Late Cretaceous asioryctitherian eutherian mammals from Uzbekistan and phylogenetic analysis of Asioryctitheria

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Archibald, J.D. and Averianov, A.O. 2006. Late Cretaceous asioryctitherian eutherian mammals from Uzbekistan and phylogenetic analysis of Asioryctitheria. *Acta Palaeontologica Polonica* 51 (2): 351–376.

Four small asioryctitheres at Dzharakuduk (Turonian), Uzbekistan are *Daulestes kulbeckensis* (= *Kumlestes olzha*), *D. inobservabilis* (= *Kennalestes*? *uzbekistanensis*), *Uchkudukodon* (gen. nov.) *nessovi* and *Bulaklestes kezbe*. *Uchkudukodon nessovi* is one of the smallest therians (molars about 1 mm long). Lower canine is two-rooted in *Uchkudukodon* gen. nov. and *Bulaklestes* (uncertain in *Daulestes*). All lower premolars in all four species are double-rooted. Teeth identified as dp1, p2 and dp2 in holotype of *Uchkudukodon nessovi* (McKenna et al. 2000) are here identified c, p1, and p2. A phylogenetic analysis weakly supported Asioryctitheria by four synapomorphies: conular basins become distinct, the number of roots reverts to two on the lower canine, the p5 becomes longer than p4, and the metaconid on p5 is reduced and lost. Other characters diagnostic of asioryctitheres are four upper and lower premolars (arguably five upper premolars in juvenile *Kennalestes*), P4 has a protocone swelling or protocone, some asymmetry of the stylar shelf on M1–2, the paraconule on M1–3 is distinctly closer to the protocone than is the metaconule, protocone is of moderate height on M1–3 (70–80% of paracone or metacone height), Meckel's groove is absent, and the mandibular foramen opens into a smaller depression on lingual side of mandibular ascending ramus. *Asioryctes* and *Ukhaatherium* are placed in Asioryctinae and along with *Kennalestes* are placed in Asioryctidae. Kennalestidae Kielan-Jaworowska, 1981 is a junior subjective synonym for Asioryctidae Kielan-Jaworowska, 1981. Because of uncertainties in the analysis, the positions of *Daulestes, Uchkudukodon* gen. nov., and *Bulaklestes* cannot be determined beyond referral to Asioryctitheria.

Key words: Mammalia, Eutheria, Asioryctitheria, *Daulestes*, *Bulaklestes*, *Uchkudukodon*, Cretaceous, Dharakuduk, Uzbekistan.

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Introduction

Daulestes kulbeckensis, based on a right dentary with the alveoli or teeth for the canine through m1 (see later discussion) was the first mammal described from the collections that Lev Nessov made at Dzharakuduk, Uzbekistan (Nessov and Trofimov 1979). It was only the second Cretaceous mammal described from the Soviet Union. The first was the poorly preserved *Beleutinus orlovi* from Kazakhstan (Bazhanov 1972). *Daulestes* and the closely related *Uchkudukodon* gen. nov. are also the smallest mammals from Dzharakuduk. *Uchkudukodon* gen. nov. is the smallest Mesozoic eutherian, and also one of the smallest known therian mammals, living or fossil, with molars of the smallest specimens about 1mm in length.

When first described, *D. kulbeckensis* (see Nessov and Trofimov 1979) was referred to Eutheria, Insectivora, Leptictoidea, Zalambdalestidae. Later it was suggested that it might belong to Palaeoryctidae rather than Zalambdalestidae (Nessov 1982). Subsequently, Nessov (1984, 1987; Nessov et al. 1994) placed *Daulestes* unquestionably in Palaeoryctidae. McKenna et al. (2000) listed the genus as Eutheria, ?Asioryctitheria, family *incertae sedis*.

In 1985 Nessov described *Bulaklestes kezbe*, based on a single M3 from Dzharakuduk. *Bulaklestes* was originally described as Proteutheria *incertae sedis* (Nessov 1985) and subsequently classified as Palaeoryctoidea (Nessov 1987), a possible kennalestid (Nessov et al. 1994), or Placentalia *incertae sedis* (McKenna and Bell 1997).

In 2000 McKenna et al. described the then oldest interpretable eutherian skull, an exquisitely preserved and expertly prepared (by W. Amaral and the authors) specimen from Dzharakuduk that had been discovered by V. Trikhin, a member of Nessov's 1989 expedition. These authors described this as a new, smaller species of *Daulestes*, *D. nessovi*.

Through the 1980s and early 1990s, before his death in 1995, Nessov described a variety of eutherians from Dzharakuduk and elsewhere. We were able to compare all of Nessov's collections as well as material collected by the URBAC (Uzbekistan, Russia, Britain, America, Canada) expeditions of 1997–2004. The exceptions were parts of the fine of the concentrate (1–2 mm) of the 1999–2002 and 2004 expeditions. The intent in this paper is to compare all available material of *Daulestes*, *Uchkudukodon* gen. nov., and *Bulaklestes* as of 2004 and include taxa named by Nessov that appear to be related. Other Dzharakuduk taxa are mentioned only as they further the discussion of the included taxa.

Thorough, recent discussions of Dzharakuduk, its localities, and its geologic setting may be found in Nessov et al. (1998), Archibald et al. (1998), Archibald and Averianov (2005), and King et al. (in press). Suffice it to note here that all localities examined by the URBAC expeditions indicate that mammal-producing sites in the Bissekty Formation are in a fluvial setting (King in Archibald et al. 1998; King et al. in press), but were probably very near the coast as suggested by otherwise marine sharks (Averianov and Ward in Archibald et al. 1998). At present, the best estimate we have for the middle–late Turonian age of these sites is based on an analysis of bracketing marine faunas (King et al. in press). Earlier these sites were thought to be late Turonian–Coniacian in age (e.g., Nessov 1997; Nessov et al. 1998). Although the sites occur at several levels in the Bissekty Formation, at this time we cannot detect any definite differences in the mammalian faunas. Thus, although locality information is provided, we treat the mammals from these sites as coeval in age and as part of the Bissekty local fauna.

Dental and geographic terminology.—We use the dental terminology in Nessov et al. (1998: fig. 1). Measurements were taken according to the method illustrated by Archibald (1982: fig. 1). Premolars are identified as upper or lower 1, 2, 4, and 5, based on information that position 3 is lost in early eutherians (Clemens 1973; Novacek 1986; Sigogneau-Russell et al. 1992; Archibald 1996; Archibald and Averianov 1997, 1998; Nessov et al. 1998). Premolars 4 and 5 correspond to numbers 3 and 4 in most other traditional descriptions of extant placentals. Other numbering schemes have been proposed such as Clemens (1973), who numbered the premolars a, b, c, 3, and 4 in *Gypsonictops hypoconus* and suggested that a = 1 and b = 2 of traditional descriptions. Premolar c would be lost. Cifelli (2000) favored calling the third site "x". Based on our unpublished observations, mostly from zhelestids, we feel that five premolar sites can be demonstrated at least in the lower dentition, but we do not know if all five sites had two generations. Given this we favor either Clemens' or our scheme as they both recognize the presence ancestrally of five premolar sites in eutherians. It has been be argued (Cifelli 2000) that such schemes could cause some confusion for extant placental premolar designations, which usually have only four premolars. The number of incisors and premolars are frequently and repeatedly further reduced in extant placentals making assessments of the homologies of teeth across the various extant placental clades nearly impossible. Accordingly, we feel comfortable in using the 1 through 5 designations for premolars in Mesozoic eutherians.

Teeth were projected on a computer screen using a video camera mounted on a binocular microscope and measured to the nearest 0.01 mm using NIH Image 1.61 software. Teeth were photographed with a Nikon CoolPix 4500 digital camera mounted on a Meiji binocular microscope. Specimens were placed on a "tilt table" to produce stereopairs.

We use the term "Middle Asia" as a region commonly and long used by Soviet geographers much as in the same way terms such as the Great Plains are used in North America. Middle Asia is in fact located more in the southwestern portion of Asia. Middle Asia 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.

Institutional abbreviations.—CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg; URBAC, Uzbek/Russian/British/American/Canadian Joint Paleontological Expedition specimens currently in San Diego State University, San Diego; ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Locality abbreviations.—CBI, central Bissekty and CDZH, central Dzharakuduk.

Systematic paleontology

Mammalia Linnaeus, 1758

Eutheria Gill, 1872

Asioryctitheria Novacek, Rougier, Wible, McKenna, Dashzeveg, and Horovitz, 1997.

Daulestes Trofimov and Nessov, 1979, in Nessov and Trofimov 1979

= *Taslestes* Nessov, 1982

= *Kumlestes* Nessov, 1985

Type species: *Daulestes kulbeckensis* Trofimov and Nessov, 1979, in Nessov and Trofimov 1979.

Included species: Type species and *D. inobservabilis* (Nessov, 1982).

Definition.—The last common ancestor of *Daulestes kulbeckensis* and *D. inobservabilis*, plus all of its descendants.

Distribution.—Uzbekistan; Late Cretaceous, Turonian.

Revised diagnosis.—Similar to *Asioryctes*, *Ukhaatherium*, and *Uchkudukodon* gen. nov., and differing from *Kennalestes* in having P2 smaller than P1 (possible ancestral character, unknown for *Bulaklestes*). Similar to *Bulaklestes* and *Uchkudukodon* gen. nov., and differing from *Kennalestes*, *Asioryctes*, and *Ukhaatherium* in P4 being two-rooted rather than three-rooted (ancestral character). Similar to *Bulaklestes* and *Uchkudukodon* gen. nov., and differing from *Kennalestes*, *Asioryctes*, and *Ukhaatherium* in P4 having small rather than large protocone swelling (ancestral character). P5 has metacone swelling that is absent in *Uchkudukodon* gen. nov. (ancestral character). (P5s are unknown for *Daulestes kulbeckensis* and *Bulaklestes*.) Similar to *Asioryctes*, *Ukhaatherium*, *Bulaklestes*, and *Uchkudukodon* gen. nov., and differing from *Kennalestes* in lacking lingual cingula on M1–3 (ancestral character). Metastylar lobe on M2 the same size or

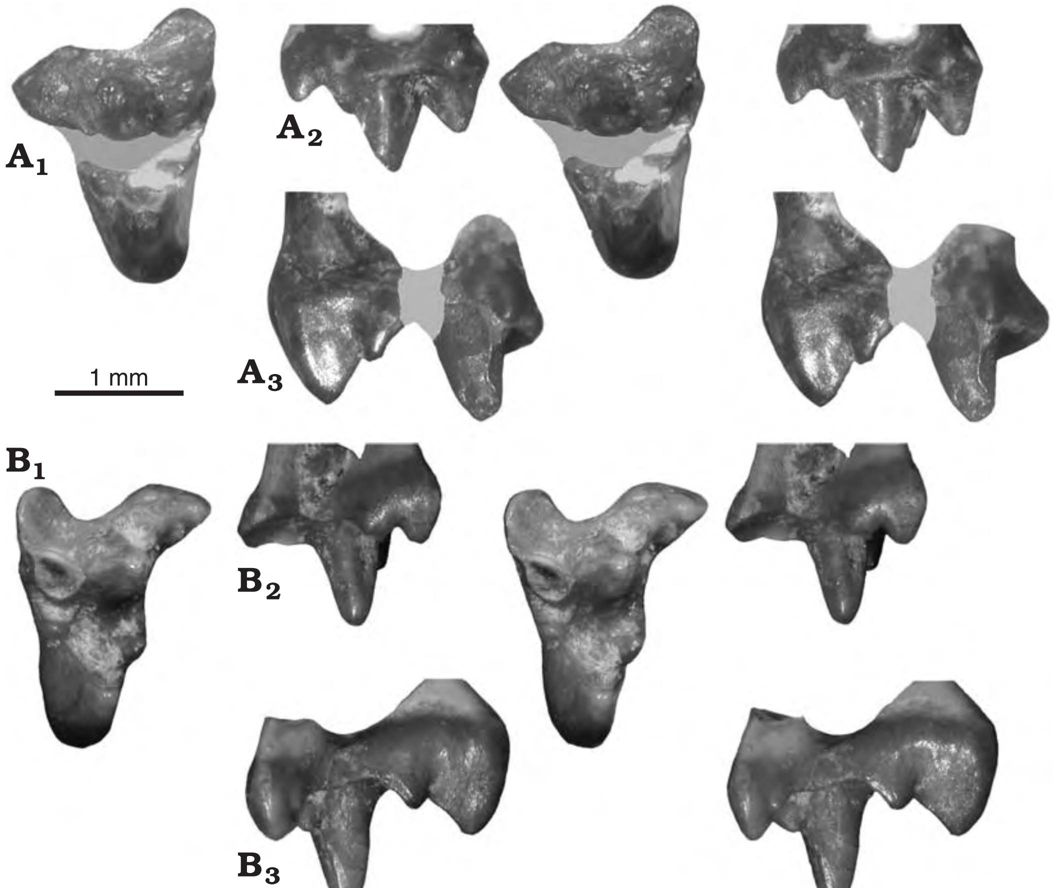

Fig. 1. Stereopairs of *Daulestes kulbeckensis* Trofimov and Nessov, 1979; Dzharakuduk, Uzbekistan, Late Cretaceous (Turonian). **A**. URBAC 98-126, probably associated lingual and labial parts of a left M1 in, occlusal (A_1), labial (A_2), and anterior (A_3) views. **B**. URBAC 98-127, a right M2 lacking the metacone, in occlusal (B_1), labial (B_2), and anterior (B_3) views.

smaller than the parastylar lobe, while in *Asioryctes*, and *Ukhaatherium* it is smaller and in *Kennalestes* it is the same size (variable character). Similar to *Bulaklestes*, *Asioryctes*, *Kennalestes*, and *Uchkudukodon* gen. nov., and differing from *Ukhaatherium* in having lower canine double-rooted rather than single-rooted (polarity uncertain). Similar to *Bulaklestes* and *Uchkudukodon* gen. nov., and differing from *Kennalestes*, *Asioryctes*, and *Ukhaatherium* in lacking diastema between p1 and p2 (ancestral character). Similar to *Kennalestes* and *Uchkudukodon* gen. nov., and differing from *Asioryctes* and *Ukhaatherium* in lacking paraconid on p4 (derived character, polymorphic in *Bulaklestes*). Similar to *Kennalestes*, *Asioryctes*, *Ukhaatherium*, and *Uchkudukodon* gen. nov., and differing from *Bulaklestes* in having p5 shorter than p4 (derived character) and in p5 talonid as wide as anterior half of tooth (derived character). Similar to *Uchkudukodon* gen. nov. in having the average length of m1 1.2–1.4 mm (ancestral character), which differs from *Bulaklestes*, *Asioryctes*, *Kennalestes*, *Ukhaatherium*, which have an average length of m1 1.6–1.9 (derived character). Similar to *Bulaklestes*, *Uckudukodon*, and *Kennalestes*, and differing from *Asioryctes* in having little or no constriction of m1–3 trigonids (ancestral character). Intermediate in size between *Uckudukodon* gen. nov. and *Bulaklestes*.

Daulestes kulbeckensis Trofimov and Nessov, 1979 in Nessov and Trofimov 1979

Figs. 1, 2, Tables 1, 2.

1979 *Daulestes kulbeckensis* sp. nov.; Nessov and Trofimov 1979: 953, fig. 1.
1981 *Daulestes kulbeckensis*; Nessov 1981: pl. 10: 18.
1982 *Daulestes kulbeckensis*; Nessov 1982: pl. 1: 6.
1985 *Kumlestes olzha* sp. nov.; Nessov 1985: 9, pl. 2: 1.
1991 *Daulestes kulbeckensis*; Nessov and Kielan-Jaworowska 1991: fig. 1.
1991 *Kumlestes olzha*; Nessov and Kielan-Jaworowska 1991: fig. 1.
1994 *Daulestes kulbeckensis*; Nessov et al. 1994: 55, pl. 1: 2.
1994 *Kumlestes olzha*; Nessov et al. 1994: 60, pl. 2: 2.
1997 *Daulestes kulbeckensis*; Nessov 1997: pl. 46: 6.
1997 *Kumlestes olzha*; Nessov 1997: pl. 45: 7.
2000 *Daulestes kulbeckensis*; Averianov 2000: fig. 30.4A, B.
2000 *Kumlestes olzha*; Averianov 2000: fig. 30.5A, B.

