentially by the presence of a single incisor, little or no unilateral hypsodonty and widely separated protoconid and hypoconid, is more disparate. *Eomylus zhigdenensis*, *E. borealis*, *Eurymylus laticeps*, the species of *Rhombomylus* and *H. orientalis* constitute a loose association. More marginal is *Khaychina oblongata* and *Zagmys*; equally distinctive is *Hypsimylus beijingensis*.

For the first group the family name Mimotonidae has been used and is often considered to represent either the first lagomorphs or those forms immediately preceding them. But lagomorph characters (as opposed to those anticipating rodents) that can be seen in available early mimotonid

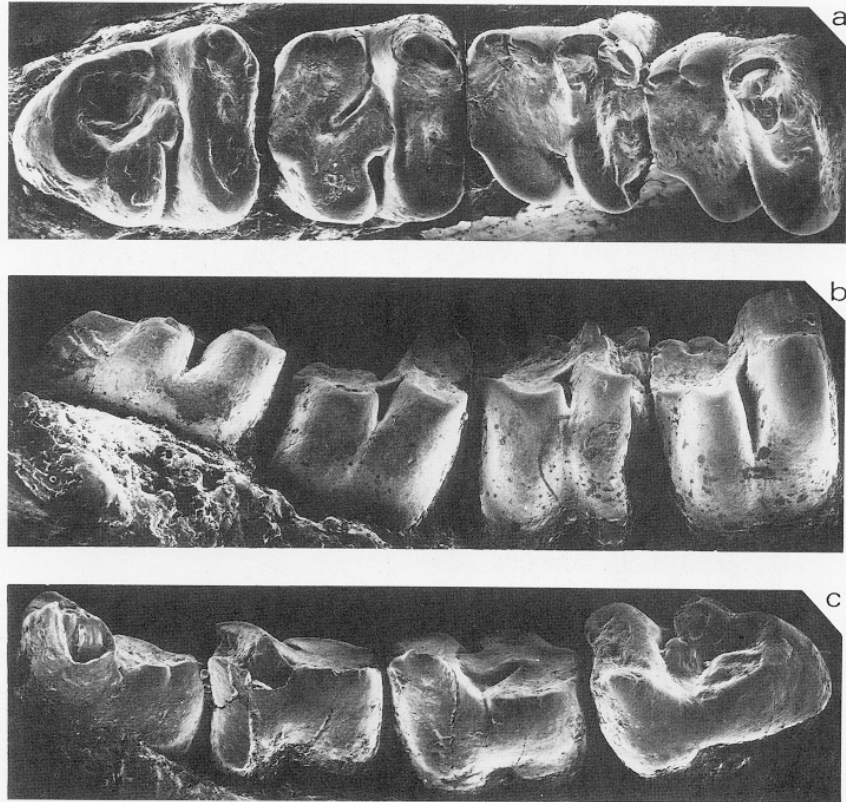


TEXT-FIG. 22. *Rhombomylus* cf. *turpanensis* Zhai, 1978. *a-c*, PSS 20-164, left maxillary with P4/-M3/. *a*, labial view; *b*, occlusal view; *c*, lingual view. All views $\times 10$. Specimen from the Bumban Member of the Naran-Bulak Beds at Quarry I, Tsagan-Khushu, Mongolia; early Eocene.

specimens are few. The presence of two upper and lower incisors is an obvious distinction, but it is probably a primitive character quite likely shared with pre-rodents and is therefore not an irrefutable indication of one or the other lineage. Another clue that is invoked for lagomorph affinity is the unilateral hypsodonty that is particularly expressed in the upper molars of lagomorphs, and which is present in *Mimolagus*, an acknowledged member of the latter group according to Bleefeld and McKenna (1985). *Mimotona*, in addition to having two incisors, also possesses the character of greater lingual than labial crown height; this difference in lingual versus labial crown height in the upper molars is more than in its contemporary *Heomys*, but not to a marked degree, and greater wear of the teeth in the *Heomys* specimen (V 4321) than in the maxillary of *M. wana* (V 4324) makes it seem less; the difference does exist, however. It is worthy of note that Dawson *et al.* (1984) exclude *Heomys* from the Rodentia in part because of the height of the tooth crowns. This character, then, is also not infallible. The condition (labial versus lingual crown height) in *Heomys* is approached by teeth

preserved in maxillaries of undescribed ctenodactyloid rodents from the early Eocene of Tsagan-Khushu.

