# Mammals from the mid-Cretaceous Khodzhakul Formation, Kyzylkum Desert, Uzbekistan

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## Abstract

Six localities in the mid-Cretaceous (early Cenomanian) Khodzhakul Formation, western Kyzylkum Desert, Uzbekistan, produced mammalian remains of a possible zalambdalestoid (*Bobolestes*), a possible zalambdalestid, and two (*Sheikhdzheilia rezvyii*, gen. et sp. nov. and *Eozhelestes mangit*) or three zhelestids ("Zhelestidae" indet., unnamed large sp. A). This is termed the Sheikhdzheili local fauna. Previously, these mammals were recognized only as being three eutherians of uncertain affinities (*Bobolestes*, *Otlestes*, and *Oxlestes*) and a possible zhelestid (*Eozhelestes*). The reinterpretation of *Bobolestes* including "*Otlestes*" as a synonym could have an impact on phylogenetic reconstructions of basal Eutheria. With five eutherian species occurring at about 95 million years ago (early Cenomanian), the Sheikhdzheili local fauna is the earliest mammalian fauna to have more than two species of eutherian. European Campanian—Maastrichtian *Lainodon* and *Labes*, which have been argued to be zhelestids (and the hadrosaurid *Telmatosaurus*), retain ancestral traits reminiscent of earlier, early Cenomanian Asian taxa such as those in the Sheikhdzheili local fauna, suggesting that they may be isolates restricted on the European Archipelago after the formation of the Turgai Strait in the Turonian.
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## 1. Introduction

The fossil record of mammals during the mid-Cretaceous (approximately Aptian, Albian through Coniacian) is poorly known. In western North America relatively diverse mammal local faunas are known from the Cedar Mountain Formation around the Albian/Cenomanian boundary, the Cenomanian Dakota Formation, and the Smoky Hollow Member of the Turonian Straight Cliff Formation (Cifelli and Eaton, 1987; Cifelli, 1990, 1993, 1999a; Eaton, 1993, 1995; Cifelli and Muizon, 1997; Cifelli et al., 1997, 1999; Cifelli and Madsen, 1998, 1999; Cifelli and Gordon, 1999; Eaton and Cifelli, 2001). In Asia only three areas have produced mid-Cretaceous mammals, and only one is relatively diverse. The two poorly sampled sites are the Cenomanian Tsondolein-Khuduk find in Gansu Province, China, which produced a single mammal axis (Bohlin, 1953; "*Khuduklestes bohlini*" of Nessov et al., 1994) and the late Cenomanian—early Turonian fossil site within the "Upper" Formation of the Mifune Group in Japan, which produced a dentary fragment with a single molar of *Sorlestes mifunensis* (Setoguchi et al., 1999).

More diverse mid-Cretaceous mammal faunas are known from what has traditionally been called Central or Middle Asia. This is a region commonly and long used

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by Soviet geographers in much the same way as terms such as the Great Plains are used in North America. Middle Asia is in fact located more in the southwestern portion of Asia. It extends approximately from the Caspian Sea in the west to the Chinese border in the east, and from the Iranian and Afghan borders in the south to southern Kazakhstan in the north. It essentially encompasses the newly independent countries of Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan.

The most diverse mammal faunas are those from the Turonian and possibly Coniacian of the central Kyzylkum Desert, Uzbekistan (see Averianov and Archibald, 2003 and Archibald and Averianov, in press for recent reviews). A lesser-known, early Cenomanian mammal fauna is known from six localities at four different places in the southwestern Kyzylkum Desert area (Karakalpakistan, western Uzbekistan; Fig. 1). All are confined to the Khodzhakul Formation (Nessov, 1993; Nessov et al., 1994; Averianov, 2000). These are the Khodzhakul site (SKH-20), Khodzhakulsai sites (SKH-5 and SKH-5a), Sheikhdzheili sites (SSHD-8 and SSHD-8a), and Chelpyk site (SCH-1). The first three localities are at different locations along a semicircular escarpment at the northern edge of the Sultanuvais [Sultanuizdag] Range, close to the Amu Darya (river). Chelpyk is an isolated hill with the ruins of a Khoresm castle at the top, some 30 km north of the escarpment. Khodzhakul is within the lower part of Khodzhakul Formation, whereas as the remaining localities are within the upper part of the formation. All localities appear to be early Cenomanian in age based on marine invertebrates that bracket the vertebrate localities (C. King, N. Morris, D. Ward, and M. Hampton, pers. comm. 2005).

Nessov first found mammals at Khodzhakul in 1978, and in 1979 at Sheikhdzheili (Nessov, 1982, 1984, 1985a). He and his team carried out surface collecting and dry screening at Sheikhdzheili in 1980, 1981, 1982, and 1985. Most intensive was dry screening in 1982 when three tons of matrix were processed and 12 mammalian specimens were recovered. The locality was visited briefly by Nessov and Archibald in 1994 and by the international URBAC expedition in 1998, but no mammals were found. Thirteen tons of matrix were screenwashed at Sheikhdzheili by URBAC in 1999 and 2003, which produced 13 mammalian specimens. Altogether, over 30 mammalian specimens belonging to five or six taxa are now known from the Khodzhakul Formation, which are here referred to as the Sheikhdzheili local fauna. The subject of this paper is a discussion of this mammalian fauna and its paleontological implications.

## 1.1. Institutional abbreviations

CCMGE, Chernyshev's Central Museum of Geological Exploration, St. Petersburg, Russia; URBAC, Uzbek-Russian-British-American-Canadian joint expedition collections, now housed at San Diego State University; ZIN, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

## 1.2. Other abbreviations

AW, anterior width; L, length; PW, posterior width; TAL, talonid length; TAW, talonid width; TRL, trigonid length; TRW, trigonid width; W, width. All measurements are in mm. Diagnoses include a combination of what we interpret as derived characters (+), primitive characters (−), and characters of uncertain polarity (?).



Fig. 1. Map of Uzbekistan showing locations of Sheikhdzheili (S) and Dzharakuduk (D) local faunas.

## 2. Systematic paleontology

Cretaceous mammals from various sites in Uzbekistan have played a prominent role in discussions of higher-level relationships among eutherian mammals. As some of the conclusions are controversial, it is worthwhile to review our usages of higher taxa.

We start by rejecting the taxon Ungulatomorpha Archibald (1996). When named it was assumed that within Placentalia there is a monophyletic Ungulata, including not only traditionally recognized ungulates such as Artiodactyla and Perissodactyla, but also paenungulates (Proboscidea, Sirenia, Hyracoidea). Molecular studies (e.g., Murphy et al., 2001) have shown that this is not the case. These taxa belong to two widely separated clades within Placentalia: Laurasiatheria and Afrotheria. Assuming such molecularly based studies are correct, Ungulatomorpha is rendered polyphyletic, and thus is rejected. Even if restricted to traditional ungulates, names already exist that incorporate parts of the clade (e.g., Ferungulata).

With the above modification, we now place "Zhelestidae" within Laurasiatheria rather than within Ungulatomorpha. Similarly, we place Zalambdalestoidea (including Zalambdalestidae) within Euarchontoglires (including Gliriformes). Both of these taxonomic assignments place these Cretaceous taxa within the crown group Placentalia rather than as stem taxa to Placentalia. Some phylogenetic analyses (Archibald, 1996; Nessov et al., 1998; Archibald et al., 2001; Luo et al., 2004) explicitly placed one or both of these Cretaceous taxa within Placentalia, while another (Meng et al., 2003) excluded these taxa, placing them as stem taxa instead. Of concern is that while the former studies included most well-known Cretaceous eutherians, it included far fewer members of the crown Placentalia. The latter study, while including many placentals, included very few Cretaceous taxa. This issue remains unresolved, but as we authored parts of the former studies, we feel inclusion of these Cretaceous taxa in Placentalia remains the best working hypothesis.

Mammalia Linnaeus, 1758
Theria Parker and Haswell, 1897
Eutheria Gill, 1872 sensu Rougier et al., 1998
Placentalia Owen, 1837 sensu Rougier et al., 1998
Euarchontoglires Murphy et al., 2001
Gliriformes Wyss and Meng, 1996
Zalambdalestoidea Gregory and Simpson, 1926
Genus *Bobolestes* Nessov, 1985, new assignment
[=*Otlestes* Nessov, 1985, syn. nov.]

*Type species.* *Bobolestes zenge* Nessov, 1985 (=*Otlestes meiman* Nessov, syn. nov.), western Uzbekistan; early Cenomanian.

*Diagnosis* (revised after the original diagnosis of *Bobolestes* and part of the original diagnosis of *Otlestes* concerning the lower dentition; Nessov, 1985a, pp. 9, 10, 15 and Nessov et al., 1994, pp. 60, 61, 63): upper molars labiolingually narrow (−); paracone larger than metacone (−); bases of paracone and metacone separated (+); stylar shelf wide (−); ectoflexus deep (−); centrocrista straight (?); stylocone weak (+); parastylar lobe large with deep parastylar groove (−); preparastyle absent (+); paracingulum extends labially well beyond paracone (+); paraconule and metaconule well developed and winged (+); paraconule positioned distinctly closer to protocone than to paracone and metaconule near midpoint between protocone and metacone (+); protocone small, distinctly lower than paracone and metacone (−), and not expanded anteroposteriorly (−); lingual cingula absent (−); posterior edge of maxillary zygomatic process situated posterior to M3 (−); c1 single rooted (+); five lower molars (−); p5 semimolariform (+); lower molars extend more ventrally on the labial than on lingual side (+); protoconid tallest trigonid cusp followed by metaconid and then paraconid (−); trigonid angle not acute (−); paraconid slightly labial on m1 and near lingual margin on m2-3 (−); trigonids tall with great height differential between trigonids and talonids (−); cristid obliqua close to protocristid notch (+); talonid slightly narrower than trigonid (−); hypoflexid deep (−); m3 paraconid higher compared to m1-2 (−); entoconulid on m3 (?). Assessments of polarities of characters are based on Archibald et al. (2001).

