

# **Paranyctoides and allies from the Late Cretaceous of North America and Asia**

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*Paranyctoides* is represented by three named, and possibly four unnamed species in the Late Cretaceous, North America. *P. aralensis* from the Late Cretaceous of Dzharakuduk, Uzbekistan, belongs in this or a closely allied taxon. Lower molars have low trigonids, well-developed paraconids not appressed against metaconids, talonids on m1–2 as wide or wider than trigonids, hypoconulids often closer to entoconids than to hypoconids. Only two upper molars are known, both have comparatively narrow crowns with wide stylar shelves and stylar cusps, paracone and metacone separated, conules well developed, and protocone low. Pre- and postcingula vary from narrow in one, *Sailestes quadrans*, to wide in the other, *Paranyctoides* sp. *Sailestes quadrans* may be an metatherian. All known species of *Paranyctoides* from North America have a submolariform ultimate premolar while *Gallolestes pachymandibularis*, also from North America, has molars not unlike those in *Paranyctoides* but may have an ultimate premolar with a molariform trigonid. A specimen from Dzharakuduk referable to *P. aralensis* is suggestive of such morphology. At least *P. aralensis* had five premolars with the third reduced as in 'zhelestids'. These findings increase the Late Cretaceous North American/Asian ties even more for eutherians, now with 'zhelestids' and the *Paranyctoides*/*Gallolestes* clades known from both.

Key words: Mammalia, Eutheria, *Paranyctoides*, *Gallolestes*, *Sailestes*, Late Cretaceous, North America, Asia, paleobiogeography.

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## **Introduction**

*Paranyctoides sternbergi* was named by Fox in 1979 based upon a series of lower dentary fragments and isolated teeth from the middle Campanian (Judithian-aged), Oldman Formation of Alberta (now referred to the Dinosaur Park Formation, Judith River Group, Eberth & Hamblin 1993). He referred the newly named *Paranyctoides* to cf. Nyctitheriidae (Lipotyphla, Erinaceoidea). In 1984 Fox named a second species, *P. maleficus*, based upon elements of both the lower and upper dentition from the

Aquilian-aged (early Campanian), upper part of the Milk River Formation, Alberta. In 1986 Lillegraven and McKenna described another species, *P. megakeros*, based upon an m1 and an mx trigonid from the Judithian-aged 'Mesaverde' Formation, Wyoming. In 1987 Rigby and Wolberg referred to *Paranyctoides* an isolated ultimate upper premolar, a questionable m3, and a lower molar talonid from the Fossil Forest Study Area (?Judithian), New Mexico (Rigby & Wolberg 1987). Montellano (1992) referred specimens from the Judith River Formation (Judithian) of Montana to both *Paranyctoides* cf. *P. maleficus* and to cf. *Paranyctoides* (now referred to the Dinosaur Park Formation, Judith River Group, Eberth & Hamblin 1993). Subsequently, Nessov *et al.* (1998) referred the single tooth, which Montellano identified as cf. *Paranyctoides*, as belonging to the then newly named *Avitotherium utahensis* Cifelli, 1990a, based upon upper and lower dental remains from the Judithian-aged Kaiparowits Formation, Utah. In the same paper in which *Avitotherium* was described, Cifelli (1990a) recognized but did not name two species each of *Paranyctoides* from the Aquilan-aged Wahweap Formation (Wahweap species A and B) and Judithian-aged Kaiparowits Formation (Kaiparowits species A and B), Utah. All four were based upon isolated teeth, the Wahweap species from lowers only and the Kaiparowits species from both uppers and lowers.

In 1993, Nessov named *Paranyctoides aralensis* from the upper Turonian–Coniacian Bissekty Formation, Dzharakuduk, Uzbekistan (Nessov 1993). This was based upon a right dentary preserving double roots for p1 through p5, a fragment of the talonid of m1, a complete m2 with a broken protoconid, and an m3 with a damaged trigonid and a missing hypoconulid (Figs. 1A, 2A, B). Nessov had been able to compare this specimen directly with type and referred material of *Paranyctoides* in the University of Alberta collections in 1991. The authors visited the Dzharakuduk localities separately with the late Lev Nessov. In 1997, the authors began what has been a cooperative project, the URBAC expeditions (Uzbekistan/Russia/Britain/America/Canada), to Dzharakuduk. This has also included the resorting, cataloguing, and further study of Nessov's original collections. One of the more enigmatic specimens was that which Nessov had ascribed to *Paranyctoides aralensis*. Before beginning the examination of this taxon, we were skeptical of the recognition of this taxon in Late Cretaceous faunas of both North America and Asia. If true, it would be the only such lower-level eutherian taxon known to both continents in the Late Cretaceous. We have been able to identify other material that is definitely or possibly referable to *P. aralensis*. Herein we describe and discuss this material, along with the type specimen. This has also necessitated a review of *Paranyctoides* as well as other possibly related taxa. Because of the fragmentary nature of much of the material, we prefer to treat this analysis as an informal discussion rather than a formal taxonomic review, although we do discuss some taxonomic consequences.

