ACTA ZOOL. CRACOV. | 33 | 3 | 37—44 | KRAKÓW, 30, IX. 1990

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New trends in adaptive radiation of Early Tertiary rodents *(Rodentia, Mammalia)*

[With 3 text-figs]

Nowe kierunki radiacji adaptatywnej wczesnotrzeciorzędowych gryzoni *(Rodentia, Mammalia)*

Abstract. Two new families of Early Eocene rodents: *Alagomyidae* and *Orogomyidae* from the Naran-Bulak Formation (Bumban Member) in the Nemegt Basin in Mongolian People's Republic are described. The former family is represented by *Alagomys inopinatus* gen. et sp. nov., the latter by *Orogomys obscurus* gen. et sp. nov. Their primitive characters permit to recognize the described forms as being at the origin of *Rodentia* and *Mixodontia*. *Eurymyloidea* and, particularly, *Heomys*, cannot be considered as ancestors of rodents.

I. INTRODUCTION

In 1976—1980 the author had the opportunity, as a member of the Soviet-Mongolian Paleontological Expedition, of washing and screening the fossiliferous deposits of the Naran-Bulak Formation (Bumban Member, Lower Eocene) in the outcrops of Tsagan Khushu in the central part of the Nemegt Basin (DASHZEVEG 1982, RUSSELL and DASHZEVEG 1986). The result was the collection of the first substantial material of Early Eocene mammals in the Mongolian People's Republic. The most important among it are fossil rodents, mainly representatives of a ctenodactylid family *Cocomyidae*. Besides them there are, in author's collection, remains of relatively primitive *Rodentia* which are the subject of the present study. The materials are stored 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.

The author would like to use this occasion to express his deep gratitude to Dr. J. L. HARTENBERGER, Dr. K. KOWALSKI and Dr. D. E. RUSSELL for their help and advice during the preparation of the present paper.

II. SYSTEMATIC PART

Order *Rodentia*

Family *Alagomyidae* fam. nov.

Diagnosis. Dimensions small, dental formula $I\frac{1}{1}\,C\frac{0}{0}\,P\frac{2}{1}\,M\frac{3}{3}$. Teeth buno- and brachyodont. $P\frac{4}{4}$ not molariform, with two roots each. M^{1-2} in the shape of an isosceles triangle, without hypocone. Proto- and metaconule distinctly developed. Parastyle not marked. Trigonid basin on M^1 and M^2 open, relatively narrow. Protocone massive, the largest of all cusps. Mesostyle developed. Posterior cingulum present on M^1 and M^2. On M_1, M_2 and M_3 trigonid much narrower than talonid. Ectolophid developed, with massive mesoconid.

Comparisons. Differs from all known families of Early Tertiary rodents by small dimensions and strongly expressed buno- and brachyodont form of cheek-teeth; from *Cocomyidae* by the lack of hypocone and distinctly triangular form of the crown of M^1 and M^2.

Contents. Genus *Alagomys* gen. nov.

Genus *Alagomys* gen. nov.

Derivation of the name. From alag (Mong.) — spotted.

Type species. *Alagomys inopinatus* sp. nov.

Diagnosis. As for the family.

Alagomys inopinatus sp. nov.

Fig. 1

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

Holotype. PSS, N° 20-176, fragment of right maxilla with P^4—M^2.

Material. PSS, N° 20-177, right M_{1-2}.

Type horizon and locality. Southern Gobi, Nemegt Basin, Tsagan Khushu, quarry I, Lower Eocene, Naran-Bulak Formation, Bumban Member.