*Remarks.* The concept of *Otlestes* was based on two lower jaws, one with a complete posterior dentition (CCMGE 7/12176, holotype of *Otlestes meiman*), and a referred maxillary fragment with M1-2 (CCMGE 8/12176), which were thought conspecific, apparently because they came from the same locality (SSHD-8). The dentaries and maxilla, however, do not match in size (the maxilla being from a larger animal) and morphology (the molar protocones are larger than what one would expect for the lower molar talonids). The ratios of LM2/Lm2 of CCMGE 8/12176 and 7/12176 are 1.33 whereas this ratio is 0.87 in *Prokennalestes trofimovi*, 1.03 in *Kennalestes*, and 1.1−1.2 in *Aspanlestes*. The lower jaws of *Otlestes* fit the size and morphology of *Bobolestes*, with an LM2/Lm2 ratio of 1.07. The lower molars of *Otlestes* have relatively narrow talonids with small talonid basins, which are too small to accommodate the large protocones of CCMGE 8/12176, but do match the much smaller protocones of *Bobolestes* (Fig. 2E). Thus, we consider CCMGE 7/12176, the holotype of *Otlestes meiman*, and the other dentary referred to this species (CCMGE 9/12176) to be conspecific with the maxillary fragment CCMGE 2/12176, the holotype of *Bobolestes zenge*.

Consequently *Otlestes meiman* Nessov, 1985 is a junior subjective synonym of *Bobolestes zenge* Nessov, 1985 by page priority (syn. nov.). The maxillary fragment CCMGE 8/12176 with M1-2, attributed previously to *O. meiman*, is referred to here as cf. *Sheikhdzheilia rezvyii* gen. et sp. nov. (see below).

In the original diagnosis of *Bobolestes*, Nessov cited a weak cusp B1. This is apparently an additional stylar cusp posterior and lingual to the stylocone in M3, which is absent in M2. In basal eutherians stylar cusps distal to the stylocone may be well developed (*Prokennalestes*, *Paranyctoides*), or virtually absent (*Murtoilestes*), and thus their presence or absence may have no great phylogenetic significance.

Nessov (1997, p. 166) questioned the presence of the jugal in *B. zenge* because of the well-developed maxillary zygomatic process and thought that it might be similar to Tenrecidae and other Soricomorpha lacking jugals. On the lateral side of the zygomatic process of the maxilla in CCMGE 2/12176 there is a marked depression that might have been overlapped by the jugal, so the absence of this bone in *B. zenge* is not conclusive.

Nessov (1985a, p. 15; Nessov et al., 1994, p. 63) reported the presence in CCMGE 7/12176 and 9/12176 of the "remnants of a coronoid bone", apparently referring to a bump-like structure on the medial side of the coronoid process at the alveolar level. Such a structure is present in a number of Cretaceous eutherians, including *Prokennalestes*, *Kennalestes*, and *Asioryctes* (Kielan-Jaworowska, 1981; Kielan-Jaworowska and Dashzeveg, 1989). There is considerable doubt that this structure is homologous to the coronoid bone and it is better referred to as a "rugosity…of uncertain meaning" (Wible et al., 2004, p. 37).

Nessov (1985a, p. 15) described the Meckelian groove for CCMGE 7/12176, but later (Nessov et al., 1994, p. 63) found that this groove "possibly does not represent this structure, as…the opening situated above this same groove and leading to a channel could represent the location of the Meckelian cartilage." The opening described above is the mandibular foramen leading to the mandibular canal serving for the n. alveolaris branch of the trigeminal cranial nerve and the ramus mandibularis of the internal carotid artery, which has no relationship to the Meckelian cartilage. A distinct ventral groove on the medial side of the dentary CCMGE 7/12176 is indeed the Meckelian groove. It has approximately the same topographic location and position relative to the mandibular foramen as in *Prokennalestes* (Kielan-Jaworowska and Dashzeveg, 1989).

*Bobolestes* was referred originally to the Pappotheriidae and subsequently to the monotypic Bobolestinae or Bobolestidae (Nessov, 1984, 1985a, b, 1987, 1989, 1997; Nessov et al., 1994), but was retained within the Pappotheriidae by McKenna and Bell (1997). According

to Kielan-Jaworowska and Dashzeveg (1989, p. 353) and Wible et al. (2001, p. 2) *Bobolestes* is an "undoubted" eutherian. *Otlestes* was placed originally in the monotypic Otlestinae within Palaeoryctidae (Nessov, 1985a), which was raised to the family level by Kielan-Jaworowska and Dashzeveg (1989) and expanded to include *Prokennalestes*. The idea of a close relationship between "*Otlestes*" and *Prokennalestes* was rejected by Averianov and Skutschas (2000) based, in particular, on a single-rooted canine in the former compared with the ancestral double-rooted canine in the latter.

*Bobolestes* has been included in relatively few phylogenetic analyses (e.g., Salles, 1996; Averianov and Skutschas, 1999), apparently because of its incompleteness; *Otlestes* has been used more widely because of the supposed association of upper and lower dentitions (Rougier et al., 1998; Cifelli, 1999b; Archibald et al., 2001). All previous phylogenetic conclusions concerning "*Otlestes*" may not be valid as they are based on chimerical data from two different taxa, and the phylogenetic position of *Bobolestes* should be reanalyzed in light of the newly associated upper and lower dentitions. We are preparing such an analysis, but we note here that there is considerable similarity in the structure of p5 between *Bobolestes* (including the lowers of "*Otlestes*") and the oldest zalambdalestid *Kulbeckia*. Both have a semimolariform p5 with a distinct metaconid and paraconid, and an enlarged and incipiently basined talonid. Although the molarization of premolars repeatedly occurred in eutherian evolution, this process had not progressed much in other lineages of Cretaceous mammals by this time. In asioryctitheres and the Cenomanian—early Turonian zhelestids p5 is not semimolariform (see below). Middle to late Turonian zhelestids had a semimolariform p5 but with a less separated metaconid and less basined talonid. Thus we consider a semimolariform p5 as a synapomorphy for Zalambdalestoidea, which possibly includes *Bobolestes* as well as more derived Zalambdalestidae. The only character that could bar *Bobolestes* from the ancestry of Zalambdalestidae is its single-rooted lower canine (double rooted in zalambdalestids). This condition may be reversed in Zalambdalestidae, or autapomorphic for *Bobolestes*. Also, there appears to be some incipient anteroposterior pinching of the para- and protocristids in the middle of the trigonid that is seen in zalambdalestids and at least some asioryctitheres, such as *Asioryctes*.

*Bobolestes zenge* Nessov, 1985
Fig. 2

Pappotheriidae [indet.]: Nessov, 1984, p. 64; Nessov, 1985b, p. 214
possibly Theria [indet.]: Nessov, 1984, fig. v; Nessov, 1997, pl. 43, fig. 3; Averianov, 2000, fig. 30.3I.

*Bobolestes zenge*: Nessov, 1985a, p. 10, pl. 1, fig. 1; Nessov and Kielan-Jaworowska, 1991, fig. 1; Nessov, 1993, fig. 5(1); Nessov et al., 1994, p. 60, pl. 2, fig. 3; Nessov, 1997, p. 166, pl. 43, fig. 1; Averianov, 2000, fig. 30.3A, B.

*Otlestes meiman* [partim]: Nessov, 1985a, p. 15, pl. 1, figs. 12, 13 [non fig. 4]; Nessov, 1993, fig. 5[2 (non 3)]; Nessov et al., 1994, p. 63, pl. 3; Nessov, 1997, p. 166, pl. 44, figs. 1, 2 [non fig. 3], pl. 45, fig. 1; Averianov, 2000, fig. 30.3G, H, O [non fig. 30.3C].

*Holotype*. CCMGE 2/12176, right maxillary fragment with M2-3 and alveoli for P5 and M1.

*Type locality and horizon*. Khodzhakul, SKH-20 site; lower Khodzhakul Formation, early Cenomanian.

*Referred specimens*. CCMGE 7/12176, left dentary with p4-5, m1-3 and alveoli for four incisors, single-rooted c, p1-3, the holotype of *Otlestes meiman* Nessov, 1985 (SSHD-8, 1982). CCMGE 9/12176, left dentary with p5, talonid of m3, and alveoli for c, p1-4, m1-2 (SSHD-8, 1981). ZIN 88437, left dentary fragment with alveoli for p2-5 (SSHD-8, 1999).

*Questionably referred specimens*. CCMGE 2/11658, left dentary fragment with alveoli for m1-3 (SKH-20, 1978). ZIN 88436, right dentary fragment with alveoli for m3 (SSHD-8, 1982).

