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The earliest rodents *(Rodentia, Ctenodactyloidea)* of Central Asia

[With 13 text-figs]

Najstarsze gryzonie *(Rodentia, Ctenodactyloidea)* Azji Centralnej

Abstract. The Eocene family *Cocomyidae* (*Ctenodactyloidea*) is divided into two subfamilies: *Cocomyinae* and *Advenimurinae* subfam. nov. *Sharomys singularis, S. parvus, Kharomys mirandus, K. gracilis, Tsagamys subitatus* and *Ulanomys mirificus* are described as new species of *Cocomyinae* from the Early Eocene of Naran-Bulak. *Boromys grandis* gen. et sp. nov. is described as a representative of *Advenimurinae* from the Middle Eocene of Khaichin-Ula II. Genus *Saykanomys* SHEVYREVA, 1972 is a junior synonym of *Advenimus* DAWSON, 1964. The problem of the time of appearance of rodents on the territory of central Asia is discussed in the light of the new material from Mongolian People's Republic.

I. INTRODUCTION

Important progress has been reached during the last 20 years in the study of Eocene rodents of Central Asia (LI 1963, DAWSON 1964, DAWSON et al. 1984, SHEVYREVA 1976 etc.). However, the determination of the systematic position of these rodents proved to be difficult. Many of them were erroneously determined and described as belonging to *Sciuravidae* and *Paramyidae*, families known before mainly from the Paleogene of North America. A. E. WOOD (1975) was the first to reconstruct correctly the paleontological history of the ctenodactyloid rodents and to connect their origin with Asia. According to his opinion, the Asiatic genera *Saykanomys* SHEVYREVA, 1972, *Tsinlingomys* LI, 1963, *Yuomys* LI, 1975 and *Advenimus* DAWSON, 1964 are phylogenetically connected and belong to the family *Ctenodactylidae* emerging as a result of Eocene Asiatic radiation.

In the years 1978—1980 the author, as a member of the Joint Soviet-Mongolian Paleontological Expedition, conducted the washing and screening of fossiliferous sediments of the Naran-Bulak Formation in the outcrops of Tsagan Khushu in the central part of the Nemegt Basin and succeeded in finding, for the first time on the territory of Mongolian People's Republic, important

material of Early Eocene mammals (DASHZEVEG 1977, 1979 a, b, DASHZEVEG and MCKENNA 1977, RUSSELL and DASHZEVEG 1986, DASHZEVEG, FLYNN, RUSSELL 1987).

The present paper contains the description of new ctenodactyloid rodents (4 new genera and 4 new species) from the Lower Eocene of Tsagan Khushu in the Nemegt Basin. It also presents the description of a new genus and species *Boromys grandis* from the Middle Eocene of Khaichin-Ula II in the Bugintsav Basin. The remains of this rodents were found by the author in the 1977 field-season, during the washing of fossiliferous sediments of the Khaichin Formation. The materials are preserved in the Division of Paleontology and Stratigraphy (PSS) of the Geological Institute of the Academy of Sciences of Mongolian People's Republic in Ulan-Bator.

Dr. D. E. RUSSELL and Dr. F. GINGERICH have sent me, on my request, the comparative material of Eocene rodents from China. Dr. J.-L. HARTENBERGER, Dr. K. KOWALSKI and Dr. D. E. RUSSELL helped with the preparation of this paper. The author expresses his best thanks to all these persons.

II. STRATIGRAPHIC SITUATION OF RODENTS IN THE EOCENE SECTIONS OF THE MONGOLIAN PEOPLE'S REPUBLIC

Eocene rodents are known on the territory of the Mongolian People's Republic from two localities of Southern Gobi: Tsagan Khushu and Khaichin-Ula II (Fig. 1).

Locality Tsagan Khushu. Remains of rodents in the Naran-Bulak Formation were discovered in two quarries in the outcrops of Tsagan Khushu in the central part of the Nemegt Basin (Fig. 2).

Quarry 1. Remains of rodents and other fossils were present in lenses of sandy gravels overlying thick green clays of the Naran Member. These lenses were rich in bones of small vertebrates and were 0.1 to 0.3 m thick. Their fauna contains insectivores: *Naranius infrequens* RUSSELL et DASHZEVEG, 1986, *Bumbanius rarus* RUSSELL et DASHZEVEG, 1986, *Tsaganius ambiguus* RUSSELL et DASHZEVEG, 1986, *Oedolius perexiguus* RUSSELL et DASHZEVEG, 1986; mixodonts: *Zagmys insolutus* DASHZEVEG, FLYNN et RUSSELL, 1987, *Rhombomylus* ZHAI, BI et YU, 1976, *Gomphos elkema* SHEVYREVA, 1975; condylarthrs: *Hyopsodus orientalis* DASHZEVEG, 1977; primates: *Altanius orlovi* DASHZEVEG et MCKENNA, 1977; and perissodactyls: *Hyracotherium gabuniaei* DASHZEVEG, 1979, *Homogalax namadicus* DASHZEVEG, 1979. Rodents are represented in this quarry by *Sharomys parvus* gen. et sp. nov. and *Kharomys gracilis* gen. et sp. nov.

Quarry 2. The fossils were discovered on the limit of Members Naran and Bumban (300 m south of quarry 1.). The lenses of fossiliferous sediments are composed of brown-grey sands and gravels and are 0.2 to 1 m thick. The composition of mammalian fauna in these lenses does not differ from that in quarry 1,

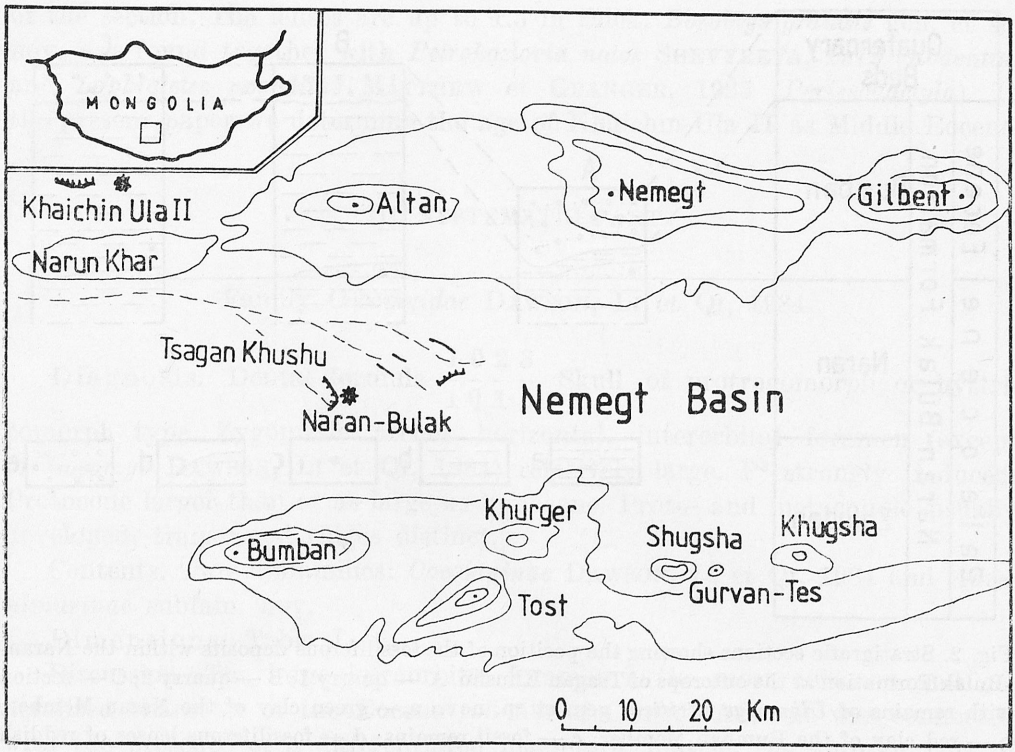

Fig. 1. Sketch map of the Nemegt Basin, Mongolian People's Republic, showing the situation of locality Tsagan Khushu and Khaichin-Ula II

but it is less diversified. It contains *Naranius infrequens*, *Bumbanius rarus*, *Tsaganius ambiguus*, *Oedolius perexiguus*, *Zagmys insolutus*, *Gomphos elkema*, *Hyopsodus orientalis*, *Altanius orlovi*, *Homogalax namadicus* and, among rodents, *Sharomys singularis* gen. et sp. nov., *S. parvus* gen. et sp. nov., and *Kharomys mirandus* gen. et sp. nov.

Remains of *Ulanomys mirificus* gen. et sp. nov. were discovered 1.5 m above the lower limit of the Member Bumban in red clays, 100 m to the south of quarry 2. Remains of *Gomphos elkema* (*Eurymyloidea*) were also found here. The age of the Naran-Bulak Formation is determined as reaching from the Upper Paleocene to the base of the Lower Eocene inclusively. The fauna of the Naran Member can be correlated with the fauna of Clark-Fork and is of Late Paleocene age. The fauna of the Bumban Member, which contains ctenodactyloid rodents and other mamals, corresponds with the zone Graybull (Wasatch) and can be dated for Early Eocene (DASHZEVEG 1982).