**Dental and geographic terminology.** — We use the dental terminology in Nessov *et al.* (1998: fig. 1). Measurements were taken according to the method illustrated by Archibald (1982: fig. 1). Premolars are identified as upper or lower 1, 2, 4, and 5, based on information that position 3 is lost in early eutherians (Novacek 1986; Sigogneau-Russell *et al.* 1992; Archibald 1996; Archibald & Averianov 1997, 1998; Nessov *et al.* 1998; Archibald & Averianov unpublished data). Premolars 4 and 5 correspond to numbers 3 and 4 in most other traditional descriptions. Teeth were projected on a computer screen using a video camera mounted on a binocular microscope and measured to the nearest



Fig. 1. Stereophotographs in occlusal views of lower dentitions of *Paranyctoides aralensis*. **A.** CCMGE 67/12455, type, right dentary with roots or alveoli for p1–5, m1 and teeth of m2–3, the latter missing the hypoconulid. **B.** ZIN C.82590, right dentary with p5. **C.** ZIN C.82588, left dentary with roots or alveoli for p5 (posterior) and m1, m2 talonid, m3. **D.** ZIN C.82592, left edentulous dentary with roots or alveoli for canine (one alveolus), p1–5 (two alveoli or roots), m1–3 (two alveoli or roots).

0.1mm using NIH Image 1.61 software. Teeth were photographed with a Nikon CoolPix 990 digital camera. We use the term ‘Middle Asia’ as a region commonly and long used by Soviet geographers much as in the same way terms such as the Great Plains are used in North America. Middle Asia is in fact located more in the southwestern portion of Asia. Middle Asia approximately extends from the Caspian Sea on the west to the Chinese border on the east, and from the Iranian and Afghan borders on the south to south-

ern Kazakhstan on the north. It essentially encompasses the newly independent countries of Kirghizia, Tadjikistan, Turkmenistan, and Uzbekistan.

**Institutional abbreviations and localities.** — CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg; UA, University of Alberta; UMNH VP, Utah Museum of Natural History Vertebrate Paleontology; ZIN C., Systematic Collections, Zoological Institute, Russian Academy of Sciences, Saint Petersburg; Localities: CBI, central Kyzylkum, Bissekty Formation.

### Affinities of *Paranyctoides*

When described by Fox (1979), he emphasized the resemblance of *Paranyctoides sternbergi* to early Tertiary nyctitheriid erinaceoids. He tentatively assigning *Paranyctoides* to Nyctitheriidae, further noting that the assignment of nyctitheriids to Erinaceoidea or Soricoidae was at that time uncertain. Later authors dealing with *Paranyctoides* (e.g., Cifelli 1990a; Montellano 1992; Nessov 1993) followed this referral to Nyctitheriidae, but with question. The most recent classification of eutherians (McKenna & Bell 1997) refers Nyctitheriidae to Soricoidae, but simply places *Paranyctoides* in Soricomorpha with no familial or superfamilial attribution. Nevertheless, this still places *Paranyctoides* within one of the 18 major extant clades (Lipotyphla) of the extant crown group Placentalia, a status allotted to only two other Late Cretaceous eutherians by McKenna & Bell (1997) – *Otlestes* (within the monotypic Otlestidae following Nessov 1985) and *Batodon*, both within Soricomorpha. We do not agree with the attribution of *Otlestes* to Soricomorpha, preferring to treat it as *Eutheria incertae sedis*. We offer no opinion regarding *Batodon*.

Fox (1979) drew particular attention to the similarities of *Paranyctoides* and *Leptacodon*, a Paleocene nyctitheriid. Some of the similarities he noted were: occlusal, labial, and lingual profiles similar; trigonids low with well-developed paraconids not appressed against metaconids; talonid on m1–2 broad, wider than trigonids; hypoconid well developed; hypoconulid closer to entoconid than to hypoconid; entoconid highest talonid cusp; cristid obliqua contacting posterior of trigonid at notch in protocristid; m3 smaller than m2, m3 talonid slightly narrower than trigonid. Although noting some differences between the two, Fox (1979: pp. 122–123) concluded that '*P. sternbergi* is more closely related to *Leptacodon*-like nyctitheriid lipotyphlans than to any other Cretaceous eutherian species.' He noted that the ultimate lower premolar, which we refer to as p5, is less molariform in *Paranyctoides* compared to other Cretaceous eutherians (and presumably *Leptacodon*), in which p5 has a more tricuspid trigonid with distinct paraconid, protoconid, and metaconid. Fox (1979: p. 123) stated that in *Paranyctoides*, the 'tooth lacks a trigonid in that the paraconid and protoconid are in line anteroposteriorly and there is no metaconid: the paraconid is small and low.' He regarded the latter condition of the p5 as close to ancestral for eutherians and thus of no particular impediment to possible ancestry of taxa with more complex p5 trigonids. Fox (1979: p. 123) finally argued that the morphology of the *Paranyctoides* lower cheek teeth 'is closer than is any other known Mesozoic mammal to what would be expected in an ancestor for the following placental groups: Lipotyphla, Tupaiidae (tree-shrews), the orders Primates, Dermoptera, and Chiroptera, and all of the ungulate mammals.'

