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## **New Material and Reinterpretation of the Late Cretaceous Eutherian Mammal Paranyctoides from Uzbekistan**

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# New material and reinterpretation of the Late Cretaceous eutherian mammal *Paranyctoides* from Uzbekistan

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*Paranyctoides aralensis*, based on a partially known set of lower postcanines from the Turonian Bissekty Formation of Uzbekistan, is proposed to be a junior subjective synonym of *Sailestes quadrans*, itself based on an M1 from the same stratigraphic unit. As a result, the latter taxon is recombined as *Paranyctoides quadrans* comb. nov. Based on newly collected or recognized specimens, we show that this species has four lower incisors, including a procumbent i1 and a relatively small i4, as well as five double-rooted premolars, the smallest of which (p3) can be lost ontogenetically. The p5 of this species is premolariform, rather than molariform as previously thought based on an erroneous identification, and resembles North American species of *Paranyctoides* in the presence of a small, cingulid-like paraconid and a distal talonid cusp, as well as the absence of a metaconid. The lower molars of *Paranyctoides* are unique among Late Cretaceous eutherians in having a larger, lingually placed paraconid. *Paranyctoides* probably is the sister taxon of the Late Cretaceous Zhelestidae.

Key words: Mammalia, Eutheria, *Paranyctoides*, Late Cretaceous, Uzbekistan.

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## Introduction

*Paranyctoides* Fox, 1979 is the only genus of Cretaceous eutherian mammal known from both Asia and North America. In North America, the genus has been reported from the Campanian (and possible Santonian) of Alberta, Canada, as well as the Campanian of Wyoming, Montana, New Mexico and Utah (Fox 1979, 1984; Lillegraven and McKenna 1986; Rigby and Wolberg 1987; Cifelli 1990; Montellano 1992), while in Asia it is known from the Turonian (and possibly Coniacian) of Uzbekistan (Nesov 1993; Archibald and Averianov 2001, 2005; Averianov and Archibald 2003). Here, we provide a taxonomic revision of *Paranyctoides* from Uzbekistan, based on the study of newly collected specimens and a reinterpretation of some previously published material. In addition, we discuss the phylogenetic relationships of this genus in light of some recently published cladistic analyses (Wible et al. 2009; Archibald and Averianov 2012).

*Institutional abbreviations and locality indexes.*—CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg; URBAC, Uzbek / Russian / British / American / Canadian Joint Paleontological Expedition specimens,

now housed in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.; ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg. CBI, Central [Kyzylkum Desert], Bissekty Formation, locality index used by L. Nesov for localities within the middle and upper parts of the Bissekty Formation. This index is used also for the localities within the Aitym Formation. CDZH, Central [Kyzylkum Desert], Dzharakuduk, locality index used by L. Nesov for localities within the lower part of the Bissekty Formation.

## Systematic paleontology

Mammalia Linnaeus, 1758

Theria Parker and Haswell, 1897

Eutheria Gill, 1872

Eutheria incertae sedis

Genus *Paranyctoides* Fox, 1979

1979 *Paranyctoides*; Fox 1979: 119.

1982 *Sailestes*; Nesov 1982: 237.

*Type species: Paranyctoides sternbergi* Fox, 1979. Irvine locality, Alberta, Canada; Oldman Formation, Judith River Group, middle Campanian, Upper Cretaceous.

*Paranyctoides quadrans* (Nesov, 1982), comb. nov.

Figs. 1, 2.

