New Late Cretaceous mammals of southern Kazakhstan

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Mammalian remains from the lower part of the Darbasa Formation (lower Campanian) at the ‘Grey Mesa’ locality in the Alymtau Range, southern Kazakhstan, are described. They include *?Bulganbaatar* sp. (Multituberculata), *Deltatheridium nessovi*, sp. n. (Deltatheroidea), and four eutherians: an undetermined *?Otlestid* kennalestoid (*?Otlestidae*), *?Alymlestes* sp. (Zalambdalestidae), *?Aspanlestes* sp. (Zhelestidae), and an undetermined eutherian. This new Cretaceous fauna is most similar to that from the Djadokhta Formation in Mongolia and may tentatively confirm an early Campanian age for the latter.

**Key words**: Mammalia, Cretaceous, Kazakhstan, Mongolia.

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**Introduction**

Mesozoic mammals from Kazakhstan are poorly known. The first Mesozoic mammal from Kazakhstan (and the first from the former USSR), found in 1962, is a mandibular fragment with heavily damaged molars, the holotype of *Beleutinus orlovii* (*?Zalambdalestidae*), from the Santonian Bostobe Formation at Zhalmauz Well, Kyzyl-Orda Region (Bazhanov 1972). Since that time only three additional mammal remains have been recognized from the Cretaceous of Kazakhstan: a cervical vertebra of a relatively large, undetermined mammal from the Zhalmauz locality (Nessov & Khisarova 1988); a dentary fragment with p5, m1–3, the holotype of *Sorlestes kara* (Zhelestidae), from the drilling core penetrating lower Turonian deposits near Ashcbikol’ Lake, Chimkent Region (Nessov 1993); and a lower molar (m1), the holotype of *Alymlestes kielanae* (Zalambdalestidae) from the lower part (Campanian) of the Darbasa Formation at the ‘Grey Mesa’ locality in the Alymtau Range, Chimkent Region (Averianov & Nessov 1995). During further search for Cretaceous mammals, undertaken by the author accompanied by I.G. Danilov and A.S. Rezvyi at the ‘Grey Mesa’ locality
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Fig. 1. Geographical and stratigraphic location of the ‘Gray Mesa’ locality at Alymtau Range, Chimkent Province, Kazakhstan.

Fig. 1) in May–June 1996, seven additional mammal fossils were discovered. They are described below.

The age of the lower part of the Darbasa Formation was determined as ?lower–middle Campanian using the tripartite division of this stage (Averianov & Nessov 1995). The Campanian is, however, a marine stage established in Europe and divided on the basis of ammonites and other marine invertebrates into two substages (Harland et al. 1989). In view of this, the tripartite division of the Campanian in Asia or North America is not appropriate. In contrast to Mongolian and Chinese Upper Cretaceous formations, the Darbasa Formation yields remains of both terrestrial, brackish water and marine animals. The marine invertebrates from the Darbasa Formation enable the precise evaluation of its age as early Campanian (Moskvin 1986). For a more detailed geological setting and a preliminary faunal list for the ‘Grey Mesa’ locality, see Averianov & Nessov (1995).

About 1440 kg of sandstone matrix were dry screened at the ‘Grey Mesa’ locality in 1996, and seven mammalian specimens were found among nearly ten thousand shark teeth, more rare osteichthyan fish remains, crocodile, theropod and hadrosaurid teeth, very rare lizard and salamander remains. This yields an average of one mammalian specimen per 200 kg of sediment. In the most productive Coniacian localities in Uzbekistan this ratio is about one mammalian remain per 600 kg (Nessov 1982). In the upper Albian Antlers Formation in Texas it varies from about 150 kg (Greenwood Canyon) to 2700 kg (Butler Farm) (Patterson 1956; Slaughter 1965), while in European
Maastrichtian localities it varies from 100 kg (Quintanilla del Coco) to 8000 kg (Champ Garimond) (Pol et al. 1992). The best obtained value for this ratio is about 24 kg per mammal specimen in Maastrichtian intertrappean beds of Naskal in Andhra Pradesh, India (Prasad et al. 1994). This review shows that the Alymtau is among the most productive Cretaceous mammal localities in the world. The possibility of further work at Alymtau is limited by the very small size of the locality.