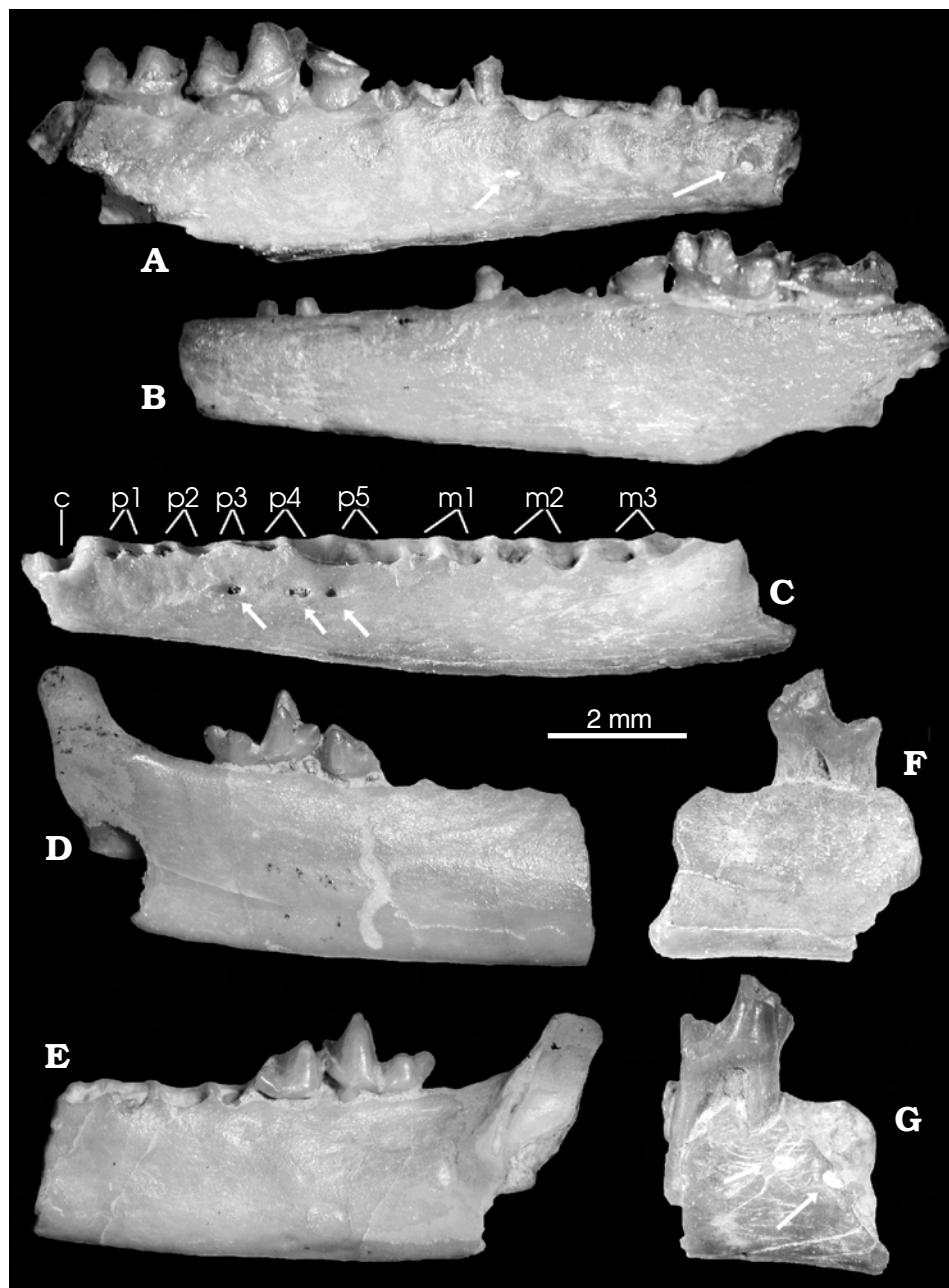


Fig. 2 Labial and lingual views of lower dentitions of *Paranyctoides aralensis*. **A, B.** Labial and lingual views, CCMGE 67/12455, type, right dentary with roots or alveoli for p1–5, m1 and teeth of m2–3, the latter missing the hypoconulid. **C.** labial view, ZIN C.82592, left edentulous dentary with roots or alveoli for canine (one alveolus), p1–5 (two alveoli or roots), m1–3 (two alveoli or roots). **D, E.** Lingual and labial views, ZIN C.82588, left dentary with roots or alveoli for p5 (posterior) and m1, m2 talonid, m3. **F, G.** Lingual and labial views, ZIN C.82590, right dentary with p5. Arrows indicate mental foramina.



In 1984 Fox named, *P. maleficus*, from the Aquilian-aged (early Campanian), upper part of the Milk River Formation, Alberta (Fox 1984). Unlike the younger Judithian *P. sternbergi*, *P. maleficus* was based upon elements of both the lower and upper dentition. He noted that *P. maleficus* differed from *P. sternbergi* only in the former taxon's 'more robust construction' of the lower dentition, the only part comparable in the two taxa. As he noted, the upper molars of *P. maleficus* show an interesting combination of ancestral and derived character states. In the former category we include wide styler shelves, ectoflexus deep, styler cuspules present (although the presence of specific cusps may well be derived), protocone lower than para- or metacone, metacone lower than paracone, molar crowns not greatly expanded transversely. These are found in the oldest undoubted eutherian *Prokennalestes* (Kielan-Jaworowska & Dashzeveg, 1989) as well as even earlier therians. In the latter category we include paracone and metacone bases separate, protocone with some anteroposterior expansion, and narrow pre- and postcingula, sometimes with a small hypocone. Although these differ some from those listed by Fox (1984), the overall conclusion remains that it is a eutherian that combines an interesting combination of ancestral and derived character states different from *most* other undoubted Late Cretaceous eutherians. Whether this combination of character states truly reflects nyctitheriid or even lipotyphlan relationships remains open to debate (e.g., Butler 1988).