- 1981 *Sailestes quadrans* [nomen nudum]; Nesov 1981: fig. 11 (29).  
 1982 *Sailestes quadrans*; Nesov 1982: 238, pl. 2: 8.  
 1985 Theria [indet.]; Nesov 1985: pl. 3: 3.  
 1991 *Sailestes quadrans*; Nesov and Kielan-Jaworowska 1991: fig. 1.  
 1993 *Paranyctoides aralensis* (new synonym); Nesov 1993: 128, fig. 2 (5).  
 1994 *Sailestes quadrans*; Nesov et al. 1994: pl. 1: 6.  
 1997 *Sailestes quadrans*; Nesov 1997: pl. 48: 3.  
 1997 *Paranyctoides aralensis* (new synonym); Nesov 1997: pl. 48: 6.  
 1997 Theria [indet.]; Nesov 1997: pl. 47: 5.  
 1999 *Marsasia* sp.; Averianov and Kielan-Jaworowska 1999: 75, figs. 3, 4.  
 2000 *Paranyctoides aralensis* (new synonym); Averianov 2000: fig. 30.7K.  
 2001 *Sailestes quadrans*; Archibald and Averianov 2001: fig. 3.  
 2001 *Paranyctoides aralensis* [partim]; Archibald and Averianov 2001: figs. 1A, C, D, 2A–E (non figs. 1B, 2F, G).  
 2004 *Sailestes quadrans*; Kielan-Jaworowska et al. 2004: fig. 113.20K.  
 2005 *Sailestes quadrans*; Archibald and Averianov 2005: figs. 2M, 3D.  
*Holotype*: CCMGE 7/11758, right M1. Found in 1979.

*Type locality*: CBI-4g, Dzharakuduk, Kyzylkum Desert, Uzbekistan.

*Type horizon*: Bissekty Formation, Upper Cretaceous (middle–upper Turonian).

*Referred specimens*.—URBAC 04-347, left M2 (CBI-14) [specimen was lost after photographs were taken]; CCMGE 8/12176, right dentary fragment with alveoli for i1–4, erupting c, and p1–5 (CBI-4b, 1980); URBAC 03-204, right dentary fragment with p5 and alveoli for i1–4, erupting c, and p1–4 (CBI-14); CCMGE 67/12455, right dentary fragment with m2–3, broken m1, and alveoli or roots for p1–5 (holotype of *Paranyctoides aralensis* Nesov, 1993; CBI-14, 1987); ZIN 82588, left dentary fragment with m3, broken m2, and alveoli for p5, m1 (CBI-14, 1984); ZIN 83131, left dentary fragment with m3 (CBI-14, 1990); URBAC 04-393, right dentary fragment with alveoli for c and p1–4 (CBI-17); URBAC 04-394, right dentary fragment with alveoli for c and p1–4 (CBI-14); ZIN 82593, left dentary fragment with alveoli for c, p1–5, and m1–2 (CBI-14, 1984); URBAC 00-48, left dentary fragment with alveoli for c, p1–5, and m1–2 (CBI-14); URBAC 02-110, right dentary fragment with alveoli for c, p1–5, and m1–2 (CBI-4e); ZIN 82592, left dentary fragment with alveoli for c, p1–5, and m1–3 (CBI-14); ZIN 82594, right dentary fragment with alveoli for c, p1–5, and m1–3 (CBI-14, 1989); URBAC 06-94, left dentary fragment with alveoli for c, p1–5, and m1–3 (CBI-4e); URBAC 04-90, right dentary fragment with alveoli for p1–5 and m1–2 (CBI-14); URBAC 03-215, right m1 or m2 (CBI-14).

*Description*.—The upper dentition of *Paranyctoides quadrans* is known from single specimens of M1 and M2. Both molars are similar in structure, but differ in their proportions. M2 is wider transversely in occlusal view, while M1 is proportionately more squared. In M1, the parastylar lobe is

Table 1. Measurements of the upper molars of the eutherian mammal *Paranyctoides quadrans* (Nesov, 1982) from the Bissekty Formation, and *Paranyctodes* sp. from the Aitym Formation at Dzharakuduk, Central Kyzylkum Desert, Uzbekistan. Abbreviations: AW, anterior width; L, length; PW, posterior width. All measurements are in mm, and were taken using a microscope-mounted reticle.

Species and specimen	M1			M2		
	L	AW	PW	L	AW	PW
<i>Paranyctoides quadrans</i>						
CCMGE 7/11758	1.5	1.6	1.8			
URBAC 04-247				–	2.1	–
<i>Paranyctoides</i> sp.						
ZIN 85293	2.1	2.2	2.3			

mostly mesial to the paracone, while in M2 it is mesiolabial to the paracone.

