Rodents from the early Paleogene Dzhylga localities in southern Kazakhstan

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Rodents from the early Paleogene Dzhylga localities in southern Kazakhstan

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With 18 figures

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Abstract: Two isolated molars, the holotypes of *Asiaparamys shevyrevae* NESSOV, 1987b and *Kazygurtia clivosa* NESSOV, 1987b from the latest Paleocene Dzhylga 1a locality are restudied, and an additional molar of *A. shevyrevae* from the same locality is described. *Asiaparamys* is referable to the rodent family Ischyromyidae by having the trigonid compressed antero-posteriorly and a ridge-like hypoconulid. *Kazygurtia* with a posteriorly closed trigonid basin, subvertical posterior trigonid wall, weak ectolophid lacking a mesoconid, cusp-like hypoconulid, and strongly bunodont molar cusps, is one of the most generalized Glires taxa; it is referred to Glires incertae sedis. The Glires species from Dzhylga 1a are among the oldest known rodents or rodent-like mammals. Enamel microstructure of five isolated Glires incisor fragments exhibits two-layered enamel with pauciserial Hunter-Schreger bands and radial enamel, which are typical for early Paleogene rodents.

Zusammenfassung: Die Holotypen von *Asiaparamys shevyrevae* NESSOV, 1987b und *Kazygurtia clivosa* NESSOV, 1987b, zwei isolierte Molaren aus der Lokalität Dzhylga 1a (oberstes Paläozän) werden erneut untersucht. Daneben wird ein weiterer Molar von *A. shevyrevae* von derselben Fundstelle neu beschrieben. *Asiaparamys* kann aufgrund seines mesio-distal komprimierten Trigonids und des gratartigen Hypoconulids zu der Nagetier-Familie Ischyromyidae gestellt werden. *Kazygurtia* stellt mit einem distal geschlossenen Trigonidbecken, nahezu senkrechtem distalem Trigonidrand, einem schwachen Ectolophid ohne Mesoconid, höckerartigem Hypoconulid und betont bunodonten Molarenhöckern eines der am stärksten generalisierten Taxa der Glires dar und wird hier als Glires incertae sedis geführt. Die Glires von Dzhylga 1a gehören zu den geologisch ältesten Nagetieren. Das Schmelzmuster von fünf gliriformen isolierten Inzisiven-Fragmenten besteht aus pauciserialen Hunter-Schreger Bändern und Radialschmelz und ist damit typisch für alt-paläogene Nagetiere.

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Introduction

In 1977 the locality Dzhylga 1 a in southern Kazhakhstan, rich in early Paleogene predominantly marine vertebrates, was discovered and sampled up to 1985 by L. A. NESSOV and his team. The vertebrate fauna consists of numerous and diverse chondrichthian and osteichthian fishes, abundant sea turtles, rarer terrestrial turtles, choristoderes, sea snakes, birds, and extremely rare but tantalizing mammals (NESSOV & UDOVICHENKO 1984; NESSOV 1987a, b, 1988a, b; NESSOV & CHKHIKVADZE 1987; NESSOV & AVERIANOV 1988; AVERIANOV et al. 1991, 1993; AVERIANOV 1995, 1997). Unfortunately, the Dzhylga 1 a locality no longer exists: it occurred at the bottom of a sand quarry which was filled subsequently by debris. The quarrying activities were moved to an adjacent locality where somewhat higher stratigraphical levels have been exposed. In 1989-1996 this new quarry was explored by one of us (A. A.) who found a less diverse and in some respects less distinct vertebrate assemblage (locality Dzhylga 1 b). A similar vertebrate assemblage was sampled also from locality Dzhylga 2, a small sand pit situated 7-8 km southeast of the Dzhylga 1 localities. Both new localities produced remains of dichobunid artiodactyls indicating an early Eocene age (AVERIANOV & ERFURT 1996). The Dzhylga 1 a level, stratigraphically situated 2-3 m lower than the Dzhylga 1 b level and differing from the latter by a relative abundance of certain shark species and by the presence of a distinct sea snake, is most probably of latest Paleocene age (see discussion in AVERIANOV et al. 1993; AVERIANOV 1999).

