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A number of typographical errors were introduced during copyediting. All that were found were corrected in this version.

Mammalian Faunal Succession in the Cretaceous of the Kyzylkum Desert

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Both metatherians and eutherians are known from the Early Cretaceous (Barremian, 125 mya; million years ago) of China, while eutherian-dominated mammalian faunas appeared in Asia at least by the earliest Late Cretaceous (Cenomanian, 95 mya). The approximately 99–93 my old (Cenomanian) Sheikhdzheili l.f. from western Uzbekistan is a small sample of only eutherians, including three zhelestids and a possible zalambdalestoid. The much better-known 90 my old (Turonian) Bissekty l.f. at Dzharakuduk iin central Uzbekistan includes 15 named and unnamed species, based on ongoing analyses. Of these, 12 are eutherians represented by at least the three groups—asioryctitheres, zalambdalestids, and zhelestids—plus an eutherian of uncertain position—*Paranyctoides*. Zalambdalestids and zhelestids have been argued to be related to the origin of the placental gliriforms (Euarchontoglires) and ferungulates (Laurasiatheria), respectively. Although there are four previously recognized metatherians, we believe three are referable to the deltatheroid *Sulestes karakshi* and the fourth, *Sailestes quadrans*, may belong to *Paranyctoides*. There is one multituberculate and one symmetrodont in the Bissekty l.f. While comparably aged (Turonian) localities in North America have somewhat similar non-therians, they have more metatherians and no eutherians. The next younger localities (early Campanian, ∼80 mya) in North America have both a zhelestid and *Paranyctoides*, suggesting dispersal of eutherians from Asia. At Dzharakuduk, the approximately 85 my old (late Turonian/Coniacian) Aitym l.f. is much less well known than the Bissekty l.f., but yields nearly identical taxa, with two non-therians, one metatherian, and six eutherians.

KEY WORDS: Mammalia, Theria, Eutheria, Metatheria, Cretaceous, Middle Asia, North America.

NOMENCLATURE

CCMGE	Chernyshev's Central Museum of Geological Exploration of Saint Petersburg, Russia
URBAC	Uzbekistan/Russian/British/American/Canadian joint paleontological expedition, Kyzylkum Desert, Uzbekistan, specimens currently held at San Diego State University, San Diego
ZIN C	Systematic Collections, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia
l.f.	Local fauna

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INTRODUCTION

During the Cretaceous, we see the appearance of taxa that underwent major radiations in the Tertiary (e.g., placental mammals and flowering plants), as well as taxa that reach their greatest ecologic diversity (e.g., non-avian dinosaurs). Among mammals, the earliest occurrences of the two great clades of therians, Metatheria and Eutheria, are some 125 mya (million years ago) from China (Ji *et al.*, 2002; Luo *et al.*, 2003). Taxonomic diversity remains relatively low throughout the Cretaceous, but quickly increases in the early Tertiary (Flynn and Wyss, 1998; Alroy, 1999; Archibald and Deutschman, 2001) with the appearance of extant clades of marsupials and placentals. Although far from complete, the fossil record indicates that by the early Late Cretaceous (Cenomanian–Turonian) that both metatherians and eutherians were undergoing what may have been their first radiations, the former in North America and the latter in Asia. Here we document our current knowledge of the mammalian radiation in Middle Asia, emphasizing the better-known faunas of Dzharakuduk, Uzbekistan, and then compare them to the similarly aged faunas of North America.

MATERIAL AND METHODS

The majority of mammals discussed in this paper that could at present be identified to at least the familial and, often the species level, are listed in Table I. This includes over 1000 dental, cranial, and postcranial remains recovered from 1978 through 2003 in the Bissekty Formation, Uzbekistan. Except for some dry screening by the crews of L. A. Nessov and the early expeditions of URBAC, before 1998, the recovery of most microvertebrates was done by methodical surface collecting. Beginning in 1998, URBAC began an extensive screenwashing program especially at the Dzharakuduk sites. From 1998 through 2003 (covering five field seasons) the URBAC crews dug, dry screened, wet screened, and sorted almost 145 metric tons of sediment. In addition to mammals, thousands of other small vertebrate remains were recovered. Discussions of the localities and faunas may be found in Nessov *et al.* (1998) and Archibald *et al.* (1998), while a discussion of the geology and ages of the faunas is found in King *et al.* (in press).

RESULTS

Faunal Succession in Middle Asia

Nessov laid the groundwork for what we currently know of Late Cretaceous vertebrate faunas (e.g., see Nessov *et al.*, 1998) of Middle Asia. We retain usage of this traditional regional name long used by Russian geographers to distinguish it from Central Asia (mostly western China and Mongolia). It is similar in extent to what English-speaking travelers referred to as Turkistan (Schuyler, 1876, although he also used Central Asia for the combined regions) and the Turkestan General Government of Russian Empire of the late 19th and early 20th centuries. In actuality Middle Asia is located more in the southwestern portion of Asia. It approximately extends 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. It essentially encompasses the newly independent countries of Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan. Most of our knowledge of this faunal succession comes from two areas in Uzbekistan (Fig. 1).

