UNGULATE-LIKE MAMMALS FROM THE LATE CRETACEOUS OF UZBEKISTAN AND A PHYLOGENETIC ANALYSIS OF UNGULATOMORPHA

LEV A. NESSOV [1]

Institute of the Earth's Crust, Faculty of Geology, St. Petersburg State University, St. Petersburg 199034, Russia

J. DAVID ARCHIBALD [2]

Department of Biology, San Diego State University, San Diego, California 92182

ZOFIA KIELAN-JAWOROWSKA [3]

Paleontologisk Museum, Universitetet i Oslo, Sars gate 1, N-0562 Oslo 5, Norway

Beard and Dawson, eds., Dawn of the Age of Mammals in Asia
Bulletin of Carnegie Museum of Natural History, 34:40–88, 1998.

Beard and Dawson, eds., Dawn of the Age of Mammals in Asia
Bulletin of Carnegie Museum of Natural History, 34:40–88, 1998.

UNGULATE-LIKE MAMMALS FROM THE LATE CRETACEOUS OF UZBEKISTAN AND A PHYLOGENETIC ANALYSIS OF UNGULATOMORPHA

LEV A. NESSOV [1]

Institute of the Earth's Crust, Faculty of Geology, St. Petersburg State University, St. Petersburg 199034, Russia

J. DAVID ARCHIBALD [2]

Department of Biology, San Diego State University, San Diego, California 92182

ZOFIA KIELAN-JAWOROWSKA [3]

Paleontologisk Museum, Universitetet i Oslo, Sars gate 1, N-0562 Oslo 5, Norway

ABSTRACT

(Supergrandorder) Ungulatomorpha Archibald, 1996*b* includes (grandorder) Ungulata and (family) "Zhelestidae." "Zhelestidae" Nessov, 1985*a* is best known from the Upper Cretaceous (upper Turonian–Coniacian) Bissekty Formation, Dzhyrakuduk, Kyzylkum Desert, Uzbekistan. Asian taxa (lower Turonian–Coniacian) include: *Kumsuperus avus* Nessov, 1984*b*, nomen dubium; *Zhelestes temirkazyk* Nessov, 1985*a*; *Sorlestes budan* Nessov, 1985*a*; *Aspanlestes aptap* Nessov, 1985*a*; *Sorlestes kara* Nessov, 1993; *Parazhelestes robustus* Nessov, 1993; *P. minor*, n. sp.; and *Eoungulatum kudukensis*, n. gen. and sp. North America taxa (mid-Campanian–early Paleocene) include: *Gallolestes pachymandibularis* Lillegraven, 1976; *G. agujaensis* Cifelli, 1994; *Alostera saskatchewanensis* Fox, 1989; and *Avitotherium utahensis* Cifelli, 1990. European taxa (Campanian–Maastrichtian) include: *Lainodon orueetxebarriai* Gheerbrant and Astibia, 1994; *Labes quintanillensis* Sigé *in* Pol et al., 1992; and *Labes garimondi* Sigé *in* Pol et al., 1992. An M_x fragment (late Santonian) from Vinton Bluff, Mississippi, U.S.A., is questionably referred to Ungulatomorpha. *Wania chowi* Wang, 1995 is not a zhelestid but may have anagalidan affinities. "Zhelestids" occur at localities in wetter, low coastal plain settings in western Asia and North America, but are absent from contemporaneous Late Cretaceous sites in higher, drier settings in Mongolia. Diverse Asian "zhelestids" with apomorphies foreshadowing much later archaic ungulates suggest that archaic ungulates reached North America near the end of the Cretaceous via Beringia. A phylogenetic analysis (18 characters of the upper dentition) strongly supports monophyly of Ungulatomorpha, which includes "Zhelestidae" and Ungulata, as represented by the exemplar *Protungulatum donnae*. A close relationship among rodents (represented by *Tribosphenomys*), primatomorphs (represented by *Purgatorius*), and ungulatomorphs is possible, but the resemblances are equally attributable to convergence.

[1] Lev A. Nessov died on October 1, 1995, during the final stages of the preparation of the review draft of the manuscript.

[2] Corresponding author.

[3] Current address: Instytut Paleobiologii PAN, 00-818 Warszawa, ul. Twarda 51/55, Poland.

Резюме. "Суперграндотряд" Ungulatomorpha Archibald 1996b, включает "грандотряд" Ungulata и "семейство" "Zhelestidae". "Zhelestidae" Nessov 1985a лучше всего известно по остаткам из верхнемеловой (поздний турон – коньяк) Бисоектинской свиты в Джиракудуке (пустыня Кызылум, Узбекистан). Азиатские таксоны желестид (ранний турон – коньяк): *Kumsuperus avus* Nessov, 1984b, nomen dubium, *Zhelestes temirkazyk* Nessov, 1985a, *Sorlestes budan* Nessov, 1985a, *Aspanlestes aptap* Nessov, 1985a, *Sorlestes kara* Nessov, 1993, *Parazhelestes robustus* Nessov, 1993, *P. minor* sp. nov., *Eoungulatum kudukensis* gen. et sp. nov. Североамериканские таксоны желестид (средний кампан – ранний палеоцен): *Gallolestes pachymandibularis* Lillegraven, 1976, *G. agujaensis* Cifelli, 1994, *Alostera saskatchewanensis* Fox, 1989, *Avitotherium utahensis* Cifelli, 1990. Европейские таксоны желестид (маастрихт): *Lainodon orueetxebarriai* Gheerbrant et Astiba, 1994 и *Labes quintanillensis* Sige in Pol et al., 1992 (Испания); *Labes garimondi* Sige in Pol et al., 1992 (Франция). Возможно унгулятоморфу принадлежит фрагмент нижнего моляра из верхнего сантона Винтон Блафф, Миссиссипи, США. *Wania chowi* Wang, 1995 не является желестидом и возможно родственен анагалидам. "Желестиды" встречаются в местонахождениях на более влажных, низких приморских низменностях, расположенных в западной Азии и Северной Америке, и отсутствуют (или очень редки) в одновозрастных позднемеловых более сухих и выше расположенных местонахождениях в Монголии. Разнообразные азиатские "желестиды" с апоморфиями, предвосхищающими намного более поздние признаки архаичных копытных, достигли Северной Америки ближе к концу мелового периода через Берингию. Филогенетический анализ 18 признаков верхних зубов подтверждает монофилию таксона Ungulatomorpha, который включает "Zhelestidae" и Ungulata (последние представлены *Protungulatum donnae*). Близкие родственные связи между грызунами (представлены *Tribosphenomys*), приматоморфами (представлены *Purgatorius*) и унгулятоморфами возможны, но сходство может быть также объяснено конвергенцией.

INTRODUCTION

For many years the oldest records of archaic ungulates (condylarths) were known from the early Paleocene of North America. Archaic ungulates are the earliest known, primarily herbivorous eutherians and are presumed to include the ancestry of many extinct and extant eutherian orders. The youngest record of this grade of ungulate was thought to be from the middle Miocene (Hoffstetter and Soria, 1986), but a more recent study shows this to be a litoptern (Cifelli and Guerrero Díaz, 1989). The youngest records now appear to be from the early Oligocene of North America (Archibald, in press).

Traditionally, archaic ungulates have been referred to as the order Condylarthra (Cope, 1881). Krause (1984) regarded the order Condylarthra as a grade; McKenna (1987:80) stated that "condylarths" are "... a scrap basket of extinct paraphyletic groups," while Prothero et al. (1988:202) claimed that "... the 'Condylarthra' is a paraphyletic waste-basket taxon that has long outlived its usefulness, and should be abandoned" (see also Archibald, in press). Prothero et al. (1988) suggested replacing "Condylarthra" with the informal term "archaic ungulate mammals." Use of this new informal term does not solve the problem of deciphering the relationships of early ungulates, but it does discontinue the use of a term that implies, but actually has, no phylogenetic meaning (i.e., it is not monophyletic, or even more precisely holophyletic).

In 1965 Sloan and Van Valen described *Protungulatum donnae* from Bug Creek Anthills, northeastern Montana, U.S.A. This was regarded as the earliest archaic ungulate (Arctocyonidae, ?Oxyclaeninae). At the time of discovery, Bug Creek Anthills was believed to be within the Upper Cretaceous (uppermost Maastrichtian, Lancian) Hell Creek Formation, but more recently is thought to lie within the lower Paleocene (lower Danian, Puercan), Tullock Formation (e.g., Archibald and Lofgren, 1990). Although most or all of the oldest archaic ungulate-bearing sites in eastern Montana are best regarded as earliest Paleocene in age, Fox (1995) has argued that latest Cretaceous (Lancian) archaic ungulates occur in the Upper Cretaceous Frenchman Formation of Saskatchewan, Canada. The age was determined palynologically.

Van Valen (1978) named four more archaic ungulate species which, like *Protungulatum donnae*, were originally thought to occur in the Hell Creek Formation but are now best regarded as coming from the Tullock Formation. These are: *Oxyprimus erikseni*, *Mimatuta morgoth*, *Protungulatum gorgun*, and *Ragnarok harbichti*. Van Valen (1978) named five additional species from the Tullock Formation, as well as new taxa from various other Paleocene localities, especially the early Paleocene Mantua lentil, Wyoming. Other workers who have described or mentioned latest Maastrichtian and/or earliest Paleocene archaic ungulates from North America include Johnston (1980), Lupton et al. (1980), Archibald (1982, in press), Johnston and Fox (1984), Lillegraven and McKenna (1986), Van Valen (1988), Fox (1989, 1995), Archibald and Lofgren (1990), Luo (1991), and Lofgren (1995).

Until recently, archaic ungulates were unknown from the Late Cretaceous or earliest Paleocene outside of North America. However, in a series of papers de Muizon and Marshall (1987*a*, 1987*b*, 1991; de Muizon, 1991) described archaic ungulates from Bolivia, South America, which were first argued to be latest Cretaceous, but are now generally regarded as early Paleocene in age (Van Valen, 1988; Archibald, 1989; Gayet et al., 1991). In 1982 Nessov figured a dentary with heavily worn M_{1-3} from Uzbekistan that he assigned to Eutheria incertae sedis. In 1984(*b*) he proposed the name *Kumsuperus avus* for the dentary, noting its resemblance to condylarths (archaic ungulates). Butler suggested omnivorous (1989) and herbivorous (1992) tendencies in the dentition of *Kumsuperus*, and later (1990, 1992) regarded it tentatively as an earlier representative of the level of dental development that appears in archaic ungulates and primates. In a series of papers Nessov and his colleagues (1985*a*, 1985*b*, 1987, 1993; Nessov and Kielan-Jaworowska, 1991; Nessov et al., 1994; see also Averianov, in press) proposed, figured, and discussed new taxa that were referred to informally as pre-ungulates.

Here, we describe and discuss material from the Bissekty Formation (Upper Cretaceous, upper Turonian–Coniacian, Uzbekistan) that we refer to the apparently paraphyletic family "Zhelestidae," and we compare these fossils with previously described taxa of archaic ungulates. Although clearly related to archaic ungulates known from elsewhere, the western Asian "zhelestids" retain some primitive characters not usually found in archaic ungulates of North America. A new taxon (Ungulatomorpha) was named (Archibald, 1996*b*) that includes "Zhelestidae" and Ungulata (archaic ungulates or "condylarths" and all other extinct and extant ungulates).

We use the dental terminology shown in Figure 1. Measurements were taken according to the method illustrated by Archibald (1982:fig. 1). Teeth were projected on a computer screen using a video camera mounted on a binocular microscope. Lines drawn on the image using the software MorphoSys version 1.25 (Meacham and Duncan, 1993) run on an AST 486DX/33 computer provided measurements that were rounded to the nearest 0.1 mm. Methods used in phylogenetic analysis are described in that section. Photographs in Figures 11B–F, 12, 14, and 16 are scanning electromicrographs, while those in Figures 7, 9, 11A, 13, 15, 17, 18, and 19 were taken using regular light photography.

Institutional abbreviations are as follows: CCMGE, Chernyshev's Central Museum of Geological Exploration of Saint Petersburg, Russia; IZANUz, Zoological Institute of the Academy of Sciences of Uzbekistan; LACM, Natural History Museum of Los Angeles County; MNA, Museum of Northern Arizona; OMNH, Oklahoma Museum of Natural History; PU, Princeton University (collections now housed at Yale University); UALVP, University of Alberta Laboratory of Vertebrate Paleontology. Material found between 1978–1993 is housed at Chernyshev's Central Museum of Geological Exploration of Saint Petersburg, Russia; material found in 1994 is housed at the Zoological Institute of the Academy of Sciences of Uzbekistan.

PALEOECOLOGICAL, GEOLOGICAL, AND BIOSTRATIGRAPHIC SETTING

Only one specimen of Cretaceous mammal was described from western Asia before 1978. This was the poorly preserved dentary from Kazakstan described as *Beleutinus orlovi* by Bazhanov in 1972. From 1974 through 1994, the first author conducted field work at a variety of sites in western Asia. This included 11 visits to the area of Dzharakuduk in the middle of the Kyzylkum Desert, western Uzbekistan, southeast of the Aral Sea (Fig. 2). He was joined by the second author for the 1994 field season.

Dzharakuduk, which means "well near the escarpment" in Kazak, refers to the small settlement and the well of the same name that lies 2 km southwest of a more than 200 m-high exposure of Upper Cretaceous sediments (Fig. 3). These exposures are the extreme southwestern extension of a much larger topographic and structural high known as the Bukantau Ridge, and they overlook to the southeast a topographic and structural basin called the Mynbulak Depression (Pyatkov et al., 1967).

All but one of the mammalian specimens from western Asia that are discussed in this paper come from a series of localities within the Bissekty Formation (previously referred to as the Taikarshin Beds by Sochava [1968], but see Nessov [1990]), which is approximately in the middle of the Dzharakuduk escarpment (Fig. 2, 3). The Bissekty Formation (Nessov, 1990) consists of 88–103 m of yellowish, cross-stratified, soft sandstones. These are intercalated with thin layers of conglomerates consisting of brown-black pebbles of clay and silt, covered by iron and manganese oxides and hydroxides. Associated paleosols sometimes preserve extensive clumps of sandstone molds of small tree trunks and *Platanus*-, Lauraceae- and *Viburum*-like leaves (Nessov, 1992:fig. 3). These beds were deposited mainly in brackish water on coastal plains; the fossils are found mostly in the interconnecting brackish, brackish-fresh, and fresh-water channels (Nessov, 1990, 1991, 1992; Nessov and Kielan-Jaworowska, 1991). The "zhelestids" are found only in channel and near-channel deposits of the Bissekty Formation.

The Bissekty Formation fauna includes heterodontid, odontaspidid, mitsukurinid, cretoxyrhinid, and other sharks; polyodontid, acipenserid(?), amiid, lepisosteid, aspidorhynchid, albulid, elopid, and enchodontid actinopterygians; frogs and salamanders including among others, scapherpetontids, batrachosauroidids, albanerpetontids, and gobiatids; adocid, trionychid, chelydrid-like, and other turtles; priscagamid, necrosaurid, teiid-like, scincid-like, and varanid-like lizards; three taxa of crocodilians; azhdarchid pterosaurs; ankylosaurid, hadrosaurid, protoceratopsid?, and ceratopsid ornithischians; sauropods; ornithomimid, therizinosaurid (including segnosaurids [Russell and Dong, 1993]), tyrannosaurid, dromaeosaurid, and avian theropods (Nessov, 1992; Nessov et al., 1994).

Fossil sites or localities at Dzharakuduk can be grouped as occurring in the lower, middle, or upper Bissekty Formation. Those producing "zhelestids" are site CDZH-17a in the lower Bissekty, CBI-4 and 14 in the middle Bissekty, and CBI-5 and 17 in the upper Bissekty Formation (Fig. 4). An entirely Turonian age for the Bissekty Formation cannot be eliminated. It appears more likely, however, that the

Fig. 1.—Dental terminology modified from Bown and Kraus (1979) and Kielan-Jaworowska and Dashzeveg (1989). Upper molar (top) is based on CCMGE 11/12953, right M^1 (reversed), holotype of *Parazhelestes minor* (Fig. 12B); and lower molar (bottom) is based on CCMGE 13/12953, right M_1 of *Sorlestes budan* (Fig. 15F).

Fig. 2.—Sketch map of the Kyzylkum Desert in western Uzbekistan showing the Dzharakuduk area (2) producing "zhelestids" in relation to other key areas that have been used to assess chronostratigraphic age. These are the same areas shown in the correlation chart in Figure 5 and are as follows: 1, Sultanvais Ridge immediately east of the Amu Dar'ya (Amu River), northwestern Uzbekistan; 2, the Dzharakuduk well area at the extreme southwestern end of the Bukantau Ridge, central Kyzylkum Desert, northwestern Uzbekistan; 3, the Tyulkeli Hill and Zhalmauz well areas in the Dzhalagash region north of the Syr Dar'ya (Syr River), northeastern Aral Sea region, southern Kazakstan; 4, the Fergana region, southwestern Kyrgyzstan.

lower site is late Turonian or possibly even Coniacian in age, while the middle and upper sites are most likely Coniacian.

As shown in Figure 5 the chronostratigraphic age of the Bissekty Formation and its included sites at Dzharakuduk can be established with considerable certainty by means of correlation with other Cretaceous sections in western Asia (a–c in Fig. 5) and by biostratigraphic assessments based on both marine invertebrates and vertebrates (1–11 in Fig. 5).

Nessov and Mertiniene (1986) argued that the middle and upper parts of the Bissekty Formation are Coniacian based on sharks, while the lower part is upper Turonian. This disagrees with Pytakov et al. (1967), who considered the entire unit to be upper Turonian. Sochava (1968) and Martinson (1969) regarded this unit as upper Turonian through Santonian. A Santonian age for the mammal-producing levels of the Bissekty Formation is unlikely because the rays from the same levels appear to be older than those of Santonian age of the Fergana depression to the east and the northeastern Aral region to the north.

The Bissekty Formation unconformably overlies a series of marine claystones, shales, and siltstones approximately 90–105 m thick (Abduazimova, 1988) that is argued to be lower Turonian in age (Pyatkov et al., 1967). The upper part of the marine section could be uppermost lower or even upper Turonian (Vereshchagin, 1979). These beds, widespread over Uzbekistan, Kyrgyzstan, Tajikistan, and southern Kazakstan, were deposited during a global transgression in the middle latitudes. They are similar in appearance and lithology to the Mancos Shale and Tropic Shale of North America (Nessov, personal observation), which were deposited under similar conditions during the transgression of a dysoxic sea. In the southwestern Kyzylkum Desert, beds that are stratigraphically equivalent to the low-

Fig. 3.—Exposures in the Dzharakuduk area. View from approximately 2 km east of the settlement of Dzharakuduk, looking toward the northeast. The units are the same as those identified in Figure 4. Distance from the base of the escarpment to the top is about 200 m.

er Turonian of central Kyzylkum (2 in the first column in Fig. 5), yield the early Turonian ammonite *Mammites nodosoides* (Schultz, 1972).

The Bissekty Formation at Dzharakuduk is overlain, sometimes with an angular disconformity of 2–5°, by the 20–61 m-thick Aitym Formation. The Aitym consists of yellowish-gray alternating siltstones and sandstones, overlain by a series of siltstones and sandstones up to 25–40 m thick. The Aitym Formation and overlying Cretaceous siltstones and sandstones contain the teeth of the shark *Hispidaspis* sp., which increases in size toward the upper part of the section. These larger teeth are found in beds referred to the Santonian and Campanian based on marine invertebrates (Sokolov, 1978). Near the top of the Cretaceous part of the section, a transgressive layer of claystones and siltstones contains Campanian marine pelecypods and gastropods. North and east of Dzharakuduk the Campanian is overlain by a thin layer of Maastrichtian sandstones (Abduazimova, 1988); west of Dzharakuduk there are also upper Paleocene marine sandstones with phosphorites (Schultz, 1972).

In the lower part of the Bissekty Formation (26 m above the lower boundary), a channel system yields mammals and other vertebrates (Nessov, 1985*a*, 1987, and references therein), including shark teeth (such as anacoracids). The simple serration and small size of the anacoracid teeth are typical for late Turonian sharks (Nessov and Mertiniene, 1986). In the middle and upper parts of the Bissekty Formation, channel deposits yield mammals and other vertebrates including shark teeth (e.g., *Ptychocorax aulaticus*). *Ptychocorax aulaticus* (see Kielan-Jaworowska and Nessov, 1990:5) occurs also in Tajikistan and northern Turkmenistan in association with Coniacian marine invertebrates. Ray teeth (e.g., *Myledaphus tritus*) occur in all levels of the Bissekty Formation. In the uppermost part, above the mammal levels, a single *Parapalaeobates*-like ray tooth was found. In other areas of Tajikistan and southern Kazakstan at the Coniacian/Santonian boundary, *Myledaphus* is replaced by a *Parapalaeobates–Baibishia–Protoplathyrina* ray assemblage. The lamnoid sharks that are common in Coniacian brackish water deposits of Uzbekistan become rare in the Santonian of Tajikistan and Kazakstan, where they are replaced almost completely by "orthodonts." The changes in fossil assemblages at the Coniacian/Santonian boundary in the region (c in Fig. 5) also involve other groups of vertebrates, such as lepisosteids, a large species of a mesosuchian crocodile (which disappears at this boundary), sawfish, turtles, theropod dinosaurs, and mammals (Nessov, 1984*b*, 1988, and references therein). The vertebrate assemblage of the Bissekty Formation is similar at the generic and familial level to that in Turonian–Coniacian beds of other regions

of Kazakstan, Uzbekistan, and Kyrgyzstan (with the exception of mammals, which are common in the Bissekty Formation but rare or absent in rocks of similar age in neighboring countries).

In the September 1994 field season at Dzharakuduk, Oleg Tsaruk (Zoological Institute of the Academy of Sciences of Uzbekistan), found a small (~8 cm diameter), well-preserved ammonite near the top of the Dzharakuduk escarpment in an unnamed unit (Fig. 4). A. A. Atabekijan (Russian Geological Institute) identified it as *Placenticeras kysylkumense*, which is characteristic of the Santonian (1994, personal communication to first author). The highest vertebrate sites in the Bissekty occur 100 m below the level at which this Santonian ammonite was found.

Thus, it is likely that most, if not all of the Bissekty Formation is Coniacian in age. The lower Bissekty could be uppermost Turonian, as the contact with the underlying, thick marine units is erosional and the Turonian/Coniacian boundary is not found in these marine units, which perhaps encompass most of the Turonian (Fig. 4, 5).

SYSTEMATIC PALEONTOLOGY

(Class) Mammalia Linnaeus, 1758
(Subclass) Trechnotheria McKenna, 1975
(Infraclass) Cladotheria McKenna, 1975
(Legion) Theria, Parker and Haswell, 1897
(Supercohort) Placentalia Owen, 1837
(Cohort) Epitheria McKenna, 1975
(Superorder) Preptotheria McKenna, 1975
(Supergrandorder) Ungulatomorpha, Archibald, 1996*b*

Included Taxa.—(Family) "Zhelestidae" and (grandorder) Ungulata (taxa included within Ungulata are listed under the rediagnosis for this taxon).

Distribution.—(Family) "Zhelestidae": Late Cretaceous of Asia, North America, and Europe; early Paleocene of North America. Ungulata: Late Cretaceous(?)–Recent of North America; late Paleocene–Recent of Europe; early Paleocene–Recent of South America; early or middle Paleocene–Recent of Asia; middle Eocene–Recent of Africa; early Eocene–Recent, most oceans and some rivers.

Definition.—(As in Archibald, 1996*b*) The most recent common ancestor of "Zhelestidae" and Ungulata and all of its descendants. This is a node-based phylogenetic definition following the protocol suggested by de Queiroz and Gauthier (1990).