Locality Khaichin-Ula II is composed of Khaichin layers, represented by light-grey soft sandstones and gravels (Fig. 3). In the lower part of the section the sandstones graduate into greenish clays with interbedded layers of the carbonates. Remains of mammals and particularly of rodents, appear in the large lanses among clayey sandstones and grey clays of the middle part

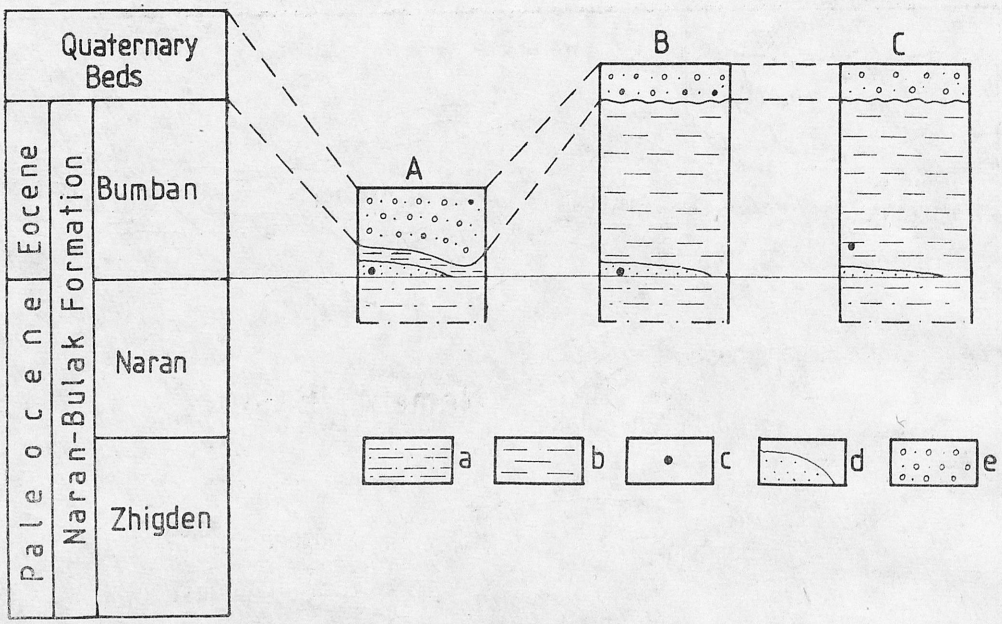

Fig. 2. Stratigrafic sections showing the position of the fossiliferous deposits within the Naran-Bulak Formation at the outcrops of Tsagan Khushu. A — quarry 1; B — quarry 2; C — section with remains of *Ulanomys mirificus* gen. et sp. nov.; a — green clay of the Naran Member; b — red clay of the Bumban Member; c — fossil remains; d — fossiliferous lenses of reddish sand and sandstone; e — Quaternary sands and gravels

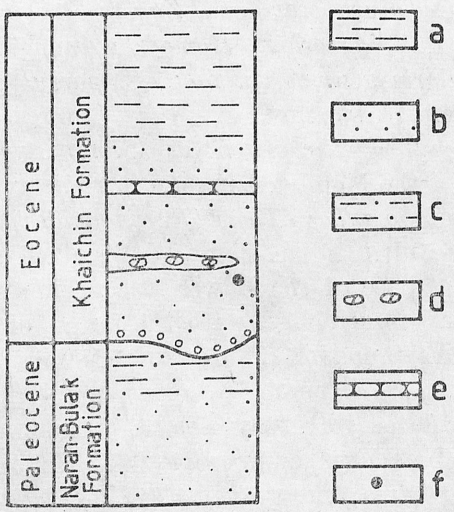

Fig. 3. Stratigraphic section of Khaichin-Ula II. a — green clay, b — gray sandstones and gravels; c — greenish mudstone; d — carbonate concretions; e — cemented sandstone: f — fossil remains of *Boromys grandis* gen. et. sp. nov.

of the section. The lenses are up to 1.5 m thick. *Boromys grandis* gen. et sp. nov. was found together with *Petrokozlovia notos* SHEVYREVA, 1972 (*Rodentia*) and *Lophialetes expeditus* MATTHEW et GRANGER, 1925 (*Perissodactyla*). In the present paper we determine the age of Khaichin-Ula II as Middle Eocene.

III. SYSTEMATIC PART

Family *Cocomyidae* DAWSON, LI et QI, 1984

Diagnosis. Dental formula $\frac{1\,0\,2\,3}{1\,0\,1\,3}$. Skull of protrogomorph or hystricomorph type. Zygomatic arches horizontal, interorbital foramen (except of *Cocomys* DAWSON, LI et QI, 1984) relatively large. P^3 strongly reduced. Protocone larger than or as large as hypocone. Proto- and metaconule usually developed, transversal ridges distinct.

Contents. Two subfamilies: *Cocomyinae* DAWSON, LI et QI, 1984 and *Advenimurinae* subfam. nov.

Dimensions: Table I.

Discussion. The large infraorbital foramen is the most common and generalized character of the Eocene rodents of Central Asia. It was connected with the presence of a differentiated masseteric muscle, the anterior part of which, m.m. medialis, penetrates across this foramen. The hystricomorph type of the skull in *Tamquammys* SHEVYREVA, 1971, *Saykanomys* and other rodents from the Middle Eocene of Asia was mentioned many times in the works of earlier authors (SHEVYREVA 1976, WOOD 1977, DAWSON et al. 1984).

The study of these materials of ctenodactyloid rodents from Mongolia in comparison with the published data makes it possible to formulate the opinion about the lower part of the infraorbital foramen and about the maxillar base of the zygomatic arch. It is evident that, in the development of ctenodactylids changes of other elements of the skull are correlated with the enlargement of the infraorbital foramen. In particular, the maxillar part of the zygomatic arch, its anterior and posterior slopes as well as the position of the masseteric crest in the relation to P^3 and P^4 are different in particular representatives of *Cocomyidae*. The preserved part of the infraorbital ring of the rodents known from Naran-Bulak points to the generally large size of the infraorbital foramen. Two types of infraorbital foramen can be distinguished (Fig. 4 A, B).

1. Large infraorbital foramens can be well studied in three specimens of the genus *Sharomys* gen. nov. Their dimensions cannot be determined exactly because of the limited material. The maxillar part of the zygomatic arch of *Sharomys* gen. nov. is rather broad, with clearly differentiated large and inclined anterior wall. Masseteric crest begins on the antero-buccal side of P^4. The type of the zygomatic arch and the large infraorbital foramen of the ge-