The assumed late Paleocene age for the Dzhylga 1 a fauna makes this site extraordinary for the understanding of the early evolution of Rodentia, because it includes two taxa described originally as rodents: *Asiaparamys shevyrevae* and *Kazygurtia clivosa* (NESSOV 1987). The first genus was attributed without explanation to Eurymylidae by MCKENNA & BELL (1997), but there is no evidence for this. The second genus was referred with some doubts to "Mixodontia" (AVERIANOV 1995, 1999; MCKENNA & BELL 1997). There are only a few other places in the world from which late Paleocene rodents have been reported: earliest Clarkforkian faunas in Montana and Wyoming, North America, revealing the ischyromyid *Paramys* [or *Acritoparamys*] *atavus*, usually considered as the earliest known rodent (JEPSEN 1937; KORTH 1984, 1994, p. 44) and four other ischyromyid and one alagomyid species (IVY 1990; DAWSON & BEARD 1996), and the Gashatan Bayan Ula fauna in Inner Mongolia, where the (?)alagomyid *Tribosphenomys minutus* comes from (MENG et al. 1994; MENG & WYSS 1994; MENG & MCKENNA 1998). For the last taxon there is some uncertainty concerning its attribution to Rodentia (MARTIN 1997), and in a later publication it was not assigned formally to Rodentia (WYSS & MENG 1996). Besides two

molars, which served as holotypes for *A. shevyrevae* and *K. clivosa*, one additional rodent molar from Dzhylga 1a level was referred to cf. *Asiaparamys* sp. (NESSOV 1987b; NESSOV & AVERIANOV 1988), but neither figured nor described. In addition to the molars, three Glires incisors were found at the Dzhylga 1a locality; the enamel type of one of the incisors was preliminarily determined as pauciserial (NESSOV 1987b). In this report we redescribe both published Glires molars from Dzhylga 1a, describe and illustrate for the first time a third molar from the same site, and Glires incisors and enamel microstructure from Dzhylga 1a, 1b, and Dzhylga 2 localities.

Institutional abbreviations: CCMGE = Czernyshev's Central Museum of Geological Exploration, Saint Petersburg; ZIN = Zoological Institute, Russian Academy of Sciences, Saint Petersburg.

Measurements: L = length; Wtl = width of talonid; Wtr = width of trigonid. All measurements are in mm.

Capital and lower-case letters: I/i (incisor), P/p (premolar) and M/m (molar), refer to upper and lower teeth.

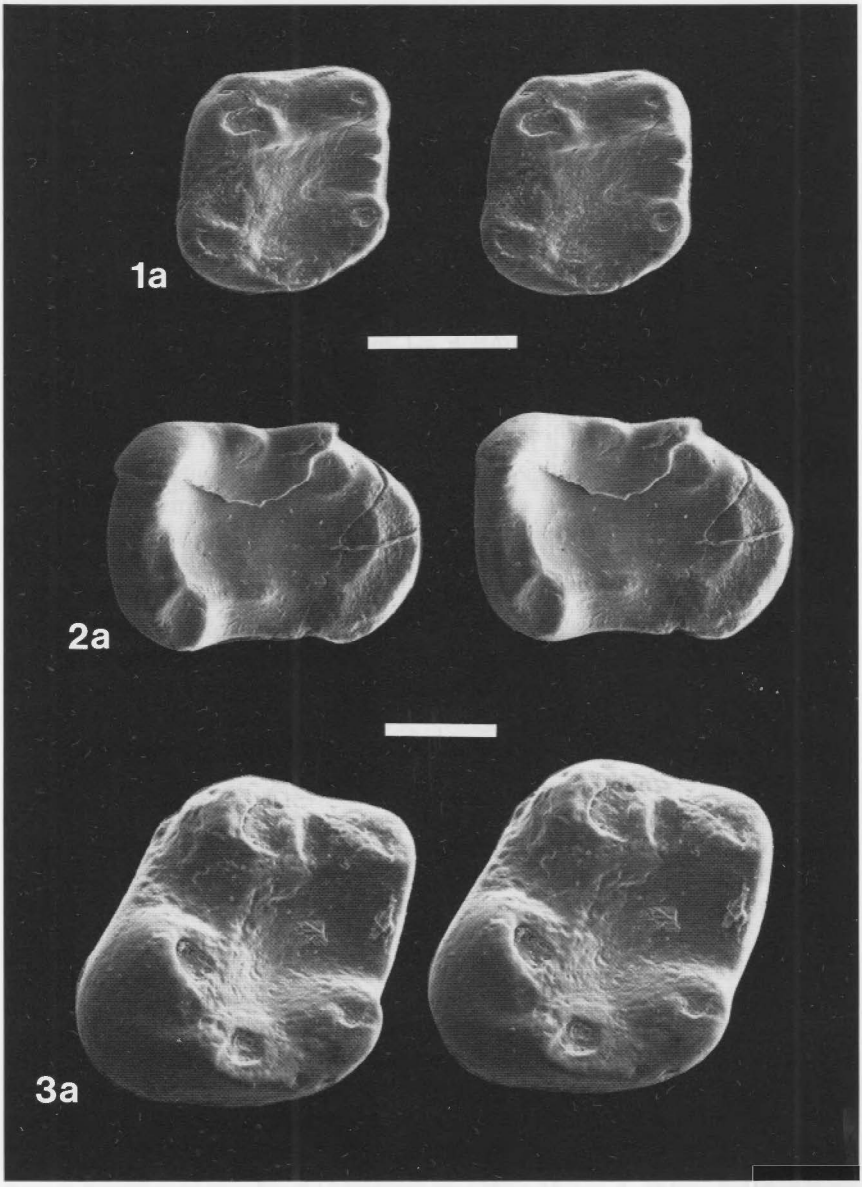
Systematic paleontology

Cohort	Glires LINNAEUS, 1758
Order	Rodentia BOWDICH, 1821
Family	Ischyromyidae ALSTON, 1876