We do agree with Fox (1984) that the dentition of *Paranyctoides* is highly suggestive of a eutherian that may be involved in lipotyphlan or archaic ungulate ancestry such as he discussed and indicated in his fig. 5. This possible tie became even more apparent with the detailed description and phylogenetic analysis of the 'zhelestids' by Nessov *et al.* in 1998. Here was a suite of as many as five Middle Asian taxa (based on upper dentitions), and two each from North American and European (and now one from Japan, Setoguchi *et al.* 1999) that seemed to embody many of the character states of the lower dentition of *Paranyctoides* with additional apomorphies in the upper dentition. This even led Nessov *et al.* (1998; Archibald 1996) to propose Ungulatomorpha for 'Zhelestidae' (the quotes indicating that the taxon was rendered paraphyletic when Cenozoic taxa were added) and all Cenozoic ungulate descendents. As with the possible *Paranyctoides* – lipotyphlan tie, the 'zhelestid' – ungulate tie emphasized the very possible association of these Late Cretaceous taxa to Cenozoic descendents or at least as sister taxa.

Not surprisingly, at least in retrospect, in the cladistic analysis by Nessov *et al.* (1998: fig. 24), *Paranyctoides* consistently clustered with the 'zhelestids' (or 'zhelestids' plus some Cenozoic taxa: fig. 25) as the closest sister taxon. *Paranyctoides* in these analyses was based on a combination of what was known for all North American representatives. In more recent analyses (Archibald & Averianov, unpublished data), including additional taxa and characters, this relationship holds.

### **Possible upper molars of *Paranyctoides aralensis***

Of the named therian taxa at the localities at Dzharakuduk in the Kyzylkum Desert, Uzbekistan, five taxa of 'zhelestids', the eutherian *Kulbeckia*, two deltatheridians, and

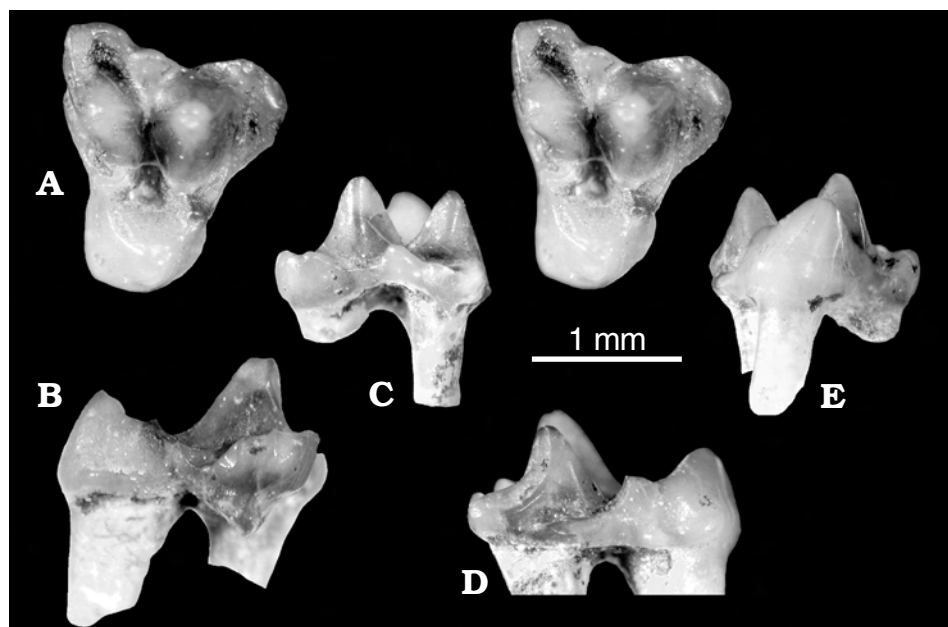


Fig. 3. *Sailestes quadrans*, CCMGE 7/117548, type, right M1. Stereophotograph in occlusal (A), anterior (B), labial (C), posterior (D), and lingual (E) views.

one marsupial constitute the medium to larger sized therian mammals (from *Mus musculus* to a well fed *Rattus norvegicus*).

The taxonomy for the small to smallest therians is in a state of flux, but probably includes three to four eutherians very similar in morphology to the recently described *Daulestes nesso* (McKenna *et al.* 2000) that range in size from the very smallest to near largest species of *Sorex*. At the larger end of this size scale is the type dentary of *Paranyctoides aralensis* described by Nesso in 1993. Morphologically, the molars in the dentary of *P. aralensis* are very similar to those discussed above for North American species (Figs. 1A, C, 2A, B, D, E). They have low, rounded trigonid cusps of similar height, little or no anteroposterior closer (i.e., compression) of the trigonid, the trigonid is quite low relative to the talonid, and the width of the talonid equals or exceeds that of the trigonid. This contrasts sharply with the higher, more trenchant-cusped trigonids and narrower talonids of the *Daulestes*-like taxa. We were able to match uppers and lowers of these small to smallest taxa except for the very smallest *Daulestes*-like lowers and the *P. aralensis* lowers.

This was the case until we compared the type lower dentition of *Paranyctoides aralensis* with the type and only known specimen of *Sailestes quadrans*, an upper molar, probably an M1. Although rather an obscure taxon, nonetheless the type had been well figured in Nesso *et al.* (1994: pl. 1: 6). To our knowledge, no one before has suggested that these taxa might be one and the same. Interestingly, in the phylogenetic analysis of Nesso *et al.* (1998), *Sailestes* was the closest sister taxon to 'zhelestids' following *Paranyctoides* spp. The closest that anyone has come to suggesting synonymy was Butler (1990: p. 546), who included only *Paranyctoides* and *Sailestes* in his

Specimen	M1																	
no.	L	AW	PW															
†CCMGE 7/11758	1.5	1.6	1.8															
ZIN C.85044	1.6	1.6	1.7															

Table 1. Measurements of *Paranyctoides aralensis* lower dentitions, M1 of *Paranyctoides* sp., (ZIN C.85044), and M1 of *Sailestes quadrans* (CCMGE 7/11758). Daggers (†) indicate types. Abbreviations as follows: L, length; W, width; TRW, trigonid width; TAW, talonid width; TRL, trigonid length; TAL, talonid length.