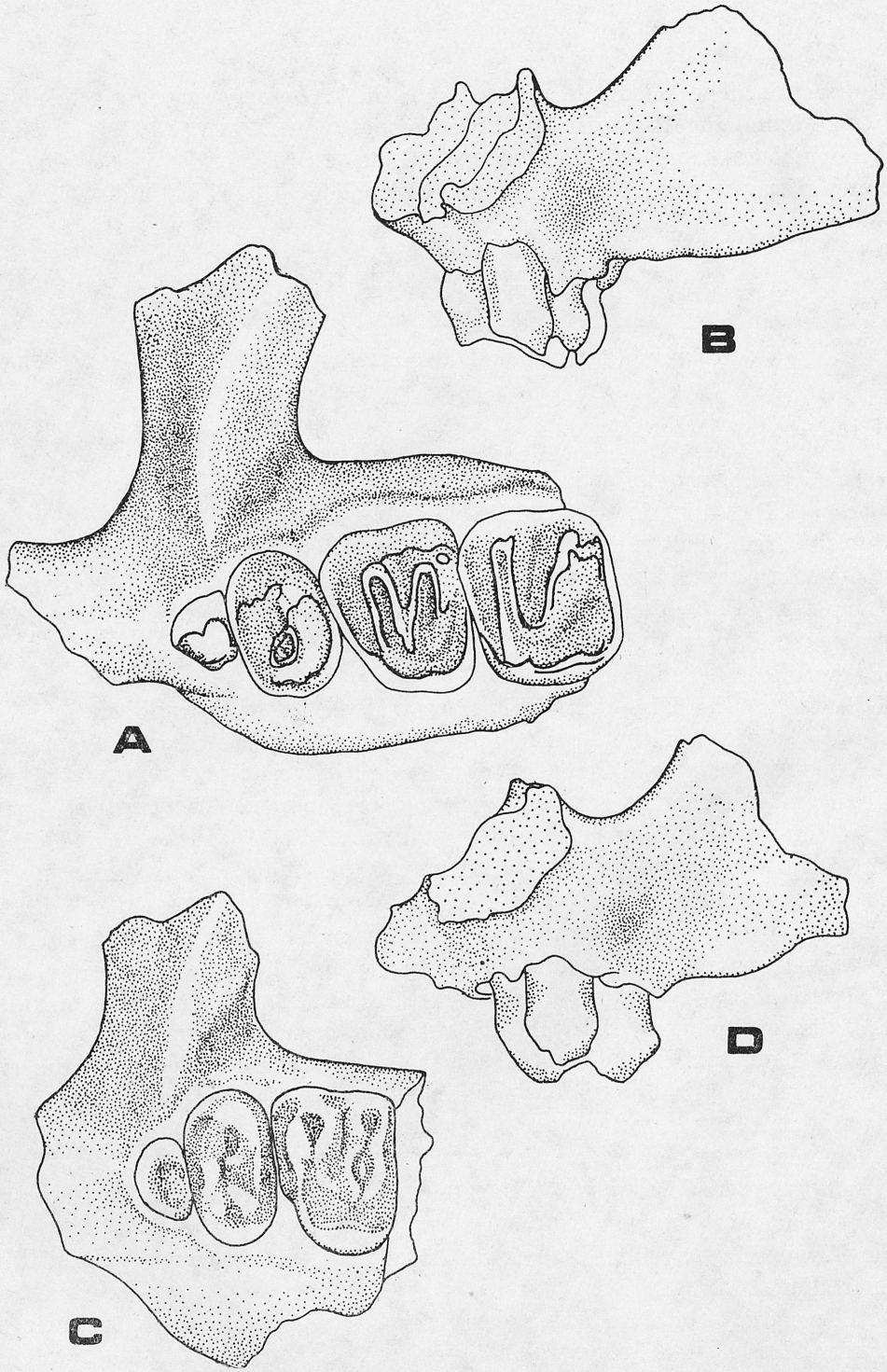

Fig. 4. The structure of maxilla and of zygomatic arch in the representatives of the family *Cocomyidae*. A — *Sharomys singularis* gen. et sp. nov., fragment of left maxilla and of zygomatic arch with P^4—M^2, top view, × 15; B — mesial view, × 15; C — *Kharomys mirandus* gen. et sp. nov., fragment of the left maxilla and of zygomatic arch with P^3—M^1, top view, × 15; D — mesial view, × 15

Table I

Tooth dimensions (in mm) of new species of *Cocomyidae*. L — length, W — width

Species	Number	P^3		P^4		M^1		M^2		M^3		dP_4		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W
Sharomys singularis sp. nov.	No. 20-282	0.8	0.8	1.1	1.7	1.6	1.8	1.6	2.0	—		—		—		—		—		—	
	No. 20-186	0.8	1.2	1.3	1.8	1.7	1.0	1.9	1.8	—		—		—		—		—		—	
	No. 20-180	—		—		—		1.7	1.9	1.8	1.9	—		—		—		—		—	
	No. 20-178	—		—		—		—		—		—		1.6	1.3	1.7	1.6	1.8	1.8	2.2	1.7
Sharomys parvus sp. nov.	No. 20-4	6.0	10.0	1.1	2.1	1.6	2.5	1.8	2.0	—		—		—		—		—		—	
	No. 20-3	—		—		—		—		—		—		—		1.7	1.6	1.7	1.7	1.9	1.6
Kharomys mirandus sp. nov.	No. 20-179	0.8	0.9	1.1	1.7	1.5	1.9	—		—		—		—		—		—		—	
Kharomys gracilis sp. nov.	No. 20-92	0.5	0.7	1.1	1.7	1.6	1.7	1.5	1.5	—		—		—		—		—		—	
Tsagamys subitus sp. nov.	No. 20-96	—		—		—		—		—		—		1.2	1.1	1.6	1.2	1.9	1.4	—	
	No. 20-183	—		1.9	1.2	—		—		—		—		—		—		—		—	
Ulanomys mirificus sp. nov.	No. 20-1	—		—		—		—		—		—		—		—		1.9	1.6	2.0	1.7
	No. 20-2	—		—		—		—		—		—		1.5	1.2	1.7	1.6	1.9	1.7	—	
Boromys grandis sp. nov.	No. 30-4	—		—		—		—		—		3.5	2.6	—		3.6	3.1	3.7	3.6	—	

nus *Advenimus* (= *Saykanomys*) make it possible to include it to this type.

2. The relatively small infraorbital foramen is characteristic for the genus *Kharomys* gen. nov. Its dimensions do not surpass the anteroposterior diameter of P^{3-4}. It is characteristic that the anterior wall of the zygomatic arch is

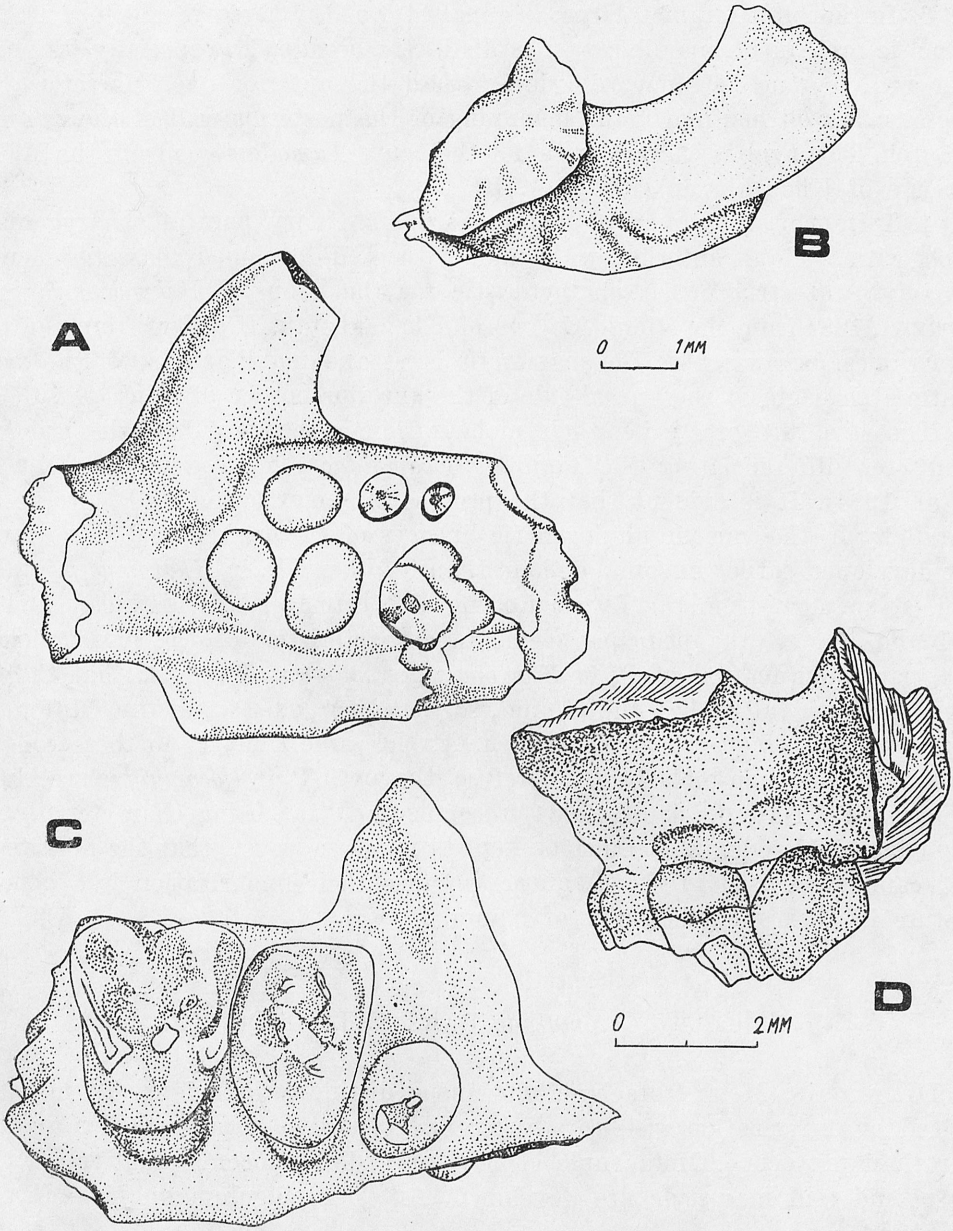

Fig. 5. The structure of maxilla and of zygomatic arch in the representatives of the family *Cocomyidae*. A — *Tamquammys tantillus* SHEVYREVA, 1971, fragment of the left maxilla and of zygomatic arch and alveoles of P^3—M^1, top view; B — mesial view; C — *Chkhikvadzomys elpima* SHEVYREVA, 1984, fragment of the left maxilla and of zygomatic arch with P^3—M^1; D — mesial view

vertical and the posterior one strongly reduced. The masseteric part, in contrast to the first type, begins buccally from P^3.

Parallelly with the described two types of structure there exist two other ones:

3. Infraorbital foramen large: it equals 4/3 of the alveolar width of P^4. Zygomatic arch in its maxillar part is distinctly broadened, especially its posterior wall is much stronger developed than the anterior one. Masseteric depression is well marked in the beginning of the posterior wall of the zygomatic arch. This type is characteristic for the genus *Tamquammys* from the Middle Eocene of Khazakhstan (Fig. 5 A, B).

4. Infraorbital foramen of medium size, maxillary part of the zygomatic arch with oblique anterior wall and with well-developed masseteric crest. This type of structure is characteristic for the genus *Chkhikvadzomys* SHEVYREVA, 1984 from the Middle Eocene of Khazakhstan. It differs from the previous ones, because here the masseteric crest and maxillar base of the zygomatic arch begin at the buccal side of the anterior border of P^3 (Fig. 5 C, D).