Table I. Preliminary List of Uzbekistan Mammaliaforms[a]

	Sheikhdzheili l.f.	Bissekty l.f.	Aitym l.f.
Taxon			
Symmetrodonta			
Spalacotheriidae			
Shalbaatar bakht		1	
cf. *Shalbaatar* sp.			1
Allotheria			
Cimolodonta			
Uzbekbaatar wardi			4
U. kizylkumensis		8	
Metatheria			
Deltatheroida			
Deltatheridiidae			
Sulestes karakshi			
(incls. *Deltatheus kizylkumensis*		30	
& in part *Marsasia aneigma*)			
Deltatheridiidae indet. A			1
Eutheria			
Asioryctitheria			
"*Daulestes*" *nessovi*		5	
D. kulbeckensis		21	
(incls. *Kumlestes olzha*, *D. nessovi*,			
& *Kennalestes*(?) *uzbekistanensis*)			
D. inobservabilis		18	
Bulaklestes kezbe		32	
Placentalia			
Euarchontoglires			
"Zalambdalestoidea"			
Bobolestes zenge			
(in part incl. *Otlestes meiman*)	6		
"Zalambdalestidae"			
Kulbeckia kulbecke		74	
Kulbeckia new smaller sp.		3	
Kulbeckia sp. cf. *K. kulbecke*& aff. *Kulbeckia* sp.			3
Kulbeckia petrosals		23	
"Zalambdalestidae" petrosal	1		
Laurasiatheria			
"Zhelestidae"			
Sheikhdzheilia rezvyii		7	
(in part incl. *Otlestes meiman*)	3		
Eozhelestes mangit	10		
Aspanlestes aptap		54	
cf. *Aspanlestes* sp.			6
Zhelestes temirkazyk		27	
(incls. *Sorlestes budan*)			
Zhelestes sp. aff. *Z. temirkayzk*			1
Parazhelestes mynbulakensis		75	
(incls. *P. minor*)			
Parazhelestes robustus		51	
(incls. *Eoungulatun kudukensis* possibly			
= *Kumsuperus avus*)			
Parazhelestes sp. cf. *P. robustus*			4
"Zhelestidae"			
edentulous dentaries		126	
"Zhelestidae" petrosals		12	
"Zhelestidae" indet.		1	
(possibly incls. *Oxlestes grandis*)	3		

Table I. Continued

	Sheikhdzheili l.f.	Bissekty l.f.	Aitym l.f.
Eutheria *incertae sedis*			
Paranyctoides aralensis (in part incls. *Marsasia aneigma* & possibly *Sailestes quadrans*)		20	
Paranyctoides sp. cf. *P. aralensis* & *Paranyctoides* sp.			6
Edentulous maxillae		3	
Skull? fragments		7	
Theria indet.			
Canines		28	
Tooth fragments	1	21	
Petrosals		7	
Mammalia indet.			
Postcrania		362	
Total	24	1016	26

[a] Mammaliaform fossils from the Sheikhdzheili, Bissekty, and Aitym local faunas, Kyzylkum Desert, Uzbekistan collected through 2003.

The Sheikhdzheili Local Fauna

The first of these includes the Khodzhakul and Sheikhdzheili localities, from the Khodzhakul Formation in the southwest Kyzylkum region of western Uzbekistan near the western shore of the Amu Darya (river), some 50 km south of the city of Nukus. We refer the fossils from these localities to the Sheikhdzheili l.f. named for the ridge to the south of

Fig. 1. Map of Uzbekistan showing locations of Sheikhdzheili (S), and Dzharakuduk (D) (Bissekty and Aitym l.f.).

these localities. Nessov believed these localities ranged in age from latest Early to earliest Late Cretaceous (late Albian to early Cenomanian). A reworked, early placenticeratid ammonite from the base of the Khodzhakul Formation suggests an early Cenomanian age, while an inoceramid bivalve from just above the Khodzhakul Formation suggests a late Cenomanian age, thus providing the Cenomanian age for the Khodzhakul Formation (D. Ward and N. Morris, personal communication, 2004).

