

Mammals from the Upper Cretaceous Aitym Formation, Kyzylkum Desert, Uzbekistan

Alexander O. Averianov^{a*}, J. David Archibald^b

^aZoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, 199034, Saint Petersburg, Russia

^bDepartment of Biology, San Diego State University, San Diego, California, 92182-4614, USA

Accepted 4 March 2003

Abstract

The Upper Cretaceous (?Santonian) Aitym Formation in the central Kyzylkum Desert, Uzbekistan, produced remains of a cimolodontan multituberculate (*Uzbekbaatar wardi*), a spalacotheriid symmetrodont (cf. *Shalbaatar* sp.), a deltatheroidan (cf. *Deltatherus* sp.), possibly the asioryctither aff. *Daulestes* sp., possibly two zalambdalestids (*Kulbeckia* sp. cf. *K. kulbecke* and aff. *Kulbeckia* sp.), two supposed lipotyphlans (*Paranyctooides* sp. cf. *P. aralensis* and *Paranyctooides* sp.), and zhelestid ungulatomorphs (cf. *Aspanlestes* sp., *Parazhelestes* sp. aff. *P. minor*, *Parazhelestes* sp. cf. *P. robustus*, and *Eoungulatum* sp. cf. *E. kudukensis*). The Aitym mammal fauna is most similar to the more diverse mammal fauna of the underlying Bissekty Formation (upper Turonian–Coniacian). *Uzbekbaatar* and *Shalbaatar* were most probably derived from North American immigrants. *Paranyctooides* and ‘Zhelestidae’ are of Middle Asian (a commonly and long used Soviet geographic region approximately extending from the Caspian Sea on the west to the Chinese border on the east, and from the Iranian and Afghan borders on the south to southern Kazakhstan on the north) origin and migrated to North America during the late Santonian–early Campanian. A dispersal route was present in Beringia during the entire Late Cretaceous, which may have worked as a cold filter, allowing intercontinental dispersals between Asia and western North America in both directions, especially during shorter, warm climatic phases.

© 2003 Published by Elsevier Ltd.

Keywords: Mammals; Aitym Formation; Late Cretaceous; Kyzylkum Desert; Uzbekistan; Intercontinental dispersals

1. Introduction

From the late 1970s onward, the Kyzylkum Desert of Uzbekistan became one of the most important places for recovery of the Cretaceous mammals (e.g., Nesson & Trofimov, 1979; Nesson, 1982, 1984, 1985a,b, 1987, 1993, 1997; Kielan-Jaworowska & Nesson, 1990, 1992; Nesson & Kielan-Jaworowska, 1991; Kielan-Jaworowska, 1992; Nesson et al., 1994, 1998; Archibald, 1996; Archibald et al., 1998, 2001; Averianov, 1999, 2000; Averianov & Kielan-Jaworowska, 1999; Cifelli, 2000; McKenna et al., 2000; Archibald & Averianov 2001, Archibald & Averianov, in press). During the Cretaceous, this region was the westernmost part of the ancient Asian landmass, bordered by the Tethys Ocean and Turgai Strait. Transgressions occurred several times

so that continental and marine deposits here are often intercalated. This makes the Kyzylkum Desert region crucial for biostratigraphic correlation throughout Asia (Archibald et al., 1998). The continental Cretaceous deposits in the Kyzylkum Desert sometimes contain diverse faunas of aquatic and terrestrial vertebrates, notably mammals. The late Lev A. Nesson discovered three successive mammalian assemblages in the Kyzylkum Desert: (1) the Khodzhakul assemblage in the lower part of the Khodzhakul Formation, latest Albian–?early Cenomanian; (2) the Sheikhdzheili assemblage in the upper part of the Khodzhakul Formation, early Cenomanian; and (3) the Dzharakuduk assemblage in the Bissekty Formation, late Turonian–Coniacian (Nesson, 1993; Nesson et al., 1994; Averianov 2000 and references therein).

For five field seasons beginning in 1997 paleontological work in the region has been carried out by a joint

* Corresponding author: Russian Academy of Sciences, Zoological Institute, Universitetskaya nab. 1, Saint Petersburg 199034, Russia

Uzbek-Russian-British-American-Canadian expedition (URBAC). The URBAC expeditions have concentrated work in the Dzharakuduk area, central Kyzylkum Desert, where screen-washing of over 55 metric tons of matrix at one fossiliferous site within the fluvial Bissekty Formation produced literally hundreds of mammalian specimens (Archibald et al., 1998). Perhaps the most unexpected find during the URBAC project was the discovery in 1998 of a new mammal locality (CBI-117 site or ‘shark locality’, approximately N 42°07′24”, E 62°39′29”) in the Dzharakuduk area within the marine age Aitym Formation directly overlying the Bissekty Formation. The new mammalian assemblage is approximately 30 m above the top of the underlying Bissekty Formation and evidently younger than the Bissekty mammal assemblage, but at the moment it is not clear exactly how much younger. The current estimate of the age of the Aitym Formation is ?Santonian (Archibald et al., 1998; Nesson et al., 1998). The study of the very diverse chondrichthyan fauna from the CBI-117 site is in progress by David J. Ward and the first author, and may provide a more precise age estimate. With the addition of this fourth mammal-bearing level, the Kyzylkum Desert is one of the few areas in the world with a 15-million-year succession of mammal assemblages during the Cretaceous.

The Aitym fauna at the CBI-117 site consists of some marine invertebrates, including oysters and ammonites (*Placenticerias kyzylkumense*), and varied marine vertebrates, e.g., especially diverse and abundant chondrichthyans and rarer osteichthyans, infrequent plesiosaurs, and sea(?) turtles. The remains of terrestrial vertebrates are extremely rare in this site. There are few bones of salamanders, lizards, crocodiles, possibly terrestrial turtles, dinosaurs, birds, and eventually mammals. Altogether some 34 mammalian specimens have been recovered from CBI-117 so far, the majority of them coming from the concentrate produced after screen-washing of 1500 kg of matrix in 1999. From these specimens, an edentulous dentary fragment of a possible zhelestid was mentioned and an isolated multituberculate p4, the holotype of *Uzbekbaatar wardi* Averianov, 1999, was described (Averianov, 1999). An isolated upper molar of *Paranyctoides* sp. from this locality was described by Archibald & Averianov (2001). The purpose of this paper is to describe all identifiable mammal specimens from CBI-117 except for some edentulous jaw fragments and postcranial elements of Mammalia indet.

Dental terminology and methods of measurement used in the paper are after Nesson et al. (1998); wear facet terminology is after Crompton & Kielan-Jaworowska (1978).

1.1. Institutional abbreviations

CCMGE, Chernyshev’s Central Museum of Geological Exploration, Saint Petersburg, Russia; URBAC,

Uzbek-Russian-British-American-Canadian joint expedition collections; ZIN C, Systematic Collections, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia; ZIN O, Osteological Collections, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia; ZPAL MgM, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland, Mongolian mammals.

1.2. Measurements

AW, anterior width; L, length; PW, posterior width; TAL, talonid length; TAW, talonid width; TRL, trigonid length; TRW, trigonid width; W, width. All measurements are in mm.

2. Systematic palaeontology

Mammalia Linnaeus, 1758

Allotheria Marsh, 1880

Multituberculata Cope, 1884

Cimolodonta McKenna, 1975

‘*Paracimexomys* group’ sensu Eaton & Cifelli, 2001

Uzbekbaatar Kielan-Jaworowska & Nesson, 1992, new assignment

Uzbekbaatar wardi Averianov, 1999

Fig. 1

1999 *Uzbekbaatar wardi* sp. n.; Averianov, p. 301, figs. 1–2

Holotype. ZIN C.83673, left p4.

Other material. ZIN C.85292, dP1?; ZIN C.85077, posterior half of right M1; ZIN C.85291, right m1.

Description. ZIN C.85292, a dP1? crown, is bulbous and triangular in occlusal view (Fig. 1a), with three conical cusps. The cusps are separated by narrow valleys. The anterior cusp is slightly smaller than the posterior cusps, which are approximately the same size and form a transverse row. The cusps are ornamented with ridges radiating from their apices. There are two roots, the anterior one (broken off for most of its length) is distinctly smaller and somewhat bent anteriorly. Based on the latter character, which is similar to the condition of dP1 in *Mesodmops dawsonae* Tong & Wang, 1994 (Tong & Wang, 1994, pl. 1), the tooth is considered to be dP1 rather than P1. The roots of P1 are of equal size in *Mesodma hensleighi* Lillgraven, 1969 (Storer, 1991, fig. 2A).

M1. ZIN C.85077 (Fig. 1b, c) lacks the anterior portion and the external cusp row. The cusp formula is ?:4+:?3. The internal cusp row is rather short and comprises three cusps, decreasing in size anteriorly. The most anterior cusp is much lower than the remaining internal cusps. There are four pyramidal to somewhat crescentic cusps preserved in the medial row; slightly

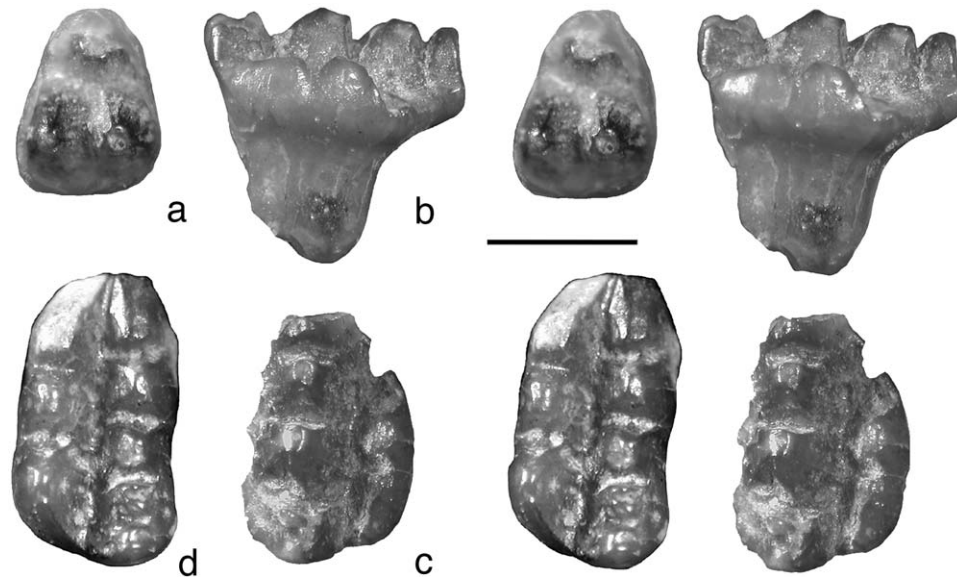


Fig. 1. *Uzbekbaatar wardi*, teeth in occlusal (a, c, d) and lingual (b) views. Locality CBI-117, Aitym Formation (?Santonian), Dzharakuduk, Kyzylkum Desert, Uzbekistan. a, ZIN C.85292, dP1?; b, c, ZIN C.85077, posterior portion of right M1; d, ZIN C.85291, right m1. All stereo-photographs; scale bar represents 1 mm.

recurved anteriorly with a concave anterior face. The penultimate cusp is larger than the preceding and following cusps. The most anterior of the cusps preserved is the smallest. There is only a minor development of ribs or pockets in the valleys between cusps. Only one posterior root is preserved.

p 4. See Averianov (1999, pp. 302–303).

m1. ZIN C.85291 (Fig. 1d) is nearly rectangular in occlusal view with a bluntly pointed anterior end and a posterior margin that bulges labially. The cusp formula is 5:3 or 4. The two posterior most external cusps are smaller and less clearly separated than the other external cusps. Damage (white area, Fig. 1d), some wear, and a particularly elongate anterolingual portion of the crown suggest there may have been two rather than one cusp in the anterolingual corner of the internal cusp row. The cusp rows are separated by a wide, straight valley with subdued ribs and pockets. The cusps are mostly pyramidal. The anterior slopes of anterior cusps in each row are anteroposteriorly elongated. In the external cusp row, the three more anterior cusps are approximately equal in size and occupy about two-thirds of the crown length. The two posteriormost external cusps are of similar size, smaller than the three preceding cusps and are restricted to the posterolabial bulge of the crown. The internal cusps are slightly taller than the external cusps. In the internal cusp row the cusps increase in size posteriorly. There are two roots of approximately equal size.

Measurements. ZIN C.85292, dP1?: L, 1.20; W, 0.92. ZIN C.83673, p4: L, 3.54; W, 1.30. ZIN C.82591, m1: L, 1.96; W, 1.12.

