



A new eutherian mammal from the Late Cretaceous of Kazakhstan

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A dentary fragment containing the last two molars (m2–3) from the Late Cretaceous (Santonian–?Campanian) Bostobe Formation exposed at the locality of Shakh Shakh, northeast Aral Sea region, Kazakhstan, is attributed to a new taxon of Zhelestidae, *Zhalmouzia bazhanovi* Averianov and Archibald gen. et sp. nov. This specimen is only the second mammal described from Shakh Shakh, the unidentifiable eutherian *Beleutinus orlovi* Bazhanov, 1972, being the first, and it is only the fifth Mesozoic mammal named from Kazakhstan. *Zhalmouzia* Averianov and Archibald gen. nov. belongs to the endemic clade of Middle Asian zhelestids (Zhelestinae), better known from the Turonian of Uzbekistan.

Introduction

The Late Cretaceous continental deposits of Middle Asia became an important source of information regarding mammal evolution after the pioneering work of Lev A. Nesov (Nesov 1997; Archibald and Averianov 2005, and references therein). In the Kyzylkum Desert of Uzbekistan, the oldest eutherian-dominated mammal faunas are known from the Cenomanian, Turonian, and possibly Coniacian (Archibald and Averianov 2001, 2003, 2005, 2006, 2012; Averianov and Archibald 2003, 2005, 2006; Averianov et al. 2010). Unfortunately, younger Cretaceous continental deposits in the Kyzylkum are absent because of a marine transgression. By contrast, the continental Cretaceous deposits east and north of the Kyzylkum were less affected by the marine transgression, and may therefore be important to our understanding of the subsequent transformations of the mammal fauna of this region. A single mammalian taxon, the zalambdalestid *Kulbeckia* sp., has been reported from the Santonian of Tajikistan (Nesov 1987; Archibald and Averianov 2003). In Kazakhstan, three Mesozoic mammal localities are known (Averianov 2000). The oldest is the Early Turonian locality of Ashchikol, a drill core of which has yielded the single specimen of the zhelestid *Borisodon kara* (Nesov 1993; Archibald and Averianov 2012). The youngest locality is the Early Campanian site of Alymtau, which produced a few isolated mammal teeth including a multituberculate, a deltatheroidan, and the zalambdalestid *Alymlestes kielanae* (Averianov and Nesov 1995; Averianov 1997). Intermediate in age between these sites is the Late Santonian locality of Shakh Shakh (Fig. 1A).

The first vertebrate fossils from the Bostobe Formation exposed at Shakh Shakh were discovered by Kseniya V. Nikiforova

and Nina A. Konstantinova in 1956. In 1957, a team from the Moscow Paleontological Institute under the direction of Anatoly K. Rozhdestvensky conducted extensive excavations at two fossiliferous sites in this region, designated as Shakh Shakh I and II (Fig. 1B, C; Rozhdestvensky 1964). During this excavation, a nearly complete hadrosaurid skull, the holotype of *Aralosaurus tuberiferus*, was found at Shakh Shakh II (Rozhdestvensky 1968; Godefroit et al. 2004). In 1961–1964, these localities were further explored by a team from the Almaty Institute of Zoology lead by T. N. Nurumov. During the 1962 field season, a mammal dentary fragment was found at Shakh Shakh during screen-washing of approximately 25 m³ of matrix, and was subsequently described as *Beleutinus orlovi*, the first Mesozoic mammal from the former USSR (Bazhanov 1972). Fifteen years later, the same sample yielded a second mammal specimen consisting of a cervical centrum (Nesov and Khisarova 1988). Additional vertebrate fossils, including some microvertebrates, were collected at Shakh Shakh by a Kazakh-American expedition in 1995 (Kordikova et al. 2001) and another international project led by Gareth Dyke and Dmitry V. Malakhov from 2003–2007 (Dyke and Malakhov 2004; Malakhov et al. 2009). Together, these expeditions have revealed a rich vertebrate assemblage including fish, amphibians, turtles, lizards, crocodiles, pterosaurs, various dinosaurs, and birds (Kuznetsov 1976; Suslov 1982; Kuznetsov and Shilin 1983; Nesov 1986, 1995, 1997; Nesov and Khisarova 1988; Storrs et al. 2000; Kordikova et al. 2001; Averianov 2004, 2007a, b; Dyke and Malakhov 2004; Danilov et al. 2007; Syromyatnikova and Danilov 2009; Vitek and Danilov 2010). The majority of the vertebrate specimens still await identification and detailed description. One of the most interesting discoveries, a dentary fragment with two molars of a new species of mammal, is described in this paper.