Table I lists the mammalian taxa recognized by Nessov (e.g., 1997) for what we term the Sheikhdzheili l.f. These are greatly modified by Averianov and Archibald (2005), and the following comments about the Sheikhdzheili l.f. taxa are from this paper. Of these taxa, *Bobolestes*, *Eozhelestes*, and *Sheikhdzheilia* are represented by dental remains. *Bobolestes* is at present represented by the type, which is a maxilla with M2-3 and alveolus for M1 (Figs. 2K and 3H) possibly three edentulous remains, and two dentaries referred previously to *Otlestes* by Nessov, including the holotype of *O. meiman*, a dentary with p4-5, m1-3, and alveoli for more anterior teeth. These dental remains, as well as a petrosal of a distinctly larger animal, show affinities with the oldest zalambdalestid, *Kulbeckia*, from the slightly younger Bissekty l.f., hence the referral of *Bobolestes* to "Zalambdalestoidea" (Averianov and Archibald, 2005). *Eozhelestes* is represented by 10 specimens, mostly edentulous dentaries that possess combined features found only in zhelestids. The type, a single lower molar, while retaining some ancestral traits, is similar to the slightly larger and younger *Aspanlestes*. *Sheikhdzheilia* is based on a lower dentary with p5 m1 and half of m2 discovered in 2003, appears to be a zhelestid smaller than *Eozhelestes* (Averianov and Archibald, 2005). A maxilla with M1-2 (Figs. 2J and 2I), referred previously to *Otlestes*, belongs to this taxon. A second cervical vertebra named *Oxlestes* by Nessov (1982) may belong to a large, unnamed zhelestid represented by two edentulous dentaries. Fused parietals referred to *Oxlestes* by Nessov (1993) may belong to this taxon as well (Averianov and Archibald, 2005).

The Sheikhdzheili l.f. is not adequately known, thus the real taxonomic diversity is surely greater. It is interesting that all mammal specimens recovered so far from the Sheikhdzheili l.f. are referable to Eutheria, while other groups such as multituberculates, symmetrodonts, and metatherians have not been found. Although poorly known, it is literally the oldest eutherian dominated fauna in the world.

Local Faunas at Dzharakuduk

The second region in Uzbekistan that samples Late Cretaceous mammalian faunal succession is in the central Kyzylkum Desert some 200 km east of Khodzhakul-Sheikhdzheili. This sequence appears to include rocks of a similar earliest Late Cretaceous (Cenomanian) age based on both turtles and dinosaurs, but mammals have not been recovered yet from this portion of the sequence.

It is in what is now called the Bissekty Formation (King *et al.*, in press) that a taxonomically rich mammalian fauna has been recovered. Based on extensive sampling of marine faunas above and below the Bissekty, the age of the Bissekty l.f. is well constrained to the Turonian.

There are some 15 mammal-producing localities in the fluvially deposited Bissekty Member, but the most productive four sites are: CDZH-17a, CBI-4, CBI-14, and CBI-5. There is up to 70 m separating the lowest from the highest locality; however, no definite