Holotype: CCMGE 1/11758, right dentary with partial alveolus for posterior root of two rooted canine, two alveoli for p1, partial anterior and posterior roots for p2, p4 lacking protoconid apex, p5 lacking protoconid apex, m1 lacking para- and metaconid apices, anterior alveolus for

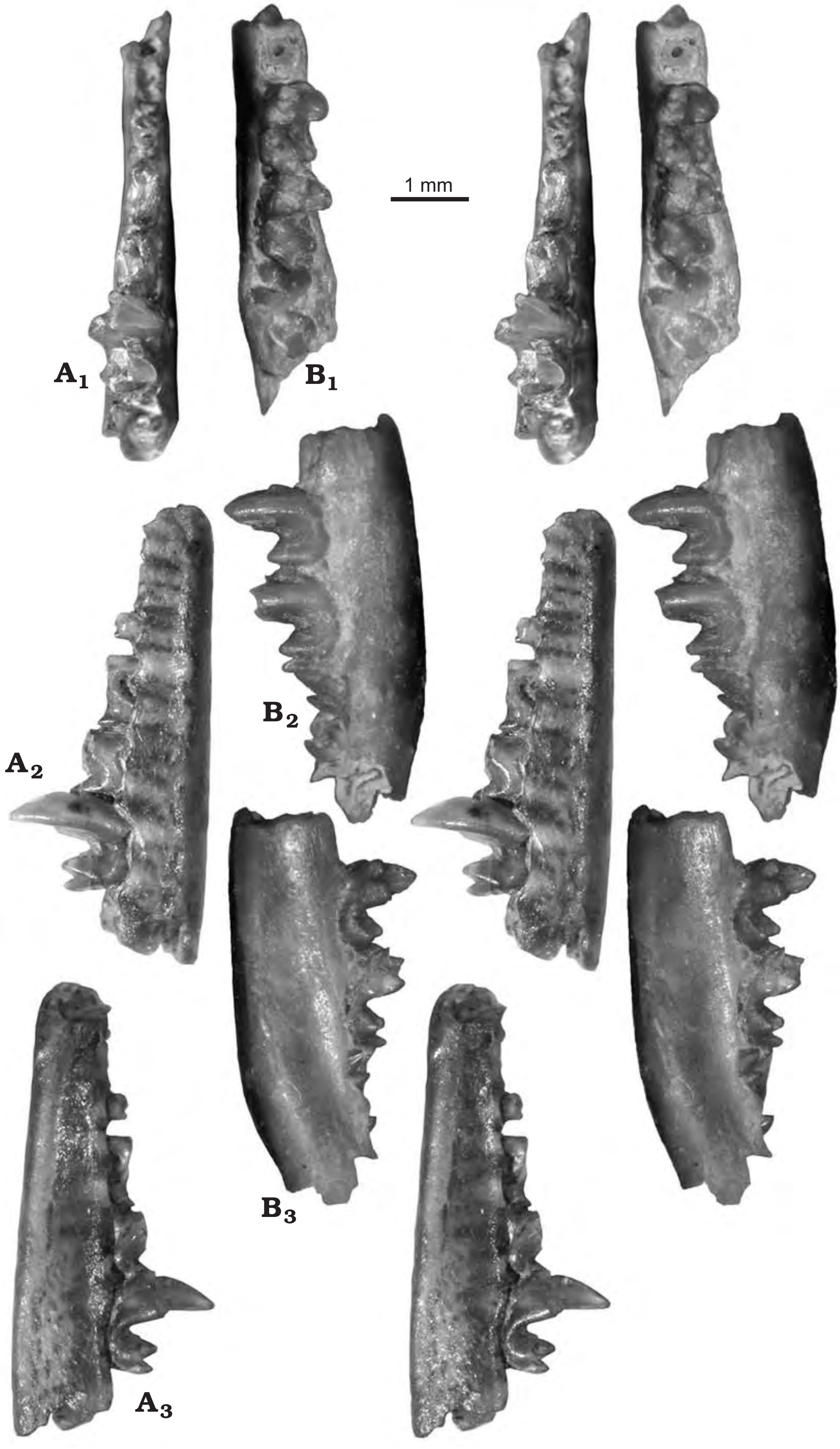
1 mm
A1
B1
A2
B2
B3
A3

Table 1. Upper tooth measurements. Italicized numbers are estimates. Parentheses are deciduous teeth. A dagger (†) indicates a type specimen. Abbreviations as follows: L, length; W, width; AW, anterior width; PW, posterior width.

Specimen no. and species	P1		P2		P4			P5 or (DP5)		
	L	W	L	W	L	AW	PW	L	AW	PW
Daulestes inobservabilis										
URBAC 02-91								1.41	1.69	1.89
URBAC 98-146					1.33	0.92	0.88			
Uchkudukodon nessovi										
ZIN 79066 † right	0.63	0.30	0.68	0.26	1.03	0.45	0.65	(0.98)	(1.03)	(1.19)
ZIN 79066 † left	0.49	0.32	0.56	0.38	1.05	0.45	0.66	(1.04)	(1.12)	(1.19)
Bulaklestes kezbe										
CCMGE 19/12176					1.70	0.93	1.26			
URBAC 99-106					1.53					

Specimen no. and species	M1			M2			M3		
	L	AW	PW	L	AW	PW	L	AW	PW
Daulestes kulbeckensis									
URBAC 98-126	1.58	1.99	2.20						
URBAC 98-127				1.59	2.07	2.03			
Daulestes inobservabilis									
URBAC 04-153	1.74	1.92	2.05						
URBAC 03-18	1.73	2.06	2.25						
URBAC 02-91	1.70	2.18	2.32						
URBAC 98-140				1.70	2.15	2.20			
URBAC 99-102				1.62					
URBAC 99-103	1.68								
Uchkudukodon nessovi									
URBAC 03-213				1.25	1.57	1.57			
URBAC 98-124	1.22	1.48	1.66						
URBAC 98-125	1.37	1.67	1.74						
ZIN 79066 † left	1.23	1.37	1.46	1.21	1.66	*1.50*			
ZIN 79066 † right	1.25	1.37	1.54	1.27	1.65	1.63			
URBAC 04-221	*1.29*	1.44	*1.55*	1.12	1.63	1.52	0.81	1.72	1.05
Bulaklestes kezbe									
ZIN 82591	2.00	2.39	2.56						
CCMGE 12/12176 †							1.36	2.28	1.48

m2 (see Discussion for the interpretation of the anterior dentition). Found 1978.

Type locality and horizon: CDZH-17a, Dzharakuduk, Kyzylkum Desert, Uzbekistan. Bissekty Formation, Upper Cretaceous (Turonian).

Referred specimens.—URBAC 98-126, probably associated lingual and labial parts of a left M1 (CBI-14); URBAC 98-127, an unworn right M2 lacking the metacone (CBI-14); URBAC 03-85, right dentary with m1–2, m3 trigonid partially erupted, and alveoli for p5 (CBI-14); CCMGE 1/12176, left dentary with damaged m1–2 and alveoli for erupting m3 (the holotype of *Kumlestes olzha* Nessov, 1985, CBI-4b); URBAC 99-25, right dentary with alveoli for m1–3, m3 was erupting (CBI-14).

Revised diagnosis.—Intermediate in size between *Uckudukodon* gen. nov. and *D. inobservabilis*, averaging 7.5% (range of 3–16%) larger based on measurements of m1 and m2 and averaging 23.5% (range of 19–28%) larger than the former species based on measurements of M1 and M2, and averaging 5.7% (range of 12% larger – 23% smaller) smaller based on measurements of m1 and m2 and averaging 4.5% (range of 0–8%) smaller based on measurements of M1 and M2 than the latter species.

← Fig. 2. Stereopairs of *Daulestes kulbeckensis* Trofimov and Nessov, 1979; Dzharakuduk, Uzbekistan, Late Cretaceous (Turonian). **A**. CCMGE 1/11758, type, right dentary with partial alveolus for posterior root of two rooted canine, two alveoli for p1, partial anterior and posterior roots for p2, p4 lacking protoconid apex, p5 lacking protoconid apex, m1 lacking para- and metaconid apices, anterior alveolus for m2, in occlusal (A_1), labial (A_2), and lingual (A_3) views. **B**. URBAC 03-85, right dentary with m1–2, m3 trigonid partially erupted, and alveoli for p5, in occlusal (B_1), labial (B_2), and lingual (B_3) views.

Table 2. Lower tooth measurements. Italicized numbers are estimates. Parentheses are deciduous teeth. A dagger(†) indicates a type specimen. Abbreviations as follows: L, length; W, width; TRW, trigonid width; TAW, talonid width; TRL, trigonid length; TAL, talonid length.

Specimen no. and species	i2		i3		c or dc		p1		p2		p4		p5 or (dp5)	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
Daulestes kulbeckensis														
1/11758 †											0.93	0.43	0.87	0.50
Daulestes inobservabilis														
URBAC 03-88													1.15	0.72
Uchkudukodon nessovi														
ZIN 79066 † right	0.47	0.30	0.26	0.32	0.66	0.32	0.44	0.19	0.67	0.31	*0.88*	*0.45*	(1.17)	(0.66)
ZIN 79066 † left					0.61	0.30	0.37	0.30	0.67	0.32	*0.81*	*0.41*	(1.03)	(0.68)
ZIN 84968											0.78	0.39	0.83	0.48
Bulaklestes kezbe														
URBAC 03-142											1.30	0.61	1.60	0.90
URBAC 00-61	0.76	0.51	0.43	0.30	1.03	0.52	0.86	0.41	1.00	0.52	1.33	0.64		

Specimen no. and species	m1					m2					m3				
	L	TRW	TAW	TRL	TAL	L	TRW	TAW	TRL	TAL	L	TRW	TAW	TRL	TAL
Daulestes kulbeckensis															
1/11758 †	1.30	0.91	0.76	0.7	0.63										
03-85	1.17	0.90	0.81	0.63	0.56	1.32	0.86	0.77	0.66	0.66					
1/12176			0.74	0.59											
Daulestes inobservabilis															
URBAC 03-88	1.34	0.94	0.83	0.83	0.53	1.35	1.04	0.89	0.74	0.60	1.32	0.95	0.68	0.66	0.65
CCMGE 8/11758 †						1.35	0.97	0.88	0.66	0.68					
CCMGE 72/12455						*1.28*		0.75		0.66					
Uchkudukodon nessovi															
ZIN 79066 † left	1.21	0.84	0.74	0.63	0.61	1.19	0.86	0.75	0.66	0.55					
ZIN 79066 † right	1.12	0.85	0.72	0.56	0.54	1.19	0.86	0.74	0.57	0.61					
ZIN 84968	1.15					1.19	0.75	0.76	0.52	0.65					
URBAC 04-181						1.14	0.78	0.75	0.54	0.58					
URBAC 98-122											1.08	0.69	0.57	0.51	0.57
URBAC 03-203											*1.05*	0.71		0.54	*0.52*
URBAC 97-9											*0.92*	*0.69*	*0.45*	*0.43*	*0.48*
URBAC 98-123												0.66		0.53	
ZIN 84967						1.04	0.88	0.74	0.49	0.54					
Bulaklestes kezbe															
URBAC 98-141	1.67	1.1	0.98	0.89	0.77										
URBAC 98-132	*1.55*	1.14	1.05	0.86	*0.68*										
URBAC 03-142	*1.49*	1.06	0.99	0.79	0.65										
URBAC 84971						*1.58*	*1.06*	0.95	*0.74*	0.81	*1.56*	*0.83*	0.77	*0.68*	0.89
URBAC 03-94						1.53	1.1	0.86	0.88	0.65					
URBAC 04-163			0.94		*0.65*	1.45	1.15	0.90	0.76	0.70	1.45	0.98	0.68	0.74	0.7
URBAC 04-170											1.48	0.97	0.71	0.76	0.75
URBAC 98-133											1.46	0.73	0.97	0.73	0.73
URBAC 99-101		1.23		0.73											
URBAC 98-129		1.17		0.82											
URBAC 98-128		1.08	1.03	0.85											
URBAC 98-131		1.07		0.99											
URBAC 98-143		1.06		0.83											

Description.—Here we describe only newly collected material of *D. kulbeckensis*. Description of the holotype dentary can be found in Nessov et al. (1994).

Only two isolated upper molars are attributable to *D. kulbeckensis*: URBAC 98-126 (M1) and 98-127 (M2). M1 consists of two parts, probably belonging to the same specimen (Fig. 1A). The ectoflexus is not deep and the stylar shelf is about twice wider labial to the metacone than labial to the paracone. The parastylar lobe is large and anteriorly protruding, with a large parastyle. A distinct small preparastyle was apparently present but has mostly worn away. The stylocone is distinct but is much smaller than the parastyle. There are no distinct stylar cusps posterior to the stylocone. The metastylar lobe is close in size to the parastylar lobe, extending a greater distance labially, but the metastylar lobe does not extend posteriorly. Preparacrista and postmetacrista are ridge-like and relatively high; both crests are heavily worn. The metacone is smaller and shorter than the paracone; the bases of the cusps are merged. The conules are sharp, large, and winged; the paraconule being closer to the protocone than is the metaconule. The sharp internal postparaconule and premetaconule cristae divide the trigon basin into concave conular basins and a deeper, concave primary trigon basin. The protocone is about the height of the metacone, but lower than the paracone, and is relatively unexpanded anteroposteriorly. There are no lingual cingula.

M2 (Fig. 1B) differs from M1 in having a parastylar lobe that extends farther anterolabially than more anteriorly as in M1, which results in a deeper ectoflexus. The preparacrista is directed towards the parastyle rather than contacting the stylocone. The preparaconule crista and paraconule bulge anteriorly from the anterior margin of the crown.

The three referred dentaries of *D. kulbeckensis* all had an m3 that was not fully erupted (hidden in crypt in URBAC 03-85) (Fig. 2B). In CCMGE 1/12176 and URBAC 99-25 the dentary is swollen surrounding the alveoli for m3, which are close to the anterior slope of the coronoid process. In URBAC 03-85 there are several very small masseteric foramina. In URBAC 99-25 on the medial side of the coronoid process there is a subhorizontal line delimiting the ventral border for the temporalis muscle. This specimen also preserves the base of the mandibular angle and a large oval-shaped and posteriorly directed mandibular foramen dorsal to the angle.

The p4–5 protoconids are mostly missing in the type specimen (CCMGE 1/11758), but enough is preserved to show that p4 is distinctly longer than p5, and that the singled-cusped talonid extends the full width of the crown (Fig. 2A).

The m1–2 (Fig. 2) are very similar in structure, differing slightly in that the m1 has a more open trigonid angle and a smaller and more labially displaced paraconid. The m2 is slightly longer as the result of a slightly more elongate talonid. On unworn m1s and m2s, the trigonid is about twice the height of the talonid. The protoconid is considerably higher and larger than the metaconid. The paraconid is smaller and shorter than the metaconid. There is a distinct, flat-bottomed, triangular trigonid basin, which is open lingually between the paraconid and metaconid bases. The precingulid is short, narrow, and terminates at the paracristid notch. The talonid is narrower than the trigonid. The hypoflexid is deep. The cristid obliqua terminates at the protocristid notch on m1 and somewhat lingual to this notch on m2. The talonid basin is deep, especially in its anterolingual corner, where it receives the protocone during centric occlusion. The hypoconid is the largest and tallest of the talonid cusps and the entoconid is the smallest. The hypoconulid is equidistant from the other talonid cusps and is posteriorly projecting.

Measurements—See Tables 1 and 2.

Daulestes inobservabilis (Nessov, 1982)

Figs. 3, 4, Tables 1, 2.

1982 *Taslestes inobservabilis* sp. nov.; Nessov 1982: 235, pl. 1: 4.
1991 *Taslestes inobservabilis*; Nessov and Kielan-Jaworowska 1991: fig. 1.
1993 Mixotheridia [indet.]; Nessov 1993: figs. 5(7) and 6(1).
1994 *Taslestes inobservabilis*; Nessov et al. 1994: 57, pl. 1: 4.
1997 *Taslestes inobservabilis*; Nessov 1997: pl. 46: 8, pl. 55: 3.
1997 *Kennalestes*(?) *uzbekistanensis* sp. nov.; Nessov 1997: 166, pl. 50: 1.
2000 *Taslestes inobservabilis*; Averianov 2000: fig. 30.4E.
2000 *Kennalestes* sp. nov.; Averianov 2000: fig. 30.5R.
2000 *Daulestes inobservabilis* [comb. nov.]; McKenna et al. 2000: 6.

Holotype: CCMGE 8/11758, right dentary with worn m2 and alveoli for m1 and m3. Found in 1979.

Type locality and horizon: CDZH-17g, Dzharakuduk, Kyzylkum Desert, Uzbekistan. Bissekty Formation, Upper Cretaceous (Turonian).

Referred specimens.—URBAC 98–146, right P4 missing small part of anterior margin (CBI-14); URBAC 02-91, right maxilla with P5, M1, and alveoli for P4 and M2–3 (CBI-4e); URBAC 04-153, right maxilla with M1 and alveoli for P5 and M2 (CBI-14); URBAC 03-18, left maxilla with M1 (CBI-14); URBAC 98-140, left M2 (CBI-14); URBAC 99-102, labial part of a right M2 (CBI-14); URBAC 99-103, labial part of a right M2 (CBI-14); URBAC 98-138, lingual part of left M1 or 2 (CBI-14); ZIN 84972, right dentary with p5, posterior alveolus for p1, and alveoli for double-rooted p2, 4 (CBI-14, 1987); URBAC 03-88, left dentary with p5, m1–3, and posterior root of p4 (CBI-14); CCMGE 72/12455, left dentary with m2 [now damaged but can be seen in Nessov's photographs] and alveoli for m1 and m3 (the holotype of *Kennalestes*? *uzbekistanensis* Nessov, 1997, CBI-4e, 1989); URBAC 00-43, right dentary with alveoli for p1–2, 4, dp5?, m1–3, and erupting m3 (CBI-14); ZIN 88441, left dentary with alveoli for p4–5, m1–2 (CBI-5a, 1989); URBAC 00-55, left dentary with alveoli for p4–5, m1 (CBI-14).

Revised diagnosis.—Similar to *D. kulbeckensis* but averaging 5.7% (range of 12% smaller – 23% larger) larger based on measurements of m1 and m2 and averaging 4.5% (range of 0–8%) larger based on measurements of M1 and M2.