There is some confusion regarding exactly where the first mammal specimen from Shakh Shakh, the holotype of *Beleutinus orlovi*, was found. Bazhanov (1972: 77) designated the type locality as “uphill near Baibolat well, somewhat east to the old route between the railway station of Dzhusaly and Karsakpai.” This corresponds to locality Shakh Shakh I of Rozhdestvensky (1964; Fig. 1B). However, according to Nesov and Khisarova (1988: 6), the screen-washing sample was taken from the outcrop closest to the Zhalmouz Well, which is located somewhere near the Baibolat Well (Fig. 1B). Nesov (1995, 1997) called this locality Zhalmouz or Baibolat, and synonymized it with Rozhdestvensky’s (1964) locality Shakh Shakh II (Fig. 1B). Because

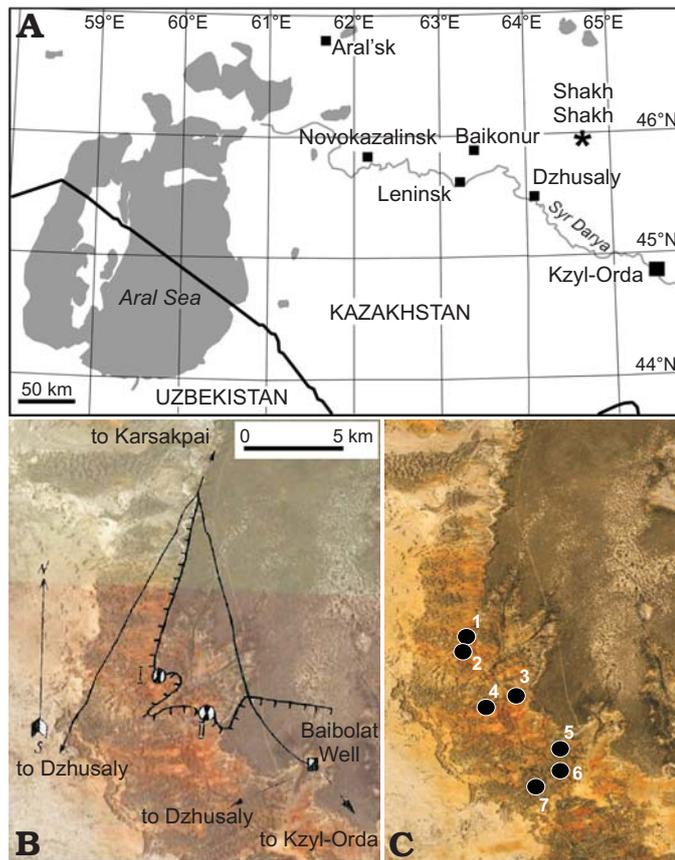


Fig. 1. Maps of the Late Cretaceous locality of Shakh Shakh in Kazakhstan. **A.** Northeast Aral Sea area with the position of the Shakh Shakh locality marked by an asterisk (modified from Averianov 2007b). **B.** Locality map (I, Shakh Shakh 1; II, Shakh Shakh 2) from Rozhdestvensky (1964: fig. 1) and Suslov (1982: fig. 1), superimposed on a Google Earth image of the area; the red beds of the Bostobe Formation in this area based on the photograph. **C.** Vertebrate localities in this area based on Malakhov et al. (2009: fig. 5); 1, Shakh-Shakh 2; 2, Shakh-Shakh 1; 3, Bird Site; 4, Turtle Site; 5, Forest; 6, Forest 2; 7, Shakh Shakh 3.

of the uncertainty about the position of the Zhalmouz Well, it is likely that Shakh Shakh I of Rozhdestvensky (1964) is the type locality of *B. orlovi*. This site generally corresponds to localities Shakh Shakh 1 and 2 of Malakhov et al. (2009; Fig. 1C, D).