Discussion. *Uzbekbaatar* was originally based on *U. kizylkumensis* Kielan-Jaworowska & Nessov, 1992 from the Bissekty Formation and referred to *Cimolodonta incertae sedis* with a note that it might be a non-specialized member of either Taeniolabidoidea or Ptilodontoidea (Kielan-Jaworowska & Nessov, 1992). An isolated multituberculate lower incisor from the Bissekty Formation, possibly completely covered by enamel, supports assignment of *Uzbekbaatar* to Ptilodontoidea (Kielan-Jaworowska & Nessov, 1992, p. 12, fig. 4 A–C), if it belongs to the same taxon. Supposed loss of the posterolabial cusp(s) on p4, however, excludes *Uzbekbaatar* from the evolutionary line leading to known taeniolabidoids or ptilodontoids (Kielan-Jaworowska & Nessov, 1992, pp. 12–13). All known multituberculate specimens from the Aitym Formation are compatible in size to each other and the type *U. wardi*. Thus, at least based upon size, there is no reason to consider the presence of more than one multituberculate species at CBI-117. Similarly, all multituberculate materials from the Bissekty fauna also seem likely to belong to a single taxon, *U. kizylkumensis*.

Recently Taeniolabidoidea was restricted to the family Taeniolabididae Granger & Simpson, 1929 (e.g., Kielan-Jaworowska & Hurum, 2001). *Uzbekbaatar* clearly differs from members of this family in M1 having a very short lingual cusp row, p3 present, p4 relatively much larger, and lower incisor uniformly covered by enamel. *Uzbekbaatar* is similar to some members of Djadochtatherioidea in having a low cusp formula for m1, but differs in having the lower incisor uniformly covered by enamel. Among families referred to Cimolodonta *incertae sedis* (Kielan-Jaworowska & Hurum,

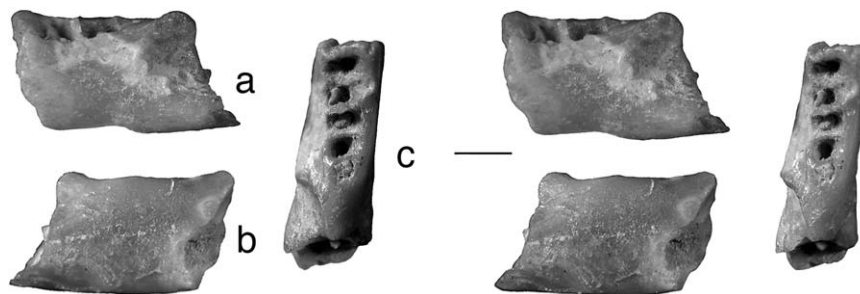


Fig. 2. cf. *Shalbaatar* sp., ZIN C.85047, left edentulous dentary fragment with alveoli of m5-7?. Locality CBI-117, Aitym Formation (?Santonian), Dzharakuduk, Kyzylkum Desert, Uzbekistan. a, labial view; b, lingual view; c, occlusal view. All stereo-photographs; scale bar represents 1 mm.

2001), *Uzbekbaatar* differs from Eucosmodontidae Jepsen, 1940, in the p4 lacking the posterolabial cusp, from Cimolomyidae Marsh, 1889, in having a more slender lower incisor and with p4 longer than m1, from Kogaionidae Radulescu & Samson, 1996, in having M1 longer and the internal cusp row occupying about half of the tooth length.

Based on limited information, *Uzbekbaatar* is most similar to the North American genera *Paracimexomys*, *Bryceomys*, and *Cedaromys* within the informal ‘*Paracimexomys* group’ recently reviewed by Eaton and Cifelli (2001). These appear to be some of the more basal genera in the ‘advanced’ suborder Cimolodonta. As in these taxa the molar cusps of *Uzbekbaatar* are asymmetric (m1 only, as the M1 lacks the external row) and the cusps are robust. *Uzbekbaatar* seems to have more pitting and ribbing on its molars than in *Paracimexomys*, but probably less than either *Bryceomys* or *Cedaromys*. *Uzbekbaatar* may differ from most members of this group in having one additional, albeit incompletely separated posteriormost external cusp, giving an external cusp count of five compared to four in at least most of the other genera. The internal cusp row may be longer on M1 as well, but because of the incompleteness of M1, this cannot be determined with certainty. For now, we believe the evidence at best argues that *Uzbekbaatar* is formally referable to Cimolodonta and informally may be aligned with the ‘*Paracimexomys* group.’

Theria Haswell & Parker, 1897
Symmetrodonta Simpson, 1925
Spalacotheriidae Marsh, 1887
Shalbaatar Nessov, 1997, new assignment

cf. *Shalbaatar* sp.
Fig. 2

Material. ZIN C.85047, left edentulous dentary fragment with alveoli of the three last molars (m5-7?).

Description. The dentary fragment consists of the posterior portion of the horizontal ramus with alveoli for m5–7? and the anterior portion of the masseteric fossa. The alveoli are oblique relative to the longitudinal axis of the dentary, with the labial side more posterior.

The alveoli slope downwards to the labial side. Posteriorly the alveoli gradually decrease in size. The alveoli indicate that the molar roots were compressed antero-posteriorly and widened transversely, except the posterior alveoli of m7?, which is rounder in outline. The coronoid process is not preserved. The masseteric crest begins as a prominent knob immediately posterolabially to the posterior alveolus for m7?, near the level of the alveolar border. Ventrally, the shallow masseteric fossa is bordered by a thick ridge. The pterygoid crest is distinct, but does not reach the alveolar border anteriorly.

Discussion. The monotypic *Shalbaatar* Nessov, 1997, was based on single specimen from the lower Bissekty Formation at Dzharakuduk, ZIN C.82622, an edentulous right dentary fragment. *Shalbaatar* was originally referred to Multituberculata (?Plagiaulacoidea), because of the ‘relatively anterior position of the coronoid process’ (Nessov, 1997, p. 162). Nessov (1997, p. 162–163) also noted distinct ‘hystricognathy’ in this specimen (i.e., deflection of the posteroventral dentary corner laterally.) He thought that *Shalbaatar* belonged to an unusual group of multituberculates, which ancestrally had a masseteric fossa that was posteriorly positioned, a p4 that was not enlarged, but which was derived in having rodent-like ‘hystricognathy’ of the dentary. According to Z. Kielan-Jaworowska (pers. comm., 2000), a posteriorly placed masseteric fossa excludes *Shalbaatar* from Multituberculata because this indicates the absence of a ‘backward masticatory power stroke,’ characteristic of multituberculates (Gambaryan & Kielan-Jaworowska, 1995).

Further examination of ZIN C.82622, the holotype of *Shalbaatar bakht* Nessov, 1997 (Fig. 3), revealed that it bears characteristics of spalacotheriid (or, even, spalacolestine; Cifelli & Madsen, 1999) symmetrodonts. These characters are: molars less than 1 mm in length, last molar smaller than the penultimate molar, molar alveoli obliquely set in the dentary and canting labially, molar roots anteroposteriorly short and transversely wide, pterygoid crest prominent and placed relatively high and extending anteriorly to the alveolar border, a

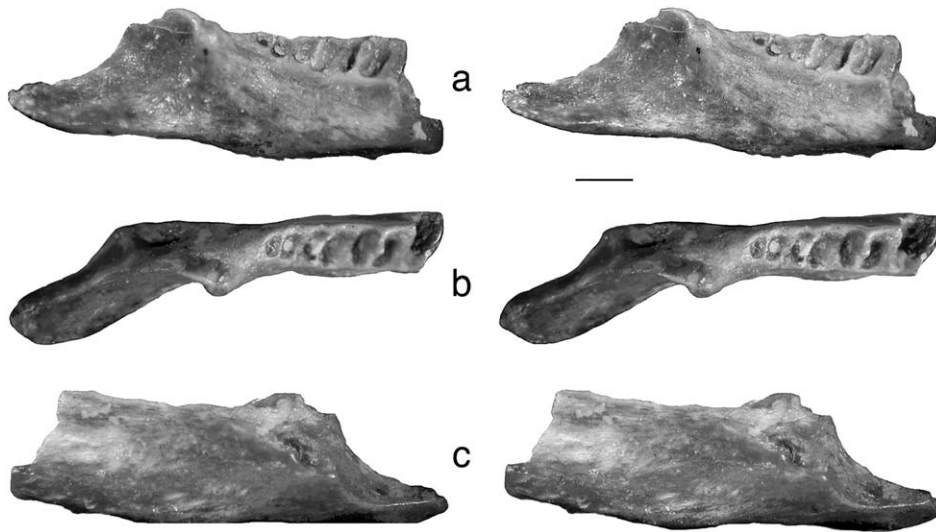


Fig. 3. *Shalbaatar bakht*, ZIN C.82622, holotype, right edentulous dentary fragment with alveoli of m4-7? Locality CDZH-17a, lower Bissekty Formation (upper Turonian), Dzharakuduk, Kyzylkum Desert, Uzbekistan. a, labial view; b, occlusal view; c, lingual view. All stereo-photographs; scale bar represents 1 mm.

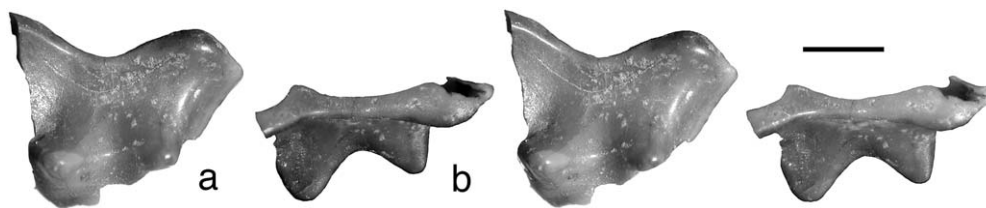


Fig. 4. cf. *Deltatherus* sp., ZIN C.85049, fragment of right upper molar (M2?). Locality CBI-117, Aitym Formation (?Santonian), Dzharakuduk, Kyzylkum Desert, Uzbekistan. a, occlusal view; b, labial view. Both stereo-photographs; scale bar represents 1 mm.

pocket posterior to the mandibular foramen and above the pterygoid crest, and angular region strongly laterally deflected. This unusual combination of dentary characters is found only in some spalacotheriids. Thus *Shalbaatar* almost certainly is a spalacotheriid symmetrodont. The Aitym specimen, ZIN C.85047, is generally similar to ZIN C.82622, differing only in minor details. The Aitym specimen is slightly larger, with a more anteriorly placed masseteric crest, a masseteric fossa bordered anteroventrally by a thick ridge (not well developed in *S. bakht*), and a pterygoid crest that does not approximate the alveolar border. These differences may indicate that the specimens belong to different species, but this question will remain unresolved until the recovery of better specimens of *Shalbaatar* from both the Bissekty and Aitym formations.

Tribosphenida McKenna, 1975

Metatheria Huxley, 1880

Deltatheroidea Kielan-Jaworowska, 1982

Deltatheridiidae Gregory & Simpson, 1926

Deltatherus Nessov, 1997

cf. *Deltatherus* sp.

Fig. 4

Material. ZIN C.85049, fragment of a right upper molar (M2?), lacking lingual and posterior portions.

Description. The preserved labial portion of the crown is almost symmetrical, with a quite shallow ectoflexus and rather wide styler shelf. There is a weak ectocingulum bearing a very small parastyle and a slightly larger stylocone. There are no other styler cusps posterior to the stylocone. The parastylar area is large, with a faint cingulum anterolingual to the parastyle. The paracone and metacone are placed well apart with little contact at their bases. The paracone is distinctly smaller and shorter than the metacone; and the apex of the paracone is directed anteriorly away from the metacone. The pre-paracrista is rather weak and does not reach the stylocone. The preceding description must be tempered by the unusual surface texture of the tooth. It is very smooth, apparently not from dental attrition as wear facets are not discernible. This might be the natural surface texture, but more likely the tooth had not erupted and the enamel was not fully mineralized when the individual died or the tooth was chemically etched.

Discussion. There are two deltatheroidans in the Bissekty Formation, *Sulestes karakshi* Nessov, 1985 and

Deltatherus kizylkumensis (Nessov, 1993), the latter known by the lower dentition and an edentulous maxillary fragment. The Aitym deltatheroid is similar with *Sulestes* (CCMGE 35/12000; Nessov, 1985b, pl. 2, fig. 1; 1997, pl. 46, fig. 5; Kielan-Jaworowska & Nessov, 1990, figs. 3, 4A; Nessov et al., 1994, pl. 4, fig. 3) in having the paracone and metacone that are less twined, compared to the Mongolian *Deltatheridium pretrituberculare* Gregory & Simpson, 1926 (e.g., ZPAL MgM-I/91 and 102, Kielan-Jaworowska, 1975, fig. 3, pl. 28, fig. 1b). It differs from *Sulestes* in lacking cuspules along the ecto-cingulum and preparacrista, and in having a much smaller stylocone, a less prominent preparacrista, and a more marked difference in height between the paracone and metacone. In the last character, ZIN C.85049 is similar to ZIN C.82193, the holotype of *Deltatheridium nessovi* Averianov, 1997, from the early Campanian Darbasa Formation in southern Kazakhstan (Averianov, 1997, fig. 3), but is different from the Mongolian species of *Deltatheridium*. *D. nessovi* differs from the Aitym molar fragment in having a more robust crown with a well-developed preparacrista. As to size, ZIN C.85049 appears to fit the M2 alveoli in CCMGE 42/12000, an edentulous maxillary fragment attributable to *D. kizylkumensis* (Nessov, 1993, fig. 2-2; 1997, pl. 45, fig. 4). The Aitym molar fragment could belong to this species.