The structure of P_4^4, i.e. their molarization is recognized as the principal character differentiating the families *Cocomyidae* and *Youmyidae* (DAWSON et al. 1984). It is evident that the process of molarization of P_4^4 progressed parallelly in the various phylogenetic lineages of *Cocomyidae* and this character developed earlier in some of them than in others. P_4 in *Kharomys mirandus* gen. et sp. nov. from the Lower Eocene of Naran-Bulak is distinctly molarized and has all the principal elements characteristic for the lower molars. The particular feature of P_4 in *Kharomys* gen. nov. is, however, that the trigonid is much taller than the talonid, so that there exists a distinct difference between respective parts of the crown. At the same time, P^4 in these rodents remains totally non-molarized. Therefore, the lower P_4 in *Cocomyidae* are ahead of upper P^4. DAWSON et al. (1984) recognized dP_4^4 as being characteristic for ctenodactyloid rodents. It must be kept in mind, however, that the milk teeth dP_4^4 cannot be used in the diagnosis because their molarization is a general feature in all principal groups of mammals.

Subfamily *Cocomyinae* DAWSON, LI et QI, 1984

Diagnosis. Molars brachyodont, cusps distinctly bunodont. P_4^4 non-molarized or molarization visible only on P_4. Hypocone always smaller and lower than protocone. Metaconule clearly marked. Hypoconid relatively large, mesoconid and mesostyle are developed. Anterior cingulum on M^1—M^2 well expressed.

Contents. Six genera: *Cocomys* DAWSON, LI et QI, 1984, *Tamquammys* SHEVYREVA, 1971, *Sharomys* gen. nov., *Kharomys* gen. nov., *Tsagamys* gen. nov., *Ulanomys* gen. nov.

Comparisons (Table II). This subfamily is distinctly different from *Advenimurinae* subfam. nov. in the following characters:

1. P_4^4 are not molarized, P^4 in Early Eocene *Cocomyinae* having one lateral root and lacking the grove which forms when two roots merge. In contradistinction, in *Advenimurinae* subfam. nov. P^4 has two lateral roots, the development of which is, evidently, connected with the distinct molarization of this tooth.

Table II

Differences in the structure of teeth in *Cocomyinae* and *Advenimurinae* subfam. nov.

Characters	*Cocomyinae*	*Advenimurinae*
P_4^4	Usually non-molarized, sometimes molarization of P_4 P^4 with one lateral root	Sub-molarized P^4 with two lateral roots
Hypocone	Always smaller and lower than protocone Valley separating hypocone from protocone poorly developed	Hypocone nearly equals protocone in dimensions
Mesostyle	Pronounced in M^1—M^3	Usually reduced or poorly developed
Metaloph	Usually lacking or poorly developed	Pronounced
Cingulum	Moderately developed on P^4—M^3	Strongly developed particularly on anterior border of M^1—M^2
Buno-brachyodonty of molars	Molars buno-brachyodont, lower with five, upper with six cusps	Molars lophodont, relatively high

2. Hypocone on P^4—M^3 in Early Eocene *Cocomyinae* is always smaller and shorter than the protocone. Enlargement of hypocone to the size of protocone and separation of these two cusps are very characteristic for the development of advenimurids. In Middle Eocene representatives of *Cocomyinae*, hypocone and protocone are nearly equal, the valley separating them being distinct on the lingual side and reaching the middle of the height of the crown.

3. Buno- and brachyodont structure of lower and upper molars is distinct. Lower teeth have five cusps, between hypo- and entoconids there is a transversal ridge uniting them. Upper teeth have six cusps, are less developed and are provided with anterior and posterior cingulum.

Genus *Sharomys* gen. nov.

Derivation of the name. From shar (Mong.) — yellow.

Type species. *S. singularis* sp. nov.

Diagnosis. Infraorbital foramen large. Anterior side of the zygomatic arch oblique, masseteric crest begins on antero-buccal side of P^4. Trigone basin in the form of V, proto- and metaloph well-developed. Lower molars distinctly bunodont, metalophulid I present, hypoconulid present on M_1 and M_3, on M_3 connected with entoconid through pasterolophid.

Contents. Two species: *S. singularis* sp. nov. and *S. parvus* sp. nov.

Comparisons. Differs from *Cocomys* in the larger infraorbital foramen of hystricomorph type, from *Tamquammys* in V-form trigone, in more distinct anterior slope of the zygomatic arch and in the lack of the hypocone on P^4, from *Chkhikvadzomys* in non-molarized P^4, in less-developed valley between the hypocone and protocone and in the presence of one external root in P^4.

Sharomys singularis sp. nov.

Fig. 4 A, B; Fig. 6 A, B, C; Fig. 7 A, B

Derivation of the name. From singularis (Lat.) — single, unique.

Holotype. PSS, N° 20-182; fragment of right maxilla with P^2—M^2; Southern Gobi, Nemegt Basin, region of Naran-Bulak, Tsagan Khushu, quarry 2; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Material. Besides holotype PSS, N° 20-178; left mandible with P_4—M_3; PSS, N° 20-180, left M^{2-3}; PSS N° 20-186, fragment of left maxilla with P^3—M^2; Tsagan Khushu, quarry 2.

Description. Preserved lower part of the infraorbital ring points to the existence of an infraorbital foramen of larger dimensions then in other forms from Naran-Bulak Formation. Its dimensions cannot, however, be determined because of fragmentary material. Posterior wall of the zygomatic arch smaller than anterior one. Traces of the masseteric plate exist in the posterior base of the zygomatic arch, at the side of P^4. Masseteric crest begins 1.5 mm from the buccal side of the anterior border of P^4. P^3 not preserved, P^4 rectangular. Its anterior and posterior cingulum is well-developed. Protocone large, metacone undistinct. Proto- and metaconule well distinguished. Trigone basin closed. There is no hypocone. M^1 of trapezoidal form, its external length larger than internal one. Para- and metacone subequal. Mesostyle present. Trigone basin distinctly V-shaped. The abrasion of proto- and hypocone begins earlier than that of external cusps (para- and metacone). The tops of two first mentioned cusps are crescent-shaped. Hypocone is much smaller than protocone; the groove dividing these two cusps is distinct. Anterior cingulum present. M^2 less worn; its principal and accessorial cusps have the structure and situation as in M^1. P^4 not molariform. In the specimen PSS N° 20-180, M^{2-3} are well preserved. M^2 has a distinctly trapezoidal form. Its metacone is of