*Description*. The anterior end of the maxillary zygomatic process is at the level of the anterior end of M2. The jugal-maxillary contact was relatively more


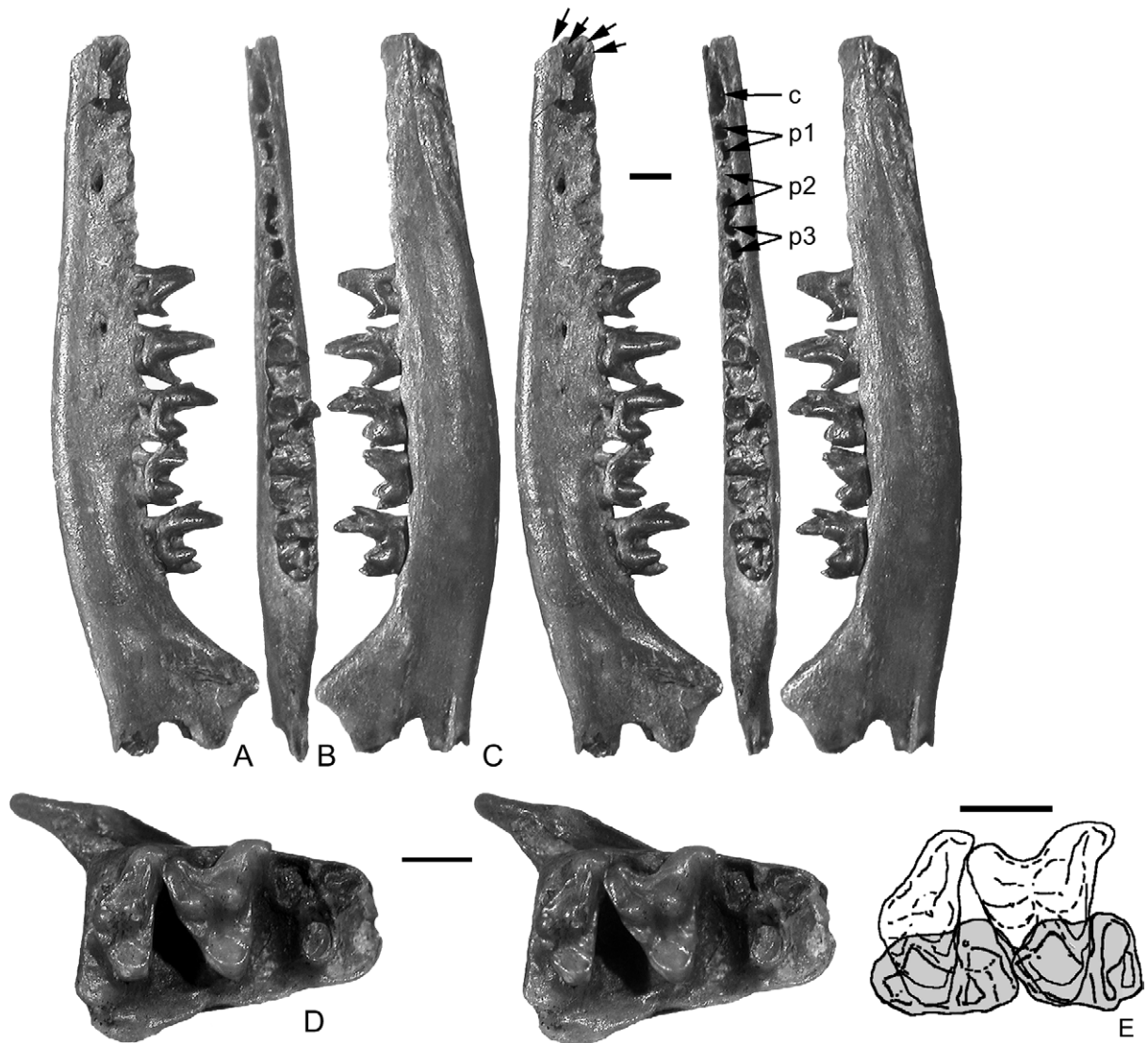
Fig. 2. *Bobolestes zenge*. Localities SSHD-8 (A–C, early Cenomanian) and SKH-20 (D, early Cenomanian), Khodzhakul Formation, Sheikhdzheili local fauna, Kyzylkum Desert, Uzbekistan. A–C, CCMGE 7/12176, stereo-photographs, left dentary with p4-5, m1-3, and alveoli for as many as four incisors (indicated by arrows in A), single-rooted canine, p1-3, holotype of *Otlestes meiman* Nessov, 1985: A, labial, B, occlusal, and C, lingual views. D, CCMGE 2/12176, stereo-photographs, right maxilla with M2-3 and partial alveoli of P5, alveoli for M1, holotype of *Bobolestes zenge* Nessov, 1985; occlusal view. E, drawing of M2-3 of CCMGE 2/12176 and m2-3 of CCMGE 7/12176; centric occlusion. Scale bars represent 1 mm.

dorsal than in, for example, zhelestids. Between the upper molars there are deep pockets or embrasures for the lower molar trigonids.

M2-3 (Fig. 2D) have a wide stylar shelf and a very small and low protocone, but the protocone height was evidently decreased by considerable wear. The conules have prominent internal cristae, delimiting conular basins placed at levels different from that of the trigon basin.

On M2 there is a deep ectoflexus with its deepest part posterior to the center of the labial side of the tooth. The parastylar lobe is much larger than the metastylar lobe. The preparacrista is long and robust, but the stylocone is not distinct, possibly having been worn away. There is a large parastyle and swelling of the crown in the region of the preparastyle, although the latter cusp does not appear to have been present. The parastylar groove is deep. The metacone is smaller than the paracone; the bases of both cusps are separate. The paraconule is slightly closer to the protocone than is the metaconule.

M3 is asymmetrical as in other primitive eutherians that have a prominent parastylar lobe and lack a metastylar lobe. On the parastylar lobe there are long, robust preparacrista, a well-developed parastyle, stylocone, and a small cusp posterior to the stylocone. The metacone is distinctly smaller than the paracone. The paraconule is much larger and closer to the protocone than the metaconule.

The dentary (Fig. 2A–C) is relatively shallow, comparable in depth with the height of molars. The anterior mental foramen is between the roots of p2. The posterior mental foramen is under the posterior root of p4 (CCMGE 9/12176), or between p4 and p5 (CCMGE 7/12176). In CCMGE 7/12176 there is a third small mental foramen under the anterior root of m1. The coronoid process is at an angle of 40–45° to the alveolar border and separated by some distance from m3. The masseteric crest is distinct but low. The masseteric fossa is shallow. The posterior end of the mandibular symphysis is between roots of p3. There is a very shallow Meckelian groove, deepened under the mandibular foramen.

Grooves on the anterior edge of the dentary of CCMGE 7/12176 suggest as many as four incisors may have been present (arrows in Fig. 2A), but only two can be identified with certainty. The lower canine is single rooted and relatively small. There are five lower premolars; all double rooted and not crowded. p2 and p4 are of similar size and larger than p1 and p3. p4 is premolariform, with a large main cusp and a distinct posterior cusp, but there is no anterior cusp. p5 is semimolariform, with a fully developed trigonid having a well-separated metaconid and a distinct paraconid. The talonid is long, with a single posterior cusp and an incipient talonid basin lingual to the longitudinal crest connecting the talonid cusp and the trigonid.

In the lower molars, the trigonid is much higher than the talonid. The metaconid is distinctly lower than the protoconid and the paraconid is relatively large, especially on m3. The bases of the metaconid and paraconid are connate. The trigonid angle varies from 43° (m1) to 55° (m3). The precingulid is distinct but short. The talonid is longer and narrower than the trigonid, and is especially long in m3. The hypoflexid is deep and the cristid obliqua terminates slightly lingual to the protocristid notch. The hypoconid is the largest of the talonid cusps, but the size difference between them is not great. The hypoconulid is approximately equidistant from the hypoconid and entoconid. On m3 there is a distinct entoconulid on the entocristid. The talonid basin is small, being dominated by the bases of the talonid cusps. There is no postcingulid.

*Measurements.* CCMGE 2/12176. M2: L, 1.7; AW, 1.9; PW, 1.8. M3: L, 1.2; AW, 1.9; PW, 1.3. CCMGE 7/12176. p4: L,1.3; W, 0.7. p5: L,1.4; W, 0.8. m1: TRL, 0.8; TRW, 1.1; TAL, 0.7; TAW, 1.0. m2: TRL, 0.8; TRW, 1.1; TAL, 0.7; TAW, 0.9. m3: TRL, 0.8; TRW, 1.0; TAL, 0.8; TAW, 0.8. CCMGE 9/12176. p5: L, 1.5; W, 0.8.

*Remarks.* B. zenge is the smallest mammal in the Sheikhdzheili local fauna. CCMGE 9/12176 is slightly larger than CCMGE 7/12176 and has a tiny labial mandibular foramen that is absent in the latter specimen.

Zalambdalestidae Gregory and Simpson, 1926

Zalambdalestidae indet.
Fig. 3

*Referred specimen.* ZIN 88500, right petrosal (SSHD-8, 2003).