Better preserved specimens of *Deltatheridium* from Mongolia (Rougier et al., 1998) reveal the presence of M4 and thus it does not differ from *Deltatheroides* in its dental formula. In *Deltatheroides cretacicus* Gregory & Simpson, 1926 (Kielan-Jaworowska, 1975, fig. 1A) and the ‘Guriliin Tsav skull’ (Szalay & Trofimov, 1996, fig. 22) M3 is a symmetrical and larger than M2, while M4 is asymmetrical, but not reduced. In *Deltatheridium* M3 is asymmetrical and M4 is very small and apparently not present in all specimens (lacking, e.g., in ZPAL MgM-I/102). The ‘Guriliin Tsav skull’ has a *Deltatheroides*-like molar pattern and differs from *Deltatheridium* in having large palatal vacuities (Szalay & Trofimov, 1996, fig. 22). Kielan-Jaworowska et al. (2000, p. 602) concluded that ‘presence of palatal vacuities is a generic, rather than family character’. Deltatheroididae Kielan-Jaworowska & Nessov, 1990, was synonymized with Deltatheridiidae Gregory & Simpson, 1926, by Kielan-Jaworowska et al. (2000, p. 602). According to the cladistic analysis by Rougier et al. (1998) and supplementary information), however, the presence of palatal vacuities is a synapomorphy for their node 14 (*Andinodelphys* + Marsupialia), convergently acquired by ‘stagodontids’ (node 22: *Eodelphis*, *Didelphodan*, and ‘Guriliin Tsav skull’). We cannot comment about proposed stagodontid affinities of the ‘Guriliin Tsav skull’, but agree with Rougier et al. (1998) that it does not belong to Deltatheridiidae; possibly it is not a deltatheroidan.

Another important character distinguishing the ‘Guriliin Tsav skull’ from *Deltatheridium* is the quite



Fig. 5. aff. *Daulestes* sp., ZIN C.85296, labial half of worn right M1, occlusal view. Locality CBI-117, Aitym Formation (?Santonian), Dzharakuduk, Kyzylkum Desert, Uzbekistan. Stereo-photographs; scale bar represents 1 mm.

large conules placed very close to the paracone and metacone. In *Deltatheridium* the conules are much smaller and approximately equidistant from the protocone and the labial cusps (e.g., Kielan-Jaworowska, 1975, fig. 3B). These appear sufficient to place *Deltatheroides*+‘Guriliin Tsav skull’ and *Deltatheridium* in different family-level taxa. In *Deltatherus*, based on CCMGE 42/12000, and in *Sulestes* (Nessov, 1985b, pl. 2, fig. 1v) M3 most probably was also asymmetrical, approximating the condition in *Deltatheridium*. *Deltatherus* also lacks palatal vacuities, and thus it is attributable to Deltatheridiidae. It differs from *Deltatheridium* in having a larger upper canine and a larger two-rooted P1. *Sulestes* has a *Deltatheridium*-like molar pattern and conules that are intermediate between the protocone and the labial cusps; thus it is also attributable to Deltatheridiidae. The systematic position of ‘*Deltatheridium*’ *nessovi* is uncertain; it may actually belong to *Deltatherus*, but more dental information is required for this assessment.

Eutheria Gill, 1872 *sensu* Rougier et al., (1998)

Asioryctitheria Novacek et al., 1997

?Asioryctitheria, *incertae sedis*

Daulestes Trofimov & Nessov, 1979, in Nessov & Trofimov, 1979

aff. *Daulestes* sp.

Fig. 5

Material. ZIN C.85296, a worn right M1 lacking the protocone.

Description and comparison. The identification of ZIN C.85296 as an M1 is suggested by the more anteriorly projecting parastylar lobe and the more labially placed metastylar lobe. It is similar to the M1 described for *Daulestes nessovi* by McKenna et al. (2000) in its small size and noticeably larger paracone compared to the metacone. ZIN C.85296 differs from the M1 in *Daulestes nessovi* in having a much more reduced stylocone, a small stylar cusp C, a less wide stylar shelf, and paracone and metacone separated at the base. It is also about 50% larger than the M1 of *Daulestes nessovi*.

Measurements. ZIN C. 85296, M1: L, 1.79.

Discussion. Larger upper molars probably referable to *Daulestes* recently recovered at sites lower in the

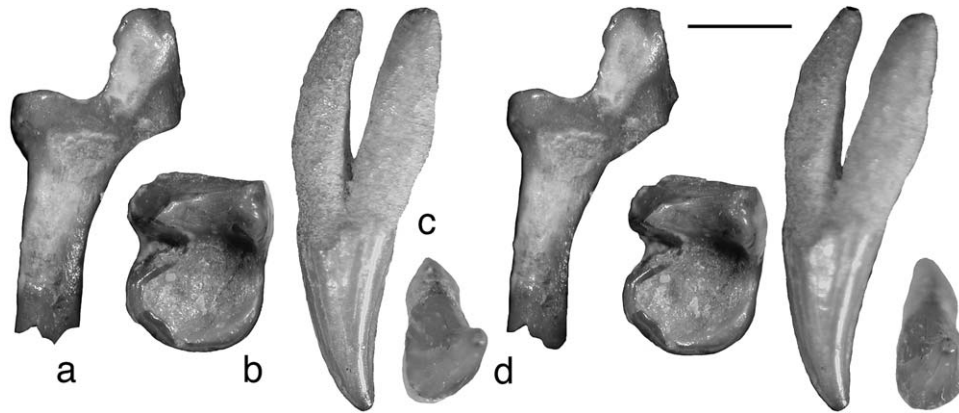


Fig. 6. *Kulbeckia* sp. cf. *K. kulbecke* (a, b) and aff. *Kulbeckia* sp. (c, d). Locality CBI-117, Aitym Formation (?Santonian), Dzharakuduk, Kyzylkum Desert, Uzbekistan. ZIN C.85050, worn left m1; a, lingual view; b, occlusal view. ZIN C.85303, upper right canine; c, labial view; d, occlusal view. All stereo-photographs; scale bar represents 1 mm.

section in the Bissekty Formation, suggest that two or more species of *Daulestes* of varying size are present in the Bissekty Formation. Thus, ZIN C.85296 may belong to one of these undescribed species. This undescribed Bissekty material is currently under study by us.

Placentalia Owen, 1837 sensu Rougier et al. (1998)

Gliriformes Wyss & Meng, 1996

Zalambdalestidae Gregory & Simpson, 1926

Kulbeckia Nessov, 1993

Kulbeckia sp. cf. *K. kulbecke* Nessov, 1993

Fig. 6a, b

Material. ZIN C.85045, right petrosal; ZIN C.85050, worn left m1.

Description. The petrosal is similar to petrosals from the Bissekty Formation referred to *Kulbeckia kulbecke* on the basis of their similarity with petrosals in the Mongolian *Zalambdalestes* Gregory & Simpson, 1926 (John Wible, pers. comm. 2000). This specimen will be described and figured elsewhere, together with the Bissekty petrosals.

The m1 (Fig. 6a, b), although very heavily worn as a result of dental attrition, strongly resembles the m1 or m2 of *Kulbeckia kulbecke* from the Bissekty Formation (Archibald & Averianov, 2003, figs. 3, 5, 6). Referral to *Kulbeckia* rather than the similarly sized *Aspanlestes* is based on what is preserved of the trigonid, suggesting that the paraconid and metaconid are closer together than in *Aspanlestes*, the protoconid and metaconid are of similar height (protoconid distinctly higher in *Aspanlestes*), the talonid does not seem as wide as in *Aspanlestes*, and is smaller than lower molars of *Aspanlestes*, closer in size to lower molars of *Kulbeckia*. Identification as an m1 rather than m2 is less certain, but is mostly because of the slightly smaller talonid relative to the trigonid in m1 compared to m2.

Measurements. ZIN C.85050, m1: L, 1.65(estimate); TRL, 0.67(estimate); TRW, 1.39; TAL, 0.99; TAW, 1.32.

Discussion. In the Bissekty fauna *Kulbeckia* is one of the most common taxa (Archibald et al., 2001; Archibald & Averianov, 2003), outnumbered only by a plethora of zhelestids. In the Aitym fauna *Kulbeckia* appears to be much rarer, rarer than the multituberculate *Uzbekbaatar*. The reason for this is not clear. One very speculative possibility is that the well-known zalambdalestids from Mongolia are all from more inland, xeric settings. The Bissekty faunas are from probably more mesic, riverine settings that were near but not at the coastline. The Aitym fauna is clearly from a marine locality into which mammal remains were transported from the shore. Possibly *Kulbeckia* simply was rarer nearer the coast and is thus much less common.

aff. *Kulbeckia* sp.

Fig. 6c, d

Material. ZIN C.85303, upper right canine.

Description. The upper canine resembles the upper canine of *Kulbeckia kulbecke* identified from the Bissekty Formation by Archibald and Averianov (2003, fig. 2A–C) and differs from lower canines of that species (Archibald & Averianov, 2003, fig. 5A–C) from the Bissekty in that it has a straighter crown and roots set more in the same plane as the crown. The Aitym canine is, however, only about two-thirds the size of the Bissekty upper canine. The Bissekty upper canine is preserved only to the base of the crown, but it appears that two roots would have been present. The Aitym upper canine preserves two complete, well-defined roots. The roots are about the same length as the crown. Both roots are mostly uniform in the anteroposterior dimension except that the posterior root bulges slightly below

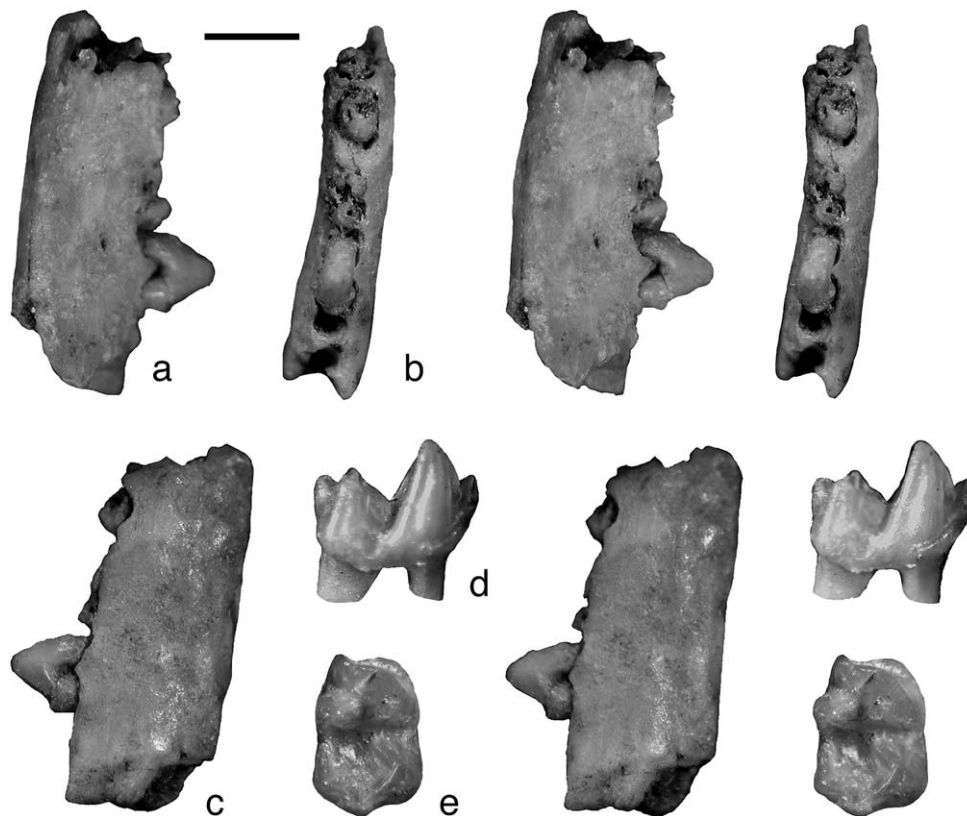


Fig. 7. *Paranyctoides* sp. cf. *P. aralensis*. Locality CBI-117, Aitym Formation (?Santonian), Dzharakuduk, Kyzylkum Desert, Uzbekistan. ZIN C.85078, left dentary with root for the posteriormost incisor and one-root for a canine (or just as likely two roots for a two-rooted canine), two roots for p1, a complete p2, two alveoli for a smaller p3; a, labial view; b, occlusal view; c, lingual view. ZIN C.85294, right m1; d, labial view; e, occlusal view. All stereo-photographs; scale bar represents 1 mm.

the base of the crown. The slight lingual curvature near the tip of the crown helps identify it as coming from the right side. Because the canine is so much smaller than its counterpart from the Bissekty Formation, we hesitate to refer it more confidently to either *Kulbeckia* sp. or cf. *Kulbeckia* sp.; hence the designation of aff. *Kulbeckia* sp.

Measurements. ZIN C.85303, C1: L, 1.13; W, 0.61.