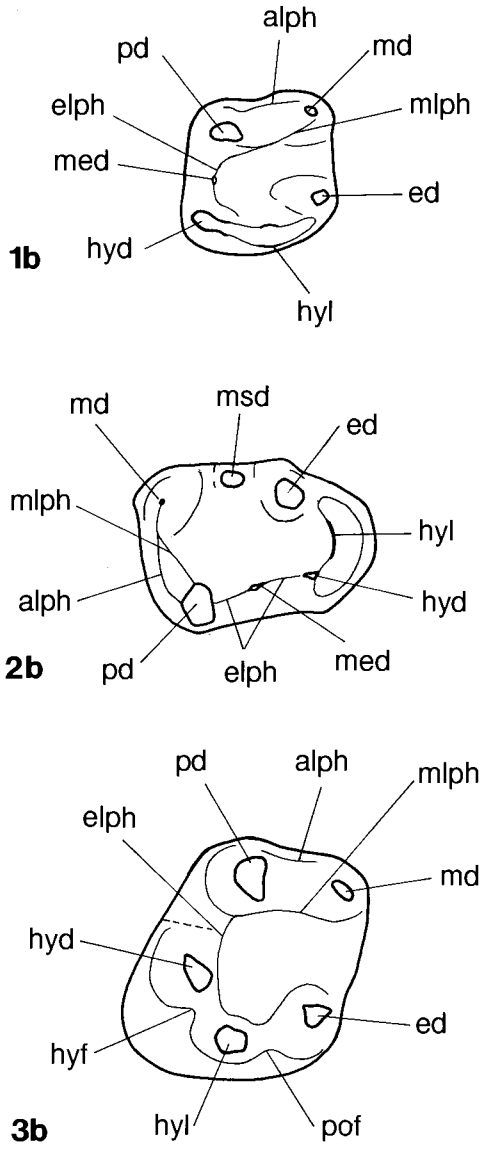
Asiaparamys NESSOV, 1987b

Type species: *Asiaparamys shevyrevae* NESSOV, 1987b, the only known species. Emended diagnosis: 1) Trigonid short antero-posteriorly. 2) Trigonid basin closed posteriorly. 3) Mesoconid small and low. 4) Ectolophid very weak and low. 5) Hypoconid relatively small. 6) Entoconid in anterior position, at level of mesoconid. 7) Hypoconulid ridge-like, connected with hypoconid. 8) Mesostylid present.

Figs. 1-3. Left lower rodent molars in occusal view; scale bar equals 1 mm; **1a.** *Asiaparamys shevyrevae*, stereo-pairs of lower m1, CCMGE 15/12455 (holotype), anterior side to the top of page; **1b.** same specimen with explanation of cusps and crests. **2a.** *Asiaparamys shevyrevae*, lower m3, ZIN 84075, anterior side to the left; **2b.** same specimen with explanation of cusps and crests. **3a.** *Kazygurtia clivosa*, left lower m2, CCMGE 14/12455, anterior side toward top of page; **3b.** same specimen with explanation of cusps and crests. Abbreviations: alph = anterolophid, ed = entoconid, elph = ectolophid, hyd = hypoconid, hyf = hypoflexid, hyl = hypoconulid, md = metaconid, med = mesoconid, mlph = metalophid, msd = mesostylid, pd = protoconid, pof = posteroflexid.



Figs. 1a - 3a (Legend see p. 485)



Figs. 1b - 3b (Legend see p. 485)

Remarks: Characters 1, 7, and 8 are derived, 2-5 are primitive, and character 6 is of uncertain polarity. Characters 1 and 7 are typical for the Ischyromyoidea, clearly separating *Asiaparamys* from the Ctenodactyloidea, which have a less compressed trigonid and a cusp-like enlarged hypoconulid. *Asiaparamys* is less advanced than the majority of the known ischyromyids in having a reduced hypoconid.

Distribution: Western part of the ancient Asian landmass, latest Paleocene.

Asiaparamys shevyrevae NESSOV, 1987b (Figs. 1 and 2)

Asiaparamys shevyrevae NESSOV, sp. nov. – NESSOV, 1987b, p. 210, pl. 2, fig. 4 cf. *Asiaparamys* sp. – Nessov 1987b, p. 205; NESSOV & AVERIANOV 1988, p. 7.