*Description.* The petrosal is nearly complete and generally well preserved. The promontorium measures about 3.5 mm by 2.5 mm (area 8.8 mm$^2$). The fenestra vestibuli is undamaged, as is the narrow shelf that received the footplate of the stapes. The dimensions are 0.8 mm by 0.4 mm, which yields a stapedial ratio of 2.0. There is a distinct sulcus on both sides of the long axis of the fenestra vestibuli indicating the presence of a stapedial artery. On the anteromedial edge of the fenestra vestibuli there also appears to be a slightly smaller diameter sulcus extending about 1 mm. This might have been for the internal carotid artery very near the point where it and the stapedial artery divide. The fenestra cochleae is not quite round in outline, being slightly narrower in the dorsoventral dimension. A prominent crista interfenestralis extends posteriorly from the promontorium between the fenestra vestibuli and fenestra cochleae. This delimits a deep fossa musculus minor immediately posterior to the fenestra vestibuli and
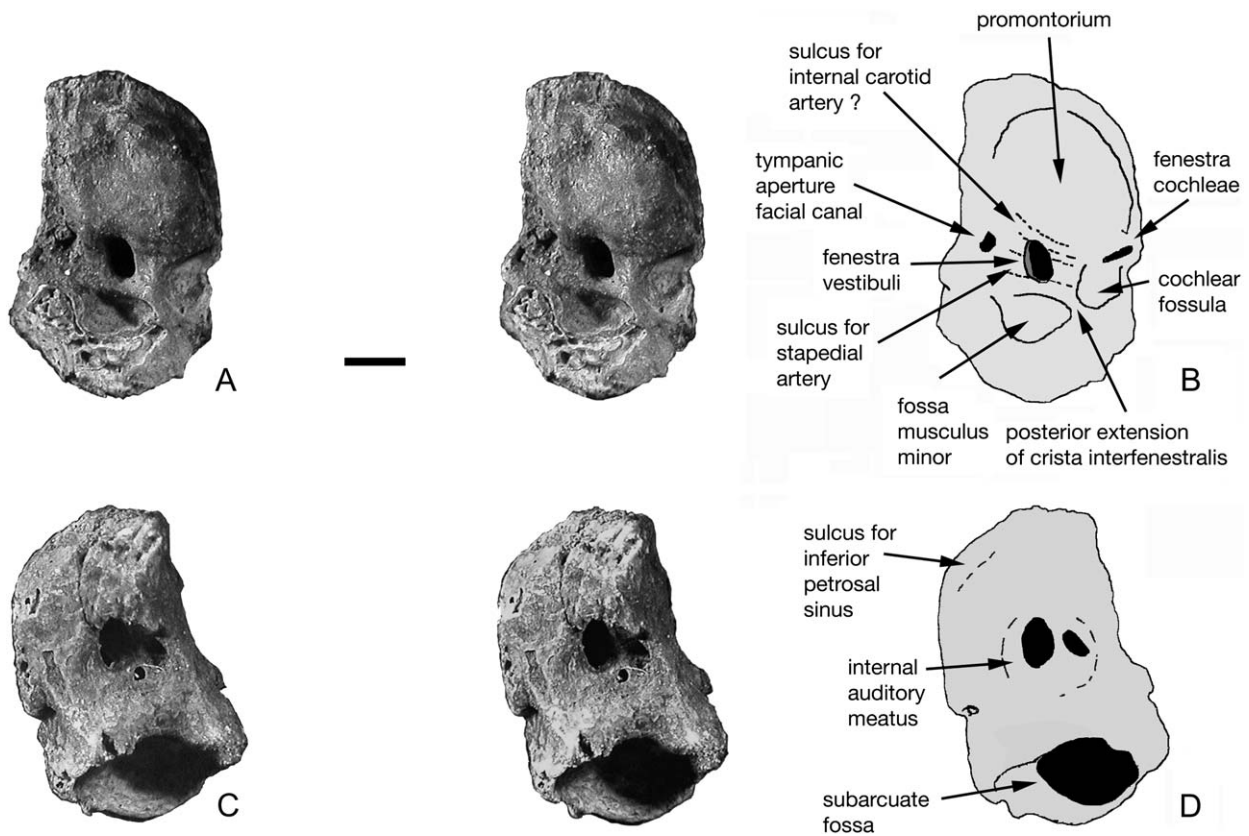
Fig. 3. Zalambdalestidae indet. Locality SSHD-8 (early Cenomanian), Khodzhakul Formation, Sheikhdzheili local fauna, Kyzylkum Desert, Uzbekistan. ZIN 88500, right petrosal; A, B, ventral view; C, D, dorsal view. A, C, stereo-photographs; B, D, explanatory drawings. Scale bar represents 1 mm.

a shallower cochlear fossula posterior to the fenestra cochleae. Immediately lateral to the fenestra vestibuli is the moderately large tympanic aperture of the facial canal. The internal auditory meatus is complete while about 75% of the subarcuate fossa is present. The hiatus Fallopii is visible on the squamosal surface.

*Remarks.* ZIN 88500 is indistinguishable in morphology and size from petrosals referred to *Kulbeckia kulbecke* by Ekdale et al. (2004). Teeth of *Kulbeckia* or any other zalambdalestid have not been recovered in the Sheikhdzheili local fauna. The closest possible phylogenetic match might be with *Bobolestes zenge*, which is thought now to be a zalambdalestoid. Even if this new phylogenetic assignment proves correct, at an m3 area of 1.7 mm$^2$, *Bobolestes* is far too small to be associated with the ZIN 88500 petrosal, which has a promontorial area of 8.8 mm$^2$. Such a promontorial area predicts an m3 with the much greater area of 2.3 mm$^2$ (Ekdale et al., 2004).

Laurasiatheria Waddell et al., 1999
"Zhelestidae" Nessov, 1985
Genus *Sheikhdzheilia* gen. nov.

*Type species. Sheikhdzheilia rezvyii* sp. nov., western Uzbekistan; early Cenomanian.

*Derivation of name.* After the Sheikhdzheili Range south of the Sheikhdzheili locality, possibly derived from a historical person of the region, Sheik Dzheili; pronounced SHAKE-ja-lee-a.

*Diagnosis.* The p5 premolariform (−); p5 paraconid well developed but positioned low on the anterior face (?); p5 with narrow, nearly complete lingual cingulid (?); p5 talonid ridge-like, not basined (−); m1 paraconid low, small, and slightly labial relative to metaconid (−); m1 trigonid relatively open, with trigonid angle ca. 60° (−); lower molar talonids wider than trigonids, with an expanded talonid basin (+); cristid obliqua below protocristid notch (+); hypoconulid close to entoconid (+); posterior mental foramen under posterior root of p5 (?). Assessments of polarities of characters are based on Archibald et al. (2001).

*Remarks. Sheikhdzheilia* gen. nov. is the smallest taxon and possibly the one retaining the greatest number of ancestral characters among known zhelestids. It is more derived than *Eozhelestes*, however, in the position of the cristid obliqua, which is more labial at least on m1. *Sheikhdzheilia* shares with "*Sorlestes*" *kara* from the lower Turonian of Kazakhstan the plesiomorphic premolariform p5, and with *Lainodon* from the Campanian

of Spain, for which p5 is unknown, a relatively open m1 trigonid, which is also considered an ancestral character. In "*Sorlestes*" *kara*, as well as in *Eozhelestes* from the Sheikhdzheili local fauna, the molars have a more typical zhelestid structure with anteroposteriorly shortened trigonids. In *Lainodon* the m1 paraconid is more lingual in position than in *Sheikhdzheilia*, being in the same anteroposterior plane as the metaconid.

*Sheikhdzheilia rezvyii* sp. nov.
Fig. 4A–C

*Holotype*. ZIN 88438, right dentary fragment with p5, m1, talonid of m2, and alveoli for p4 and m3.

*Type locality and horizon*. Sheikhdzheili, site SSHD-8 (2003); upper Khodzhakul Formation, early Cenomanian.

*Derivation of name*. After Anton S. Rezvyi, who found the holotype.

*Diagnosis*. As for the genus.

*Description*. The p5 is relatively long, only slightly shorter than m1. Its paraconid is narrower labiolingually relative to the remaining part of the crown. There is a narrow, but nearly complete lingual cingulid, an anterolabial cingulid that contacts the paraconid, and a posterolabial cingulid that contacts the hypoconulid.

The m1 has a narrow, but well-developed precingulid. In the m2 the talonid is slightly wider than in the m1.

*Measurements*. ZIN 88438. p5: L, 1.5; W, 0.9. m1: TRL, 0.8; TRW, 1.1; TAL, 0.8; TAW, 1.1. m2: TAW, 1.2.

cf. *Sheikhdzheilia rezvyii* gen. et sp. nov.
Fig. 4D

*Otlestes meiman* [partim]: Nessov, 1985a, p. 15, pl. 1, fig. 4 [non figs. 12, 13]; Nessov and Kielan-Jaworowska, 1991, fig. 1; Nessov, 1993, fig. 5[3 (non 2)]; Nessov, 1997, p. 166, pl. 44, fig. 3 [non figs. 1, 2]; Averianov, 2000, fig. 30.3C [non figs. 30.3G, H, O].