Description. Cheek-teeth brachyodont, their cusps distinctly bunodont. P^3 not preserved but remains of its posterior alveole present. P^4 not molariform, with two roots. This tooth is markedly elongate in lingual-buccal direction. Two isolated cusps are developed on P^4: the lingual one, much lar-

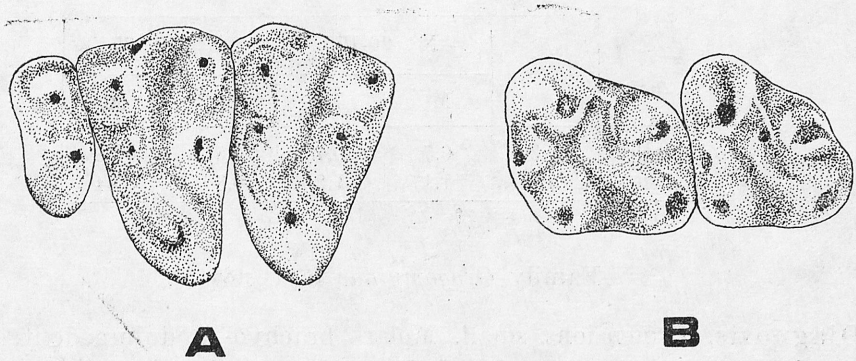

Fig. 1. *Alagomys inopinatus* n. sp. A — holotype, PSS, N° 20-176, A — right P^4—M^2, × 30, top view; Southern Gobi, Nemegt Basin, Tsagan Khushu, quarry 1; Lower Eocene, Naran-Bulak Formation, Bumban Member. B — right M_{1-2}, from the same locality, top view

ger than the buccal, represents the protocone. Both cusps are separated by a relatively deep groove.

M^1 in the form of isosceles triangle. Talonid basin is open and extends from the anterior end of the protocone to the exterior border of the crown; it is relatively narrow. Paracone well developed, its top has a markedly round-oval shape in occlusal view. Metacone slightly larger and situated more buccally than paracone. Accessorial cusps strongly developed: protoconule slightly smaller than metaconule. Protocone is the largest of all cusps, hypocone is not developed; not even a trace of it is preserved. Mesostyle situated on the elevated part of ectoloph, posteriorly from the bucco-posterior edge of the paracone. Anterior cingulum weakly developed, posterior one clearly visible on the whole length of the crown of M^1. M^2 triangular, its anterior part slightly longer then posterior one. Para- and metacone subequal in dimensions. Metaconule distinctly larger than protoconule and isolated from neighbouring cusps. Protoconule connected with paracone by small transversal ridge. Protocone massive and large, in the shape of a regular pyramid. Between protoconule and protocone there is a tiny but distinct cusp, nearly fully isolated from neighbouring cones. Mesostyle developed as in M^1. Trigone basin well developed, slightly curved in the region of proto- and metaconule. Posterior cingulum developed. M^3 not preserved, there are only traces of its anterior root.

The dimensions of molars increase from the first to the third, their lingual cusps are higher than labial ones. Main cusps pyramidal in shape, relatively high and pointed. On M_1, M_2 and M_3, trigonid distinctly narrower than talonid. Ectolophid well developed, with large mesoconid, situated nearer the protoconid than the hypoconid. Anterior cingulum present, but relatively small. Trigonid basin marked. Mesoconid slightly taller and larger than protoconid. Hypoconid is the largest cusp on talonid, entoconid is intermediate in dimensions between hypoconid and distinctly developed hypoconulid.

Dimensions, in mm:

		N° 20-176		N° 20-177	
		M^1	M^2	M_1	M_2
Length	0.3	0.7	0.7	0.81	0.88
Width	0.7	1.1	1.2	0.84	0.84

Family *Orogomyidae* fam. nov.

Diagnosis. Dimensions small. Molars brachyo- and bunodont, protoconule and metaconule well developed. M^{1-2} of triangular shape, parastyle massive, distinct. Mesostyle present. Hypocone weakly developed. Anterior and posterior cingulum on upper molars well developed. On M_{1-3} basins of trigonids not developed. Lingual cusps shifted anteriorly in relation to labial ones. Metaconid on M_{1-3} always larger and higher than protoconid.