Diagnosis.—(Expanded and modified from Archibald, 1996*b*). Those character states labeled with a dagger (†) appear to be apomorphic for Ungulatomorpha while those not so labeled appear to be plesiomorphic or their polarity cannot be determined. Differs from other Late Cretaceous eutherian mammals (including earliest anagalidans) and earliest primatomorphs (i.e., *Purgatorius*) in the following: protocone anteroposteriorly expanded, if only slightly (some expansion also in *Paranyctoides*); upper molar crown in occlusal view at most only slightly constricted through conular region; parastylar region with two cuspules in earliest diverging taxa (also in *Kennalestes* and *Sailestes*), reduced to one or none in later taxa; paracone/metacone and protocone relatively far apart in earlier diverging taxa (in later diverging taxa protocone migrates labially), with conules closer to paracone/metacone; paraconid lingual to sublingual with some appression to metaconid (†); entoconid and hypoconulid twinned (†) (also in some zalambdalestids). Differs from other Late Cretaceous eutherian mammals (including earliest anagalidans) but shares with earliest primatomorphs (i.e., *Purgatorius*): molar crown shape in occlusal view trapezoidal (also *Paranyctoides*), subrectangular, or rectangular, but not triangular; trigonid height lower relative to talonid height (†); talonid expanded to same or greater width than trigonid (†). Differs from most other Late Cretaceous eutherian mammals (including earliest anagalidans) but shares with *Gypsonictops*, the earliest primatomorphs (i.e., *Purgatorius*), and some later anagalidans (e.g., the rodent *Tribosphenomys*) a stylar shelf that is narrow (†) (possibly also *Barunlestes*). Shares with *Gypsonictops*, *Asioryctes*, *Batodon*, *Kennalestes*, and *Paranyctoides* pre- and postcingula consistently present, but differs from these taxa and is (convergently?) like *Purgatorius* and *Tribosphenomys* in having pre- and postcingula that reach or extend below the conules (†). Shares with *Sailestes*, *Zalambdalestes*, *Gypsonictops*, *Purgatorius*, and *Tribosphenomys* paracone and metacone of similar height. Shares with *Kennalestes*, *Zalambdalestes*, *Gypsonictops*, *Purgatorius*, and *Tribosphenomys* ultimate upper premolar has metacone or swelling (metaconid or swelling on lower). Shares with *Paranyctoides*, *Otlestes*, *Sailestes*, *Zalambdalestes*, *Gypsonictops*, *Purgatorius*,

and *Tribosphenomys* paracone and metacone with separate base.

Discussion.—We include in Ungulatomorpha the Late Cretaceous species of ungulate-like mammals from Asia, Europe, and North America ("Zhelestidae") plus (the grandorder) Ungulata, which includes all later archaic ungulates and ungulates. A rediagnosis and discussion of Ungulata follow a description of the "zhelestids."

Soon after the Cretaceous/Tertiary boundary, archaic ungulates began a tremendous morphological and taxonomic radiation leading to the great diversity we see today in ungulates, sub-ungulates, and whales. If our systematic hypotheses are even broadly correct, the above diagnostic characters were very quickly modified as ungulates began to radiate, leaving us with no dental synapomorphies with which to unite extant ungulates.

We presented an exhaustively detailed formal taxonomy at the beginning of this section. This was to provide a phylogenetic framework for understanding where we place Ungulatomorpha. The additional categories (ranks) and taxa are those used by McKenna (*in* Stucky and McKenna, 1993). We do not agree among ourselves as to the merits and need to use categories (ranks), but they have been provided in parentheses for those who wish them. Rather than invent a wholly new categorical name for Ungulatomorpha, however, we simply modified an existing category by adding the prefix "super" to "grandorder" to signify its greater inclusivity.

(Family) "Zhelestidae" Nessov, 1985*a*

As Nessov et al. (1994) noted, Zhelestinae Nessov, 1985*a* was proposed for *Zhelestes temirkazyk*, which is based on an upper dentition. In 1990 Nessov raised this to Zhelestidae. In his 1985(*a*) paper Nessov also erected the taxon Mixotheridia (including Zhelestidae) as a suborder with phylogenetic ties to Scandentia. As originally conceived, Mixotheridia included taxa based on lower dentitions: *Gallolestes*, *Sorlestes*, *Taslestes*, and *Aspanlestes*. With subsequent field work by the first author in the Kyzylkum Desert of Uzbekistan (Nessov et al., 1994), it became clear that zhelestids represented the upper dentitions of mixotheridians.

Our analysis, confirming early suggestions (e.g., Butler, 1990; Nessov, 1993), shows that among the named Late Cretaceous eutherians, there is a group based on both upper and lower dentitions that has phylogenetic affinities to ungulates, notably the early Tertiary archaic ungulates. Using the synapomorphies in the preceding diagnosis, we unite these

Fig. 4.—Geological section in the Dzharakuduk area. Stratigraphic occurrence of vertebrate localities is shown to the right of the section, as are occurrences of other fossils discussed in the text and in the caption of Figure 5.

Uzbek species, along with species from Kazakstan, North America, and Europe, with Ungulata (sensu stricto) in (the supergrandorder) Ungulatomorpha. The species are as follows: Uzbek species: *Zhelestes temirkazyk* Nessov, 1985*a*; *Sorlestes budan* Nessov, 1985*a*; *Aspanlestes aptap* Nessov, 1985*a* (including *Zhelestes bezelgen* Nessov, 1993); *Parazhelestes robustus* Nessov, 1993; *Parazhelestes minor* n. sp.; *Eoungulatum kudukensis* n. gen. and sp.; and *Kumsuperus avus* Nessov, 1984*b*, nomen dubium; the Kazak species *Sorlestes kara* Nessov, 1993; and the North American species *Avitotherium utahensis* Cifelli, 1990; *Alostera saskatchewanensis* Fox, 1989; *Gallolestes pachymandibularis* Lillegraven, 1976; and *G. aguajensis* Cifelli, 1994; *Lainodon orueetxebarriai* Gheerbrant and Astibia, 1994 and *Labes quintanillensis* Sigé *in* Pol et al., 1992, from Spain; and *Labes garimondi* Sigé *in* Pol et al., 1992 from France. Questionably included is: the fragmentary M_1 or M_2 from Vinton Bluff, Mississippi, U.S.A., described by Emry et al. (1981).

Other taxa, such as *Taslestes*, do not appear to belong to the ungulatomorph clade and are accordingly excluded. We also remove "zhelestids" from Mixotheridia.

Further, we detected no apomorphies that clearly link all Uzbek ungulatomorphs into a clade that is, in turn, the sister taxon to Ungulata (sensu stricto). This means that Zhelestidae is paraphyletic and is indicated as such by double quotation marks. We retain "Zhelestidae" as a convenient name to use when referring to these Asian, European, and North American ungulatomorphs.

"Zhelestids" do share character states with one another; however, as will be shown in our phylogenetic analysis, these are either primitive retentions of Late Cretaceous eutherians or are also shared with later ungulates. The characters states shared by "zhelestids" and ungulates are those given in the diagnosis of Ungulatomorpha. These are not regarded as synapomorphies of "zhelestid" species.

There are some character states seen in "zhelestids" as well as in a variety of other Late Cretaceous eutherians (see Table 4). This strengthens our view that these states are primitive for some earlier node within Eutheria, if not for the taxon as a whole. The primitive character states that "zhelestids" share with some or all other Late Cretaceous eutherians are: well-developed postparaconular and premetaconular cristae on the upper molars; metacingulum formed of only the postmetaconule crista, while the metacrista runs from the apex of the metacone to the metastylar region (also in some Paleocene taxa such as *Purgatorius*); a definite parastylar lobe; five teeth present (at the same time) between the canine and the molars in the maxilla and dentary; a metacone or similar swelling on the ultimate upper premolar (which we call P^5), and a metaconid or similar swelling on the ultimate lower premolar (which we call P_5). The last two character states could be primitive retentions; otherwise they evolved convergently among Late Cretaceous eutherians.

Although five teeth present (at the same time) between the canine and the molars in the maxilla and dentary have not been demonstrated in most "zhelestids," they are present or represented by alveoli in *Zhelestes temirkazyk* and *Sorlestes budan*, which may be conspecific (see Fig. 10), and in a larger "zhelestid" (see Fig. 19A–C.) We identify these teeth as P_1^1 through P_5^5 mostly for convenience, although we have no clear basis to argue that all five positions are second generation or successional premolars. Other Late Cretaceous eutherians that possess five teeth at the same time (sometimes based only on alveoli) between the canine and the molars in the maxilla and/or dentary in some individuals are *Gypsonictops hypoconus* (Clemens, 1973), *G. illuminatus* (Lillegraven, 1969), *Kennalestes gobiensis* Kielan-Jaworowska (1981), and *Otlestes meiman* (Nessov, 1985*a*). In addition, Kielan-Jaworowska and Dashzeveg (1989) reported five premolars in Early Cretaceous *Prokennalestes trofimovi* and *P. minor*.

Unlike *Gypsonictops* and "zhelestids," in which P^3 and P_3 are distinctly smaller than immediately adjacent teeth, in *Kennalestes*, *Otlestes*, and *Prokennalestes* P_3^3 (also referred to as Px or Pc in *Kennalestes*) is not a distinctly smaller tooth. Also, in taxa in which it is preserved, the penultimate upper premolar (what we call P^4) is distinctly higher and piercing in *Kennalestes*, and possibly *Prokennalestes*, compared to the condition in *Gypsonictops* and "zhelestids." No clear phylogenetic inferences can be drawn from these differences, although one could reasonably argue that the reduction in size of P^3 and P_3 is derived, unless, of course, this is the retention of a normally smaller, deciduous tooth.

The relatively small size of the tooth at position three in most of the Late Cretaceous eutherians may indicate that it is a tooth undergoing evolutionary reduction and loss. In a study assessing dental homologies in both marsupials and placentals, Luckett (1993) noted that loss of a tooth at this position would be quite unusual given what we know concerning most extant and fossil placentals. He further noted that in an analysis under preparation he sug-

Fig. 5.—Cretaceous chronostratigraphic age estimates and correlations in western Asia. The four geological columns correspond to numbered localities shown in Figure 2. Numbered triangles are biostratigraphic age estimates as follows: 1, ammonites of *Acanthohoplites nolani* Zone, uppermost Aptian (Schultz, 1972); 2, ammonites of *Mammites nodosoides* Zone, lower Turonian (Schultz, 1972); 3, ammonites, upper Turonian (Schultz, 1972); 4, foraminiferans, lower Turonian (various sources); 5, foraminiferans, lower Turonian (Pyatkov et al., 1967), the ammonite *Proplacenticeras kharesmense* and the pelecypod *Inoceramus labiatus* 80 km east of Dzharakuduk

gests that this small tooth at position three may be a retained, reduced, deciduous P2. Supporting Luckett's argument that it is a retained deciduous premolar (whether dP2 or dP3) is the observation that only some individuals of *Gypsonictops hypoconus* and *Kennalestes gobiensis*, and, in one case, only one side of the dentary of *Kennalestes gobiensis*, possess this third position tooth. The small size and variable occurrence of this third premolariform tooth argues that evolutionary reduction was occurring, but does not clarify whether the tooth was deciduous or permanent. Its occurrence among as many as nine Late Cretaceous and two Early Cretaceous eutherian species does suggest, however, that possession of five such teeth is a primitive retention from an earlier stage in eutherian evolution.

The "zhelestid" material consists of isolated lower and upper teeth, some fragmentary maxillae or dentaries with teeth, and some edentulous maxillae and dentaries. As upper and lower teeth and jaws have not been found in occlusion and because of the fragmentary nature of the material, we cannot confidently match taxa based on upper and lower teeth, with one exception. We argue that the uppers of *Zhelestes bezelgen* can be associated with the lowers of *Aspanlestes aptap*, the latter name having priority. We also compare (Fig. 10) the uppers of *Zhelestes temirkazyk* with the lowers of a specimen referred to *Sorlestes budan*. These taxa may also be conspecific, but because of several similarly sized species known by uppers alone, we cannot confidently synonymize these two species.

Aspanlestes Nessov, 1985*a*

Type and Only Known Species.—*Aspanlestes aptap* Nessov, 1985*a*.

Distribution.—Late Cretaceous (late Turonian and Coniacian), western Uzbekistan.

Revised Diagnosis.—Same as for type and only species.

Aspanlestes aptap Nessov, 1985*a* (Fig. 7, 8, 20, 21, 22F)

cf. *Cimolestes* (in part); Nessov, 1984*b*:63, unnumbered fig.

Aspanlestes aptap Nessov, 1985*a*:14, pl. 2, fig. 11; ?non-plate 2, fig. 10. Nessov et al., 1994:62, pl. 4, fig. 1; Archibald, 1996*b*: 1151, fig. 2E, F; 3C.

Aspanlestes cf. *aptap* Nessov, 1985*a*:pl. 2, fig. 7.

?*Zhelestes bezelgen* Nessov, 1987:207, pl. 1, fig. 1.

"Zhelestinae (Kennalestidae)" Nessov, 1987:pl. 1, fig. 3.

?non-?*Aspanlestes* sp. Nessov, 1987:pl. 6, fig. 6; Nessov, 1995: pl. 2, fig. 22.

Zhelestes bezelgen Nessov, 1987. Nessov and Kielan-Jaworowska, 1991:fig. 1; Nessov et al., 1994:63, pl. 5, fig. 1.

?*Zhelestes* sp., cf. *Z. bezelgen* Nessov, 1987. Nessov, 1993:125, pl. 2, fig. 3; pl. 5, fig. 5.

Holotype.—CCMGE 4/12176, right dentary with alveoli for P_3, crowns of P_{4-5}, M_{1-2}.

Type Locality.—Locality CDZH-17a, lower part of Bissekty Formation, Upper Cretaceous (upper Turonian), Dzharakuduk, western Uzbekistan.

Referred Specimens.—Lower dentition: CCMGE 6/12176, fragment of left dentary with talonid of M_2 and M_3; CCMGE 69/12455, left dentary with worn M_{2-3}; CCMGE 7/12953, chemically weathered right M_1; CCMGE 8/12953, left M_2; with some reservation, CCMGE 9/12953, left dentary fragment with one or more incisor alveoli, erupting canine, P_1 alveolus(i), P_2, anterior alveolus for P_3. Upper dentition: CCMGE 1/12455, left maxilla with three-rooted P^5, M^{1-2} (type of *Zhelestes bezelgen*); CCMGE 19/12953, right P^5 missing parastylar lobe; CCMGE 3/12455, left M^1; CCMGE 68/12455, left maxilla with alveoli for three-rooted P^5, alveoli for M^1, M^2, alveoli for M^3; IZANUz P No 2155-M-2, left M^2.

Localities.—All referred specimens except CCMGE 9/12953, 68/12455, and 7/12953 are from locality CBI-14, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan. CCMGE 9/12953 is from locality CDZH-17a, lower part Bissekty Formation (upper

←

(Vereshchagin, 1979); 6, the shark *Hispidaspis* sp., larger specimens suggest Santonian or Campanian (Nessov, personal observation); 7, the ammonite *Placenticeras kysylkumense*, Santonian (A. A. Atabekijan, personal communication, 1994); 8, oysters and gastropods suggestive of middle to upper Campanian transgression (Nessov, personal observation); 9, marine pelecypods, lower Turonian (Verzilin, 1967); 10, ammonites, upper Turonian (Krymholts, 1977:table 12); 11, brackish-water pelecypods, same as Chinese Santonian species in northern Fergana (G. G. Martinson, personal communication). Numbered ellipsoids are correlations as follows: a, turtles *Kizylkumemys schultzi* and *Fergenemys* sp., cf. *F. itemirensis* in both the upper Khodzhakul Formation and Dzharakuduk Beds (Nessov, 1984*a*); b, similar or same hadrosaurids, crocodiles, and turtles in both the Bissekty and Zhirkindek formations (Nessov, personal observation); c, aridization at or near the Coniacian/Santonian boundary, with shift from grey to red beds and shift from relatively larger to smaller angiosperm leaves (Shilin, 1986), gars become locally extinct and are replaced by other "ganoid" fishes, taxonomic turnover in species of rays, crocodilians, and hadrosaurids (Nessov, personal observation).

Fig. 6.—Graphs comparing maximum anteroposterior length (Y axis) versus maximum labiolingual width (X axis) for M^1, M^2, and M^3 (left), and maximum length (Y axis) versus maximum width (X axis) for M_1, M_2, and M_3 (right). Measurements are those given in Tables 1 and 2. Numbers refer to tooth position. Numbers enclosed by squares are from dentary or maxilla, others are isolated teeth. Tooth positions for holotype specimens are identified by an asterisk. Dashed line in upper left graph given only to provide visual separation of species; it does not have statistical significance. Abbreviations are as follows: *Aa*, *Aspanlestes aptap* (including *Zhelestes bezelgen*); cf. *Ek*, cf. *Eoungulatum kudukensis*; *Ek*, *Eoungulatum kudukensis*; *Ka*, *Kumsuperus avus*; *Pm*, *Parazhelestes minor*; *Pr*, *Parazhelestes robustus*; *Sb*, *Sorlestes budan*; *Zt*, *Zhelestes temirkazyk*.

Turonian); CCMGE 68/12455 is from locality CBI-4, middle part, Bissekty Formation (Coniacian), and CCMGE 7/12953 is from locality CBI-5a, upper part of Bissekty Formation, (Coniacian); Upper Cretaceous, Dzharakuduk, western Uzbekistan.

Revised Diagnosis.—Compared with other "zhelestids": upper molar crowns slightly constricted through conular region, but similar to *Parazhelestes minor*; ectoflexus moderately deep; protocone with slight anteroposterior expansion; protocone with little or no labial shift of apex; smallest in size. Of these five characters only the last might be an autapomorphy. The first four are shared with some or all other Late Cretaceous non-"zhelestids." Upper dentition averages 83% (ranging from 76–92% for three measurements each on P^5, M^1, and M^2) of size of next larger "zhelestid," *Parazhelestes minor*. As in lower dentition of other "zhelestids": trigonid

Table 1.—*Measurements (in mm) of Uzbek ungulatomorph upper dentitions. Italicized numbers are estimates. Daggers (†) indicate type specimens. Abbreviations are as follows: L, length; W, width; AW, anterior width; PW, posterior width.*

	P^2		P^4		P^5			M^1				M^2				M^3		
Specimen no.	L	W	L	W	L	AW	PW	L	AW	PW	L/PW	L	AW	PW	L/PW	L	AW	PW
Zhelestes temirkazyk																		
†10/12176	1.5	0.9	2.5	1.6	2.5	3.0	3.6	2.7	3.7	4.2	0.64	2.9	3.9	4.3	0.67	2.3	3.8	3.2
Aspanlestes aptap																		
3/12455	—	—	—	—	—	—	—	2.2	2.6	2.9	0.76	—	—	—	—	—	—	—
19/12953	—	—	—	—	—	—	2.6	—	—	—	—	—	—	—	—	—	—	—
†1/12455	—	—	—	—	2.0	2.2	2.7	2.4	2.6	3.1	0.77	2.4	2.9	3.2	0.75	—	—	—
68/12455	—	—	—	—	—	—	—	—	—	—	—	2.4	3.1	3.3	0.73	—	—	—
2155-M-2	—	—	—	—	—	—	—	—	—	—	—	2.4	3.2	3.4	0.71	—	—	—
Averages	—	—	—	—	—	—	2.7	2.3	2.6	3.0	—	2.4	3.1	3.3	—	—	—	—
Parazhelestes robustus																		
†70/12455	—	—	2.2	1.5	2.6	3.1	3.7	3.0	3.7	4.0	0.75	3.2	3.8	4.0	0.80	2.3	3.1	2.6
20/12953	—	—	—	—	—	—	—	3.2	3.8	4.2	0.76	—	—	—	—	—	—	—
10/12953	—	—	—	—	—	—	—	—	—	—	—	—	—	*3.9*	—	—	—	—
Averages	—	—	—	—	—	—	—	3.1	3.8	4.1	—	—	—	4.0	—	—	—	—
Parazhelestes minor																		
21/12953	—	—	—	—	—	—	3.2	—	—	—	—	—	—	—	—	—	—	—
22/12953	—	—	—	—	—	—	—	2.9	3.5	3.8	0.76	—	—	—	—	—	—	—
†11/12953	—	—	—	—	—	—	—	2.7	3.1	3.5	0.77	—	—	—	—	—	—	—
11/12176	—	—	—	—	2.4	2.9	3.3	2.8	3.3	3.7	0.76	2.6	3.7	3.9	0.67	—	—	—
12/12953	—	—	—	—	—	—	—	—	—	—	—	—	—	3.6	—	—	—	—
Averages	—	—	—	—	—	—	3.3	2.8	3.3	3.7	—	—	—	3.8	—	—	—	—
Eoungulatum kudukensis																		
†2/12455	—	—	—	—	—	—	—	—	—	—	—	3.2	4.0	4.3	0.74	—	—	—
cf. *Eoungulatum kudukensis*																		
35/12176	—	—	—	—	2.5	3.2	3.2	—	—	—	—	—	—	—	—	—	—	—

low relative to talonid, slight appression of paraconid and metaconid, pre- and postcingulids present, labial and lingual cingulids absent, entoconid and hypoconulid with some twinning, unlike in cf. *Eoungulatum kudukensis* and *Sorlestes budan* M_3 hypoconulid not posteriorly shifted and no suggestion of apical closure of cusps. Lower dentition averages 78% (ranging from 69–100% for two measurements each on P_4 and P_5, and for five measurements each on M_1 and M_2) of size of next larger "zhelestid," *Sorlestes budan*, and 72% (ranging from 67–87% for five measurements each on M_2 and M_3) of size of largest "zhelestid," cf. *Eoungulatum kudukensis*.

Description.—The maxilla of *Aspanlestes aptap* (CCMGE 1/12455; type of *Zhelestes bezelgen*) preserves two labial roots for the penultimate two-rooted premolar. As discussed under *Zhelestes temirkazyk*, this and the ultimate premolar are interpreted as P^4 and P^5, respectively. The P^5 in CCMGE 1/12455 (Fig. 7A), is a submolariform, three-rooted tooth. The well-developed protocone reaches as far lingually as the lingual margin of M^{1-2}. The stylar shelf is narrow and almost nonexistent labial to the paracone. The only stylar cusp is a well-developed parastyle formed as a distinct parastylar lobe. The metastyle lobe is also well developed, but lacks cusps. A prominent, slightly anteroposteriorly elongate paracone lacks a preparacrista, but has a distinct postparacrista that extends posterolabially onto the metastyle lobe. The postparacrista has a swelling in the region where a metacone would be expected. Distinct pre- and postparaconular cristae, and a subdued preprotocrista join, forming an indistinct paraconule. There is no metaconule or associated pre- and postmetaconule cristae. Very narrow but distinct pre- and postcingula are present. CCMGE 19/12953, a right P^5 missing the parastylar lobe, is similar in size to the P^5 in the type of *Z. bezelgen*, CCMGE 1/12455, and is tentatively referred to *Aspanlestes aptap*. This P^5 is slightly longer anteroposteriorly across the protocone. Two subdued cristae run posterolabially from the protocone. One is probably the postprotocrista, but the homology of the other is unknown. Except for the preceding differences and a slightly shorter, thicker paracone, this P^5 resembles the P^5 in the type maxilla.

In CCMGE 1/12455, M^{1-2} are similar except in the stylar region and the fact that M^2 is slightly narrower anteroposteriorly relative to its labiolingual width. On both M^1 and M^2, the stylar shelf is moderately wide labial to the metacone, forming a distinct metastylar lobe. The shelf remains relatively wide between the paracone and metacone, but narrows considerably labially to the paracone, especially on M^1. On both molars, there is a distinct parastylar lobe with a stylocone (formed by the juncture of the edge of the stylar shelf and the preparacrista), parastyle, and preparastyle. There are no other stylar cusps. The preparastyle appears to be present on M^2, but is partly obscured by the me-

Fig. 7.—*Aspanlestes aptap* Nessov, 1985*a*. A. CCMGE 1/12455 (holotype of *Zhelestes bezelgen*), cast of left maxilla preserving P^5–M^2 in occlusal view. B, C. CCMGE 4/12176, cast of holotype right dentary preserving P_4–M_2 in occlusal (B) and buccal (C) views. D, E. CCMGE 6/12176, cast of left dentary preseving talonid of M_2 and M_3 in occlusal (D) and buccal (E) views. Scale = 2 mm.

tastylar lobe of M^1. Also, CCMGE 68/12455, another M^2, has a preparastyle. The parastylar lobe is more labially expanded on M^2. As a result, there is a shallow but distinct ectoflexus on M^2, which is essentially absent on M^1. The following description refers to both M^1 and M^2. There are distinct pre- and postparacristae and distinct pre- and postmetacristae. The postmetacrista merges with the metastylar lobe. The paracone and metacone are similar in height, and both are moderately low. The paracone is only slightly larger in girth than the metacone. The well-developed paraconule and metaconule are situated relatively closer to the paracone and metacone than to the protocone. The conules have distinct pre- and postparaconule cristae and pre- and postmetaconule cristae forming prominent conular wings. The preparaconule and postmetaconule cristae continue labially, merging with the tooth below (dorsal to), respectively, the anterior margin of the paracone and posterior margin of the metacone. The apex of the protocone is as tall as the paracone and metacone. This cusp is lingually positioned, with some anteroposterior expansion. There are well-developed pre- and postcingula that begin lingually below the protocone, merging with the tooth below and just labial to the conules. One M^1 (CCMGE 3/12455) and two M^2s (CCMGE 68/12455 and IZANUz P No 2155-M-2) are also tentatively referred to *Aspanlestes aptap*. They do not differ in any significant way from the above description of CCMGE 1/12455, except that one M^2, IZANUz P No 2155-M-2, is anteroposteriorly wider than is the case in CCMGE 1/12455. Although M^3 is unknown, the alveoli of M^3 in CCMGE 68/12455 (Nessov, 1993:pl. 2, fig. 3) show that this tooth was not reduced as the lingual margin of M^1 through M^3 are extended lingually to the same degree.