Description.—The most complete maxillary fragment is URBAC 02-91 with P5, M1 and partial alveoli for P4 and M2–3 (Fig. 3B). On the labial side there appears to be a jugal

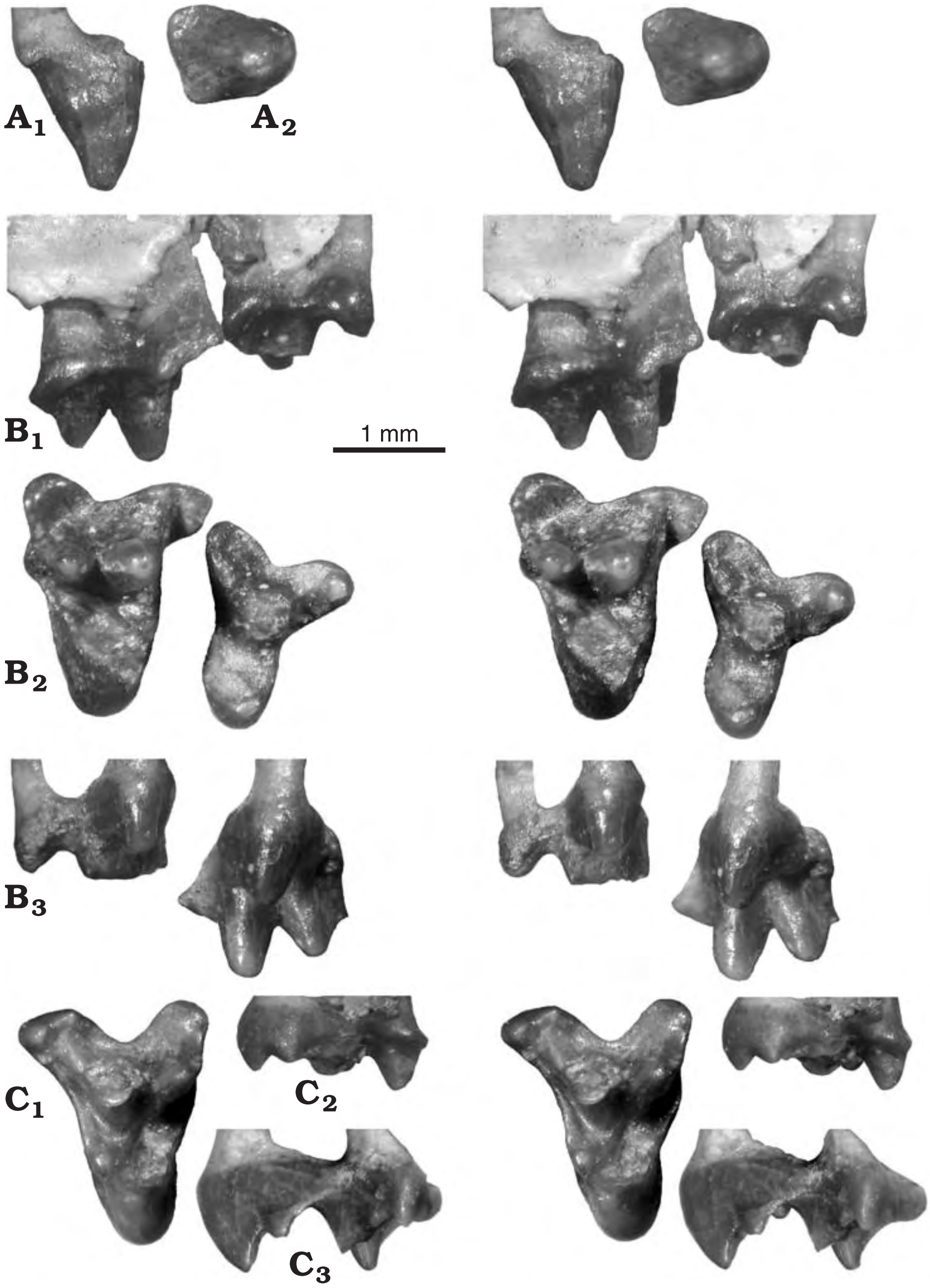

Fig. 3. Stereopairs of *Daulestes inobservabilis* (Nessov, 1982); Dzharakuduk, Uzbekistan, Late Cretaceous (Turonian). **A**. URBAC 98-146, right P4 missing small part of anterior margin, in labial (A_1) and occlusal (A_2) views. **B**. URBAC 02-91, P5 and M1 from right maxilla with P5, M1, and alveoli for P4 and M2–3, in labial (B_1), occlusal (B_2), and lingual (B_3) views. **C**. URBAC 98-140, left M2, in occlusal (C_1), labial (C_2), and anterior (C_3) views.

facet from the middle of M1 toward the posterior end of the fragment. In URBAC 04-153 there is an infraorbital foramen dorsal to P4.

P4 (Fig. 3A) is very high, with anterior and posterior crests, and small anterior and posterior cusps. The base of labial side of the crown is nearly straight. There are a complete lingual cingulum and a small lingual swelling just posterior of the middle of the crown. This swelling is supported by the posterior root, which is slightly subdivided. Thus there are two roots, with the posterior of the two being slightly larger.

The P5 is a semimolariform, three-rooted tooth (Fig. 3B). There is a small but distinct metacone swelling on the postparacrista. The paracone is large and occupies a central position on the crown. The ectoflexus is deep and the labial margin is almost symmetrical with prominent metastylar and parastylar lobes. There is no stylocone or preparastyle and the preparacrista connects to a rather large parastyle. The trigon is transversely wide and anteroposteriorly narrow, with a prominent but low protocone. There are no conules or lingual cingula. The preprotocrista is straight and terminates labially at the anterior end of paracone. The postprotocrista

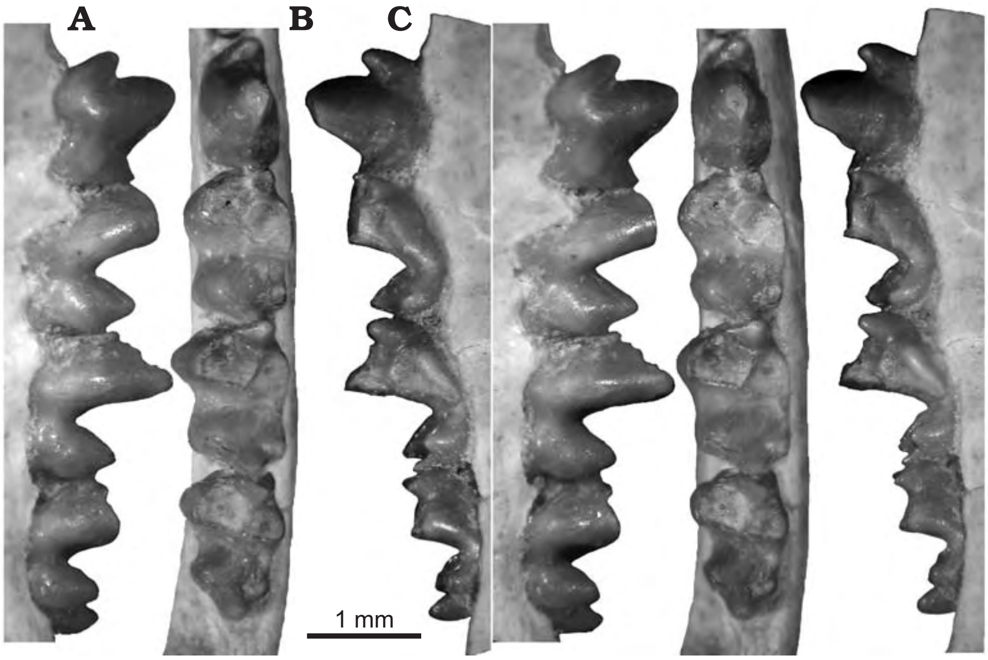

Fig. 4. Stereopairs of *Daulestes inobservabilis* (Nessov, 1982); Dzharakuduk, Uzbekistan, Late Cretaceous (Turonian). URBAC 03-88, left dentary with p5, m1–3 (ventral margin is damaged and thus not shown); in labial (**A**), occlusal (**B**), and lingual (**C**) views.

extends posterodorsally from the protocone and turns labially, ending dorsal to the posterior end of the metastylar lobe.

The M1 is transversely wider than P5 (Fig. 3B). Except for being larger, this tooth differs from M1s in *Uchkudukodon nessovi* in only a few details: the labial margin of the stylar shelf forms a more consistent ridge, the premetaconule crista is weaker (absent in the worn URBAC 02-91), and the metacingulum is wider. On the worn URBAC 02-91 there is a distinct parastylar groove. With wear, the preparaconule crista shifts its labial terminus posterolingually from the preparastyle to the anterior margin of the paracone. The parastylar lobe of the M1 of URBAC 02-91 is slightly more labial than in other M1s of this species. There are narrow but distinct pre- and postcingula on URBAC 02-91 but not on other M1s.

The M2 differs from M1 mostly in its more symmetrical stylar lobes, deeper ectoflexus, and relatively longer preparacrista. Compared with *Uchkudukodon nessovi*, M2s of *D. inobservabilis* appear to have more symmetrical stylar lobes, with a relatively less reduced metastylar lobe. URBAC 99-102 is an exception to this, with the parastylar lobe being distinctly larger than the metastylar lobe. This specimen also has a cusp-like preparacrista, which is not characteristic for other specimens.

In URBAC 00-43, an edentulous dentary, there are alveoli for the posterior root of p1, double-rooted p2, p4, dp5?, m1–2, and a hole for an unerupted m3. Judging from alveoli, p1–2, 4 gradually increased in size posteriorly. A long slit-like posterior mental foramen is under the alveoli for dp5?. In other specimens (URBAC 00-55, 03-88, ZIN 88441), the posterior mental foramen is under the posterior root of p5.

Premolars anterior to p5 are not known, but the relative size of the p5 and alveoli for p4 in ZIN 84972 suggest that p5 in *D. inobservabilis* was shorter than p4, as in *D. kulbeckensis* and *Uchkudukodon nessovi*.

The p5 (ZIN 84972, URBAC 03-88) (Fig. 4) has a distinct paraconid, a broad but very short talonid with one posterior cusp (absent in ZIN 84972), and anterolingual and posterior cingulids. The talonid cusp in URBAC 03-88 is higher than the paraconid.

The m1–2s are generally similar in structure to lower molars of *Uchkudukodon nessovi* and *Daulestes kulbeckensis*. In URBAC 03-88 (Fig. 4) the protocristid is set more obliquely than in other specimens. The cristid obliqua attaches slightly lingual to the protocristid notch in all molars.

Measurements.—See Tables 1 and 2.

Genus *Uchkudukodon* nov.

Type and only species: *Daulestes nessovi* McKenna, Kielan-Jaworowska, and Meng, 2000.

Derivation of the name: Named for the Uzbekistan city of Uchkuduk, derived from Kazkh for three (uch) and well (kuduk), and Greek for tooth (odon); masculine gender; pronounced ("u" as in sue throughout, and "ch" as in chase) UCH-ku-duk-o-don.

Definition.—The type and all species more closely related to *U. nessovi* than to other asioryctitheres.

Distribution.—Uzbekistan; Late Cretaceous, Turonian.

Diagnosis.—Similar to *Asioryctes*, *Ukhaatherium*, and *Daulestes*, and differing from *Kennalestes* in having P2 smaller than P1 (possible ancestral character, unknown for *Bulaklestes*). Similar to *Bulaklestes* and *Daulestes*, and differing from *Kennalestes*, *Asioryctes*, and *Ukhaatherium* in P4 being two-rooted rather than three-rooted (ancestral character). Similar to *Bulaklestes* and *Daulestes*, and differing from

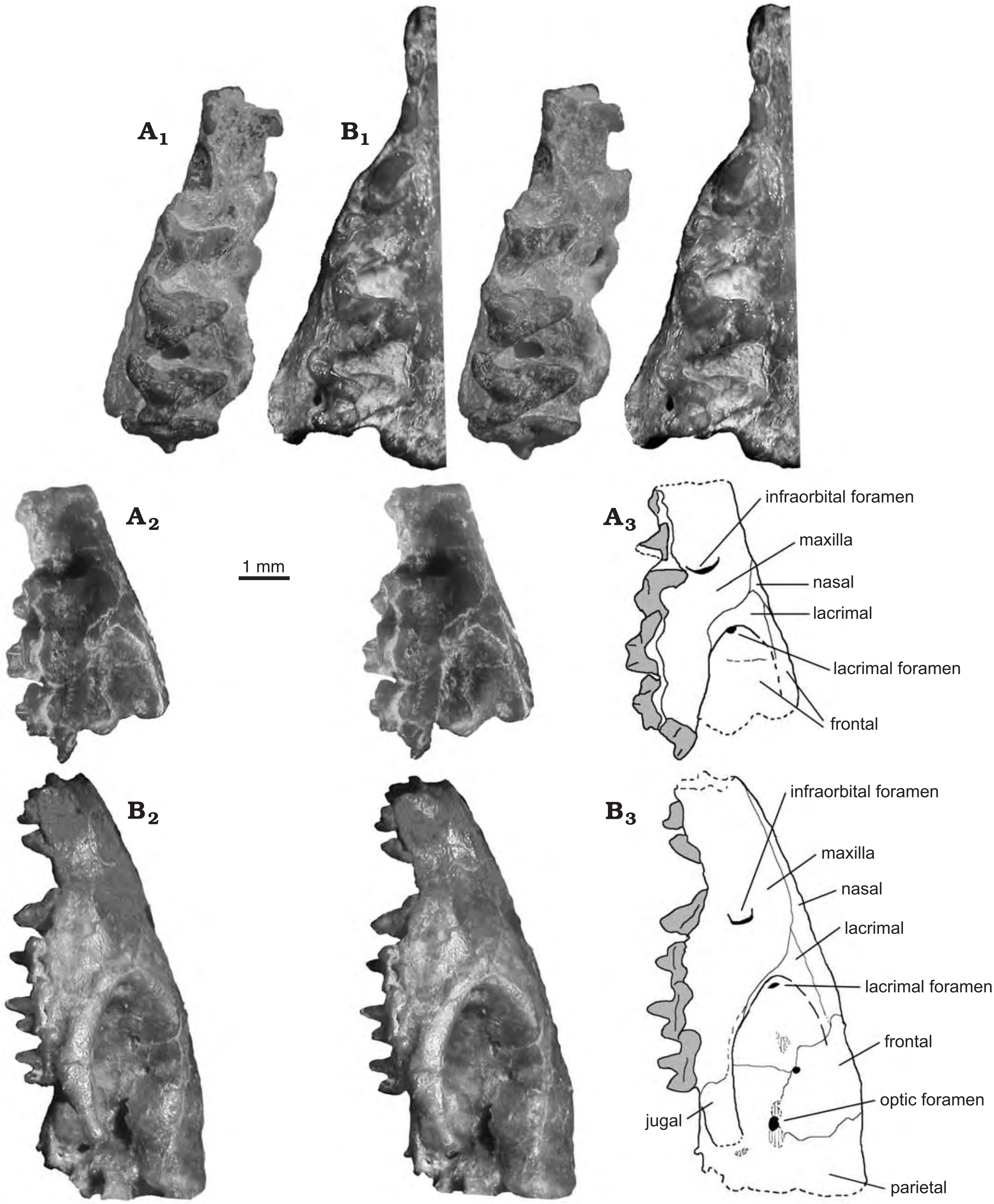

Fig. 5. *Uchkudukodon nessovi* (McKenna, Kielan-Jaworowska, and Meng, 2000); Dzharakuduk, Uzbekistan, Late Cretaceous (Turonian). **A**. URBAC 04-221, skull fragment with right (reversed in A_2 and A_3) P5, M1–3, broken P2 and root for P4, in occlusal (A_1, stereopair) and labial (A_2, stereopair) views; A_3, labeled labial drawing showing P4 fragment before loss during preparation. **B**. ZIN 79066, a skull with occluded dentaries of a sub-adult, type, only left anterior two-thirds of skull shown here, in occlusal (B_1, stereopair, reversed) and labial (B_2, stereopair) views; B_3, labeled labial drawing.

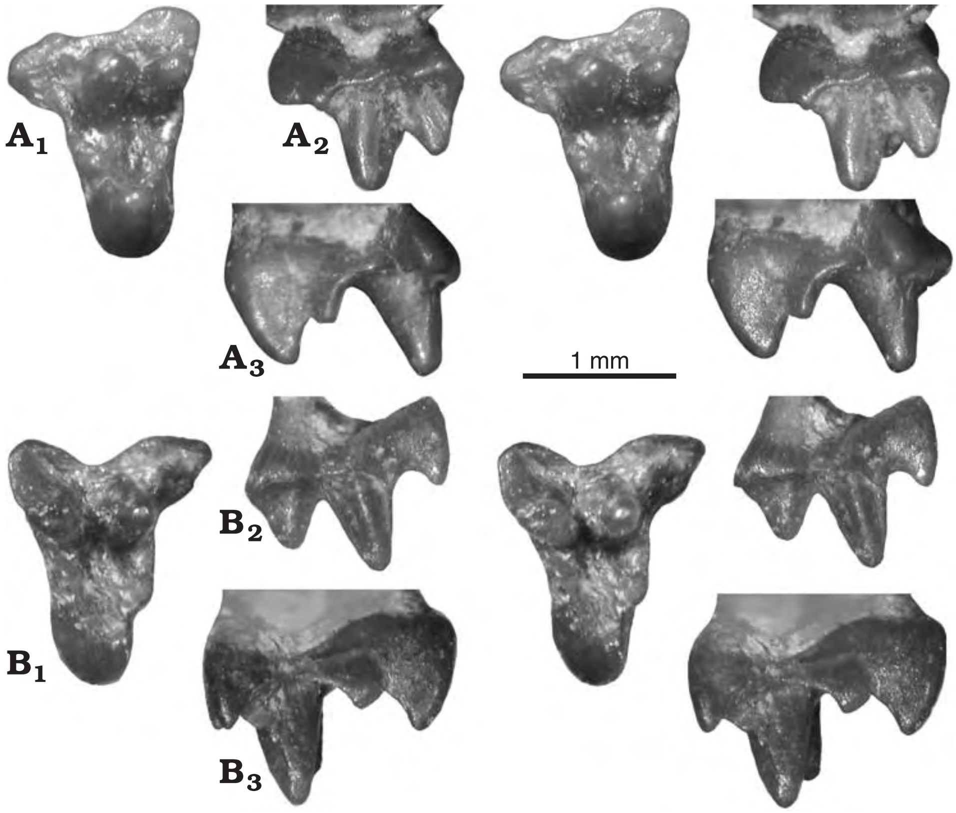

Fig. 6. Stereopairs of *Uchkudukodon nessovi* (McKenna, Kielan-Jaworowska, and Meng, 2000); Dzharakuduk, Uzbekistan, Late Cretaceous (Turonian). **A**. URBAC 98-124, M1 from left maxilla with M1 and alveoli or partial alveoli for P5 and M2, in occlusal (A_1), labial (A_2), and anterior (A_3) views. **B**. URBAC 03-213, right M2, in occlusal (B_1), labial (B_2), and anterior (B_3) views.