Comparisons. Existing material permits to determine the specific characters of the family and its differences in comparison with the most primitive rodents of the families *Ischyromyidae* and *Cocomyidae*. It differs from the representatives of the above-mentioned families by small dimensions, much less developed hypocone and the presence of a strong parastyle on M^{1-2}. *Orogomyidae* fam. nov. as opposed to *Cocomyidae* and *Ischyromyidae*, have a distinctly triangular shape of the crown of M^1 and M^2 and more bunodont structure of molars; they are particularly characterized by the lack of meta- and protoloph.

They differ from *Alagomyidae* fam. nov. by the presence of parastyle and by a more developed hypocone on M^{1-2}. Also, *Alagomyidae* fam. nov., in contrast to *Orogomyidae* fam. nov., have a relatively narrow trigonid in relation to the talonid and the more developed mesoconid on M_1—M_3.

Contents. Genus *Orogomys* gen. nov.

Genus *Orogomys* gen. nov.

Derivation of the name. From orog (Mong.) — grey, ash-grey.

Type species. *Orogomys obscurus* sp. nov.

Diagnosis. As for the family.

Orogomys obscurus sp. nov.

Fig. 2

Derivation of the name. From obscurus (Lat.) — enigmatic.

Holotype. PSS, N° 20-174, left M^1 or M^2.

Material. PSS, N° 20-175, right M_{1-3}.

Dimensions (in mm): M^1 or M^2 — length (L) (1.74), width (W) (1.49); M_1-L (0.83), W (0.61); M_2-L (0.82), W (0.67); M_3-L (0.81), W (0.59).

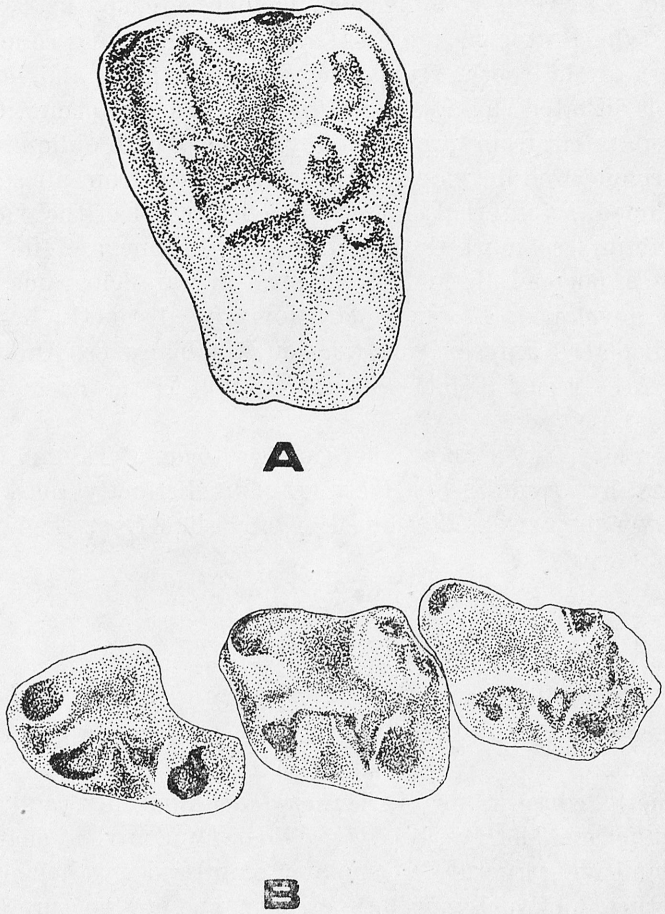

Fig. 2. *Orogomys obscurus* sp. nov. A — holotype, PSS, N° 20-174, left M^1 or M^2 × 17.5, top view; Southern Gobi, Nemegt Basin, Tsagan Khushu, quarry 1; Lower Eocene, Naran-Bulak Formation, Bumban Member. B — right M_2—M_3, from the same locality, top view

Type horizon and locality. Southern Gobi, Nemegt Basin, Tsagan Khushu, quarry I; Lower Eocene, Naran-Bulak Formation, Bumban Member.