The following description of the lower dentition, except where noted, is based on the type, CCMGE 4/12176, a right dentary with alveoli for P_3, P_{4-5}, M_{1-2}; and CCMGE 6/12176, a fragment of the left dentary with a talonid of M_2 and M_3 (Fig. 7D, E). On P_{3-4}, the protoconid is the dominant cusp. On both, a cristid runs posteriorly from the apex of the protoconid to the posterior margin of the tooth, which divides the trenchant heel into a slightly larger lingual part and a smaller labial part. There are no distinct talonid cusps on either P_4 or P_5. On P_5, the lingual part of the talonid forms an incipient basin. A distinct, anteroposteriorly elongate metaconid and a narrow precingulid are found on P_5. Neither is present on the P_4. The dentary fragment CCMGE 9/12953, which we refer to *Aspanlestes aptap* with some reservation, preserves a P_2. It is similar to the P_4 just described, except that it is smaller, the cristid on the posterior side of the protoconid is faint, and the tooth is canted anteriorly. The molars do not differ greatly in length, with even the smallest molar, M_3 (preserved in CCMGE 6/12176; see Fig. 7D, E), only 0.2 mm shorter than the longest molars (see Table 2). This M_3, however, is considerably narrower than the talonid of M_2 preserved in the same dentary fragment (Fig. 7D). This suggests some labiolingual narrowing, but not anteroposterior shortening of M_3. All three molars are similar in having a distinct precingulid, narrower postcingulid, and no labial or lingual cingulids. On M_{1-2}, but less so on M_3, the hypoconulid is slightly closer to the entoconid (twinning) than to the hypoconid. On M_{1-2} the trigonid and talonid are of similar width, while on M_3 the talonid is narrower than the trigonid. On M_1 the trigonid and talonid are of similar length, but on M_{2-3} the trigonid is usually shorter. These length differences are the result of the differing placement of the paraconid on these molars. On M_1 the paraconid, which is rather crest-like, is near the anteroposterior midline, while on M_{2-3} it is distinctly more lingual. On M_1 the paraconid is less appressed to the metaconid than on M_{2-3}.

Discussion.—*Aspanlestes aptap* has the smallest lower teeth of any Asian "zhelestid." It closely corresponds in size to the upper molars of *Zhelestes bezelgen*. As shown in Figure 8, when the uppers and lowers of these taxa are superposed, the match is relatively good. We have little doubt that these two species belong to the same genus, *Aspanlestes*. At the species level, however, there are some apparent differences, all of which seem to relate to the size of the talonid in *Aspanlestes aptap*. As seen in Figure 8, the anteroposterior dimension of the protocone of M^1 and M^2 in the type of *Zhelestes bezelgen* appears to be slightly too large for the talonid basin of M_1 and M_2, respectively, in the type of *Aspanlestes aptap*. Further, almost 27 m of stratigraphic section separate the types of these two taxa.

Fig. 8.—Superimposed occlusal outlines of the maxillary dentition of the holotype of *Zhelestes bezelgen* and the mandibular dentition (reversed) of the holotype of *Aspanlestes aptap*. The very close similarity in size and correspondence in occlusal morphology indicate that these specimens probably belong to the same species, *Aspanlestes aptap*. Scale = 2 mm.

Stratigraphic position is not an intrinsic character that is inherited and passed on, and thus should not be coded in a phylogenetic analysis; it may be, however, a cue that the above morphological differences are more than individual variation. Lacking more specimens to estimate whether this is specific or individual variation, we err on the side of the latter and tentatively treat *Zhelestes bezelgen* Nessov, 1987 as a junior synonym of *Aspanlestes aptap* Nessov, 1985*a*.

Based on the phylogenetic analysis presented later, *Aspanlestes aptap* retains more primitive character states relative to other "zhelestids." It is possible that this is an allometric phenomenon, which may or may not have a phylogenetic basis. Arguing against this is the fact that, of the two next larger Asian "zhelestids," one (*Zhelestes temirkazyk*) retains the next higher number of primitive retentions, while the other (*Parazhelestes minor*), does not. Thus, it is unclear whether size and retentions of primitive character states are in any way related.

Zhelestes Nessov, 1985*a*

Type and Only Known Species.—*Zhelestes temirkazyk* Nessov, 1985*a*.

Distribution.—Late Cretaceous (late Turonian and Coniacian), western Uzbekistan.

Revised Diagnosis.—Same as for type and only species.

Zhelestes temirkazyk Nessov, 1985*a* (Fig. 9, 10, 20)

Zhelestes temirkazyk Nessov, 1985*a*:16, pl. 3, fig. 14. Nessov et al., 1994:63, pl. 5, fig. 1; Archibald, 1996*b*:1152, fig. 4A.
non-*Zhelestes* cf. *temirkazyk* Nessov, 1985*a*:16, pl. 3, fig. 5.

Holotype and Only Known Specimen.—CCMGE 10/12176, left maxilla with part of alveolus for large, single-rooted C^1, alveolus for small, single-rooted P^1, two-rooted P^2, bilobed root for small P^3, two-rooted P^4, three-rooted P^5, M^{1-3} (molars very worn).

Type and Only Known Locality.—Locality CBI-17, upper part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

Revised Diagnosis.—Of the following character states, only the relative narrowness of M^1 and M^2 are arguably autapomorphic for *Zhelestes temirkazyk*. Upper molar crowns not constricted through conular region as is also the case in other Asian ungulatomorphs except *Aspanlestes aptap* and *Parazhelestes minor*; at least shallow ectoflexus as found in all "zhelestids" except *Eoungulatum kudukensis*; protocone with slight anteroposterior expansion as is also the case in *Aspanlestes aptap*; protocone with little or no labial shift of apex as is also the case in *Aspanlestes aptap*, although this is conjectural because of extreme wear; closest in size to *Parazhelestes robustus* and *P. minor*. Compared with other "zhelestids": upper molar crowns anteroposteriorly shorter (narrower) relative to labiolingual width, with a ratio of 0.64 for M^1 compared to an average of 0.77 for all other known Asian "zhelestid" M^1s (seven specimens) and a ratio of 0.67 for M^2 compared to an average of 0.73 for all other known Asian "zhelestid" M^2s (six specimens). The narrowness of M^2 is only matched by that of M^2 in *Parazhelestes minor*.

Description.—The occlusal surfaces are obliterated by dental attrition on most occlusal surfaces in the single specimen known for *Zhelestes temirkazyk*, so that little can be described of the crown morphology. Much of the left maxillary region is preserved, however, providing considerable information (Fig. 9, 10).

The posterior margin of a large canine alveolus and an alveolus for a single-rooted P^1 are preserved, as are a little-worn, two-rooted P^2, single-rooted fragment of a smaller P^3, somewhat worn P^{4-5}, and very heavily worn M^{1-3}. A large infraorbital foramen lies dorsal to the posterior root of P^4. The two-rooted P^2 has a single dominant cusp with a small anterior cingular cuspule and a posterior margin that is slightly expanded but which bears no cusps. Unlike P^2, which is implanted vertically, P^4 is canted slightly posteriorly because the anterior root slants posteriorly before joining the crown. P^4 is probably only two-rooted, but the posterior margin is linguolabially expanded into an incipient protocone. The crown is dominated by a single cusp, but there are also anterior cingular and posterior cingular cuspules. The P^3 root shows this to be a smaller tooth than P^2 or P^4. P^5 is slightly less worn than the molars. It is a submolariform, three-rooted tooth. The well-developed protocone reaches as far lingually as the lingual margin of M^{1-2}. The stylar shelf is narrow, being almost nonexistent labial to the paracone. A parastyle appears to be the only stylar cusp on a distinct parastylar lobe. The metastylar lobe

Fig. 9.—*Zhelestes temirkazyk* Nessov, 1985*a*, CCMGE 10/12176, holotype left maxilla preserving part of alveolus for large, single-rooted C^1; alveolus for small, single-rooted P^1; crown of P^2; roots of small P^3; crowns of P^4–M^3 in labial (A) and occlusal (B) views. Scales = 2 mm.

Fig. 10.—Left labial view of maxilla of *Zhelestes temirkazyk* shown in Figure 9 compared to dentary of *Sorlestes budan* shown in Figure 19D–F. Lower view is occlusal view of dentary showing alveoli. Reconstructed teeth are shown by dotted lines. Diagonal lines are broken areas. Stippling on dentary shows alveoli. Stippling on maxilla shows suture with jugal. Note the evidence for five premolars in maxilla, and relative size of premolars, $P^5 > P^4 > P^2 > P^3 > P^1$. Scale = 2 mm. See text for discussion.

is also well developed, but lacks cusps. The prominent but heavily worn paracone preserves a distinct postparacrista with an obvious swelling, suggesting that a metacone may have been present. There are very narrow and possibly worn pre- and postcingula.

The occlusal surfaces of M^{1-3} are nearly obliterated, so that nothing can be said about the disposition (or even presence or absence) of the conules and their related cristae. It does appear that the molars possessed pre- and postparacristae and pre- and postmetacristae. The stylar shelves are moderately narrow except for the parastylar region on M^{2-3} and the metastylar region on M^{1-2}. With both para- and metastylar lobes, M^2 has a distinct but shallow ectoflexus. There appear to be three cusps on the parastylar lobe on at least M^1: stylocone, parastyle, and preparastyle. There is a distinct cuspule on the metastylar lobe of M^2. Otherwise, the crowns are so worn that wear has reached to the level of the narrow, but distinct pre- and postcingula.

Discussion.—Even with considerable wear, enough morphology is preserved that there is little doubt that *Zhelestes temirkazyk* is a "zhelestid." In Figure 10 these affinities are reinforced by a comparison of the type of *Zhelestes temirkazyk* with a dentary referred here to *Sorlestes budan*. This comparison permits a suggested reconstruction for missing teeth in both species. Most notable is the assessment of five premolars in both the upper and lower jaws. Further, P^3 and P_3 appear to be smaller than adjacent P^2 and P_2, and P^4 and P_4. We refer an edentulous dentary (Fig. 19A) to "Zhelestidae" because it possesses this same size pattern and also because it is similar in size to the larger Asian "zhelestids." As discussed previously under "Zhelestidae," we have no clear evidence as to whether the smaller, third tooth between the canine and molars is a permanent premolar or a retained deciduous tooth.

Parazhelestes Nessov, 1993

Type Species.—*Parazhelestes robustus* Nessov, 1993.

Included Species.—Type species and, tentatively, *Parazhelestes minor*, n. sp.

Distribution.—Late Cretaceous (Coniacian), western Uzbekistan.

Revised Diagnosis.—Upper molar crowns only slightly (*Parazhelestes minor*) or not constricted through conular region (*Parazhelestes robustus*) as is also the case in other Asian "zhelestids"; at least shallow ectoflexus as found in all "zhelestids" except *Eoungulatum kudukensis*; protocone intermediate among "zhelestids" in amount of anteroposterior expansion and amount of labial shift of apex; intermediate in size among "zhelestids"; M^3 markedly linguolabially narrowed compared to M^{1-2} in *P. robustus* (condition unknown in *Parazhelestes minor*).

Comments.—Without knowledge of the size of M^3 in *Parazhelestes minor*, it is difficult to be con-

fident regarding the referral of this species to *Parazhelestes*. *Parazhelestes robustus* and *P. minor* show a similar degree of labial shift of the protocone relative to that seen in *Aspanlestes aptap* and *Eoungulatum kudukensis*. Depending on whether *P. minor* ultimately proves to have M^3 markedly linguolabially narrowed compared to M^{1-2}, this character is either an autapomorphy of *Parazhelestes* or of *P. robustus*.

Parazhelestes robustus Nessov, 1993 (Fig. 11, 20, 21)

Parazhelestes robustus Nessov, 1993:124, pl. 2, fig. 1; note that this figure was incorrectly published at 87% of the size indicated in the figure caption, as were all others in Nessov, 1993.

Holotype.—CCMGE 70/12455, left maxilla with two-rooted P^4, three-rooted P^5, worn M^1–M^3.

Type Locality.—Locality CBI-14, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

Referred Specimens.—CCMGE 20/12953, left M^1, and CCMGE 10/12953, worn and damaged right M^2.

Localities.—All referred specimens are from the type locality.

Revised Diagnosis.—Compared to *Parazhelestes minor*: size averages about 10% larger (ranging from 3–19% for three measurements each on the P^5, M^1, and M^2); molar crowns not constricted through conular region; M^2 less linguolabially extended.

Description.—The type maxilla, CCMGE 70/12455 (Fig. 11A), preserves a two-rooted penultimate premolar and a three-rooted ultimate premolar, which, as discussed under *Zhelestes temirkazyk*, are interpreted as P^{4-5}. P^4 is dominated by a single cusp, but there are also anterior cingular and posterior cingular cuspules. The posterior margin is linguolabially expanded into an incipient protocone. P^5 is a submolariform, three-rooted tooth. The well-developed protocone reaches as far lingually as the lingual margin of M^{1-2} and is anteroposteriorly wide compared with the same region in *Aspanlestes aptap* and *Zhelestes temirkazyk*. The stylar shelf is narrow, being almost nonexistent labial to the paracone. A parastyle appears to be the only stylar cusp on a distinct parastylar lobe. The metastylar lobe is also well developed and bears a single cuspule. Although somewhat worn and slightly damaged, there is a distinct metacone swelling and a metacone may have been present. The centrocrista (postparacrista + premetacrista) and postmetacrista are well developed, but there is no preparacrista. There appears to have been a small postparaconular crista but no premetaconular crista. There is only a hint of widening in the area of the pre- and postcingula.

In CCMGE 70/12455 M^{1-2} (Fig. 11A) are similar except for the stylar region and the fact that M^1 is slightly wider anteroposteriorly, with more distinct pre- and postcingula. On both M^1 and M^2 the stylar shelf is generally narrower than in either *Aspanlestes aptap* or *Zhelestes temirkazyk* (Fig. 20). The shelf remains recognizable between the paracone and metacone. It narrows considerably labial to the paracone on both M^{1-2}, but this narrowing is slightly less pronounced labial to the metacone on both molars. The remainder of the molar description is based mostly on a very well-preserved left M^1, CCMGE 20/12953 (Fig. 11B–F). The less worn and damaged parts of the type maxilla, CCMGE 70/12455, and a left M^2, CCMGE 10/12953, agree with this description. On CCMGE 20/12953 there is a distinct parastylar lobe on which there are three small cuspules: stylocone, parastyle, and preparastyle. There is also a small, distinct metastyle labial to the metacone. The postparacrista, and pre- and postmetacristae are distinct, but the preparacrista is not expressed on most of the height of paracone, but is present near its base. This crista, although worn, seems slightly better developed on the M^{1-2} in the type maxilla. This may be the result of considerable dental attrition of the parastylar groove, which accentuated the unworn area of the preparacrista. The postmetacrista merges with the metastylar lobe. The paracone and metacone are similar in height, which is moderately low, and they are separate at their bases. The well-developed paraconule and metaconule are situated approximately midway between the paracone and metacone labially and the protocone lingually. The conules have distinct pre- and postparaconule cristae and pre- and postmetaconule cristae, forming prominent conular wings. The preparaconule crista continues anterolabially, forming a broad paracingulum with the parastylar lobe. The postmetacrista forms the metacingulum, which merges with the tooth below (dorsal to) the posterior margin of the metacone. The apex of the protocone is as tall as the paracone and metacone. This cusp lies approximately on the middle of the lingual half of the M^1, as it is in *Parazhelestes minor*, but is more labial than in *Aspanlestes aptap* and more lingual than in *Eoungulatum kudukensis* (Fig. 21). The degree of anteroposterior expansion of the protocone is also intermediate between conditions in the latter two taxa. There are well-developed pre- and postcingula beginning lingually below the protocone, merging with the tooth below and just labial to the conules. CCMGE 20/12953 shows a slight amount of constriction of the crown through the conular area (slightly exaggerated in Fig. 11B), which is not seen in the other two specimens. The surface of M^3 in the type specimen is obscured by wear, but there is no doubt that this tooth is considerably narrower linguolabially than M^{1-2} (Fig. 11A). M^3 in *P. robustus* is also narrower than that in *Zhelestes temirkazyk*; alveoli for this tooth in a maxilla of *Aspanlestes aptap* (see earlier description) suggest that *Zhelestes temirkazyk* and *Aspanlestes aptap* were similar for this character.

Parazhelestes minor, **new species** (Fig. 12, 13, 20, 21)

Zhelestes cf. *temirkazyk* Nessov, 1985*a*:16, pl. 3, fig. 5.
"gen. indet." Nessov et al., 1994, pl. 7, fig. 8.
Parazhelestes n. sp. Archibald, 1996*b*:1151, fig. 2G, H.

Holotype.—CCMGE 11/12953, right M^1.

Type Locality.—Locality CBI-4, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

Referred Specimens.—CCMGE 11/12176, right maxilla with two roots of P^4, three-rooted P^5, M^{1-2}, all showing some wear; CCMGE 21/12953, right P^5 lacking the parastylar lobe; CCMGE 22/12953, left M^1; CCMGE 12/12953, right M^2.

Localities.—All referred specimens are from lo-

Fig. 11.—*Parazhelestes robustus* Nessov, 1993. A. CCMGE 70/12455, cast of holotype left maxilla preserving P^4–M^3 in occlusal view. B–F. CCMGE 20/12953, left M^1 in occlusal (B), buccal (C), posterior (D), anterior oblique (E), and lingual (F) views. Occlusal view in B is stereopair. Scales = 2 mm (upper scale corresponds to A, lower scale corresponds to B–F).

cality CBI-14, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

Etymology.—Latin *minor*, less. In reference to the smaller size of this species compared to *P. robustus*.

Diagnosis.—Compared to *Parazhelestes robustus*: size averages about 10% smaller (ranging from 3–19% for three measurements each on the P^5, M^1, and M^2); molar crowns slightly constricted through the conular region; M^2 more linguolabially extended.

Fig. 12.—*Parazhelestes minor*, n. sp. A–E. CCMGE 11/12953, holotype right M^1 in occlusal (A), lingual oblique (B), buccal (C), posterior oblique (D), and anterior oblique (E) views. Occlusal view in A is stereopair. F–H. CCMGE 21/12953, right P^5 lacking the parastylar lobe in occlusal (F), anterior oblique (G), and lingual oblique (H) views. Scales = 2 mm (upper scale corresponds to A–E, lower scale corresponds to F–H).

Description.—CCMGE 11/12176, a right maxilla, preserves two roots of P^4 and a three-rooted P^5, as well as M^{1-2}, all showing some wear (Fig. 13). An isolated P^5, CCMGE 21/12953, lacking the parastylar lobe, differs from the P^5 in the maxilla in some possibly significant ways (Fig. 12F–H). Because of their close similarity in size, however, the P^5s seem best referred to the same species for now. Both P^5s are submolariform, three-rooted teeth. The well-developed protocone on P^5 reaches as far lingually as the lingual margin of M^{1-2} in CCMGE 11/12176, and is only exceeded by *Parazhelestes robustus* in terms of its anteroposterior dimension. The stylar shelf is narrow, being almost nonexistent labial to the paracone. The parastylar lobe, which is distinct, is preserved only on the P^5 on CCMGE 11/12176. It is sufficiently worn that no cuspules can be recognized, if indeed they were present. A small preparacrista is detectable at the base of the paracone. Both P^5s preserve a well-developed metastylar lobe, neither of which have cuspules. The centrocrista and postmetacrista are well developed on both P^5s. CCMGE 11/12176, however, has only a very slight swelling in the region of the metacone, while the isolated P^5, CCMGE 21/12953, has a small but distinct metacone. Both P^5s have distinct but weak pre- and postparaconular cristae, so that a small paraconule is defined. Both lack a premetaconule crista, but the isolated P^5 has a postmetaconule crista. Narrow but distinct pre- and postcingula are present on the isolated P^5. Only the postcingulum is similarly developed on the P^5 in the maxilla, while there is only a hint of a precingulum.

The upper molars referred to *Parazhelestes minor* have a narrow stylar shelf compared with most other Late Cretaceous eutherians; this structure appears to be slightly wider than in *Parazhelestes robustus* but similar to that in *Aspanlestes aptap* and *Zhelestes temirkazyk* (Fig. 20). The shelf remains recognizable between the paracone and metacone. It narrows considerably labial to the paracone on both M^1 and M^2, but is slightly broader labial to the metacone on both molars. The type specimen, CCMGE 11/12953, is the best preserved, although it is the smallest of the three M^1s referred to *P. minor* (Fig. 12A–E). It compares favorably in most respects with the well-preserved M^1, CCMGE 20/12953, assigned to *Parazhelestes robustus* (Fig. 11B–F). The photographs suggest that the protocone is slightly more labial in *Parazhelestes robustus*. This is illusory because when posterior outlines of these M^1s are drawn to the same size, they almost completely overlap (top position, Fig. 21). The metastylar and parastylar lobes are both well developed on referred M^1s and M^2s. There are no cuspules on the metastylar lobe. The ridge bordering the stylar shelf is interrupted on M^2 in the maxilla (CCMGE 11/12176), with the edges bordering this interruption being slightly swollen. On less worn M^1s and M^2s, there are three cuspules on the parastylar lobe: stylocone, parastyle, and preparastyle. The postparacrista, and pre- and postmetacristae are distinct and present on all molars. The preparacrista is present on all the molars, but is usually more subdued. The postmetacrista merges with the metastylar lobe. The paracone and metacone are both moderately low and are separate at their bases. The

Fig. 13.—*Parazhelestes minor*, n. sp., CCMGE 11/12176, cast of right maxilla preserving roots for P^4 and crowns of P^5–M^2 in occlusal view. Scale = 1 mm.

well-developed paraconule and metaconule are situated approximately midway between paracone and metacone on the one hand and protocone on the other. The conules have distinct pre- and postparaconule cristae and pre- and postmetaconule cristae, forming prominent conular wings. The preparaconule crista continues anterolabially, forming a well-defined paracingulum with the parastylar lobe. The postmetacrista forms the metacingulum, which merges with the tooth below (dorsal to) the posterior margin of the metacone. The apex of the protocone is as tall as the paracone and metacone. This cusp is situated approximately on the middle of the lingual half of M^1, as it is in *Parazhelestes robustus*, but is more labial than in *Aspanlestes aptap* and more lingual than in *Eoungulatum kudukensis* (Fig. 21). The degree of anteroposterior expansion of the protocone is similar to that in *Parazhelestes robustus*. There are well-developed pre- and postcingula beginning lingually below the protocone, merging with the tooth below and just labial to the conules. The molars show a slightly greater degree of constriction of the crown through the conular area compared to *Parazhelestes robustus*.

Comments.—There is enough variation in size and morphology of the three M^1s placed in *Parazhelestes minor* to question whether only one species is represented. The problem, however, is that we do not have enough upper molars of any "zhelestid" to investigate meaningfully the issue of variation. The holotype M^1, CCMGE 11/12953, is the smallest of these M^1s. It is also the least worn (Fig. 12A–E). It is very similar to the somewhat worn M^1 in the maxilla, CCMGE 11/12176 (Fig. 13), except that the M^1 in the maxilla is slightly larger, has a less lingually extended postcingulum, has a slightly larger parastylar lobe, and has a protocone with a slightly more expanded lingual face. The most heavily worn M^1 referred to *P. minor*, CCMGE 22/12953, in addition to being larger than the holotype, has a relatively more lingually extended protocone and is relatively narrower across the conular region. This tooth may belong to *Zhelestes temirkazyk*, or it may be an M^2 of *P. minor* rather than an M^1. The latter possibility seems more likely.