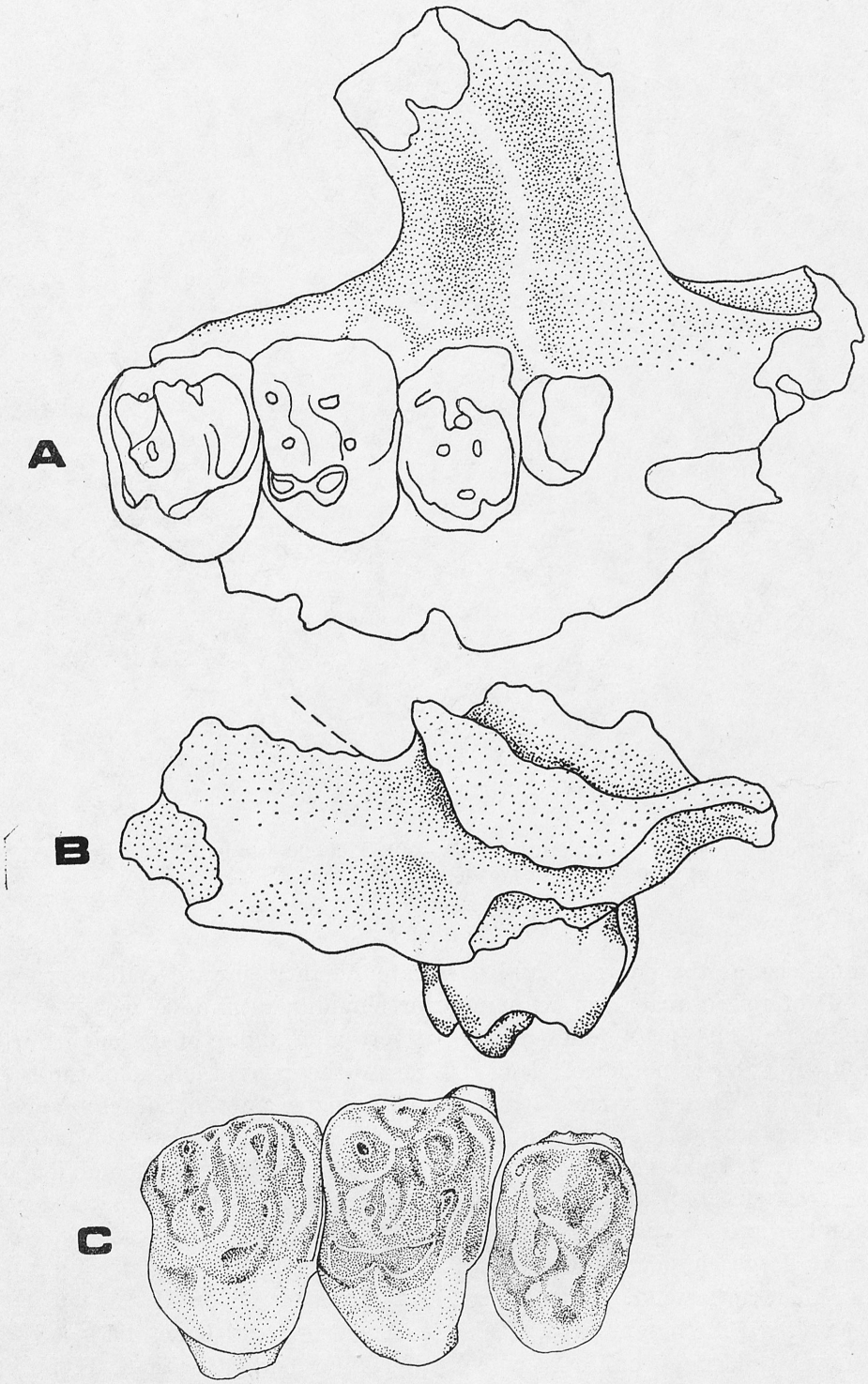

Fig. 6. *Sharomys singularis* gen. et sp. nov. A — holotype, PSS, N° 20-182, fragment of the right maxilla and of zygomatic arch with P^4—M^2, top view, × 12; B — mesial view, ×12; C — right P^4—M^2 (specimen 20-182), top view, × 15

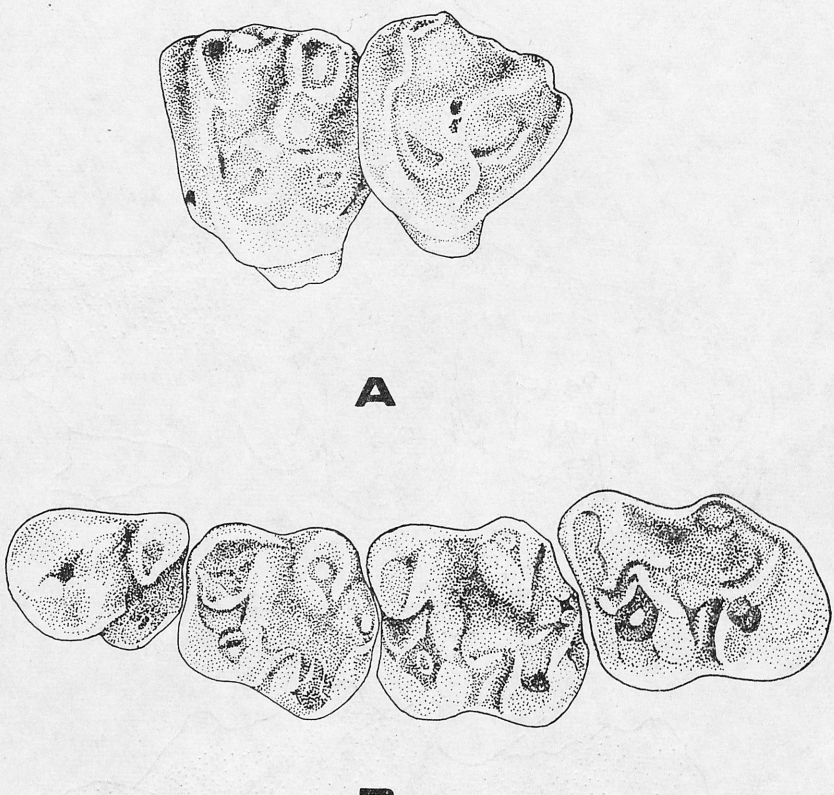

Fig. 7. *Sharomys singularis* gen. et sp. nov. A — PSS, N° 20-180, left M^{2-3}, top view, × 15; B — PSS, N° 20-178, left P_4—M_3, top view, × 15

the same size as the paracone and is situated slightly inwards. Mesostyle present. M^3 of round-oval form with anterior cingulum well-developed.

The mandibule in its dental part relatively high, index of its height on the level of the anterior border of M_3 in relation to the general lenght of the tooth-row is 33.3%. Incisor narrow (transversal diameter on the border of alveole 9.0 mm, antero-posterior 20 mm). Its transversal section has the shape of a narrow oval. Mental foramen situated below the anterior border of P_4. Masseteric crest distinct, anterior border of the masseteric fossa situated on the level of the anterior part of M_3. Molarization of P_4 is well marked, hypoconid relatively large, hypoconulid weakly marked. Entoconid slightly lower and smaller than hypoconid. Trigonid narrower than talonid on M_1. Anterior cingulum present, metalophulid II weakly marked. Trigonid basin distinct. Ectoloph developed, mesoconid present. Hypoconulid barely marked. Hypoconid large. M_2 differs from M_1 by its larger dimensions. Its hypoconulid is better developed. M_3 more elongated than M_2. Trigonid basin narrow. Hypoconid united with entoconid by posterior cingulum. Mesoconid present.

Sharomys parvus sp. nov.
Fig. 8 A, B, C

Derivation of the name. From parvus (Lat.) — small.

Holotype. PSS, N° 20-4; fragment of left maxilla with P^3—M^2; Southern Gobi, Nemegt Basin, region of Naran-Bulak, Tsagan Khushu, quarry 1; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Material. Apart from the holotype, fragment of the left mandible with M_1—M_3; PSS, N° 20-3, from the same locality.

Description. Structure of the maxillar part of the zygomatic arch does not differ from that in *S. singularis* sp. nov. Masseteric crest for the attachment of the masseteric muscle distinct; it begins 1.6 mm buccally from the anteroexterior border of P^4. Infraorbital foramen round-oval in shape. Its largest diameter about 1.4 mm longer than antero-posterior diameter of P^{3-4}. P^3 strongly reduced, of oval shape. P^4 molarized, lacking metacone. Paracone, situated on the external side of the tooth, is its largest and highest cusp. Protoloph distinct. Metaconule well-developed. Trigone basin closed. Protocone, situated on lingual side of the crown, opposite to paracone, is distinctly shaped. Hypocone is much smaller and lower than the protocone. M^1 of trapezoidal shape, its external side being slightly longer than internal one. Protoloph distinct. Protoconule barely marked. Metacone well-developed, oval in outline. Metaconule, isolated from neighbouring cusps and well-developed, is distinctly bunodont. Protocone occupies a large surface in the lingual part of the crown. Hypocone smaller than protocone, situated near the latter and separated from it by the internal fold. Mesostyle, distinct and situated at the beginning of the trigone valley, approaches the base of paracone. Trigone basin deep, open from buccal side. Between the metaconule and lingual cusps (protocone--hypocone) there is a narrow fissure, behind which trigone basin is distally open. M^2 is less worn than M^1. Protoloph distinct. Anterior border of masseteric fossa situated in the level of posterior border of M_2. Lower cheek-teeth relatively short in antero-posterior diameter and rather broad on the transversal axis of the talonid. M_1 trapezoidal in shape, its crown being the broadest in the region of talonid. As the anterior cingulum is lacking, the trigonid basin is not developed. Protoconid slightly more massive than metaconid. The particular character of these two latter cusps is that they are separate, as there exists a characteristic oblique fissure between them. Talonid basin broad. Hypoconid large and situated more externally in relation to protoconid. Entoconid smaller and lower than other cusps. Ectolophid differentiated. Hypoconulid well-developed and in central position. M_2 differs from M_1 by its larger dimensions. The distribution of cusps on M_2 is more or less the same as on M_1. Ectolophid better developed, with distinct mesoconid. M_3 differs from anterior molars by its more rounded end. Its protoconid is distinctly larger and taller than metaconid, the oblique fissure between them clearly visible. Mesoconid less developed.