Holotype: CCMGE 15/12455, left m1. Dzhylga 1a, Kazakhstan. Latest Paleocene.
Additional material: ZIN 84075, left m3. Dzhylga 1a, Kazakhstan. Latest Paleocene.
Diagnosis: As for the genus.

Description: The m1 metaconid is located far anteriorly and near the lingual corner of the tooth. The anterior cingulid (anterolophid) connecting the metaconid with the protoconid is weak, nearly indistinct. It meets the protoconid near the lingual margin of the cusp and is separated from the protoconid. The trigonid basin is narrow and very short antero-posteriorly. The metalophid is complete and closes the trigonid basin posteriorly. It extends onto the slope of the metaconid. The mesoconid is a small, but distinct swelling on the ectolophid. It is separated from the protoconid by a shallow valley and its base is joined with the hypoconid by the short posterior ectolophid ridge. The hypoconid is small, low, and antero-posteriorly compressed. The hypoconulid is a low semicircular ridge connected with the hypoconid and the entoconid. The entoconid is a relatively small rounded cusp, shifted anteriorly with respect to the hypoconid. It is separated from the metaconid by a wide valley, slightly elevated above the level of the talonid basin. There is a minute mesostylid.

The m3 is about twice as large as m1. The trigonid is very short antero-posteriorly and bucco-lingually wider than the talonid. The tooth differs from m1 by a more antero-posteriorly elongated ridge-like mesoconid and a longer posterior part of the ectolophid. The mesostylid is much larger than on m1, with a bulbous base, and it is larger than the mesoconid. The hypoconid is very low. The entoconid is in an anterior position, as in m1.

Remarks: The holotype of *A. shevyrevae* was originally interpreted as m2. Taking in account its conspicuous smaller size relative to m3, attributed to the same species (ZIN 84075), it is m1 rather than m2.

Measurements: m1 (holotype): L = 1.4 mm, Wtr = 1.2 mm, Wtl = 1.3 mm; m3: L = 2.1 mm, Wtr = 1.5 mm, Wtl = 1.4 mm.
Distribution: As for the genus.

Glires incertae sedis

Kazygurtia Nessov, 1987b

Kazygurtia Nessov, gen. nov. – Nessov, 1987b, p. 209

Type species: *Kazygurtia clivosa* Nessov, 1987b, the only known species.
Emended diagnosis: 1) Molar cusps bunodont. 2) Trigonid basin open posteriorly. 3) Posterior trigonid wall relatively high. 4) Metaconid only slightly higher than protoconid. 5) Ectolophid weak, without a mesoconid. 6) Hypoconulid cusp-like. 7) Talonid basin wide and relatively deep.

Remarks: Characters 1 and 3-6 are primitive, whereas 2 and 7 are derived. The systematic position of *Kazygurtia* is uncertain due to the scarcity of the material and its primitive condition. It combines traits wich are characteristic both for "mixodontians" (1, 3, 4) and rodents (2 and 7). Because *Kazygurtia* shares derived characters with rodents, its attribution to Rodentia is preferable. *Kazygurtia* differs from "mixodontians" by lacking a mesoconid and possessing a wider talonid basin.

Distribution: Western part of the ancient Asian landmass, latest Paleocene.

Kazygurtia clivosa Nessov, 1987b Fig. 3

Kazygurtia clivosa Nessov, sp. nov. – Nessov, 1987b, p. 210, pl. 2, fig. 2.

Holotype: CCMGE 14/12455, left m2. Dzhylga 1a, Kazakhstan. Latest Paleocene.
Material: The holotype only.
Diagnosis: As for the genus.

Description: The trigonid of m2 is narrower than the talonid. The anterior cingulid (anterolophid) is short, connected with the protoconid and the metaconid. The protoconid is a large rounded cusp, larger than the metaconid. The metaconid is somewhat higher than the protoconid, but it is not shifted anteriorly in relation to the protoconid. The trigonid basin is small and opens posteriorly. The posterior trigonid wall is relatively high. The ectolophid is a weak continuous ridge connecting the protoconid and the hypoconid, without