Eoungulatum, **new genus**

Type and Only Known Species.—*Eoungulatum kudukensis*, n. gen. and sp.

Distribution.—Late Cretaceous (Coniacian), western Uzbekistan.

Etymology.—Greek *eos*, dawn, early; and Latin *ungula*, hoof. In reference to the very early age and resemblance to archaic ungulates.

Diagnosis.—Same as for type and only known species.

Eoungulatum kudukensis, **new species** (Fig. 14A–E, 20, 21, 19I)

"Advanced form of Proteutheria, intermediate to Condylarthra" Nessov, 1987, pl. 1, fig. 2.

"Archaic ungulate mammals" Nessov and Kielan-Jaworowska, 1991, fig. 1, shown as left M^2.

"Condylarthra of the family Periptychidae" Nessov, 1993, pl. 1, fig. 3 (not pl. 6, as indicated in Nessov, 1993).

"gen. et sp. nov." Archibald, 1996*b*:1151, fig. 2D, 3D.

Holotype and Only Known Specimen.—CCMGE 2/12455, left M^2.

Type Locality.—Locality CBI-14, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

Etymology.—Kazak *kuduk*, well. In reference to the general Dzharakuduk region, which means "well near the escarpment" in Kazak, where the type and tentatively referred specimens were found.

Diagnosis.—Compared with other "zhelestids": upper molar crown without ectoflexus; protocone with greatest anteroposterior expansion; protocone with greatest labial shift of apex; largest in size. Upper dentition is comparable in length, but about 6% wider (only two measurements of M^2) than the slightly smaller "zhelestid," *Parazhelestes robustus*. If the lower teeth described below are correctly referred to *E. kudukensis*, the lower dentition averages 8% (three measurements of M_2) greater in length and 20% (two measurements of M_2) greater in width than the slightly smaller *Sorlestes budan*.

Description.—The holotype, a left M^2 (CCMGE 2/12544) has three roots. The enamel shows chemical weathering that obscures some details of the crown. The occlusal outline of the crown is nearly rectangular, with the lingual part almost as long as the labial. The parastylar lobe is quite prominent, but the metastylar region is less so. The stylar shelf is narrow, with no distinct ectoflexus. There may have been three cuspules on the parastylar

lobe: preparastyle, parastyle, and stylocone. There are small bumps on the stylar shelf labial to both the paracone and metacone, but we cannot determine if these are real or a result of weathering. There may not have been a preparacrista, but a prominent postmetacrista extends from the metacone to the metastylar region. The paracone and metacone are conical and similar in size, with an indistinct (possibly because of wear) centrocrista. The apices of both the paracone and metacone are broken. As in all other upper molars of "zhelestids," the para- and metaconules have prominent wings with strong cristae forming especially strong shearing facets on their internal surfaces. The preparaconule crista forms a narrow, continuous paracingulum that merges labially with the parastylar lobe. The postmetaconule crista forms a narrow metacingulum that continues labially below (dorsal to) the metacone, where it terminates. The protocone is the largest cusp, with a broad, rounded lingual face and well-developed but subdued (possibly because of weathering) pre- and postprotocristae. Both the pre- and postcingula, but especially the precingulum, are weathered. The precingulum originates as a faint vertical crest below the paracingulum. It then turns horizontally and broadens slightly to form the precingulum. Just anterior to the protocone it narrows to form a faint triangular facet on the anterior face of the protocone. It broadens slightly again as it continues to form a lingual cingulum that merges with the postcingulum. There is a slight apical expansion of the postcingulum posterolingually below the protocone (in the position of a hypocone). The postcingulum then narrows slightly, and continues around the posterior margin of the molar. At a point between and below the metaconule and metacone, the postcingulum becomes very narrow, sharply turns vertically, and contacts the metacingulum.

cf. *Eoungulatum kudukensis*, **new species**
(Fig. 14F–Q, 20)

Four specimens probably belong to *Eoungulatum kudukensis* based on size and morphology, but given the fragmentary nature of the material, a more definite assignment is not currently possible. These specimens are: CCMGE 35/12176, right P^5; CCMGE 17/12953, right M_2; CCMGE 18/12953, left M_3; CCMGE 16/12953, left M_3. CCMGE 17/12953, CCMGE 18/12953, and CCMGE 16/12953 are from locality CBI-14, and CCMGE 35/12176 is from locality CBI-4b, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

The right P^5, CCMGE 35/12176 (Fig. 14P, Q, 20), could easily be mistaken for the ultimate upper premolar of a small periptychid, even though this family is unknown in the fossil record until some 20 million years later. There is no stylar shelf. The metastylar and parastylar lobes are small, as in the holotype M^2 of *Eoungulatum kudukensis*. The paracone and protocone are both robust, slightly swollen, and worn apically. There is a distinct metacone swelling. Probably because of cusp swelling, there are no cristae between or emanating from the paracone and metacone. There are traces of pre- and postparaconule cristae and there may have been a paraconule. Para- and metacingula are present. Unlike on P^5s or upper molars of other "zhelestids," but as in archaic ungulates, the metacingulum is at the level of and continues onto the metastylar lobe. There are narrow pre- and postcingula.

The three lower molars that may belong to *Eoungulatum kudukensis*, one M_2 and two M_3s, seem to cluster together based on size (Fig. 6). In morphology, however, there is some indication that at least two taxa may be represented. The lower molar that seems most likely to belong to *E. kudukensis* is a left M_3, CCMGE 16/12953 (Fig. 14F–J). As in other "zhelestids," the trigonid is low relative to the talonid compared with other Late Cretaceous eutherians. The overall height of both the trigonid and talonid appear to be greater than in any other "zhelestid." The paraconid is almost, but not completely lingual, and is slightly appressed to the larger metaconid. As in other "zhelestids" there are small pre- and even smaller postcingulids, but no labial or lingual cingulids. Individual cusps do not appear to be swollen, but the whole crown is slightly swollen at its base, so that the apices of the cusps seem slightly more crowded. This is especially clear for the talonid basin and the talonid cusps. This closure of the cusps is seen to a much greater extent in some earlier Tertiary periptychids. There seems to be little or no twinning of hypoconulid and entoconid, probably because the hypoconulid is set slightly separate and more posterior. This more posterior placement of the hypoconulid on M_3 is seen to a greater extent in many, if not all, early Tertiary archaic ungulates.

The other M_3, CCMGE 18/12953, is only slightly larger than CCMGE 16/12953; the trigonid and talonid widths are comparable in the two, but the talonid is relatively longer in the former specimen (Table 2). The height of both the trigonid and the talonid are less than on CCMGE 16/12953. The base of the crown has little or no swelling and the apices of the cusps do not seem to show crowding, although there is some wear. The hypoconulid shows slight twinning with the entoconid, but as in CCMGE 16/12953, it is positioned more posteriorly than in M_2s. The trigonid and its cusps are comparable on the two M_3s. In CCMGE 18/12953 the pre- and postcingulids are not as small, and there is a small ectostylid. Based on overall size, the next possible candidate to which CCMGE 18/12953 might be referred is *Parazhelestes robustus*. In this species, however, M_3 is labiolingually reduced, yet there is no sign of such a reduction in CCMGE 18/12953. The next likely candidate based on size

Fig. 14.—A–E. *Eoungulatum kudukensis*, n. gen. and sp., CCMGE 2/12455, holotype left M^2 in occlusal (A), lingual (B), anterior (C), posterior (D), and buccal (E) views. Occlusal view in A is stereopair. F–Q. cf. *Eoungulatum kudukensis*, n. gen. and sp. F–J. CCMGE 16/12953, left M_3 in occlusal (F), anterior (G), posterior oblique (H), buccal (I), and lingual (J) views. K–O. CCMGE 17/12953, right M_2 in occlusal (K), posterior (L), lingual (M), buccal (N), and posterobuccal (O) views. P, Q. CCMGE 35/12176, right P^5 in occlusal (P), and anterior (Q) views. Occlusal views in A, F, and K are stereo pairs. Scales = 2 mm (upper scale corresponds to A–E; middle scale corresponds to F–J and M–Q; and lower scale corresponds to K–L).

Table 2.—*Measurements (in mm) of Uzbek ungulatomorph lower dentitions. Italicized numbers are estimates. Daggers (†) indicate type specimens. Abbreviations are as follows: L, length; W, width; TRW, trigonid width; TAW, talonid width; TRL, trigonid length; TAL, talonid length.*

	P_2		P_4		P_5		M_1				M_2					M_3				
Specimen no.	L	W	L	W	L	W	L	TRW	TAW	TAL	L	TRW	TAW	TRL	TAL	L	TRW	TAW	TRL	TAL
Sorlestes budan																				
13/12953	—	—	—	—	—	—	2.4	1.5	1.6	1.3	—	—	—	—	—	—	—	—	—	—
1/12953	—	—	—	—	2.2	1.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2/12953	—	—	2.3	1.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3/12953	—	—	—	—	—	—	*2.4*	1.5	—	*1.3*	—	—	—	—	—	—	—	—	—	—
36/12000	—	—	—	—	—	—	—	—	—	—	2.4	1.8	1.8	1.1	1.3	—	—	—	—	—
†3/12176	—	—	—	—	—	—	—	—	—	—	2.8	1.8	1.8	1.3	1.5	—	—	—	—	—
4/12953	—	—	—	—	—	—	2.4	1.5	1.5	1.3	—	—	—	—	—	—	—	—	—	—
5/12953	—	—	—	—	—	—	2.4	1.5	1.6	1.3	—	—	—	—	—	—	—	—	—	—
14/12953	—	—	—	—	—	—	—	—	—	—	2.6	1.8	1.8	1.2	1.4	—	—	—	—	—
6/12953	—	—	—	—	—	—	—	—	—	—	2.6	1.7	1.7	1.2	1.4	—	—	—	—	—
15/12953	—	—	2.0	1.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2155-M-1	—	—			—	—	—	—	—	—	—	—	—	—	—	2.5	1.8	1.5	1.0	1.5
Averages	—	—	2.2	1.3	—	—	2.4	1.5	1.6	1.3	2.6	1.8	1.8	1.2	1.4	—	—	—	—	—
Kumsuperus avus																				
†13/11758	—	—	—	—	—	—	—	—	1.8	1.3	2.5	1.8	1.8	1.2	1.3	*2.3*	*1.5*	1.0	—	1.3
Aspanlestes aptap																				
7/12953	—	—	—	—	—	—	2.1	1.1	1.4	1.0	—	—	—	—	—	—	—	—	—	—
6/12176	—	—	—	—	—	—	—	—	—	—	—	—	1.6		*1.7*	1.9	1.4	1.1	0.9	1.0
†4/12176	—	—	1.6	0.9	2.1	1.0	2.1	1.5	1.5	1.1	2.2	1.6	1.6	1.0	1.2	—	—	—	—	—
69/12445	—	—	—	—	—	—	—	—	—	—	2.0	*1.5*	*1.5*	0.9	1.1	2.0	1.3	1.2	0.8	1.2
8/12953	—	—	—	—	—	—	—	—	—	—	2.0	1.6	1.6	0.9	1.1	—	—	—	—	—
9/12953	1.5	0.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Averages	—	—	—	—	—	—	2.1	1.3	1.5	1.1	2.1	1.6	1.6	0.9	1.3	2.0	1.4	1.2	0.9	1.1
cf. *Eoungulatum kudukensis*																				
16/12953	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.8	2.1	1.7	1.3	1.5
17/12953	—	—	—	—	—	—	—	—	—	—	2.8	2.2	2.1	1.3	1.5	—	—	—	—	—
18/12953	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.9	2.1	1.8	1.1	1.8
Averages	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.9	2.1	1.8	1.2	1.7

Fig. 15.—*Sorlestes budan* Nessov, 1985*a*. A–E. CCMGE 3/12176, cast of holotype right dentary with M_2 and alveoli for M_3 (not shown) in occlusal (A), posterior (B), anterior (C), lingual (D), and buccal (E) views. F–J. CCMGE 13/12953, cast of right M_1 in occlusal (F), posterior (G), anterior (H), lingual (I), and buccal (J) views. Occlusal views in A and F are stereopairs. Scale = 2 mm.

is the slightly smaller *Zhelestes temirkazyk*. This allocation cannot be eliminated as a possibility, but without stronger evidence, we prefer to refer both of these M_3s to cf. *Eoungulatum kudukensis*.

On the right M_2, CCMGE 17/12953, the only swelling of the crown seems to be at the base of the hypoconid (Fig. 14K–O). The other talonid cusps show some twinning. The paraconid is smaller than on either M_3, is slightly appressed to the metaconid, and is lingual to the midline of the tooth, but is not situated on the lingual margin of the molar. The pre- and postcingulids are very small and there are no labial or lingual cingulids. CCMGE 17/12953 shows some increase in the height of the trigonid and talonid, almost as much as on the M_3, CCMGE 16/12953, but more than on the other M_3, CCMGE 18/12953.

Sorlestes Nessov, 1985*a*

Type and Only Known Species.—*Sorlestes budan* Nessov, 1985*a*.

Distribution.—Late Cretaceous (late Turonian and Coniacian), western Uzbekistan.

Revised Diagnosis.—As for the type species.

Sorlestes budan Nessov, 1985*a*
(Fig. 10, 15, 16, 17)

Sorlestes budan Nessov, 1985*a*:14, pl. 2, fig. 13. Nessov and Kielan-Jaworowska, 1991:fig. 1; Nessov et al., 1994:18, pl. 1, fig. 7; Archibald, 1996*b*:1152, fig. 4C.

?*Zalambdalestes mynbulakensis* Nessov 1985*b*:212, pl. 2, fig. 2. Nessov et al., 1994:24, pl. 5, fig. 2.

Holotype.—CCMGE 3/12176, right dentary with M_2 and alveoli for M_3.

Type Locality.—Locality CBI-14, middle part of

Fig. 16.—*Sorlestes budan* Nessov, 1985*a*. CCMGE 14/12953, left M_2 in occlusal (A), posterior (B), anterior (C), lingual (D), and buccal (E) views. Occlusal view in A is stereopair. Scale = 2 mm.

Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

Referred Specimens.—CCMGE 2/12953, left P_4; CCMGE 5/12953, chemically weathered left M_1; CCMGE 13/12953, right M_1; CCMGE 3/12953, chemically weathered right M_1; CCMGE 14/12953, left M_2; CCMGE 6/12953, right M_2; CCMGE 36/12000 (type of ?*Zalambdalestes mynbulakensis)*, left dentary with M_2 and alveoli for M_3; CCMGE 1/12953, left dentary with P_5, alveoli for M_1, roots of M_2, and alveoli for M_3; CCMGE 15/12953, left dentary with canine, two roots of P_1, two alveoli each for P_{2-3}, P_4; IZANUz P2155-M-1, left dentary with unerupted M_3.

Localities.—CCMGE 3/12953 is from locality CDZH-17a, lower part of Bissekty Formation, upper Turonian. CCMGE 5/12953 is from locality CBI-4b, middle part Bissekty Formation, Coniacian. CCMGE 36/12000, CCMGE 13/12953, CCMGE 14/12953, CCMGE 6/12953, CCMGE 1/12953, CCMGE 2/12953, and CCMGE 15/12953 are from locality CBI-14, middle part of Bissekty Formation, Coniacian. All localities are from the Upper Cretaceous, Dzharakuduk, western Uzbekistan.

Revised Diagnosis.—As in lower dentition of other "zhelestids": trigonid low relative to talonid, slight appression of paraconid and metaconid, pre- and postcingulids present, labial and lingual cingulids absent, entoconid and hypoconulid with some twinning. Lower dentition averages 22% larger (ranging from 0–31% for two measurements each on P_{4-5}, and for five measurements each on M_{1-2}) than smallest "zhelestid," *Aspanlestes aptap*, and 8% smaller (three measurements of M_2) in length and 20% smaller (two measurements of M_2) in width than the slightly larger cf. *Eoungulatum kudukensis*. The only possible autapomorphy is the intermediate size of this species, but as many as three species could be included.

Description.—A left dentary, CCMGE 15/12953, preserves a large, single-rooted canine, six alveoli or root fragments, and a two-rooted premolar. It appears that the canine may not be fully erupted. The premolar, which has some apical wear, is about 25% larger than (but similar in morphology to) the unworn penultimate premolar in the holotype dentary of *Aspanlestes aptap* (CCMGE 4/12176). Both are two-rooted, have a large protoconid, no paraconid, a cristid on the metaconid region, a small heel, and no cingulids. Both teeth are broadest just posterior to the protoconid, although CCMGE 15/12953 is slightly more bulbous, probably because of its slightly larger size. This dentary is too large to be referred to *Aspanlestes aptap*, but seems to be within the size range of *Sorlestes budan*. An isolated premolar (CCMGE 2/12953) is slightly larger than but comparable to the premolar in CCMGE 15/12953, both of which we feel are best regarded as P_4s (Fig. 10, 19D–F).

There are three specimens of M_1, four M_2s, including the holotype M_2, CCMGE 3/12176, and one M_3 assigned to *Sorlestes budan*. Two of the M_2s, including the type, are preserved in dentary fragments that also preserve the roots or alveoli for M_3. Based on these associations, plus differences in crown morphology and comparisons with the type dentary of *Aspanlestes aptap*, we are confident about our identifications as to locus of isolated molars assigned here to *Sorlestes budan*.

The M_1s average about 92% of the size of the M_2s except in the trigonid width of M_1, which is even smaller (about 83%). From what can be gleaned from the alveoli of M_3, this tooth was probably only slightly smaller than M_1 and M_2. Both M_1 and M_2 are similar in having a distinct precingulid, narrower postcingulid, and no labial or lingual cingulids. On both, the hypoconulid is slightly closer to the entoconid (twinning) than to the hypoconid. On M_1, the paraconid is nearer the anteroposterior midline than it is on M_2, in which it is distinctly more lingual. On M_1, the paraconid is less appressed to the metaconid than on M_2.

A left dentary fragment, IZANUz P2155-M-1, preserves the mandibular condyle, angular process, alveoli for M_2, and unerupted M_3 that has been exposed (Fig. 17A–D). This dentary fragment is of particular interest as it preserves both the mandibular condyle and the angular process. The dentary is dorsoventrally shallow, yet the preserved alveoli for M_2 are quite large (Fig. 17D), about the size for roots of M_2 in *Sorlestes budan* or *Aspanlestes aptap*. Such large alveoli relative to dentary size are often indicative of a young mammal. For example, compare the alveolar size relative to the size of the dentary in IZANUz P2155-M-1 versus CCMGE 23/12953 in Figure 19A. When originally collected, the dentary had a small foramen behind the second alveolus in IZANUz P2155-M-1 that was interpreted as the locular opening above an unerupted molar, which we surmised was M_3. When X-rayed, a tooth was detected. Most of the bone surrounding the tooth, which is clearly an M_3, was removed (Fig. 17B, D). In both the trigonid and talonid basins enamel had not completely formed, but enough is present to show "zhelestid" characteristics. The trigonid is slightly anteroposteriorly compressed and the hypoconulid and entoconid are somewhat twinned. This tooth is larger than M_3 in *Aspanlestes aptap*, but smaller than the M_3 tentatively referred to *Eoungulatum kudukensis* (Table 2). Also, if the M_3 in *Kumsuperus avus* is sufficiently preserved to indicate the true size of this tooth, it is similar in length but noticeably narrower than the M_3 in IZANUz P2155-M-1 (Table 2). If true, this suggests that *Kumsuperus*, with a reduced (especially narrowed) M_3, may be a senior generic synonym of *Parazhelestes*, at least one species of which (*P. robustus*) has a linguolabially narrow M^3.

The mandibular condyle in IZANUz P2155-M-1 is cylindrical, with the long axis labiolingually oriented; the labial end is higher (Fig. 17C). The condyle is posterior to the angular process and is just barely dorsal to the alveolar row. This is the presumed primitive position of the condyle in eutherians, if not therians. The well-preserved dentary of *Sorlestes kara* from Kazakstan described by Nessov (1993:pl. 1) preserves a condyle at or only slightly higher than that in IZANUz P2155-M-1. In earliest Tertiary ungulates (sensu stricto), such as *Protungulatum* or *Oxyprimus*, the mandibular condyle is dorsal to the occlusal surface of the tooth row.

The angular process in IZANUz P2155-M-1 is slightly inflected. A considerably more inflected angle is primitive for metatherians. The angle is unknown for most Late Cretaceous eutherians. For this reason we cannot assess whether the more modestly

Fig. 17.—*Sorlestes budan* Nessov, 1985*a*. IZANUz P2155-M-1, left dentary preserving the mandibular condyle, angular process, posterior alveolus for M_2, and unerupted M_3 from which the surrounding bone has been removed. Views are buccal (A), lingual (B), posterior (C), and occlusal (D). Dashed lines indicate broken or removed surfaces. Occlusal view in D is stereopair. Scales = 2 mm (upper scale corresponds to A–C, lower scale corresponds to D).

inflected angle is an apomorphy of "zhelestids" or a larger clade of eutherians.

Discussion.—Figure 10 compares the type maxilla of *Zhelestes temirkazyk* and the fragmentary left dentary described above. As shown in this figure, the uppers and lowers are very similar in size, and the comparable teeth and alveoli align quite well. This fragmentary left dentary may belong to *Z. temirkazyk*. However, based on the material that we currently have available, it seems more prudent to refer this dentary fragment to *Sorlestes budan*, a taxon founded on lower teeth. The more recently named *S. budan* (founded on lower teeth) may prove to be a synonym of *Z. temirkazyk* (founded on upper teeth). Indeed, *S. budan* may include specimens belonging to as many as three taxa known from upper teeth: *Z. temirkazyk*, *Parazhelestes robustus*, and *P. minor*. Thus, we feel synonymization of *S. budan* with *Z. temirkazyk* is premature.

We are making the admittedly major assumption that the premolar count of five in the type specimen of *Zhelestes temirkazyk* (Fig. 9A, 10) and in a much larger edentulous dentary described below (Fig. 19A–C) is representative of all species we refer to "Zhelestidae." Given this assumption, the premolar preserved in CCMGE 15/12953 is P_4, as is an isolated premolar (CCMGE 2/12953) also referred to *Sorlestes budan*. This is also part of the basis for identifying the various submolariform upper premolars as P^5 and the two premolars in the type of *Aspanlestes aptap* (CCMGE 4/12176) as P_{4-5}.

Comments.—Nessov (1993:pl. 1, top three figures; Nessov et al., 1994:pl. 7, fig. 4) recently described a new species of *Sorlestes*, *S. kara*, based on a very well-preserved right dentary with P_5 and M_{1-3}. The specimen, CCMGE 106/12455, was recovered from a well core (Ashchikol locality) in south-central Kazakstan. It is believed to be early Turonian in age, which is slightly older than the late Turonian and Coniacian age advocated here for the "zhelestids" from the Dzharakuduk area in western Uzbekistan. Although the species is not included in our phylogenetic analysis because only the lower dentition is known, some characters distinguishing it from other taxa are included.

On the P_5 of *Sorlestes kara* compared to *Aspanlestes aptap*: the protoconid is higher, sharper, and more posteriorly curved; the metaconid is not developed; the precingulid on the labial side is stronger and bears a sharp cuspule; the postcingulid is much better developed; and the talonid basin is narrower labiolingually and strongly inclined lingually. Thus, P_5 in *S. kara* is not submolariform as it is in *A. aptap*.

M_2 in *Sorlestes kara* is similar to that in *S. budan*, but the latter is approximately 20% larger. Some differences are as follows: M_2 in *S. kara* has an incipient ectocingulid (absent in *S. budan*); the crown of M_2 in *S. kara*, especially the talonid, is not as high as in *S. budan*; the trigonid basin of M_2 in *S. kara* is shallower than in *S. budan*; and the paraconid of M_2 in *S. kara* is blade-like, but in *S. budan* the tip of the paraconid is slightly bulbous.

Fig. 18.—*Kumsuperus avus* Nessov, 1984*b*, nomen dubium. CCMGE 12/11758, holotype left dentary with heavily worn and slightly broken M_{1-3} in lingual (A), occlusal (B), and buccal (C) views. Scale = 2 mm.