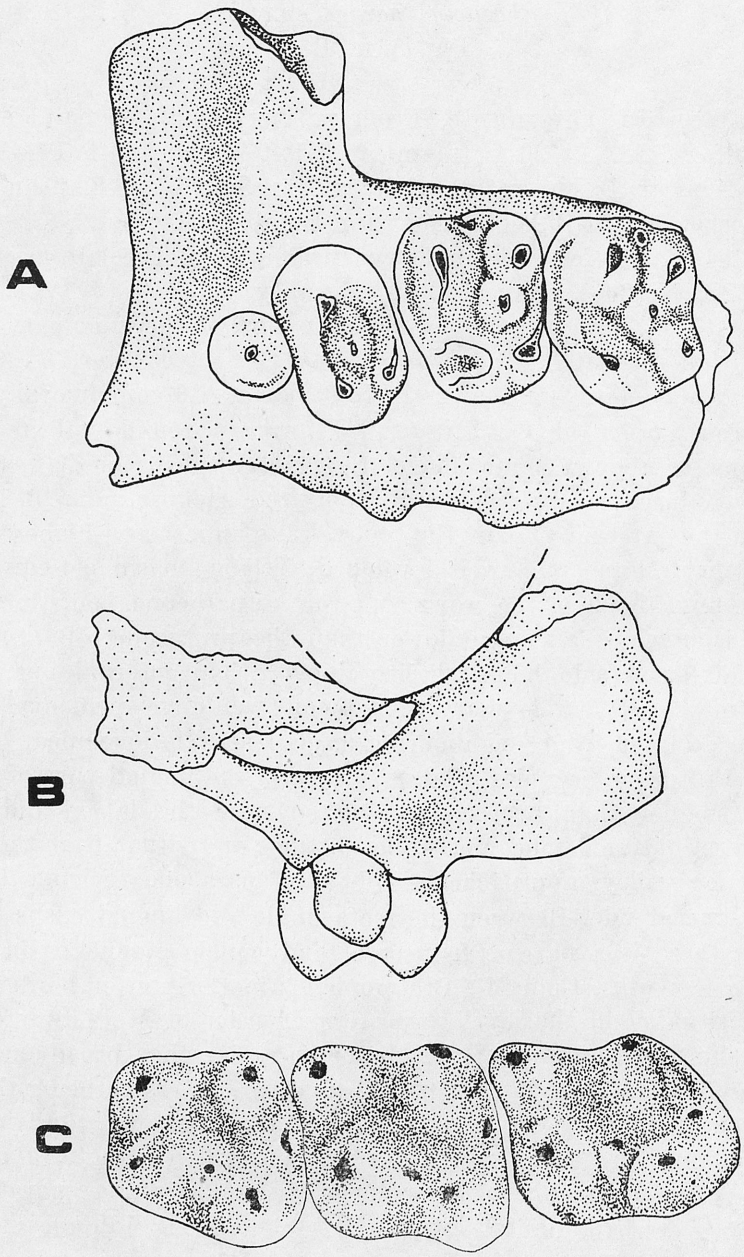

Fig. 8. *Sharomys parvus* gen. et sp. nov. A — holotype, PSS, N° 20-4, fragment of left maxilla and of zygomatic arch with P^3—M^2, top view, × 15; B — mesial view, × 15; C—PPS, N° 20-3, left M_{1-3}, top view, × 15

Comparisons. Differs from *S. singularis* sp. nov. by the lack of metaloph on M^1—M^3, by a more developed protoconule on upper molars and by the presence of a small hypocone on P^4.

Genus *Kharomys* gen. nov.

Derivation of the name. From khar (Mong.) — black.

Type species. *K. mirandus* sp. nov.

Diagnosis. Infraorbital foramen smaller than in *Sharomys* gen. nov. Anterior slope of the zygomatic arch much larger than in *Sharomys* gen. nov. Masseteric crest begins opposite to buccal side of P^3. Metaloph not differentiated, protoloph well developed, with a small protoconule.

Contents. Two species: *K. mirandus* sp. nov. and *K. gracilis* sp. nov.

Comparisons. Differs from *Cocomys* by the relatively larger infraorbital foramen which is of hystricomorph type, by the lack of metaloph and by the less developed posterior slope of the zygomatic arch and from *Sharomys* gen. nov. by the relatively smaller infraorbital foramen, a less developed anterior wall of the zygomatic arch and by a less expressed protoconule and metaloph on M^{1-2}.

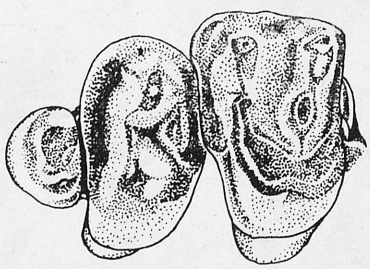

Fig. 9. *Kharomys mirandus* gen. et sp. nov. PSS, N° 20-178, left P^3—M^1 (holotype), top view, × 15

Kharomys mirandus sp. nov.
Fig. 4 C, D; Fig. 9

Derivation of the name. From mirandus (Lat.) — miraculous.

Holotype. PSS, N° 20-179, fragment of left maxilla with P^3—M^1; Nemegt Basin, region of Naran-Bulak, Tsagan Khushu, quarry 2; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Description. Interorbital foramen of large dimensions, its diameter about as large as the width of P^4. Maxillar part of the zygomatic arch narrower than in *Sharomys* gen. nov. Anterior slope of the zygomatic arch steep, posterior one weakly developed. Masseteric crest begins directly buccally from the external side of P^3. This tooth is round-oval in shape, on external side of its crown a distinct cusp represents the highest part of the tooth. P^4 rectangular, its proto- and metaconule are developed. Hypocone is barely marked. Trigone basin closed. M^1 of trapezoidal form. Protoloph well developed, with small protoconule. Metaloph not developed. Metaconule distinct, low, isolated from neighbouring cusps. Hypocone lower and smaller than protocone. Groove dividing these two cusps is poorly marked from lingual side.

Kharomys gracilis sp. nov.
Fig. 10 A, B

Derivation of the name. From gracilis (Lat.) — graceful.

Holotype. PSS, N° 20-92; fragment of left maxilla with P^3—M^2; Nemegt Basin, region of Naran-Bulak, Tsagan Khushu, quarry 1; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Material. Holotype only.

Description. Dimensions slightly smaller than in *K. mirandus* sp. nov. P^3 strongly reduced, oval, its top blunted be wear. P^4 rectangular, its paracone occupies the central position on the labial side of the crown. Protoloph developed, without protoconule. Metaconule minute, yet distinct. Protocone is the second largest cusp after paracone. Hypocone hardly marked. M^1 of trapezoidal shape, its external side longer than internal one. Paracone more massive

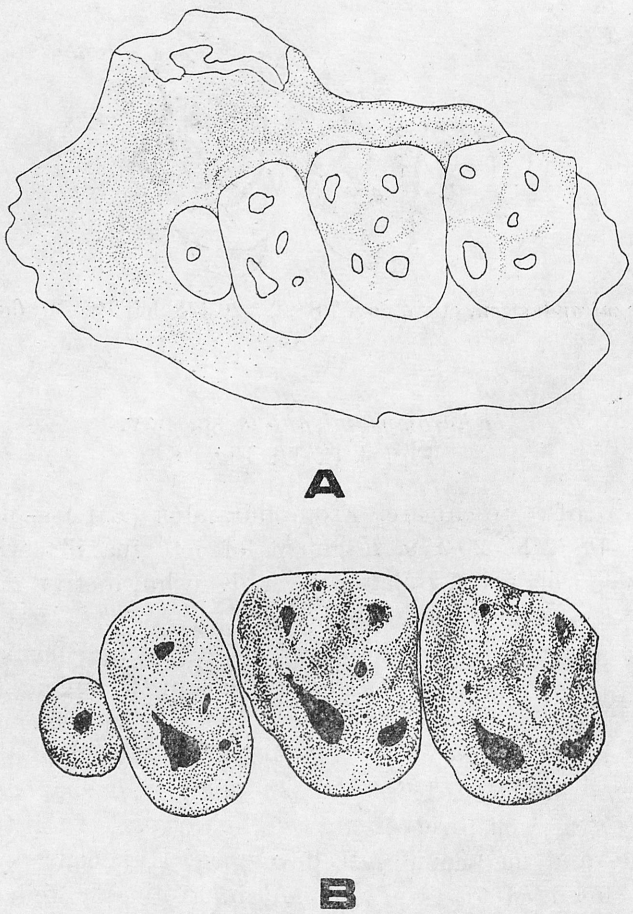

Fig. 10. *Kharomys gracilis* gen. et sp. nov. A — holotype, PSS, N° 20-92, fragment of left maxilla and of a base of the zygomatic arch with P^3—M^2, top view, × 15; B — left P^3—M^2, top view, × 15

than metacone, mesostyle weak. Protoloph developed, paraconule lacking. Proto- and hypocone are close one another, the former being larger and higher than the latter. Metaconule distinct, low and isolated from metacone. M^2 has the same shape as M^1. Anterior cingulum better developed. Para- and metacone are well isolated by broad trigone valley. Mesostyle present, approaches posterior slope of the paracone.

Comparisons. Differs from *K. mirandus* sp. nov. by its generally smaller dimensions of teeth and by the presence of hypocone on P^4.

Tsagamys gen. nov.

Derivation of the name. From tsaga (Mong.) — white.

Type species. *T. subitus* sp. nov.

Diagnosis. P_4^4 considerably molarized, with well-developed hypoconulid. Ectolophid weakly marked.

Contents. Type species only.

Comparisons. Differs from *Cocomys* in considerably molarized premolars and in better developed hypoconid, and well-developed hypoconulid on M_1 and M_2. It differs from all here described new genera of cocomyins by the strongly molarized P_4^4; at the same time its P_4 is characterized by the presence of well-developed hypoconulid and P^4 of metacone. From all other genera of subfamily differs in smaller dimensions, less developed ectolophid and small hypoconulid on M_1 and M_2.

Tsagamys subitus sp. nov.
Fig. 11 A, B

Derivation of the name. From subitus (Lat.) — unexpected.