The other mixodont family, the Eurymylidae, is regarded here in a sufficiently elastic view to encompass the genera enumerated above; the division into subfamilies will probably be useful as more taxa become known.



TEXT-FIG. 23. *Gomphos elkema* Shevyreva, 1975. a-c, PSS 20-163, right mandible with P/4-M/3. a, occlusal view; b, labial view; c, lingual view. All views $\times 10$. Specimen from the Bumban Member of the Naran-Bulak Beds above Quarry II, Tsagan-Khushu, Mongolia; early Eocene.

Our classification of the Mixodontia is as follows:

Cohort Glires Linnaeus, 1758

Order Mixodontia Sych, 1971

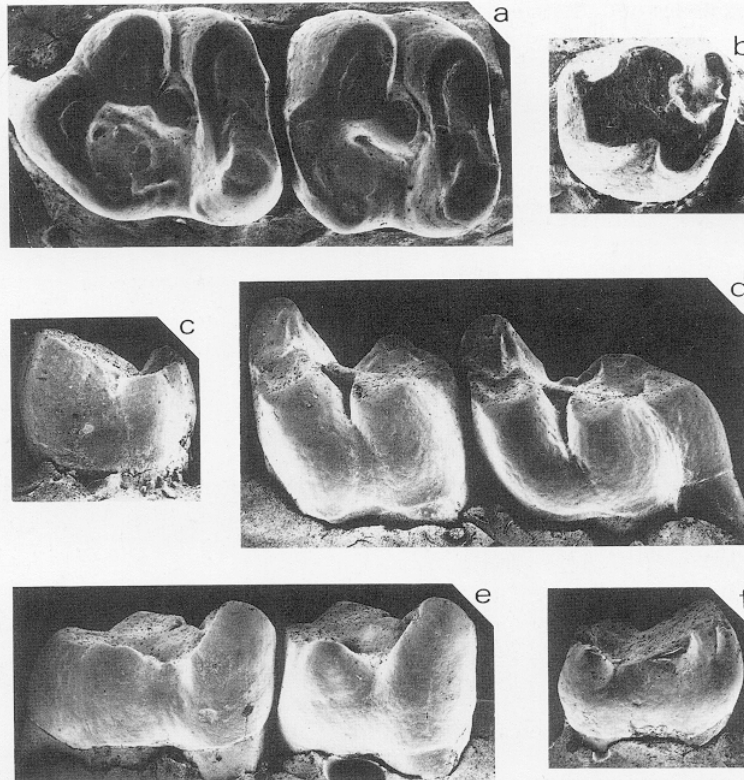
Family Eurymylidae Matthew, Granger and Simpson, 1929