Kennalestes, *Asioryctes*, and *Ukhaatherium* in P4 having small rather than large protocone swelling (ancestral character). P5 lacks a metacone swelling that is present in *Daulestes* (derived character). (P5s are unknown for *Daulestes kulbeckensis* and *Bulaklestes*.) Similar to *Asioryctes*, *Ukhaatherium*, *Bulaklestes*, and *Daulestes*, and differing from *Kennalestes* in lacking lingual cingula on M1–3 (ancestral character). Metastylar lobe on M2 the same size or smaller than the parastylar lobe, while in *Asioryctes*, and *Ukhaatherium* it is smaller and in *Kennalestes* it is the same size (variable character). Similar to *Bulaklestes*, *Asioryctes*, *Kennalestes*, and *Daulestes*, and differing from *Ukhaatherium* in having lower canine double-rooted rather than single-rooted (ancestral character). Similar to *Bulaklestes* and *Daulestes*, and differing from *Kennalestes*, *Asioryctes*, and *Ukhaatherium* in lacking diastema between p1 and p2 (ancestral character). Similar to *Kennalestes* and *Daulestes*, and differing from *Asioryctes* and *Ukhaatherium* in lacking paraconid on p4 (derived character, polymorphic in *Bulaklestes*). Similar to *Kennalestes*, *Asioryctes*, *Ukhaatherium*, and *Daulestes*, and differing from *Bulaklestes* in having p5 shorter than p4 (derived character) and in p5 talonid as wide as anterior half of tooth (derived character). Similar to *Bulaklestes*, *Daulestes*, and *Kennalestes*, and differing from *Asioryctes* in having little or no constriction of m1–3 trigonids (ancestral character). Similar to *Asioryctes* and *Ukhaatherium* in having the ratio of the M1 average length to ml average length of 1.1, which differs from *Bulaklestes*, *Daulestes*, and *Kennalestes* which have a ratio of 1.3 (derived character). By far the smallest asioryctithere and smallest Cretaceous eutherian. Compared to *Daulestes* averaging at least 7.5% (range of 3–16%) smaller based on measurements of m1 and m2 and averaging at least 23.5% (range of 19–28%) smaller based on measurements of M1 and M2.

Uchkudukodon nessovi (McKenna, Kielan-Jaworowska, and Meng, 2000)

Figs. 5–7, Tables 1, 2.

1991 Proteutheria [indet.]; Nessov and Kielan-Jaworowska 1991: fig. 1.
1993 Eutheria gen. and sp. nov.; Nessov 1993: fig. 1(4).
1995 Proteutheria gen. and sp. nov.; Nessov 1995: pl. 11: 7.
1997 Placentalia, probably *Daulestes* sp. nov.; Nessov 1997: pl. 48: 1.
2000 Eutheria [indet.]; Averianov 2000: fig. 30.8A, B.
2000 *Daulestes nessovi* sp. nov.; McKenna et al. 2000: 6, figs. 2–19.

Holotype: ZIN 79066, a skull with occluded dentaries of a sub-adult, see McKenna et al. 2000 for a more complete description. Found in 1989.

Type locality and horizon: CBI-5a, Dzharakuduk, Kyzylkum Desert, Uzbekistan. Bissekty Formation, Upper Cretaceous (Turonian).

Referred specimens.—URBAC 04-221, skull fragment with right P5, M1–3, broken P2 and root for P4 (CBI-14); URBAC 98-124, left maxilla with M1 and alveoli or partial alveoli for P5 and M2 (CBI-14); URBAC 98-125, right M1 (CBI-14);

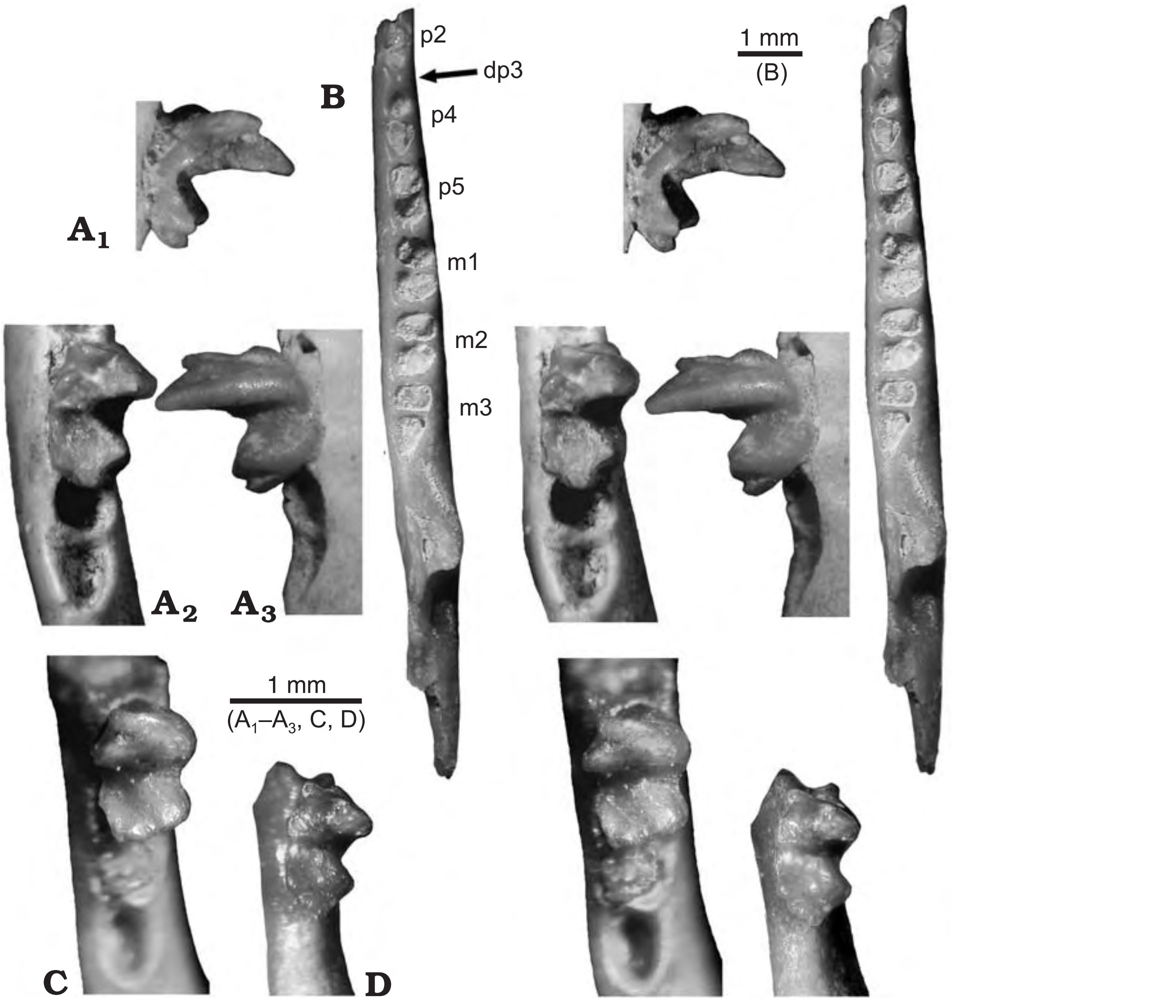

Fig. 7. Stereopairs of *Uchkudukodon nessovi* (McKenna, Kielan-Jaworowska, and Meng, 2000); Dzharakuduk, Uzbekistan, Late Cretaceous (Turonian). **A**. URBAC 04-181, m2 from right dentary with m2 and alveoli for p5, m1, 3; in lingual (A_1), occlusal (A_2), and labial (A_3) views. **B**. URBAC 04-42, right denary with alveoli for p2–5, m1–3 and angular process, in occlusal view. **C**. ZIN 84967, m2 from right dentary with worn m2 and alveoli for m3; occlusal. **D**. URBAC 98-122, m3 from right dentary with worn m3, in occlusal view.

URBAC 03-213, right M2 (CBI-14); ZIN 84968, right dentary with damaged p4–5, m1–2, and m3 in matrix and roots for p2 (CDZH-17a, 1978[1983]); URBAC 04-181, right dentary with m2 and alveoli for p5, m1, 3 (CBI-14); ZIN 84967, right dentary with worn m2 and alveoli for m3 (CBI-14); URBAC 98-122, right dentary with worn m3 (CBI-14); URBAC 97-9, right dentary with erupting m3, posterior alveolus for p4 and alveoli for p5, m1–2 (CBI-14, 1997); URBAC 03-205, right dentary with talonid of erupting m3 and alveoli for p5 and m1–2 (CBI-14); URBAC 98-25, left dentary with talonid of erupting m3, posterior alveolus for m2 and parts of coronoid and angular processes (CBI-14); URBAC 03-203, left dentary with m3 erupting and alveoli for m1–2 (CBI-14); URBAC 98-123, right dentary with erupting m3 and alveoli for m1–2 (CBI-14); URBAC 04-42, right denary with alveoli for p2–5, m1–3 and angular process (CBI-14); URBAC 04-131, left dentary with posterior alveolus for p2 and alveoli for p4–5, m1–3 (CBI-14); ZIN 88443, right dentary with alveoli for p5, m1–3 (CBI-14, 1985); ZIN 88444, right dentary with alveoli for p5, m1–3 (CBI-14, 1987); URBAC 03-106, left dentary with alveoli for p5, m1–3 (CBI-14); URBAC 03-1, left dentary with alveoli for m1–2 and erupting m3, and parts of coronoid and angular processes (CBI-14); URBAC 03-3, right dentary with alveoli for m1–3 (CBI-14); URBAC 03-159, right dentary with alveoli for m1–3 (CBI-14); URBAC 03-191, left dentary with alveoli for m1–3 (CBI-4e); URBAC 97-11, right dentary with alveoli for m2–3 (CBI-14); URBAC 98-145, right dentary with alveoli for m2–3 (CBI-14); URBAC 99-107, right dentary with alveoli for m2 and erupting m3 (CBI-14); URBAC 03-198, left dentary with alveoli for m2 and erupting m3 (CBI-14); ZIN 88445, left dentary with alveoli for m2 and erupting m3 (CBI-14, 1984-1985).

Diagnosis.—As for the genus.

Description.—Here we describe only newly collected material of *Uckudukodon nessovi*. Description of the holotype skull and dentition (ZIN 79066) can be found in McKenna et al. (2000); the specimen is illustrated herein for comparative purposes (Fig. 5B). URBAC 04-221 is a skull fragment including the right maxilla and lacrimal, parts of the nasal, frontal, and orbitosphenoid, and bearing P2, 5, M1–3, and roots of P4 (Fig. 5A; the partial P4 was lost during preparation). A large infraorbital foramen lies dorsal to the anterior part of P5. On the labial side of URBAC 98-124 there appears to be a jugal facet, which extends anteriorly almost to the posterior alveolar border of M1.

P2 is a two-rooted premolar with single-cusped low crown, heavily worn in URBAC 04-221. The posterior root is slightly longer than anterior root.

P5 is known only in URBAC 04-221. It is a semimolariform, three-rooted premolar. The paracone is large and occupies a central position on the crown. There is no metacone or metacone swelling, which may be a derived character for the genus. The ectoflexus is deep and the labial margin is almost symmetrical, with prominent metastylar and parastylar lobes. There is no stylocone or preparastyle and the preparacrista connects to the parastyle. The trigon is transversely wide and anteroposteriorly narrow, with a distinct protocone missing the posterior margin of the apex. There are no conules.

In addition to the M1s preserved in the skull (ZIN 79066), M1 is known from three other specimens (URBAC 98-124, 98-125 and 04-221), which are similar in morphology. The following description utilizes information from all specimens (see Fig. 6A). The ectoflexus is shallow to moderately deep and the stylar shelf is about twice wider labial to the metacone than to the paracone. The parastylar lobe is large and anteriorly protruding, with a large parastyle and small preparastyle. The stylocone is intermediate in size between the parastyle and preparastyle. There are no distinct stylar cusps posterior to the stylocone. The metastylar lobe is close in size to the parastylar lobe, extending labially, but not very much posteriorly. The preparacrista is ridge-like but low, while the postmetacrista is ridge-like but higher. The metacone is smaller than the paracone and the bases of the cusps are merged. The conules are sharp, large, and winged; the paraconule is closer to the protocone than is the metaconule. The sharp internal cristae divide the trigon basin into concave conular basins and a deeper, concave primary trigon basin. The preparaconule crista, and to a lesser extent, the postmetaconule crista protrude beyond the margins of the crown creating lobe-like conules. The preparaconule crista extends anterolabially to the preparastyle forming a well-developed paracingulum. The postmetaconule crista is shorter and terminates dorsal to the posterior margin of the metacone. The protocone is lower than the paracone, but close in height to the metacone. The protocone ranges from quite narrow anteroposteriorly (URBAC 04-221) to slightly expanded (URBAC 98-124). In URBAC 98-125 there are very faint pre- and postcingula.

M2 is known from the holotype skull fragment, URBAC 04-221, and an isolated tooth, URBAC 03-213 (Fig. 6B). It differs from M1 mostly in its more symmetrical stylar lobes, a parastylar lobe that protrudes anterolabially rather than anteriorly, deeper ectoflexus, and a relatively longer preparacrista. The metastylar lobe is large, being only slightly smaller than the parastylar lobe in URBAC 03-213, but is considerably smaller than the parastylar lobe in URBAC 04-221.

M3 is known only in URBAC 04-221 (Fig. 5A). It is similar in morphology to CCMGE 12/12176, the holotype of *Bulaklestes kezbe*. The parastylar lobe is very wide (about a third of the tooth width) and protrudes much more labially than anteriorly (more anterolabially in *D. kezbe*). The metacone is only half the size of the paracone (broken), but is still a distinct cusp. The paraconule is larger and is closer to the protocone than is the metaconule.

Ten of 21 specimens that preserve the posterior portion of the dentary come from individuals with m3 in some stage of eruption. In these specimens the dentary is swollen surrounding the m3 alveoli, which are positioned sufficiently posteriorly so that they are on the anterior slope of the coronoid process. In adult specimens there is space between the m3 and the coronoid process. The depth of the dentary increases markedly with age (deepest in URBAC 03-106 at 2.2 mm). The posterior mental foramen is ventral to the anterior root of p5 (holotype, ZIN 84986), between the roots of p5 (URBAC 04-131), ventral to the posterior root of p5 (URBAC 97-9, 04-181), or between p5 and m1 (URBAC 04-42). The masseteric fossa is deep and the coronoid is high. Usually there are more than two very small to small masseteric foramina, one of which is usually distinctly larger than others (URBAC 03-1, 03-3, 04-42, 04-181, ZIN 88443, 88444, 84967). On the medial side of the coronoid process (URBAC 98-25, 03-3, 04-181) there is a distinct, nearly horizontal line below the level of the alveolar border, delimiting ventrally the area for attachment of the temporalis muscle ("medial flange" of Kielan-Jaworowska 1981, but not of Kermack et al. 1973). URBAC 98-25 and 03-1 preserve the base of the mandibular angle and a large oval-shaped and posteriorly directed mandibular foramen.

In URBAC 04-42 there is a distinct diastema between two-rooted alveoli for p2 and p4, with a small round hole in the middle, apparently representing the partially filled alveolus for the unreplaced dp3 (Fig. 7B). In ZIN 84968 there are two roots for p2 and double-rooted p4 and p5, each lacking the protoconid apices. The p5 appears to be shorter than p4, although its length cannot be accurately measured as this tooth is not fully erupted and it remains partially encrusted with matrix. The labial side of p5 is exposed, showing that the talonid is expanded to the greatest labial extent of the crown.

The m1–2 are similar in structure, except that m1 has a smaller and more labially placed paraconid and a more open trigonid lingually. The m2 is longer than m1 in ZIN 84968 and in the right ramus of the holotype, but shorter than m1 in the left ramus of the holotype (Table 2). The trigonid is twice the height of the talonid on unworn m1s and m2s. The protoconid is considerably higher than the metaconid. The paraconid is smaller than the metaconid and more labial in position on m1 compared to m2. There is a distinct, flat-bottomed, triangular trigonid basin, which is open lingually between the paraconid and metaconid bases. The precingulid is short, narrow, and terminates at (m1) or lingual to the paracristid notch (m2). The talonid is narrower than the trigonid. The hypoflexid is deep. The cristid obliqua terminates at the protocristid notch on m1 and at or slightly lingual to this notch on m2. The talonid basin is deep, especially in its anterolingual corner, where it received the protocone during centric occlusion. The hypoconid is the largest and tallest of the talonid cusps and the entoconid is the smallest. The hypoconulid is equidistant from the other talonid cusps and is (URBAC 04-181, Fig. 7A) or is not (ZIN 84967, Fig. 7C) posteriorly projecting.

The m3 was not known previously for *Uchkudukodon nessovi*. In the new sample it is represented by four specimens, but fully erupted only in URBAC 98-122 (Fig. 7D). The trigonid is much higher than the talonid, showing little anteroposterior compression, with a relatively large paraconid. The trigonid basin is distinct and open lingually between the paraconid and metaconid. The talonid is narrower and longer than the trigonid, with a rather small talonid basin and a deep hypoflexid. The cristid obliqua attaches to the trigonid at the protocristid notch and extends only slightly dorsal along the posterior trigonid wall. The talonid cusps are roughly equal in size and equidistant, and the hypoconulid is posteriorly projecting.

Measurements.—See Tables 1 and 2.

Bulaklestes Nessov, 1985

Type species: *Bulaklestes kezbe* Nessov, 1985.

Included species: Only the type species.

Definition.—The type and all species more closely related to *B. kezbe* than to other asioryctitheres.

Distribution.—Uzbekistan; Late Cretaceous, Turonian.