Abbreviations: Upper and lower case letters, P/p (premolar) and M/m (molar), refer to upper and lower teeth, respectively. The described mammal remains are housed in the Zoological Institute, Russian Academy of Sciences, Saint Petersburg (ZIN).

Measurements: L - length, W - width, TAW - talonid width, TRL - trigonid length, TRW - trigonid width. All measurements are in mm.

**Systematic Palaeontology**

Order Multituberculata Cope, 1884

*Bulganbaatar* Kielan-Jaworowska, 1974

*Bulganbaatar* sp.

Fig. 2.

**Material.** — ZIN 82192, left P4. The ‘Grey Mesa’ locality in the Alymtau Range, southern Kazakhstan; lower part of the Darbasa Formation, lower Campanian.

**Description.** — Cusp formula 3:5. The tooth bears two cusp rows. The external row consists of a very small anterobasal cusp and two larger cusps that increase in size posteriorly. The posterior-most cusp is almost as tall and is noticeably larger than cusps of the internal row. The penultimate internal cusp is nearly twice smaller and slightly shorter than the posterior-most cusp. The internal row consists of a slightly smaller anterior cusp, connected by a short cingulum to the external anterobasal cusp, and four slightly larger, approximately equally sized and closely-spaced cusps. The posterior-most cusp has a relatively elongate posterior slope. The third cusp is probably the highest (the tip of the fourth cusp is broken). The anterior root of the tooth is higher than the posterior one, but both roots are nearly equal in length.

**Comparisons.** — None of the Mongolian Late Cretaceous multituberculates has 3:5 cusp formula for P4. If the very small size of the first cusp in the external row is taken into account, the closest cusp formula would be 2:5. Only three Late Cretaceous Mongolian multituberculates have such a cusp formula for P4; these are *Sloanbaatar mirabilis* and *Bulganbaatar nemegtbaataroides*, both from the Djadokhta Formation at Bayn Dzak (Kielan-Jaworowska 1970, 1974); and a new genus from the ?equivalent of the Djadokhta Formation at Ukhaa Tolgod (Rougier et al. in press). In relatively large samples of Mongolian Late Cretaceous multituberculates there is almost no variation in cusp formulae of fourth premolars (Kielan-Jaworowska et al. in press), permitting a relatively reliable determination for ZIN 82192. The P4 from Alymtau (2.7 mm long) is larger than that of *S. mirabilis* (1.7 mm) and nearly identical in size to the P4 of *B. nemegtbaataroides*, which is 2.6 mm long. In the general shape and proportions the Alymtau P4 is similar to P4 of the Mongolian *Bulganbaatar* and differs from it only in having an incipient additional cusp in the external row. From the above new
multituberculate taxon from Ukhaa Tolgod, ZIN 82192 differs in its smaller size and more developed area of the external row, with relatively larger cusps.

In having the cusp formula 3:5, the P4 of ?Bulganbaatar sp. from Alymtau is intermediate in morphology between those in Mongolian Bulganbaatar nemegibaataroides (Djadokhta Formation; cusp formula 2:5) and Nemegibaatar gobiensis (Barun Goyot Formation; cusp formula 3:6:1). ZIN 82192 differs from the latter in having a smaller number of cusps in the main row, in lacking of the third cusp row, and in having a less elongated crown relative to the width.

Order Deltatheroida Kielan-Jaworowska, 1982
Family Deltatheridiidae Gregory & Simpson, 1926
Deltatheridium Gregory & Simpson, 1926
Deltatheridium nessovi, sp. n.

Fig. 3.
Holotype: ZIN 82193, right M2 missing the protocone. The ‘Grey Mesa’ locality in the Alymtau Range, southern Kazakhstan; lower part of the Darbasa Formation, lower Campanian.
Etymology: In memory of the late Dr. Lev A. Nessov, who found the first deltatheroidans in the former USSR (Nessov 1985).

**Diagnosis.** — Species of Deltatheridium that differs from D. pretrituberculare and D. tardum from the Djadokhta and the Barun Goyot formations in Mongolia, respectively,
Fig. 3. Deltatheridium nessovi sp. n., partial right M2, ZIN 82193, holotype. A. Labial view. B. Occlusal view. SEM stereo-micrographs. Scale bar is 1 mm. Anterior is up.

by having a ectoflexus shallower, stylar shelf relatively shorter, metastylar and para-stylar lobes less developed (of which the former is smaller), preparacrista much weaker, and metacone relatively larger and not compressed labiolingually.