Lipotyphla Haeckel, 1866

?Soricomorpha Gregory, 1910

?Nyctitheriidae Simpson, 1928

Paranyctoides Fox, 1979

Paranyctoides sp. cf. *P. aralensis* Nessov, 1993

Fig. 7

2001 *Paranyctoides* sp.; Archibald & Averianov, p. 542, fig. 4

Material. ZIN C.85044, left M1; ZIN. C.85300, right M1(?) fragment preserving the crown from the conules lingually; ZIN C.85078, left dentary with root for the posteriormost incisor and one-root for a canine (or just as likely two roots for a two-rooted canine), two roots for p1, a complete p2, and two alveoli for a smaller p3; ZIN C.85294, right m1.

Description. M1. See Archibald & Averianov (2001, p. 542).

A right upper molar fragment, ZIN. C.85300 (possibly M1), preserves the crown from the conules lingually. It is very similar to ZIN C.85044, hence is also referred to *Paranyctoides* sp. cf. *P. aralensis*.

Dentary ZIN C. 85078 (Fig. 7a–c) resembles *Paranyctoides aralensis* quite closely, and we are quite confident that ZIN C.85044 also can be referred to *Paranyctoides* sp. cf. *P. aralensis* along with the lower dentition and lower molar. The dentary is relatively deep, more than exceeding twice the height of the p2 crown, and only slightly tapering anteriorly. The single small mental foramen is located below the anterior root of p2. Judging from the alveoli, most likely the canine was relatively large, one- or two-rooted, p1 was two-rooted, and p3 was of slightly smaller size than p2. The p2 is two-rooted with a single-cusped crown, with labial widening at the posterior end. There is a very small posterior accessory cusp.

The m1 (Fig. 7d, e) is well preserved and matches the size of the dentary, ZIN C. 85078, and the previously described left M1, ZIN C.85044 (Archibald & Averianov, 2001). No m1s are known of *P. aralensis*

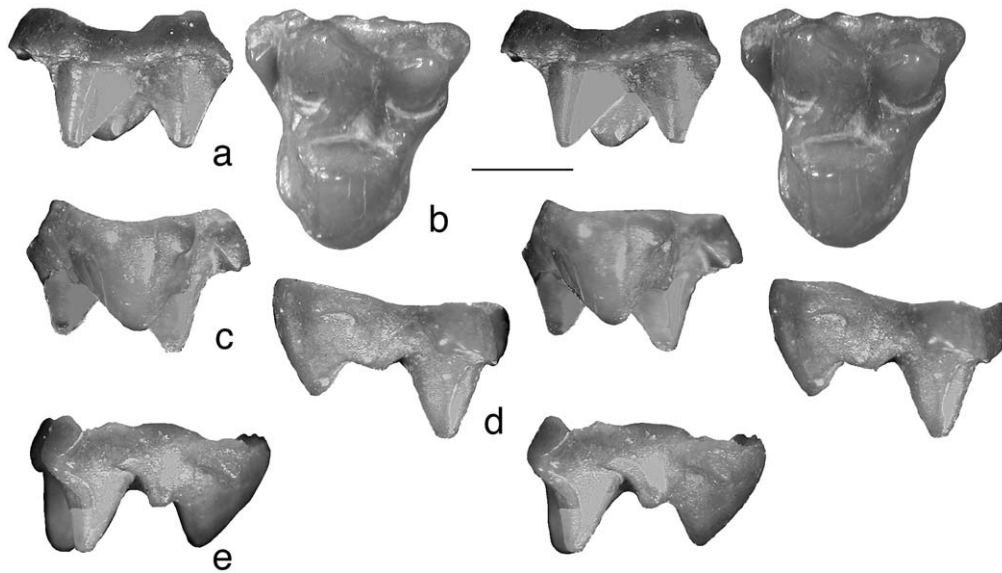


Fig. 8. *Paranyctoides* sp., ZIN C.85293, left M1; a, labial view; b, occlusal view; c, lingual view; d, anterior view; e, posterior view. Locality CBI-117, Aitym Formation (?Santonian), Dzharakuduk, Kyzylkum Desert, Uzbekistan. All stereo-photographs; scale bar represents 1 mm.

from the underlying Bissekty Formation, but ZIN C.85294 does match well with the morphology of m2 and m3 in that species described by Archibald & Averianov (2001). The trigonid is quite low relative to the talonid. The trigonid cusps are all well developed and separate, increasing in girth and height from paraconid to metaconid to protoconid. The paraconid is set well forward of the metaconid with no indication of closure of the trigonid lingually. The anterior margin of the paraconid narrows into a vertical crest, a feature more commonly seen in Cretaceous metatherians. There is a narrow but continuous precingulid. The talonid is slightly wider than the trigonid. The entoconid, hypoconulid, and hypoconid are all well developed and equidistant from each other. The hypoconid is the largest of the three talonid cusps. ZIN C.85294 is most likely to be an m1 because of the more anterior placement of the paraconid and the slightly greater width of the talonid relative to the trigonid.

Measurements. ZIN C.85044, M1: L, 1.55; AW, 1.62; PW, 1.72. p2: L, 0.8; W, 0.45. ZIN C.85294, m1: L, 1.60; TRL, 0.77; TRW, 1.05; TAW, 1.07; TAL, 0.84.

Discussion. The relatively large lower canine may suggest attribution of ZIN C.85078 to a zhelestid, but the relatively unreduced p3 argues against this. Almost certainly this fragment belongs to *Paranyctoides*, although the latter also appears to have a somewhat reduced p3 (Archibald & Averianov, 2001). *Paranyctoides aralensis* from the Bissekty Formation is known only by lower dentitions and edentulous dentaries (Nessov, 1993; Archibald & Averianov, 2001). The Aitym *Paranyctoides* specimens seem to fit the size of CCMGE 67/12455, the holotype of *P. aralensis*, very

well and is best attributed to this species. We, however, retain the Aitym specimens as *Paranyctoides* sp. cf. *P. aralensis* for now as comparable parts of the dental anatomy are not known from the Aitym and Bissekty Formation.

Paranyctoides sp.

Fig. 8

Material. ZIN C.85293, left M1.

Description. The styler shelf of the M1 is narrow to almost completely lacking labial to the paracone. The parastylar lobe is well developed with a small parastyle and a distinct preparastyle just lingual to the parastyle. The tooth is almost unworn, so there is not a distinct parastylar groove separating the parastylar lobe from the small, distinct stylocone. A weak preparacrista from the anterolabial base of the paracone contacts the very small stylocone. The styler shelf is (as noted above) narrowest immediately labial of the paracone. Just posterior to this point on the styler shelf, midway between the paracone and metacone, are two small cusps in the cusp 'c' region. Immediately posterior is a slightly smaller cusp 'd'. Posteriorly is the metastylar lobe, which is large but lacks a distinct cusp. A somewhat muted postmetacrista extends from the metastylar lobe to near the posterior side of the apex of the metacone. There is no discernible notch on the postmetacrista. The paracone and metacone are separate, with the former cusp being the taller and larger of the two. A distinct but weak centrocrista connects the apices of these two cusps. The paraconule is only slightly larger than the metaconule, and is positioned very slightly more lingually, approximately equidistant between the protocone and paracone.

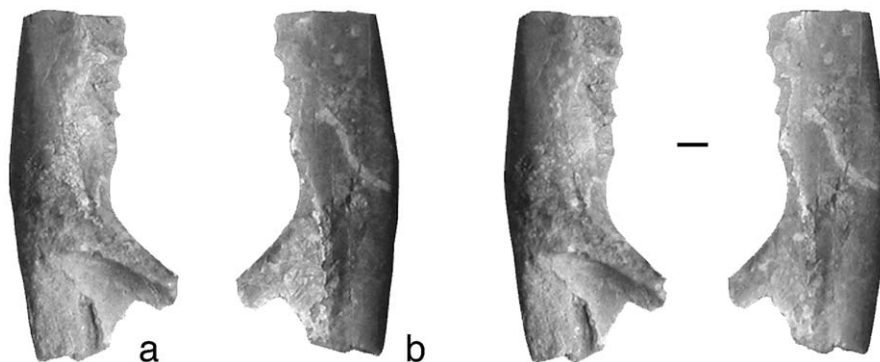


Fig. 9. cf. *Aspanlestes* sp., ZIN C.85048, left edentulous dentary fragment with alveoli of m1-3. Locality CBI-117, Aitym Formation (?Santonian), Dzharakuduk, Kyzylkum Desert, Uzbekistan; a, labial view; b, lingual view. All stereo-photographs; scale bar represents 1 mm.

Both conules have distinct conular cristae. The preparaconular crista continues labially as a narrow but distinct paracingulum that merges with the anterior base of the paracone. The only clear dental attrition is on the paraconule and its cristae. A distinct metacingulum continues labially from the postmetacrista, merging with the crown dorsal to the midpoint of the postmetacrista. The moderately developed protocone is not as tall as either the paracone or metacone. It has some antero-posterior expansion. The preprotocrista contacts the paraconule while the postprotocrista contacts the metaconule. There is a short, narrow, distinct precingulum and postcingulum, which are not as well developed as in ZIN C.85044, the M1 of *Paranyctoides* sp. cf. *P. aralensis*.

Measurements. ZIN C.85293, M1: L, 2.09; AW, 2.18; PW, 2.28.

Discussion. This specimen is a complete left upper molar crown lacking roots. It appears to be an M1 judging by the overall narrowness of the crown and the greater narrowness of the crown labial to the paracone. This is similar to the Aitym M1 listed above as *Paranyctoides* sp. cf. *P. aralensis* and described and figured by Archibald & Averianov (2001), but contrasts with the relatively wider upper molars of *P. maleficus* shown in Fox (1984), which he did not identify as to tooth site. Also, in both Aitym specimens the parastylar lobe extends somewhat more anterolabially compared to the more labially extending metastylar lobe so that the ectoflexus is shallower than on the Mx's illustrated by Fox (1984). Together these features are highly suggestive of an M1.

Paranyctoides sp. ZIN C.85293, M1, and ZIN C.85044, the M1 of *Paranyctoides* sp. cf. *P. aralensis* are quite similar. The latter tooth, is notably smaller and is somewhat more squared in occlusal view, mostly because of a larger postcingulum. Otherwise, they appear to be closely related.

One possibility that cannot be dismissed is that ZIN C.85293 might be a deciduous last upper premolar, but it seems unlikely because of the large size of this tooth.

Ungulatomorpha Archibald, 1996

'Zhelestidae' Nesso, 1985

Aspanlestes Nesso, 1985

cf. *Aspanlestes* sp.

Figs. 9, 10

Material. ZIN C.85051, left m1 or m2 lacking posterior portion of the talonid; ZIN C.85048, left edentulous dentary fragment with alveoli of m2-3 and posterior root of m1; URBAC 02-101, right M2 lacking the parastylar lobe. Possibly also ZIN C.85299, a right P4? (penultimate premolar) and ZIN C.85079, left edentulous maxillary fragment with M1(?) alveolus.

Description. The dentary (Fig. 9) is relatively shallow and of consistent depth along the molar series. The coronoid process is relatively steeply rising, at an angle of about 55° from the alveolar level. The masseteric crest is very sharp and the masseteric fossa is deep.

ZIN C.85299 (Fig. 10a, b) is possibly a penultimate premolar (P4) of cf. *Aspanlestes* sp. It is a complete crown without roots. There is no protocone but a bulge in that area as in the P4 of zhelestids. Other such teeth in zhelestids are often worn in this area and do not have clear, narrow posterolingual and posterolabial cingula as in this unworn tooth. It is in the size range of *Aspanlestes*.

Although missing the parastylar region, the size and morphology of URBAC 02-101 (Fig. 10c) is very like that of M2s of *Aspanlestes aptap* from the Bissekty Formation. Like molars of zhelestids in general, it has well-developed pre- and postcingula, a moderately broad trigon, and para- and metaconules closer to the para- and metacone, respectively, than to the protocone.