The new mammal specimen described here was collected from the Shakh Shakh 2C site in 2007, after screen-washing of approximately 925 kg of matrix. Thus, both mammal dentaries from Shakh Shakh come from approximately the same locality (Fig. 1). The matrix from Shakh Shakh 2C was wet sieved through a 1 mm mesh screen. Once wet, the clay and silt quickly disintegrated, leaving about 10% of the original weight composed mostly of small rock fragments and rare bones. The concentrate was picked in Almaty in 2007.

Institutional abbreviations.—IZK, Institute of Zoology, Kazakh Academy of Sciences, Almaty, Russia; ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

Other abbreviations.—L, length; TAW, talonid width; TRW, trigonid width.

Systematic paleontology

Mammalia Linnaeus, 1758

Theria Parker and Haswell, 1897

Eutheria Gill, 1872

Zhelestidae Nesov, 1985

Genus *Zhalmouzia* Averianov and Archibald nov.

Type species: *Zhalmouzia bazhanovi* Averianov and Archibald sp. nov.; type and only known species.

Etymology: After the Zhalmouz Well.

Diagnosis.—As for the type and only known species.

Stratigraphic and geographic range.—Late Cretaceous (Santonian–?Campanian) of Asia (Kazakhstan).

Zhalmouzia bazhanovi Averianov and Archibald sp. nov.

Fig. 2A.

Etymology: Named after Valerian Semenovich Bazhanov (1907–1984), who described *B. orlovi* from Shakh Shakh.

Holotype: ZIN 100639, left dentary fragment with m2–3 and alveoli for c, p1–5, and m1.

Type locality: Shakh Shakh 2 locality of Malakhov et al. (2009) [= Shakh Shakh I of Rozhdestvensky 1964], about 70 km northeast of Dzhusaly railway station, Kyzylorda Province, Republic of Kazakhstan.

Type horizon: Bostobe Formation (Late Cretaceous, Santonian–?Campanian).

Diagnosis.—*Zhalmouzia bazhanovi* is referred to Zhelestidae because the protoconid in this specimen is subequal to the para- and/or metaconid, the protocristid is transverse, and the hypococonid closely approximates the entoconid. *Z. bazhanovi* differs from *Avitotherium* Cifelli, 1990 because the paraconid is not on the lingual margin of the tooth, and from *Borisodon* Archibald and Averianov, 2012 in the presence of a rounded mesiolingual vertical crest of the paraconid and the absence of the Meckelian groove; differs from *Borisodon*, *Gallolestes* Lillegraven, 1976, and *Eozhelestes* Nesov, 1997 in having a trigonid less than twice the height of the talonid, and from *Gallolestes*, *Avitotherium*, and *Parazhelestes* Nesov, 1993 in a trigonid angle of 36–49° (as opposed to 35° or less in the latter taxa); differs from *Borisodon* and *Parazhelestes* in having the mandibular symphysis extending to the level of p3 or further posteriorly; differs from *Eozhelestes* in having a protoconid subequal to the para- and/or metaconid, and a cristid obliqua contacting the protocristid labial to the protocristid notch; differs from *Avitotherium* and *Eozhelestes* in having a transverse protocristid, and from *Gallolestes* in having a mesiolabial cuspule f with a distinct cingular shelf. *Z. bazhanovi* resembles *Eoungulatum* Nesov, Archibald, and Kielan-Jaworowska, 1998, and differs from all other zhelestids in having an ultimate lower molar smaller than the penultimate one (the state of this character is unknown for *Avitotherium*). *Z. bazhanovi* differs from *Eoungulatum* in having a short and erect hypoconulid on the ultimate lower molar, and because the ventral border of the masseteric fossa is present as a well-defined crest. Finally, *Z. bazhanovi* differs from all other known zhelestids in having a posteriormost mental fora-