Specimen	p5?					m1					m2					m3				
no.	L	TRW	TAW	TRL	TAL	L	TRW	TAW	TRL	TAL	L	TRW	TAW	TRL	TAL	L	TRW	TAW	TRL	TAL
†CCMGE 67/12455											1.8	1.3	1.3	0.9	0.9	?	1.2	1.1	0.0	?
ZIN C.85044	1.7	1.2	1.1	1.0	0.7															
ZIN C.82588											?	?	1.2	?	0.8	1.7	1.1	1.0	0.8	0.9
ZIN C.82589						?	1.1	?	1.0	?										

eutherian group ‘c’ that were characterized as having ‘comparatively narrow upper molars, on which the stylar shelf is nevertheless fairly wide and bears stylar cusps. The main cusps are low, the paracone and metacone are separated, conules are strongly developed, and there is a postcingulum.’ (It must be emphasized that Butler’s insight was based upon a comparison of North American *Paranyctoides* and the Middle Asian *Sailestes*, as Nessov did not name or figure *P. aralensis* until 1993.) We also reread the original description of the upper molars given by Fox (1984) for *P. maleficus*, and this also matches closely the morphology of *Sailestes quadrans*. The following description of *Sailestes quadrans* and comparison with upper molars of *P. maleficus* rely heavily on the description of Fox (1984).

The type and only known specimen, CCMGE 7/11758, appears to be a right M1 (Fig. 3) as judged by the relative narrowness of the crown (Table 1). This contrasts with the relatively wider upper molars of *P. maleficus* shown in Fox (1984), which he did not identify as to tooth site. Also, in CCMGE 7/11758 the parastylar lobe extends somewhat more anterolabially compared to the more labially extending metastylar lobe so that the ectoflexus is shallower than on the MX’s illustrated by Fox (1984). Together these features are highly suggestive of an M1. The stylar shelf is moderately wide except labial to the paracone. The parastylar lobe is well developed with a small but distinct parastyle, and with a smaller preparastyle just lingual to the parastyle. Fox (1984) notes the same cusps and the occasional presence of a third. We regard such double cusps on the parastylar lobe as an ancestral retention, as it is known in the earliest eutherians referred to various species of *Prokennalestes* (Kielan-Jaworowska & Dashzeveg 1989) and to *Murtoilestes abramovi* (Averianov & Skutschas 2000, 2001), and apparently retained in all ‘zhelestids’, *Kennalestes*, and the *Paranyctoides* spp. that Cifelli (1990b) described from Utah. A well-worn parastylar groove separates the parastylar lobe posteriorly from the small stylocone. A weak preparacrista joins the stylocone to the anterolabial margin of the paracone. The stylar shelf is (as noted above) narrowest immediately labial of the paracone. Just posterior to this point on the stylar shelf, midway between the paracone and metacone is a cusp ‘c’ that is the largest or at least most distinct cusp on the stylar shelf. Immediately posteriorly is a smaller,



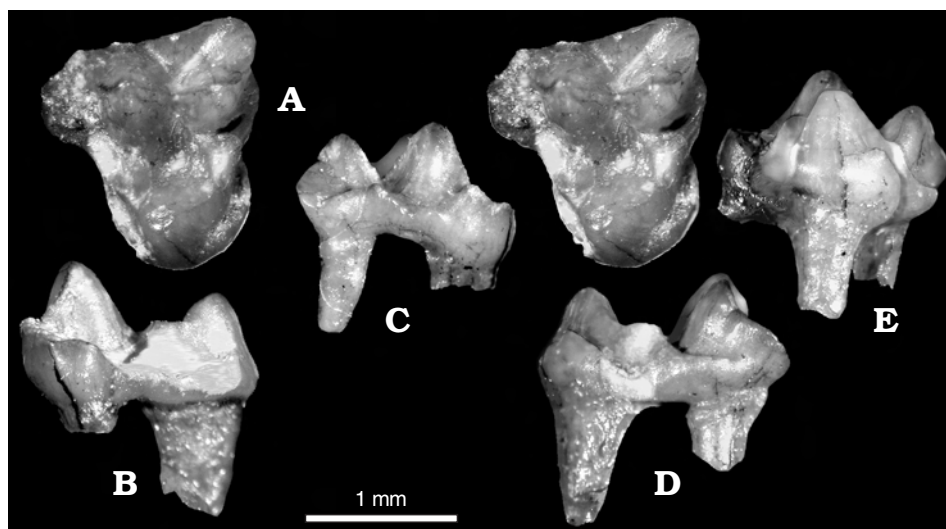


Fig. 4. *Paranyctoides* sp., ZIN C.85044, left M1. A. Stereophotograph in occlusal (A), anterior (B), labial (C), posterior (D), and lingual (E) views.

but distinct cusp 'd'. On the upper molars of *P. maleficus*, Fox (1984) reports that the second of these last two cusps is larger. Most posteriorly is the metastylar lobe; it is large but bears no distinct cusp. A distinct postmetacrista extends from the metastylar lobe to near the posterior side of the apex of the metacone. A well-developed postvallum wear facet marks its entire length. There is no discernable notch on the postmetacrista.