The m1 or 2 (Fig. 10d, e) has a prominent precingulid anteriorly and the crown is higher on the labial side than on the lingual side. The paraconid is considerably

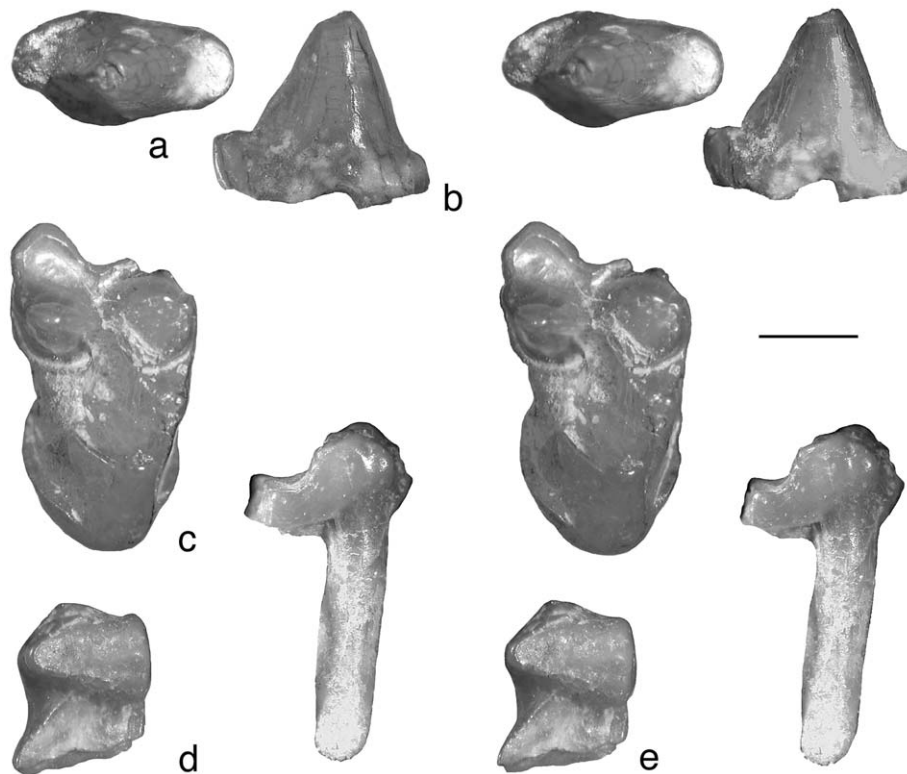


Fig. 10. cf. *Aspanlestes* sp. Locality CBI-117, Aitym Formation (?Santonian), Dzharakuduk, Kyzylkum Desert, Uzbekistan. ZIN C. 85299, right P4 (penultimate premolar); a, occlusal view; b, lingual view. URBAC 02-101, right M2 lacking the parastylar lobe; c, occlusal view. ZIN C.85051, left m1 or 2 lacking posterior portion of the talonid; d, occlusal view; e, lingual view. All stereo-photographs; scale bar represents 1 mm.

reduced compared with the metaconid and these cusps are appressed. The talonid is wider than the trigonid. The anterior root is vertically projecting and quite long. Although small relative to the P4 and M2 described above, this tooth does fall within the range of lower molars of *Aspanlestes aptap* from the Bissekty Formation.

Measurements. ZIN C.85051, m1 or 2: LTR, 0.76; WTR, 1.24. ZIN C.85299, P4?: L, 2.18; W, 1.18; URBAC 02-101, M2: PW, 3.21.

Discussion. Known teeth and jaw fragments of cf. *Aspanlestes* sp. agree in dimensions and morphology with those in *A. aptap* Nessov, 1985, the smallest zhelestid from the Bissekty Formation (Nessov et al., 1998, table 2, fig. 7).

Parazhelestes Nessov, 1993

Parazhelestes sp. cf. *P. robustus* Nessov, 1993
Fig. 11a-c

Material. ZIN C.85055, badly worn left(?) M1 or 2; ZIN C.85301, left M3.

Description. The crown of M1 or 2 has almost completely been eliminated by wear. It is relatively wide buccolingually, with a very shallow ectoflexus.

The M3 (Fig. 11a–c) is complete and generally well preserved, except for the missing tip of the metacone. It has the labially expanded parastylar lobe and very reduced metastylar lobe characteristic of other known zhelestid M3 specimens and many other Cretaceous eutherians. There are no distinctive cusps on the stylar shelf. The paracone has an anterolabially positioned, subdued preparacrista that does not extend on to the stylar shelf. There is no discernable postmetacrista. A centrocrista connected the paracone to the damaged metacone. The paracone is significantly larger than the metacone (even accounting for damage to the metacone) as is normal for M3s. The paraconule is well developed and wing-like with well-defined post- and preparaconular cristae; the latter shows dental wear. The metaconule is very reduced with no well-defined post- and premetaconular cristae. As is the case in zhelestids, the conules are positioned distinctly closer to the paracone and metacone. The protocone is large, with a lingually expanded base. Its labially positioned apex is somewhat anteroposteriorly expanded and is almost as tall as the paracone. It was probably taller than the damaged metacone. There are well-defined, narrow pre- and postcingula extending from near the lingual margin of the protocone to the level of the conules. Thus, there is no constriction through the conular region.

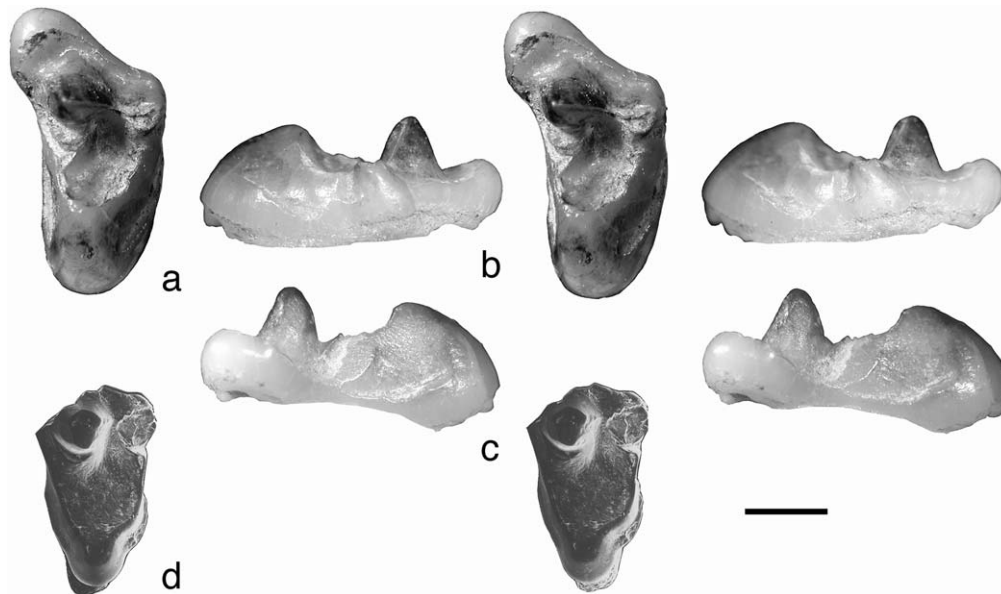


Fig. 11. *Parazhelestes* sp. cf. *P. robustus* (a–c) and *Parazhelestes* sp. aff. *P. minor* (d). Locality CBI-117, Aitym Formation (?Santonian), Dzharakuduk, Kyzylkum Desert, Uzbekistan. ZIN C.85301, left M3; a, occlusal view; b, posterior view; c, anterior view. ZIN O.35054, partial right M3, reversed; d, occlusal view. a–c are stereo-photographs and d is an SEM stereo-micrograph; scale bar represents 1 mm.

Measurements. ZIN C.85055, M1 or 2: L, 2.90; AW, 4.00; PAW, 2.90. ZIN C.85301, M3: L, 1.91; AW, 3.30; PAW, 2.71.

Discussion. The M3 referred to *Parazhelestes* sp. cf. *P. robustus* sp. is more similar in size and shape to the rather labiolingually narrowed M3 of *P. robustus* (Nessov et al., 1998, fig. 11A) than to that of *Zhelestes temirkazyk* (Nessov et al., 1998, fig. 9B), hence its possible referral the former taxon. For further comments, see the discussion of *Parazhelestes* sp. aff. *P. minor* below.

Parazhelestes sp. aff. *P. minor* Nessov, Archibald & Kielan-Jaworowska, 1998

Fig. 11d

Material. ZIN O.35054, right M3.

Description. M3 (Fig. 11d) lacks only the parastylar lobe and part of the metacone. The crown is not constricted through the conular area. The remaining labial margin of the crown is obliquely orientated, indicating that the missing parastylar lobe was large and anterolabially projecting, as in other known zhelestid M3 specimens (see above) and in many other Cretaceous eutherians. A part of the stylar shelf is preserved only between the paracone and metacone; it is quite narrow here. Labial to the metacone the stylar shelf is virtually absent. There is no metastyle. The postparacrista is distinct. The preparacrista is expressed as an enamel thickening only. The metacone base is approximately 1.5 times smaller than the paracone base. The cusps are separate at their bases. The paracone is the tallest crown

cusps. Its apex is flattened by wear. On the posterior slope of the paracone a broad wear facet 3 could be recognized. The paraconule and metaconule are situated approximately one-quarter of the distance between the paracone and metacone labially and the protocone lingually. The paraconule is almost eliminated by dental attrition (facet 1b) so that the remaining part of the preparaconule crista is shifted toward the paracone base and has become separated by a considerable space (=wear facet 1b) from the preprotocrista. A similar stage of wear can be seen on CCMGE 11/12176, a specimen of *Parazhelestes minor* (Nessov, 1985a, pl. 3, fig. 5a; Nessov et al., 1998, fig. 13), obliterating the paracingulum. The remaining part of the preparaconule crista is long and distinct, approaching close to the paracone base. The postparaconule crista is much shorter, terminating near the paracone base (part of it may be obliterated by wear facet 3). The metaconule is still preserved; it is a prominent cusp bearing a wear facet, which is inclined posteriorly. The premetaconule crista is long and prominent. It terminates close to the junction between the postparacrista and premetacrista. The postmetaconule crista is much shorter and nearly vertical, extending directly towards a weak cingulum at the base of the molar crown. The apex of the protocone lies well lingual to the middle of the lingual half of the tooth; this lingual position is evidently caused by wear; in the unworn tooth it probably occupied a more labial position. The apex of the protocone is much lower than the paracone and heavily worn by transverse movements against the talonid basin and the lingual hypoconid wall (facet 9). The postcingulum is well developed. It begins posterior

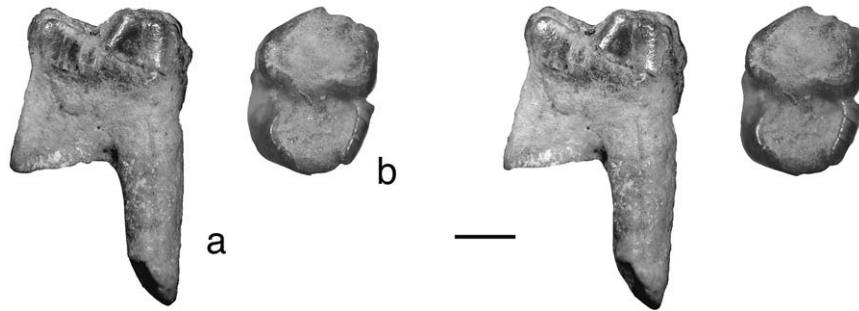


Fig. 12. *Eoungulatum* sp. cf. *E. kudukensis*, ZIN O.35052, left m3; a, lingual view; b, occlusal view. Locality CBI-117, Aitym Formation (?Santonian), Dzharakuduk, Kyzylkum Desert, Uzbekistan. All stereo-photographs; scale bar represents 1 mm.

to the protocone and merges with the tooth lingual of the metaconule. The precingulum is less distinct; it is a thickening of the enamel. It also terminates lingual to the paraconule.

Measurements. M3: PAW, 2.47.

Discussion. An M3 has been described only for two Bissekty zhelestid specimens: CCMGE 10/12176, the holotype maxilla of *Zhelestes temirkazyk* Nessov, 1985 (Nessov, 1985a, pl. 3, fig. 14; Nessov et al., 1994, pl. 5, fig. 1; Archibald, 1996, fig. 4A; Nessov, 1997, pl. 52, fig. 1; Nessov et al., 1998, fig. 9) and CCMGE 70/12455, the holotype maxilla of *Parazhelestes robustus* (Nessov, 1993, pl. 2, fig. 1; Nessov, 1997, pl. 53, fig. 2; Nessov et al., 1998, fig. 11A). The M3 differs in these two taxa. In *Parazhelestes* it is markedly buccolingually narrowed compared to M1-2, while in *Zhelestes* it is roughly equal in buccolingual width to M2. This character was considered to be diagnostic and included in the revised diagnosis of *Parazhelestes* (Nessov et al., 1998, p. 54). In proportions ZIN O.35054 agrees more with the *Parazhelestes* condition, i.e. it is relatively short buccolingually. *Parazhelestes* currently consists of two species, *P. robustus* (type species) and *P. minor*. The second species differs mostly in its smaller size and in having molar crowns slightly constricted through the conular region. ZIN O.35054 is closer in size to *P. minor* and smaller than ZIN C.85301 referred above to *Parazhelestes* sp. cf. *P. robustus*. Neither shows any crown constriction through the conular region. Both ZIN C.85301 and ZIN O.35054 differ from M3 of *P. robustus* and *Z. temirkazyk* in having a somewhat better developed postcingulum. In both of these taxa, the known M3s are quite worn. For the most derived Bissekty zhelestid, *Eoungulatum kudukensis*, M3 is not known. ZIN O.35054, is smaller than the M3 of *P. robustus*, and thus does not appear to be attributable to *E. kudukensis*, which is the largest Bissekty zhelestid. When all evidence is weighed, both ZIN C.85301 and ZIN O.35054 from the Aitym are best referred to *Parazhelestes* sp. cf. *P. robustus* and *Parazhelestes* sp. aff. *P. minor* respectively. The greater uncertainty regarding the referral of ZIN

O.35054 to *P. minor* (hence the ‘aff.’ assignment) only reflects the fact that M3 for this taxon is unknown.