**Description.** — The holotype lacks the crown lingual to the paracone and metacone. The remaining part of the tooth is nearly symmetrical; the parastylar lobe is larger than the metastylar one. The ectoflexus is relatively shallow. The stylocone and the parastyle are nearly equal in size. There is a deep groove for the protoconid between them and lingually. There are no other stylar cusps, nor distinct metastyle. There is a prominent wear facet 2a (facet nomenclature after Crompton & Kielan-Jaworowska 1978) on the postmetacrista. The premetacrista and postparacrista carry strong wear facets 3 and 4, that extend to the tips of the metacone and paracone, respectively. The preparacrista is relatively weak and not worn. The metacone is somewhat taller than the paracone; both cusps have rounded bases approximately equal in size.

**Remarks.** — The Mongolian species D. pretrituberculare and D. tardum are distinguished on the basis of snout proportions and number of lower incisors (Kielan-Jaworowska 1975). In general the labial half of M2 in the Kazakhstanian species is more robust than in molars of the Mongolian species. In possessing a larger metacone, stronger postmetacrista and weaker preparacrista, the new species approaches more
closely the condition of marsupials, than that of the Mongolian deltatheridiids. It is more primitive than the Mongolian species and *Sulestes karakshi* from the Coniacian of Uzbekistan (Nessov 1985; Kielan-Jaworowska & Nessov 1990) in having the parastylar lobe relatively larger than the metastylar lobe, and in having a shorter postmetacrista. In this respect it is reminiscent of *Pappotherium*.

**Measurements.** — *L* = 2.7.

Superfamily Kennalestoidea Kielan-Jaworowska, 1981

*Family Otlestidae* Nessov, 1985

Genus et species indet.

Fig. 4.

**Material.** — ZIN 82194, trigonid of left molar. The ‘Grey Mesa’ locality in the Alymtau Range, southern Kazakhstan; lower part of the Darbasa Formation, lower Campanian.

**Description.** — The trigonid is slightly compressed anteroposteriorly, having an outline approaching that of an isosceles triangle in occlusal view. It bears three cusps, among which the protoconid is the tallest. The apex of the protoconid is slightly bent posteriorly.

Fig. 4. An *?otlestid kennalestoid*, trigonid of left *m3*?, ZIN 82194. A. Occlusal view. B. Lingual view. SEM stereo-micrographs. Scale bar is 0.5 mm. Anterior is to the right.
The metaconid is broken; but its base is equal to that of the protoconid and possibly it was not much smaller than the latter. The paraconid is the smallest trigonid cusp, but not much reduced and is about one half of the protoconid height. The paraconid and the metaconid are connate at their bases. The trigonid basin is small and opens lingually. In anterior view there is an anterolabial cingulid that extends nearly vertically to the paracristid notch between protoconid and paraconid bases, closer to the latter. The posterior trigonid wall is concave, bearing no evidence of the cristid obliqua.

**Comparison.** — The trigonid appears to be primitive with respect to most other Eutheria. It is less antero-posteriorly compressed and has a less reduced paraconid than in other known Kennalestoidea (including Prokennalestes, Otlestes and Kennalestes) and Palaeoryctoidea, resembling in these features the molars of Early Cretaceous ‘Trinity therians’ (Patterson 1956). Among Palaeoryctoidea, ZIN 82194 is most similar to trigonids in Daulestes kulbeckensis from the late Turonian of Uzbekistan (Nessov *et al.* 1994) but differs from the latter in having a smaller protoconid, connate paraconid and metaconid, and possibly a relatively larger paraconid. The paraconid connate at the base with the metaconid is characteristic of Kennalestoidea. Among the latter ZIN 82194 is remarkably similar to the m3 trigonid in the holotype of Otlestes meiman from the early Cenomanian of Uzbekistan (Nessov *et al.* 1994: pl. 3, fig. 1c, d), in having unreduced a relatively high paraconid and the protoconid apex bent posteriorly. The Alymtau specimen, however, is somewhat larger.

**Measurements.** — TRL = 1.1, TRW = 1.3.

‘Supergrandorder’ Ungulatomorpha Archibald, 1996
Family Zhelestidae Nessov, 1985
*Aspanlestes* Nessov, 1985
*?Aspanlestes* sp.