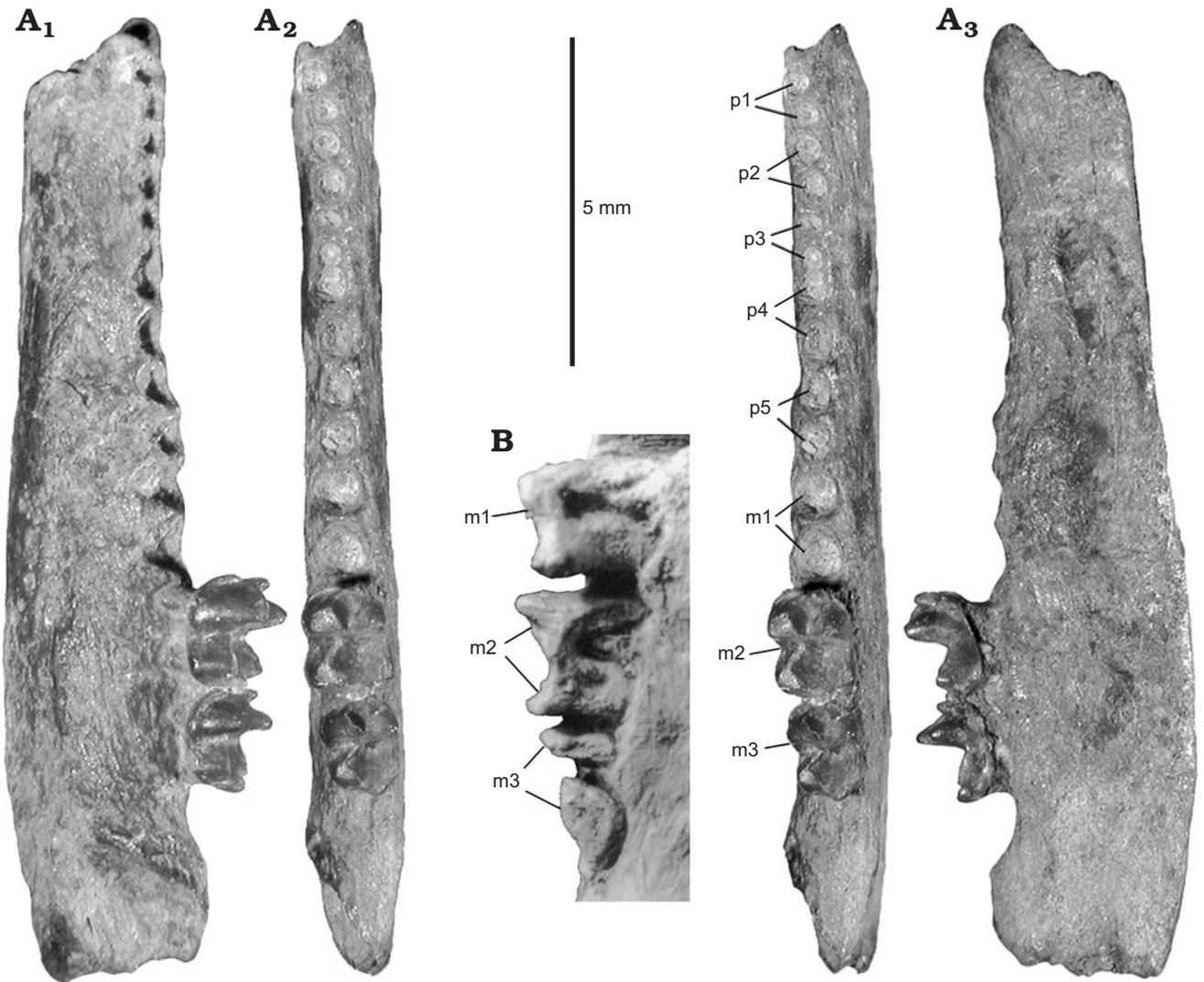


Fig. 2. Eutherian mammals from Shakh Shakh, Kazakhstan, Late Cretaceous. **A.** *Zhalmouzia bazhanovi* Averianov and Archibald gen. et sp. nov., ZIN 100639, holotype, left dentary fragment with m2–3 in situ and alveoli for c, p1–5 and m1, in labial (A₁), occlusal (A₂, stereopair), and lingual (A₃) views. **B.** *Beuletinus orlovi* Bazhanov, 1972, IZK I-751/III-1962, holotype, heavily abraded right m1–3 in labial view (modified from Nesov et al. 2004: pl. 1: 1a).

men located below the penultimate premolar (state unknown in *Avitotherium*).