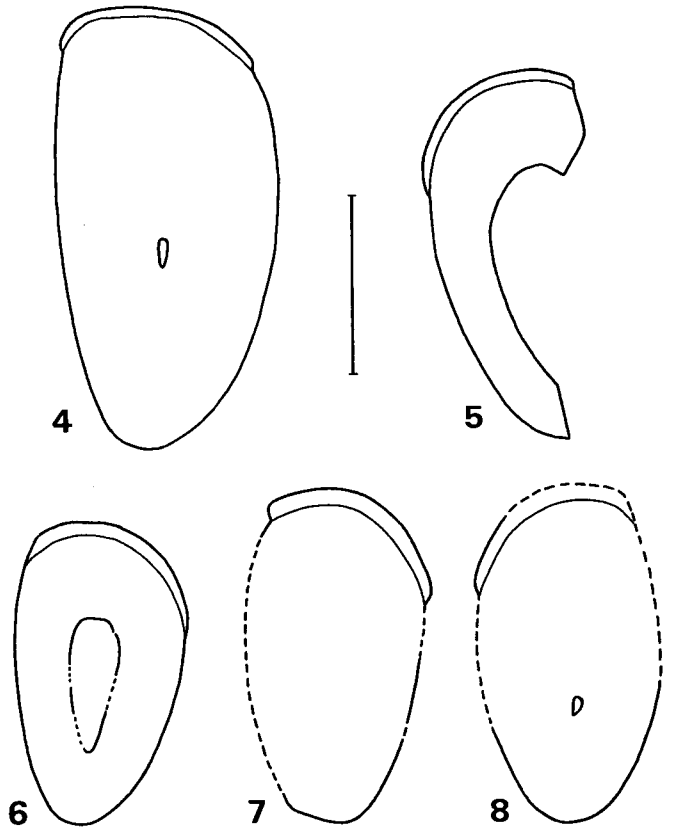
a mesoconid. The hypoconid is a relatively large rounded cusp, approximating the size of the protoconid. The hypoconid and the hypoconulid are separated by a distinct oblique valley (hypoflexid). The hypoconulid is large and cusp-like, separated from the entoconid by a shallow broad valley (posteroflexid). The entoconid is smaller than the hypoconid, but higher. It is separated from the metaconid by a wide valley, elevated above the level of the talonid basin. The talonid basin is wide and relative deep.

Measurements: L = 2.8 mm, Wtr = 2.0 mm, Wtl = 2.3 mm.
Distribution: As for the genus.

Incisor morphology and enamel microstructure

From Dzhylga 1a two fragments of gliriform incisors have been collected (MA 174 and MA 175), which were attributed to an upper jaw position based on their curvature. In both incisors, enamel is restricted to the anterior surface and overlaps somewhat laterally, which is typical for rodent incisors (Figs. 4 and 5). The enamel (Figs. 9-12) of both incisors is two-layered with an inner layer (portio interna, PI) of pauciserial Hunter-Schreger bands (HSB) and an outer layer (portio externa, PE) of radial enamel (for enamel type definition and terminology, see MARTIN 1992, 1993, 1997, and 1999). HSB width is 1 - 4 prisms, and interprismatic matrix (IPM) surrounds the prisms and runs parallel to the prisms' long axes in the PI. Transition zones between the HSB are missing and HSB are not inclined. In the PE, prisms are inclined 50° apically; prisms' cross sections are ovally rounded and prisms are embedded in a thick IPM. A prismless external layer (PLEX) is missing. Enamel thickness is 43 μm (MA 174) and 58 μm (MA 175) resp.; PE comprises 35 % (MA 174) and 25 % (MA 175) resp. of the total enamel thickness.

From Dzhylga 1b one (?upper) gliriform incisor fragment was collected (MA131). Enamel is restricted to the anterior side and extends somewhat laterally (Fig. 6). The enamel (Figs. 13 and 14) is two-layered, with pauciserial HSB in the PI and radial enamel in the PE. HSB width is 1-4 prisms and thick IPM surrounds the prisms and runs parallel to the prisms' long axes. HSB are not inclined, and transition zones between the HSB are missing. In the PE, prisms are inclined 60° apically. Prism cross sections are ovally rounded and are embedded in a thick IPM. A PLEX is missing. Enamel thickness is 60 μm and PE comprises 35 % of the total enamel thickness.



Figs. 4-8. Rodent incisor cross sections from Dzhylga localities. Scale bar equals 1 mm. **4.** MA 174, ?upper left incisor from Dzhylga 1a; **5.** MA 175, ?upper right incisor from Dzhylga 1a; **6.** MA 131, ?upper left incisor from Dzhylga 1b; **7:** MA 132/1 and **8.** MA 132/2, incisors from Dzhylga 2.

Two gliriform incisor fragments from Dzhylga 2 (MA 132/1 and 132/2), which cannot be attributed to an upper or lower jaw position, correspond in enamel distribution (Figs. 7 and 8) and schmelzmuster (Figs. 15-18) to the incisors from Dzhylga 1a and 1b. Both have a two-layered enamel, paucispiral HSB without transition zones in the P1, and radial enamel in the PE. In