Diagnosis.—Ratio of M1 average length to ml average length of 1.3 as in *Daulestes* (derived character), compared to 1.1 for *Uchkudukodon* gen. nov. (ancestral character). Compared to the next smaller Dzharakuduk asioryctithere, *Daulestes inobservabilis*, averaging at least 12.6% (range of 2–32%) larger based on measurements of m1 and m2 and averaging at least 16.7% (range of 16–17%) larger based on measurements of M1 (M2 not known for *Bulaklestes*). Similar to *Daulestes* and *Uchkudukodon* gen. nov. but differing from *Kennalestes*, *Asioryctes*, and *Ukhaatherium* in having P4 two-rooted rather than three-rooted (ancestral character). Similar to *Daulestes* and *Uchkudukodon* gen. nov., but differing from *Kennalestes*, *Asioryctes*, and *Ukhaatherium* in having P4 with smaller rather than large protocone swelling (ancestral character). Similar to *Daulestes*, *Uchkudukodon* gen. nov., *Asioryctes*, and *Kennalestes* but differing from *Ukhaatherium* in having lower canine double-rooted rather than single-rooted (ancestral character). Similar to *Daulestes* and *Uchkudukodon* gen. nov., but differing from *Kennalestes*, *Asioryctes*, and *Ukhaatherium* in lacking diastema between p1 and p2 (ancestral character). Differs from *Daulestes*, *Uchkudukodon* gen. nov., *Kennalestes*, *Asioryctes*, and *Ukhaatherium* in having p5 longer than p4 (possibly ancestral character) and having p5 talonid not extending full width of crown (possibly ancestral character) (not reported in *Ukhaatherium*).

Bulaklestes kezbe Nessov, 1985

Figs. 8–10, Tables 1, 2.

1985 *Bulaklestes kezbe* sp. nov.; Nessov 1985: 16, pl. 3: 6.
1985 Theria [indet.]; Nessov 1985: pl. 3: 2.
1993 *Bulaklestes kezbe*; Nessov 1993: pl. 4: 10.
1994 *Bulaklestes kezbe*; Nessov et al. 1994: 64, pl. 4: 2.
1997 *Bulaklestes kezbe*; Nessov 1997: pl. 48: 2.
1997 Theria [indet.]; Nessov 1997: pl. 48: 4.

Holotype: CCMGE 12/12176, right M3.

Type locality and horizon: CBI-4b, Dzharakuduk, Kyzylkum Desert, Uzbekistan. Bissekty Formation, Upper Cretaceous (Turonian). Found in 1980.

Referred specimens.—CCMGE 19/12176, right P4 (CBI-4v); URBAC 99-104, right P4 (CBI-14); ZIN 82591, left M1 lacking paracone (CBI-14, 1998); URBAC 00-61, left dentary with i3?–4?, c, p1–2, 4 (CBI-14); URBAC 03-142, right dentary with p4 missing most of the crown, p5, m1, and alveoli for two-rooted c and p1–2 (CBI-14); URBAC 98-132, left m1 (CBI-14); URBAC 98-141, left m1 (CBI-14); URBAC 99-101, left m1 lacking paraconid, metaconid and hypoconulid (CBI-14); URBAC 98-128, right m1 lacking metaconid and hypoconulid (CBI-14); URBAC 98-129, left m1 trigonid (CBI-14); URBAC 98-131, right m1 trigonid (CBI-14); URBAC 98-143, left m1 trigonid lacking protoconid (CBI-14); URBAC 04-163, left dentary with m2–3, m1 lacking most of the crown, and alveoli for p5 (CBI-14); ZIN 84971, right dentary with m2–3 talonids, m1 roots, and alveoli for c, p1–2, 4–5 (CBI-14, 1985); URBAC 03-94, left dentary with m2 and alveoli for p5, m1, and m3 (CBI-14); URBAC 04-170, right dentary with erupting m3 and posterior alveolus for m2 (CBI-14); URBAC 02-22, left dentary with m3 in crypt and alveoli for m1–2 (CBI-4e); URBAC 03-22, left dentary with m3 in crypt and alveoli for m2 (CBI-14); ZIN 84970, left dentary with m3 talonid and posterior alveolus for c, double-rooted alveoli for p1–2, 3–4, m1–2, and anterior alveolus for m3 (CBI-14, 1980); URBAC 04-51, right dentary with m3 lacking trigonid and part of the coronoid process (CBI-14); URBAC 02-37, left dentary with m3 lacking most of the trigonid and alveoli for m1–2 (CBI-4e); URBAC 04-21, left dentary with m3 lacking metaconid and alveoli for m2 (CBI-14); URBAC 98-133, left m3 (CBI-14); ZIN 88440, right dentary with alveoli for p1–2, 4 (CBI-4a, 1989); URBAC 03-140, right dentary with alveoli for p2, 4–5 and posterior alveolus for p1 (CBI-14); URBAC 02-39, left dentary with fragments of p4–5 and alveoli for m1–2 (CBI-4e); URBAC 04-83, right dentary with alveoli for p4–5, m1–3 (CBI-14); URBAC 03-201, right dentary with alveoli for p4–5, m1–2 (CBI-14); URBAC 04-210, left dentary with alveoli for p4–5, m1–2 (CBI-14); ZIN 88439, left dentary with posterior alveolus for p5, alveoli for m1–3 and part of angular process (CBI-14, 1989); URBAC 02-11, left dentary with alveoli for p5, m1–3 (CBI-4e); URBAC 03-82, left dentary with alveoli for p5, m1–3 (CBI-14);

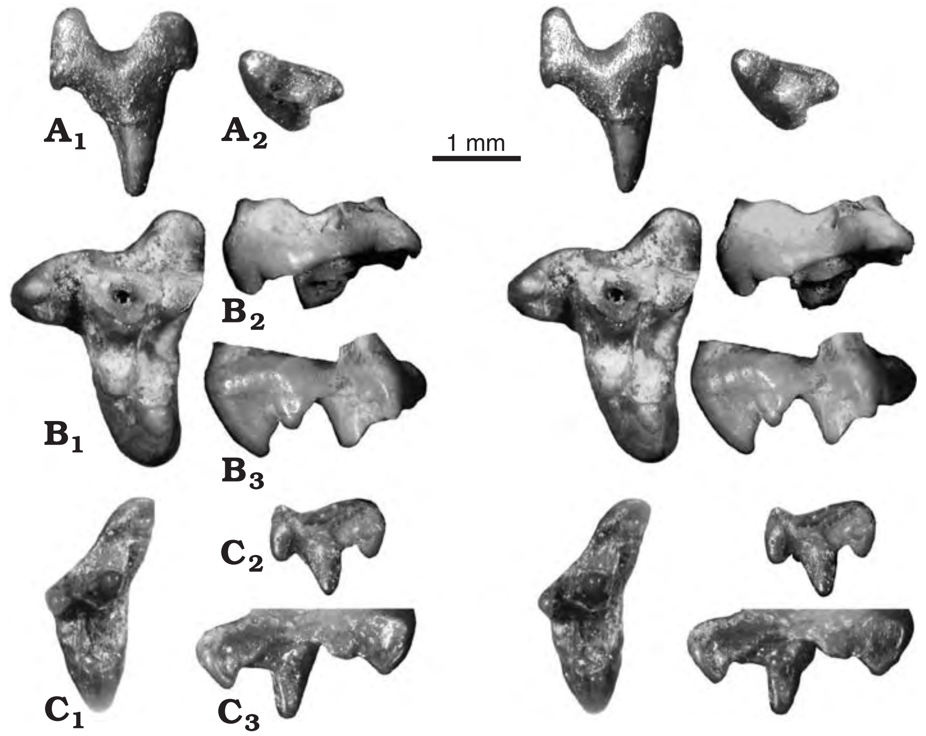

Fig. 8. Stereopairs of *Bulaklestes kezbe* Nessov, 1985; Dzharakuduk, Uzbekistan, Late Cretaceous (Turonian). **A**. 1985. CCMGE 19/12176, right P4; in labial (A_1) and occlusal (A_2) views. **B**. ZIN 82591, left M1 lacking paracone; in occlusal (B_1), labial (B_2), and anterior (B_3) views. **C**. CCMGE 12/12176, type, right M3; in occlusal (C_1), labial (C_2), and anterior (C_3) views.

URBAC 97-12, left dentary with alveoli for m1–3 and parts of coronoid and angular processes (CBI-14); ZIN 88927, left dentary with alveoli for m1–3 and parts of coronoid and angular processes (CBI- uncertain locality); URBAC 03-149, left dentary with alveoli for m1–3 and part of angular process (CBI-14); ZIN 88960, left dentary with roots of m1–3 (CBI-14, 1987); URBAC 00-58, left dentary with alveoli for m1–3 (CBI-14); ZIN 88442, left dentary with alveoli for m1–3 (CBI-14, 1989); ZIN 88487, right dentary with alveoli for m1–3 (CBI-4a, 1989); URBAC 02-31, left dentary with posterior alveolus for m1 and alveoli for m2–3 (CBI-4e); URBAC 00-38, right dentary with alveoli for m2 and erupting m3 (CBI-4e); ZIN 88492, left dentary with alveoli for m2–3 (CBI-14, 1987); ZIN 88496, left dentary with alveoli for m2–3 (CBI-14, 1980); URBAC 04-78, left dentary with alveoli for m2–3 (CBI-14); URBAC 04-167, left dentary with alveoli for m2–3 (CBI-14); URBAC 04-216, left dentary with alveoli for m2–3 (CBI-14); URBAC 04-222, left dentary with alveoli for m2–3 (CBI-14); URBAC 03-1999, right dentary with alveoli for m2–3 (CBI-14); ZIN 88956, right dentary with alveoli for m1–3 (CBI-15, 1985); URBAC 98-144, left dentary with alveoli for m3 (CBI-14); URBAC 02-42, left dentary with alveoli for m3 (CBI-4e); URBAC 04-142, left dentary with alveoli for m3 (CBI-14).

Diagnosis.—As for the genus.

Description.—There are two P4s referred to this species. They differ slightly in size, but are similar in morphology. The crown is very high, with the apex canted slightly posteriorly (Fig. 8A). The faint anterior and posterior crests extend from the apex toward the anterior and posterior basal cusps respectively. The posterior crest possesses a distinct swelling. The labial side of the single, large cusp is gently concave. On the lingual side there is a swelling in the middle of the crown, which is not complete on either specimen. This swelling possibly was supported by a small separate (third) root, but this is not certain. There is a faint posterolingual cingulum.

Except in size, M1 differs from M1s in *D. inobservabilis* in having a relatively larger parastyle (also pronounced in M3) and a thickened, cusp-like crest between the stylocone and parastyle. There are no pre- or postcingula (Fig. 8B).

For a description of M3 see the description of CCMGE 12/12176 in Nessov et al. (1994: 64–65), here shown in Fig. 8C. This tooth has some very faint swellings in the postcingular region.

The dentary symphysis terminates below p1 or p2 (URBAC 00-61, URBAC 03-142, ZIN 84971) (Fig. $9B_3$). There are two anterior mental foramina. The first is below i4? (URBAC 00-61), while the second is below the anterior root of p1 (ZIN 84970, 84971), the posterior root of p1 (URBAC 00-61), or between c and p1 (URBAC 03-142) (Fig. $9B_2$). The posterior mental foramen is below the anterior root of p5 (ZIN 84970, 84971, URBAC 02-11, 02-39, 03-94, 03-142, 04-210), or the middle of this tooth (URBAC 03-82, URBAC 03-142) (Fig. $9A_2$). In ZIN 84971 there is a smaller, second posterior mental foramen below the posterior root of p5. The depth of the dentary increases markedly with age (deepest in URBAC 04-163 at 2.7 mm, Fig. $10D_1$).

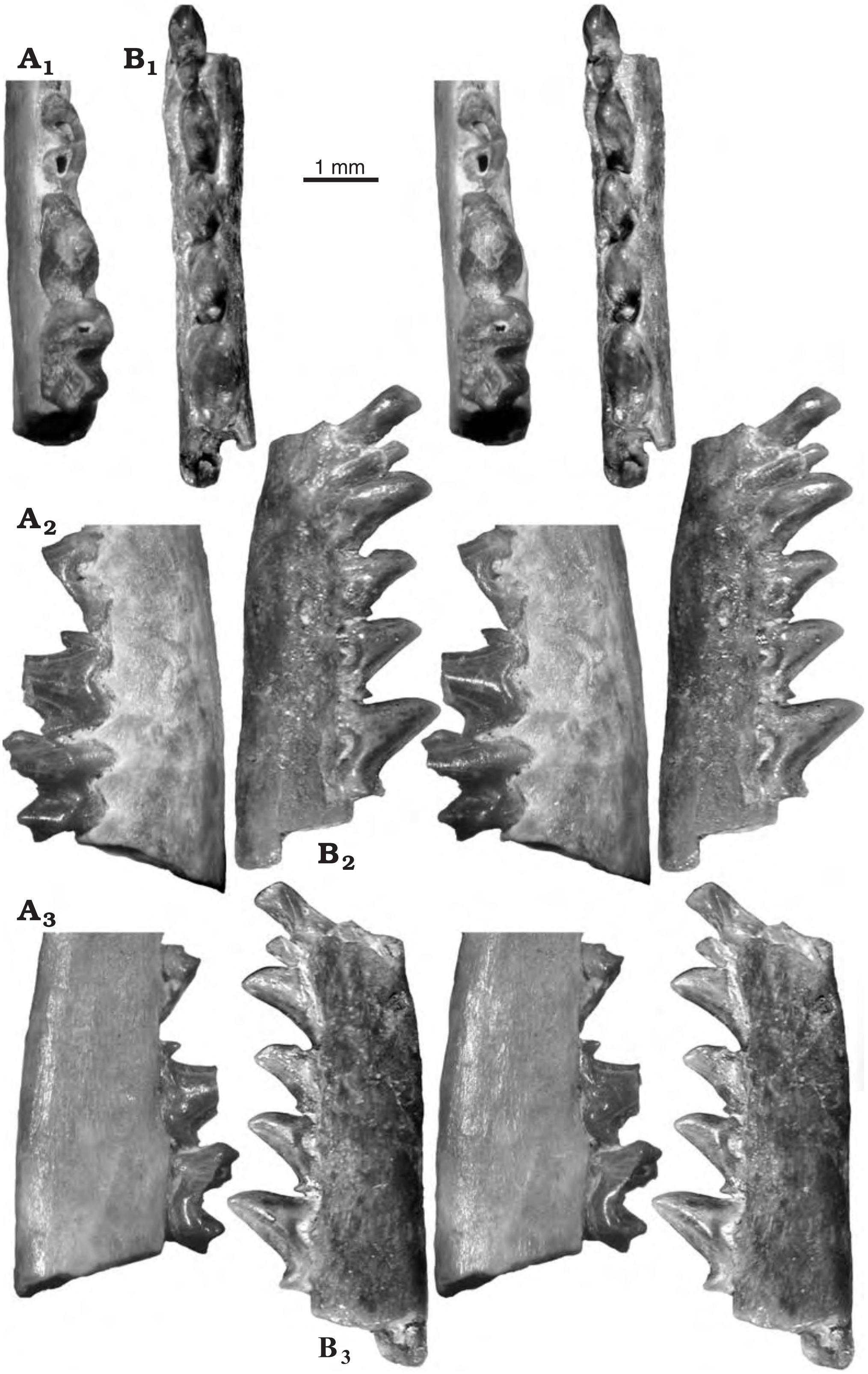

Fig. 9. Stereopairs of *Bulaklestes kezbe* Nessov, 1985; Dzharakuduk, Uzbekistan, Late Cretaceous (Turonian). **A**. URBAC 03-142, right dentary with p4 missing most of the crown, p5, m1, and alveoli for two-rooted c and p1–2 (p4–5, m1 shown), in occlusal (A_1), labial (A_2), and lingual (A_3) views. **B**. URBAC 00-61, left dentary with i3?–4?, c, p1–2, 4, in occlusal (B_1), labial (B_2), and lingual (B_3) views.