Subfamily Eurymylinae, new usage

Eurymylus laticeps Matthew and Granger, 1925

Heomys orientalis Li, 1977

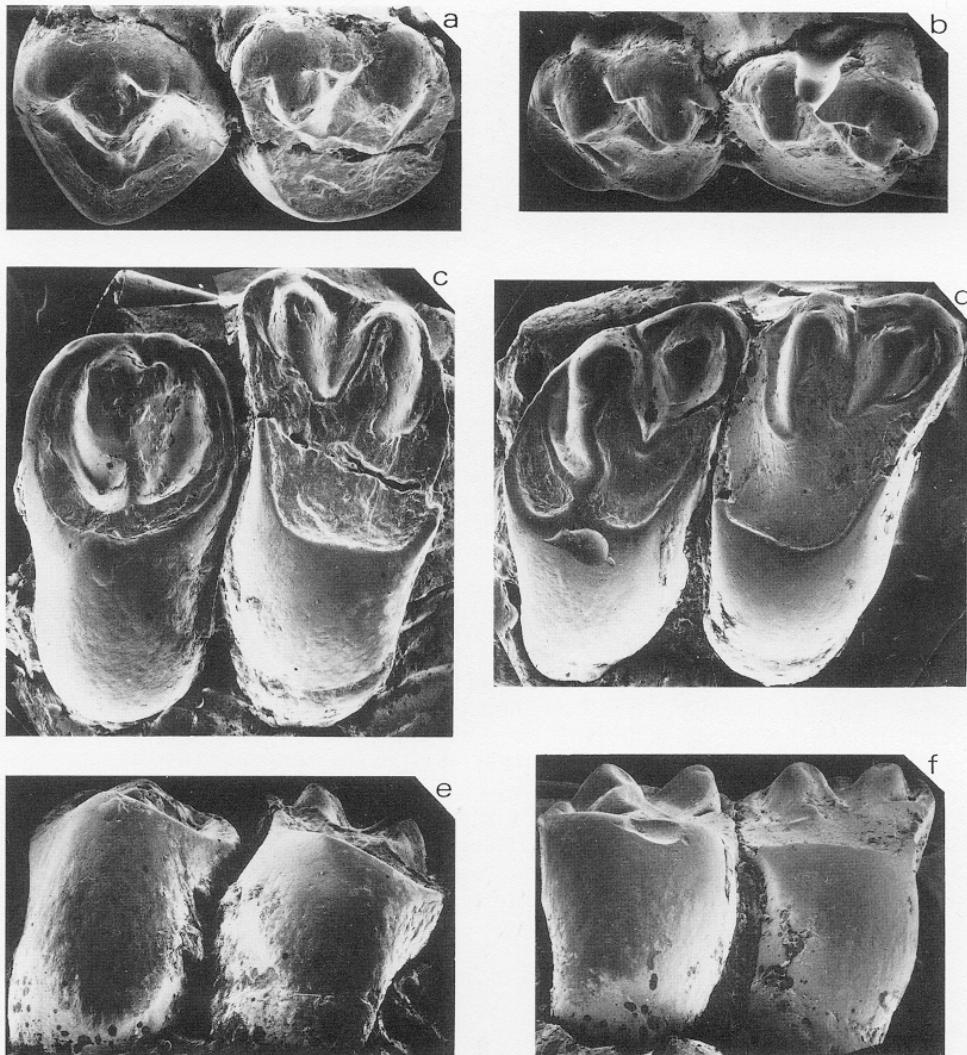
Rhombomylus laianensis Zhai *et al.*, 1976 or *R. turpanensis* Zhai, 1978



TEXT-FIG. 24. *Gomphos elkema* Shevyreva, 1975. a-f, PSS 33-11, left P/3, M/2-M/3. a, b, occlusal views; c, d, labial views; e, f, lingual views. All views $\times 10$. Specimen from Bed 11 of 'Svita 2' at the locality of Gashato, Ulan-Nur Basin, Mongolia; probably early Eocene.

- R. nitidulus* (Li *et al.*, 1979), new combination
Eomylus zhigdenensis n. gen., n. sp.
E. borealis (Chow and Qi, 1978), new combination
Amar aleator n. gen., n. sp.
 Subfamily Khaychininae nov.
Khaychina elongata n. gen., n. sp.
 Subfamily Zagmyinae nov.
Zagmys insolitus Dashzeveg *et al.*, 1987
 Subfamily Hypsimylinae nov.
Hypsimylus beijingensis Zhai, 1977
 Family Mimotonidae Li, 1977
Mimotona wana Li, 1977
M. robusta Li, 1977
M. lili, n. sp.
Gomphos elkema Shevyreva, 1975.

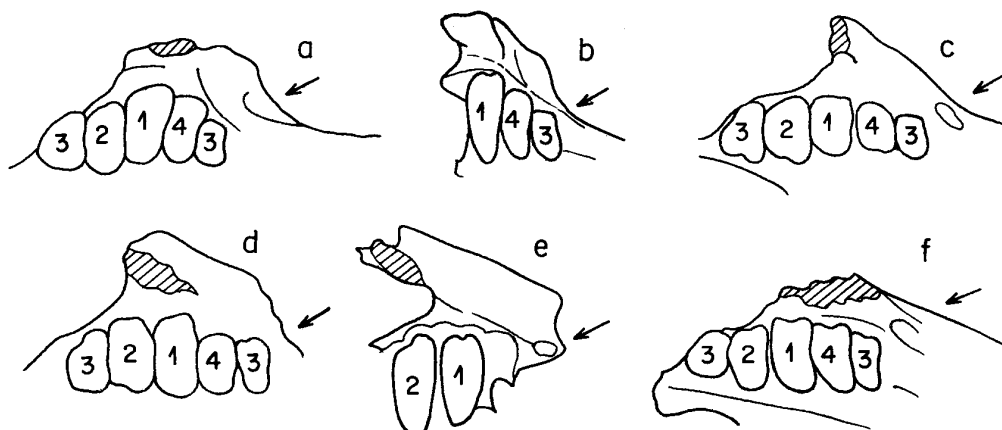
These new subfamilies are characterized by the single genus and species that each one includes. The



TEXT-FIG. 25. *Gomphos elkema* Shevyreva, 1975. *a, c, e*, PSS 20-166, left maxillary with P4/-M1/. *a*, labial view; *c*, occlusal view; *e*, lingual view. *b, d, f*, PSS 20-167, right maxillary with M1/-M2/. *b*, labial view; *d*, occlusal view; *f*, lingual view. All views $\times 10$. Both specimens from the Bumban Member of the Naran-Bulak Beds above Quarry II, Tsagan-Khushu, Mongolia; early Eocene.