Kumsuperus Nessov, 1984*b*, nomen dubium

Type and Only Known Species.—*Kumsuperus avus* Nessov, 1984*b*, nomen dubium.

Distribution.—Late Cretaceous (Coniacian), western Uzbekistan.

Kumsuperus avus Nessov, 1984*b*, nomen dubium (Fig. 18)

"Lower jaw of advanced placental mammal with M_1–M_3" Nessov, 1982:pl. 2, fig. 2.

Kumsuperus avus Nessov, 1984*b*:63, lower left, center left, and center images in figure. Nessov et al., 1994:14–15, pl. 2, fig. 1.

Holotype and Only Known Specimen.—CCMGE 12/11758, left dentary with heavily worn and slightly broken M_{1-3}.

Type Locality.—Locality CBI-4b, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

Discussion.—*Kumsuperus avus* Nessov, 1984*b* was based on a partial dentary with heavily worn M_{1-3} from the Bissekty Formation in Dzharakuduk. It was originally figured by Nessov (1982:fig. 2a) as an "advanced placental mammal," and in 1984(*b*) he named and referred it to Eutheria incertae sedis. There is a slight suggestion of anteroposterior shortening of the trigonid in *Kumsuperus* compared to *Sorlestes budan*, but this can be attributed to either dental attrition or postmortem abrasion. When the lower teeth of these two taxa are plotted together (Fig. 6), and when their sizes are compared (Table 2), there is no detectable difference except for the linguolabial narrowing of M_3 in *K. avus*.

It may well be that *Kumsuperus avus* and *Sorlestes budan* are congeneric, if not conspecific. The problem is in attempting to determine which uppers and lowers go together. As already discussed, lowers of *Aspanlestes aptap* can be associated with considerable confidence with uppers previously attributed to *Zhelestes bezelgen*; and possible lowers of *Eoungulatum kudukensis* can be identified with less certainty. In the midsize range, we recognize three taxa of "zhelestids," *Zhelestes temirkazyk*, *Parazhelestes robustus*, and *Parazhelestes minor*. As noted above, the linguolabially narrow M_3 in *K. avus* is suggestive of possible synonymy between this taxon and *Parazhelestes*. It may ultimately be shown that some of the taxa discussed above are invalid or that different taxa are grouped under *Sorlestes budan*. For now, we think it is best to retain both *Sorlestes budan* and *Kumsuperus avus*, while recognizing that the latter taxon is questionable.

"Zhelestidae" genus and species indeterminate (Fig. 19A–F)

A number of fragmentary teeth and edentulous dentaries may belong to "Zhelestidae." We briefly comment on only one of these specimens, CCMGE 23/12953, a right edentulous dentary with alveoli for canine (posterior portion only), P_{1-5}, M_{1-3} (Fig. 19A–C). Based on size alone, CCMGE 23/12953 is very likely a "zhelestid" as no other mammal of this size is known from the Bissekty Formation. Also as discussed earlier, this dentary preserves alveoli for five premolars, of which P_3 appears to have been smaller than P_2 and P_4. This size pattern is found in at least one other "zhelestid" dentary that preserves teeth (Fig. 19D–F, CCMGE 15/12953, *Sorlestes budan*). The very deep excavation of the masseteric fossa (Fig. 19B) may also be characteristic of "zhelestids."

NORTH AMERICAN "ZHELESTIDS"

Fox (1989) named *Alostera saskatchewanensis* based on material from the Scollard and Frenchman formations of Alberta and Saskatchewan, Canada, and the Hell Creek Formation, Montana, U.S.A. There is universal agreement that the localities in the Scollard Formation are latest Cretaceous (Lancian) in age. More recently studied localities in the Frenchman Formation are of less certain age, although Fox (1995) argued that, based on palynological data, these sites are also latest Cretaceous in age. The site in Montana that yielded specimens of *Alostera saskatchewanensis* is Bug Creek Anthills, which (as discussed in the Introduction) we regard as probably lying within the lowermost Paleocene Tullock Formation rather than the latest Cretaceous Hell Creek Formation.

Alostera saskatchewanensis is a rather curious species. Fox (1989) noted similarities with *Gypsonictops* and *Purgatorius*. Although not denying these similarities, we feel that the most likely evolutionary affinities are with Ungulatomorpha, more specifically "zhelestids." *Alostera* is similar to "zhelestids" and some other Late Cretaceous eutherians in having only a slight expansion of the protocone and in maintaining large conular wings, yet it is very much like early Tertiary archaic ungulates in having even greater reduction of the stylar shelf and accompanying cuspules, loss of parastylar groove and reduction to one parastylar cusp, and a metacingulum formed by the continuation of postmetaconule crista onto the metastylar lobe. These character states suggest that *Alostera* could simply be an odd archaic ungulate, but our phylogenetic analysis (presented next) suggests that it is an ungulatomorph of uncertain affinities. The variable presence of a distinctive mesostylar cusp is probably autapomorphic for this taxon (Fig. 22H).

Fox described and figured (1989:pl. 3, fig. 8) a lower molar (UALVP 3685) that he referred to *Alostera saskatchewanensis*. This tooth is almost identical in size and is similar in morphology to the M_1 of *Sorlestes budan* described earlier and illustrated in Figure 15F–J. Fox (1989) noted that the hypoconulid was equidistant from the entoconid and hypoconid. The tip of the hypoconulid is broken, however, so that it is difficult to say whether or not there would have been some slight twinning of hypoconulid and entoconid. Another possibly significant way in which the M_1 of *A. saskatchewanensis* differs from that of *Sorlestes budan* is the presence of a slightly larger and more cusp-like paraconid in the former species. It may also be less appressed to

Fig. 19.—Dentary fragments of "zhelestids." A–C. CCMGE 23/12953, right edentulous dentary preserving alveoli for C_1–M_3 in occlusal (A), buccal (B), and lingual (C) views. D–F. CCMGE 15/12953, *Sorlestes budan*, left dentary preserving C_1, two roots of P_1, two alveoli each for P_{2-3}, and crown of P_4 (alveoli as marked in Figure 10). Scale = 5 mm.

Fig. 20.—Comparative occlusal views of the upper left dentitions of zhelestids (except for *Parazhelestes minor* and cf. *Eoungulatum kudukensis*, which are reversed from the right side). The bottom two dentitions preserve P^5–M^2, the middle two preserve P^5–M^3, and the uppermost is isolated P^5 and M^2. Diagonal lines indicate areas of dental attrition. Scale = 2 mm (see Table 3).

the metaconid in the former species. However, because the metaconid is missing in UALVP 3685, this cannot be properly assessed. Another lower molar (SMNH P1927.454) from the latest Cretaceous of Saskatchewan was referred to *A. saskatchewanensis* by Fox (1989), and was mentioned and figured by Storer (1991). Although similar in length to M_1s of *S. budan*, it is distinctly narrower. Finally, Fox (1989) noted that a dentary with a complete lower molar and part of a second that was the basis of the species *Paranyctoides megakeros* from the "Mesaverde" Formation (Judithian) of Wyoming (Lillegraven and McKenna, 1986) likely belongs to a species of *Alostera*.

Avitotherium utahensis (Fig. 22G) is from the mid-Campanian (Judithian) Kaiparowits Formation of south-central Utah (Cifelli, 1990). Cifelli (1990) noted its similarities to both *Paranyctoides* and *Alostera*. Especially of relevance here is his statement (1990:357) that *Avitotherium* resembles *Alostera* in the "reduction of labial shearing structures, with concomitant development of crushing and grinding wear patterns (also seen in *Purgatorius* and *Protungulatum*)." We agree with this as well as his other assessments of *Avitotherium*, but note that (although from separate continents and separated by as much as 10 million years) *Avitotherium* and *Aspanlestes aptap* show even greater similarities (both primitive retentions and apomorphies), including two cuspules in the parastylar region. Comparing the types of *A. utahensis* (MNA V4650; Cifelli, 1990:fig. 6A, B) and *A. aptap* (CCMGE 1/12455, Fig. 7A), the only differences are a slightly smaller size, slightly more lingually placed protocone, and a closer approximation in size for the paracone and metacone in *A. utahensis*. Even the slightly more lingual placement of the protocone is duplicated in other upper molars we refer to *A. aptap*. These taxa may eventually be synonymized at least at the generic level, but given the fragmentary nature of the material we avoid such a step at this time.

Cifelli (1990:fig. 6) also figured a lower molar (M_1 or M_2, OMNH 20424) and a lower premolar in a dentary fragment (P_3, OMNH 20532), both of which he assigned to *Avitotherium utahensis*. The M_x is very close in length to both M_1s and M_2s

referred to *Aspanlestes aptap*. With its slightly larger and slightly more labially placed paraconid, the trigonid of M_x referred to *A. utahensis* resembles the trigonid of M_2s more than the trigonid of M_1s assigned to *A. aptap*. The widths of both the trigonid and talonid of M_x are closer to the comparable widths seen in M_1s referred to *A aptap*. The two greatest differences between the M_x of *A. utahensis* and M_1s or M_2s of *A. aptap* are a noticeably shorter talonid and an apparent lack of twinning of the entoconid and hypoconulid on the M_x of *A. utahensis*. P_3 in the dentary fragment referred to *A. utahensis* by Cifelli (1990) appears to have been larger than the fragmentary tooth preceding it in the dentary, identified as P_2 by Cifelli (1990). No complete P_3s of any "zhelestids" are known, but what evidence is available strongly argues that this two-rooted tooth is smaller than P_2. It is possible that the tooth identified as P_3 in Asian "zhelestids" has been lost in *A. utahensis*, and thus the tooth identified as P_3 in *A. utahensis* is homologous with the tooth identified as P_4 in Asian "zhelestids." Even if this highly speculative homology is correct, the premolar of *A. utahensis* has a more basined talonid (with two cusps) compared to a more trenchant talonid on P_4 of *A. aptap*. Further, the premolar of *A. utahensis* has no suggestion of a metaconid, while the P_4 of *A. aptap* has a swelling in this region (Fig. 7).

An upper molar, either M^1 or M^2, figured and briefly described as cf. *Paranyctoides* by Montellano (1992) from the middle Campanian (Judithian) Judith River Formation of north-central Montana is referable to *Avitotherium*, or possibly even *Aspanlestes*. Except for being 0.1 mm longer, this tooth is within the size range of M^1 of *Aspanlestes*, but is slightly larger than upper molars of *Avitotherium*. Based on Montellano's drawing of the specimen (1992:fig. 29), it differs from M^1s of *Aspanlestes* only in having a slightly anteroposteriorly wider protocone, a possibly narrower postcingulum (unless it is broken), and more widely spaced preparastyle and parastyle.

Gallolestes pachymandibularis Lillegraven, 1976 is based on three dentary fragments and two isolated molars collected from the "El Gallo Formation" in the state of Baja California del Norte, Mexico. The teeth known in the type specimen (LACM 42633) have been identified tentatively as P_{3-4} and M_{1-3}. Other material confirms the relative positions of these teeth. The tentative nature of the identification centers on the tooth identified as P_4. The complete trigonid is molariform with three cusps,

Fig. 21.—Posterior outlines of relatively unworn M^1s and M^2s of *Aspanlestes aptap* (*Aa*), *Eoungulatum kudukensis* (*Ek*), *Parazhelestes robustus* (*Pr*), and *Parazhelestes minor* (*Pm*). All molars shown as if from left side. Width is standardized so that the lingual margin and the outline of the metacone are approximated on all the molars. Arrows delimit the three states (different line patterns) in the labial shift of protocone (Table 3, character 2).

and although the talonid is mostly missing, what remains suggests a basined structure as seen on molars (Lillegraven, 1976). Lillegraven (1976) reviewed most if not all the likely possibilities, appearing to favor the interpretation that the tooth is a molariform P_4 in a eutherian insectivore, unlike known Cenozoic taxa. Clemens (1980) followed Lillegraven's assignations of teeth, but concluded that *Gallolestes* was not clearly a eutherian or metatherian, but was probably a separate derivative of a metatherian–eutherian grade mammal. Butler (1977, 1990) argued that the tooth in question is a "molariform milk-molar." This seems reasonable especially because the tooth is more heavily worn than the succeeding three "molars." As Clemens (1980) pointed out, retention of the last deciduous premolar until the M_3 is erupted is quite unusual. Butler (1990) responded that a specimen of *Barunlestes* retains the last two deciduous premolars (with an unerupted permanent premolar below the last deciduous premolar) although the M_3 is erupted. This seems the most plausible explanation. Perhaps Late Cretaceous eutherians in general retained their deciduous premolars longer.

Given this interpretation of "P_4" as a deciduous

P_4 in *Gallolestes pachymandibularis*, the remainder of the dentition looks remarkably like that of a "zhelestid," hence our assignment of this taxon to this group. Expanding on Lillegraven (1976), Clemens (1980) listed a number of characters of *Gallolestes* that he regarded as apomorphies relative to other Late Cretaceous eutherians, but which are also shared with zalambdalestids: 1) trigonid of last premolar molariform; 2) paraconid on molars slightly labial, close to metaconid, and trigonid canted anteriorly; 3) molar talonids broad; 4) hypoconulid and entoconid approximated; 5) M_3 hypoconulid nearly medial and salient; and 6) trigonid of M_3 narrower than talonid of M_2. The P_5 in "zhelestids" is not quite as molariform as the possibly comparable "P_4" in *Gallolestes* but, as noted in the previous paragraph, we regard this tooth in *Gallolestes* as deciduous P_4.

A second species of *Gallolestes*, *G. agujaensis*, was named by Cifelli (1994) based on six lower molars and molar fragments, and three upper molar fragments from the Judithian Terlingua local fauna, Big Bend area, Texas. Cifelli (1994) indicated that *G. agujaensis* is 40% smaller, has more delicately constructed molar cusps, and has more vertically developed shearing surfaces than *G. pachymandibularis*. Otherwise, *G. agujaensis* is similar to *G. pachymandibularis*. If correctly assigned, the upper molar fragments that he includes are the first known uppers for a species of *Gallolestes*. As noted by Cifelli (1994), the two lingual fragments of M^1 or M^2 possess pre- and postcingula, although a distinct hypocone is not present on either. He did not comment on the presence or absence of conular wings; further, this area is not well preserved on the specimen figured by Cifelli (1994:fig. 9F). The labial part of the M^3 he referred to *G. agujaensis* (Cifelli, 1994:fig. 9G) cannot be compared easily with the two worn M^3s known for Asian "zhelestids," although what can be seen does not argue against "zhelestid" affinities. Too little is known to provide further comparisons of the upper molars in these taxa.

The following characters found in both species of *Gallolestes* appear to be derived for "zhelestids" (including *Gallolestes*) relative to zalambdalestids: lower trigonid relative to talonid, overall lower crown height, relatively larger talonid basin, and possibly greater hypoconulid–entoconid twinning. Relative to zalambdalestids, *G. pachymandibularis* also has a greater robustness of the dentary (dentary unknown for *G. agujaensis*) and is larger. *Gallolestes* and "zhelestids" also retain two characters that appear to be primitive relative to conditions in zalambdalestids. These are less anteroposterior compression of the trigonid and less size reduction of M_3 relative to M_2.

?UNGULATOMORPHA: A QUESTIONABLE NORTH AMERICAN "ZHELESTID"

Emry et al. (1981) described a fragmentary molar preserving the labial half of the trigonid and the complete talonid from the upper Santonian Eutaw Formation in the vicinity of Vinton Bluff, Mississippi, U.S.A. The authors argued that, based on what could be determined, the specimen resembled the archaic ungulate *Protungulatum* to a greater extent than either *Gallolestes* or *Purgatorius*. The trigonid is low relative to the talonid, the talonid is quite broad, the entoconid and hypoconulid are somewhat approximated, and the tooth is mildly bulbous. The tooth is only slightly larger than M_2s we assign to cf. *Eoungulatum kudukensis*. This tooth is probably a "zhelestid."

EUROPEAN "ZHELESTIDS"

Gheerbrant and Astibia (1994) named *Lainodon orueetxebarriai* from the Maastrichtian locality of Laño in the Basque region, Spain. They compared it with *Labes quintanillensis* Sigé (*in* Pol et al., 1992) from the Maastrichtian locality of Quintanilla del Coco in northern Spain and *Labes garimondi* Sigé (*in* Pol et al., 1992) from the Campanian locality of Champ-Garimond near the village of Fons in southern France. *Lainodon orueetxebarriai* is based on two possible M_1s, one possible M_2, a P_2 or P_3, and two molar talonids (Gheerbrant and Astibia, 1994; Gheerbrant, personal communication). *Labes quintanillensis* is based on a left lower molar, identified as M_3, and a fragment of the lingual portion of M_x. *Labes garimondi* is based on two lower molars, one of which had been referred to as the "Champ-Garimond tooth" (Ledoux et al., 1966) prior to its formal systematic description, and the second of which was reported and figured by Pol et al. (1992) at the time *Labes garimondi* was named.

In their discussion of these three taxa from Spain and France, Gheerbrant and Astibia (1994) con-

Fig. 22.—Occlusal views of M^1s or M^2s (all shown as if from left side). A. *Kennalestes gobiensis* M^2. B. *Gypsonictops illuminatus* M^2. C. *Purgatorius unio* M^2. D. *Tribosphenomys minutus* M^1. E. *Paranyctoides* sp., cf. *P. maleficus* M^1 or M^2. F. *Aspanlestes aptap* M^2. G. *Avitotherium utahensis* M^1 or M^2. H. *Alostera saskatchewanensis* M^1. I. *Eoungulatum kudukensis* M^2. J. *Protungulatum donnae* M^2. Molars drawn at same width. Scales (horizontal lines) = 1 mm. Sketches are after figures from the following sources, supplemented by casts or specimens: A–C, J (Kielan-Jaworowska et al., 1979); D (Meng et al., 1994); E (Montellano, 1992); G (Cifelli, 1990); and H (Fox, 1989). Note the following character states: ectoflexus (bracket) ranges from deep to shallow (e.g., A vs. D, respectively); postmetacrista continuous with metastylar area so that metacingulum is formed only by the postmetaconule crista (thick black line) or metacingulum formed by postmetaconular crista continuing onto metastylar region (thick gray line) (e.g., F vs. J, respectively); degree of waisting of molar occlusal outline (thick, diagonally hatched lines) ranges from very waisted to only slightly or not waisted (e.g., A vs. I, respectively); internal conular cristae (arrows) are pronounced to weak or absent (F vs. J, respectively) (see Table 3).

cluded that they appear to form a suprageneric group showing affinities with the mixotheridians ("zhelestids" as used here), as characterized by Nessov (1985*a*). Although Gheerbrant and Astibia (1994) entertained several phylogenetic hypotheses for these European Cretaceous eutherians, such as derivation from North American *Gypsonictops* or a sister group relationship to zalambdalestids, their favored hypothesis advocated a close relationship with "zhelestids," essentially in the sense we use the group here. Earlier, Butler (1990) thought that the "Champ-Garimond tooth," now *Labes garimondi*, was probably a first molar similar to *Gallolestes* and his "group d," which, along with several other taxa, includes what we call "zhelestids." Sigé (*in* Pol et al., 1992) argued that *Labes* has closer phylogenetic affinity to archaic ungulates ("condylarths") than does North American *Protungulatum donnae*. Although *P. donnae* may be more advanced in some characters than taxa such as the similarly aged North American *Oxyprimus* sp., (e.g., *P. donnae* has more bulbous teeth, has a larger and more lingual paraconid, has little or no metaconid on the ultimate premolar; see Luo, 1991), there is no doubt that it is an archaic ungulate showing closer affinities to other ungulates than does *Labes*.

The three European taxa are very similar to "zhelestids," notably in having an expanded talonid and greater tendency for bunodonty. Gheerbrant and Astibia (1994) noted that *Lainodon* and *Labes* differ from "zhelestids" in having: more massive cusps, less difference in trigonid and talonid height (the trigonid is lower), the paraconid transversely reduced, the precingulid large and high on the trigonid contacting the midpoint of the paracristid, the labial surface of the protoconid with a slightly concave profile, the postcingulid absent, and noticeably less overhang (exodaenodonty) of the lower labial margin of the molar crown. In comparing casts and/or specimens of *Lainodon*, *Labes*, and Asian "zhelestids," E. Gheerbrant and D. Archibald observed that *Lainodon* and *Labes* differ from Asian "zhelestids" in having a more lingual placement of the paraconid, which aligns this cusp and the metaconid, and in having the paraconid and metaconid more rounded than transversely elongate in occlusal view. The possible phylogenetic significance of these differences are under study by E. Gheerbrant, but they suggest that *Lainodon* and *Labes* form a clade, either within "Zhelestidae" or as a very close sister clade.

TAXA REMOVED FROM "ZHELESTIDAE"

Wang (1995) described a new middle Paleocene mammal, *Wania chowi*, from the Qianshan Basin, Anhui Province, China, which he referred to Mixotheridia, Zhelestidae. The taxon was based on dentaries and maxillary fragments of the same individual. The upper molars do show some similarities to taxa here assigned to "Zhelestidae," such as narrowing of the stylar shelf, increase in the linguolabial dimension of upper molars, and reduction of M^3 and M_3 (*Parazhelestes robustus* and *Kumsuperus avus*). Aside from the reduction of M^3 and M_3, which is not found in all "zhelestids," the other two resemblances are widespread in Late Cretaceous and early Tertiary mammals. Thus, we see no basis to suggest that *W. chowi* is a "zhelestid." This taxon does, however, bear some resemblance to anagalidans, and it is to this group that *W. chowi* may be related. The second author (J.D.A.) was kindly shown the specimens of *Wania chowi* by its describer, Wang Yuanqing. This brief examination confirmed our earlier assessment that *Wania chowi* is not a "zhelestid."

As recently as 1994 Nessov retained *Taslestes inobservabilis* in "Zhelestidae" with reservations (Nessov et al., 1994). As noted earlier in this paper, we remove *T. inobservabilis* from "Zhelestidae." At the time of his death, the first author (L.A.N.) was working on manuscripts dealing with the non-"zhelestid" therians from southwestern Asia, including Uzbekistan. This unpublished work included more complete argumentation for the removal of *T. inobservabilis* from "Zhelestidae." The second and third authors have not seen these manuscripts; thus, the following comments, although probably agreeing with Nessov's unpublished assessments, are ours alone.

Taslestes inobservabilis is based on a right dentary preserving M_2 and alveoli for M_1 and M_3 from the lower part of the Bissekty Formation (locality CDZH-17b) at Dzharakuduk, the general area from which most "zhelestids" have been recovered. The M_2 of *T. inobservabilis* is only about 60% of the size of M_2 in the smallest Asian "zhelestid," *Aspanlestes aptap*. In proportions of the crown the two species are similar, except that the greatest width of the M_2 (especially on the talonid) of *T. inobservabilis* is at the base of the crown, while the occlusal surface of the M_2 of *A. aptap* is relatively more

Fig. 23.—Upper molars of a generalized "zhelestid" (above) and an archaic ungulate (below) in posterior view. In "zhelestids" and Late Cretaceous eutherians, the postmetaconule crista forms the metacingulum (arrow), while in ungulates the metacingulum is formed by the postmetaconule crista continuing onto the metastylar lobe (arrows) (see Table 3, character 4).

expanded. Further, the paraconid is larger and less appressed to the metaconid on the M_2 of *T. inobservabilis* than is the case in *A. aptap*. The degree of entoconid/hypoconulid twinning is comparable in both species. Although these differences are relatively minor, they are sufficient to exclude *T. inobservabilis* from "Zhelestidae" at the present time. A partial skull with lower jaws recovered at locality CBI-5a at Dzharakuduk may be congeneric or conspecific with *T. inobservabilis*, and thus may provide more answers about the affinities of this taxon.

(Grandorder) Ungulata Linnaeus, 1766

Included Taxa.—The paraphyletic assemblage "Condylarthra" that is here informally termed archaic ungulates (Archibald, in press), the South American native ungulates listed by Cifelli (1993, i.e., Litopterna, Astrapotheria, Notoungulata, Pyrotheria, and Xenungulata), Desmostylia, Embrithopoda, Artiodactyla, Cetacea, Hyracoidea, Perissodactyla, Proboscidea, Sirenia, and questionably Tubulidentata. Following Lucas (1993), taxa explicitly excluded from Ungulata (sensu stricto) are Pantodonta, Tillodontia, and Dinocerata.