The paracone and metacone are separate, with the former cusp being the taller and larger of the two. A weak but distinct centrocrista runs in a straight line between the apices of these two cusps. The paraconule is only slightly larger than the metaconule, and is positioned slightly more lingually, closer to the protocone than to the paracone. Both conules have distinct conular cristae, although because of its position closer to the metacone, the premetaconular crista is considerably shorter than the postparaconular crista. The preparaconular crista continues labially as a narrow but distinct paracingulum terminating between the anterior margin of the paracone and the parastylar groove. Its counterpart, a distinct metacingulum, continues labially from the postmetacrista, merging with the crown dorsal to the midpoint of the postmetacrista. Like the postmetacrista, it bears a wear facet for postvallum shear. The moderately developed protocone is not as tall as either the para- or metacone. It is slightly expanded anteroposteriorly, which accounts for the specific epithet 'quadrans,' and the apex is canted anteriorly. The short preprotocrista contacts the paraconule while the longer, slightly posteriorly convex postprotocrista contacts the metaconule. There is a short, very narrow precingulum and an even shorter, equally narrow postcingulum. These cingula appear to be better developed in *P. maleficus* (Fox, 1984).

Another upper molar that bears a more striking resemblance to uppers of *Paranyctoides maleficus* was found at Dzharakuduk. Unlike almost all the better known taxa from Dzharakuduk, including *Sailestes quadrans* and *P. aralensis*, which come

from late Turonian–Coniacian aged localities in the Bissekty Formation, this specimen is from a Coniacian or Santonian aged locality, CBI-117, some 48 meters higher in the Aitym Formation (King, unpublished data). The site has produced very few mammals, but notable are zhelestids and multituberculates. The separation in time between the localities in these two formations is at most a few million years.

The specimen from CBI-117, ZIN C.85044, is a left upper molar, probably an M1 (Fig. 4). In many aspects it resembles the probable M1, type of *Sailestes quadrans* described above (Fig. 3). Also, the two teeth are similar in size (Table 1). ZIN C.85044 is almost complete and little worn except for the parastylar groove. There is some chemical damage that has slightly corroded and lightened the enamel along the anterolingual and to a lesser extent posterolingual portion of the tooth. Compared to the M1 of *S. quadrans*, ZIN C.85044 has slightly more robust primary cusps and conules. The para- and metacone are also relatively lower on ZIN C.85044 (compare Figs. 3 and 4). Compared to the M1 of *S. quadrans*, pre- and postcingula are much better developed on ZIN C.85044 as in other upper molars referred to species of *Paranyctoides*. On the stylar shelf, there is no ectoflexus in ZIN C.85044, compared to the slight ectoflexus on the M1 of *S. quadrans*. Each molar has a small preparastyle, parastyle, stylocone, and larger cusp ‘c’. Also both molars have a well-developed metastylar lobe but not distinct metastyler cusp. ZIN C.85044 lacks the small but distinct cusp ‘d’ present on the stylar shelf of the M1 of *S. quadrans*. ZIN C.85044 also has a very small cuspule labial to the paracone and the postmetacrista is slightly swollen at its midpoint but there is no distinct notch in the postmetacrista. For the present we think it best to refer ZIN C.85044 to *Paranyctoides* sp.

The probable M1’s of *Paranyctoides* sp. and *Sailestes quadrans* offer tantalizing but somewhat conflicting information as to what the uppers of *P. aralensis* might be like. Because of the slightly lower and slightly more robust cusps, and better developed pre- and postcingula on the probable M1 of *Paranyctoides* sp., one is tempted to refer it to *P. aralensis*. A possible, but less convincing argument is that the slightly biochronologically older M1 of *Sailestes quadrans* might be expected to have not yet evolved better developed pre- and postcingula or as robust cusps. We do not have enough evidence to decide among these two or other alternatives, but lean towards the former of the two arguments. A further concern is the possibility that molar of *Sailestes quadrans* may not even be a eutherian, but rather might be that of a non-deltatherid metatherian. The reasons are the overall morphology of the crown, the notable postvallum shear, and the fact that the marsupial *Marsasia* (Averianov & Kielan-Jaworowska 1999) is known from the same locality as *Sailestes*, CBI-4b. *P. aralensis* is not known from CBI-4b, but this in itself is not of great concern as other taxa are known from multiple localities at Dzharakuduk. We cannot resolve these matters now, but only point out our concerns.

It is also appropriate at this juncture to comment on Nessel’s (1997) naming of Sailestinae in which he placed *Sailestes*, the adapisoricolid *Bustylus* from the Paleocene of Europe (Gheerbrant & Russell 1991), and possibly the tribotherid *Bistius* from the Late Cretaceous of North America (Clemens & Lillegraven 1986). While the outline of the crown of *Bistius* is similar to that of *Sailestes*, *Bistius* has massive stylar cusps that are similar in height to the primary trigon cusps (Clemens & Lillegraven 1986). Thus, we can find no reason to suggest affinities. For *Bustylus*, comparisons

cannot be so easily dismissed. Both the upper and lower molars, and ultimate lower premolar figured by Gheerbrant & Russell (1991) bear an uncanny resemblance not just to *Sailestes* but also to the teeth of *Paranyctoides maleficus*. While rejecting the taxon Sailestinae, a more thorough comparison of *Bustylus*, *Paranyctoides*, and *Sailestes* is well warranted, but is beyond the scope of our study.