*Referred specimens*. CCMGE 8/12176, left maxillary fragment with M1-2 and alveoli for P5 and M3 (SSHD-8, 1982). ZIN 88432, left maxillary fragment with alveoli for M1-3 (SKH-20, 1982).

*Description*. The anterior end of the maxillary zygomatic process is at the level of M2. There is a well-developed, pocket-like articulation for the jugal, which is placed somewhat more dorsally than in other zhelestids. P5 was three-rooted and thus at least semimolariform, similar in width to M1. M1-2 are similar in structure, differing in the shape of their labial sides. In M1 the ectoflexus is shallower and the metastylar lobe is directed mostly anteriorly, while in M2 it is directed more anterolabially. The stylar shelf is narrow on both M1
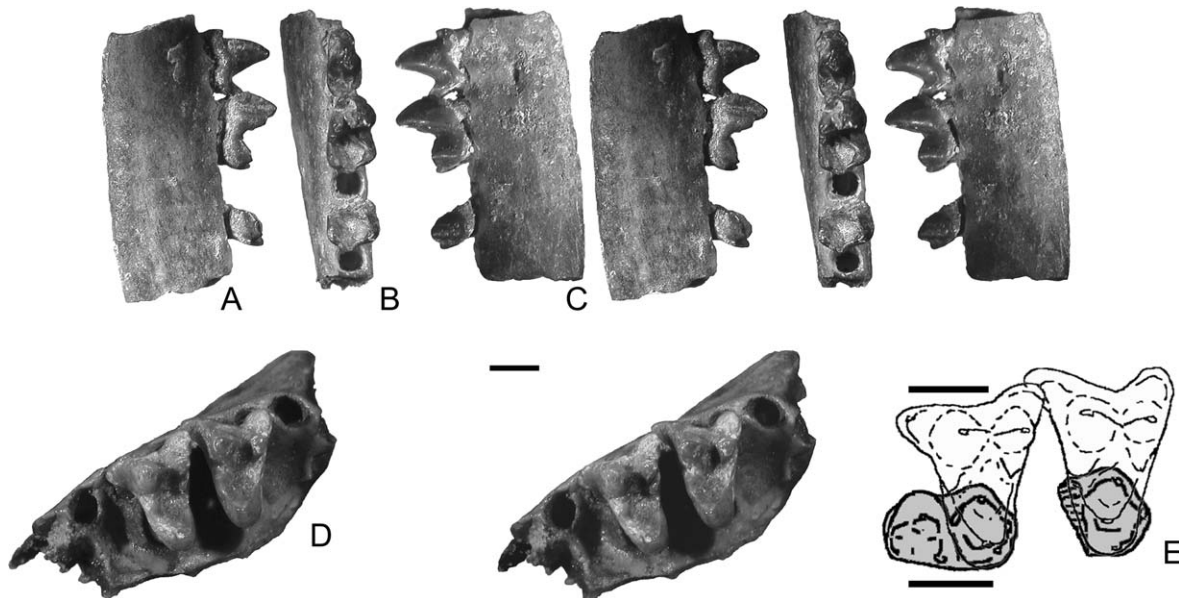


Fig. 4. *Sheikhdzheilia rezvyii* gen. et sp. nov. (A–C) and cf. *Sheikhdzheilia rezvyii* gen. et sp. nov. (D). Locality SSHD-8 (early Cenomanian), Khodzhakul Formation, Sheikhdzheili local fauna, Kyzylkum Desert, Uzbekistan. A–C, ZIN 88438, stereo-photographs, right dentary with p5, m1, talonid of m2, partial posterior alveolus for p4, and anterior alveolus for m3, holotype; A, lingual, B, occlusal, and C, labial views. D, CCMGE 8/12176, stereo-photographs, left maxilla with M1-2 and alveoli for P5 and M3; occlusal view. E, drawing of M1-2 of CCMGE 8/12176 and m1 and talonid of m2 of ZIN 88438; centric occlusion (upper molars are somewhat reduced to fit the size of lowers, and M1 slightly turned to a more anatomically correct position). Scale bars represent 1 mm.

and M2. The preparacrista is shorter in M1 than in M2. The postmetacrista is cusp-like. The metacone is distinctly lower than the paracone; the cusps are separated at their bases. The conules are roughly equidistant from the protocone and are closer to the paracone and metacone, but not as close as in other zhelestids. The internal cristae are well developed but short. The preparaconule and postmetaconule cristae are relatively short, extending labially to the bases of the paracone and metacone, respectively. The protocone is large, slightly expanded anteroposteriorly, and only slightly lower than the paracone, which is in part a result of moderate wear. There are no lingual cingula.

*Measurements.* CCMGE 8/12176. M1: L, 1.9; AW, 2.1; PW, 2.5. M2: L, 2.0; AW, 2.3; PW, 2.5.

*Remarks.* The M1 and M2 in CCMGE 8/12176 bear resemblances to the same teeth in zhelestids, notably in *Aspanlestes aptap*, in what appear to be characters derived relative to the ancestral eutherian condition. The protocone is relatively larger compared to, for example, *Bobolestes zenge*, and is slightly expanded anteroposteriorly. The stylar shelves are almost as narrow as those in *Aspanlestes*. Also as in this taxon, the paracone and metacone are separated at their bases, the metacone is slightly smaller and lower, the conules are wing-like and closer to the paracone and metacone than to the protocone. Unlike zhelestids, the M1 and M2 in CCMGE 8/12176 lack lingual cingula and probably do not have a preparastyle.

CCMGE 8/12176 is morphologically suitable for the lower dentition of *Sheikhdzheilia rezvyii* gen. et sp. nov. (Fig. 4E), but slightly larger; hence it is identified here as cf. *Sheikhdzheilia rezvyii*.

Nessov (1997, p. 166) proposed that CCMGE 8/12176 might not have had a jugal and zygomatic arch, like some soricomorph insectivores. There is a distinct pocket-like articulation facet for the jugal on the maxillary zygomatic process, better preserved in ZIN 88432 than in CCMGE 8/12176, thus suggesting the presence of a jugal.

Genus *Eozhelestes* Nessov, 1997

*Type species.* *Eozhelestes mangit* Nessov, 1997. western Uzbekistan; early Cenomanian.

*Diagnosis* (revised after Nessov, 1997, p. 169). Four lower incisors (−); five lower premolars (−); lower canine single rooted (+); p1 not transverse (−); p3 somewhat reduced at least in some specimens (+); m1 trigonid relatively open, with trigonid angle ca. 45° (−); lower molar talonids narrower than trigonids (−); cristid obliqua lingual to protocristid notch in m1 (−); hypoconulid close to entoconid (+); posterior mental foramen

under anterior root of p5 (?). Assessments of polarities of characters are based on Archibald et al. (2001).

*Remarks.* The holotype of *E. mangit* is generally similar in morphology and close in size to the m1 of *Aspanlestes aptap* from the Turonian of the central Kyzylkum, but differs in a number of ancestral retentions: the trigonid is relatively higher than the talonid, so that the height differential between the trigonid and talonid is greater; there is a greater height differential between the protoconid and metaconid; the cristid oblique is lingual to the protocristid notch rather than at the at the notch as in *Aspanlestes*; the talonid is narrower than the trigonid (wider or of the same width in *Aspanlestes*); and the talonid basin is relatively less expanded. In the m3, the position of the cristid obliqua is more labial, under the protocristid notch, but this derived condition is achieved by an almost right angle deflection of the cristid obliqua's anterior end, thus in the depth of the hypoflexid m3 is close to m1.

*Eozhelestes mangit* Nessov, 1997
Figs. 5, 6

Mixotheridia [indet.]: Nessov, 1985a, pl. 1, fig. 3.
Theria [indet.]: Nessov, 1985a, pl. 1, fig. 11; Nessov, 1997, p. 139, pl. 43, fig. 5; Averianov, 2000, fig. 30.3F.
Gen. indet.: Nessov et al., 1994, pl. 7, fig. 2.
'Mixotheridia' cf. 'Zhelestidae': Nessov, 1997, p. 139.
*Eozhelestes mangit* Nessov, 1997, p. 170, pl. 43, fig. 4.
'Zhelestidae' gen. et sp. nov.: Averianov, 2000, fig. 30.3D, E.

*Holotype.* CCMGE 26/12176, left m1.

*Type locality and horizon.* Sheikhdzheili, site (SSHD-8, 1982); upper Khodzhakul Formation, early Cenomanian.

*Diagnosis.* As for the genus.

*Referred specimens.* ZIN 88430, incomplete and worn left dp5 (SSHD-8, 1999). CCMGE 15/12176, left(?) p4 (SSHD-8). ZIN 82579, left m3 lacking anterior side of the trigonid (SSHD-8, 1999). ZIN 88433, left dentary fragment with heavily worn m1(?) and alveoli for p5(?) and m2(?) (SSHD-8, 1982). ZIN 82578, left dentary fragment with alveoli for three incisors (i1-3?), single-rooted c, p1-5, m1 (SSHD-8, 1999). ZIN 88431, right dentary fragment with alveoli for i1-4, single-rooted c, p1-4, dp5, m1 (SSHD-8, 2003). ZIN 82577, left dentary fragment with alveoli for c, p1-5 (SSHD-8, 1982). ZIN 88434, right dentary fragment with alveoli for m3 (SSHD-8, 2003).