Distribution.—See distribution under Ungulatomorpha.

Definition.—All ungulates sharing a more recent common ancestor with each other than with any other eutherians. This is a node-based phylogenetic definition following the protocol suggested by de Queiroz and Gauthier (1990).

Diagnosis.—In addition to character states shared with other Ungulatomorpha ("zhelestids"), taxa referable to Ungulata (at least the earlier occurring taxa) have the following synapomorphies that also are seen (presumably convergently) in earliest primatomorphs (i.e., *Purgatorius*) and some later (but not earliest) anagalidans (e.g., the early rodent *Tribosphenomys*): molar conules with little or no internal wings; parastylar region reduced and with one cusp (a reversal, also found in the "zhelestid" *Alostera*); premolars four or fewer in number (although sirenians have five upper premolars, a reversal); parastylar groove (and lobe) reduced (also found in *Alostera*); metacingulum formed by postmetaconular crista continuing onto the metastylar region (also found in *Alostera*, but not earliest primatomorphs, i.e., *Purgatorius*). Differs from earliest primatomorphs (i.e., *Purgatorius*), some later (but not earliest) anagalidans (e.g., the early rodent *Tribosphenomys*), and from "Zhelestidae" in having upper molars rectangular in occlusal view, upper molar conules closer to protocone than to the midpoint of the tooth, mandibular condyle dorsal to the occlusal surface of the tooth row.

Discussion.—Some other autapomorphies suggested for Ungulata by Prothero (1993) are: more bunodont, lower-crowned teeth; molar trigonids anteroposteriorly shortened; M_3 with a large, posteriorly projecting hypoconulid; and astragalus with a shorter, robust head. Of these character states, the first two are found in all ungulatomorphs, the second is hinted at on the M_3 tentatively referred to *Eoungulatum kudukensis* (Fig. 13), and the fourth was not evaluated by us. Prothero (1993) also listed additional autapomorphies known with confidence only in living ungulates.

Many of the above-listed apomorphies of Ungulata are subsequently transformed or reversed within the tremendous taxonomic and ecologic radiation of ungulates. Thus, we feel that comparisons are justifiably limited to earliest Tertiary ungulates. We examined casts or specimens of most earliest Paleocene North America ungulates and found that the above character states are consistently present with the exception of some upper molars of *Mimatuta*

minuial. In PU 14211, cast of *M. minuial* figured by Van Valen (1978:pl. 7, fig. 4), the M^2 does not have a strong metacingulum formed by the postmetaconular crista continuing onto the metastylar region. Rather, as in "zhelestids" there is a moderate metacingulum formed only by the postmetaconular crista, while the metacrista runs from the apex of the metacone to the metastyle. We regard this as the primitive condition. On M^1 and M^3, however, the derived condition is found, in which the metacingulum is formed by the postmetaconular crista continuing onto the metastylar region. On the same cast, distinct postparaconule and premetaconule cristae are present. These cristae are only weakly developed compared to the much more prominent (and we believe, more primitive) wing-like cristae found in the western Asian Cretaceous ungulatomorphs.

The last apomorphy in the above diagnosis is the position of the mandibular condyle. As discussed earlier, a dentary assigned to *Sorlestes budan* preserves the mandibular condyle and is tentatively identified as a "zhelestid." If this is correct, "zhelestids" retain the primitive condition of having the inferior margin of the condyle at or near the level of the alveoli. The well-preserved dentary of *Sorlestes kara* from Kazakstan described by Nessov (1993:pl. 1) possesses a mandibular condyle at or only slightly higher than that of *Sorlestes budan* (Fig. 17A, B). When this position of the condyle is compared to that in earliest Tertiary ungulates (Archibald, 1996*b*:fig.4C, D), it is clear that, even in the earliest known archaic ungulates such as *Protungulatum donnae*, the mandibular condyle has shifted dorsally to a level above the occlusal surface of the tooth row.

This shift to a more dorsally placed mandibular condyle is correlated with herbivory, in which there is an increased emphasis on the masseter and pterygoid musculature and a concomitant reduction in the importance of the temporalis musculature (Janis, 1995). This dorsal shift of the condyle also results in the development of a simultaneous rather than sequential occlusion of the teeth (as seen in many modern carnivores), although the masticatory process can be considerably more complex (Greaves, 1995).

PHYLOGENETIC ANALYSIS OF UNGULATOMORPHA

Ungulate monophyly has been open to question, but studies using fossil or living taxa, or both, and various anatomical and macromolecular approaches suggest that at least six orders of living ungulate eutherians may form a monophyletic grouping (Novacek, 1992; Prothero, 1993). These are Artiodactyla, Cetacea, Hyracoidea, Perissodactyla, Proboscidea, and Sirenia. Interrelationships among these orders are still debated (e.g., see various articles in Szalay et al., 1993). Various extinct groups of eutherians are assigned to Ungulata, in part based on their resemblances to extinct archaic ungulates ("condylarths") and in part based on their possession of characters that are thought to be typical of ungulates (e.g., reduction of lateral digits, elongation of limbs, dental modifications towards herbivory). None of these approaches has proven especially strong, although several recent studies have argued for similar higher-level relationships among supposed extinct as well as extant ungulates (Prothero et al., 1988; Prothero, 1993; Archibald, in press), including archaic ungulates.

The major problem of diagnosing Ungulata, at least on anatomical characters, is that there is a tremendous amount of variation among extinct and extant orders, arguably more so than among any other hypothesized superordinal grouping of mammals. Archaic ungulates retain so many characters primitive for eutherians and lack so many of the characters found in later ungulate orders that the monophyly of Ungulata, including archaic ungulates is difficult to test. This means that the defining characters of Ungulata are essentially the same as those uniting archaic ungulates relative to other contemporary eutherians. The discovery by the first author of new ungulatomorphs (the "zhelestids") from the Late Cretaceous of western Asia, and their recognition in the Late Cretaceous of North America (Nessov, 1993), helps to clarify characters seen in earliest Paleocene archaic ungulates in North America and permits a more testable hypothesis of ungulate monophyly.

Figure 24 is the result of a phylogenetic analysis of ungulatomorphs ("zhelestids" and Ungulata) for which the upper dentition is known. *Protungulatum donnae* is used as an exemplar for Ungulata. We believe that it shows the primitive character states for Ungulata for most if not all of the characters that we examined. As noted in the discussion of the analysis in Figure 24, *Oxyprimus ericksoni* may be somewhat more primitive for some character states

Fig. 24.—A. Strict consensus tree for all "zhelestids" and other Late Cretaceous mammals for which the upper dentition is reasonably known. B. Strict consensus tree for all taxa considered in A, plus the archaic ungulate *Protungulatum donnae*. Circled numbers in B refer to nodes discussed in text. In both analyses all taxa except the hypothetical ancestor were treated as a single polytomy. Tree length, consistency index (CI), homoplasy index (HI), retention index (RI), and rescaled consistency index (RC) shown in the lower right part of A and B are taken from the PAUP analysis for the number of trees (as indicated) with equal length. Tree lengths in the lower middle parts of A and B are from MacClade. In some cases (but not this one), tree lengths vary from PAUP to MacClade because PAUP treats polytomies as hard or as real polytomous speciations, while MacClade treats polytomies as uncertainties.

than is *Protungulatum donnae* (Luo, 1991), but choosing either of these taxa in the analysis does not affect the outcome.

Although the lower dentition was also examined, problems in differentiating taxa using lower dentitions and in assigning upper and lower dentitions to the same species precluded the effective use of lower dentitions in this analysis. Lower dental charac-

Table 3.—*Characters and character states of the upper dentition in a hypothetical ancestor, Late Cretaceous eutherians, the primatomorph* Purgatorius, *the rodent* Tribosphenomys, *and ungulatomorphs ("zhelestids" plus Ungulata, represented by* Protungulatum donnae*). Primitive or ancestral state = 0. derived states = 1–3. See Figures 20–23.*

1) Degree of anteroposterior expansion of protocone: none (0); slight (1); moderate (2); substantial (3).
2) Degree of labial shift of protocone: none (0); moderate (1); substantial (2).
3) Postparaconular and premetaconular cristae: strong and wing-like (0); weak or absent (1).
4) Metacingulum: formed only by the postmetaconule crista and terminates dorsal to postmetacrista, which is continuous with the metastylar lobe (0); formed by the postmetaconule crista continuing onto the metastylar lobe (1).
5) Stylar shelf: wide (0); narrow (1).
6) Number of cuspules in parastylar region: one (0); two (1).
7) Pre- and postcingula: absent or poorly developed (0); present but do not reach or extend below the conules (1); present and reach or extend below the conules (2).
8) Height and size of paracone and metacone: paracone higher and larger (0); cusps of similar height and size (1).
9) Metacone or metaconal swelling on P^5 (or ultimate upper premolar): absent (0); present (1).
10) Number of premolars: five (0); four or fewer (1).
11) Shape of molar crown in occlusal view: triangular (0); trapezoidal (1); subrectangular (2); rectangular (3).
12) Constriction of crown through conular region with or without cingula present: no constriction, no cingula (0); marked constriction with cingula (1); slight constriction with cingula (2); no constriction with cingula (3).
13) Ectoflexus: deep (0); shallow (1); none (2).
14) M^3 linguolabial width relative to other molars: not markedly narrowed (0); markedly narrowed (1).
15) Parastylar groove: well developed (0); very reduced or absent (1).
16) Base of paracone and metacone: merged (0); separate (1).
17) Distance between paracone or metacone and protocone relative to total anterior or posterior width, respectively: between 45–55% of crown width (0); more than 55% of crown width (1); less than 45% of crown width (2).
18) Position of conules (especially paraconule) relative to paracone and metacone versus protocone: conules closer to midposition (0); conules closer to protocone than to the midposition (1).

ters are noted when they might provide further information about relationships. Characters and character states are described in Table 3; a taxon–character matrix is provided in Table 4.

In the two analyses shown in Figure 24, we chose to use as outgroups all demonstrably Late Cretaceous eutherians for which enough of the upper dentition is known to allow the coding of most of the 18 characters. One taxon not included in this analysis is *Kulbeckia* (Nessov, 1993), because at the time that the phylogenetic analysis was performed, specimens were not available for comparions. For the two analyses in Figure 25, which we discuss at the end of this section, we also added the upper dentitions of the earliest known primatomorph, *Purgatorius unio*, and one of the better known early rodents, *Tribosphenomys minutus*. *Purgatorius unio* and *Tribosphenomys minutus* were included in this second set of analyses because their orders often have been placed in the grandorders Archonta and Anagalida respectively, which in turn have been linked to the grandorder Ungulata (McKenna, 1992; MacPhee and Novacek, 1993; Salles, 1995). These two species were chosen only as exemplars. They cannot be assumed to be primitive for all characters for their order or grandorder. Some of these issues are further discussed in the review of the analysis that follows.

We feel confident in assigning the primitive states for the 18 characters in the most recent common ancestor of all the taxa used in the analysis. This is based on the very wide distribution of these presumed primitive character states in Early Cretaceous eutherians, metatherian–eutherian grade mammals, and marsupials, as well as the outgroup taxa used in the analysis. These primitive states were assigned to the hypothetical ancestor given in Table 4 and shown in Figure 24. This was done in order to assess polarity for as many of the characters as possible that were used in the analysis. We could have also used the two-step analysis of Maddison et al. (1984) to help assess polarity of characters. The problem, however, is in choosing which of the 12 outgroups in Table 4 we believe is the sister taxon to ungulatomorphs. The arguments for such a choice are difficult to defend. We feel that running all outgroup and ingroup taxa as a single polytomy (unrooted tree) with one hypothetical ancestor was the more conservative and more justifiable approach given the present limited state of our knowledge. Further, using this approach, we feel justified in concluding that results are more robust because we have not limited potential sister-taxon relationships and we have not assumed monophyly of the ungulatomorphs. This is similar if not identical to the one-step method of Maddison et al. (1984).

Table 4.—*Character matrix for characters and states described in Table 3. Queried states (0?) were run using the state shown. Multistate characters were run as unordered. When more than one state occurs in a given taxon (0, 1), the state was run as polymorphic.*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Outgroups (all Late Cretaceous eutherians represented by upper teeth)																		
Asiorycetes nemegetensis	0	0	1**	0	0	0	1	0	?	1	0	0	0	0	0	0	0	0
Batodon tenuis	0	0	0	0	0	0	1	0	0	1	0	1	1	?	0	0	0	0
Barunlestes butleri	0	0	1	0	1?	0?	0	0	0	1[a]	0	0	0, 1	1	0	0	0	0
Cimolestes spp.	0	0	0	0	0	0	0, 1	0	0	1	0	0, 1	0, 1	0	0	0	0	0
Gypsonictops spp.	0	0	0	0	1	0	1	0?	1	0, 1	0	1	0, 1	0	0	0	0	0
Kennalestes gobiensis	0	0	0	0	0	1	1	0	0, 1	0, 1	0	1, 2	0	0	0	0	0	0
Paranyctoides maleficus	1, 2	0	0	0	0	0	1	1	0	?	1	1, 2	0	0	0	1	0	0
Otlestes meiman	0	0	0, 1	0	0	0?	0	0	?	0	0	0	0	0?	0	1	0	0
Sailestes quadrans	1	0	0	0	0	1	1	0?	?	?	0	2	1	?	0	1	1	0
Zalambdalestes lechei	0	0	1?	0	0, 1	0	0	0	1?	1	0	0	0	1	0	1	0	0
Outgroups (possible other zhelestid relatives with modern descendants, including ungulates)																		
Purgatorius unio	1	0	1**	0	1	0	2	1	1	1	3[c]	1	1	0?	1	1	0	0
Tribosphenomys minutus	1	1	1	1	1	0	2	1	?[d]	1?	1	3	2	0?	1	1	2	0
Protungulatum donnae	3	2	1	1	1	0	2	1	0, 1	1[b]	3	3	1, 2	0	1	1	2	1
Ingroup (presumptive zhelestids)																		
Alostera saskatchewanensis	1	0	0	1	1	0	2	1	1	?	1	2	2	?	1	1	1	0
Avitotherium utahensis	1	0	0	0	1	1	1, 2	1	1	?	1	2	0, 1	?	0	1	1	0
Aspanlestes aptap	1	0	0	0	1	1	2	1	1	0?	1	2	0, 1	0	0	1	0	0
Zhelestes temirkazyk	1	0?	0	0	1	1	2?	1?	1	0	1	3	1	0	0	1?	2?	0
Parazhelestes robustus	2	1	0	0	1	1	2	1	1	0?	1	3	1	1	0	1	2	0[e]
Parazhelestes minor	1, 2	1	0	0	1	1	2	1	0, 1	0?	1	2	1	?	0	1	2	0
Eoungulatum kudukensis	3	2	0	0	1	1	2	1?	1?	?	2	3	2	?	0	1	2	0

* Data for "outgroups" was obtained from casts, specimens, and the following sources: Lillegraven (1969), Kielan-Jaworowska (1975, 1981), Kielan-Jaworowska et al. (1979), Fox (1984, 1989), Cifelli (1990), Nessov et al. (1994), and Meng et al. (1994).

** Metaconule reduced.

[a] Premolars reduced to three.

[b] Although *P. donnae* is derived in having only four premolars, some ungulates such as sirenians have five upper premolars.

[c] The shape is actually more hourglass than rectangular because the hypoconal region is appended to the posterior part of the molar rather than forming a more integrated part of the crown as in most Ungulata. Thus, homology of the character in these two taxa is doubtful.

[d] The ultimate premolars described and figured by Meng et al. (1995) appear to be deciduous, and thus the condition of the permanent ultimate premolars remains unknown (Wyss, personal communication).

[e] Character state was incorrectly coded as "1" in Archibald (1996*b*).

Fig. 25.—Strict consensus trees for all "zhelestids" and other Late Cretaceous mammals for which the upper dentition is reasonably known, plus *Protungulatum donnae* (an archaic ungulate), *Purgatorius unio* (an early primtomorph), and *Tribosphenomys minutus* (an early rodent). In the analysis in A all taxa, except the hypothetical ancestor, were treated as a single polytomy. In the analysis in B, "zhelestids" plus *P. donnae* were constrained to be monophyletic, while all other taxa, except the hypothetical ancestor, were treated as a single polytomy. Tree length, consistency index (CI), homoplasy index (HI), retention index (RI), and rescaled consistency index (RC) shown at lower right are taken from the PAUP analysis for the number of trees with equal length as indicated. The alternative tree lengths shown at lower middle are from MacClade. In some cases, tree lengths vary from PAUP to MacClade because PAUP treats polytomies as "hard" or as real polytomous speciations, while MacClade treats polytomies as "soft" or as uncertainties, hence the lower tree lengths for MacClade.

The taxon–character matrix in Table 4 was created on MacClade 3.01 (Maddison and Maddison, 1992) and analyzed using PAUP 3.1.1 (Swofford, 1993). All multistate characters were treated as unordered in all analyses. Opinions vary on the efficacy of ordering, from those arguing against it (Hauser and Presch, 1991) to those arguing for it in some cases (Campbell and Frost, 1993). Although we do not have a strong opinion, we do feel that when well demarcated, biologically defensible transitions can be discerned that ordering is a reasonable approach. In the case of the present study, however, changes between taxa are generally small, forming a graded series. Thus, without more clearly demarcated changes, ordering seems unjustified for our study.

For the two analyses in Figure 24, we employed the branch-and-bound algorithm in PAUP and, as noted, ran the analysis starting with the hypothetical ancestor as the single outgroup, with all the remaining outgroup taxa and the ingroup taxa as a single polytomy. For the two analyses in Figure 25, we employed the heuristic search algorithm in PAUP. For the analysis in Figure 25A we started with all the outgroup and ingroup taxa as a single polytomy and the hypothetical ancestor as the single outgroup. For Figure 25B we started with all ungulatomorph taxa ("zhelestids" plus *Protungulatum donnae*) as a polytomy that was, in turn, monophyletic relative to the outgroup taxa. The outgroup taxa were run as a single polytomy and the hypothetical ancestor as the single outgroup.

The number of equally parsimonious trees, tree lengths, and measures (consistency index, homoplasy index, retention index, and rescaled consistency index) from each PAUP run are given in Figures 24 and 25. For the strict consensus trees we employed the "soft polytomy" option in MacClade, which assumes uncertainty at these polytomies, rather than the "hard polytomy" option in PAUP, which assumes multiple speciations. Thus, the tree lengths for the strict consensus trees generated from MacClade (shown in Fig. 25) are slightly lower than the tree lengths for the comparable PAUP run.

In the following discussion, characters and their states are identified by the same numbering system used in Tables 3 and 4. For example, the derived state of the stylar shelf (5) is narrow (1), and is referred to as [5.1], while the primitive wide shelf is [5.0]. Relevant nodes in Figures 24A and B are numbered and circled. These are the nodes to which we refer in the following discussion. The character state changes are the same at the similarly numbered nodes in Figures 24A and B unless indicated otherwise. As each node is discussed, it is noted whether an apomorphy is shared only at that node (unambiguous) or occurs among other taxa (see Table 4) in the analysis (ambiguous). Possible autapomorphies for each terminal taxon are also noted. Only those nodes and terminal taxa that directly include "zhelestids" and/or *Protungulatum donnae* are considered in the following discussion.

As noted earlier, there are no synapomorphies that unite "zhelestids" as a monophyletic taxon whenever ungulates such as *Protungulatum donnae* (Fig. 24B) are included in the analysis, but for convenience we use the term for this paraphyletic assemblage (with quotation marks). Some character states, such as the twinning of cusps on the talonid, appression of trigonid cusps, reduction of M^3 and M_3, and closeness of conules to paracone and metacone were first thought to be possible synapomorphies of the Asian "zhelestid" taxa. On further analysis, which is detailed below, some of these character states, such as reduction of M^3 and M_3, appear to be derived for only some species of "zhelestids." Other character states are more easily explained as transitions to later taxa, for example, twinning of cusps on the talonid and appression of trigonid cusps appear related to the expansion of the talonid and the "squaring" of the molar seen in later archaic ungulates.

Node 1 in Figure 24A unites the clade Zhelestidae as a monophyletic taxon, while in Figure 24B "Zhelestidae" is not monophyletic with the inclusion of *Protungulatum donnae* (an ungulate). However, a more inclusive clade containing "Zhelestidae" and *P. donnae* remains monophyletic in Figure 25B, and this assemblage ("zhelestids" + ungulates) was earlier named Ungulatomorpha (Archibald, 1996*b*). Ungulatomorpha in Figure 24B (and Zhelestidae in Figure 24A) share the following three apomorphies: stylar shelf narrow [5.1], pre- and postcingula reach or extend below conules [7.2], and metacone or metaconal swelling on ultimate upper premolar [9.1]. Among Late Cretaceous eutherians, narrowing of the stylar shelf [5.1] occurred at least two times (*Barunlestes* + *Zalambdalestes* and *Gypsonictops*) and a metacone or metaconal swelling [9.1] arose up to three other times (possibly *Kennalestes*, *Gypsonictops*, and *Zalambdalestes*).

In addition to these apomorphies of the upper dentition, the lower dentition (where known) of ungulatomorphs has four apomorphies and one possible apomorphy that were not included in the phy-

logenetic analysis. We regard the expansion of the talonid, twinning of the entoconid and hypoconulid, lowering of the trigonid height relative to the talonid, and slight appression (or anteroposterior shortening) of the trigonid cusps as ungulatomorph apomorphies. The expansion of the talonid is unarguably related to the expansion of the protocone in the upper molars. Luo (1991) noted, however, that the talonid on the M_1 of at least some early Tertiary ungulates such as *Protungulatum*, *Oxyprimus*, and *Mimatuta* is actually the smallest relative to the size of the trigonid as compared to at least four other Late Cretaceous and early Tertiary eutherians (*Cimolestes*, *Procerberus*, *Gypsonictops*, and *Purgatorius*). How widespread this relative size pattern for the talonid is, and whether it is primitive or derived for these early Tertiary ungulates, remains to be studied. The twinning of the entoconid and hypoconulid could be an autapomorphy that would argue for the monophyly of "Zhelestidae." It seems more likely that this twinning is also a result of the expansion of the protocone, caused as the hypoconid moved away from the other two talonid cusps, similar to the twinning that occurred in marsupials (Marshall and Kielan-Jaworowska, 1992). By the time the ungulate grade is reached, further expansion of the talonid basin has forced the entoconid and hypoconulid apart. Nessov (personal observation) felt, however, that he could detect some twinning of the entoconid and hypoconulid on some specimens of early Tertiary ungulates such as the M_2s of species of *Mimatuta* and *Ragnarok* (see various figures in Archibald, 1982; Lofgren, 1995). Appression of the trigonid cusps and lowering of the trigonid relative to the talonid are related to the early stages of the "squaring" of molars leading to herbivory. As with the metacone on the P^5 [9.1], the metaconid on P_5 probably evolved convergently in other Late Cretaceous eutherians.

At node 2, (Fig. 24A, B) all ungulatomorphs except *Aspanlestes* can be distinguished by the apomorphy of having the distance between the paracone or metacone and protocone relative to the anterior or posterior width, respectively, either more than 55% of the crown width [17.1] or less than 45% of the crown width [17.2]. *Aspanlestes* retains the primitive state [17.0] of having the distance between paracone or metacone and protocone relative to anterior or posterior width, respectively, at between 45% and 55%. This is the state found in all other Late Cretaceous eutherians examined except *Sailestes*, which exhibits the derived state [17.1]. This appears to be convergent with the "zhelestids" *Avitotherium* and *Alostera* that also have state 17.1, because the relatively greater distance between paracone and metacone and protocone in *Sailestes* is a result of the transverse narrowing of the entire crown.

At node 3, (Fig. 24A, B) all ungulatomorphs except *Aspanlestes* and *Avitotherium* can be distinguished by the apomorphy of having the ectoflexus either shallow [13.1] or absent [13.2]. Depth of the ectoflexus is a rather homoplastic character, having become at least somewhat shallow in a wide variety of other Late Cretaceous eutherians (*Barunlestes*, *Batodon*, *Cimolestes*, *Gypsonictops*, and *Sailestes*). Even in *Aspanlestes* and *Avitotherium*, there is some suggestion of shallowing.

Neither *Aspanlestes* nor *Avitotherium* possess any autapomorphies in either the upper or lower dentition that convincingly argue for their respective monophyly. Their character states are primitive retentions of other Late Cretaceous eutherians or all ungulatomorphs. These species are, however, distinctly smaller than all other "zhelestids," which is a questionable autapomorphy for these species.