Description. Molar teeth brachyodont, cusps of the grinding surface distinctly bunodont, ridges connecting principal cusps not expressed. M^1 and M^2 of distinctly triangular shape, their length smaller than their width. Parastyle elongate, relatively small and separated from the paracone by a well-developed depression. Para- and metacone subequal; between them there is a minuscule and low cusp; this unnamed cusp approaches the paracone with the wear of the tooth. Metaconule relatively large, but much lower than paracone and well isolated from the protocone. The wearing of the metaconule joins it to the metacone. Protoconule much smaller than metaconule and well connected with protocone by internal cone. It is totally isolated from the paracone. Mesostyle is distinctly expressed on the labial side of the tooth. In

its neighbourhood there is a minuscule, elongated cusp, markedly differing from the mesostyle. Protocone represents a large and strong cone which forms the highest part of the tooth. Hypocone is much smaller and lower than the protocone and is situated slightly more inwards than the former. On the plane, hypocone is separated from protocone by a deep and oblique groove. The valley of the trigone well-developed and nearly closed from all sides. Anterior cingulum developed, its internal end situated before 1/4 of the width of crown. Posterior cingulum less marked than the anterior one and its internal end approaches the hypocone. M_1 and M_2 in form of parallelograms, their principal cusps well developed. Lower molars low and distinctly bunodont, their lingual cusps displaced anteriorly in relation to labial ones. Anterior cingulum relatively low. As a result of lack of metalophulid II the basin of trigonid is almost unmarked.

Metaconid on M_{1-2} larger and higher than protoconid. Talonid basin narrow. Hypoconid large, hypoconulid relatively low, but distinctly marked. Posterior cingulum on lower molars not developed or only slightly marked.

III. DISCUSSION

The new material from Mongolia permits to formulate following preliminary conclusions:

1. Phylogenetic connections of *Alagomyidae* fam. nov. and *Orogomyidae* fam. nov. are unclear. The family *Alagomyidae* fam. nov. is characterized by a markedly primitive structure of molars, expressed in their brachyo- and bunodont structure, lack of hypocone etc. This type of structure of their teeth permits, without any doubt, to recognize them as being at the origin of rodents and of the cohort Glires in general. *Orogomyidae* fam. nov. are, in comparison with them, more derived, as evidenced by the presence of hypocone and by more perfect structure of the trigone on M^1 and M^2. In the same time, on M^1 and M^2 of *Orogomyidae* fam. nov. there is a well developed parastyle, the presence of which is not characteristic for *Alagomyidae* fam. nov. and for primitive rodents of the family *Cocomyidae*. The position of *Orogomyidae* fam. nov. remains so far uncertain because of limited material. It is reasonable to suppose that both families of this group are at the origin of the orders *Rodentia* and *Mixodontia*.

2. The high diversification of Early Eocene rodents on the family level in Mongolia suggests that their radiation took place during the Paleocene or Eocene. This is in accord with earlier expressed opinion of HARTENBERGER (1977) about the Paleocene dichotomy of rodents (Fig. 3).

The characters listed above, such as undifferentiated or slightly differentiated hypocone and the distinct bunodonty of the molars in the families *Alagomyidae* fam. nov. and *Orogomyidae* fam. nov., are the best indicators of their