The M1 (holotype of *Sailestes quadrans* Nesov, 1982) was figured and described in detail by Archibald and Averianov (2001: 540–541, fig. 3). The newly collected M2 is lacking part of the metastylar lobe and part of the apex of the metacone (Fig. 1A). The paracone and metacone are relatively low, and at least the paracone is compressed mesio-distally, and separated from the metacone by a deep transverse groove interrupting the centrocrista. The paracone is somewhat larger at its base and taller than the metacone. The tips of the paracone and metacone bear prominent wear facets, which are incompletely preserved on the metacone. The centrocrista consists mostly of the postparacrista, whereas the premetacrista is virtually absent. The ectoflexus is a deep embayment between the large, wing-like parastylar lobe and the partly missing metastylar lobe. On the ectocingulum, opposite the notch separating the labial cusps, there is a large, spine-like stylar cusp C. A much smaller, minute stylar cusp D is located on the ectocingulum halfway between cusp C and the transversely oriented, incompletely preserved post-metacrista. The stylar shelf is narrow between the labial cusps, but wide (more than 25% of the crown width) labial to the paracone, owing to the protruding parastylar shelf. The stylar shelf is partly missing labial to the metacone; however, based on the part that remains, it was wide, although probably not as wide as that labial to the paracone. This condition is in contrast to M1, in which the width of the stylar shelf is minimal labial to the paracone. The M2 parastylar lobe is prominent and projecting mesiolabially. The preparacrista and the parastylar groove (= protoconid notch) are heavily worn. The stylocone is not discernable; if it was present before wear, it would have been quite small. There is a small additional cusp labial to the paracone; however, this cusp is not connected with the preparacrista, and therefore cannot be a stylocone. The parastyle is small and almost completely worn away. Because of the wear, it is not clear if a pre-parastyle as seen in M1 was present. The crown is mesio-distally constricted in the conular region. The paraconule and metaconule are well developed, with the former cusp being slightly larger and located closer to the protocone. There is a