**Material.** — ZIN 82197, talonid of left lower molar (m1 or m2). The ‘Grey Mesa’ locality in the Alymtau Range, southern Kazakhstan; lower part of the Darbasa Formation, lower Campanian.

**Description.** — The talonid is wide, apparently wider than the trigonid, separated from the latter by strong constriction. The talonid basin is large and deep. The hypoconulid and the entoconid are strongly twinned, nearly fused. The distances between the tips of hypoconulid and hypoconid and the notch separating the bases of these cusps are nearly equal. The hypoconulid is taller than the hypoconid. The tip of the entoconid is broken, its base is smaller than that of the hypoconulid.

**Comparison.** — In size and general appearance, ZIN 82197 is similar to the talonids in m1–2 of the Coniacian zhelestids *Aspanlestes aptap* and *Sorlestes budan* from Uzbekistan (Nessov *et al.*, in press). In size it is closer to *Sorlestes* (for m1 and m2 TAW = 1.6 and 1.8 in average), than to *Aspanlestes* (for m1 and m2 TAW = 1.5 and 1.6 in average, Nessov *et al.* in press.), but it is more similar to *Aspanlestes* in having the talonid wider than the trigonid. ZIN 82197 is most similar to the relatively unworn m2 in the specimen referred to *A. aptap* (Nessov *et al.* in press: fig. 7D), differing from the latter by having a relatively higher hypoconulid and a deeper talonid basin. In *Aspanlestes* and *Sorlestes*, as in other zhelestids, the hypoconulid and the entoconid are only
slightly twinned and the hypoconulid is much closer to the notch separating the base of that cusp from the base of the hypoconid. In this feature ZIN 82197 is more similar to the Mongolian Zalambdalestidae. From the Alymtau zalambdalestid, Alymlestes kielanae, ZIN 82197 differs by its smaller size (in Alymlestes for m1 TAW = 2.1), shallower talonid basin, more strongly twinned hypoconulid and entoconid, and less marked unilateral hypsodonty. Although the described molar talonid is only tentatively assigned to Aspanlestes, it is confidently attributed to the Zhelestidae.

**Measurements.** — TAW = 1.7.

Order Anagalida Szalay & McKenna, 1971
Family Zalambdalestidae Gregory & Simpson, 1926
Aspanlestes Averianov & Nessov, 1995

Fig. 6A, B.

**Material.** — ZIN 82195, right ?dp3; ZIN 82196, right dentary fragment with p2–3. The ‘Grey Mesa’ locality in the Alymtau Range, southern Kazakhstan; lower part of the Darbasa Formation, lower Campanian.

**Description.** — The crown of dp3 has one main cusp, situated at the anterior end of the tooth, with tip bent somewhat posteriorly, and distinct posterior basal cusp. Both cusps are connected by a ridge carrying an elevation at its midpoint. This ridge and the whole crown are curved labially. The tooth has two roots, anterior of which is bent anteriorly. The roots are resorbed and between them there is a considerable space for the permanent tooth. This shows that the tooth belongs to the deciduous tooth generation. The dp4 should be submolariform as in most eutherians (for example, in *Asioryctes nemegetensis*: Kielan-Jaworowska 1981: pl. 18, fig. 2a, b), the dp2 usually has more simple morphology; it follows that ZIN 82196 most probably is dp3.

The dentary is relatively deep, possibly with a diastema in front of p2. The p2 is more than twice lower than p3 and has two roots. The p3 is relatively small, without
basal tubercles, two rooted, its posterior end is broken off. The specimen is badly eroded, possibly it passed through the digestive system of a carnivorous animal.

**Comparison.** — The deciduous tooth is similar to p3 in *Asioryctes* (Kielan-Jaworowska 1981: pl. 18, fig. 3b, e), but differs by midpoint elevation on the shearing ridge, labially bent crown and larger size. ZIN 82195 approaches in size the p3 attributed to *Alymlestes* sp. from the same locality (ZIN 82196), but the latter tooth is more robust than the supposed dp3. It seems possible that the described milk tooth belongs to *Alymlestes kielanae*, known previously only from the holotype (m1) from the same locality (Averianov & Nessov 1995).