At node 4, (Fig. 24A, B) all ungulatomorphs except *Aspanlestes*, *Avitotherium*, and *Alostera* possess the following two apomorphies: the crown is not constricted through the conular region and cingula are present [12.3] (except in *Parazhelestes minor*, which shows a presumed reversal to a slight constriction, but cingula are present [12.2]); and the distance between the paracone or metacone and protocone relative to the anterior or posterior width, respectively, is less than 45% of the crown width [17.2].

Alostera saskatchewanensis shows three autapomorphies that are convergent on ungulates such as *Protungulatum donnae*. These are: metacingulum formed by the postmetaconule crista continuing onto the metastylar lobe [4.1], number of cuspules on parastylar region is one [6.0], and parastylar groove absent [15.1]. If the lowers of *Alostera saskatchewanensis* are properly referred to this species (Fox, 1989; Storer, 1991), the probable loss of twinning of the entoconid and hypoconulid is another autapomorphy. This combination of character states suggests that *Alostera* could simply be an odd archaic ungulate, but the parsimony argument of our analysis suggests otherwise.

At node 5, (Fig. 24A, B) *Zhelestes*, *Parazhelestes robustus*, and *Parazhelestes minor* are united by the rather weak character of possessing a shallow ectoflexus [13.1], presumably reversed from having none [13.2]. An equally likely possibility is that the

ectoflexus became shallow [13.1] at node 4 (Fig. 24A, B) and then disappeared at least twice [13.2], once leading to *Alostera* and again on the stem leading to the *Eoungulatum* + Ungulata clade.

Zhelestes temirkazyk does not possess any clear autapomorphies arguing for its monophyly. Further, it is based on a single, heavily worn maxillary dentition. Assuming that it is a taxon separate from other "zhelestids," a possible autapomorphy is the relatively anteroposteriorly narrow crowns of M^{1-2}. This can be seen in a comparison of "zhelestid" upper molars in Figure 20, as well as the offset placement of this species in the graph of lengths versus widths in Figure 6. Only the M^2 of *Parazhelestes minor* shows a similar placement on these graphs (Fig. 6).

At node 6 (Fig. 24A, B), *Parazhelestes robustus* and *P. minor* are united by the following apomorphies: amount of anteroposterior expansion is slight to moderate [1.1/2] or moderate [1.2], amount of labial shift of the protocone is moderate [2.1]. These are rather weak potential synapomorphies, being minor intermediate states possibly within an evolutionary gradient. A potentially much better apomorphy uniting these two species is the linguolabial narrowness of M^3 [14.1]. Unfortunately, M^3 is unknown in *P. minor* and this character was therefore coded as missing [14.?] for this species.

Parazhelestes minor does not possess any clear autapomorphies. Its smaller size compared to *P. robustus* could be derived or ancestral. The relative anteroposterior narrowing of the crown of M^2, similar to the condition seen in *Zhelestes temirkazyk*, could be an autapomorphy. We retain *P. minor* as monophyletic, but realize that it could also be a metaspecies (i.e., a previously named portion of a polytomy for which positive evidence of monophyly or paraphyly is lacking, in this case at the species level where the included organisms lack any synapomorphies that would unite them; Archibald, 1994). In *Parazhelestes robustus*, the M^3 is distinctly narrowed lingually [14.1] (Fig. 11, 20). Because we do not have information on the size of M^3 in *P. minor*, we do not know whether the reduction of M^3 is characteristic of both species of *Parazhelestes*. For now, we treat this as a possible autapomorphy for *P. robustus*. We also do not know whether reduction of M^3 is shared with any other species of "zhelestid," although it is known that M^3 is not linguolabially narrowed [14.0] (Fig. 9, 20) in *Zhelestes temirkazyk* and *Aspanlestes aptap*. Some reduction of M^3 and M_3 may be characteristic of some or all "zhelestids," and, of course, occurs in other ungulate clades as well. The M_3 in *Kumsuperus avus* is similar in width to M_3 in the smaller *Aspanlestes aptap*, but is substantially narrower compared to that in the similarly sized *Sorlestes budan*. In *Eoungulatum kudukensis*, if M_3 is correctly associated with M_2 (both teeth are tentatively assigned), M_3 appears to be unreduced in this species. The possible importance of M^3 and M_3 reduction in "zhelestids" awaits the recovery of additional specimens.

In Figure 24A *Eoungulatum kudukensis* has the following three autapomorphies: amount of anteroposterior expansion of the protocone is substantial [1.3], amount of labial shift of the protocone is substantial [2.2], and shape of the molar crown is subrectangular [11.2].

At node 7 in Figure 24B, when Ungulata (as represented by *Protungulatum donnae*) is added to the analysis, all three of these character states unite *E. kudukensis* and Ungulata (as represented by *P. donnae*). The shape of the molar crown is further modified in *P. donnae* by becoming rectangular [11.3].

Finally, the phylogenetic analysis in Figure 24B argues strongly for the monophyly of (grandorder) Ungulata (as represented here by *Protungulatum donnae*). The following seven states are interpreted as derived relative to all other members of Ungulatomorpha (i.e., "Zhelestidae"): molar conules with little or no internal wings [3.1]; metacingulum formed by postmetaconular crista continuing onto the metastylar region [4.1]; parastylar region reduced with one cusp [6.0 reversal]; premolars four or fewer in number [10.1], although sirenians have five upper premolars (Gingerich et al., 1994), which we regard as a reversal; upper molars rectangular in occlusal view [11.3]; parastylar groove (and lobe) reduced [15.1]; and conules closer to the protocone than to the midposition of the crown [18.1]. Of these, only two, [11.3] and [18.1], are unique to Ungulata as compared to the other taxa used in this analysis.

For the analyses shown in Figures 25A and B we added the earliest known primatomorph *Purgatorius unio* and the early rodent *Tribosphenomys minutus*. The overall pattern was similar to that in Figure 25A, other than the addition of these two taxa, described above (Fig. 24A, B). In Figure 25B the one difference was that the analysis started by holding all ungulatomorph taxa as a monophyletic polytomy.

Unsurprisingly, in the analysis shown in Figure 25A, Ungulatomorpha was rendered nonmonophyletic. *Purgatorius*, *Tribosphenomys*, *Protun-*

gulatum, and *Alostera* were united by three character states: conular wings weak or absent [3.1], reduction of premolars from five to four or fewer [10.1], and parastylar groove (and parastylar lobe) reduced or absent [15.1]. The possible clustering of the grandorders Archonta (including *Purgatorius*), Anagalida (including *Tribosphenomys*), and Ungulata (including *Protungulatum* and *Alostera*) is suggested by various authors (McKenna, 1992; MacPhee and Novacek, 1993; Salles, 1995). Of the three character states uniting the above taxa, the first and second are also found in a variety of other Late Cretaceous eutherians. These include *Zalambdalestes* and *Barunlestes*, which are sometimes placed together with a variety of other eutherians, including rodents, within Anagalida (Stucky and McKenna, 1993). If this alignment is true, the above character states are convergent in at least rodents and ungulates.

There is nothing that we currently know about the dentition of "zhelestids" that would preclude them from giving rise to rodents such as *Tribosphenomys minutus*. There is, however, nothing that especially links "zhelestids" and anagalidans, the more inclusive taxon to which rodents such as *T. minutus* may belong. Further, some of the outgroup taxa such as *Zalambdalestes* and *Barunlestes* that have either been implicated in anagalidan ancestry or sometimes even included in Anagalida (Stucky and McKenna, 1993; but see Kielan-Jaworowska, 1978, for arguments against anagalidan affinities of Zalambdalestidae) retain a number of primitive eutherian upper dental features (as well as showing specializations) not found in "zhelestids." For example, these two genera retain the primitive states in characters 1, 7, 11–13, and 17 that are derived in "zhelestids" (see Table 4). The retention of these primitive dental features in alleged anagalidans but not in ungulatomorphs suggests that most if not all of the apomorphic dental similarities of "ungulatomorphs" and *T. minutus* are convergent adaptations for herbivory.

As to a primatomorph–ungulatomorph connection, some of the upper dentitions of "zhelestids" such as *Aspanlestes* and *Avitotherium* (which retain more primitive character states) suggest possible primate as well as ungulate ancestry. When the lower dentitions (especially of the better-known *Aspanlestes*) are examined, however, a possible primatomorph–ungulatomorph link seems less likely. In "zhelestids" the molar trigonids already have greater anteroposterior shortening than that seen in early primatomorphs. Thus ancestry of primatomorphs, although possibly near that of "zhelestids," would probably be outside this taxon.

In Figure 25B, in which Ungulatomorpha was constrained to be monophyletic, *Purgatorius* and *Tribosphenomys*, unsurprisingly, form the second and first outgroups, respectively, to Ungulatomorpha. This possible primatomorph–rodent (or anagalidan)–ungulatomorph relationship is intriguing. However, until we have more definitive data, we prefer to err in the more conservative direction in excluding rodents and primatomorphs from Ungulatomorpha.

BIOGEOGRAPHIC AND PALEOECOLOGICAL CONSIDERATIONS

As discussed in the Introduction, there is some issue as to the age of the earliest archaic ungulates in North America. Archaic ungulate-bearing sites in the Frenchman Formation, Saskatchewan, Canada (Fox, 1995), appear to be latest Cretaceous (Lancian) in age, while those to the south in eastern Montana, U.S.A., appear to be earliest Paleocene (Puercan) in age. Ungulatomorphs, however, are clearly present (barring rampant convergence) in North America in the form of the "zhelestid" *Avitotherium* by the middle Campanian (Judithian) at sites in south-central Utah (Cifelli, 1990) and north-central Montana (Montellano, 1992:fig. 29; upper molar identified by her as cf. *Paranyctoides*), both U.S.A.; and linger as the "zhelestid" *Alostera* in latest Cretaceous (Lancian) and earliest Paleocene (Puercan) sites in eastern Montana, U.S.A., and southern Saskatchewan and Alberta, Canada.

As is clear from our alpha-level taxonomy of "zhelestids," their known center of greatest and oldest diversity is in western Asia. It thus may seem surprising that ungulatomorphs, both as "zhelestids" and archaic ungulates, are found in the Late Cretaceous and early Paleocene of North America, and even the early Paleocene of South America, but are unknown from comparably aged faunas in China and Mongolia. The absence of early Paleocene ungulatomorphs from central and eastern Asia may well be the result of the absence of sites of the appropriate age there. However, this is not the case for the Late Cretaceous of central Asia, for which very

rich Late (but not latest) Cretaceous mammal sites are known. Ungulatomorphs are most likely absent from Late Cretaceous faunas in central and eastern Asia for paleoecological reasons.

In the Gobi Desert of central Asia, the Upper Cretaceous Djadokhta and Barun Goyot formations (Kielan-Jaworowska, 1984) were deposited in more inland areas with semi-arid and arid climates (Verzilin, 1978; Jerzykiewicz, 1989; Jerzykiewicz and Russell, 1991). In sharp contrast, most of the Upper Cretaceous formations in North America that have produced extensive vertebrate faunas were formed on low coastal plains (Archibald, 1996*a*) that were seasonally dry but certainly not arid (Fastovsky and McSweeny, 1987). This is especially well demonstrated by similarities in the Late Cretaceous nonmammalian vertebrate faunas of western North America (Estes, 1964; Estes et al., 1969; Estes and Berberian, 1970; Bryant, 1989) and western Asia (Nessov, 1992; Nessov et al., 1994), compared to central Asia. The former two regions have a number of elements in common, including sharks, bony fishes, amphibians, turtles, and crocodilians. These faunal elements are far less common or absent at the central Asian sites.

We are hard pressed to draw similarly strong paleoecological inferences using Late Cretaceous mammals. This is in part because of the poor quality of preservation for North American forms; more importantly, the mammal material usually does not permit us to draw similarly strong ecological conclusions by analogy with modern mammals as is possible for many nonmammalian fossil vertebrates (e.g., fishes and amphibians). Nevertheless, the profound differences among the Late Cretaceous mammal faunas of western Asia, central Asia, and western North America may well have been ecologically driven. This may explain the absence of ungulatomorphs from the more arid central Asian sites, while they are the most common mammalian taxa in the more lowland western Asian sites and even have a small presence in the lowland sites of western North America.

In sharp contrast to the above pattern, multituberculates are a very common taxonomic component in Late Cretaceous faunas of both central Asia and western North America, while they are very rare in western Asia. In numbers of collected specimens, they comprise on average about 70% in central Asia (Kielan-Jaworowska, 1992) but only 1% in western Asia (Kielan-Jaworowska and Nessov, 1992). Comparable estimates are not available for the Late Cretaceous of western North America, but multituberculates undoubtedly comprise 50% or more of the mammal specimens. Multituberculates are predominantly or totally taeniolabidoids in central Asia while in western North America they are predominantly ptilodontoids. Thus, the similarity in the multituberculate faunas between these two areas is more illusory than real. It is only near the Cretaceous/Tertiary boundary that taeniolabidoids become an important component of the mammal fauna in North America, presumably via invasion through Beringia from central Asia (e.g., Lillegraven et al., 1979). Lacking earliest Paleocene sites in central Asia, we cannot say whether the opposite pattern of migration into central Asia was also true for ptilodontoids.

The extremely low presence of multituberculates in western Asia seems anomalous. The only named multituberculate from western Asia is *Uzbekbaatar kizylkumensis*, which cannot be confidently identified as taeniolabidoid or ptilodontoid (Kielan-Jaworowska and Nessov, 1992). If one hypothesizes that "zhelestids" and multituberculates were ecological competitors, then the absence of the latter in western Asia might be explained. Based on dentitions, "zhelestids" may have filled an ecological role similar to the abundant marsupials in the Late Cretaceous of North America, yet there is a considerable diversity and abundance of multituberculates in the Late Cretaceous of North America.

Archaic ungulates appear in North America just before, at, or just after the Cretaceous/Tertiary boundary, which is similar to the pattern of taeniolabidoid appearance in North America. Unlike the taeniolabidoids, most of which can be confidently traced to central Asia, we are not certain from whence the archaic ungulates came. Ancestral archaic ungulates may have been evolving in situ in North America at least since the middle Campanian (Judithian) from "zhelestids" such as *Avitotherium*, but the relatively well-documented Late Cretaceous record of this continent shows no such trace except for the rather enigmatic *Alostera*. Archaic ungulates also might have come from Europe or even eastern North America near the close of the Cretaceous, arising from the questionable "zhelestids" known from those regions. A more appealing, but equally unsubstantiated hypothesis is that they came from western Asia along coastal routes over Beringia to North America (Nessov et al., 1994; Archibald, 1996*a*). This is appealing because of the considerable diversity of "zhelestids" in western Asia and because of the precocious presence of such advanced "zhe-

lestids" as *Eoungulatum* in western Asia, which is almost at the archaic ungulate grade of evolution. The most sobering aspect of this scenario is the tremendous amount of time separating the western Asian "zhelestids" and the earliest North American archaic ungulates, probably more than 20 million years from the Coniacian (~87 million years ago) to the Cretaceous/Tertiary boundary at ~65 million years. Much could and did transpire during this 20+ million year interval for which we have little fossil evidence at present.

ACKNOWLEDGMENTS

The authors thank A. O. Averianov, D. V. Bugaenko, M. N. Kaznyshkin, D. V. Logunov, L. A. Nalbandyan, D. D. Povshedny, O. I. Tsaruk, and B. G. Veretennikov for help in the field; D. A. Azimov and O. I. Tsaruk for logistical support while in Uzbekistan for the 1994 field season; R. L. Cifelli, W. A. Clemens, R. C. Fox, P. Holroyd, D. E. Russell, D. Sigogneau-Russell, Y. Wang, and A. Wyss for casts, the loan of material, or the opportunity to examine specimens in their care; D. A. Henderson and C. Smith for providing X-ray photographs; L. O. Salles for general discussion of early ungulates; J. Hunter, S. G. Lucas, D. E. Russell, D. Sigogneau-Russell, and A. Wyss for reading and providing comments on the manuscript; A. O. Averianov for providing a Russian translation of the abstract; E. Gheerbrant for providing unpublished information on European "zhelestids"; R. L. Cifelli and Z. Luo for their very exhaustive formal reviews that greatly improved the manuscript; A. O. Averianov, R. Etheridge, P. Mabee, M. J. Novacek, and M. Simpson for comments and help on systematic methodology; and K. C. Beard and M. R. Dawson for inviting us to participate in their symposium on Asian Cretaceous–Paleogene mammals. All scanning-electron micrographs were taken at the Paleontological Museum in Oslo by L. A. Nessov and Z. Kielan-Jaworowska. All photographs except Figure 9A were taken by J. D. Archibald at SDSU on a Wild microscope in the lab of M. Simpson. Figure 9A is a modified version of plate 5, figure 1a in Nessov et al., 1994, and is used with the kind permission of D. Sigogneau-Russell and D. E. Russell. The contributions of Z. Kielan-Jaworowska were supported by grants of Norwegian Science Foundation ABC/LR 441.91/001, 441.92/001, and 441.95/001. Visits to Oslo by L. Nessov were supported by the University of Oslo, and grants ABC/LR 441.91/001 and 441.92/001 (Norwegian Science Foundation to Z.K.J.). The 1994 field season and preparation of this manuscript were supported by a National Geographic Grant #5087-93 (L. A. Nessov and J. D. Archibald).

LITERATURE CITED

[Except for commonly used authors' names, Russian language citations are transliterated using the "British" or "European" system (Kielan-Jaworowska, 1993).]

ABDUAZIMOVA, I. M. 1988. [Recognition of suites in the Upper Cretaceous deposits of Central Kyzylkum.] Uzbyekskii Gyeologichyeskii Zhurnal, 2:64–69. (In Russian with English summary)

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

———. 1989. South American Paleocene dinosaurs, Cretaceous archaic ungulates, or neither? National Geographic Research, 5:137–138.

———. 1994. Metataxon concepts and assessing possible ancestry using phylogenetic systematics. Systematic Biology, 43:27–40.

———. 1996*a*. Dinosaur Extinction and the End of an Era: What the Fossils Say. Columbia University Press, New York, New York.

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

———. In press. Archaic ungulates ("Condylarthra"). *In* Evolution of Tertiary Mammals of North America: Volume 1: Terrestrial Carnivores, Ungulates and Ungulate-like Mammals (C. M. Janis, K. M. Scott, and L. L. Jacobs, eds.). Cambridge University Press, Cambridge, United Kingdom.

ARCHIBALD, J. D., AND D. L. LOFGREN. 1990. Mammalian zonation near the Cretaceous–Tertiary boundary. Pp. 31–50, *in* Dawn of the Age of Mammals in the Rocky Mountain Interior, North America (T. M. Bown and K. D. Rose, eds.). Geological Society of America Special Paper 243, Boulder, Colorado.

AVERIANOV, A. O. In press. Mammals from the Mesozoic of Kyrgyzstan, Uzbekistan, Kazakhstan and Tajikistan. *In* The Age of Dinosaurs in Russia and Mongolia (M. Benton and D. Unwin, eds.). Cambridge University Press, Cambridge, United Kingdom.

BAZHANOV, V. S. 1972. First Mesozoic Mammalia (*Beleutinus orlovi* Bazhanov) from the USSR. Tyeriologiya, Akadyemiya Nauk SSSR, Novosibirsk, 1:74–80. (In Russian with English summary)

BOWN, T. M., AND M. J. KRAUS. 1979. Origin of the tribosphenic molar and metatherian and eutherian dental formulae. Pp. 162–171, *in* Mesozoic Mammals: The First Two-thirds of Mammalian History (J. A. Lillegraven, Z. Kielan-Jaworowska, and W. A. Clemens, eds.). University of California Press, Berkeley, California.

BRYANT, L. J. 1989. Non-dinosaurian lower vertebrates across the Cretaceous–Tertiary boundary in northeastern Montana. University of California Publications in Geological Sciences, 134:1–107.

BUTLER, P. M. 1977. Evolutionary radiation of the cheek teeth of Cretaceous placentals. Acta Palaeontologica Polonica, 22: 241–271.

———. 1989. Early trends in evolution of tribosphenic molars.

VIII International Symposium on Dental Morphology, Jerusalem, Israel. Abstracts:14.

———. 1990. Early trends in the evolution of tribosphenic molars. Biological Reviews, 65:529–552.

———. 1992. Tribosphenic molars in the Cretaceous. Pp. 125–138, *in* Structure, Function, and Evolution of Teeth (P. Smith and E. Tchernov, eds.). Freund Publishing House Ltd., Tel Aviv, Israel.

CAMPBELL, J. A., AND D. R. FROST. 1993. Anguid lizards of the genus *Abronia*: Revisionary notes, descriptions of four new species, a phylogenetic analysis, and key. Bulletin of the American Museum of Natural History, 216:1–121.

CIFELLI, R. L. 1990. Cretaceous mammals of southern Utah. IV. Eutherian mammals from the Wahweap (Aquilan) and Kaiparowits (Judithian) formations. Journal of Vertebrate Paleontology, 10:346–360.

———. 1993. The phylogeny of the native South American Ungulates. Pp. 195–216, *in* Mammal Phylogeny, Volume 2: Placentals (F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds.). Springer Verlag, New York, New York.

———. 1994. Therian mammals of the Terlingua local fauna (Judithian), Aguja Formation, Big Bend of the Rio Grande, Texas. Contributions to Geology, University of Wyoming, 30:117–136.

CIFELLI, R. L., AND J. GUERRERO DÍAZ. 1989. New remains of *Prothoatherium colombianus* (Litopterna, Mammalia) from the Miocene of Colombia. Journal of Vertebrate Paleontology, 9:222–231.

CLEMENS, W. A. 1973. Fossil mammals of the type Lance Formation, Wyoming: Part III. Eutheria and summary. University of California Publications in Geological Sciences, 94: 1–102.

———. 1980. *Gallolestes pachymandibularis* (Theria, incertae sedis; Mammalia) from Late Cretaceous deposits in Baja California del Norte, Mexico. Paleobios, 33:1–10.

COPE, E. D. 1881. On some Mammalia of the lowest Eocene beds of New Mexico. Proceedings of the American Philosophical Society, 19:484–495.

DE MUIZON, C. 1991. La fauna de mamíferos de Tiupampa (Paleoceno inferior, Formación Santa Lucía), Bolivia. Pp. 575–624 *in* Fosiles y Facies de Bolivia. Volume I, Vertebrados (R. Suarez-Soruco, ed.). Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos, 12(3–4), Santa Cruz, Bolivia.

DE MUIZON, C., AND L. G. MARSHALL. 1987*a*. Le plus ancien condylarthre (Mammalia) sud-américain supérieur, Bolivie. Comptes Rendus de l'Académie des Sciences, Paris (Série II), 304:771–774.

———. 1987*b*. Deux nouveaux condylarthres (Mammalia) du Maastrichtien de Tiupampa (Bolivie). Comptes Rendus de l'Académie des Sciences, Paris (Série II), 304:947–950.

———. 1991. Nouveaux condylarthres du Paléocène inférieur de Tiupampa (Bolivie). Bulletin du Muséum National d'Histoire Naturelle, Paris (4e Série, Section C), 13:201–227.

DE QUEIROZ, K., AND J. GAUTHIER. 1990. Phylogeny as a central principle in taxonomy. Systematic Zoology, 6:307–322.

EMRY, R. J., J. D. ARCHIBALD, AND C. C. SMITH. 1981. A mammalian molar from the Late Cretaceous of northern Mississippi. Journal of Paleontology, 55:953–956.

ESTES, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. University of California Publications in Geological Sciences, 49:1–187.

ESTES, R., AND P. BERBERIAN. 1970. Paleoecology of a Late Cretaceous community from Montana. Breviora, 343:1–35.

ESTES, R., P. BERBERIAN, AND C. MESZOELY. 1969. Lower vertebrates from the Late Cretaceous Hell Creek Formation, McCone County, Montana. Breviora, 337:1–33.

FASTOVSKY, D. E., AND K. MCSWEENY. 1987. Paleosols spanning the Cretaceous–Paleogene transition, eastern Montana and western North Dakota. Geological Society of America Bulletin, 99:66–77.

FOX, R. C. 1984. *Paranyctoides maleficus* (new species) an early eutherian mammal from the Cretaceous of Alberta. Pp. 9–20, *in* Papers in Vertebrate Paleontology Honoring Robert Warren Wilson (R. M Mengel, ed.). Carnegie Museum of Natural History Special Publication no. 9.