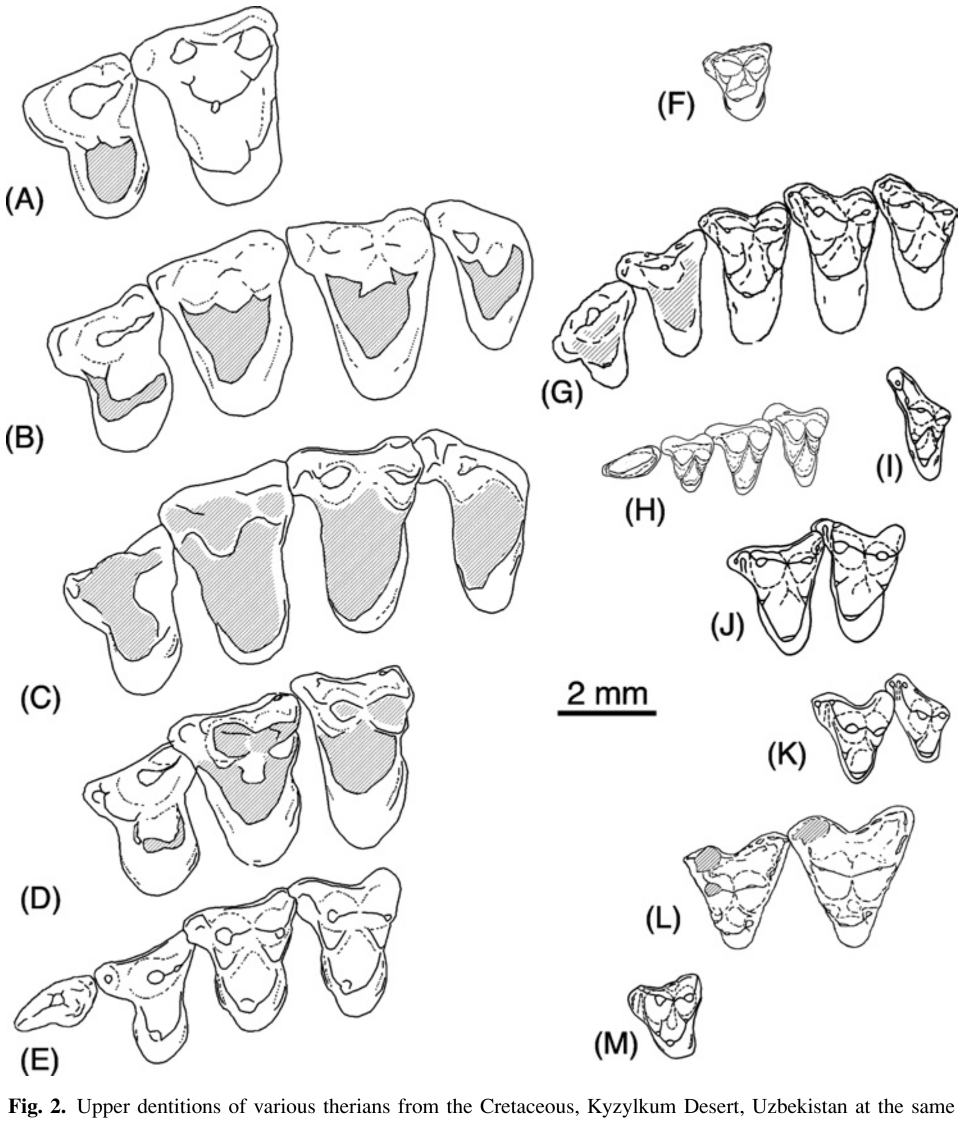

Fig. 2. Upper dentitions of various therians from the Cretaceous, Kyzylkum Desert, Uzbekistan at the same scale to emphasize size diversity. (A) *Parazhelestes robustus* (= *Eoungulatum kudukensis*), isolated P5 (CCMGE 35/12176) and M1 (identified as M2 by Nessov *et al.*, 1998, CCMGE 2/12455). (B) *P. robustus* maxilla with P5-M3 (CCMGE 70/12455). (C) *Zhelestes temirkazyk* maxilla with P5-M3 (CCMGE 10/12176). (D) *Parazhelestes mynbulakensis* (= *Parazhelestes minor*) maxilla with P5-M2 (CCMGE 11/12176). (E) *Aspanlestes aptap* maxilla with P4-M2 (CCMGE 1/12455). (F) *Paranyctoides* sp. M1 (ZIN C.85293). (G) *Kulbeckia kulbecke* based on partial skull including P4-5 (URBAC 99-53) and isolated M1-3 (CCMGE52/12455, ZIN C.82565, CCMGE54/12455, respectively). (H) "*Daulestes*" *nessovi* P4, DP5, M1-2 (ZIN C.79066). (I) *Bulaklestes kezbe* M3 (CCMGE 35/12000). (J) *Sheikhdzheilia rezvyii* (identified as *Otlestes meiman* by Nessov, 1985a), maxilla with M1-2 (CCMGE 8/12176). (K) *Bobolestes zenge* maxilla with M2-3 (CCMGE 2/12176). (L) *Sulestes karakshi* maxilla with M2-3 (35/12000). (M) *Sailestes quadrans* (most likely belongs in *Paranyctoides aralensis*) M1 (CCMGE 7/117548). All specimens have been oriented as if from upper left dentition. Shaded areas are heavily worn or damaged areas. For the zhelestids showing such wear, most tooth sites are known by less worn isolated teeth. (A)–(E) modified after Nessov *et al.* (1998).