A single larger mandibular foramen or several smaller masseteric foramina are present. In ZIN 88439, URBAC 97-12, and 03-149 the base of the mandibular angle and the mandibular foramen are preserved, which are similar to those

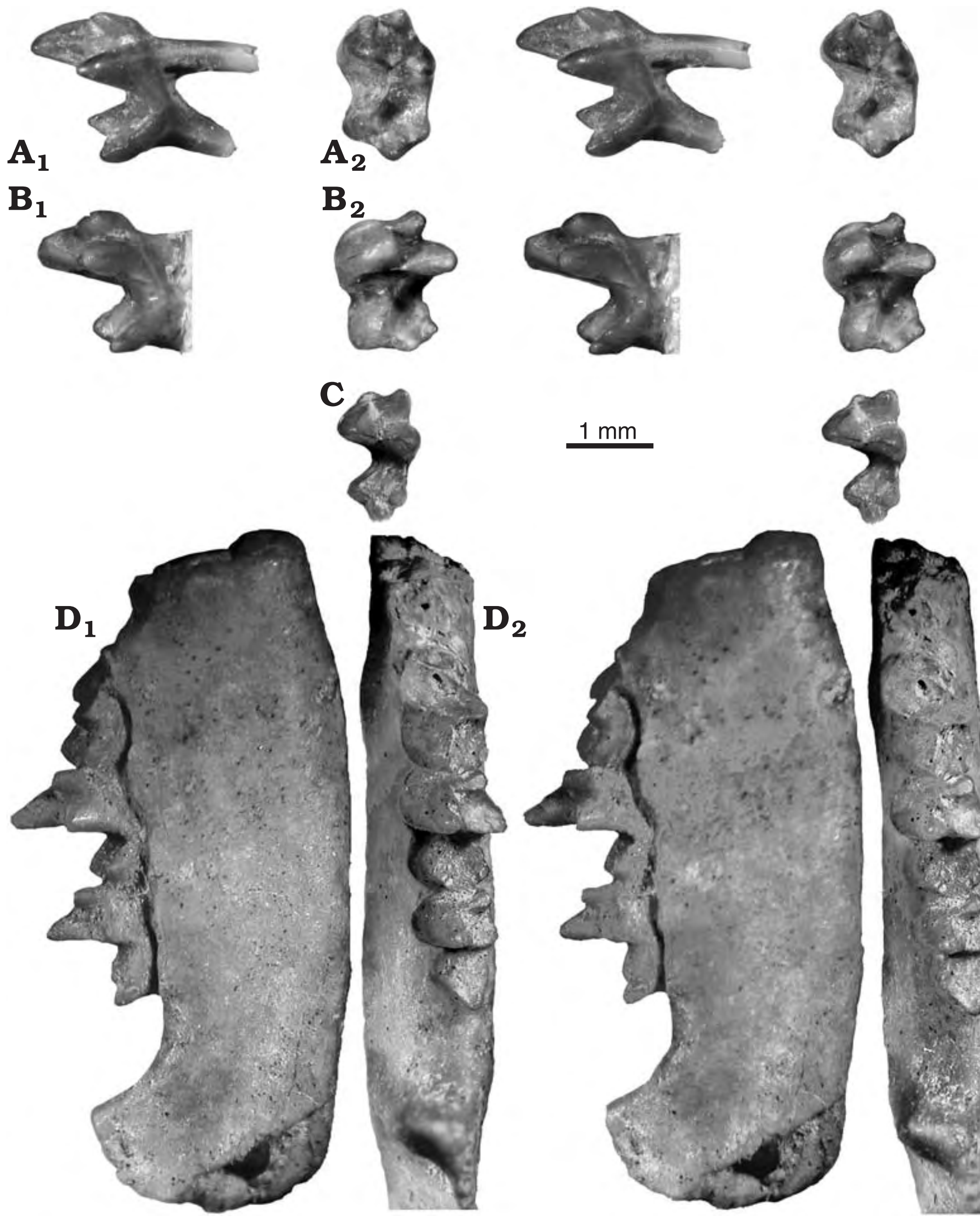

Fig. 10. Stereopairs of *Bulaklestes kezbe* Nessov, 1985; Dzharakuduk, Uzbekistan, Late Cretaceous (Turonian). **A**. URBAC 98-141, left m1, in lingual (A_1) and occlusal (A_2) views. **B**. URBAC 03-94, m2 from left dentary with m2 and alveoli for p5, m1, and m3, in lingual (B_1) and occlusal (B_2) views. **C**. URBAC 04-170, erupting m3 from right dentary with erupting m3 and posterior alveolus for m2; occlusal. **D**. URBAC 04-163, left dentary with m2–3, m1 lacking most of the crown, and alveoli for p5, in lingual (D_1) and occlusal (D_2) views.

in *Uchkudukodon nessovi*. The angle is somewhat inflected medially. On the medial side of the coronoid process on ZIN 88439 and URBAC 04-83, there is a subhorizontal line delimiting the ventral border for the temporalis muscle. Only three of 32 specimens that preserve the posterior portion of the dentary come from individuals with m3 in some stage of eruption.

What we here identify as i3 and i4 (known only in URBAC 00-61) are slightly procumbent (Fig. 9B). The presumed i4 is less than half the size of the presumed i3, but both have similar crown construction. The crown is anteroposteriorly expanded, with a single cusp and short anterior and longer keels, and a lingual cingulid, which is more pronounced on the presumed i3. In URBAC 00-61, the presumed i4 is displaced labially compared to the presumed i3.

The lower canine is double-rooted and higher than the presumed i3. There is a very faint posterior cusp (Fig. 9B).

The p1–2 and 4 are double-rooted and similar in structure, gradually increasing in size posteriorly (URBAC 00-61) (Fig. 9B). The same is characteristic for other specimens. There is no paraconid and the talonid cusp is small on p1–2 and 4 of URBAC 00-61, while p4 in URBAC 03-142 has a small paraconid (Fig. 9A_1). The p4 is similar in height to the lower canine. In p5 the paraconid is much larger and there is a dis-

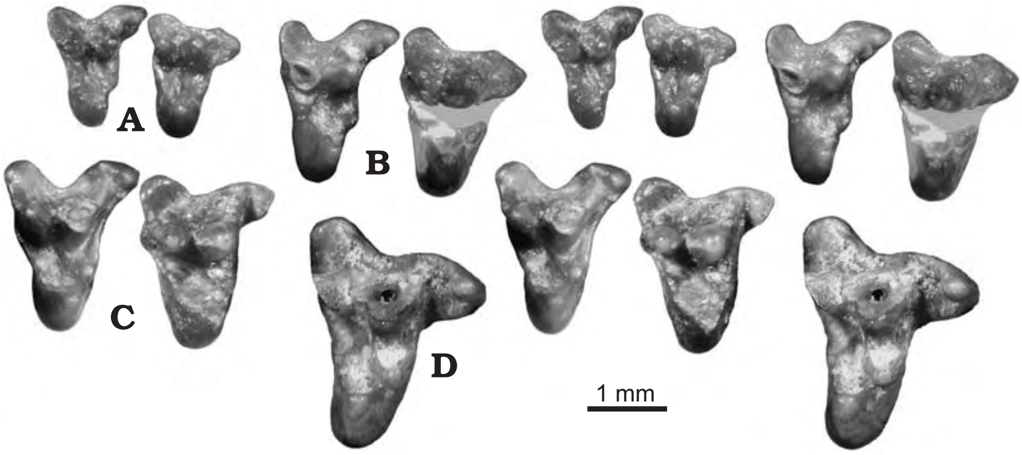

Fig. 11. Stereopairs of composite occlusal views of M1's and M2's. All specimens from Dzharakuduk, Uzbekistan, Late Cretaceous (Turonian). **A**. *Uchkudukodon nessovi* (McKenna, Kielan-Jaworowska, and Meng, 2000) (URBAC 98-124, left M1 reversed and URBAC 03-213, right M2). **B**. *Daulestes kulbeckensis* Trofimov and Nessov, 1979 (URBAC 98-126, probably associated lingual and labial parts of a left M1, reversed and URBAC 98-127, a right M2 lacking the metacone). **C**. *Daulestes inobservabilis* (Nessov, 1982) (URBAC 02-91, right M1 and URBAC 98-140, left M2, reversed). **D**. *Bulaklestes kezbe* Nessov, 1985 (ZIN 82591, left M1 lacking paracone, reversed).

tinct anterolingual cingulid (URBAC 03-142). The talonid cusp is similar to the paraconid in size, but positioned higher on the crown. The very short and narrow talonid occupies only the lingual side of the crown, not extending as far labially as the anterior portion of the crown (Fig. 9A).

Lower molars (Figs. 9, 10) are similar to those in *D. inobservabilis*, with a rather oblique protocristid on m1, and the cristid obliqua is lingual to or at the protocristid notch. The m3 hypoconulid is posteriorly procumbent, as in other Dzharakuduk asioryctitheres.

Measurements.—See Tables 1 and 2.

Discussion

Our revision of asioryctitherians from Dzharakuduk reveals four species that differ in relative size of p4 and p5, proportions of M1 to m1, and in size (Fig. 11), which are, from smallest to largest: *Uchkudukodon nessovi*, *Daulestes kulbeckensis*, *D. inobservabilis*, and *Bulaklestes kezbe*. *Uchkudukodon nessovi* includes specimens that are among the smallest therian mammals known, with molars about 1 mm in length. The smallest specimens of *U. nessovi* are similar in size to the minute *Batodon tenius* from the Campanian– Maastrichtian of North America (Wood and Clemens 2001), but larger than the Eocene *Batodonoides vanhouteni* from North America (Bloch et al. 1998). In addition to being the largest Dzharakuduk asioryctithere, *Bulaklestes kezbe* retains two characters that appear to be ancestral relative to other asiorytitheres (but see Phylogenetic Analysis). In *Bulaklestes* p4 is distinctly shorter than p5 while in other asiorytitheres p4 is equal to or longer than p5, and in *Bulaklestes* the simple p5 talonid is narrower than the greatest width of the crown while in other asiorytitheres the p5 talonid reaches the greatest labial extent of the crown (not reported for *Ukhaatherium*).

The interpretation of the anterior dentition in *Daulestes* has been problematic. Originally the holotype of *D. kulbeckensis* was interpreted as having c, p2, 3, 4, m1 and alveoli for the last incisor (designated as i3, or i?), and m2 (Nessov and Trofimov 1979). Using the number of alveoli or root fragments preserved, this interpretation implies a single-rooted small c and a double-rooted p1 (its small anterior alveolus was not depicted in Nessov and Trofimov 1979: fig. 1), a single rooted p2, and a double-rooted p3 and p4. This interpretation contradicts the original statement (Nessov and Trofimov 1979: 953) that "premolars have two roots". Nessov (1982: 235) corrected the latter, indicating that p1 is double-rooted and p2 is single-rooted. The issue was further complicated by Nessov et al. (1994: 56) who proposed several hypotheses interpreting the anterior dentition in *D. kulbeckensis*: "either [it] had 5 premolars, the three anterior teeth having only one root; or there were only 4 premolars; or the 'canine' was in fact a p1; finally the respective sizes of the last two premolars might suggest that the antepenultimate could be a milk tooth [...]".

Subsequently, McKenna et al. (2000) accepted a single-rooted p2 hypothesis for *D. kulbeckensis* and used this character to differentiate it from their new species *Daulestes nessovi*, which has a double-rooted p2. The newly collected materials of *Daulestes, Uchkudukodon* gen. nov., and *Bulaklestes*, including a dentary fragment URBAC 00-61 of *B. kezbe* with two complete last incisors, c, p1–2, 4, as well as several edentulous anterior dentary fragments, indicate that none of these hypotheses is correct (Figs. 9B and 12). Like *Asioryctes* and *Kennalestes*, *Daulestes, Uchkudukodon* gen. nov., and *Bulaklestes* had a double-rooted lower canine (single-rooted in *Ukhaatherium*) and four double-rooted lower premolars (also seen in *Ukhaatherium*). As was noted earlier, these premolars are designated here as p1, p2, p4, and p5, in contrast to p1, p2, p3, and p4 in most previous studies.

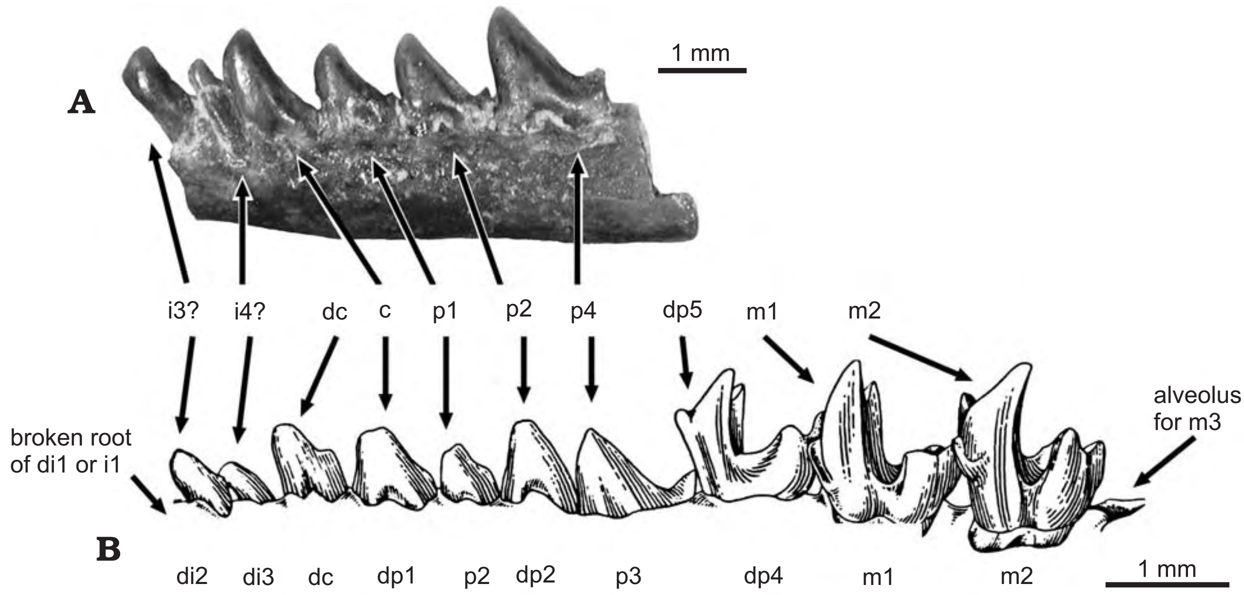

Fig. 12. Labial views, lower anterior dentitions of *Bulaklestes kezbe* Nessov, 1985 (**A**) and of *Uchkudukodon nessovi* (McKenna, Kielan-Jaworowska, and Meng, 2000) (**B**, drawing from McKenna et al. 2000: fig. 16D). Both from Dzharakuduk, Uzbekistan, Late Cretaceous (Turonian). Our interpretations of tooth identifications for both taxa are between the dentaries and those of McKenna et al. (2000) for *U. nessovi* are below the lower dentary.

The newly collected material allows us to also modify the interpretation of the anterior dentition in the juvenile skull ZIN 79066, the holotype of *Uchkudukodon nessovi*, which was thought to be di2, di3, dc, dp1, p2, dp2, p3, and dp4 (Fig. 12; McKenna et al. 2000: fig. 16C–E). The tooth designated as delayed "dp2" is distinctly larger than the anteriorly placed "p2" and thus would not likely be a deciduous predecessor. Based on our observations, milk teeth in Cretaceous eutherians are smaller or occasionally similar in size, but not larger than their permanent analogs. We interpret the same dentition as probably di3, probably di4, dc, c, p1, p2, p4, and dp5 (Fig. 12). The uncertainty regarding incisor identification is a result of the anterior margin of the dentary being absent. Thus the pattern of eruption of the postcanine lower dentition would be (p1, 2, m1, 2) – p4–m3–p5. In this interpretation the shedding of dc is delayed until the complete eruption of c, a situation that is not infrequent in modern mammals, notably in some terrestrial carnivorans and pinnipeds (Averianov, personal observations). As was pointed out to us (John Wible, personal communication 2005), if our interpretations are correct, in ZIN 79066, although dc is anterior to DC (see fig. 7 in McKenna et al. 2000), what we interpret as c is posterior to DC. We attribute this to the young age of the individual, so that as the animal increased in size, c would migrate anterior to C when it erupts and as dc is lost. The number of lower incisors is unknown for all Dzharakuduk asioryctitheres, but all other known asioryctitherians for which the anterior end of the dentary is known have four lower incisors, and this number would be a reasonable guess for Dzharakuduk asioryctitheres.

Reinterpretation of the lower dentition in ZIN 79066 suggests that the upper premolars in this specimen are P1–2, 4, DP5, rather than DP1, DP2 (or P2), P3, and DP4 (McKenna et al. 2000: fig. 16A, B).

In their revised diagnosis of *Daulestes*, McKenna et al. (2000: 5) noted that this taxon "[s]hares with *Asioryctes* and *Ukhaatherium* a strongly asymmetrical stylar shelf on the upper molars, especially on M2, with a large parastylar and small metastylar lobe region." New materials show that the M1–2 metastylar lobe is more variable in Dzharakuduk asioryctitheres, varying in size from reduced to similar in size to that of the parastylar lobe. There may be differences between species in the relative size of the stylar lobes, but based on available samples, this cannot be determined.

McKenna et al. (2000: 5) cited as diagnostic for *Daulestes* the lack of a single masseteric foramen. Again, new material shows that this structure is more variable in Dzharakuduk asioryctitheres, ranging from a single large foramen to several small foramina. Masseteric foramina or a single foramen are also variably present in *Prokennalestes* and *Bobolestes* (= *Otlestes*), present among most if not all triconodontids and *Vincelestes*, lacking in *Kuehneotherium* and *Morganucodon* (Cifelli et al. 1998) and variably present in metatheres (Cifelli and Muizon 1998). Possibly this character has no great phylogenetic significance.