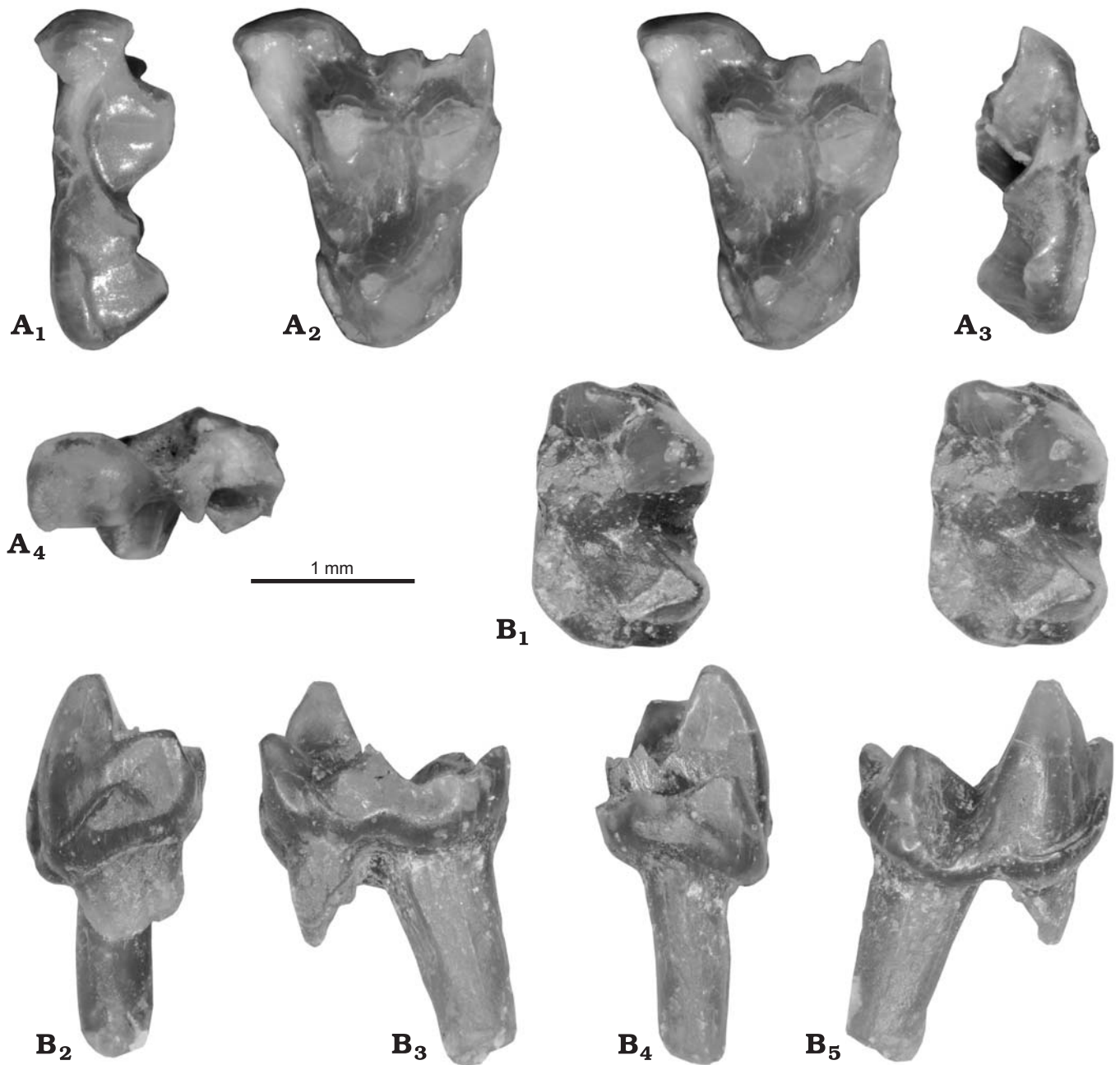


Fig. 1. Isolated molars of the eutherian mammal *Paranyctoides quadrans* (Nesov, 1982) from the Bissekty Formation at Dzharakuduk, Central Kyzylkum Desert, Uzbekistan. **A.** URBAC 04-347, left M2, in mesial (A<sub>1</sub>), occlusal (A<sub>2</sub>, stereopair), distal (A<sub>3</sub>), and labial (A<sub>4</sub>) views (specimen subsequently lost). **B.** URBAC 03-215, right m1 or m2, in occlusal (B<sub>1</sub>, stereopair), mesial (B<sub>2</sub>), lingual (B<sub>3</sub>), distal (B<sub>4</sub>), and labial (B<sub>5</sub>) views.

small wear facet on the apex of each of these conules. The conular basins are prominent, with distinctive, wing-like internal conular cristae, and a paracingulum and metacingulum extending labially beyond the bases of the paracone and metacone, respectively. The deepest point of the trigon basin is equidistant from the protocone and paracone/metacone. The protocone is prominent, and almost approaches the labial cusps in height. The difference in height between the protocone and the labial cusps is apparently diminished by greater wear of the labial cusps. In M1, the protocone is distinctly lower than the paracone. It almost has no labial shift

(sensu Wible et al. 2009), and is located close to the lingual margin of the crown, somewhat mesial to the line separating the paracone and metacone (Archibald and Averianov 2001: fig. 3). The preprotocrista on M1 is one-third the length of the postprotocrista. The postprotocrista on M2 is less convex compared with M1. The lingual cingula are more prominent than on M1, but do not extend labially beyond the conules and are widely interrupted lingually. The postcingulum is better developed than the precingulum in M2, while in M1 the condition is reversed.