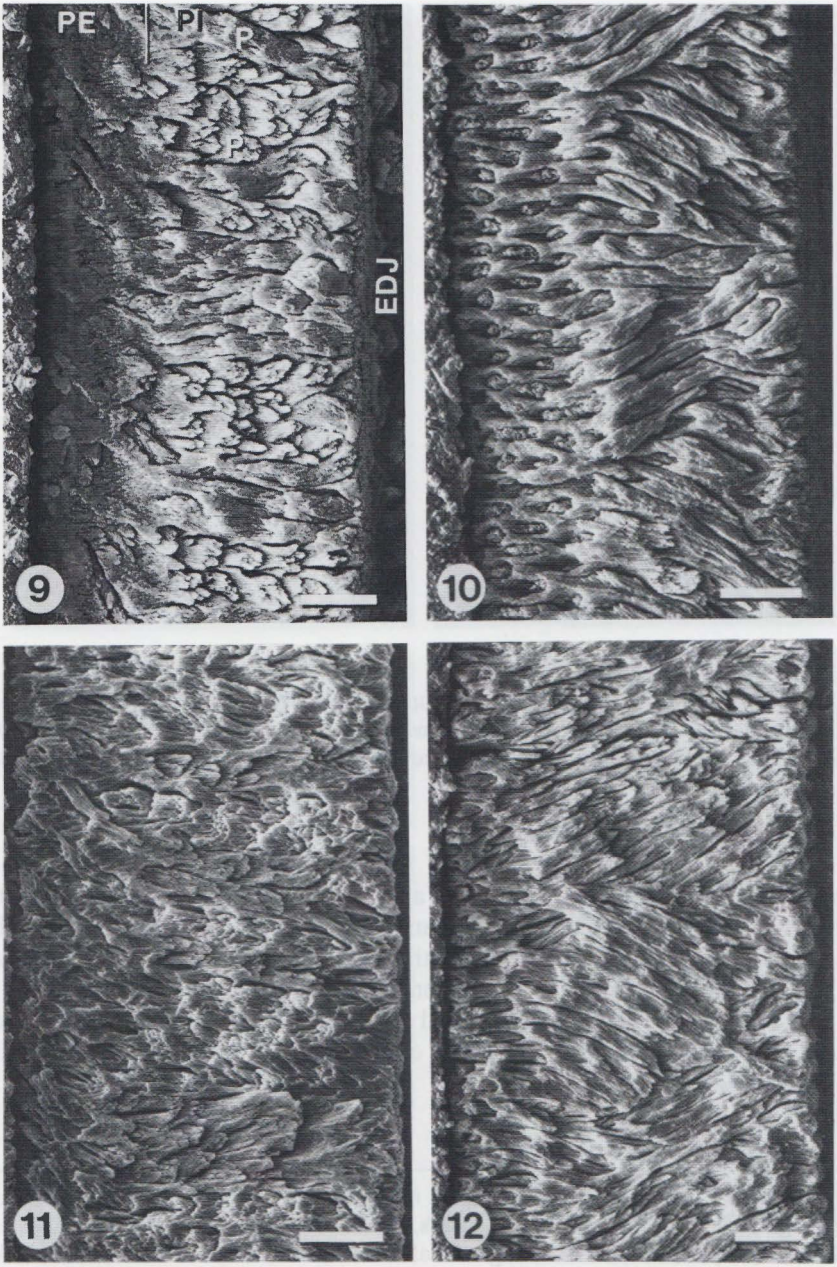
the P1, thick IPM surrounds the prisms and runs parallel to the prisms': long axes. In MA 132/1, HSB width is 1-3 prisms and HSB are not inclined. In the PE, prisms are inclined 50° apically; prisms' cross sections are ovally rounded and are embedded in a thick IPM. Enamel thickness is 75 μm and PE comprises 25-30 % of the total enamel thickness. A PLEX is missing. The schmelzmuster of MA 132/2 has been described in MARTIN (1999). HSB can be somewhat thicker (1-5 prisms) than in MA 132/1. Enamel thickness is 95 μm and PE comprises 25 % of the total enamel thickness.