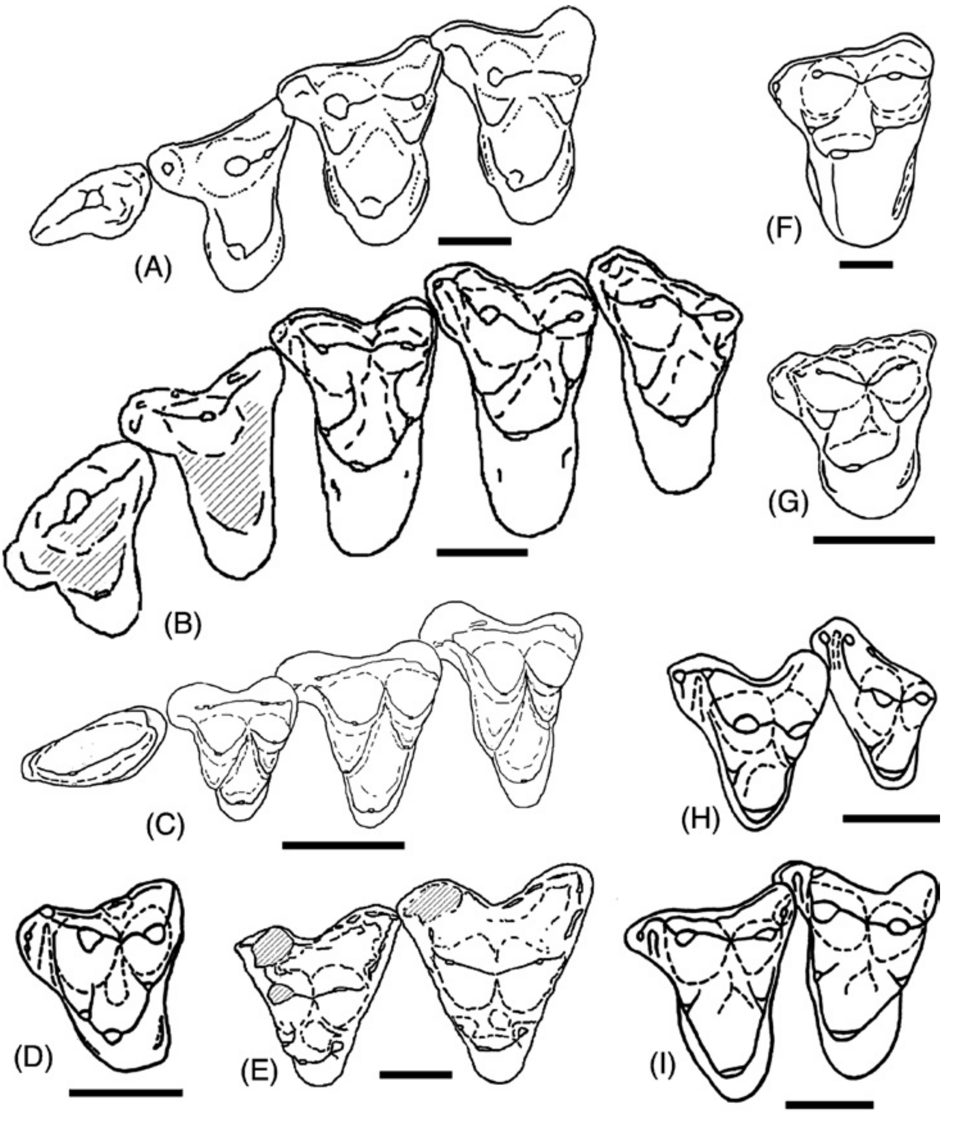

Fig. 3. Upper dentitions of various therians from the Cretaceous, Kyzylkum Desert, Uzbekistan standardized using M1 and M2 length to permit comparisons of mostly unworn teeth. (A) *Aspanlestes aptap* maxilla with P4-M2 (CCMGE 1/12455). (B) *Kulbeckia kulbecke* based on partial skull including P4-5 (URBAC 99-53) and isolated M1-3 (CCMGE52/12455, ZINC.82565, CCMGE54/12455, respectively). (C) "*Daulestes*" *nessovi* P4, DP5, M1-2 (ZIN C.79066). (D) *Sailestes quadrans* (most likely belongs in *Paranyctoides aralensis*) M1 (CCMGE 7/117548). (E) *Sulestes karakshi* maxilla with M2-3 (CCMGE 35/12000). (F) *Parazhelestes robustus* M1 (CCMGE 20/12953). (G) *Paranyctoides* sp. M1 (ZIN C.85293). (H) *Bobolestes zenge* maxilla with M2-3 (CCMGE 2/12176). (I) *Sheikhdzheilia rezvyii* (identified as *Otlestes meiman* by Nessov, 1985a), maxilla with M1-2 (CCMGE 8/12176). All specimens have been oriented as if from upper left dentition. Shaded areas are heavily worn or damaged areas. Scale bar equals one millimeter. (A) modified after Nessov *et al*. (1998).

faunal differences have been detected among the mammals. As noted, these localities are collectively termed the Bissekty l.f. As Table I shows, this includes one spalacotheriid, one multituberculate, one metatherian, and 12 eutherians. While both non-therians and metatherians are quite rare, the Bissekty l.f. is unarguably the taxonomically richest eutherian fauna known for the Cretaceous. The following taxonomic synopsis includes specimens collected through the 2003 field season.

A less rich fauna comes from the Aitym Formation (Averianov and Archibald, 2003). This rock unit is now regarded to be late Turonian to Coniacian in age (King *et al*., in press).

The Bissekty Local Fauna

Allotheria and Symmetrodonta

These mammals are represented by two genera in the Dzharakuduk local faunas, the spalacotheriid symmetrodont, *Shalbaatar*, and the multituberculate, *Uzbekbaatar*. Both taxa are components of the Bissekty l.f. *Shalbaatar* (Nessov, 1997), is monotypic and is based on one edentulous partial right dentary (ZIN C.82622) fragment. As suggested by the suffix of the generic name 'baatar,' meaning hero in Mongolian, which is frequently used for Asian multituberculates, *Shalbaatar* was originally thought to be a multituberculate (Nessov, 1997). On further study by the second author, it was found that *Shalbaatar* shares a number of characters (Averianov and Archibald, 2003) with spalacotheriid (or, even, spalacolestine: Cifelli and Madsen, 1999) symmetrodonts. Among these characters, two are especially noteworthy: The molars are less than 1 mm in length and the molar roots are anteroposteriorly short and transversely wide. A second dentary fragment tentatively referable to *Shalbaatar* was recovered from the Aitym l.f. (Averianov and Archibald, 2003).