Description.—The horizontal ramus of the dentary of ZIN 100639 gradually tapers anteriorly, but its depth slightly increases at the canine alveolus. However, only the posterior margin of the canine alveolus is preserved, and it is not clear if the canine was single or double-rooted. The bone surface of this specimen is also somewhat abraded, and the articular surface of the mandibular symphysis is poorly defined; nevertheless, it appears that the symphysis terminates at the mesial root of p3. On the labial surface of the dentary, there is a small mental foramen below the mesial root of p1, close to the alveolar border. The posterior mental foramen is distinctly larger and is located below the distal root of p4, closer to the mid-height of the ramus than the anterior foramen.

The postcanine alveoli are closely spaced. The alveoli for p1 are slightly rotated relative to the long axis of the dentary, while the alveoli for the other postcanine teeth are in line with

this axis. All the premolars are double-rooted and the relative sizes of their alveoli are as follows: p1 < p2 > p3 < p4 > p5. The total length of the p4 alveoli is greater than that of p5, while the individual alveoli for the p4 roots are smaller than those for p5. As in other zhelestids and *Paranyctoides*, p3 is the smallest premolar, although p1 is only slightly larger. Although only a small part of the coronoid process is preserved, there is some space between the last molar and the coronoid process, suggesting that this animal was fully mature. The masseteric fossa is deep; it is bordered anteriorly by a laterally flared coronoid crest, and ventrally by a low, wide crest extending across less than half of the depth of the horizontal ramus. Within the masseteric fossa, there is a single labial mandibular foramen of moderate size. The ventral margin of the horizontal ramus is gently convex below m2–3 and the base of the coronoid process, but straight below m1 and the premolars.

The lower molars (m2–3) are hardly worn and almost completely preserved, except for the missing apex of the protoc-