### **Additional lower teeth of *Paranyctoides aralensis* and resemblance to *Gallolestes* spp.**

In addition to comparisons of our dentaries of *Paranyctoides aralensis* with published accounts, we were able to compare this material with the following: a cast of the type of *Gallolestes pachymandibularis*, (LACM 42633) named by Lillegraven (1976), a dentary, which, as discussed below, we tentatively identified as damaged penultimate and ultimate premolars, m1–2, and m3 trigonid (provided by R. Cifelli); a cast of a left dentary (LACM 27600) with worn m1 talonid and worn m1–2 (Lillegraven, 1972) later referred to *G. pachymandibularis* (Lillegraven, 1976), and photos provided by R. Cifelli of an undescribed left dentary of *Paranyctoides* sp. A, (UMNH VP1301) from the lower Kaiparowits Formation, Utah, under study by R. Cifelli and J. Eaton.

*Gallolestes pachymandibularis* from the Late Cretaceous (Campanian) of Baja California del Norte, Mexico, was named and described by Lillegraven in 1976 based upon parts of several dentaries and lower molars. The most complete was the type specimen (LACM 42633) preserving the heel of the possible penultimate premolar, the molariform trigonid of the ultimate premolar (p5), complete m1–2, and m3 talonid.

*Gallolestes* could not be easily classified, mostly because of aspects of the molariform trigonid of the ultimate premolar. Lillegraven (1976) suggested three possibilities, only the second of which he deemed unlikely. The first interpretation was that the four more posterior teeth represented a pattern usual in many Cenozoic (but not Mesozoic) mammals, in which there is a molariform ultimate premolar (which we term p5) and three molars. This interpretation was problematic because of the kind of wear on the teeth. Wear was greatest on the presumptive ultimate premolar becoming progressively less on posterior teeth. In the majority of extant mammals, m1 erupts before p5 and thus it should have more wear than p5.

Lillegraven's second interpretation was this is marsupial with the normal count of four molars. This was deemed as unlikely based on the general eutherian appearance of individual molars. Third, this was an aberrant eutherian that has four rather than three molars. A fourth interpretation by Butler (1977) was that the ultimate premolar is probably not a permanent tooth, but rather the deciduous precursor that had been retained at least until the eruption of m3. This was given credence because of the considerable wear, smaller size, and slightly different preservation of this tooth. The greatest problem with this interpretation is that the roots are well formed, very unusual for a deciduous tooth that was soon destined to be shed. Fifth, in a description of an additional m3 and a review of the previous hypotheses, Clemens (1980) suggested that *Gallolestes* was neither a eutherian nor a metatherian but represented a third albeit aborted lineage of therian mammals.

One of the lower dental remains from Dzharakuduk referable to *Paranyctoides aralensis* is relevant to discussions of *Gallolestes*. It is ZIN C.82590, a right dentary with what we believe are most likely alveoli for p4 and a complete p5 missing the tips of the trigonid cusps (Figs. 1C, 2F, G). We cannot reject the possibility that the tooth is m1, but several lines of evidence suggest the p5 identification is most likely.

The tooth in ZIN C.82590 is of the right size and morphology to belong to *P. aralensis*. The anterior root is slightly smaller and rounder than the posterior root, matching quite well, except a slightly larger size, the partial root and alveolus preserved for p5 in the type specimen, CCMGE 67/12455. The type has one mental foramen ventral and midway between the posterior root of p4 and anterior root of p5 (Fig. 2A). A second smaller foramen is ventral to the roots of p1. ZIN C.82590 has one such foramen in the same position between p4 and p5, although positioned more dorsally on the dentary. What appears to be another foramen is situated ventral to the anterior root of p4. Fox (1984) noted two such closely spaced mental foramina in UA 16174, which he identified as the ultimate (p5) of *P. maleficus*. An edentulous dentary, ZIN C.82592 (Fig. 1D, 2C) also has one mental foramen ventral and midway between the posterior root of p4 and anterior root of p5, as well as one below the posterior root of p4. ZIN C.82592 preserves more of the anterior portion of the dentary, which has a third mental foramen below and between the two roots of the small p3 (Fig. 2C). Another edentulous dentary referable to *P. aralensis*, ZIN C.82593, repeats the pattern of the above specimens in having a mental foramen ventral and midway between the posterior root of p4 and anterior root of p5. Finally, a third edentulous dentary referable to *P. aralensis*, ZIN C.82594 is somewhat different in that the most posterior mental (elongate) foramen is ventral and midway between the posterior root of p5 and anterior root of m1. It also has a foramen below the anterior root of the small p3. Except for this last specimen, which suggests the tooth in ZIN C.82590 is m1, the position of the most posterior mental foramen in the other specimens discussed in this paragraph supports the view that the tooth in ZIN C.82590 is p5. It should be noted that ZIN C.82594 is a young individual and thus the position of the mental foramina in this individual may not reflect the adult condition.

There are three trigonid cusps forming a nearly equilateral triangle on the p5 of ZIN C.82590. There was some apparently preburial damage to the cusp apices, but it appears the protoconid was not only the largest but tallest followed by the metaconid and then the paraconid. The trigonid alone might suggest an aberrant molar trigonid, but the talonid is not fully comparable in size to that of a molar. The talonid is almost as wide as the trigonid but is quite short. The actual talonid basin is composed of a smaller, shallow, rimmed basin occupying only the lingual half of the talonid. The labial half forms a sloping surface.

Four possibilities seem most likely for the identification of ZIN C.82588. It is an m1, p5 (ultimate premolar), dp5, or is a molar of another taxon. It does not match the morphology of any other taxon known from Dzharakuduk but does match that seen in *Paranyctoides aralensis*. Thus, we feel the last alternative is the least likely. Identification as a dp5 also seems unlikely. The roots of this tooth are well formed and the dentary is deeper than in the type specimen, which has a fully erupted m3. This suggests that individual preserving this tooth was an older individual than the type specimen. Retention of a dp5 until after the m3 is erupted is rare in eutherians. The two

most likely identifications are an m1 or p5. Based on the preceding discussion of the positions of mental foramina, crown morphology, and wear, we tentatively identify the tooth in ZIN C.82590 as a p5 or ultimate premolar. With this major assumption, it would appear that ZIN C.82588 is similar *Gallolestes* in the morphology of its ultimate premolar.