The dentary is known from several fragmentary speci-

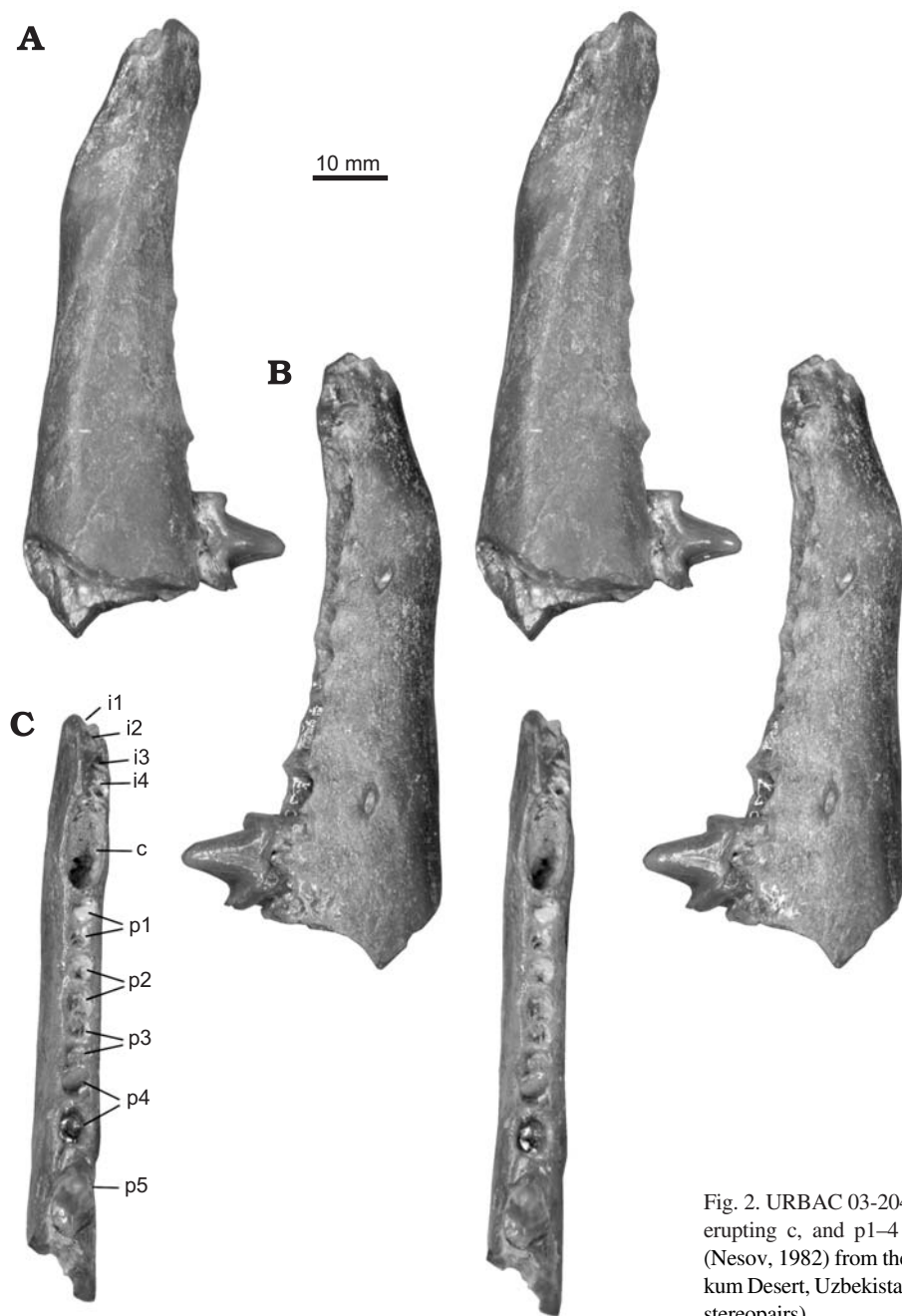


Fig. 2. URBAC 03-204, right dentary fragment with p5 and alveoli for i1–4, erupting c, and p1–4 of the eutherian mammal *Paranyctoides quadrans* (Nesov, 1982) from the Bissekty Formation at Dzharakuduk, Central Kyzylkum Desert, Uzbekistan, in lingual (A), labial (B), and occlusal (C) views (all stereopairs).

mens, variably preserving the horizontal ramus and sometimes the base of the coronoid process. The horizontal ramus is deepest ventral to the molar series, where it is about twice as high as the molar crowns. The horizontal ramus tapers anteriorly, and bends slightly dorsally along the mandibular symphysis. The mandibular symphysis terminates posteriorly between p1–2 (three specimens), at p2 (two specimens), or p3 (two specimens). Most dentary fragments are broken at the posterior end of the canine alveolus. The anterior end of the dentary with the alveoli for the incisors and the canine is preserved in only two specimens, CCMGE 8/12176 (Nesov 1985: pl. 3: 3) and URBAC 03-204 (Fig. 2). Both specimens have an enormous single canine alveolus, which is about twice as long as the p1 alveolus. It is likely that the lower canine had

not fully erupted in these specimens, with the entire alveolus being occupied by the canine crown. In ZIN 85078 of *Paranyctoides* sp. from the Aitym Formation, the lower canine is large and double-rooted (see below). It is likely that the lower canine was double-rooted in *P. quadrans* as well, but we have no specimens to demonstrate this.