Holotype. PSS, N° 20-96; fragment of left mandible with P_4—M_2; Southern Gobi, Nemegt Basin, region of Naran-Bulak, Tsagan-Khushu, quarry 1; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Material: Apart from holotype, PSS, N° 20-187, right P^4, Tsagan Khushu, quarry 1.

Description. Anterior border of the masseteric depression at the level of posterior border of M_2. Mental foramen situated below P_4. P_4 rectangular, its trigonid much higher than talonid. Metaconid slightly larger than protoconid and situated slightly anteriorly of it. All three cusps: entoconid, hypoconulid and hypoconid are conspicuous on its talonid, among them entoconid being the largest and the tallest, hypoconid second in size. Hypoconulid low but massive. Peaks of these cusps are connected by a weak transversal ridge. Presence of hypoconulid on P_4 points clearly to the existence of metacone on P^4. In this way it can be stated that P_4^4 were conspicuously molarized. M_1 is much broader than P_4, trapeziform. Its talonid much broader than trigonid,

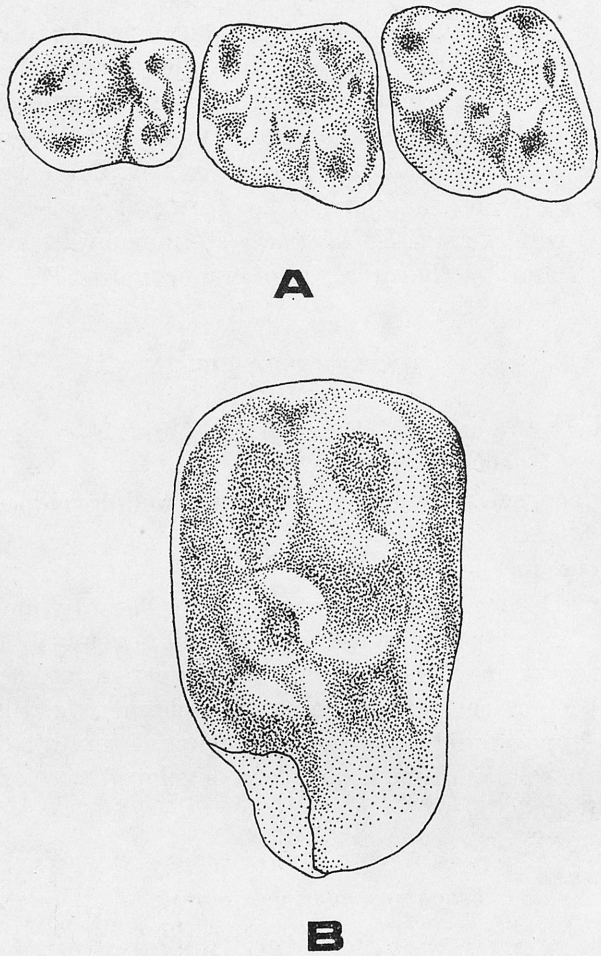

Fig. 11. *Tsagamys subitus* gen. sp. nov. A — holotype, PSS, N° 20-96, left P_4—M_2, top view, × 15; B — PSS, N° 20-183, right P^4, × 54, top view

trigonid basin developed, ectolophid not marked, mesoconid distinct. Hypoconid relatively large, entoconid smaller and lower than all other cusps of the grinding surface. In M_2, in opposition to M_1, trigonid and talonid are of the same width. Situation and proportions of principal cusps are the same as in M_1. The small hypoconulid occupies the central position between hypoconid and entoconid.

Genus *Ulanomys* gen. nov.

Derivation of the name. From ulan (Mong.) — red.

Type species. *U. mirificus* sp. nov.

Diagnosis. Trigonid basin on M_1—M_3 present. Hypoconid large, parti-

cularly on last molar. Entoconid much smaller than other cusps. Hypoconulid minuscule but distinct on M_1—M_3.

Contents. Type species only.

Comparisons. Differs from *Cocomys* in large dimensions, better development of hypoconid and presence of metalophulid I on lower molars, from *Sharomys* gen. nov. and *Kharomys* gen. nov. in conspicuously developed trigonid basin and relatively large hypoconid on M_1—M_3.

Ulanomys mirificus sp. nov.
Fig. 12

Derivation of the name. From mirificus (Lat.) — strange.

Holotype. PSS, N° 20-1, fragment of right mandible with M_1—M_3, Nemegt Basin, region of Naran-Bulak, Tsagan Khushu; Lower Eocene, Naran Bulak-Formation, Bumban Member.

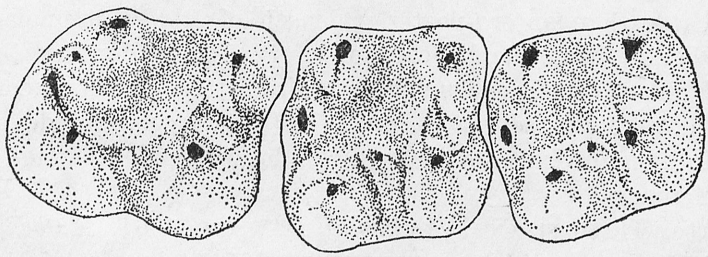

Fig. 12. *Ulanomys mirificus* gen. et sp. nov. Holotype, PSS, N° 20-1, right M_{1-3}, top view, × 10

Material. Apart from holotype, fragment of right mandible with M_2—M_3, PSS, N° 20-2; from the same locality.

Description. Mandible massive, its horizontal branch relatively high. Masseteric crests conspicuously marked, anterior border of masseteric fossa situated on the level of the middle of M_2. Mental foramen situated 1.2 mm below P_4. Molars very low, conspicuously bunodont. M_1 has nearly rectangular shape, its trigonid narrower than talonid. Trigonid basin small but distinct because of the presence of metalophulid I, mesoconid developed and situated lingually. Hypoconid distinct, anterior and posterior cingulum developed. M_2 rhomboidal, its lingual cusps situated slightly anteriorly in relation to external ones. Metaconid taller than protoconid, trigonid valley well-developed. M_3 relatively elongated in comparison to M_2, its posterior edge more rounded. Metaconid conspicuously displaced anteriorly in relation to protoconid, trigonid valley less developed. Hypoconid large, much larger and more massive than other cusps. Entoconid minute and short.

Subfamily *Advenimurinae* subfam. nov.

Diagnosis. Molars relatively high, conspicuously lophodont. P_4^4 submolarized. P^4 with two lateral roots. Hypocone slightly smaller than or nearly as large as protocone. The groove dividing these two cusps distinct. Cingulum well developed on P^4—M^3.

Contents. Four genera: *Advenimus* DAWSON, 1964, *Tsinlingomys* LI, 1963, *Chkhikvadzomys* SHEVYREVA, 1984, *Boromys* gen. nov.

Genus *Advenimus* DAWSON, 1964

Advenimus; DAWSON 1964, p. 4, fig. 1—6.
Saykanomys; SHEVYREVA 1972, p. 132, fig. 1; 1976, p. 27, fig. 5; WOOD 1977, p. 122, fig. 2.

Type species. *A. burkei* DAWSON, 1964.

Diagnosis. Infraorbital foramen large. Its largest diameter no less than 4 times greater than antero-posterior length of P^4. P_4^4 submolarized. Masseteric crest begins from the buccal side of P^4. P_4^4 smaller than molars. Teeth buno-lophodont, their dimensions increase from P_4 to M_3. Hypoconulid well-developed and distinctly separated on P_4—M_3. Anterolophid developed. Metalophulid II distinct. Proto- and metaconulid present. Anterior cingulum on P^4—M^3 well marked.

Contents. Three species: *A. burkei* DAWSON, 1964, *A. bohlini* DAWSON, 1964 (= *Saykanomys chalchae* SHEVYREVA, 1972), *A. wilsoni* DAWSON, LI et QI 1984.

Discussion. Genus *Saykanomys*, described by N. S. SHEVYREVA (1972) from the Middle Eocene of Khaichin Ula II, has following principal characteristics: large infraorbital foramen of hystricomorph type, P_4^4 smaller than molars, successive increase of dimensions from P_4 to M_3; well-developed hypoconulid on all lower teeth, conspicuously expressed anterolophid on P_4—M_3.

As to the first character, N. S. SHEVYREVA, correctly remarked that infraorbital foramen of *Saykanomys* is larger than in any other representative of *Sciuravidae*. This feature, undoubtedly appears as typical and general in Eocene ctenodactyloids of Asia (WOOD 1975). Fragmentary paleontological material does not permit to express opinion about the structure of the skull, and particularly about the infraorbital foramen in the genus *Advenimus*. Nevertheless, the above-mentioned characters of the genus *Saykanomys* are typical for *Advenimus* from the Middle Eocene of Northern China (DAWSON 1964). Index $\frac{M1}{P4}$ in both genera is the same: in *A. burkei* — 1.05, *A. bohlini* — 1.07, *S. chalchae* — 1.15. The increase of dimensions of successive teeth P_4 to M_3 is identical in *Advenimus* and *Saykanomys*. In both genera trigonid is

slightly narrower than talonid in lower teeth. Of particular importance is the presence in both *Advenimus* and *Saykanomys*, of anterolophid and of a transversal ridge connecting protoconid and metaconid. Hypoconulid is massive and very distinct on all lower teeth in *Advenimus* and *Saykanomys*. The tendency to the confluence of hypolophid and ectolophid anteriorly of the hypoconid on M_1—M_3 is visible in both genera. Apart from that, the position of mental foramina and the depression of masseteric plate on the mandible in these genera are identical. All this demonstrates that *Saykanomys* is a junior synonym of *Advenimus*. My opinion about the identity of *Advenimus bohlini* with *Saykanomys chalchae* is in accord with the data of M. DAWSON et al. (1984).