*Questionably referred specimens.* ZIN 88435, right dentary fragment with alveoli for m3 (SSHD-8, 1982).
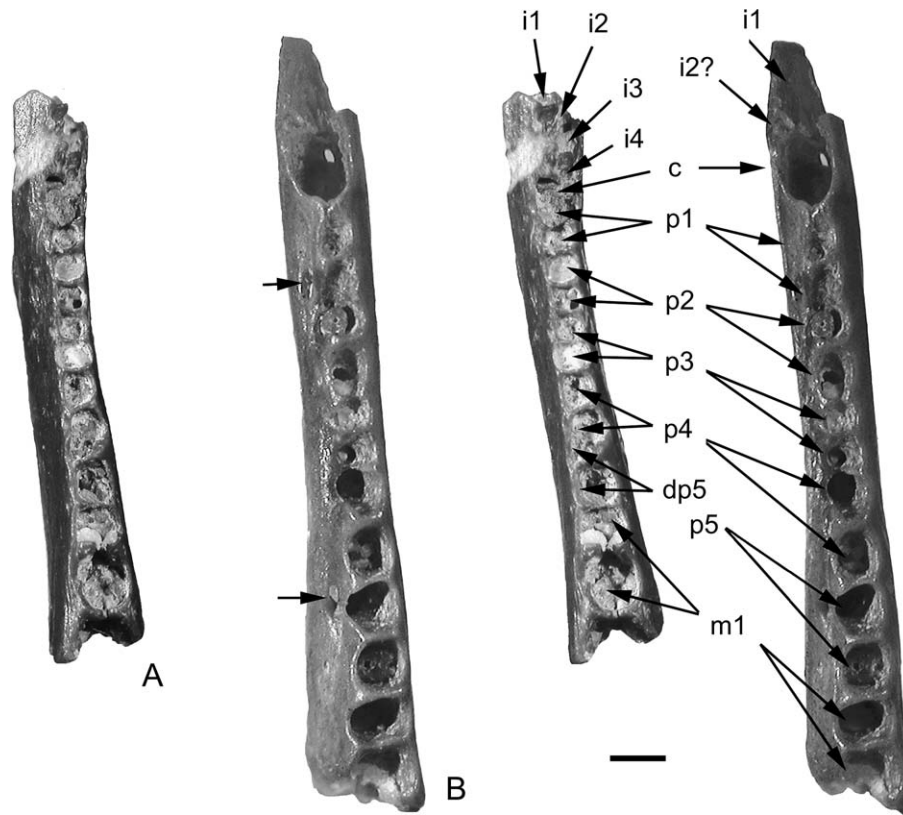
Fig. 5. *Eozhelestes mangit*. Locality SSHD-8 (early Cenomanian), Khodzhakul Formation, Sheikhdzheili local fauna, Kyzylkum Desert, Uzbekistan. A, ZIN 88431, stereo-photographs, right dentary with alveoli for i1-4, c, p1-5, dp5, and most of m1; occlusal view. B, ZIN 82578, stereo-photographs, left dentary with alveoli for i1, i2?, c, p1-5, and most of m1; occlusal view; arrows indicate mental foramina. Scale bar represents 1 mm.

ZIN 88501, left dentary fragment with alveoli for m2-3 (SCH-1, 1980).

*Description.* There are alveoli for four incisors in ZIN 88431 and for two incisors in ZIN 82578 (Fig. 5). In the latter specimen the dorsal border of the dentary is incomplete in this region and the alveoli for the posterior incisors are missing. The canine, judging from the alveolus in at least two specimens, was single rooted and not very large. Its root in ZIN 82578 extends posteriorly to between p1 and p2. There are five lower premolars, all double rooted, and not crowded in adult specimens (crowded in the juvenile, ZIN 88431). The p1 is relatively smaller than the other premolars in ZIN 82577, compared to the p1 in both ZIN 82578 and 88431. In the juvenile specimen, ZIN 88431, the anterior alveolus for p1 is confluent with the canine alveolus. The p1 crown was probably canted anteriorly, at least in ZIN 82578, judging from its posteriorly directed alveoli and remaining roots. In ZIN 82578 and 82577, p3 is slightly smaller than the neighboring teeth, but in ZIN 88431, it is almost equal in size to p2. The anterior mental foramen is below the posterior root of p1 (ZIN 82578), under the anterior root of p2 (ZIN 88431), or between p2 and p3 (ZIN 82577). The posterior mental

foramen is under anterior root of p5 (or dp5 in ZIN 88431). The symphysis terminates posteriorly under p3, or between p2 and p3 (ZIN 88431).

p4. This tooth has a distinct anterior cusp and a larger talonid cusp. In ZIN 88431 the posterior alveolus for p4 is partly confluent with the anterior alveolus for dp5.

dp5. ZIN 88430 is heavily worn with most of its enamel and anterior part of the trigonid lacking. The talonid is relatively long. The talonid basin is expanded so that the talonid is almost equal to the trigonid in width, but the hypoflexid is deep. The trigonid was high and there is a trace of the cristid obliqua reaching quite high on the trigonid posterior slope. The root is rather long, exceeding the talonid height by more than twice.

m1. The trigonid is tall, with the primary cusps forming a wide angle. The metaconid is distinctly lower and smaller than the protoconid (Fig. 6A–E). The paraconid is small and positioned slightly labial to the metaconid. There is a distinct trigonid basin. The precingulid is distinct but narrow, placed rather low below the paracristid notch. The talonid is slightly narrower than the trigonid, with a deep hypoflexid and deep talonid basin. The cristid obliqua contacts the

trigonid somewhat lingually to the protocristid notch. The hypoconulid and entoconid are close in size and position. The postcingulid is distinct and rather long.

m3. The ultimate molar (Fig. 6F, G) is known from a single specimen lacking the anterior part of the trigonid (ZIN 82579). The remaining trigonid cusps are robust, and they may have formed a wide angle. They are somewhat inclined forward. There is a distinct trigonid basin. The protoconid is noticeably higher than the metaconid. The talonid is slightly narrower than the trigonid, with an expanded but shallow basin and with shallow hypoflexid. The cristid obliqua bears a cusp-like swelling and terminates below the protocristid notch. The talonid cusps are relatively low; the hypoconid is the largest and the entoconid is the smallest. The hypoconulid is approximately equidistant from the hypoconid and entoconid.

*Measurements*. CCMGE 26/12176. m1: TRL, 1.1; TRW, 1.5; TAL, 1.1; TAW, 1.4. ZIN 82579. m3: TAL, 1.1; TAW, 1.1.

*Remarks*. ZIN 88430 is identical in other aspects of morphology compared to dp5s of other zhelestids (e.g., CCMGE 37/12000, dp5 of *Zhelestes temirkazyk*, Nessov, 1985b, pl. 2, fig. 3, identified in that publication as ?m1). It is interesting that this tooth is rather worn but its root is long and has no trace of resorption. This may indicate rather late replacement in the fifth post-canine locus in this species. This, and the small anterior alveolus are the bases for identification of the dp5 alveoli in the juvenile, ZIN 88431.

"Zhelestidae" indet., unnamed large sp. A
Fig. 7

possibly *Oxlestes grandis* [nomen nudum]: Nessov, 1981, fig. 9(23).
possibly *Oxlestes grandis*: Nessov, 1982, p. 236, pl. 1, fig. 1; Nessov and Kielan-Jaworowska, 1991, fig. 1; Nessov et al., 1994, p. 57, pl. 1, fig. 5; Nessov, 1997, pl. 43, fig. 6; Averianov, 2000, fig. 30.3N.
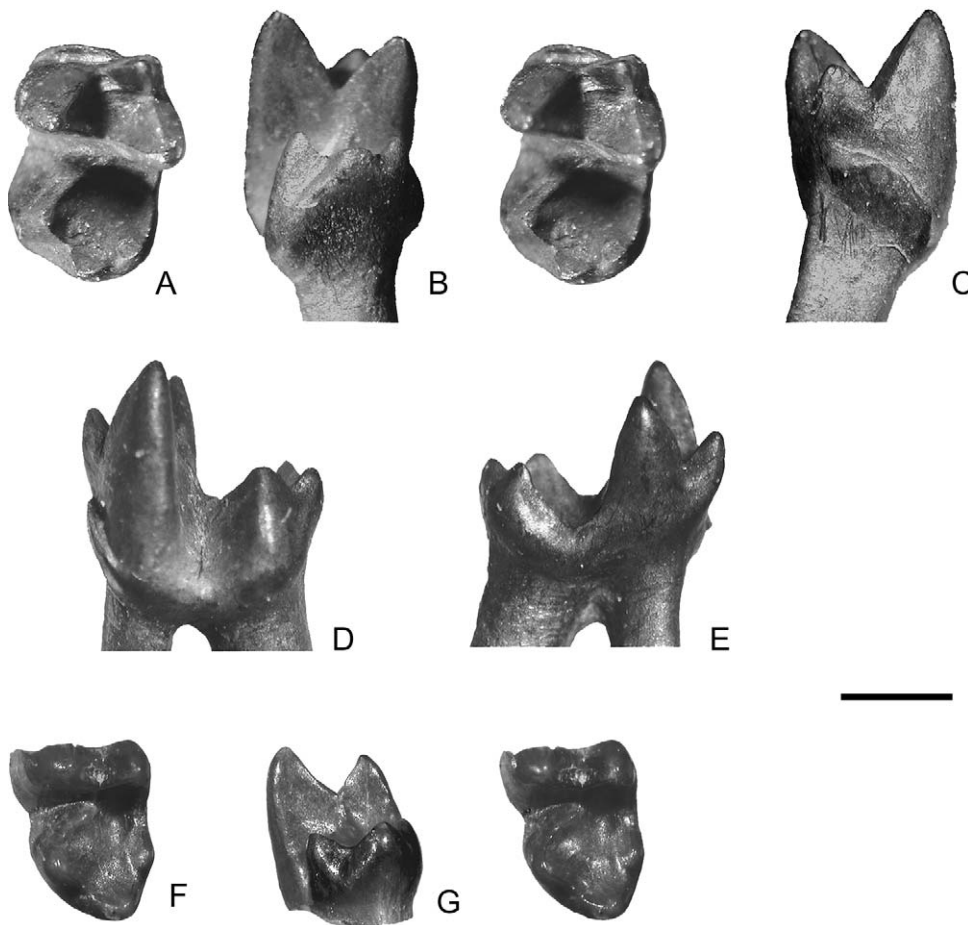