There are four alveoli for single-rooted incisors. The alveoli for i1–3 are similar in diameter and compressed mesio-distally, while the alveolus for i4 is round and only half as wide in diameter. The alveolus for i1 is not visible in dorsal view, owing to its almost horizontal, i.e., procumbent, orientation. All five lower premolars are double-rooted. The relative sizes of the premolar alveoli in descending order are p5 > p4 > p2 > p1 > p3, indicating the presence of a reduced p3. In

URBAC 06-94, p3 was evidently shed and its alveoli almost completely filled with secondary bone. Both the reduction in the size of p3 and the ontogenetic loss of the latter are features also found in zhelestids. The molar alveoli gradually increase in size from m1 to m3.

On the labial side of the horizontal ramus, there are four or five mental foramina varying in position and size. The two smaller anterior foramina are located below i3 and i4, while the next largest mental foramen is found either below p1 (six specimens) or p2 (two specimens). The largest mental foramen is located below the distal root of p4 (four specimens) or below p5 (two specimens). However, in ZIN 82592 and URBAC 04-90 there are two small, closely spaced foramina below p5 or between p4 and p5, instead of a large posterior mental foramen. In addition, there is an additional small mental foramen below the mesial root of p4 in ZIN 82592 and URBAC 00-48.

There is no Meckelian groove on the medial side of the horizontal ramus. The coronoid process is angled away from the alveolar margin at an angle of approximately 125°. On the medial side of the base of the coronoid process, posterior to and in line with m3, there is a prominent swelling, possibly for the attachment of the m. temporalis pars profunda (this structure is sometimes described as a “coronoid” facet) (ZIN 82588; Archibald and Averianov 2001: figs. 1C, 2D). The coronoid process is partially preserved in ZIN 82588 (Archibald and Averianov 2001: fig. 2D, E). The coronoid crest is distinct and prominent. In ZIN 82588, there is a single, large lateral mandibular foramen connected dorsally to a vertical groove, apparently for a blood vessel, which is located within the masseteric fossa close to the coronoid crest.

Among the lower premolars, only p5 is known (URBAC 03-204; Fig. 2). It is preserved in a dentary fragment with alveoli for the complete anterior dentition. The crown is premolariform with signs of submolarization, and bears a high main cusp (protoconid), a small cingulid mesial cusp (paraconid), and a somewhat larger distal talonid cusp. The protoconid is slightly tilted distally, has a convex mesial margin, and bears a faint vertical line with a barely discernible central swelling on its lingual side. The paraconid is located on the

lingual side of the crown. The distal half of the tooth is slightly wider than the mesial half. The strong distal crest of the protoconid runs past a small, flattened area located on its lingual side, and extends to the talonid cusp. The distolingual cingulid connects to the vertical line on the lingual side of the protoconid, terminates lingually and labially at the protoconid base, and does not extend to the talonid. It is best developed in the mesial half of the crown, where it contacts the paraconid. Both roots are of similar mesiodistal length, but the distal root is slightly wider transversely.

The lower molars are known from a single isolated m1 or m2 (URBAC 03-215; Fig. 1B), a dentary fragment bearing m2–3 (CCMGE 67/12455; Archibald and Averianov 2003: figs. 1A, 2A, B), a dentary fragment with the talonid of m2 and a complete m3 (ZIN 82588; Archibald and Averianov 2003: figs. 1C, 2D, E), and a dentary fragment including m3 (ZIN 83131; Averianov and Kielan-Jaworowska 1999: figs. 3, 4). The lower molars are characterized by distinct, unilateral hypsodonty, with the crown extending further ventrally on the labial side than on the lingual side.