Multituberculates are richer than spalacotheriids in the Bissekty and Aitym local faunas, but are nevertheless rare. *Uzbekbaatar kizylkumensis* was named for material from the Bissekty Member. Although referred to Cimolodonta *incertae sedis*, possible affinities to either "Taeniolabidoidea" or Ptilodontoidea were also noted (Kielan-Jaworowska and Nessov, 1992). Remains referable to *U. kizylkumensis* include the holotype p4, a completely enamel-covered lower incisor, three edentulous dentaries, an edentulous maxilla, and several postcranial elements. A second species, *Uzbekbaatar wardi*, was named from the Aitym l.f. (Averianov, 1999) and is now based on four isolated teeth (Averianov and Archibald, 2003). Together, this limited sample suggests affinities with the informal '*Paracimexomys* group' recently reviewed by Eaton and Cifelli (2001). This includes the more basal cimolodont taxa *Paracimexomys*, *Bryceomys*, and *Cedaromys*; these, like *Uzbekbaatar*, have robust, asymmetric molar cusps.

Metatheria

Three metatherians were named from the Bissekty l.f., *Sulestes karakshi* (Nessov, 1985b) and *Deltatherus kizylkumensis* (Nessov, 1993, originally referred to *Deltatheroides*) referred to Deltatheridiidae, and *Marsasia aenigma* (Nessov, 1997; Averianov and Kielan-Jaworowska, 1999) referred to Asiadelphia. These three taxa are now represented by 30 dental, maxillary, and dentary remains, eight of which were recovered in the 2002 and 2003 seasons. With this considerable increase in the sample size of the latter three metatherians and a review of the material now underway by the authors, it appears that these three taxa are best treated as a single species, *S. karakshi*, with *D. kizylkumensis* and *M. aenigma* treated as synonyms.

Eutheria

With 12 species of eutherians, the Bissekty l.f. is unarguably the taxonomically richest Cretaceous eutherian fauna in the world. There are at least the three clades—asioryctitheres, zalambdalestids, and zhelestids—plus an eutherian of uncertain position—*Paranyctoides*. At 90 mya, it is also one of the oldest eutherian-dominated mammalian faunas. Not until near the end of the Cretaceous some 65 mya in North America do we see faunas with six or seven eutherians in sites from North America (Lillegraven, 1969; Archibald, 1982). There are some interesting implications for this richness of eutherians at 90 mya in Middle Asia. These are discussed following a synopsis of the eutherian taxa in the Bissekty l.f.

The smallest of the eutherians in this local fauna appear to be most like the asioryctitheres of the Late Cretaceous (Campanian) of Mongolia—*Asioryctes*, *Ukhaatherium*, and *Kennalestes* (Kielan-Jaworowska, 1981; Novacek *et al*., 1997; McKenna *et al*., 2000). These taxa include four species that we here refer to *Daulestes* and *Bulaklestes* (Figs. 2H, I and 3C). Size groupings are at present the main differences among these taxa. McKenna *et al*. (2000) described a nearly complete skull of a mammal from the Bissekty l.f., which they named *Daulestes nessovi*. With over 75 specimens now referable to *Daulestes*, we have far more specimens than were available to McKenna *et al*. (2000). (Figs. 2H, 3C, and 4A). In what is almost certainly a combination of ancestral and derived characters these Mongolian and Uzbek taxa share a moderately wide stylar shelf, anteroposteriorly narrow protocone, little or no lingual cingula, tall trigon and trigonid cusps, small talonid, and an emphasis on shearing surfaces.

The next clade, "Zalambdalestidae" is not taxonomically diverse. There is one currently recognized species, *Kulbeckia kulbecke*, and almost certainly a second, new species also referable to *Kulbeckia*. *Kulbeckia* is the single most abundant mammal in the Bissekty l.f. comprising 96 specimens (Table I) including two partial skulls, 22 isolated petrosals, as well as 72 dental remains (Figs. 2G, 3B, and 4B). Until recently, *Kulbeckia* could be regarded as the most basal and oldest member of the "Zalambdalestidae," which is best known by *Zalambdalestes* from 15 million years later in Mongolia (Wible *et al*., 2004). As described earlier, the approximately 95 million year old (porobably early Cenomanian)

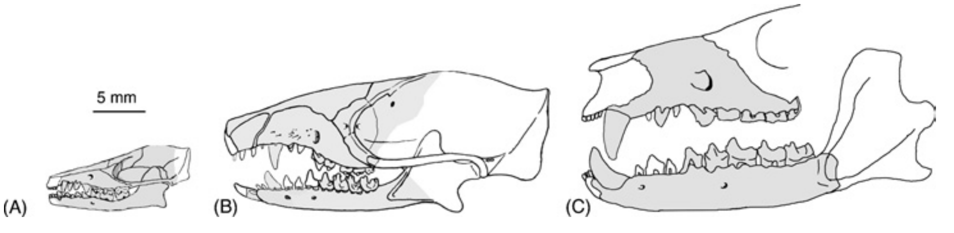

Fig. 4. Reconstructions of three eutherians from the Bissekty l.f. (A) "*Daulestes*" *nessovi* is based on a skull (ZIN C.79066) described by McKenna *et al*. (2000). (B) *Kulbeckia kulbecke* is based on various specimens described by Archibald and Averianov (2003) and a partial skull discovered in 2003. (C) Composite zhelestid skull based mostly on material identified as *Zhelestes temirkazyk*, most of which was described by Nessov *et al*. (1998). Shaded areas are those parts of the skull known by one or more specimens.