Eurymylinae is comprised of mixodont species showing none of the peculiarities (no proclive incisor with an exaggerated diastema, no strong paraconid, no excessive hypsodonty of P/4) that distinguish the members of the other subfamilies.

Rodents, like lagomorphs, are probably derived from mixodont ancestors. As yet (and as usual) an ideal ancestral form is lacking, although *Heomys* is often cited as a borderline case. If it is rejected as a rodent by specialists (Hartenberger (1980), among others), its characters display a tantalizing resemblance to those of early Ctenodactylidae.



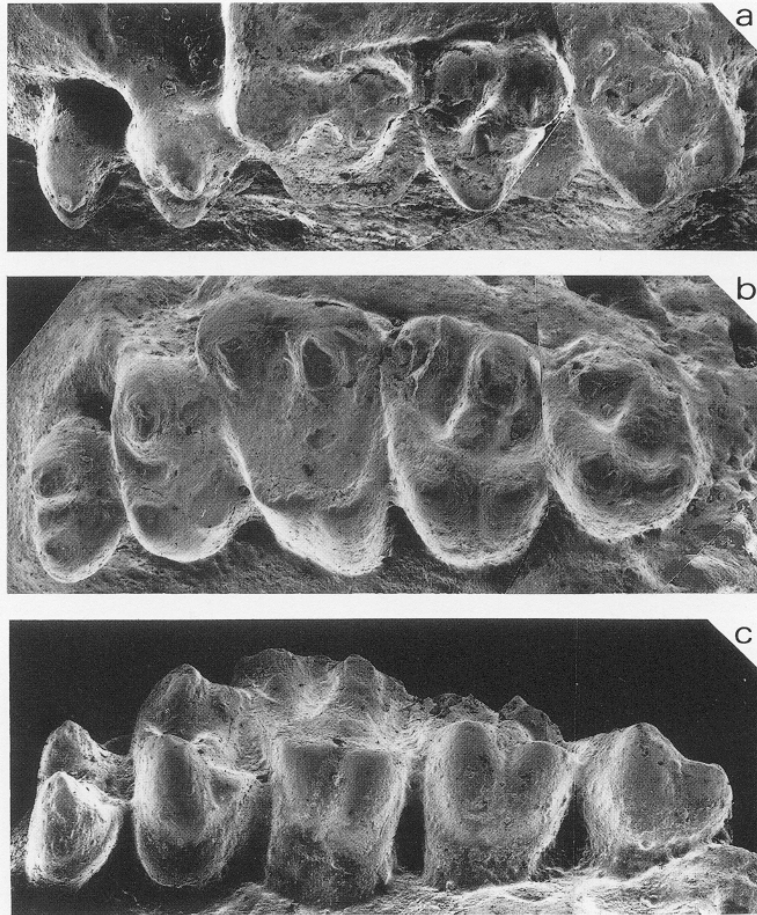
TEXT-FIG. 26. *a*, *Heomys orientalis*, V 4321, $\times 4$; modified from Li & Ting 1985. *b*, *Eurymylus laticeps*, MgM II/62, $\times 2.6$; modified from Sych 1971. *c*, *Rhombomylus* sp., V 5289, $\times 2$; modified from Li & Ting 1985. *d*, *Mimotona wana*, V 4324 (reversed), $\times 3.8$; modified from Li 1977. *e*, *Eomylus zhigdenensis*, PSS 20-139, $\times 4$. *f*, *Rhombomylus nitidulus*, V 5354 (reversed), $\times 2$; modified from Li *et al.* 1979. Arrows indicate the infraorbital foramen.

The lower jaw, V 4322 (text-fig. 28), that was referred to *H. orientalis* by Li (1977) but which apparently does not come from the same locality as the type partial skull, has badly worn teeth. Nevertheless, enough remains so that it can be said that, particularly in labial view, they are unlike those of *M. wana*, *M. robusta*, or *M. lii*. More resemblance to *E. zhigdenensis* is apparent (the P/4 is quite similar), although the M/3 of the latter is much larger. There is less similarity to *E. borealis* and still less to any of the other known mixodonts. If this lower jaw is not of *Heomys* (but it could well be) it is different in any case from that of *Mimotona*, which was found in the same locality. For the reasons cited earlier that distinguish rodents, it cannot belong to that group.