Uchkudukodon gen. nov. for which a reasonably complete, nicely preserved skull has been described (McKenna et al. 2000), is one of the best-known Cretaceous eutherians. At present, however, cranial characters of *Uchkudukodon* gen. nov. are of little use for assessment of its phylogenetic position because the majority of other Cretaceous eutherians are not known from skulls. McKenna et al. (2000) proposed affinities of *Daulestes* with Mongolian asioryctitherians, mostly because of the supposed reduction of the metastylar lobe on upper molars. Originally, Asioryctitheria were diagnosed exclusively based on cranial characters (Novacek et al. 1997), but these taxa, indeed, have some reduction of the

Table 3. Character matrix. See text for explanation.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Eomaia	0	0	0	0	?	?	?	?	0	0	0
Prokennalestes	0	0	0	0, 1	1, 2	0	0	0	0	0	0
Bulaklestes	0	1	0	1	3	?	1	?	0	1	1
Kennalestes	0	0, 1	1	2	3	0	0	0	0	1	2
Asioryctes	0	1	1	2	2	0	0	1	0	2	3
Ukhaatherium	0	1	1	2	2	0	0	1	0	2	3
Uchkudukodon nessovi	0	1	0	1	2	0	1	0	0	1	1
Daulestes kulbeckensis	0	?	?	?	3	0	1	0	0	1	1
Daulestes inobservabilis	0	?	0	1	3	0	0, 1	0	0	1	1
Parazh. mynbulakensis	0	0	0	1	2	2	1	2	1	0	2
Parazh. robustus	0	?	0	1	2	1	1	2	1	0	2
Zhelestes	0	0	0	1	2	1	1	2	1	0	2
Aspanlestes	0	0	0	1	2	1	1	2	1	0	2
Kulbeckia	1	1	1	2	0	1	0	0	1	1	1
Zalambdalestes	1	1	1	2	0	1	0	0	1	0	2
Bobolestes	0	?	?	?	?	0	?	0	0	0	1
	12	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**
Eomaia	0	?	0	?	0	0	0	?	1	0	1
Prokennalestes	0	0	0	0	0	0	0	0	0	0	0
Bulaklestes	1	0	0	0	1	1	?	?	0	1	0
Kennalestes	1	0	1	0	1	1	1	0	0	1	1
Asioryctes	1	0	0	0	1	1	0	0	0	1	1
Ukhaatherium	1	0	0	0	?	?	0	0	1	1	1
Uchkudukodon nessovi	1	0	0	0	1	1	?	?	0	1	0
Daulestes kulbeckensis	1	0	0	0	1	1	?	?	0	1	0
Daulestes inobservabilis	1	0	0	0	1	1	?	?	0	1	0
Parazh. mynbulakensis	1	2	1	1	1	1	0	0	0	0	0
Parazh. robustus	1	3	1	1	1	1	0	0	1	0	0
Zhelestes	1	1	1	0	1	1	0	0	1	0	0
Aspanlestes	1	1	1	0	1	1	0	0	?	0	0
Kulbeckia	1	0	0, 1	0	1	1	0	1	0	1	1
Zalambdalestes	1	0	0	1	1	1	0	1	1	1	1
Bobolestes	0	0	0	0	1	1	1	0	1	0	0
	23	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**
Eomaia	0	0	?	?	?	0	0	?	0	?	0
Prokennalestes	0	0	0	0	0, 1	0	0	0	0	0	0
Bulaklestes	0, 1	0	0	0	1	0	0	0	0	0, 1	0
Kennalestes	1	1	0	1	1	0	0	0	0	1	0
Asioryctes	0	1	0	1	1	0	0	1	1	1	0
Ukhaatherium	0	1	?	?	?	0	0	?	?	?	?
Uchkudukodon nessovi	1	1	?	1	0	0	0	0	0	1	0
Daulestes kulbeckensis	1	1	0	1	0	0	0	0	0	1	0
Daulestes inobservabilis	1	1	0	1	0	0	0	0	0	1	0
Parazh. mynbulakensis	0	0	1	1	2	1	1	1	0	2	1
Parazh. robustus	1	0	1	1	2	1	1	1	0	2	1
Zhelestes	?	0	?	1	2	1	1	0	0	2	1
Aspanlestes	0	0	1	1	2	1	1	0	0	2	1
Kulbeckia	1	0	1	1	1	1	1	0	1	2	0
Zalambdalestes	1	0	1	1	2	1	1	1	1	2	0
Bobolestes	1	0	1	0	0	0	0	0	1	1	0

metastylar lobe on M1–2. As noted earlier, this character is more variable in Dzharakuduk asioryctitheres, with some upper molars having the metastylar lobe nearly as large as the parastylar lobe. Dzharakuduk asioryctitheres are some 15 my older than other asioryctitherians and such variation could be expected.

Phylogenetic analysis

In order to address phylogenetic relationships of *Daulestes*, *Uchkudukodon* gen. nov., and *Bulaklestes*, we performed a phylogenetic analysis including these taxa as well as *Kennalestes*, *Asioryctes*, and *Ukhaatherium* (Kielan-Jaworowska 1969, 1981, personal communication to JDA; Novacek et al. 1997; and personal observation by both authors of the original materials and casts of *Kennalestes* and *Asioryctes*). In addition, zalambdalestids, based on *Kulbeckia kulbecke* and *Zalambdalestes lechei* (Kielan-Jaworowska 1969; Archibald and Averianov 2003; Wible et al. 2004; and personal observation by both authors of the original materials and casts) and the Uzbek zhelestids, *Aspanlestes aptap*, *Parazhelestes mynbulakensis*, *Parazhelestes robustus*, and *Zhelestes temirkazyk* (Nessov et al. 1998; and personal observation by both authors of the original materials) were included. These four taxa of zhelestids were chosen, because they are demonstrably a clade, unlike for "Zhelestidae" as a whole when Tertiary placentals are included (e.g., Archibald et al. 2001). The mid-Cretaceous, questionable zalambdalestoid *Bobolestes zenge*, which now includes *Otlestes meiman* (Averianov and Archibald 2005) was included in the ingroup. The Early Cretaceous eutherian taxa *Eomaia scansoria* and *Prokennalestes* spp. (both *P. trofimovi* and *P. minor*) were used as outgroups (coding of *Eomaia* is after Ji et al. 2002 and coding of *Prokennalestes* is after Kielan-Jaworowska and Dashzeveg 1989; Sigogneau-Russell et al. 1992; and an extensive collection of this taxon from the Moscow Paleontological Institute studied by AA), with the remaining ingroup taxa treated as monophyletic. It should be noted that treating *Bobolestes* as a member of the ingroup or outgroup did not affect the topology of the remainder of the tree. All default settings were employed, including no weighting of characters and all multistate characters were unordered. The analysis employed the following 33 characters.

1) Shape of snout: with moderate tapering anteriorly (0), with marked narrowing anterior of posterior premolars (1).
2) Number of upper premolars: five (0), four or fewer (1).
3) Number of roots on P4: two (0), three (1).
4) Protocone on P4: absent (0), small protocone swelling (1), distinct protocone present (2).
5) M1 average length / m1 average length: 0.9 (0), 1.0 (1), 1.1 (2), 1.3 (3).
6) Stylar shelf on M1, 2: on both M1, 2 widest point of stylar shelf (centrocrista to greatest labial extent) equal or greater than 29% of total crown width (0), on both M1, 2 widest point of stylar shelf (centrocrista to greatest labial extent) from 19% to 27% of total crown width (1), on M1 widest point of stylar shelf (centrocrista to greatest labial extent) from 19% to 27% of total crown width and on M2 widest point of stylar shelf (centrocrista to greatest labial extent) equal or greater than 29% of total crown width (2).
7) M1 parastylar lobe relative to paracone: parastylar lobe is anterolabial to the paracone (0), parastylar lobe is anterior to the paracone (1).
8) M2 parastylar and metastylar lobe positions: both lobes extend same distance labially (0), parastylar lobe is more labial than metastylar lobe (1), metastylar lobe is more labial than parastylar lobe (2).
9) Bases of paracone and metacone: partially fused (0), bases separate (1).
10) Conular basins: distinct para- and metaconular basins not present (0), distinct para- and metaconular basins present (1), metaconule very small or absent and metaconular basin absent (2).
11) Position of para- and metaconule: para- and metaconule closer to protocone than to para- and metacone, respectively (0), paraconule distinctly closer to protocone than is metaconule (1), paraconule and metaconule in approximately same labiolingual plane and midway or closer to paracone and metacone, respectively, than to protocone (2), metaconule may be very reduced or absent (3).
12) Height of protocone relative to paracone on M1–3: protocone distinctly lower (less than 70%) (0), protocone of intermediate height (70–80%) (1).
13) Antero-posterior expansion of protocone: none (0), slight (1), moderate (2), substantial (3).
14) Lingual cingula on M1–3: absent (0), present (1).
15) M3/m3 size relative to other M2/m2: not noticeably reduced (0), reduced (1).
16) Meckel's groove on dentary: present (0), absent (1).
17) Mandibular foramen (posterior opening of the mandibular canal): positioned on ventral shelf of a larger pterygoid fossa (0), opens into smaller depression on lingual side of ascending ramus of mandible (1).
18) Number of lower incisors: four (0), three (1).
19) Medial lower incisor: not distinctly larger than other lower incisors (0), greatly enlarged and procumbent (1).
20) Number of roots on lower canine: two (0), one (1).
21) Number of lower premolars: five (0), four or fewer (1).
22) Diastema separating p1 and p2: absent (0), present (1).
23) Paraconid on p4: present (0), absent (1).
24) Length of p5: longer than length of p4 (0), equal to or less than length of p4 (1).
25) Metaconid on p5: absent (0), present (1).
26) Talonid of p5: narrower than anterior portion of crown (0), as wide as anterior portion of crown (1).
27) Average length of m1 (in mm): 1.2–1.4 (0); 1.6–1.9 (1); 2.1–2.4 (2).

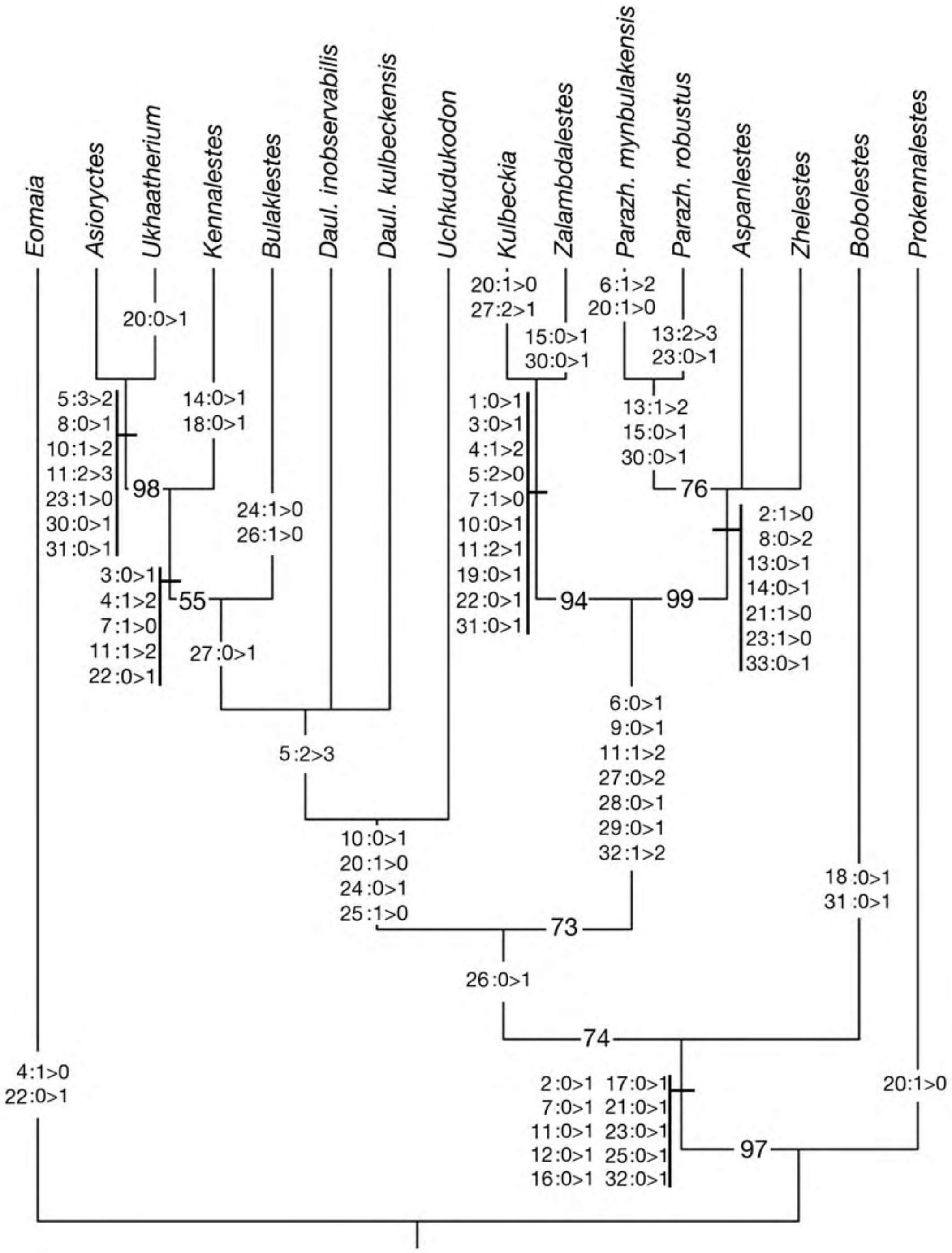

Fig. 13. Strict consensus tree of three equally parsimonious trees produced by reweighting the 33 characters listed in the text using the maximum value of the rescaled consistency indices, resulting in more internal resolution of Asioryctitheria. The single numbers on each tree are bootstrap values greater than 50 that were each produced from 10,000 replicate runs. The characters and state changes are those listed and discussed in the text.

28) Trigonid width relative to talonid width of m1–2: trigonid wider than talonid (0); trigonid narrower than talonid (1).
29) Trigonid height relative to talonid height of m1–3: trigonid twice or more the height of talonid (0); trigonid less than twice the height of the talonid (1).
30) Anterior-posterior constriction of trigonid on m1–3: none apparent (0); some constriction apparent, especially on m2 (1).
31) Pinching of trigonid at its midpoint: absent (0), present (1)
32) Cristid obliqua on m1–3: contact closest to middle posterior of metaconid (0), contact closest to protocristid notch (1), labial to protocristid notch (2).
33) Entoconid and hypoconulid relative to hypoconid: entoconid and hypoconulid slightly closer to each other ("twinned") (0), entoconid and hypoconulid not closer to each other (1).

A branch-and-bound PAUP (version 4.0b10) search of the data matrix present in Table 3 yielded nine most parsimonious trees. A strict consensus tree yielded almost no resolution within the ingroup. In order to recover more internal resolution, the characters were reweighted by PAUP using the maximum value of the rescaled consistency indices and then the PAUP analysis was rerun using a branch-and-bound search. The result was three most parsimonious trees with tree length 39.715, CI = 0.766, RI = 0.870, RC = 0.667, and HI = 0.293.

Fig. 13 shows the strict consensus tree for these three trees. The character state changes are those reconstructed directly from PAUP for the strict consensus tree. Bootstrap values of over 50 based on 10,000 replicates are shown on the tree. As can be seen, there is weak support for Asioryctitheria. Two reasons for this are that the Dzharakuduk asioryctitheres retain a number of ancestral eutherian traits and this analysis by necessity was largely limited to dental characters.

While previous studies have strongly supported monophyly of zhelestids and zalambdalestids relative to other Cretaceous eutherians (e.g., Archibald et al. 2001; Wible et al. 2004), their apparently strong association in the present analysis must be viewed cautiously. The included taxa in these two clades tend to share characters related to the lessening of shear and the increase of crushing in the dentition. While we cannot demonstrate it, we feel that these traits may have evolved in parallel. This is suggested by the equivocal evidence that the mid-Cretaceous *Bobolestes* shares characters with zalambdalestids such as a somewhat molarized ultimate premolar and a pinching of the molar trigonids at their midpoints. Note that even given these possible synapomorphies, *Bobolestes* clearly falls as the most basal member of the ingroup in the present analysis rather than with zalambdalestids. Similarly, the mid-Cretaceous zhelestids *Eozhelestes* and *Sheikdzheilia* share some but not all characters with the Dzharakuduk zhelestids used in this analysis (Averianov and Archibald 2005). This is suggestive but not demonstrable that the traits that unite zhelestids and zalambdalestids evolved in parallel.

Because the results of this analysis only weakly support the monophyly of Asioryctitheria, we do feel that changes in current taxonomy are not warranted. Accordingly, based on this analysis we suggest the (indented) classification in Table 4. For those who wish, categories may be added to the taxa.

Table 4. Indented classification of Asioryctitheria.

Asioryctitheria
- *Uchkudukodon nessovi*
- (unnamed taxon)
  - *Daulestes kulbeckensis*
  - *Daulestes inobservabilis*
  - (unnamed taxon)
    - *Bulaklestes kezbe*
    - Asioryctidae
      - *Kennalestes gobiensis*
      - Asioryctinae
        - *Asioryctes nemegetensis*
        - *Ukhaatherium nessovi*

Asioryctitheria.—*Kennalestes* and *Asioryctes* have long been considered as representatives of two different lineages of early eutherians, leptictoids and palaeoryctoids respectively (e.g., Kielan-Jaworowska 1969, 1975, 1981; Kielan-Jaworowska et al. 1979), until Novacek et al. (1997) demonstrated, based on cranial characters, that both taxa belong to an endemic Asiatic clade Asioryctitheria. Novacek et al. (1997) grouped the newly described *Ukhaatherium* and *Asioryctes* within Asioryctidae and separated these two genera from *Kennalestes* by the following characters: P2 smaller than P1, upper molars more strongly widened transversely and lacking pre- and postcingula, lower molars with smaller paraconids and more compressed trigonids, mastoid exposure rectangular in outline with large lower foramen, anterior contact of jugal with maxilla strongly bifurcate. In our analysis (Fig. 13) the association of *Ukhaatherium*, *Asioryctes*, and *Kennalestes* is also supported, but only weakly so, by five largely dental character state changes. In our analysis, Asioryctitheria is also weakly supported but by only the four following character state changes: (character 10) conular basins become distinct, (character 20) the number of roots reverts to two on the lower canine, (character 24) the p4 becomes longer than p5, and (character 25) the metaconid on p5 is reduced and lost. Except for character 25, each of the other characters undergoes further change in one or more taxa within Asioryctitheria. One of these characters, number 24, appears to revert to the probably ancestral eutherian condition in which the p4 is shorter than p5 in one asioryctithere, *Bulaklestes*. Given the instability of the tree, it seems equally likely that *Bulaklestes* could be the basalmost asioryctithere.

Asioryctidae.—Kielan-Jaworowska et al. (2004) distinguished two families within Asioryctitheria, Asioryctidae and Kennalestidae. According to these authors, Asioryctidae differ from Kennalestidae in having a longer mesocranial region, P2 smaller than P1, very slender and strongly elongated transversely upper molars, with parastylar region more expanded labially, lack of pre- and postcingula, noticeably reduced metastylar region, five/four rather than four/three incisors, lower molars with smaller paraconids and more compressed trigonids. Some of these characters require comment. P2 is also smaller than P1 in *Uckudukodon* (unknown for *Bulaklestes* and *Daulestes*), *Eomaia*, and possibly in *Prokennalestes*, and thus this condition might be ancestral for Eutheria, not derived for the Asioryctidae. Lingual cingula on upper molars are known for the asioryctitherian *Kennalestes*, an autapomorphy of this taxon (this character was independently acquired in a number of Cretaceous eutherian taxa). Reduction of the metastylar region of upper molars is variably present in *Daulestes* and consistent presence of this character might be a synapomorphy for *Asioryctes* and *Ukhaatherium*.