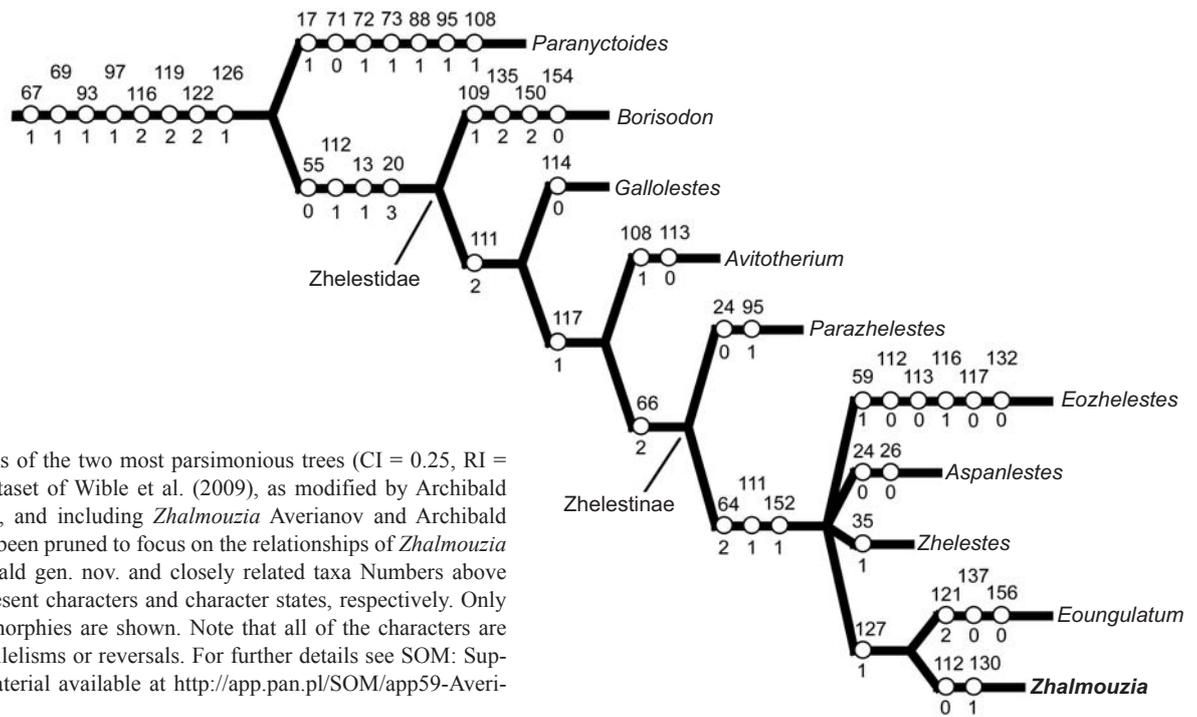


Fig. 3. Strict consensus of the two most parsimonious trees (CI = 0.25, RI = 0.55) based on the dataset of Wible et al. (2009), as modified by Archibald and Averianov (2012), and including *Zhalmouzia* Averianov and Archibald gen. nov. The tree has been pruned to focus on the relationships of *Zhalmouzia* Averianov and Archibald gen. nov. and closely related taxa. Numbers above and below nodes represent characters and character states, respectively. Only unambiguous synapomorphies are shown. Note that all of the characters are homoplastic, i.e., parallelisms or reversals. For further details see SOM: Supplementary Online Material available at http://app.pan.pl/SOM/app59-Averianov_et_al_SOM.pdf.

nid of m2. The preserved molars are similar in morphology, but differ in size: m3 is about 10% shorter and narrower than m2. Additionally, the m2 talonid is relatively more expanded than in m3 and wider than the trigonid, whereas the opposite is true for m3. The trigonid is moderately compressed (trigonid angle is $\sim 42^\circ$ in m2 and 47° in m3). The protoconid (unworn in m3) is only slightly higher than the metaconid. The paraconid is less than half the height of the metaconid and is offset from the lingual margin of the crown. The trigonid basin is filled by the bases of the trigonid cusps and is closed lingually. The protocristid is nearly transverse, with a wide angle between the protocristid arms, while the paracristid is more angled on m3 than on m2, with a smaller angle between the arms. The precingulid is a prominent shelf extending along most of the mesial side of the crown, and lingually abuts the hypoconulid of the preceding tooth. The talonid is about half the height of the trigonid. The talonid basin is extensive and rather deep, with its deepest point being adjacent to the protocristid notch. The cristid obliqua terminates somewhat labial to the protocristid notch. The hypoconid is the largest talonid cusp. The entoconid is taller than the hypoconid, but because the crown is higher labially than lingually, the total height of hypoconid is greater than that of the entoconid. The hypoconulid is only slightly smaller than the entoconid and closer to the latter than to the hypoconid (a feature related to the labiolingual expansion of the talonid). On m3, the hypoconulid is short, erect (i.e., not procumbent distally), and relatively larger and located somewhat more distally than on m2. The labial postcingulid is faint, but rather long; on m2, its wear matches that of the m3 precingulid. The labial cingulid is extremely faint and hardly recognizable. The distal root of m3 is only a little longer (mesiodistally) than the mesial root.

Measurements (all measurements in mm).—ZIN 100639, m2, L = 1.8, TRW = 1.3, TAW = 1.3; m3, L = 1.6, TRW = 1.2, TAW = 1.1.

Remarks.—The lower molars of the holotype of *Beleutinus orlovi* from Shakh Shakh (Fig. 2B) are heavily abraded, preventing us from comparing the molar morphologies of these two taxa. The holotype of *B. orlovi* is about 25–30% larger than ZIN 100639 and likely belongs to a distinct taxon. In *B. orlovi*, the distal root of m3 is labiolingually compressed and longer than the mesiodistally compressed mesial root, while in ZIN 100639 both roots are of similar size. *B. orlovi* was referred provisionally to Zalmobalestidae (Nesov 1987; Nesov et al. 2004), but this assignment was later challenged in light of the fragmentary nature of the only known specimen (Wible et al. 2004). In its large size and laterally compressed distal root of m3, *B. orlovi* is similar to the zhelestid *Eoungulatum* from the Turonian of Uzbekistan (Archibald and Averianov 2012), but differs in having a relatively larger m3. *Beleutinus orlovi* should be considered a nomen dubium, not identifiable beyond Eutheria indet.