———. 1989. The Wounded Knee local fauna and mammalian evolution near the Cretaceous–Tertiary Boundary, Saskatchewan, Canada. Palaeontographica A, 208:11–59.

———. 1995. "Paleocene aspect" mammals from the Late Cretaceous of Alberta and Saskatchewan. Geological Society of America, Abstracts with Programs, 27:11.

GAYET, M., L. G. MARSHALL, AND T. SEMPERE. 1991. The Mesozoic and Paleocene vertebrates of Bolivia and their stratigraphic context: A review. Revista Tecnica de Yacimientos Petroliferas Fiscales Bolivianos, Santa Cruz (Bolivia), 12: 393–433.

GHEERBRANT, E., AND H. ASTIBIA. 1994. Un nouveau mammifère du Maastrichtien de Laño (Pays Basque espagnol). Comptes Rendus de l'Académie des Sciences, Paris (Série II), 318: 1125–1131.

GINGERICH, P. D., D. P. DOMNING, C. E. BLANE, AND M. D. UHEN. 1994. Cranial morphology of *Protosiren fraasi* (Mammalia, Sirenia) from the middle Eocene of Egypt: A new study using computed tomography. Contributions from the Museum of Paleontology, University of Michigan, 29:41–67.

GREAVES, W. S. 1995. Functional predictions from theoretical models of the skull and jaws in reptiles and mammals. Pp. 99–115, *in* Functional Morphology in Vertebrate Paleontology (J. J. Thomason, ed.). Cambridge University Press, Cambridge, United Kingdom.

HAUSER, D. L., AND W. PRESCH. 1991. The effect of ordered characters on phylogenetic reconstruction. Cladistics, 7:243–266.

HOFFSTETTER, R., AND M. F. SORIA. 1986. *Neodolodus colombianus* gen. et sp. nov., un nouveau Condylarthre (Mammalia) dans le Miocène de Colombie. Comptes Rendus de l'Académie des Sciences, Paris (Série II), 303: 1619–1622.

JANIS, C. M. 1995. Correlations between craniodental morphology and feeding behavior in ungulates: Reciprocal illumination between living and fossil taxa. Pp. 76–98, *in* Functional Morphology in Vertebrate Paleontology (J. J. Thomason, ed.). Cambridge University Press, Cambridge, United Kingdom.

JERZYKIEWICZ, T. 1989. 1988 Sino–Canadian Dinosaur Project Expedition successful in Inner Mongolia. Geos, 18:1–6.

JERZYKIEWICZ, T., AND D. A. RUSSELL. 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Desert. Cretaceous Research, 12:345–377.

JOHNSTON, P. A. 1980. First record of Mesozoic mammals from Saskatchewan. Canadian Journal of Earth Sciences, 17:512–519.

JOHNSTON, P. A., AND R. C. FOX. 1984. Paleocene and Late Cre-

taceous mammals from Saskatchewan, Canada. Palaeontographica A, 186:163–222.

KIELAN-JAWOROWSKA, Z. 1975. Preliminary description of two new eutherian genera from the Late Cretaceous of Mongolia. Palaeontologica Polonica, 33:5–16.

———. 1978. Evolution of the therian mammals in the Late Cretaceous of Asia. Part III. Postcranial skeleton in Zalambdalestidae. Palaeontologica Polonica, 38:3–41.

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

———. 1984. Evolution of the therian mammals in the Late Cretaceous of Asia. Part VII. Synopsis. Palaeontologia Polonica, 46:173–183.

———. 1992. Interrelationships of Mesozoic mammals. Historical Biology, 6:185–202.

———. 1993. Citing Russian papers. Society of Vertebrate Paleontology News Bulletin, 159:53–54.

KIELAN-JAWOROWSKA, Z., AND D. DASHZEVEG. 1989. Eutherian mammals from the Early Cretaceous of Mongolia. Zoologica Scripta, 18:347–355.

KIELAN-JAWOROWSKA, Z., AND L. A. NESSOV. 1990. On the metatherian nature of the Deltatheroida, a sister group of the Marsupialia. Lethaia, 23:1–10.

———. 1992. Multituberculate mammals from the Cretaceous of Uzbekistan. Acta Palaeontologica Polonica, 37:1–17.

KIELAN-JAWOROWSKA, Z., T. M. BOWN, AND J. A. LILLEGRAVEN. 1979. Eutheria. Pp. 99–149, *in* Mesozoic Mammals: The First Two-thirds of Mammalian History (J. A. Lillegraven, Z. Kielan-Jaworowska, and W. A. Clemens, eds.). University of California Press, Berkeley, California.

KRAUSE, D. W. 1984. Mammalian evolution in the Paleocene: Beginning of an era. Pp. 87–109, *in* Mammals: Notes for a Short Course Organized by P. D. Gingerich and C. E. Badgley (T. W. Broadhead, ed.). University of Tennessee Department of Geological Sciences, Studies in Geology, 8.

KRYMHOLTS, G. YA. (ED.). 1977. Ryeshyeniya Myezhvyedomstvyennogo Stratigrafichyeskogo Sovyeshchaniya po Myezozoyu Sryednyei Azii, Samarkand, 1971 [Resolutions of the Interdepartmental Stratigraphic Conference on the Mesozoic of Middle Asia, Samarkand, 1971]. Lyeningrad, USSR. (In Russian)

LEDOUX, J.-L., J.-L. HARTENBERGER, J. MICHAUX, J. SUDRE, AND L. THALER. 1966. Découverte d'un Mammifère dans le Crétacé supérieur à Dinosaures de Champ-Garimond près de Fons (Gard). Comptes Rendus de l'Académie des Sciences, Paris (Série D), 262:1925–1928.

LILLEGRAVEN, J. A. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial–placental dichotomy in mammalian evolution. Paleontological Contributions, University of Kansas, 50 (Vertebrata 12):1–122.

———. 1976. A new genus of therian mammal from the Late Cretaceous "El Gallo Formation," Baja California, Mexico. Journal of Paleontology, 50:437–443.

LILLEGRAVEN, J. A., AND M. C. MCKENNA. 1986. Fossil mammals from the "Mesaverde" Formation (Late Cretaceous, Judithian) of the Bighorn and Wind River basins, Wyoming, with definitions of Late Cretaceous North American land-mammal "Ages." American Museum Novitates, 2840:1–68.

LILLEGRAVEN, J. A., M. J. KRAUS, AND T. M. BOWN. 1979. Paleogeography of the world of the Mesozoic. Pp. 277–308, *in* Mesozoic Mammals: The First Two-thirds of Mammalian History (J. A. Lillegraven, Z. Kielan-Jaworowska, and W. A. Clemens, eds.). University of California Press, Berkeley, California.

LINNAEUS, C. 1758. Systema naturae regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Laurentii Salvii, Stockholm, Sweden. (In Latin)

———. 1766. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Editio duodecima, reformata. Laurentii Salvii, Stockholm, Sweden. (In Latin)

LOFGREN, D. L. 1995. The Bug Creek problem and the Cretaceous–Tertiary transition at McGuire Creek, Montana. University of California Publications in Geological Sciences, 140:1–185.

LUCAS, S. G. 1993. Pantodonts, tillodonts, uintatheres and pyrotheres are not ungulates. Pp. 182–194, *in* Mammal Phylogeny, Volume 2: Placentals (F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds.). Springer Verlag, New York, New York.

LUCKETT, W. P. 1993. An ontogenetic assessment of dental homologies in therian mammals. Pp. 182–204, *in* Mammal Phylogeny, Volume 1: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials (F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds.). Springer Verlag, New York, New York.

LUO, Z. 1991. Variability of dental morphology and the relationships of the earliest arctocyonid species. Journal of Vertebrate Paleontology, 11:452–471.

LUPTON, C., D. GABRIEL, AND R. M. WEST. 1980. Paleobiology and depositional setting of a Late Cretaceous vertebrate locality, Hell Creek Formation, McCone County, Montana. Contributions to Geology, University of Wyoming, 18:117–126.

MACPHEE, R. D. E., AND M. J. NOVACEK. 1993. Definition and relationships of Lipotyphyla. Pp. 13–31, *in* Mammal Phylogeny, Volume 2: Placentals (F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds.). Springer Verlag, New York, New York.

MADDISON, W. P., AND D. R. MADDISON. 1992. MacClade: Analysis of Phylogeny and Character Evolution, Version 3. Sinauer Associates, Inc., Sunderland, Massachusetts.

MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Systematic Zoology, 33: 83–103.

MARSHALL, L. G., AND Z. KIELAN-JAWOROWSKA. 1992. Relationships of the dog-like marsupials, deltatheroidans and early tribosphenic mammals. Lethaia, 25:353–460.

MARTINSON, G. G. 1969. Biostratigrafiya i fauna myelovykh kontinyentalnykh otlozhyenii Tadzhikskoi dyepryessii, i Kyzylkumov Pritashkyentskikh Chulyei [Biostratigraphy and fauna of the Cretaceous continental deposits of the Tajik Depression, Kyzylkum Desert and Pritashkentshie Chuli]. Pp. 18–51, *in* Kontinyentalnyye obrazovaniya vostochnykh raionov Sryednyei Azii i Kazakhstana (litologiya i biostratigrafiya) [Continental Deposits of the Eastern Regions of Middle Asia and Kazakstan (Lithostratigraphy and Biostratigraphy)] (G. G. Martinson, ed.). Izdatyelstvo Nauka, Lyeningrad, USSR. (In Russian)

MCKENNA, M. 1975. Toward a phylogenetic classification of the Mammalia. Pp. 21–46, *in* Phylogeny of the Primates: A

Multidisciplinary Approach (W. P. Luckett and F. S. Szalay, eds.). Plenum Press, New York, New York.

———. 1987. Molecular and morphological analysis of high-level mammalian interrelationships. Pp. 55–95, *in* Molecules and Morphology in Evolution: Conflict or Compromise? (C. Patterson, ed.). Cambridge University Press, Cambridge, United Kingdom.

———. 1992. The alpha crystallin A chain of the eye lens and mammalian phylogeny. Annales Zoologici Fennici, 28:349–360.

MEACHAM, C. A., AND T. DUNCAN. 1993. Morphosys, version 1.29, computer software. Regents of the University of California.

MENG, J., A. R. WYSS, M. R. DAWSON, AND R. ZHAI. 1994. Primitive fossil rodent from Inner Mongolia and its implications for mammalian phylogeny. Nature, 370:134–136.

MONTELLANO, M. 1992. Mammalian fauna of the Judith River Formation (Late Cretaceous, Judithian), north-central Montana. University of California Publications in Geological Sciences, 136:1–115.

NESSOV, L. A. 1982. Dryevnyeishiye mlyekopitayushchiye SSSR [Ancient mammals of the USSR]. Yezhyegodnik Vsyesoyuznogo Palyeontologichyeskogo Obshchyestva, 25: 228–243. (In Russian)

———. 1984*a*. Data on late Mesozoic turtles from the USSR. Studia Geologica Salmanticensia. Studia Palaeocheloniologica, 1:215–223.

———. 1984*b*. O nyekotoryye nakhodkakh octatkov mlyekopitayushchikh v myelov otloshchyeniyakh sryednyei Azii [On some Cretaceous mammmals from the Soviet Middle Asia]. Vyestnik Zoologii, Kiyev, 2:60–65. (In Russian with English summary)

———. 1985*a*. Novyye mlyekopitayushchiye myela Kyzylkumov [New mammals from the Cretaceous of the Kyzylkum Desert]. Vyestnik Lyeningradskogo Univyersityeta Syeriya 7, 17:8–18. (In Russian with English summary)

———. 1985*b*. Ryedkiye kostnyye ryby nazyemnyye Yahchyeritsy i mlyekopitayushchiye zony limanov i primorskikh nizmyennostyei myela Kyzylkumov [Rare bony fish, terrestrial lizards and mammals of the zone of estuaries and coastal plains of the Cretaceous Kizylkum Desert]. Yezhyegodnik Vsyesoyuznogo Palyeontologichyeskogo Obshchyestva, 24: 199–218. (In Russian)

———. 1987. Ryezultaty poiskov i isslyedovaniya myelovykh i rannyepalyeogyenovykh mlyekopitayushchikh na territorii SSSR [Results of search and study on the Cretaceous and Early Paleogene mammals on the territory of the USSR]. Yezhyegodnik Vsyesoyuznogo Palyeontologichyeskogo Obshchyestva, 30:199–218. (In Russian)

———. 1988. Komplyeksy pozvonochnykh pozdnyego myezozoya i palyeotsyena Cryednyei Azii [Assemblages of late Mesozoic and Paleocene vertebrates of middle Asia]. Pp. 93–101, *in* Stanovlyeniye i evolyutsiya kontinentaln biot [Appearance and Evolution of the Continental Biotas] (T. N. Borgdanova and M. V. Oshurkova, eds.). Izdatyelstvo Nauka, Lyeningrad, USSR. (In Russian)

———. 1990. Myelkii ikhtiornis i drugiye nakhodki kostyei ptits v bissyektinskoi svitye (vyerkhnii myel) Tsyentrlnykh Kyzylkumov [Small ichthyornithiform bird and other bird remains from the Bissekty Formation (Upper Cretaceous) of Central Kyzylkum Desert]. Trud Zoologichyeskogo instituta Akadyemiya Nauk SSSR, 21:59–62. (In Russian with English summary)

———. 1991. Gigantskiye lyetayushchiye iashchyery syemyeistva Azhdarchidae. II. Sryeda obitaniya, syedimyentologitsyeskaya obstanovka zakhoronyeniya ostatkov [Giant flying reptiles of the family Azhdarchidae. II. Environments, sedimentological conditions under burial of remains]. Vyestnik Lyeningradskogo Univyersityeta Syeriya 7, 21:16–24. (In Russian with English summary)

———. 1992. Mesozoic and Paleogene birds of the USSR and their paleoenvironments. Pp. 465–478, *in* Papers in Avian Paleontology Honoring Pierce Brodkorb (K. E. Campbell, ed.). Natural History Museum of Los Angeles County Museum, Contributions in Science, 36.

———. 1993. Novyye mlyekopitayushchiye myezozoya sryednyei Azii i Kazakhstana i zamyechaniya po évolyutsii tyeriofaun primorskikh nizmyennostyei myela dryevnyei Azii [New Mesozoic mammals of middle Asia and Kazakstan and comments about evolution of theriofaunas of Cretaceous coastal plains of Asia]. Trud Zoologichyeskogo Instituta, Rossiiskaya Akadyemiya Nauk, 249:105–133. (In Russian with English summary)

———. 1995. Dinozavrý Syevyernoi Yevrazii: novýye dannýye osostavye komplyesov, ékologii i palyeobiogyeografii [Dinosaurs of northern Asia: New data about assemblages, ecology and paleobiogeography]. Sankt-Pyetyerburgskii Gosudarstvyennýi univyerityet Naucho-isslyedovatyelskii institut zyemnoi korý, Russia. (In Russian with English summary)

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

NESSOV, L. A., AND R. A. MERTINIENE. 1986. Ostatki khryashchyevykh ryb myela sryednyei Azii i Kazakhstana kak istochnik svyedyenii o vozrastye i gyenyezisye otlozhyenii [Fragments of chondrichthyan fishes from the Cretaceous of middle Asia and Kazakstan as a source of information on the age and origin of the deposits]. Pp. 35–41, *in* Palyeontologiya i dyetalnaya stratigrafichyeskaya korryellatsiya [Paleontology and Detailed Stratigraphic Correlation] (G. Ya. Krymholts and V. S. Belenkova, eds.). Izdatyelstvo Nauka, Lyeningrad, USSR. (In Russian with English summary)

NESSOV, L. A., D. SIGOGNEAU-RUSSELL, AND D. E. RUSSELL. 1994. A survey of Cretaceous tribosphenic mammals from middle Asia (Uzbekistan, Kazakhstan and Tajikistan), of their geological setting, age and faunal environment. Palaeovertebrata, 23:51–92.

NOVACEK, M. J. 1992. Mammalian phylogeny: Shaking the tree. Nature, 356:121–125.

OWEN, R. 1837. Teeth. Pp. 864–935, *in* The Cyclodapia of Anatomy and Physiology, Volume 4, Part 2 (R. B. Todd, ed.). Sherwood, Gilbert, and Piper, London, Great Britain.

PARKER, T. J., AND W. A. HASWELL. 1897. A Textbook of Zoology, Volume 2. Macmillan and Company, London, Great Britain.

POL, C., A. D. BUSCALIONI, J. CARBELLEIRA, V. FRANCÉS, N. LÓPEZ MARTINEZ, B. MARANDAT, J. J. MORATALLA, J. L. SANZ, B. SIGÉ, AND J. VILLATTE. 1992. Reptiles and mammals from the Late Cretaceous new locality Quintanilla del Coco (Burgos Province, Spain). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 184:279–314.

PROTHERO, D. R. 1993. Ungulate phylogeny: Molecular vs. morphological evidence. Pp. 173–181, *in* Mammal Phylogeny, Volume 2: Placentals (F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds.). Springer Verlag, New York, New York.

PROTHERO, D. R., E. M. MANNING, AND M. FISCHER. 1988. The phylogeny of the ungulates. Pp. 201–234, *in* The Phylogeny and Classification of the Tetrapods, Volume 2: Mammals (M. J. Benton, ed.). Systematics Association, Special Volume 35B. Clarendon Press, Oxford, United Kingdom.

PYATKOV, K. K., I. A. PYANOVSKAYA, A. K. BUKHARIN, AND YU. K. BYKOVSKIJ. 1967. Gyeologichyeskoye stroyeniye Tsyentrlnykh Kyzylkumov [Geological Structure of the Central Kyzylkum]. Izdatyelstvo Fan, Tashkent, Uzbekistan, USSR. (In Russian)

RUSSELL, D. A., AND DONG, Z.-M. 1993. The affinities of a new theropod from the Alxa Desert, Inner Mongolia, People's Republic of China. Canadian Journal of Earth Sciences, 30: 2107–2127.

SALLES, L. O. 1995. Phylogénie des ongulés basaux: L'évolution du complexe dentaire (morphologie des dents jugales superieures) chez les "condylarthres" de Crétacé superieur à l'Eocène et l'émergence des cétacés (Ungulata, Mammalia) (avec la formulation d'un nouvel indice de cohérence stratophylogénétique: "L'indice de Gaudry"). Thése de Doctorat, Université de Paris VII, Paris, France.

SCHULTZ, S. S., JR. 1972. Gyeologichyeskoye stroyeniye zony sochlyenyeniya Urala i Tyan-Shanya [Geological Structure of the Contact Zone of Ural and Tian Shan Mountains]. Izdatyelstvo Nyedra, Moskva, USSR. (In Russian)

SHILIN, P. V. 1986. Pozdnyemyelovyye Flory Kazakhstana. Sistemyematichyeskii sostav, istoriya razvitiya, stratigrafichyeskoye znachyeniye [Late Cretaceous Floras of Kazakstan. Systematics, history of the development, stratigraphical implications]. Izdatyelstvo Nauka, Alma-Ata, Kazakstan, USSR. (In Russian)

SLOAN, R. E., AND L. VAN VALEN. 1965. Cretaceous mammals from Montana. Science, 148:220–227.

SOCHAVA, A. V. 1968. Krasnotsvyety Myela Sryednyei Azii [Red-colored Cretaceous Sediments of Middle Asia]. Izdatyelstvo Nauka, Lyeningrad, USSR. (In Russian)

SOKOLOV, M. I. 1978. Zuby akul kak rukovodyashchiye iskopayemyye pri zonalnom raschlyenyenii myelov otlozhyenii Turanskoi Plity [Teeth of Sharks as Guide Fossils for Zonal Dividing of Cretaceous Deposits of Turan Platform]. Izdatyelstvo Nyedra, Moskva, USSR. (In Russian)

STORER, J. 1991. The mammals of the Gryde Local Fauna, Frenchman Formation (Maastrichtian: Lancian), Saskatchewan. Journal of Vertebrate Paleontology, 11:350–369.

STUCKY, R. K., AND M. C. MCKENNA. 1993. Mammalia. Pp. 739–771, *in* The Fossil Record II (M. J. Benton, ed.). T. Chapman and Hall, London, United Kingdom.

SWOFFORD, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

SZALAY, F. S., M. J. NOVACEK, AND M. C. MCKENNA (EDS.). 1993. Mammal Phylogeny, Volume 2: Placentals. Springer Verlag, New York, New York.

VAN VALEN, L. 1978. The beginning of the age of mammals. Evolutionary Theory, 4:45–80.

———. 1988. Paleocene dinosaurs or Cretaceous ungulates in South America? Evolutionary Monographs, 10:1–79.

VERESHCHAGIN, V. N. (ED.). 1979. Stratigrafichyeskii slovar SSSR. Trias. Yura. Myel. [Stratigraphic Dictionary of the USSR. Triassic. Jurassic. Cretaceous.]. Izdatyelstvo Nauka, Lyeningrad, USSR. (In Russian)

VERZILIN, N. N. 1967. Myelovyye otloshchyeniya yuga fyerganskoi vpadiny i ikhnyeftyegazonosnost [Cretaceous deposits of the south of Fergana Depression and their oil bearing]. Trudy Lyeningradskogo Obshchyestva Yestyestvoispytatyelyei, 71:1–139. (In Russian)

———. 1978. [Origin of the Upper Cretaceous deposits of southern Mongolia inferred from taphonomic observations.] Vyestnik Lyeningradskogo Univyersityeta, 12, Gyeologiya, Gyeografiya, 2:7–13. (In Russian)

WANG, Y. 1995. A new zhelestid (Mixotheridia, Mammalia) from the Paleocene of Qianshan, Anhui. Vertebrata PalAsiatica, 33:114–137 (In Chinese with English translation)

Note added in proof:

In 1997, L. B. Golovneva and A. O. Averianov edited a posthumously published monograph by L. A. Nessov in which the unpublished names *Parazhelestes minor* (pp. 148 and 213), *Eoungulatum* (p. 150), and *Eoungulatum kudukensis* (p. 213) were used without being "accompanied by a description or definition that states in words characters that are purported to differentiate that taxon. . ." (Article 13[a][i] of the International Code of Zoological Nomenclature, Third Edition, 1985). Accordingly, the aforementioned taxonomic names are nomina nuda in Nessov, 1997. When used in the article by Nessov (1997), these nomina nuda were accompanied by the citations Nessov et al. or Nessov et al., in press, in reference to the publication here presented, but without this citation in the references of Nessov, 1997. Thus, the correct attribution of these taxonomic names is the present work (Nessov, Archibald, and Kielan-Jaworowska, 1998). The complete citation for Nessov, 1997 is: Nyemorskiye pozvonochnýye myelovogo pyerioda Syevyernoi Yevrazii (Cretaceous nonmarine vertebrates of northern Eurasia). Sankt-Pyetyerburgskii Gosudarstvyennýi univyerityet Nauchko-isslyedovatyelskii institut zyemnoi korý (in Russian with English summary).

Two new genera and species were described and figured in Nessov (1997) as belonging to Zhelestidae. The first is *Eozhelestes mangit* based on a single, lower molar identified as a left M_1 from the Cenomanian-aged Sheikhdzheili locality (SSHD-8), western Uzbekistan. The second is *Ortalestes tostak* based on a single upper tooth identified as a left M^1 from the Coniacian-aged Dzharakuduk locality (CBI-4). These specimens were examined by the second author (JDA). Space does not permit a full discussion, but a few comments are in order. The type of *Eozhelestes mangit* does appear to be either M_1 or M_2. Although there is nothing precluding a mammal with this kind of lower molar and of this earlier age from being

ancestral to "zhelestids," it lacks the expanded talonid of "zhelestids" and later ungulatomorphs. Accordingly, it is excluded from Ungulatomorpha (including "Zhelestidae"). The upper tooth identified as a left M^1 from Dzharakuduk has been somewhat damaged since the time of being photographed. It is slightly smaller than M^1s but similar in size to P^5s of *Aspanlestes aptap,* also from Dzharakuduk. It has dental attrition, a lack of roots, and a somewhat linguolabially narrowed crown suggestive of a dP^5. Thus, it seems quite likely that the single and only known tooth of *Ortalestes tostak* is a dP^5 of *Aspanlestes aptap.*