Sheikhdzheili l.f., has yielded a petrosal showing affinities with the *Kulbeckia* (Averianov and Archibald, 2005). Parts of the rather specialized postcrania have also been identified for *Kulbeckia* from the Bissekty l.f. (Szalay *et al*., 2003). Although retaining some ancestral features, such as the retention of more premolars, *Kulbeckia* already shows derived zalambdalestid dental features: An enlarged central incisor with enamel restricted to the labial surface, smaller canine, and diastemata between premolars. Archibald *et al*. (2001) found zalambdalestids to nest with basal gliriforms (Euarchontoglires) rather than with other Cretaceous eutherians, thus placing them within the crown taxon Placentalia. This result has been disputed in another analysis (Meng *et al*., 2003).

"Zhelestidae" may be the taxonomically richest clade in the Bissekty l.f. They are known from 227 specimens, most of which are dental remains (Table I). At least 12 isolated petrosals have also been identified. They retain several ancestral therian(?) traits such as the presence of a petrosal sinus and a low stapedial length-to-width ratio, both of which are retained in extant marsupials (Ekdale *et al*., 2004). Going from approximately smallest to largest, we currently recognize five taxa—a new genus and species, *Aspanlestes aptap*, *Parazhelestes mynbulakensis*, *Zhelestes temirkazyk*, and *Parazhelestes robustus* (Figs. 2A–E, 3A, F, and 4C). Until recently, only *A. aptap* could be identified confidently based on both upper and lower dentitions. With the recovery of much additional material by URBAC crews, we can now confidently assign both upper and lower dentitions to all five taxa based on criteria of size and morphology (Archibald and Averianov, in preparation).

In comparison to most other Cretaceous eutherians, zhelestids have de-emphasized shearing and increased the grinding and crushing function of the cheek teeth. Thus, these teeth are lower crowned, individual cusps are more bulbous, the trigonid is lowered relative to the talonid, and the upper molars have narrow lingual cingula. Phylogenetic analyses consistently place zhelestids either with archaic ungulates within Placentalia (Archibald, 1996; Archibald *et al*., 2001; Luo *et al*., 2003) or as sister to the crown taxon Placentalia (Ji *et al*., 2002).

The final taxa in the Bissekty l.f. are *Paranyctoides aralensis* (Figs. 2F and 3G) and *Sailestes quadrans* (Figs. 2M and 3D). The affinities of *Paranyctoides* are uncertain beyond placement within Eutheria *incertae sedis*. Archibald and Averianov (2001) compared *P. aralensis* to congeneric taxa as well as the taxon *Gallolestes* known from the Campanian of North America. In various phylogenetic analyses (e.g., Archibald *et al*., 2001), *Paranyctoides* is the sister taxon to zhelestids. Both share the general lowering of molar cusps and the trigonid relative to the talonid. *S. quadrans* (Nessov, 1982) is represented by a single M1. In their discussion of the eutherian *Paranyctoides*, Archibald and Averianov (2001) noted that this M1 might be an upper molar of *P. aralensis*, but as well might be a molar of a metatherian. While still possible, with the referral of all other metatherian material to the deltatheroid *Sulestes karashi*, which is known by upper molars, *Sailestes* once again seems more likely to be an upper molar of *Paranyctoides*. Also, a dentary fragment with worn last molar (ZIN C83131), identified by Averianov and Kielan-Jaworowska (1999) as *Marsasia* sp., is attributable to *Paranyctoides*.

The Aitym Local Fauna

The single locality that represents the Aitym l.f., CBI-117, occurs about 30 m above the Bissekty l.f. localities within the Aitym Formation; its age could be late Turonian or Coniacian (Averianov and Archibald, 2003). The mammalian fauna is very similar in composition to that of the Bissekty l.f. Both faunas include the spalacotheriid *Shalbaatar* and the multituberculate *Uzbekbaatar*, although separate species of *Uzbekbaatar* are recognized from the two faunas (Table I). A fragment of an M2? (ZIN C.85049) from the Aitym l.f. that was tentatively referred to *Deltatherus* by Averianov and Archibald (2003) should be treated as Deltatheridiidae indet. Among eutherians, the upper molar fragment (ZIN C.85296) identified as aff. *Daulestes* by these authors is best treated as belonging to *Paranyctoides*, along with five other specimens. An upper tooth that had been identified by these authors as M1 (ZIN C.85293) of *Paranyctoides* is a dP5 of a small zhelestid. The following eutherian taxa (or closely related taxa) appear to be present in the Aitym l.f.—*Kulbeckia kulbecke*, *Aspanlestes aptap*, *Zhelestes temirkayzk*, *Parazhelestes robustus*, and *Paranyctoides aralensis* (Table I).