Eoungulatum Nessov, Archibald & Kielan-Jaworowska, 1998

Eoungulatum sp. cf. *E. kudukensis* Nessov, Archibald & Kielan-Jaworowska, 1998

Fig. 12

Material. ZIN O.35052, badly worn left m3; ZIN C.85054, left dentary fragment with alveolus of m3.

Description. The coronoid process of the dentary gradually rises just posterior to the m3 alveolus. The masseteric crest is rather sharp and the masseteric fossa is deep. The posterior root alveolus of m3 is labiolingually narrower and about twice as long as the anterior root alveolus.

The m3 (Fig. 12) has a badly worn and eroded crown, but it appears that the labial side was higher than the lingual side. There is a remnant of the precingulid anteriorly. The talonid is narrower than the trigonid, without remnants of any talonid cusps. The hypoconulid region is most heavily worn; thus the crown may have been shortened anteroposteriorly by wear. There is a faint ectostylid. The posterior root is distinctly longer than the anterior root, and directed posteroventrally. Both roots are merged proximally and separated distally.

Measurements. ZIN O.35052, m3: L, 2.62; TRL, 1.38; TAL, 1.23; TRW, 2.05; TAW, 2.06.

Discussion. In ZIN C.85054 the length of the m3 alveolus is 3.8 mm; the m3 appears to fit this alveolus. The size of the latter coincides with the m3 size of the largest Bissekty zhelestid, cf. *Eoungulatum kudukensis* (Nessov et al., 1998, table 2). The talonid is narrower than the trigonid, as in m3 of cf. *Eoungulatum kudukensis* and ‘*Kumsuperus avus*’ from Bissekty Formation (Nessov et al., 1998, figs. 14F, 18B).

Eutheria indet.

Material. There are four other dental remains that are listed here for completeness. Because of the poor quality

of preservation we elect to not formally identify these specimens beyond Eutheria.

ZIN C.85295 is almost certainly the parastylar region and paracone of the left M3 of a large zhelestid. It is similar to the specimen attributed above to *Parazhelestes* sp. cf. *P. robustus*.

ZIN C.85297 is a very worn left M1 or 2 missing the posterior part of the tooth in a line just posterior to the metacone. If ZIN C.85293, referred to *Paranyctoides* sp., is an M1, then ZIN C.85297 could be an M2 of the same species. It could also be a small zhelestid, but the protocone is rather labiolingually narrow so that the lingual area is rather 'squared up' as in *Paranyctoides*. The presence of well-developed lingual cingula suggests that this is not a metatherian tooth.

ZIN C.85298 is a worn and damaged right P4 or 5. Its has three roots. It is eutherian, not metatherian. In size it is similar to a zhelestid or *Kulbeckia* but it matches neither of these in morphology. We do not know what the morphology of such teeth are in *Paranyctoides*. It is too large for this but could be the correct size for the other upper molar, ZIN C.85293, referred to *Paranyctoides* sp.

ZIN C.85302 is possibly a left lower canine. It is two-rooted, about the size of a lower canine for *Kulbeckia kulbecke*, but it does not appear to have the backward sweep of the roots as in this taxon. It is more robust. It could be an anterior left lower premolar. What argues against this is a well-developed wear facet on the posterolabial margin that could be for the anterior edge of an upper left canine.

3. General discussion

3.1. Comparison with other Kyzylkum and Mongolian Cretaceous mammal faunas

Although the Aitym mammal assemblage is incompletely known, some comparisons with other Cretaceous mammal assemblages from the Kyzylkum Desert can be made. Eleven mammal taxa are currently known from the Aitym fauna, which is more than half of the Bissekty assemblage and four times that of the Khodzhakul assemblage (Table 1). The Khodzhakul mammal fauna at the moment contains only eutherians. *Oxlestes grandis* Nessov, 1982 from this assemblage, based on the fused cervical vertebrae II and III, was considered a deltatheroidan (e.g., Nessov et al., 1994, p. 58), but these vertebrae could be referable to the purported zhelestid *Eozhelestes mangit* Nessov, 1997, the largest mammal in the assemblage. The absence of multituberculates, symmetrodonts, and metatherians at Khodzhakul is almost certainly in part a sampling bias. Multituberculates and symmetrodonts are the rarest elements in the well-

sampled Bissekty fauna, but they are also found in much smaller Aitym fauna. This may mean that these groups became more abundant by Aitym time, and thus may reflect some currently unknown changes in the environment. *Uzbekbaatar wardi* and possibly *Paranyctoides* sp. are the only species from the Aitym Formation thus far recovered that are almost certainly distinct from species known from the underlying Bissekty Formation, yet these species are referable to Bissekty genera. This suggests some discernible time separates these two faunas. Deltatheroidans are present in both the Bissekty and Aitym faunas and everywhere are relatively rare. Asiadelphian metatherians are not found in the Khodzhakul and Aitym faunas, and very rare in the Bissekty fauna. The Khodzhakul eutherian assemblage contains the stem-group archaic eutherians *Bobolestes zenge* Nessov, 1985 and *Otlestes meiman* Nessov, 1985, not known in later Kyzylkum complexes. In the Bissekty fauna they are replaced by more derived, diverse and abundant asioryctitherians, which were very rare, if present, in the Aitym fauna. A eutherian of uncertain affinities, *Paranyctoides*, is present in both the Bissekty and Aitym faunas, but is not very abundant. In the Bissekty and Aitym mammal assemblages archaic ungulatormorphs ('Zhelestidae') are a dominant group, while in the Khodzhakul fauna they may be represented by a single taxon, *Eozhelestes mangit*. In the Bissekty fauna five taxa of zhelestids are currently recognized based on the upper dentition (Nessov et al., 1998; Table 1), although this figure may require amendment after revision of the group based on more recently recovered material. In the Aitym fauna at least four taxa of zhelestids are recognized. In all three Kyzylkum faunas more than half of the identifiable mammal specimens belong to zhelestids. Finally, the Bissekty fauna contains a zalambdalestid *Kulbeckia kulbecke*, which is the most abundant single species in the fauna (Archibald & Averianov, 2003), but the same or a related taxon is rarer in the Aitym Formation. The zalambdalestids are also known from the early Campanian Darbasa Formation in southern Kazakhstan (Averianov, 1997), where they are represented by a more derived taxon, *Alymlestes kielanae* Averianov & Nessov, 1995. There is some morphological difference between the Turonian–Coniacian *Kulbeckia* and the Campanian *Alymlestes*, but currently the geologically intermediate Aitym cf. *Kulbeckia* sp. is too poorly known to be compared with these taxa. The rarity of zalambdalestids in the Aitym Formation is interesting, because they were the first or only mammals found from the Santonian of regions adjacent to the Kyzylkum Desert. The lower Santonian Yalovach Formation in Tajikistan produced three molars of *Kulbeckia* sp. and *Kulbeckia kansaica* Nessov, 1993 (a junior synonym of *K. kulbecke*; Archibald & Averianov, 2003), and the upper Santonian Bostobe Formation in the Aral Sea region, Kazakhstan produced

Table 1

Faunal lists of mammals from the Cretaceous of the Kyzylkum Desert, Uzbekistan (data from Nesson, 1993; Nesson et al., 1994, 1998; Averianov, 2000; and unpublished information).

Khodzhakul Formation	Bissekty Formation	Aitym Formation
upper Albian?–lower Cenomanian	upper Turonian-Coniacian	?Santonian
Theria	Multituberculata	Multituberculata
Eutheria	Cimolodonta	Cimolodonta
Bobolestidae	<i>Uzbekbaatar kizylkumensis</i>	<i>Uzbekbaatar wardi</i>
<i>Bobolestes zenge</i>	Theria	Theria
Otlestidae	Symmetrodonta	Symmetrodonta
<i>Otlestes meiman</i>	Spalacotheriidae	Spalacotheriidae
Ungulatomorpha	<i>Shalbaatar bakht</i>	cf. <i>Shalbaatar</i> sp.
‘Zhelestidae’	Tribosphenida	Tribosphenida
<i>Eozhelestes mangit</i>	Metatheria	Metatheria
(?= <i>Oxlestes grandis</i>)	Deltatheriidae	Deltatheriidae
	<i>Sulestes karakshi</i>	cf. <i>Deltatherus</i> sp.
	<i>Deltatherus kizylkumensis</i>	Eutheria
	Asiadelphia	Zalambdalestidae
	<i>Sailestes quadrans</i>	<i>Kulbeckia</i> cf. <i>K. kulbecke</i>
	<i>Marsasia aenigma</i>	aff. <i>Kulbeckia</i> sp.
	<i>Marsasia</i> sp.	?Soricomorpha
	Eutheria	?Nyctitheriidae
	Asioryctitheria	<i>Paranyctoides</i> sp. cf.
	<i>Daulestes kulbeckensis</i>	<i>P. aralensis</i>
	(= <i>Taslestes inobservabilis</i> ,	<i>Paranyctoides</i> sp.
	= <i>Kumlestes olzha</i> , = <i>Kennalestes</i>	Ungulatomorpha
	<i>uzbekistanensis</i> , ?= <i>Daulestes</i>	‘Zhelestidae’
	<i>nessovi</i>)	cf. <i>Aspanlestes</i> sp.
	<i>Daulestes</i> sp. nov.	<i>Parazhelestes</i> sp. cf.
	Asioryctitheria gen. & sp. nov.	<i>P. robustus</i>
	<i>Bulaklestes kezbe</i>	<i>Parazhelestes</i> sp. aff.
	Zalambdalestidae	<i>P. minor</i>
	<i>Kulbeckia kulbecke</i>	<i>Eoungulatum</i> sp. cf.
	(= <i>Kulbeckia rara</i>)	<i>E. kudukensis</i>
	?Soricomorpha	
	?Nyctitheriidae	
	<i>Paranyctoides aralensis</i>	
	(= <i>Ortallestes tostak</i>)	
	Ungulatomorpha	
	‘Zhelestidae’	
	<i>Aspanlestes aptap</i>	
	(= <i>Zhelestes bezelgen</i>)	
	<i>Sorlestes budan</i>	
	(= <i>Zalambdalestes</i>	
	<i>mynbulakensis</i>)	
	<i>Zhelestes temirkazyk</i>	
	<i>Parazhelestes robustus</i>	
	<i>Parazhelestes minor</i>	
	<i>Eoungulatum kudukensis</i>	
	(?= <i>Kumsuperus avus</i>)	

a dentary fragment with broken teeth of a possible zalambdalestid ‘*Beleutinus orlovi*’ Bazhanov, 1972 (*nomen dubium*; Nesson, 1987, 1993; Averianov, 2000). The size, relatively unreduced m3, and relatively posterior position of the masseteric fossa of ‘*Beleutinus orlovi*’ are more similar to *Kulbeckia* than to Mongolian zalambdalestids.

The Mongolian Late Cretaceous mammal faunas are dominated by endemic and diverse multituberculates, with more rare deltatheroidans, asiadelphians, asioryc-

titherians, kennalestids, and zalambdalestids (Kielan-Jaworowska et al., 2000). Although there are some similarities in the therian components of the Mongolian and Kyzylkum faunas, the former faunas are notable for their absence of zhelestids and the Kyzylkum faunas appear to lack taxa such as *Kennalestes* Kielan-Jaworowska, 1969. When the faunas from these two regions share higher level taxa, such as zalambdalestids, the Mongolian faunas have more derived representatives. These differences between mammal assemblages of

Uzbekistan and Mongolia can be explained by differing environmental conditions (more mesic coastal plains versus more xeric, elevated inland areas, respectively) and by at least a 10 million year younger geological age for Mongolian sites (Kielan-Jaworowska et al., 2000 and references therein).

3.2. Problems of intercontinental dispersals

The sequence of Late Cretaceous mammal assemblages in Middle Asia and Kazakhstan is the most complete after that of western North America (Table 2); only Maastrichtian mammal faunas are lacking in Middle Asia. In Mongolia only the Campanian Stage is well known. In both Europe and eastern North America, which were isolated during most of the Late Cretaceous from Asia and western North America, respectively, Cretaceous mammals are very poorly known. The Campanian assemblages from eastern North America and Europe are similar to those of western North America, but in the Maastrichtian the European fauna became more endemic. In the Maastrichtian, Europe was broken into an archipelago, and the known records come from two island areas, the Iberian (*Labes*, *Lainodon*) and Transylvanian (*Barbatodon*, *Hainina*, *Kogaionon*) regions. The data presented in Table 2 clearly show considerable endemism of Asian and North American Late Cretaceous mammal faunas. There are only two genera found on both continents: *Deltatheroides* in the Campanian of Mongolia and cf. *Deltatheroides* in the Campanian–Maastrichtian of North America, and *Paranyctoides* in the Coniacian–Santonian of Middle Asia and Campanian–Maastrichtian of North America. Both taxa most probably migrated from Asia to North America, because they or their relatives are found in older deposits in Asia (Archibald & Averianov, 2001). There are some other mammal taxa indicating intercontinental interchange during the Late Cretaceous. In Middle Asia there is a spalacotheriid (spalacolestine?) symmetrodont *Shalbaatar* and a basal cimolodontan multituberculate *Uzbekbaatar*. In North America, Spalacolestinae underwent a radiation from the end of the Early Cretaceous to the Campanian, and previously were not recorded on other continents (Cifelli & Madsen, 1999).