Genus *Boromys* gen. nov.

Derivation of the name. From bor (Mong.) — grey.

Type species. *B. grandis* sp. nov.

Diagnosis. Ectolophid distinct, without mesoconid. Hypoconulid on lower molars massive and distinct. M_1 and M_2 square in outline.

Contents. Type species only.

Comparisons. Differs from the nearest genus *Advenimus* by the lack of mesoconid and by a more external position of hypoconulid on M_1 and M_2, by the square outline of crowns of M_1 and M_2, a more straight entoconid crest, a distinct valley between entoconid and hypoconid and by relatively high molars (relation of height to length in M_1 — 0.68, in M_2 — 0.71). It differs from *Chkhikvadzomys* by its larger dimensions, more molarized P^4 and trapezoidal shape of M^1—M^2, and from *Tsinlingomys* by the well-developed hypoconulid and lack of metalophulid II on M_1 and M_2.

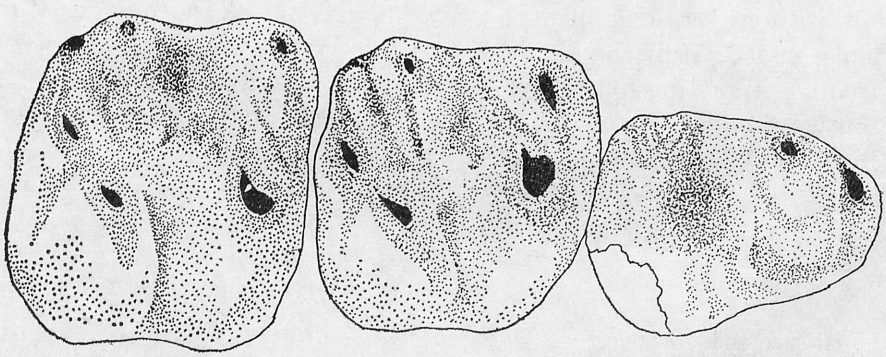

Fig. 13. *Boromys grandis* gen. et sp. nov. Holotype, PSS N° 30-4, right P_4—M_2, top view, × 10

Discussion. M. Dawson (1964) described a fragment of the right mandible with P_2—M_3 under the name of *Advenimus* sp. from the Middle Eocene Ulan Shire Formation in the outcrops of Chimney Butte in China. This specimen very much resembles *Boromys* gen. nov. Such characters as general dimensions, square outline of molars and position of the masseteric depression of the mandible are very similar in both cases. At the same time there are some differences between them: in the rodent from Ulan Shire, P_4 is slightly reduced, there are two mental foramina, etc.

Boromys grandis sp. nov.
Fig. 13

Derivation of the name. From grandis (Lat.) — large.

Holotype. PSS, N° 30-4, fragment of right mandible with dP_4, M_1, M_2; Southern Gobi, Bugintsav Basin, Khaichin-Ula II, Middle Eocene, Khaichin Formation, Khaichin level.

Description. Dimensions similar to those of *Advenimus burkei*. Anterior border of masseteric depression situated on the level of the limit between M_1 and M_2. One mental foramen, situated anteriorly of P_4. Dimensions of molars increase from M_1 to M_3 (judging after alveoles the last molars were the largest), dP_4 elongated, its trigonid narrower than talonid. This tooth is relatively long. Talonid is strongly worn and partly destroyed, so that it is difficult to judge about its structure. Protoconid low, distinct and in lingual position. Metaconid high, its posterior side oblique. Protoconid blunt, a crest originating at its top in lingual direction is distinct. Talonid basin broad. Entoconid small. Anterior cingulum well-developed. M_1 square in outline. Metaconid taller and less massive than protoconid. Metalophulid II very distinct. Trigonid basin present. Ectolophid well-developed. Mesoconid almost lacking. Entoconid smaller than hypoconid, entoconid crest directed nearly straight (transversely), it ends without reaching lingual wall of hypoconid. Hypoconid very massive, its top rounded. Hypoconulid large, occupies relatively external position and is situated near the hypocone. Posterior cingulum well-developed. Talonid basin very distinct. Ectolophid better developed than in M_1. Hypoconid large, hypoconulid close to hypoconid.

IV. DISCUSSION

Until recently, *Ischyromyoidea*, known from the Upper Paleocene and Eocene of North America and from the Lower Eocene of Western Europe, were recognized as ancestors of all rodents. In the last years an important progress has been reached in the study of ctenodactyloid rodents and of archaic

lagomorphs of Asia. This made possible a new approach to the problem of the origin of rodents (HARTENBERGER 1980, 1985). Interesting in this respect is the contribution of BRUIJN et al. (1982), who described fragmentary remains of rodents (ctenodactyloids and ischyromyids) from the Lower Eocene of Pakistan and also discussed the problems of the origins of these groups. The authors stated the existence of fully molarized P_4 in the representatives of Early Eocene fauna of Barbara Banda. The presence of a large hypocone on this tooth, the lack of metalophulid I and of hypoconulid were used to refer this rodent to *Ischyromyoidea*. The presence of *Ctenodactyloidea* (non-molariform P_4, multiserial type of enamel) and of *Ischyromyoidea* (molariform P_4, pauciserial type of enamel) in the Lower Eocene of Pakistan are, in the opinion of the authors, a strong support for HARTENBERGER'S opinion about the Paleocene dichotomy of rodents.

As stated earlier, P_4 in *Tsagamys subitus* gen. et sp. nov. from the Lower Eocene of Mongolia is considerably molariform. On its trigonid, proto- and metaconid are distinct and on the talonid, hypo- and entoconid as well as hypoconulid are developed. Notwithstanding the molarization of P_4, this tooth differs from the molars in its trigonid which is tall in relation to the talonid.

The new material from Mongolia indicates that molariform P_4 from the Lower Eocene of Pakistan determined as belonging to *Ischyromyoidea* (BRUIJN et al. 1982) belongs in fact to *Ctenodactyloidea*. In any case, the presence of ischyromyoid rodents in the Eocene of Barbara Banda cannot be taken as granted without new data and more convincing arguments.

The finds of rodents and other fossils are associated with very base of the Bumban section (DASHZEVEG 1982). As there is a continuity of sections in the region of Naran-Bulak during the passage from the Paleocene to the Eocene, it must be supposed that the association known from Bumban Member developed much earlier than the beginning of sedimentation of this member. Therefore, the origins of this fauna are to be expected in the Paleocene. So far, however, no traces of this fauna have been found, neither in Naran-Bulak itself, nor in other Late Paleocene faunal localities in Asia. It is possible that the lack of remains of this fauna in Late Paleocene sections of Naran-Bulak can be explained by taphonomic reasons. We can suppose that the fauna, composed of ctenodactyloid rodents, perissodactyls (*Hyracotherium*, *Homogalax*), condylarthrs (*Hyopsodus*) and others did not play an important role at that time. The biotope inhabited by it could be situated far from the region from which originated the material accumulated in the formation. It is well known that there is a relation between the composition of faunal remains and the distance between the place of existence and place of deposition of organisms (EFREMOV 1950). If the biotope of the Paleocene community was remote from the place of deposition, the probability of conservation of its members was reversely proportional to the distance from their living area. In this case it would be a very limited chance for the preservation of the elements of the

fauna of such a distant biotope. It is therefore not impossible that ctenodactyloid rodents and some other mammals (*Perissodactyla*) appeared on the territory of Central Asia before the Eocene.

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STRESZCZENIE

Eoceńska rodzina gryzoni *Cocomyidae* (*Ctenodactyloidea*) podzielona jest w niniejszej pracy na dwie podrodziny: *Cocomyinae* i *Adenimurinae* subfam. nov. Materiał *Cocomyinae* z wczesnego eocenu formacji Naran-Bulak w basenie Nemegt z Mongolskiej Republiki Ludowej należy do sześciu nowych gatunków skupionych w czterech nowych rodzajach (*Sharomys singularis*, *S. parvus*, *Kharomys mirandus*, *K. gracilis*, *Tsagamys subitus* i *Ulanomys mirificus*). Podrodzina *Advenimurinae* subfam. nov. jest reprezentowana przez *Boromys grandis* gen. et sp. nov. opisany ze środkowego eocenu stanowiska Khaichin Ula II w basenie Bugintsav z Mongolskiej Republiki Ludowej. Rodzaj *Saykanomys* SHEVYREVA, 1972 jest synonimem *Advenimus* DAWSON, 1964. W pracy dyskutuje się problemy pojawienia się gryzoni w Azji Centralnej w świetle nowych materiałów z Mongolskiej Republiki Ludowej.

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