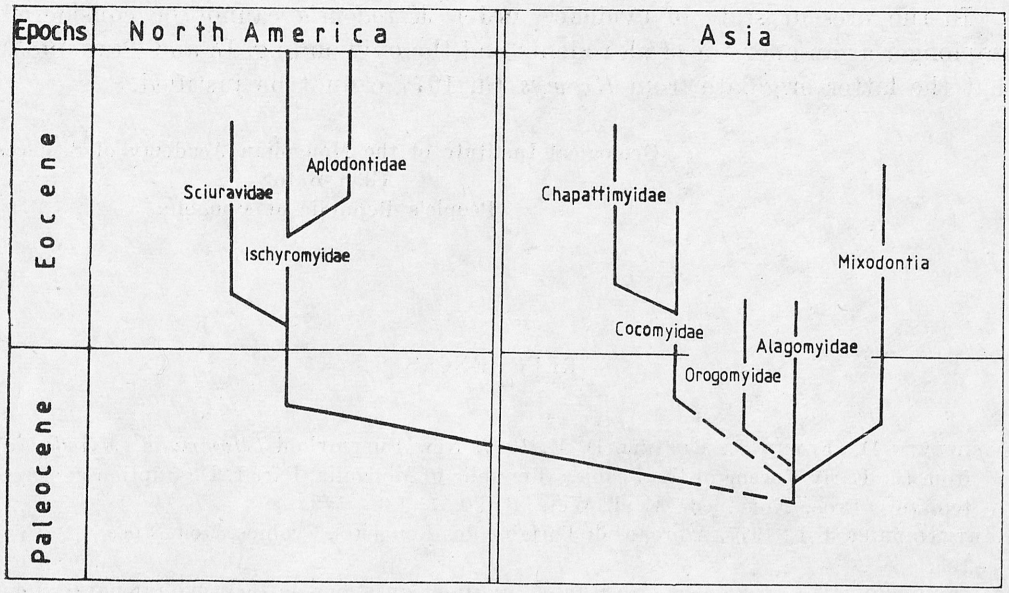

Fig. 3. Phylogenetic relationships of Early Tertiary rodents

low level of evolution and their place at the beginning of the phylogenetic history of rodents.

From the cladistic point of view it must be supposed that a species with most primitive characters is to be expected inside the oldest part of the area of a higher taxon, i.e. in the center of origin. New Mongolian discoveries corroborate the Central Asiatic origin of *Rodentia*.

3. What groups of mammals were ancestral for the rodents? This problem still remains open and that is why so many theoretical hypotheses have been formulated (see LUCKETT and HARTENBERGER 1985, HARTENBERGER 1985).

The study of the microstructure of incisors and of the structure of teeth in Early Eocene *Eurymyloidea* from Mongolia permits to include *Mixodontia* into the cohort Glires, together with *Rodentia* and *Lagomorpha* (DASHZEVEG et al. 1987).

There is no doubt that rodents and mixodonts developed from a common ancestor and that their evolution was parallel during the Paleocene and Early Eocene. In the evolutionary lineages of *Mixodontia* more primitive characters can be observed, particularly the sectorial type of the structure of molars, the presence of the paraconid, the contrast between the trigonid and talonid and so on, evidently the heritage of ancestral forms.

Phyletic radiations inside the *Eurymyloidea* and *Cocomyidae* demonstrate a parallelism which can be seen in nearly all branches diverging from the common stock.

„Rodent type" develops parallelly in several evolutionary lines of *Eurymyloidea*, most evidently in the genus *Zagmys* DASHZEVEG, FLYNN et RUSSELL, 1987 (DASHZEVEG et al. 1987).

In the present state of evidence, order *Mixodontia* cannot be considered any longer as an ancestor of all rodents and the opinion (e.g. Li and Ting 1985) that the latter originate from *Heomys* Li, 1977 cannot be justified.

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STRESZCZENIE

Praca zawiera opis materiału kopalnego z dwóch nowych rodzin wczesnoeoceńskich gryzoni z formacji Naran-Bulak (poziom Bumban) w basenie Nemegt w Mongolskiej Republice Ludowej. Pierwsza z rodzin *Alagomyidae* fam. nov. jest reprezentowana przez *Alagomys inopinatus* gen. et sp. nov., a druga, *Orogomyidae* fam. nov., przez *Orogomys obscurus* gen. et sp. nov. Oba gatunki wykazują bardzo prymitywne cechy i mogą być traktowane jako formy wyjściowe dla rzędów *Rodentia* i *Mixodontia*. W tej sytuacji *Eurymyloidea*, a szczególnie rodzaj *Heomys*, nie mogą być traktowane jako przodkowie gryzoni.

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