Discussion

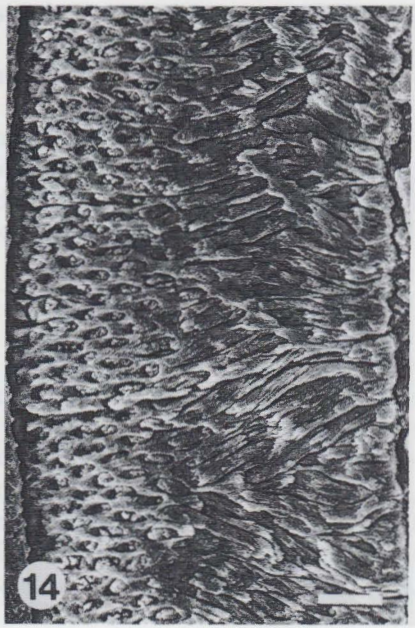
Molar pattern

Both *Asiaparamys* and *Kazygurtia* are among the most generalized Glires taxa and extend our knowledge about the diversity of rodent-like mammals in the early Paleogene of Asia. They clearly differ from the known Alagomyidae and Ivanantoniidae. The Alagomyidae currently includes two genera, *Alagomys* DASHZEVEG, 1990 from the latest Paleocene - Early Eocene of Mongolia, China and western USA (DASHZEVEG 1990; TONG & DAWSON 1995; DAWSON & BEARD 1997), and *Tribosphenomys* MENG, WYSS, DAWSON & ZHAI, 1994 from the latest Paleocene of northern China (MENG et al. 1994; MENG & WYSS 1994). *Asiaparamys* is similar to *Tribosphenomys* in having an antero-posteriorly compressed trigonid, but differs by the lack of a paraconid and by the presence of a ridge-like hypoconulid on m3. *Kazygurtia* differs from *Tribosphenomys* by a more square crown outline and bunodont cusps. *Alagomys* is distinct from both Dzhylga Glires by the rhomboidal shape of the lower molars, posteriorly open trigonid basin, and a stronger ectolophid. *Ivanantonia efremovi* SHEVYREVA, 1989 from the Early Eocene of Mongolia, the only known member of the Ivanantoniidae (SHEVYREVA 1989; HARTENBERGER et al. 1997), differs from the Dzhylga Glires by having an extensive antero-posterior groove on the protocone and hypocone made by movement of the lower teeth, indicating an important propalinal component during the chewing cycle. Subsequently, *Ivanantonia*

Figs. 9-12. SEM micrographs of rodent incisor enamel from Dzhylga 1a. EDJ (enamel-dentine junction) is to the right and, in the longitudinal sections, tip of the incisor is toward top of page. Scale bar equals 10 μm. P = prism, PE = portio externa, PI = portio interna. **9** and **10**: MA 174, ?upper left incisor, in longitudinal and cross section, respectively. **11** and **12**: MA 175, ?upper right incisor in longitudinal and cross section, respectively.



Figs. 9-12 (Legend see p. 492)