According to published information the type material of both *M. orientalis* and *H. wana* came from locality 71017 in the upper part of the Doumu Formation, Qianshan Basin, Anhui. An additional specimen, V 4326, with I1/-I2/, was referred to *M. wana* but comes from the upper part of the

The stratigraphic distribution of the members of the mixodont families

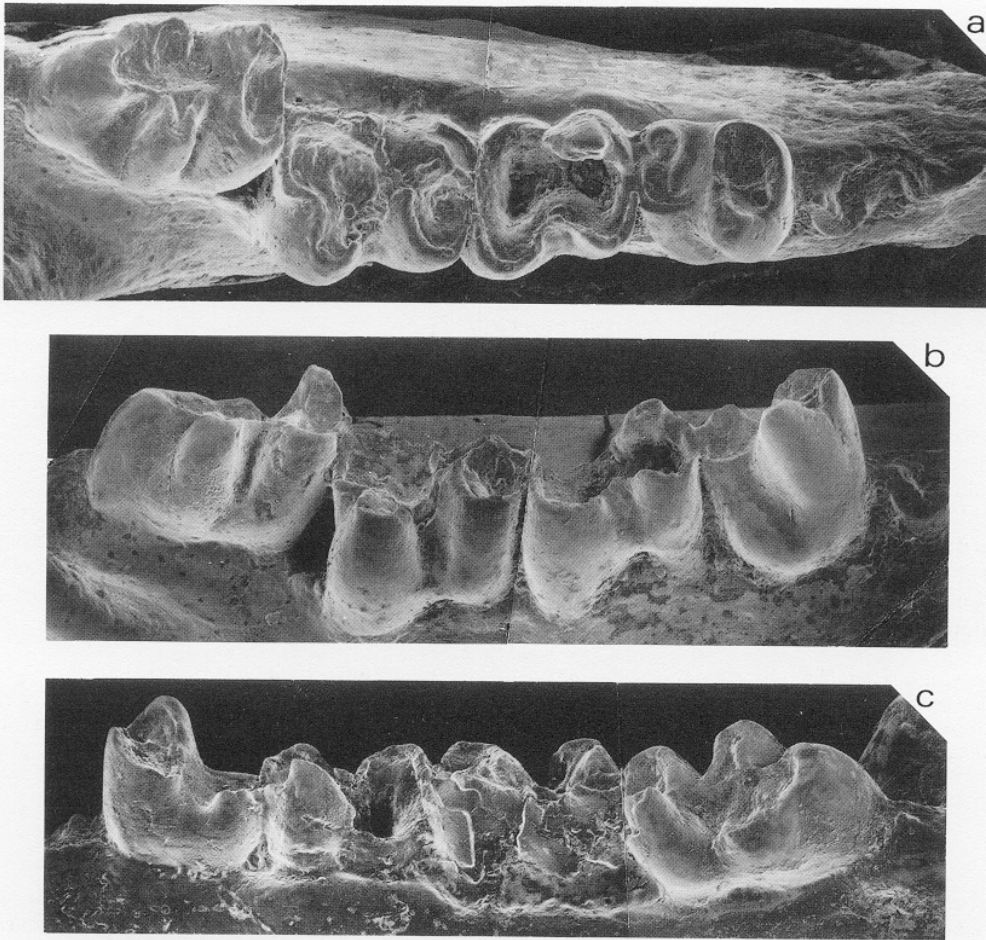
late Eocene	<i>Hypsomylyus beijingensis</i>	
early Eocene	<i>Rhombomylus</i> spp. (including <i>Matutinia</i>)	<i>Gomphos elkema</i>
	<i>Zagmys insolitus</i>	
late Palaeocene	<i>Eurymylus laticeps</i>	<i>Mimotona wana</i>
	<i>Heomys orientalis</i>	<i>M. robusta</i>
	<i>Eomylus zhigdenensis</i>	
	<i>E. borealis</i>	
	<i>Khaychina elongata</i>	
	<i>Amar aleator</i>	
middle Palaeocene		<i>M. lii</i>
	EURMYLIDAE	MIMOTONIDAE
	1 incisor, little or no unilateral hypsodonty, protoconid and hypoconid widely separated by a deep groove.	2 incisors, unilateral hypsodonty, protoconid and hypoconid close together and separating shallow groove.