The trigonid is about twice the height of the talonid. On m1–2, the trigonid is as long as the talonid; by contrast, the talonid is somewhat shorter on m3, owing to an expanded hypoconulid (Table 2). The trigonid angle varies from 48–50° (URBAC 03-215, ZIN 82588) to about 40° (ZIN 83131), although in the latter specimen the trigonid angle might have been diminished by a prominent wear facet along the paracristid. The protoconid is the highest trigonid cusp, though only slightly higher than the metaconid, with a complete, unworn metaconid only preserved on the m3 of ZIN 82588. The protoconid has a vertical ridge on the lingual slope between the sharp edges of the paracristid and protocristid. The most remarkable feature of the lower molars is a relatively unreduced paraconid, which was one of the reasons for identification of ZIN 83131 as a marsupial by Averianov and Kielan-Jaworowska (1999). The paraconid is located at the lingual margin of the trigonid and almost at the same level as the metaconid, with its apex being directed dorsomesially. The mesial side of the paraconid has a distinct concavity for reception of the hypoconulid of

Table 2. Measurements of lower dentition of the eutherian mammal *Paranyctoides quadrans* (Nesov, 1982) from the Bissekty Formation, and *Paranyctodes* sp. from the Aitym Formation at Dzharakuduk, Central Kyzylkum Desert, Uzbekistan. Abbreviations: L, length; TAL, talonid length; TAW, talonid width; TRL, trigonid length; TRW, trigonid width; W, width. All measurements are in mm, and were taken using a microscope-mounted reticle.

Species and specimen	p2		p5		m1 or m2					m3				
	L	W	L	W	L	TRL	TAL	TRW	TAW	L	TRL	TAL	TRW	TAW
<i>Paranyctoides quadrans</i>														
URBAC 03-204			1.3	0.7										
URBAC 03-215, m1 or m2					1.6	0.8	0.8	1.1	1.2					
CCMGE 67/12455, m2 and m3					1.8	0.9	0.9	1.3	1.3	–	0.8	–	1.2	1.1
ZIN 82588, m2 and m3					–	–	0.8	–	1.2	1.7	0.8	0.9	1.1	1.0
<i>Paranyctoides</i> sp.														
ZIN 85078	0.8	0.5												
ZIN 85294, m1 or m2					1.6	0.8	0.8	1.0	1.1					

the preceding molar. The trigonid basin is open lingually, and restricted to a narrow, Y-shaped groove between the bases of the trigonid cusps. The protocristid is oriented obliquely. The precingulid is robust and extends into a variably developed labial cingulid. While the labial cingulid of the trigonid is almost lacking in ZIN 82588, and faint in CCMGE 67/12455, it is prominent and reaches the hypo-flexid in URBAC 03-215 (Fig. 1B).

The talonid is somewhat longer and wider than the trigonid. The largest talonid cusp is the hypoconid, while the hypoconulid is the smallest, although in m3 the hypoconulid is as large as the entoconid and projects distally beyond it. The hypoconulid is equidistant from the two other talonid cusps. The cristid obliqua extends mesially to a point just labial to the protocristid notch. The talonid basin is moderately expanded, and deepest at the entocristid. The labial postcingulid is small or moderately developed.

*Comments.*—ZIN 82590, a right dentary fragment with semi-molariform p5 referred to *P. aralensis* by Archibald and Averianov (2001: figs. 1B, 2F, G) is better identified as the zalambdalestid *Kulbeckia*, known from the Bissekty local fauna (Archibald and Averianov 2003). ZIN 82589, a right molar trigonid referred to *Paranyctoides* by Archibald and Averianov (2003: 545) is excluded here from the hypodigm of this genus. It is certainly larger than the molars of *Paranyctoides*, and has a more reduced paraconid; more probably, this specimen belongs to the zhelestid *Aspanlestes*.

### *Paranyctoides* sp.

2003 *Paranyctoides* sp. cf. *P. aralensis* [partim]; Archibald and Averianov 2003: 178, fig. 7.

2003 *Paranyctoides* sp.; Averianov and Archibald 2003: 179, fig. 8.

2005 *Paranyctoides* sp.; Archibald and Averianov 2005: figs. 2F, 3G.

*Referred specimens:* ZIN 85044, left M1 (CBI-117, 1998); ZIN 85078, left dentary fragment with p2 and alveoli for c, p1, and p3–4 (CBI-117, 1998); ZIN 85294, left m1 or m2 (CBI-117, 1999). From locality CBI-117, Dzharakuduk, Kyzylkum Desert, Uzbekistan; Aitym Formation, Upper Cretaceous (upper Turonian–Coniacian?).