Both family group names Kennalestidae and Asioryctidae appeared on the same paper and the same page (Kielan-

Jaworowska 1981: 67), albeit the first name appeared earlier on the page. We choose the name Asioryctidae Kielan-Jaworowska, 1981 as the senior subjective synonym for the name Kennalestidae Kielan-Jaworowska, 1981 by the principle of the first reviser (ICZN Article 24). Although Kennalestinae could be retained for *Kennalestes*, we do not follow this, as *Kennalestes* would be the only included taxon, thus making the subfamilal designation redundant.

Dzharakuduk Asioryctitheria.—*Bulaklestes*, *Daulestes*, and *Uchkudukodon* gen. nov., are now known only from the middle–late Turonian Bissekty local fauna of Dzharakuduk. Earlier reports of aff. *Daulestes* sp. from the late Turonian–?Coniacian Aitym local fauna of Dzharakuduk, based on the labial part of M1 (Averianov and Archibald 2003: fig. 5) are not confirmed by this study. This tooth has a labially placed metaconule and is possibly attributable to *Paranyctoides* or a small zhelestid.

As shown in the cladogram in Fig. 13 and discussed above, the Dzharakuduk asioryctitheres can be weakly united with the asioryctitheres from the 15 million year younger sites in the Gobi Desert, Mongolia. Within Asioryctitheria, however, the relationships of the Dzharakuduk asioryctitheres to the Gobi asioryctitheres are even less certain. All asioryctitheres except *Uchkudukodon* gen. nov. are united by a single character (5) in which the ratio of average M1 versus that of m1 increases from 1.1 to 1.3, but this is reversed in asioryctines. Next, all asioryctitheres except *Daulestes* and *Uchkudukodon* gen. nov. are also united by a single character (27) in which the average length of m1 (in mm) increases from a range of 1.2–1.4 to that of 1.6–1.9. This reflects a general increase in size of those taxa united by this character state change.

Asioryctitherians and other eutherians.—Asioryctitherians, like zalambdalestids have at most four upper (character 2) and four lower premolars, that are further reduced in more derived zalambdalestids (Wible et al. 2004). While this is shown as occurring at the base of the ingroup in our analysis, we feel that it is as likely to have occurred later in parallel within asioryctitheres and zalambdalestids. This is suggested by the fact that zhelestids most commonly retain five upper and lower premolars, and the lowers of *Bobolestes* are also known to have five premolars. The condition is unknown for the uppers in this taxon. To this we can add the similarity in the structure of the upper molar conules between *Daulestes*, *Uchkudukodon* gen. nov., *Bulaklestes* and the oldest zalambdalestid *Kulbeckia* (see Archibald and Averianov 2003) from the same Bissekty local fauna in Uzbekistan. In all these taxa the paraconule is distinctly closer to the protocone than is the metaconule. Archibald et al. (2001) concluded that in known specimens of *Zalambdalestes* and *Barunlestes* the disposition of the conules could not be made because of wear. Wible et al. (2004) concurred with Crompton and Kielan-Jaworowska (1978) that the conules are in the same labiolingual plane and closer to the paracone and metacone than to the protocone. The first author (JDA) examined (2004) specimens of *Zalambdalestes* and *Barunlestes* housed in Warsaw, in part to examine conular positions. The left M1 and, with less certainty, the left M2 of ZPAL MgM-I/16 of *Zalambdalestes* preserve the conules in the same labiolingual plane, equidistant between the paracone and metacone labially and the protocone lingually, as does the M2 of ZPAL MgM-I/72 of *Barunlestes*. Thus, we agree with Wible et al. (2004) that the conules are in the same labiolingual plane but we found them to be in a central position on the crown rather than closer to the paracone and metacone.

The characters in this analysis are mostly dental in nature because we wished to maximize the number of relatively completely sampled species that could be included. Further, we emphasized those characters that might better elucidate relationships among presumed asioryctitheres. Our results also indicate that zhelestids and zalambdalestids may be more closely related to one another than either is to asioryctitheres. Seven character state changes (Fig. 13) rather strongly suggest this and the bootstrap value of 73 also supports this. As discussed earlier, however, these similarities may be a result of parallel evolution of a more crushing dentition. Other studies (Wible et al. 2004) including additional characters have suggested zalambdalestids and asioryctitheres may be closely related but these studies did not include zhelestids, thus this question remains open.

These results in the present study support the emerging view that there are three major clades of eutherians in the Late Cretaceous of Asia: asioryctitheres, zhelestids, and zalambdalestids. The first and third of these are well represented in the mammalian faunas of both Uzbekistan and Mongolia, while the Asian record of the second clade remains at least for now limited to Uzbekistan.

Acknowledgements

The continued cooperation of the Zoological Institute, National Academy of Sciences of Uzbekistan, Tashkent, notably Djalaliddin Azimov and Yuri Chikin is much appreciated. We thank the URBAC expedition members Alexi Abramov (Zoological Institute, St. Petersburg), Gennady Cherepanov (St Petersburg State University, St. Petersburg), Igor Danilov (Zoological Institute, St. Petersburg), Sky Dominguez (San Diego State University, San Diego), Chris King (University of Greenwich, London), Eleni Kochkomazova (Zoological Institute, St. Petersburg), Tatiana Malyshkina (Institute of Geology and Geochemistry, Ekaterinburg), Noel Morris (Natural History Museum, London), Cory Redman (San Diego State University, San Diego), Anton Resvyi (St. Petersburg State University, St. Petersburg), Catherine Skrabec (Royal Ontario Museum, Toronto), Pavel Skutschas (St. Petersburg State University, St. Petersburg), Hans-Dieter Sues (National Museum of Natural History, Washington, D.C.), and David Ward (University of Greenwich, London) for their myriad field help and scientific expertise. The members of the URBAC field staff (Nicholai Sukhoverikov, Erkin Salikhbaev, Shukhrat Salikhbaev, and Boris Veretennikov, all from Tashkent), our liaison in Tashkent (Oleg Tsaruk), and the Navoi Mining and Metallurgy Combinat and their subsidiaries, Nikolai Kuchersky (Navoi), Vladimir Novikov (Uchkuduk), Vasily Poverennov (Zarafshon), Gennady Prokhorenko (Zarafshon), Nicholai Pronin (Uchkuduk), have been paramount in our continued success. The first author thanks George Shkurkin (Berkeley) for making available his 1981 English translation of Nessov and Trofimov (1979) and

Jennifer Valentine (San Diego State University, San Diego), for various help in the lab with specimens. We thank Richard Cifelli (University of Oklahoma, Norman) and an anonymous reviewer for helpful comments on the manuscript, William Clemens and Patricia Holroyd (University of California, Berkeley) for the loan of specimens from the University of California Museum of Paleontology, Zofia Kielan-Jaworowska (Institute of Paleobiology, Warsaw) for permission to study specimens and photographs in her care, and Jørn Hurum for photographs of these same specimens. The financial support of the National Geographic Society (5901-97 and 6281-98), the National Science Foundation (EAR-9804771 and 0207004), the Navoi Mining and Metallurgy Combinat, and the Civilian Research and Development Foundation (RU-G1-2571-ST-04) are gratefully acknowledged. The work of AA was supported by the President's of Russia grant MD-255.2003.04, by the Russian Fund of Basic Research grants 04-04-49113 and 04-04-49637, and by the Russian Science Support Foundation.

References

Archibald, J.D. 1982. A study of Mammalia and geology across the Cretaceous–Tertiary boundary in Garfield County, Montana. *University of California Publications in Geological Sciences* 122: 1–286.

Archibald, J.D. 1996. Fossil evidence for a Late Cretaceous origin of "hoofed" mammals. *Science* 272: 1150–1153.

Archibald, J.D. and Averianov, A.O. 1997. New evidence for the ancestral placental premolar count. *Journal of Vertebrate Paleontology* 17(Supplement to No. 3): 29A.

Archibald, J.D. [Arčibal'd J.D.] and Averianov, A.O. 1998. Original tooth formula fundamental for placental mammals (Mammalia, Eutheria) [in Russian]. *Zoologičesij Institut Rossiiskoj Akademii Nauk, Otčyetnaya Naučnaya Syesseya po Itogam Rabot 1997 goda*, 7. Sankt-Peterburg.

Archibald, J.D. and Averianov, A.O. 2003. The Late Cretaceous placental mammal *Kulbeckia*. *Journal of Vertebrate Paleontology* 23: 404–419.

Archibald, J.D. and Averianov, A.O. 2005. Mammalian faunal succession in the Cretaceous of the Kyzylkum Desert. *Journal of Mammalian Evolution* 12: 9–22.

Archibald, J.D., Averianov, A.O., and 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., King, C., Ward, D.J., Tsaruk, O.I., Danilov, I.G., Rezvyi, A.S., Veretennikov, B.G., and Khodjaev, A. 1998. Précis of the Cretaceous paleontology, biostratigraphy and sedimentology at Dzharakuduk (Turonian?–Santonian), Kyzylkum Desert, Uzbekistan. *In*: S.G. Lucas, J.I. Kirkland, and J.W. Estep (eds.), Lower to Middle Cretaceous Terrestrial Ecosystems. *Bulletin of the New Mexico Museum of Natural History and Science* 14: 21–28.

Averianov, A.O. 2000. Mammals from the Mesozoic of Kyrgyzstan, Uzbekistan, Kazakhstan and Tajikistan. *In*: M.J. Benton, M.A. Shishkin, D.M. Unwin, and E.N. Kurochkin (eds.), *The Age of Dinosaurs in Russia and Mongolia*, 627–652. Cambridge University Press, Cambridge.

Averianov, A.O. and Archibald, J.D. 2003. Mammals from the Upper Cretaceous Aitym Formation, Kyzylkum Desert, Uzbekistan. *Cretaceous Research* 24: 171–191.

Averianov, A.O. and Archibald, J.D. 2005. Mammals from the mid-Cretaceous Khodzhakul Formation, Kyzylkum Desert, Uzbekistan. *Cretaceous Research* 26: 593–608.

Bazhanov, V.S. [Bažanov, V.S.] 1972. First Mesozoic Mammalia (*Beleutinus orlovi* Bashanov) from the USSR [in Russian]. *Teriologiâ* 1: 74–80.

Bloch, J.I., Rose, K.D., and Gingerich, P.D. 1998. New species of *Batodonoides* (Lipotyphla, Geolabididae) from the Early Eocene of Wyoming: smallest known mammal? *Journal of Mammalogy* 79: 804–827.

Cifelli, R.L. 2000. Counting premolars in early eutherian mammals. *Acta Palaeontologica Polonica* 45: 195–198.

Cifelli, R.L. and Muizon, C. de. 1998. Marsupial mammal from the Upper Cretaceous North Horn Formation, central Utah. *Journal of Paleontology* 72: 532–537.

Cifelli, R.L., Wible, J.R., and Jenkins, F.A. Jr. 1998. Triconodont mammals from the Cloverly Formation (Lower Cretaceous), Montana and Wyoming. *Journal of Vertebrate Paleontology* 18: 237–241.

Crompton, A.W. and Kielan-Jaworowska, Z. 1978. Molar structure and occlusion in Cretaceous therian mammals. *In*: P.M. Butler and K.A. Joysey (eds.), *Development, Function and Evolution of Teeth*, 249–287. Academic Press, London.

Gill, T.N. 1872. Arrangement of the families of mammals. With analytical tables. *Smithsonian Miscellaneous Collections* 11: 1–98.

ICZN 1999. *International Code of Zoological Nomenclature, Fourth Edition*. 306 pp. International Trust for Zoological Nomenclature, c/o The Natural History Museum, London.

Kermack, K.A., Mussett, F., and Rigney, H.W. 1973. The lower jaw of *Morganucodon*. *Zoological Journal of the Linnean Society* 71: 1–158.

Kielan-Jaworowska, Z. 1969. Preliminary data on the Upper Cretaceous eutherian mammals from Bayn Dzak, Gobi Desert. *Palaeontologia Polonica* 19: 171–191.

Kielan-Jaworowska, Z. 1975. Preliminary description of two new eutherian genera from the Late Cretaceous of Mongolia. *Palaeontologia Polonica* 33: 5–16.

Kielan-Jaworowska, Z. 1981. Evolution of the therian mammals in the Late Cretaceous of Asia. Part IV. Skull structure in *Kennalestes* and *Asioryctes*. *Palaeontologia Polonica* 42: 25–78.

Kielan-Jaworowska, Z. and Dashzeveg, D. 1989. Eutherian mammals from the Early Cretaceous of Mongolia. *Zoologica Scripta* 18: 347–355.

Kielan-Jaworowska, Z., Bown, T.M., and Lillegraven, J.A. 1979. Eutheria. *In*: J.A. Lillegraven, Z. Kielan-Jaworowska, and W.A. Clemens (eds.), *Mesozoic Mammals: the First Two-Thirds of Mammalian History*, 221–258. University of California Press, Berkeley.

Kielan-Jaworowska, Z., Cifelli, R.L., and Luo, Z.-X. 2004. *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*. 630 pp. Columbia University Press, New York.

King, C., Morris, N.J., Ward, D.J., and Hampton, M.J. (in press). Late Cretaceous stratigraphy of the central and western Kyzylkum Desert, Uzbekistan. *Cretaceous Research*.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1: Regnum animale. Editio decima, reformata*. 824 pp. Laurentii Salvii, Stockholm.

McKenna, M.C. and Bell, S.K. 1997. *Classification of Mammals.* 631 pp. Columbia University Press, New York.

McKenna, M.C., Kielan-Jaworowska, Z., and Meng, J. 2000. Earliest eutherian mammal skull, from the Late Cretaceous (Coniacian) of Uzbekistan. *Acta Palaeontologica Polonica* 45: 1–54.

Nessov, L.A. [Nesov, L.A.] 1981. Cretaceous salamanders and frogs of Kizylkum Desert [in Russian]. *Trudy Zoologičeskogo Instituta AN SSSR* 101: 57–88.

Nessov, L.A. [Nesov, L.A.] 1982. The most ancient mammals of the USSR [in Russian]. *Ežegodnik Vsesoyuznogo Paleontologičeskogo Obŝestva* 25: 228–242.

Nessov, L.A. [Nesov, L.A.] 1984. On some remains of mammals in the Cretaceous deposits of the Middle Asia [in Russian]. *Vestnik Zoologii* 2: 60–65.

Nessov, L.A. [Nesov, L.A.] 1985. New mammals from the Cretaceous of Kyzylkum [in Russian]. *Vestnik Leningradskogo Universiteta, Seriâ 7*, 17: 8–18.

Nessov, L.A. [Nesov, L.A.] 1987. Results of search and study of Cretaceous and early Paleogene mammals on the territory of the USSR [in Russian]. *Ežegodnik Vsesoûznogo Paleontologičeskogo Obŝestva* 30: 199–218.

Nessov, L.A. [Nesov, L.A.] 1993. New Mesozoic mammals of Middle Asia and Kazakhstan and comments about evolution of theriofaunas of Cretaceous coastal plains of Asia [in Russian]. *Trudy Zoologičeskogo Instituta RAN* 249: 105–133.

Nessov, L.A. [Nesov, L.A.] 1995. *Dinozavry Severnoj Evrazii: novye* *dannye o sostave kompleksov, ekologii i paleobiogeografii*. 156 pp. Izdatel'stvo Sankt-Peterburgskogo Universiteta, Sankt-Peterburg.

Nessov, L.A. [Nesov, L.A.] 1997. *Melovye nemorskie pozvonočnye Severnoj Evrazii*. (Posthumous edition by L.B. Golovneva and A.O. Averianov). 218 pp. University of Saint Petersburg, Institute of the Earth Crust, Saint Petersburg.

Nessov, L.A. and Kielan-Jaworowska, Z. 1991. Evolution of the Cretaceous Asian therian mammals. *In*: Z. Kielan-Jaworowska, N. Heintz, and H.-A. Nakrem (eds.), Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota. Extended Abstracts. *Contributions from the Paleontological Museum, University of Oslo* 364: 51–52.

Nessov, L.A. [Nesov, L.A.] and Trofimov, B.A. 1979. The oldest insectivore of the Cretaceous of the Uzbek SSR [in Russian]. *Doklady Akademii Nauk SSSR* 247: 952–954.

Nessov, L.A., Archibald, J.D., and Kielan-Jaworowska, Z. 1998. Ungulate-like mammals from the Late Cretaceous of Uzbekistan and a phylogenetic analysis of Ungulatomorpha. *Bulletin of the Carnegie Museum of Natural History* 34: 40–88.

Nessov, L.A., Sigogneau-Russell, D., and 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.

Novacek, M.J. 1986. The ancestral eutherian dental formula. *Journal of Vertebrate Paleontology* 6: 191–196.

Novacek, M.J., Rougier, G.W., Wible, J.R., McKenna, M.C., Dashzeveg, D., and Horovitz, I. 1997. Epipubic bones in eutherian mammals from the Late Cretaceous of Mongolia. *Nature* 389: 483–486.

Sigogneau-Russell, D., Dashzeveg, D., and Russell, D.E. 1992. Further data on *Prokennalestes* (Mammalia, Eutheria *inc. sed.*) from the Early Cretaceous of Mongolia. *Zoologica Scripta* 21: 205–209.

Wible, J.R., Novacek, M.J., and Rougier, G.W. 2004. New data on the skull and dentition in the Mongolian Late Cretaceous eutherian mammal *Zalambdalestes*. *Bulletin of the American Museum of Natural History* 281: 1–144.

Wood, C.B. and Clemens, W.A. 2001. A new specimen and a functional reassociation of the molar dentition of *Batodon tenuis* (Placentalia, incertae sedis), latest Cretaceous (Lancian), North America. *Bulletin of the Museum of Comparative Zoology* 156: 99–118.