Basal cimolodontan multituberculates of the '*Paracimexomys* group' were known only from the Cretaceous of North America (Eaton & Cifelli, 2001) and *Uzbekbaatar* was probably derived from an American immigrant.

The multituberculates of the '*Paracimexomys* group' are clearly of Asian origin, originating from the Central Asian (Mongolian area) Early Cretaceous Eobaatarinae and giving rise to more derived North American

multituberculates (Montellano et al., 2000; Eaton & Cifelli, 2001). Similarly 'Zhelestidae', an abundant element of Middle Asian coastal plains since possibly the Cenomanian, gave rise to more derived archaic ungulates ('condylarths') in North America after arriving there in the late Santonian (Nessov et al., 1998). Interestingly, in most cases Asian immigrants in North America were successful, undergoing considerable radiations, whereas American immigrants to Asia were less successful. They usually remained rare faunal elements, as in the Early Eocene Chinese Wutu fauna (Tong & Wang, 1998). The only exception of this rule is cf. *Deltatheroides*, which had limited distribution in North America, possibly as a result of competition with more derived and numerous North American marsupials.

The considerable endemism of Asian and North American mammal faunas indicates that intercontinental dispersal was rather difficult. Only three dispersal events can be more or less confidently detected in the Cretaceous:

1. Dispersal of plagiaulacoid multituberculates referable to Eobaatarinae and the amphilestine 'triconodont' *Gobiconodon* from Central Asia to Europe and then to North America. Eobaatarinae and *Gobiconodon* are known from the Aptian–Albian of Mongolia (Kielan-Jaworowska et al., 1987; Kielan-Jaworowska & Dashzeveg, 1998), Barremian of Spain (Hahn & Hahn, 1992; Cuenca-Bescós & Canudo, 1999), and *Gobiconodon* is known from the Aptian–Albian of USA (Jenkins & Schaff, 1988). In North America multituberculates of the *Paracimexomys* group, derived from Eobaatarinae, were first recorded in the Aptian–Albian (Krause et al., 1990; Cifelli, 2000). This argues for this dispersal event to have occurred no later than the Barremian. At this time Asia was connected with Europe (the Turgai Strait was not open until the early Turonian), and both the Atlantic Ocean and the Western Interior Seaway were not open, which would have promoted intercontinental dispersal. As this dispersal route was located in relatively low latitudes, climate was not a major factor; thus it can be classified as a typical biogeographic corridor (*sensu* Simpson, 1965; see also McKenna, 1973). The endemic European multituberculates (*Barbatodon*, *Hainina*, *Kogaionon*) are quite primitive and resemble the North American '*Paracimexomys* group'. They may have developed from Asian Eobaatarinae and persisted until the end of Cretaceous or Paleocene (Vianey-Liaud, 1986; Gheerbrant et al., 1999; Peláez-Compomanes et al., 2000) of Europe in island isolation.

2. Dispersal of 'Zhelestidae', *Paranyctoides*, and *Deltatheroides* from Asia to western North America via Beringia. These taxa are clearly known in North America since the Campanian, but 'Zhelestidae' may have appeared in this continent as early as late Santonian (Nessov et al., 1998). This would give late Santonian as minimal time estimate for this dispersal

Table 2

Comparison of Late Cretaceous mammals faunas (after Averianov, 2000; Cifelli, 2000; Kielan-Jaworowska et al., 2000 and other sources). Genera known from two continents are marked by bold.

Europe	Middle Asia and Kazakhstan	Central Asia and Japan	West North America	East North America
Latest Albian – Cenomanian				
	<i>Bobolestes</i>	' <i>Khuduklestes</i> '	<i>Astroconodon</i>	
	<i>Otlestes</i>	<i>Sorlestes</i>	<i>Corviconodon</i>	
	<i>Eozhelestes</i>		<i>Jugulator</i>	
			? <i>Plagiaulacidae</i>	
			indet.	
			<i>Janumys</i>	
			<i>Paracimexomys</i>	
			<i>Cedaromys</i>	
			<i>Bryceomys</i>	
			<i>Ameribaatar</i>	
			<i>Spalacolestes</i>	
			<i>Spalacotheridium</i>	
			<i>Dakotadens</i>	
			Picopsidae indet.	
			Pappotheriidae indet.	
			<i>Kokopellia</i>	
			<i>Alphadon</i>	
			<i>Protalphadon</i>	
			<i>Pariadens</i>	
Turonian-Coniacian				
	<i>Uzbekbaatar</i>		<i>Bryceomys</i>	
	<i>Shalbaatar</i>		<i>Paracimexomys</i>	
	<i>Sulestes</i>		<i>Cimolodon</i>	
	<i>Deltatherus</i>		<i>Spalacotheridium</i>	
	<i>Sailestes</i>		<i>Symmetrodontoides</i>	
	<i>Marsasia</i>		Deltatheriidae indet.	
	<i>Daulestes</i>		Picopsidae indet.	
	Asioryctitheria gen. nov.		? <i>Anchistodelphys</i>	
	<i>Bulaklestes</i>		<i>Alphadon</i>	
	<i>Paranyctoides</i>		<i>Protalphadon</i>	
	<i>Aspanlestes</i>			
	<i>Sorlestes</i>			
	<i>Zhelestes</i>			
	<i>Parazhelestes</i>			
	<i>Eoungulatum</i>			
	<i>Kulbeckia</i>			
Santonian				
	<i>Uzbekbaatar</i>		<i>Paracimexomys</i>	
	cf. <i>Shalbaatar</i>		<i>Bryceomys</i>	
	cf. <i>Deltatherus</i>		<i>Cimolodon</i>	
	af. <i>Daulestes</i>		? <i>Cimolomys</i>	
	<i>Paranyctoides</i>		<i>Meniscoessus</i>	
	cf. <i>Aspanlestes</i>		<i>Symmetrodontoides</i>	
	cf. <i>Parazhelestes</i>		'Zhelestidae'? indet.	
	cf. <i>Eoungulatum</i>		cf. <i>Picopsis</i>	
	<i>Kulbeckia</i>		<i>Alphadon</i>	
	' <i>Beleutinus</i> '			
Campanian				
cf. <i>Alphadon</i>	<i>Bulganbaatar</i>	<i>Chulsanbaatar</i>	<i>Alticonodon</i>	Cimolodontidae
cf. <i>Pediomys</i>	<i>Deltatheridium</i>	<i>Catopsbaatar</i>	? <i>Bryceomys</i>	indet.
cf. <i>Leptacodon</i>	Kennalestoidea indet.	<i>Djadochtatherium</i>	<i>Cimexomys</i>	cf. <i>Cimolomys</i>
	<i>Alymlestes</i>	<i>Kryptobaatar</i>	<i>Paracimexomys</i>	<i>Protalphadon</i>
<i>Labes</i>	cf. <i>Aspanlestes</i>	<i>Tombaatar</i>	<i>Viridomys</i>	
		<i>Bulganbaatar</i>	<i>Cimolodon</i>	
		<i>Nemegtbaatar</i>	<i>Cimolomys</i>	
		<i>Kamptobaatar</i>	<i>Meniscoessus</i>	
		<i>Nessovbaatar</i>	? <i>Stygimys</i>	
		<i>Sloanbaatar</i>	<i>Mesodma</i>	
		<i>Deltatheridium</i>	<i>Symmetrodontoides</i>	

Table 2 (continued)

Europe	Middle Asia and Kazakhstan	Central Asia and Japan	West North America	East North America
		<i>Deltatheroides</i>		
		<i>Hyotheridium</i>	Dryolestidae indet.	
		<i>Asiatherium</i>	<i>Potamotelses</i>	
		<i>Asioryctes</i>	<i>Zygiocuspis</i>	
		<i>Ukhaatherium</i>	<i>Picopsis</i>	
		<i>Kennalestes</i>	cf. <i>Deltatheroides</i>	
		<i>Barunlestes</i>	<i>Falepetrus</i>	
		<i>Zalambdalestes</i>	<i>Palaeomolops</i>	
			<i>Iugomortiferum</i>	
			<i>Albertatherium</i>	
			<i>Aenigmadelphys</i>	
			<i>Alphadon</i>	
			<i>Protalphadon</i>	
			<i>Turgidodon</i>	
			<i>Anchistodelphys</i>	
			<i>Varalphadon</i>	
			<i>Aquiladelphys</i>	
			<i>Iqualadelphys</i>	
			<i>Pedionys</i>	
			<i>Eodelphis</i>	
			<i>Paranyctooides</i>	
			<i>Gallolestes</i>	
			<i>Avitotherium</i>	
			<i>Gypsonictops</i>	
			<i>Cimolestes</i>	
Maastrichtian			<i>Essonodon</i>	
<i>Barbatodon</i>		<i>Buginbaatar</i>	<i>Cimexomys</i>	
<i>Hainina</i>		‘Guriliin Tsav’	<i>Paracimexomys</i>	
<i>Kogaionon</i>		taxon’	<i>Cimolodon</i>	
<i>Labes</i>			<i>Cimolomys</i>	
<i>Lainodon</i>			<i>Meniscoessus</i>	
			<i>Clemensodon</i>	
			<i>Stygimys</i>	
			<i>Mesodma</i>	
			? <i>Neoplagiaulax</i>	
			<i>Parectypodus</i>	
			<i>Kimbetohia</i>	
			<i>Catopsalis</i>	
			<i>Bistius</i>	
			cf. <i>Deltatheroides</i>	
			<i>Aenigmadelphys</i>	
			<i>Alphadon</i>	
			<i>Glasbius</i>	
			<i>Protalphadon</i>	
			cf. <i>Peradectes</i>	
			<i>Turgidodon</i>	
			<i>Aquiladelphys</i>	
			<i>Pedionys</i>	
			<i>Didelphodon</i>	
			<i>Eodelphis</i>	
			<i>Paranyctooides</i>	
			<i>Gypsonictops</i>	
			<i>Cimolestes</i>	
			<i>Batodon</i>	
			<i>Procerberus</i>	
			<i>Telacodon</i>	
			<i>Alostera</i>	
			<i>Baioconodon</i>	
			<i>Oxyprimus</i>	
			<i>Protungulatum</i>	
			<i>Mimatuta</i>	

event. The dispersal route was located at higher latitudes and thus would have been more strongly dependent on climate; thus it is a biogeographic filter using the Simpson (1965) classification. The presence of the Beringian bridge during all of the Late Cretaceous was a requirement for this dispersal and a late Santonian–early Campanian warming was sufficient for this dispersal to have occurred.

3. Dispersal of a spalacotheriid (spalacolestine?) symmetrodont, giving rise to *Shalbaatar*, and a basal cimolodontan multituberculate, giving rise to *Uzbekbaatar*, from western North America via Beringia to Middle Asia. The minimal time estimate of this event is late Turonian. Possibly, during this dispersal, marsupials first came from North America to Asia, where they give rise to an endemic Asian clade Asiadelphia, first recorded in the Coniacian of Middle Asia (*Marsasia-Sailestes*; Averianov & Kielan-Jaworowska, 1999; Archibald & Averianov, 2001). This issue is more complicated, because asiadelphians have no clear relatives in North America and may have appeared earlier in Asia than the record now indicates.

Impressed by the absence of Marsupialia and Ptilodontoidea in Asia, Kielan-Jaworowska earlier (1974, 1980, p. 172) argued that ‘the distribution of the Cretaceous multituberculate and therian faunas indicated that during the Late Cretaceous North America and Asia were separated by a sea-way. Rare dispersals of a sweepstakes route type took place from Asia to North America but not vice versa.’ The subsequent discovery of Cretaceous Marsupialia (Szalay & Trofimov, 1996; Averianov & Kielan-Jaworowska, 1999), spalacotheriid symmetrodonts and ptilodontoidean multituberculates (this paper) in Asia indicates the presence of a dispersal route via Beringia during the Late Cretaceous, which probably worked as a cold zone filter, allowing intercontinental dispersals in both directions during the short warm climatic phases.

Acknowledgements

AOA is grateful to Z. Kielan-Jaworowska for her hospitality during his stay in Warsaw in December 1999, when this paper was started, and to C. Kulicki for taking SEM micrographs (Fig. 11d) at the Institute of Paleobiology, Polish Academy of Sciences. This visit to Warsaw was supported by the interchange program between the Russian and Polish Academies of Sciences. We thank all the participants of URBAC-98-00 for field assistance and good company. We especially thank A. V. Abramov for help with the excavations at the CBI-117 site and A. S. Rezvyi for help with sorting of the concentrate. We thank J. Eaton for comments on

multituberculates and R. Cifelli for comments on spalacotheriids, and the comments of two anonymous reviewers. JDA thanks J. Valentine for help in the laboratory. Fieldwork was supported by the National Science Foundation (EAR-9804771) and by the National Geographic Society (6281-98), also with assistance from the Navoi Mining and Metallurgy Combinat. Laboratory work in Russia was supported by Russian Fund of Basic Research (RFBR) grants (00-15-99355 and 01-04-49548) and in the US by National Science Foundation grants (EAR-9804771 and 0207004).