Phylogenetic position of *Zhalmouzia*

To assess the phylogenetic position of *Zhalmouzia* Averianov and Archibald gen. nov., we performed a parsimony-based phylogenetic analysis using the data matrix of Wible et al. (2009), including the modifications of Archibald and Averianov (2012), who incorporated new specimens of Zhelestidae from Uzbekistan. The data matrix comprised 72 taxa and 408 characters (see Appendix 1 for scorings of *Zhalmouzia bazhanovi* Averianov and Archibald gen. et sp. nov.), and was analyzed using the new technology search algorithm of TNT version 1.1 (Goloboff et al. 2003; ratchet algorithm). All characters were considered

non-additive, and branch support was assessed using Bremer support values (Bremer 1994).

The analysis produced two most parsimonious trees of 2324 steps, a consistency index (CI) of 0.25, and a retention index (RI) of 0.55. A subset of the strict consensus of these trees, detailing the position of *Zhalmouzia* Averianov and Archibald gen. nov. and closely related taxa, is shown in Fig. 3. The clade comprising *Paranyctoides* + Zhelestidae is supported by eight unambiguous synapomorphies, while Zhelestidae is supported by four synapomorphies; however, these clades, as well as subclades within Zhelestidae, are not robust (Bremer support = 1). Our results confirm the Early Turonian *Borisodon* as the most basal zhelestid, followed by *Gallolestes* and *Avitotherium* from the Campanian of North America. The clade containing the remaining taxa is mostly comprised of Middle Turonian zhelestids from Uzbekistan (Zhelestinae). The inclusion of the Early Cenomanian *Eozhelestes* from Uzbekistan into this clade could be an artifact caused by the incompleteness of the specimens referred to this taxon, as implied by the 6 autapomorphic reversals which apparently characterize it. A constrained analysis enforcing a monophyletic Zhelestidae to the exclusion of *Eozhelestes* resulted in eight most parsimonious trees of the same length (2324 steps, CI = 0.25, RI = 0.55) as in the unconstrained analysis. In the strict consensus of those trees, *Eozhelestes* is placed as sister taxon to the clade comprising *Paranyctoides* + Zhelestidae. Within Zhelestinae, *Zhalmouzia* Averianov and Archibald gen. nov. forms the sister taxon of the Turonian *Eoungulatum* from Uzbekistan. However, this clade is supported by just one synapomorphy (ultimate lower molar smaller than penultimate), independently acquired in a number of eutherian lineages (including Zalambdalestidae). The only character unique to *Zhalmouzia* Averianov and Archibald gen. nov. is the position of the posterior mental foramen below p4 instead of p5, as in other zhelestid taxa.

To date, only two mammals are known from the Bostobe Formation of Kazakhstan: the unidentifiable eutherian *Beleutinus orlovi* and the zhelestid *Zhalmouzia bazhanovi* Averianov and Archibald gen. et sp. nov. Future discoveries will show if the mammalian fauna of the Bostobe Formation was dominated by eutherians, as in Middle Asia, or multituberculates, as in Central Asia (Archibald and Averianov 2005).

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Appendix 1

Character scores for *Zhalmouzia bazhanovi* Averianov and Archibald gen. et sp. nov., based on the matrix of Wible et al. (2009):

1(0), 2(0), 3(0), 29(0), 47(0), 48(0), 49(0), 50(1), 51(0), 61(1), 63(0), 106(0), 107(0), 108(0), 109(0), 110(0), 111(1), 112(1), 113(1), 114(1), 115(1), 116(2), 117(1), 118(2), 119(2), 120(3), 121(0), 122(2), 123(0), 124(0), 125(0), 126(1), 127(1), 130(1), 131(0), 132(1), 136(1), 137(2), 138(0), 139(1), 151(0), 152(1), 153(0), 154(1), and 156(1).