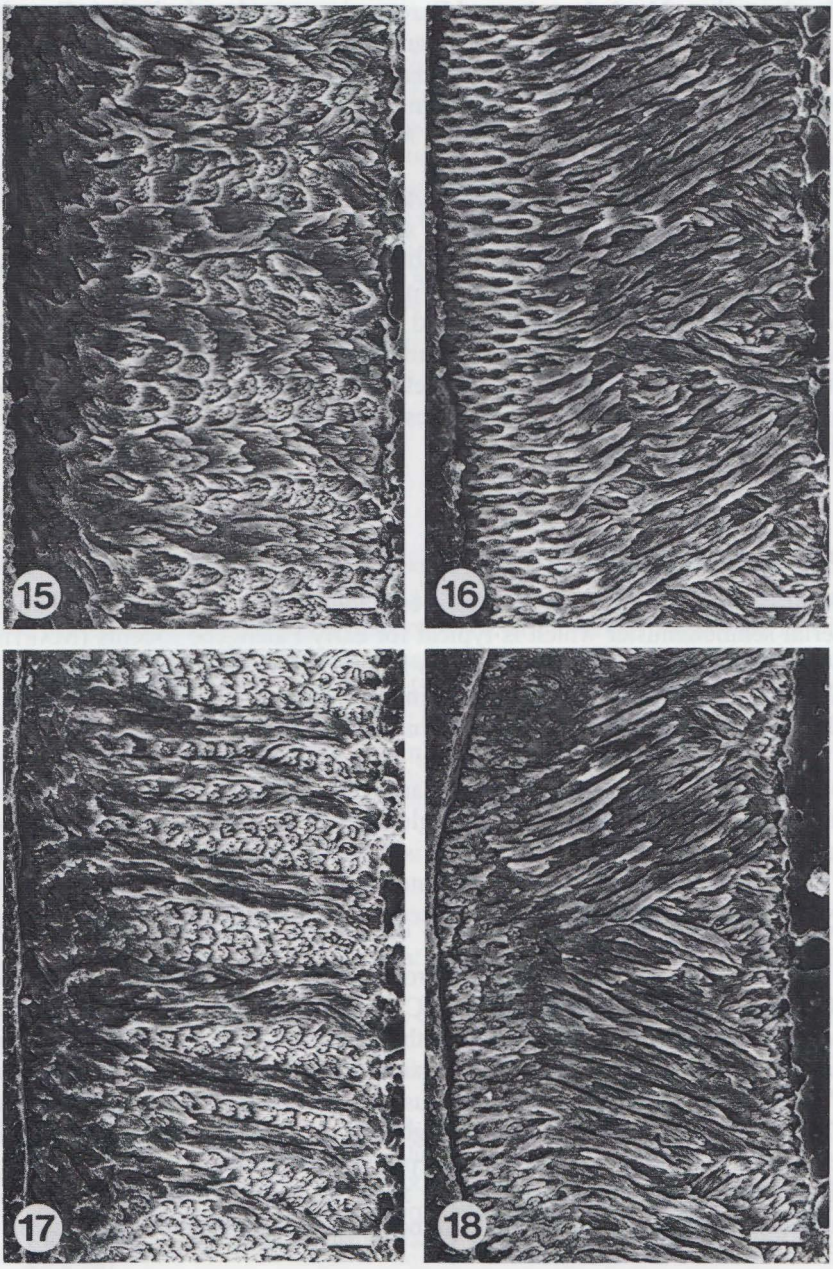


Figs. 13 and 14. SEM micrographs of ?upper left rodent incisor enamel (MA 131) from Dzhylga 1b. EDJ is to the right and, in the longitudinal sections, tip of the incisor is toward top of page. Scale bar equals 10 μm. **13** longitudinal and **14** cross section.

has a trigonid basin open posteriorly and a large mesoconid connected with the protoconid by a strong ridge (anterior part of the ectolophid). Both characters are very different from the condition present in the Dzhylga Glires, so we can exclude their relationships with the Ivanantoniidae.

In addition to Alagomyidae and Ivanantoniidae, Ischyromyidae and Ctenodactyloidea are the two major clades of early rodents, the first con-

Figs. 15-18. SEM micrographs of rodent incisor enamel from Dzhylga 2. EDJ is to the right and, in the longitudinal sections, tip of the incisor is toward top of page. Scale bar equals 10 μm. **15** (longitudinal section) and **16** (cross section) of MA 132/1. **17** (longitudinal section) and **18** (cross section) of MA 132/2.



Figs. 15-18 (Legend see p. 494)

fined mostly to North America and Europe, the second exclusively to Eurasia and Africa. The compressed trigonid and the ridge-like hypoconulid suggest ischyromyid affinities for *Asiaparamys* and this genus is placed here, following NESSOV's original attribution, in the Ischyromyidae (contra MCKENNA & BELL 1997). Although *Kazygurtia* has a general ctenodactyloid appearance and was originally included in that clade by NESSOV (1987b), its similarity with ctenodactyloids is based exclusively on primitive characters, among which the most striking is a cusp-like hypoconulid. Although this does not falsify the attribution of the poorly known *Kazygurtia* to the Ctenodactyloidea, we prefer to place this genus within Glires incertae sedis. The posteriorly closed trigonid basin, subvertical posterior trigonid wall, very weak ectolophid lacking a mesoconid, cusp-like hypoconulid, and strongly bunodont molar cusps, characteristic for *Kazygurtia*, are interpreted here as very ancient characters, ancestral to the more typical rodent condition.

Incisor enamel microstructure

All incisors from the Dzhylga localities studied exhibit a two-layered pauciserial schmelzmuster which is typical for early Paleogene rodents (MARTIN 1993, 1997, 1999). Enamel thickness is rather low in all specimens, which also is a primitive character. The incisor enamel microstructure of the Dzhylga rodents differs clearly from that of *Tribosphenomys* (MENG & WYSS 1994) and some small late Paleocene mixodontians from Mongolia by the presence of HSB. *Tribosphenomys* and the Paleocene Mongolian mixodontians lack HSB and have a single-layered enamel consisting only of radial enamel (MARTIN 1999), which is the primitive condition for Eutheria. *Tribosphenomys* originally was attributed to the Rodentia (MENG et al. 1994) but later was removed from it and placed as its sister taxon (MENG & WYSS 1994, WYSS & MENG 1996).

The hitherto oldest unquestioned rodents are *Acritoparamys atavus* and *Alagomys* from the late Paleocene (Clarkforkian). Both possess a typical two-layered rodent schmelzmuster with pauciserial HSB in the PI and radial enamel in the PE (MARTIN 1999). Apparently, in Rodentia already in the late Paleocene a two-layered schmelzmuster with HSB was achieved when (?most) mixodontians still had a single layered schmelzmuster with radial enamel. This corroborates the interpretation that the incisor fragments from Dzhylga studied indeed derive from Rodentia, since up to now no unquestioned rodent lacking HSB in the incisor enamel has been detected.

Faunal aspects

Although the mammal assemblage from the Dzhylga locality is known only from a dozen specimens, it includes two taxa of primitive Glires. This may suggest a possible past diversity and abundance of Glires in the Late Paleocene - Early Eocene on the western coast of the Asian ancient landmass. The fossil vertebrates from Dzhylga indicate a tropical or semitropical and humid paleoenvironment at that time. In this respect the Dzhylga fauna is similar to the Early Eocene Wutu fauna in Shandong Province, China (TONG & WANG 1998), which includes a number of American immigrants, particularly the ischyromyids (TONG & DAWSON 1995). Otherwise, ischyromyids were very rare in Asia, especially on the continental mainland. Possibly, they were restricted to the humid environments in Asia, which generally have a poor fossil record.

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