The dentary fragment resembles the mandibles of *Zalambdalestes* in some respects (p2 present, half as high as p3, mandible is not very deep under p3), but is closer to *Barunlestes* (p3 relatively smaller, without an anterior basal cusp, possibly there was a diastema to the rear of p1) (Kielan-Jaworowska & Trofimov 1980; Kielan-Jaworowska 1984). The structure of p2–3 in ZIN 82196 is, however, different from that in *Zalambdalestes* and *Barunlestes*. Crowns in these teeth are more robust and possibly were adapted for crushing a more solid food. The third lower premolar of ZIN 82196 is somewhat smaller than in *Barunlestes butleri* (Kielan-Jaworowska &
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Trofimov 1980), whereas m1, the holotype of A. kielanae, is close in size to that in B. butleri (Averianov & Nessov 1995).

**Measurements.** — dp3: L = 1.7, W = 0.9, p2: L = 1.5, W = 0.7, p3: L = approximately 1.9, W = 0.9, depth of mandible under p3 3.3.

Eutheria incertae sedis
Genus et species indet.
Fig. 6C.

**Material.** — ZIN 82198, left dentary fragment with alveoli for m2–3(?) or dp3–4(?)
The ‘Grey Mesa’ locality in the Alymtau Range, southern Kazakhstan. Lower part of the Darbasa Formation, lower Campanian.

**Description and comparison.** — The dentary is small and very shallow. Judging from the alveoli, the two teeth probably are nearly equal in length, with roots extending nearly to the ventral edge of the dentary. The massetteric crest begins anterior to the last tooth locus represented; this tooth was situated internal to the coronoid process in contrast to the other Cretaceous eutherians, where there is a space between m3 and the base of the coronoid process. The massetteric crest is poorly defined, which may be a juvenile trait. Possibly, this specimen belonged to a juvenile animal with deciduous teeth. In this case, the coronoid process would move posteriorly and the dentary become deeper during later growth stages. But, tooth germs of permanent teeth nor cavities for them are not visible in transmitted light.

The described dentary fragment belongs to the smallest mammal in the Alymtau fauna. The supposed deciduous tooth of Alymlestes (ZIN 82195) belonged to a considerably larger mandible.

**Measurements.** — Alveolar length for the two last teeth is 1.3 and approximately 1.3.

**Discussion**

Six mammalian taxa are determined with different degree of confidence from the Alymtau locality:
Multituberculates
  ?Bulganbaatar sp.
Deltatheroidans
  Deltatheridium nessovi sp. n.
Eutherians
  ?Otlestidae
    Gen. et sp. indet.
Zhelestidae
  ?Aspanlestes sp.
Zalambdalestidae
  Alymlestes kielanae (= ?Alymlestes sp.)
Eutheria incertae sedis
  Genus et species indet.
As many as five mammalian families may be represented, which approximates the richest known Late Cretaceous mammalian faunas of Asia: 9 families may be represented in the fauna of the Bissekty Formation (Uzbekistan) (family for Uzbekbaatar, Deltatheroididae, Deltatheridiidae, ?Palaeoryctidae [Daulestes], family for Sailestes, Kulbeckiidae, ?Nyctitheriidae [Paranyctoides], Kennalestidae [undescribed taxon], and Zhelestidae); as compared with 7 families (Eucosmodontidae, Sloanbaataridae, Taeniolabididae, Deltatheroididae, Deltatheridiidae, Kennalestidae, and Zalambdalestidae) from the Djadokhta Formation (Mongolia) and 6 (Eucosmodontidae, Taeniolabididae, Deltatheridiidae, Asiatheriidae, family for Asioryctes, and Zalambdalestidae) from the Barun Goyot Formation (Mongolia).