DISCUSSION

Faunal and Biogeographic Comparisons

The only other mammal-bearing localities in the world that are comparable in age to the Turonian-Coniacian sites at Dzharakuduk are the two localities from the Smoky Hollow Member of the Straight Cliffs Formation, southern Utah. From these two localities as many as seven multituberculates, two symmetrodonts, one therian of uncertain affinities, and five metatherians have been described (Cifelli, 1990a; Eaton, 1995). The local fauna from the Smoky Hollow Member is similar to the Bissekty l.f. in numbers of taxa, but the faunal composition of the two are very different. Nevertheless, several comparisons are noteworthy.

While Eaton (1995) recognized seven different multituberculate morphs that might represent as many taxa in the local fauna from the Smoky Hollow Member, the Bissekty l.f. has only one species known, and this is very rare. As noted earlier, *Uzbekbaatar* from Dzharakuduk is quite similar to the more basal cimolodontan taxa *Paracimexomys*, *Bryceomys*, and *Cedaromys* known as early as the Early Cretaceous/Late Cretaceous boundary in North America (Eaton and Cifelli, 2001). *Paracimexomys* was reported with some reservation from the late Early Cretaceous (Albian) of Texas (Krause *et al.*, 1990), and definitely from the late Early Cretaceous (Aptian-Albian) of Oklahoma (Cifelli, 1997). This quite basal grade of multituberculates is known by the Albian in North America, but only by the Turonian in Asia. Although it is not possible to suggest with any certainty where these multituberculates originated, their possible affinities with the Mongolian Eobaataridae (Eaton and Cifelli, 2001) hints at an Asiatic origin.

Spalacotheriids are first known from the Berriasian of the UK and are well represented in Aptian-Albian (Cloverly and Antlers fms.) and Albian-Cenomanian (Cedar Mountain Fm.) of NA. Recent finds in the Early Cretaceous of Japan (Tsubamoto *et al.*, 2004) indicate that spalacotheriids were widely spread by the Early Cretaceous.

Both local faunas have metatherians, with the Bissekty l.f. being much less diverse. In the local fauna from the Smoky Hollow Member there are three metatherians (Cifelli, 1990a), probably stem marsupials (?*Anchistodelphys*, *Alphadon*, and *Protalphadon*) that provide an inkling of the greater diversity of this clade that comes later in the Late Cretaceous of North America. Greater metatherian diversity actually occurs even earlier in North America, as five taxa are known from the Cenomanian aged Dakota Fm. (Eaton, 1993).

Metatherians are also found in the earlier Albian–Cenomanian sites in North America (Cifelli, 1993; Cifelli and Muizon, 1997), while (as with the multituberculates and splacotheriids) there are no comparably sampled localities of this age from Asia that yield a diversity of metatherians. As discussed earlier, there is only one metatherian now recognized in the Bissekty l.f., the deltatheroid, *Sulestes*.

It is only among the eutherians that we find enough information to suggest biogeographic patterns between North America and Asia. Of particular note is the lack of eutherians from the Smoky Hollow localities. This might be a result of sampling, but no eutherians of a comparable age or earlier are known from North America with the notable exception of the Aptian-Albian *Montanalestes* from Montana, which Averianov (in preparation) believes may not be a eutherian. In the same faunal sequence as the local fauna from the Smoky Hollow Member of southern Utah, but in the slightly higher Wahweap Fm., the eutherian *Paranyctoides* sp. occurs at sites of early Campanian age (Cifelli, 1990a,b). Fox (1984) recognized *Paranyctoides maleficus* from the Milk River Fm. of Canada, also thought to be early Campanian in age. Until *Montanalestes* was described, these were the oldest eutherian occurrences in North America. The Turonian sites at Dzharakuduk already have 12 species of eutherians representing three major groups—asioryctitheres, zalambdalestids, and zhelestids, plus the eutherian of uncertain affinities, *Paranyctoides*. By the mid-Campanian in North America, both zhelestids (*Avitotherium*) and *Paranyctoides* are known. Zalambdalestids have never been recovered from North America, but some asioryctitheres have been thought to be related to the cimolestids of North America, which are common by the Maastrichtian (Clemens *et al.*, 1979). This biogeographic and temporal pattern suggests that there were at least two and possibly three eutherian dispersal events from Asia to North America between the Turonian and early Campanian.

The recent identifications of both the earliest eutherian and metatherian from 125 my old beds in China (Ji *et al.*, 2002; Luo *et al.*, 2003) point to the origin of these two major therian clades in Asia. Given the time gap between these and the later known faunas from about 100 to 90 mya in both Asia and North America, one can say little of the intervening biogeographic and evolutionary history of eutherians and metatherians. By at least 90 mya, and possibly as early as 100 mya the first known radiations of eutherians in Asia and metatherians in North America were underway.

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