TEXT-FIG. 27. *Heomys orientalis* Li, 1977. a-c, V 4321, holotype, left maxillary with P3/-M3/. a, labial view; b, occlusal view; c, lingual view. All views $\times 15$. Specimen from the Doumu Formation, Qianshan Basin, Anhui Province, China; late Palaeocene.

underlying Wanghudun Formation. The determination of these incisors as belonging to *M. wana*, which would indicate the presence of the species in this lower level, seems rather dubious as none are associated with the type or referred material from the Doumu Formation.

A recent effort made to decipher lagomorph origins is that of McKenna (1982) who sought illumination among the anagalids in the genera *Huaiyangale* and *Hsiuannania*. The former is stated by McKenna to be a non-lagomorph. Its upper molars, however, possess the same unilateral hypsodonty that is found in *Mimotona*, coupled with a broadly expanded postcingulum and a much more developed anterocingulum, very reminiscent of the condition in *Hsiuannania*, a genus that is included in McKenna's concept of the Lagomorpha. Dentally (in the upper cheek teeth), *Huaiyangale* seems as good a lagomorph as does *Hsiuannania* and better than *Mimotona*. Based on the morphology of the anterior part of the lower jaw, however, it is clear that *Huaiyangale* is a member of the Anagalida



TEXT-FIG. 28. *Heomys?* sp. a-c, V 4322, right mandible with P/4-M/3. a, occlusal view; b, labial view; c, lingual view. All views $\times 15$. Specimen questionably from the Doumu Formation, Quinshan Basin, Anhui Province, China; late Palaeocene.

(since it completely lacks gliriform incisor adaptation), while *Mimotona* is a mixodontian. *Hsiuanania* possesses non-gliriform incisors, a canine and three premolars (in the lower jaw, V 4314, at least) and can no more be a mixodontian than is *Huaiyangale*.

Cheek tooth morphology, then, is not enough, for on this basis there is no reason to exclude *Huaiyangale* from lagomorph affinity and tenuous reason to include *Mimotona*, wherein the anterocingulum is low placed and faint or absent—and thus not in the line of creatures that produced (eventually) a hypostris. Concerning cusp homologies in the upper molars of Eocene and later lagomorphs, we follow Lopez Martinez (1985) and Butler's (1985) analyses, based on wear facets, in regarding the protocone as being lingually placed.

Since the early fossil record of the groups in question is known to be extremely incomplete, designating the first possible lagomorph is difficult or even illusory. *Mimotona* could be a candidate for this position, but it might be more prudent to say only that it approaches the lagomorph condition.

We would not say that *Hsiuannania* shares this quality. The absence of gliriform adaptation would place it securely, in our opinion, in the Anagalida; it is contemporary with both *Mimotona* and *Heomys*.

CONCLUSION

The Mixodontia can be considered an evolutionary grade; it is thereby transitional. With an increase in discovered material it is conceivable that some day better established lineages would bring about its dissolution. However, in our opinion, none of the known forms can be properly classed as either an undoubted rodent or lagomorph. This is opposition to McKenna (1982) and Bleefeld and McKenna (1985) who regard *Mimotona* as already a lagomorph and the eurymylids as rodents. If one follows this reasoning it is necessary to add a totally new dimension to both Rodentia and Lagomorpha. At this stage in their unfolding history, and perhaps until the time when skulls and skeletons become available, the authors feel that the concept of Mixodontia is useful and unconfusing.

The new taxa that we have been able to add to this group furnish a suggestion as to what its variety must have been in Asia during the later part of the Palaeocene and the early part of the Eocene. It follows that our present classification is only temporary. Of the five genera here placed in the Eurymylinae, *Rhombomylus* and *Eurymylus* seem to be the most prevalent and hence the most characteristic. Considerable mystery still shrouds *Heomys*, particularly as concerns its lower dentition; *Eomylus* is very distinctive and too little is known of *Amar* even to be certain of its placement in the Eurymylidae. Even more uncertainty applies to the familial situation of *Khaychina* and *Zagmys*. *Hypsomyilus* has already been placed in the Mimotonidae (by Li and Ting 1985), but its unique dental morphology does not provide irrefutable evidence for such an attribution. Our concept of the Mimotonidae includes only *Gomphos* and the species of *Mimotona*.

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