“Note added in proof: Recent work by C. King, N. J. Morris, D. J. Ward, M. J. Hampton (written comm., 2003) indicates that the Aitym fauna described here is late Turonian to Coniacian in age and that the underlying Bissekty fauna is middle to late Turonian in age.”

References

- Archibald, J.D., 1996. Fossil evidence for a Late Cretaceous origin of ‘hoofed’ mammals. *Science* 272, 1150–1153.
- Archibald, J.D., Averianov, A.O., 2001. *Paranyctoides* and allies from the Late Cretaceous of North America and Asia. *Acta Palaeont. Pol.* 46, 533–551.
- Archibald, J.D., Averianov, A.O., 2003. The Late Cretaceous placental mammal *Kulbeckia*. *J. Vert. Paleont.* 23, 404–409.
- Archibald, J.D., Averianov, A.O., Ekdale, E.G., 2001. Late Cretaceous relatives of rabbits, rodents, and other extant eutherian mammals. *Nature* 414, 62–65.
- Archibald, J.D., Sues, H.-D., Averianov, A.O., et al., 1998. Précis of the paleontology, biostratigraphy, and sedimentology at Dzharakuduk (Turonian?–Santonian), Kyzylkum Desert, Uzbekistan. In: Lucas, S.G., Kirkland, J.L., Estep, J.W. (Eds.), Lower to Middle Cretaceous Terrestrial Ecosystems, Bulletin of the New Mexico Museum of Natural History and Science, 14, 21–28.
- Averianov, A.O., 1997. New Late Cretaceous mammals of southern Kazakhstan. *Acta Palaeont. Pol.* 42, 243–256.
- Averianov, A.O., 1999. A new species of multituberculate mammal *Uzbekbaatar* from the Late Cretaceous of Uzbekistan. *Acta Palaeont. Pol.* 44, 301–304.
- Averianov, A.O., 2000. Mammals from the Mesozoic of Kirgizstan, Uzbekistan, Kazakhstan and Tadzhikistan. In: Benton, M.J., Shishkin, M.A., Unwin, D.M. et al. (Eds.), *The Age of Dinosaurs in Russia and Mongolia*, Cambridge University Press, Cambridge, pp. 627–652.
- Averianov, A.O., Kielan-Jaworowska, Z., 1999. Marsupials from the Late Cretaceous of Uzbekistan. *Acta Palaeont. Pol.* 44, 71–81.
- Cifelli, R.L., 2000. Cretaceous mammals of Asia and North America. *Paleontological Society of Korea. Special Publication* 4, 49–84.
- Cifelli, R.L., Madsen, S.K., 1999. Spalacotheriid symmetrodonts (Mammalia) from the medial Cretaceous (upper Albian or lower Cenomanian) Mussentuchit local fauna, Cedar Mountain Formation, Utah, USA. *Geodiversitas* 21, 167–214.
- Crompton, A.W., Kielan-Jaworowska, Z., 1978. Molar structure and occlusion in Cretaceous therian mammals. In: Butler, P.M., Joysey, K.A. (Eds.), *Studies in the Development, Function and Evolution of Teeth*, Academic Press, London, pp. 249–287.

- Cuenca-Bescós, G., Canudo, J.I., 1999. A Lower Cretaceous traveler: *Gobiconodon* ('triconodont', Mammalia) from Vallipón (Upper Barremian, Teruel, Spain). In IV European Workshop on Vertebrate Palaeontology, Albarracín (Teruel, Spain), Programme and Abstracts Field Guide, p. 41 (Servicio Publicaciones Universidad de Zaragoza).
- Eaton, J.G., Cifelli, R.L., 2001. Multituberculate mammals from near the Early-Late Cretaceous boundary, Cedar Mountain Formation, Utah. *Acta Palaeont. Pol.* 46, 453–518.
- Fox, R.C., *Paranyctoides maleficus* (new species), an early eutherian mammal from the Cretaceous of Alberta. In: Dawson, M.R. (Ed.), *Papers in Vertebrate Paleontology Honoring Robert Warren Wilson*, Carnegie Museum of Natural History Special Publication 9, 9–20.
- Gambaryan, P.P., Kielan-Jaworowska, Z., 1995. Masticatory musculature of Asian taeniolabidoid multituberculate mammals. *Acta Palaeont. Pol.* 40, 45–108.
- Gheerbrant, E., Codrea, V., Hosu, A., et al., 1999. Découverte de vertébrés dans les Calcaires de Rona (Thanétien ou Sparnacien), Transylvanie, Roumanie: les plus anciens mammifères cénozoïques d'Europe Orientale. *Ecolae Geol. Hel.* 92, 517–535.
- Hahn, G., Hahn, R., 1992. Neue Multituberculaten-Zähne aus der Unter-Kreide (Barremium) von Spanien (Galve und Uña). *Geol. Palaeont.* 26, 143–162.
- Jenkins, F.A. Jr., Schaff, C.R., 1988. The Early Cretaceous mammal *Gobiconodon* (Mammalia, Triconodonta) from the Cloverly Formation in Montana. *J. Vert. Paleont.* 6, 1–24.
- Kielan-Jaworowska, Z., 1974. Migrations of the Multituberculata and the Late Cretaceous connections between Asia and North America. *Ann. SA Mus.* 64, 231–243.
- Kielan-Jaworowska, Z., 1975. Evolution of the therian mammals in the Late Cretaceous of Asia. Part I. *Deltatheridiidae*. *Palaeont. Pol.* 33, 103–132.
- Kielan-Jaworowska, Z., 1980. Absence of ptilodontoidean multituberculates from Asia and its palaeogeographic implications. *Lethaia* 13, 169–173.
- Kielan-Jaworowska, Z., 1992. Interrelationships of Mesozoic mammals. *Hist. Biol.* 6, 185–202.
- Kielan-Jaworowska, Z., Dashzeveg, D., 1998. Early Cretaceous amphilestid ('triconodont') mammals from Mongolia. *Acta Palaeont. Pol.* 43, 413–438.
- Kielan-Jaworowska, Z., Dashzeveg, D., Trofimov, B.A., 1987. Early Cretaceous multituberculates from Mongolia and a comparison with Late Jurassic forms. *Acta Palaeont. Pol.* 32, 3–47.
- Kielan-Jaworowska, Z., Hurum, J.H., 2001. Phylogeny and systematics of multituberculate mammals. *Palaeontology* 44, 389–429.
- Kielan-Jaworowska, Z., Nesson, L.A., 1990. On the metatherian nature of the *Deltatheroidea*, a sister group of the Marsupialia. *Lethaia* 23, 1–10.
- Kielan-Jaworowska, Z., Nesson, L.A., 1992. Multituberculate mammals from the Cretaceous of Uzbekistan. *Acta Palaeont. Pol.* 37, 1–17.
- Kielan-Jaworowska, Z., Novacek, M.J., Trofimov, B.A., et al., 2000. Mammals from the Mesozoic of Mongolia. In: Benton, M.J., Shishkin, M.A., Unwin, D.M. et al. (Eds.), *The Age of Dinosaurs in Russia and Mongolia*, Cambridge University Press, Cambridge, pp. 573–626.
- Krause, D.W., Kielan-Jaworowska, Z., Turnbull, W.D., 1990. Early Cretaceous Multituberculata (Mammalia) from the Antlers Formation, Trinity Group, of southcentral Texas. *J. Vert. Paleont.* 10 (Supplement to no. 3), 31A.
- McKenna, M.C., 1973. Sweepstakes, filters, corridors, Noah's arks, and beached Viking funeral ships in palaeogeography. In: Tarling, D.H., Runcorn, S.K. (Eds.), *Implications of Continental Drift to the Earth Sciences Volume 1*, Academic Press, London, pp. 295–308.
- McKenna, M.C., Kielan-Jaworowska, Z., Meng, J., 2000. Earliest eutherian mammal skull from the Late Cretaceous (Coniacian) of Uzbekistan. *Acta Palaeont. Pol.* 45, 1–54.
- Montellano, M., Weil, A., Clemens, W.A., 2000. An exceptional specimen of *Cimexomys judithae* (Mammalia: Multituberculata) from the Campanian Two Medicine Formation of Montana, and the phylogenetic status of *Cimexomys*. *J. Vert. Paleont.* 20, 333–340.
- Nesson, L.A., 1982. The ancient mammals of the USSR. *Ezheg. Vses. Paleont. Obshch.* 25, 228–242. [In Russian].
- Nesson, L.A., 1984. On some remains of mammals in the Cretaceous deposits of the Middle Asia. *Vest. Zool.* 2, 60–65. [In Russian].
- Nesson, L.A., 1985a. New mammals from the Cretaceous of Kyzylkum. *Vestnik Leningradskogo Universiteta. Seriya 7* (17), 8–18. [In Russian].
- Nesson, L.A., 1985b. Rare bony fishes, terrestrial lizards and mammals from the zone of estuaries and coastal plains of the Cretaceous of Kyzylkum. *Ezheg. Vses. Paleont. Obshch.* 28, 199–219. [In Russian].
- Nesson, L.A., 1987. Results of search and study of Cretaceous and early Paleogene mammals on the territory of the USSR. *Ezhe. Vses. Paleont. Obshch.* 30, 199–218. [In Russian].
- Nesson, L.A., 1993. New Mesozoic mammals of Middle Asia and Kazakhstan and comments about evolution of theriofaunas of Cretaceous coastal plains of Asia. *Trudy Zoologicheskogo Instituta. Ross. Akad. Nauk* 249, 105–133. [In Russian].
- Nesson, L.A., 1997. Cretaceous Nonmarine Vertebrates of Northern Eurasia. In: Golovneva, L.B., Averianov, A.O. (Eds.), 218 pp. (University of Saint Petersburg, Institute of Earth Crust, Saint Petersburg). [In Russian].
- Nesson, L.A., Archibald, J.D., Kielan-Jaworowska, Z., 1998. Ungulate-like mammals from the Late Cretaceous of Uzbekistan and a phylogenetic analysis of Ungulatomorpha. In: Beard, C.K., Dawson, M.R. (Eds.), *Dawn of the Age of Mammals in Asia*, Bulletin of the Carnegie Museum of Natural History, 34, 40–88.
- Nesson, L.A. & Kielan-Jaworowska, Z. 1991. Evolution of the Cretaceous Asian therian mammals. In: Kielan-Jaworowska, Z., Heintz, N., Nakrom, H.-A. (Eds.), *Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota. Extended Abstracts, Contributions from the Paleontological Museum, University of Oslo*, 364, 51–52.
- Nesson, L.A., Sigogneau-Russell, D., Russell, D.E., 1994. A survey of Cretaceous tribosphenic mammals from Middle Asia (Uzbekistan, Kazakhstan and Tajikistan), of their geological setting, age and faunal environment. *Palaeovertebrata* 23, 51–92.
- Nesson, L.A., Trofimov, B.A., 1979. The oldest insectivore of the Cretaceous of the Uzbek SSR. *Doklady Akad. Nauk SSSR* 247, 952–954. [In Russian].
- Peláez-Compomanes, P., Daams, R., López-Martínez, N., et al., 2000. The earliest mammal of the European Paleocene: the multituberculate *Hainina*. *J. Paleont.* 74, 701–711.
- Rougier, G.W., Wible, J.R., Novacek, M.J., 1998. Implications of *Deltatheridium* specimens for early marsupial history. *Nature* 396, 459–463.
- Simpson, G.G., 1965. *The Geography of Evolution*, 249 pp. (Chilton Books, Philadelphia and New York).
- Storer, J.E., 1991. The mammals of the Gryde local fauna, Frenchmen Formation (Maastrichtian: Lancian), Saskatchewan. *J. Vert. Paleont.* 11, 350–369.
- Szalay, F.S., Trofimov, B.A., 1996. The Mongolian Late Cretaceous *Asiatherium*, and the early phylogeny and paleobiogeography of Metatheria. *J. Vert. Paleont.* 16, 474–509.
- Tong, Y., Wang, J., 1994. A new neoplagiulacid multituberculate (Mammalia) from the lower Eocene of Wutu Basin, Shandong. *Vert. Palasiatica* 32, 275–284. [In Chinese, English summary].
- Tong, Y., Wang, J., 1998. A preliminary report on the early Eocene mammals of the Wutu fauna, Shandong Province, China. In:

Beard, C.K., Dawson, M.R. (Eds.), Dawn of the Age of Mammals in Asia, *Bulletin of the Carnegie Museum of Natural History*, 34, 186–193.

Vianey-Liaud, M., 1986. Les multituberculés thanétiens de France, et leurs rapports avec les multituberculés nord-américains. *Paleontographica. Abteilung A* 191, 85–171.