Fig. 6. *Eozhelestes mangit*. Locality SSHD-8 (early Cenomanian), Khodzhakul Formation, Sheikhdzheili local fauna, Kyzylkum Desert, Uzbekistan. A–E, CCMGE 26/12176, left m1, holotype in A, occlusal, B, posterior, C, anterior, D, labial, and E, lingual views. F, G, ZIN 82579, left m3 lacking anterior part of the trigonid; F, occlusal, and G, posterior views. A, F, stereo-photographs; scale bar represents 1 mm.

Eutheria [indet.]: Nessov, 1984, figs. a, b.

Gen. indet.: Nessov et al., 1994, pl. 7, fig. 3.

'Mixotheridia' cf. 'Zhelestidae', or Eutheria [indet.]: Nessov, 1997, p. 139, pl. 43, fig. 9.

*Referred specimens.* CCMGE 1/11658, left dentary with alveoli for p1-2, 4-5, m1-3 (SSHD-8, 1980). ZIN 82576, left dentary fragment with alveoli for c, p1-2, 4-5, m1-2 (SSHD-8, 1982).

*Questionably referred specimen.* CCMGE 6/11758, axis, the holotype of *Oxlestes grandis* Nessov, 1982 (SSHD-8a, 1979).

*Description.* The dentary is deep and robust, with a convex ventral border (Fig. 7). There are two smaller mental foramina under the posterior root of p1 and anterior root of p5 (CCMGE 1/11658), or two larger mental foramina under p2 and p4 (ZIN 82576). The masseteric crest is prominent and the masseteric fossa is deep. The posterior end of the mandibular symphysis is under the posterior root of p2. The lower premolars are not crowded; p1 and p2 are of similar size; in ZIN 82576 they are separated by a small diastema. The p3 is lost with its alveoli plugged in both specimens; thus p2 and p4 are separated by a long diastema. The m3 had a large posterior root.

*Remarks.* As noted by Nessov (1984, p. 64), CCMGE 1/11658 was part of an old individual based on the size,

depth and robustness of the dentary, and the narrow pulp cavities in the remaining roots of p2 and p4. This specimen (Nessov, 1997, p. 56) and ZIN 82576 had lost p3 and its alveoli were plugged, which produced a long diastema between p2 and p4. These specimens and other such zhelestid specimens from Dzharakuduk confirm that the p3 locus was lost in an evolutionary reduction from five to four premolars in Eutheria (Archibald and Averianov, 1997; Nessov, 1997). CCMGE 1/11658 is otherwise similar to dentaries of zhelestids in its steep coronoid process and in the shape of the masseteric fossa.

The holotype of *Oxlestes grandis* is a rather large (L, 12.8) mammalian axis. Nessov and Kielan-Jaworowska (1991) and Averianov (2000) erroneously considered this specimen to be fused second and third cervicals (C2 and C3), apparently because of a distinct transverse suture. This suture is possibly between the axis intercentrum and axis centrum, not between the atlas centrum and axis centrum, as thought by Nessov et al. (1994), because the atlas centrum is homologous with the axial odontoid process (Romer, 1997). The same suture is visible on the axis in *Asioryctes* and *Barunlestes* (Kielan-Jaworowska, 1977, 1978). The cervical rib possibly was not fused with the axis. Unique to CCMGE 6/11758 are two pairs of distinct foramina anterior and posterior to the transverse suture on its dorsal side. Nessov et al. (1994) interpreted these foramina as openings for blood vessels. In recent mammals only a posterior pair of these
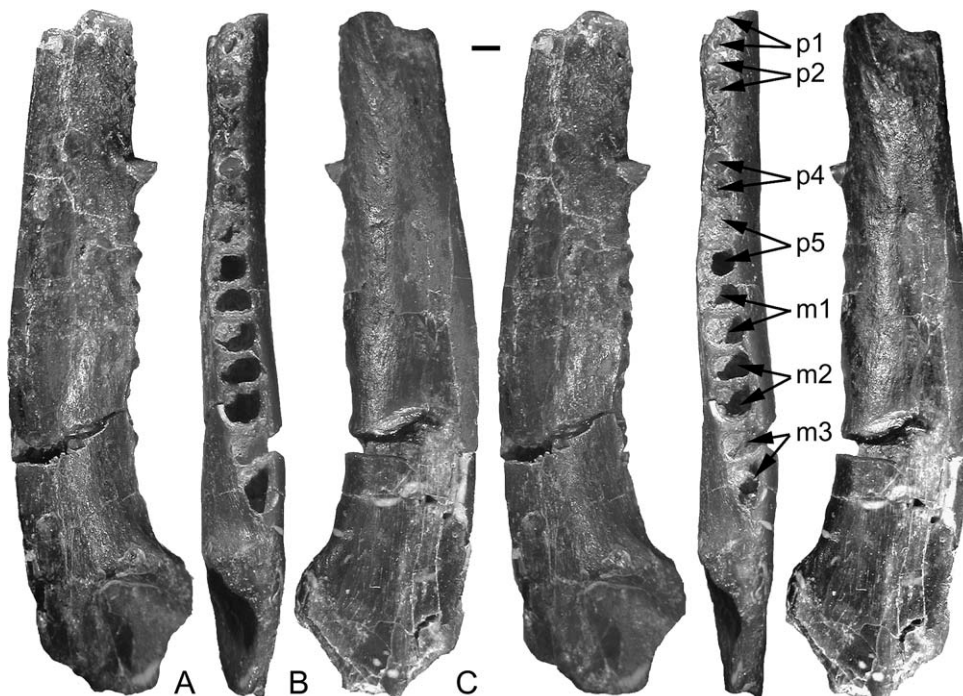


Fig. 7. "Zhelestidae" indet., unnamed large sp. A. Locality SSHD-8 (early Cenomanian), Khodzhakul Formation, Sheikhdzheili local fauna, Kyzylkum Desert, Uzbekistan. A−C, CCMGE 1/11658, stereo-photographs, left dentary with alveoli for p1-2, 4-5, m1-3: A, labial, B, occlusal, and C, lingual views. Scale bar represents 1 mm.

foramina is present. Nessov (1982, p. 237) estimated the skull length of *Oxlestes* as close to 100 mm based on the axis/skull ratio in *Zalambdalestes*, *Barunlestes* and *Asioryctes*. This estimate is apparently exaggerated because of the unusually long snout and small axis in zalambdalestids. CCMGE 6/11758 is distinctly shorter but anteriorly wider than the axis of a rabbit, *Oryctolagus cuniculus*, with the skull length 77.5 mm. The preserved length of the CCMGE 1/11658 dentary is 24 mm and this specimen and the axis may belong to animals of similar size.

*Oxlestes* was placed originally in Palaeoryctidae(?) (Nessov, 1982, 1984). Later Nessov (in Nessov et al., 1994, p. 58) thought *Oxlestes* "might be…a large deltatheroid", or "a deltatheroid, or a palaeoryctoid predator" based on possible association of its holotype with fused parietals and large canine. He (Nessov, 1997) subsequently referred this taxon to Deltatheroida(?), or Palaeoryctidae(?). In most recent classifications (McKenna and Bell, 1997; Kielan-Jaworowska et al., 2004). *Oxlestes* is assigned to Deltatheroida. It is more parsimonious, however, to think that the holotype of *O. grandis* belongs to the similarly large, undetermined zhelestid from the Sheikhdzheili local fauna. Unfortunately, there is a little chance of proving this association and the name "*Oxlestes grandis*" is possibly best considered a nomen dubium.

Nessov (1985a, 1987, 1993, 1997; Nessov et al., 1994) also referred relatively large fused parietals with a prominent sagittal crest to *Oxlestes* (CCMGE 13/12176, SSHD-8, 1980; Nessov, 1985a, pl. 2, fig. 1; Nessov et al., 1994, pl. 7, fig. 1; Nessov, 1997, pl. 43, fig. 7; Averianov, 2000, fig. 30.3J, K). The size of these bones suggests they may belong to "Zhelestidae" indet., unnamed large sp. A.