The Alymtau fauna appears to be intermediate in composition between the late Turonian–Coniacian fauna of the Bissekty Formation and the Campanian faunas of Mongolia: it shares two families with the former and three families with faunas from both Mongolian formations. One family (?Otlestidae) was known previously from ?Aptian–Albian and Cenomanian deposits of Mongolia and Uzbekistan (Kielan-Jaworska & Dashzeveg 1989). Its possible presence in the Alymtau fauna is not of biostratigraphic importance. The presence of Zhelestidae in the Campanian of Kazakhstan and their absence in the Campanian of Mongolia may be due to climatic and environmental factors. The latest Santonian–latest early Campanian was the warmest period in the high latitudes of the Northern Hemisphere (Nessov & Golovneva 1990). This climatic event led to marked aridification in the continental landmass of ancient Asia, particularly in Mongolia (Jerzykiewicz et al. 1993). During the Campanian, the Kazakhstanian locality was situated at the sea coast and the aridification was not so strong there: the site has yielded remains of hydrophilous salamanders and hadrosaurs, which are absent or very rare in the Djadokhta and the Barun Goyot formations. This is why the zhelestids, the dominant group in the Bissekty Formation fauna, that lived there on the coastal plain under tropical or subtropical humid conditions (Nessov et al. in press), are present in the Campanian deposits in Kazakhstan, but could not live in Mongolia, or were extremely rare there. One can speculate that the zhelestids, that were able to live also on the humid coastal plains of North America, possibly migrated there via Beringia from Asia during the latest Santonian–early Campanian thermal maximum. The geologically oldest zhelestid from North America is Avitotherium utahensis from the mid-Campanian (Judithian) Kaiparowits Formation of Utah (Cifelli 1990). As was pointed out by Nessov et al. (in press), A. utahensis and Coniacian Aspanlestes aptap from Uzbekistan are almost indistinguishable. Early Campanian ?Aspanlestes sp. from the Alymtau fauna fills both geographical and geochronological gaps between these taxa. Its presence in the Alymtau fauna extends eastward the known Asian geographic distribution of the zhelestids. It also shows that they survived in Asia longer than hitherto known, which supports the conclusion of Nessov et al. (in press) that they reached North America during the latest Santonian–early Campanian warming. At the same time an American crocodile, Brachychampsa, and a theropod dinosaur, Troodon, migrated in the opposite direction to Asia and occur in the Alymtau fauna (Averianov & Nessov 1995; Nessov 1995). It is possible to predict from this scenario that zhelestids and other preungulates will not be found in America in deposits older than the latest Santonian. This hypothesis can be useful for biostratigraphy of continental deposits containing preungulate remains in America.
Two genera from the Alymtau fauna occur in the Djadokhta Formation: Bulganbaatar and Deltatheridium. From the known evidence, the Kazakhstani Bulganbaatar is very close to the Mongolian species. The Kazakhstani Deltatheridium possess more primitive characters than the Mongolian species. There is only one common genus (Deltatheridium) between faunas of the Alymtau and Barun Goyot formations. But this is not helpful in biochronological considerations, as this genus has a wide stratigraphic range.

The last Alymtau species, the zalambdalestid Alymlestes kielanae, although an endemic genus, is a close relative of the Mongolian zalambdalestids Zalambdalestes and Barunlestes. It shows somewhat more derived molar morphology than either Mongolian genus. This may be explained rather by the heterochrony in evolution between mammals that lived on wet coastal plains near the sea (Uzbekistan and Kazakhstan) and mammals that inhabited dry steppes and semideserts far away from the sea (Mongolia) (Nessov 1993), rather than by the younger geological age of the Alymtau fauna.

The Alymtau mammalian fauna is generally similar to both of the above Mongolian faunas. The presence of Bulganbaatar at Alymtau, which is not known from the Barun Goyot Formation, suggests that the Alymtau fauna may be better correlated with the fauna of the Djadokhta Formation, rather than with that of the Barun Goyot Formation. Gradziński et al. (1977) regarded the Djadokhta Formation tentatively as of ?late Santonian and/or ?early Campanian age. Fox (1978: fig. 1) placed it between the upper Milk River and Judith River plus Oldman Formations, and thus attributed to it the middle Campanian age. Lillegren & McKenna (1986: p. 58), however, stated: 'we concur with Fox (1978) that the Djadokhta of eastern Asia and the Judith River and Oldman faunas of North America are essentially of the same age and that, more indirectly, the Djadokhta Formation is therefore late Campanian or even early Maastrichtian in age.' The evidence from this paper, although inconclusive as the tentative correlation presented above is on the generic level, supports in part the conclusion of Gradziński et al. (1977) in suggesting a somewhat earlier, perhaps early Campanian age for the Djadokhta Formation.

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References


Новые позднемеловые млекопитающие южного Казахстана

АЛЕКСАНДР АВЕРЬЯНОВ

Резюме