*Description.*—See Averianov and Archibald (2003: 178–180).

*Comments.*—We now consider ZIN 85044, a left upper molariform tooth previously interpreted as an M1 of *Paranyctoides* sp. (Archibald and Averianov 2001: fig. 4) or *Paranyctoides* sp. cf. *P. aralensis* (Averianov and Archibald 2003: 178) to be a zhelestid DP5 (Archibald and Averianov 2012). It is similar to the DP5s of several zhelestid taxa, and differs from the upper molars of *Paranyctoides* in its beveled labial margin, less protruding parastylar lobe, and more expanded labial cingula.

Although the M1 from the Aitym Formation (ZIN 85044) is structurally very similar to the M1 of *P. quadrans* (CCMGE 7/11758), it is more robust, less constricted at the conular region, and bears more expanded lingual cingula. With the limited sample of upper molars of *Paranyctoides* from Dzharakuduk, it is impossible to determine the taxonomic significance of these differences. The lower molar from the Aitym Formation is likely an m1 because of the rel-

atively large difference between trigonid and talonid widths. Otherwise, this specimen is indistinguishable from the lower molars of *Paranyctoides* from the Bissekty Formation.

## Discussion

Originally, *Paranyctoides* was referred to the Nyctitheriidae, a group of Paleogene lipotyphlans (see Archibald and Averianov 2003 for a detailed account of its earlier classification). The first phylogenetic analyses employing the generic name *Paranyctoides* (Nesov et al. 1998; Archibald et al. 2001) suggested affinities with Zhelestidae, a diverse and widely distributed clade of Late Cretaceous eutherians (Archibald and Averianov 2012), while Archibald and Averianov (2001) argued for a close relationship between *Paranyctoides* and *Gallolestes* from the Campanian of Mexico. However, it is now evident that this view was based on misinterpretations of certain specimens. First, the Uzbek *Paranyctoides* does not have a submolariform p5. While the dentary fragment with a submolariform p5 (ZIN 82590), previously referred to *P. aralensis* by Archibald and Averianov (2001), is now attributed to the zalambdalestid *Kulbeckia*, the newly collected dentary fragment URBAC 03-204 (Fig. 2) includes a simpler p5. In this regard, the Uzbek *P. quadrans* does not differ from the North American *Paranyctoides*. Secondly, the tooth in the holotype of *Gallolestes pachymandibularis* Lillegraven, 1976, interpreted by Archibald and Averianov (2001) as a molariform p5, is more likely a milk tooth, dp5. Recent phylogenetic analyses by Wible et al. (2007, 2009) placed *Gallolestes* within the Zhelestidae.

Wible et al. (2007, 2009) also recovered a clade comprising *Paranyctoides* and *Eozhelestes* Nesov, 1997 from the Cenomanian of Uzbekistan (revised by Averianov and Archibald 2005). On their cladogram, this clade was positioned above Zhelestidae, and was supported by three synapomorphies, including small lower canines, the presence of a distinctive paraconid on the penultimate lower premolar, and the presence of a labial postcingulid on m2 (Wible et al. 2007, 2009). This clade seems to be an artifact of miscoding of *Eozhelestes* and *Paranyctoides*. While the lower canine is large in *Eozhelestes* (see Averianov and Archibald 2005: fig. 5), none of the known North American specimens of *Paranyctoides* preserve the lower canine or even its alveolus. In the Uzbek *Paranyctoides*, the lower canine is quite large. The penultimate lower premolar (p4) is not known for *Paranyctoides*. A labial postcingulid on the molars is present in a number of Cretaceous eutherian genera, and thus the presence of this character does not convincingly suggest a close relationship between *Paranyctoides* and *Eozhelestes*. Archibald and Averianov (2012) presented a novel analysis of Wible et al.'s (2009) data matrix, modified by new or emended scorings for zhelestids and *Paranyctoides* based on newly described specimens. In all versions of the analysis, *Paranyctoides* was found to be the sister taxon of Zhelestidae (including or excluding *Eozhelestes*).

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