?"Zhelestidae"
Fig. 8

*Referred specimen*. ZIN 88691, right petrosal (SSHD-8, 2004).

*Description*. The petrosal is nearly complete and generally well preserved. The promontorium measures about 4 mm by 3 mm (area 12 mm²). The fenestra vestibuli is mostly intact, as is the narrow shelf that received the footplate of the stapes. The dimensions are 0.8 mm by 0.3 mm, which yields a stapedial ratio of 2.7. There is a shallow but distinct sulcus on both sides of the long axis of the fenestra vestibule, indicating the presence of a stapedial artery. The fenestra cochleae is ovoid in outline, being narrower in the dorsoventral dimension. A faint crista interfenestralis extends posteriorly from the promontorium between the fenestra vestibuli and fenestra cochleae. This delimits a shallow fossa musculus minor immediately posterior to the fenestra vestibuli and an equally shallow cochlear fossula posterior to the fenestra cochleae. Immediately lateral to the fenestra vestibuli is a rather slit-like (although possibly damaged) tympanic aperture of the facial canal. Slightly posterolaterally is a shallow, fairly large groove that continues on to the squamosal surface. This may be part of the prootic canal. The internal auditory meatus is complete, although slightly damaged, while less than 50% of the subarcuate fossa is present. The hiatus Fallopii is visible on the squamosal surface.

*Remarks*. ZIN 88691 combines an unusual suite of characters. As in the zalambdalestid *Kulbeckia kulbecke* it has a sulcus for the stapedial artery crossing the fenestra vestibuli, a high stapedial ratio of 2.7, and a crista interfenestralis, although it is subdued (Ekdale et al., 2004). The one character that suggests that it could be a zhelestid is the apparent presence of part of a prootic canal. If this structure is incorrectly identified, then it might be a zalambdalestid petrosal. Even if it is a prootic canal, this is a therian trait that could have been retained in the earliest members of the zalambdalestoid clade.

## 3. General discussion

Mammals are extremely rare in the coastal marine Khodzhakul locality, but are better represented in the fluvial Sheikhdzheili locality. Similarity of at least the mammalian taxa permits us to treat the collections from these two localities as representatives of a single local fauna, the Sheikhdzheili local fauna. There may be some difference in age between the localities, but this is not discernible based upon the non-marine vertebrates.

Revision of the Sheikhdzheili mammalian local fauna considerably changes its composition (see Averianov and Archibald, 2003 and references cited herein for previous data). Rather than three eutherians of uncertain affinities (*Bobolestes*, *Otlestes*, and *Oxlestes*) and one zhelestid (*Eozhelestes*), it now appears to include a possible zalambdalestoid (*Bobolestes*), a possible zalambdalestid, and two (*Sheikhdzheilia rezvyii*, gen. et sp. nov. and *Eozhelestes mangit*) or three zhelestids ('Zhelestidae' indet., unnamed large sp. A) (Table 1). With five eutherian species at least 95 million years ago (early Cenomanian), it is the earliest mammalian fauna to have more than two species of eutherians. This eutherian-dominated Middle Asian local fauna is very different from the Cenomanian–Turonian mammalian faunas of North America, which are dominated by multituberculates and marsupials, with occurrences of "symmetrodonts" and "triconodonts" (Averianov and Archibald, 2003, table 2).
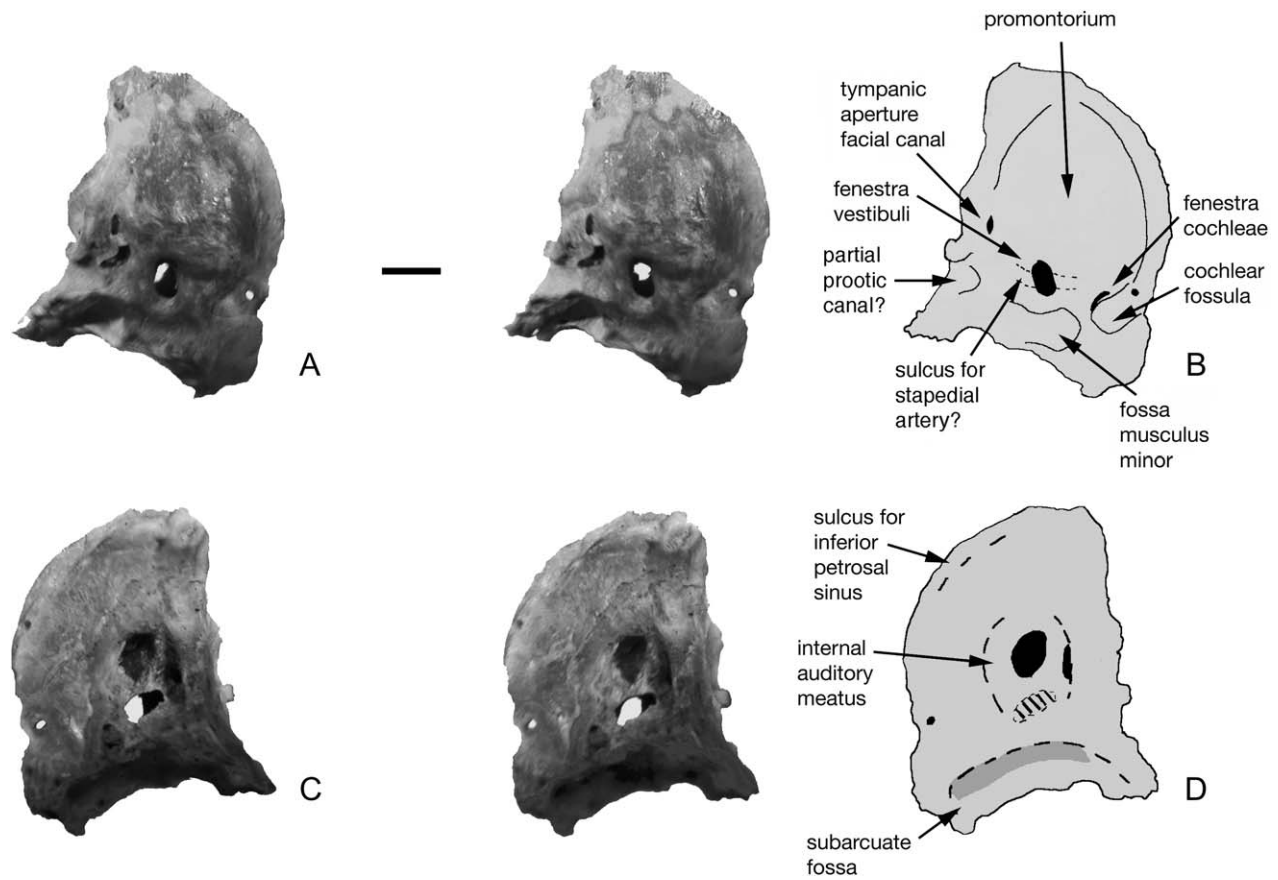
Fig. 8. ?"Zhelestidae". Locality SSHD-8 (early Cenomanian), Khodzhakul Formation, Sheikhdzheili local fauna, Kyzylkum Desert, Uzbekistan. ZIN 88691, right petrosal; A, B, ventral view; C, D, dorsal view. A, C, stereo-photographs; B, D, explanatory drawings; scale bar represents 1 mm.

Synonymy of *Bobolestes* and "*Otlestes*" and interpretation of *Bobolestes* as a possible zalambdalestoid could have an impact on phylogenetic reconstructions of basal Eutheria. If indeed a zalambdalestoid and if zalambdalestoids are crown eutherians (i.e., placentals) as suggested by Archibald et al. (2001), this taxon could corroborate the "long fuse" model of eutherian evolution (Archibald and Deutschman, 2001).

Table 1
Faunal list of mammals from Khodzhakul and Sheikhdzheili localities, Sheikhdzheili local fauna, southwest Kyzylkum Desert, Uzbekistan; early Cenomanian

| Taxa | Khodzhakul | Sheikhdzheili |
|---|---|---|
| **Zalambdalestoidea** | | |
| *Bobolestes zenge* | 1 (or 2) | 3 (or 4) |
| Zalambdalestidae indet. | | 1 |
| **"Zhelestidae"** | | |
| *Sheikhdzheilia rezvyii*, gen. et sp. nov. | | 1 |
| cf. *Sheikhdzheilia rezvyii*, gen. et sp. nov. | 1 | 1 |
| *Eozhelestes mangit* | | 9 (or 10) |
| 'Zhelestidae' indet. sp. A (?= *Oxlestes grandis*) | | 2 (or 4) |

Numbers refer to the number of identifiable specimens.

In the Cenomanian, before the formation of the Turgai Strait in the Turonian, Europe was still connected to Asia, and by this time basal zhelestids, such as *Sheikhdzheilia* gen. nov., as well as primitive hadrosauroids (Arkhangelsky and Averianov, 2003) may have reached Europe from Asia. Subsequent isolation of the European Archipelago may thus have facilitated survival of more primitive taxa in Europe until Campanian–Maastrichtian times. Such taxa include *Lainodon* and *Labes*, which have been suggested to be zhelestids but have not been included in any phylogenetic analyses with other zhelestids, and the hadrosaurid *Telmatosaurus*. By the Turonian in Asia, zhelestids already showed added diversification in form and in number of taxa, and definite zalambdalestids appeared.

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