Of further note, the type specimen, CCMGE 67/12455, as well as three edentulous dentaries (ZIN C.82592, 82593, and 82594) preserve alveoli or roots for five premolars. The third premolar is distinctly reduced as seen in the (larger) 'zhelestids' from Dzharakuduk.

Two other dental specimens that we refer to *Paranyctoides aralensis* do not add as much intriguing information as the dentary with p5, but do provide information on other aspects of the lower dentition. ZIN C.82588, a left dentary with the posterior alveolus for p5, alveoli for m1, m2 talonid, and complete m3 is very similar to the type dentary, CCMGE 67/12455, in its preserved portions of the dentary and dentition (Figs. 1C, 2D, E). Unlike in the type, however, the m3 of ZIN C.82588 is complete, and the m2 talonid and m3 show little wear. As in the m2 trigonid of the type, the m3 trigonid of ZIN C.82588 shows little or no anteroposterior shortening with the bases of the para- and metaconid separate. On both, the paraconid is slightly labial of the metaconid.

The second additional dental specimen, ZIN C.82589, a molar trigonid, is similar in morphology to the trigonid in the other specimens, except that the paraconid is slightly more labial, suggesting, as is often the case in Late Cretaceous therians, that this is a m1. This specimen has a very marked postvallid wear facet. In only the m3 of ZIN C.82588 can we estimate trigonid cusp height (Figs. 1C, 2E). The larger protoconid and metaconid are of similar height, while the paraconid is lower. The anterolingual edge of the paraconid has a faint vertical ridge that is very well developed in most, if not all Late Cretaceous metatherians. At least in part this seems to be the result of the hypoconulid appressing tightly against the paraconid and paracristid of the next more posterior molar.

Both the trigonid and talonid cusps are somewhat inflated. As is usual for most Late Cretaceous eutherians, the talonid is about half the height of the trigonid, but both are notably lower than in most Late Cretaceous eutherians. This contributes to the somewhat robust appearance of the cusps. The cristid obliqua contacts the posterior of the trigonid at the notch in the protocristid. The hypoconid is the largest but shortest talonid cusp, with height increasing from the hypoconulid to entoconid. On m3, the hypoconulid is set somewhat apart and more posterior than on m2. This is the usual pattern for Late Cretaceous eutherians. There is a precingulid on the more anterolabial aspect of the molars. There is a hint of a postcingulid on the posterolabial margin of the m2 hypoconid.

At first glance, viewed occlusally, the hypoconulid appears almost equidistant between hypoconid and entoconid, or ever so slightly closer to the entoconid on m3 (Fig. 1A, C). On closer inspection on both m2 and m3 there is a shallow anterolingually oriented trough that separates the hypoconid on one side from the hypoconulid and entoconid on the other. Viewed lingually these latter two cusps seem to be part of the same subdivided ridge. The talonids on m2 and m3 (and probably the unknown m1 talonid) are nearly as wide or are as wide as the trigonid. Nessov *et al.* (1998) argued



that the increased width in the talonid of eutherians such as in ‘zhelestids’ seems to begin by a labial expansion of the hypoconid, with the result that the hypoconulid and entoconid may be more approximated. This pattern seen in *Paranyctoides aralensis* is reported for at least some molars of *P. sternbergi* (Fox 1979), *Gallolestes pachymandibularis* (Lillegraven 1976), and *G. agujaensis* (Cifelli 1994). This is synapomorphic with ‘zhelestids’ (Nessov *et al.* 1998).

A similar expansion of the hypoconid may have occurred in Late Cretaceous metatherians, but in these taxa a much more obvious ‘twinning’ of the entoconid and hypoconulid is the usual result. In such metatherians these cusps are usually much closer and are normally lined up in an anteroposterior axis compared to any Late Cretaceous eutherians, such as those listed above that show only some approximation of hypoconulid and entoconid.

The lower molars of *Paranyctoides aralensis* differ from those of *Gallolestes pachymandibularis* and of other species assigned to *Paranyctoides* in several ways. Although in all of these species there is a general decrease in molar height, in all except *P. aralensis* the talonid is approximately half the height of trigonid. In *P. aralensis* the talonid ranges from about half the height of the trigonid (m3) to almost three-quarters the height of trigonid (m2’s). Also, in *P. aralensis* compared to these other taxa, the molar talonids (only known definitely from m2 and m3 in *P. aralensis*) are relatively anteroposteriorly shorter, and both the trigonids and talonids are relatively wider with more robust cusps. In addition to the overall shortening of the talonid on m3 of *P. aralensis*, the m3 hypoconulid is not as distinctly extended posteriorly as in the m3’s of these other taxa. Although we have not analyzed the polarity of these characters, we suggest that all the states seen in *P. aralensis* are derived relative to the states seen in these other taxa. This is in spite of the fact that *P. aralensis* is the biochronologically oldest of these taxa. We next consider the phylogenetic implications of these as well as other characters.

## Phylogenetic considerations

Fig. 5A and B show what we regard as two of the more likely scenarios for the relationships between ‘zhelestids’ and the *Paranyctoides/Gallolestes* clade. In the phylogenetic analyses of Nessov *et al.* (1998; Archibald 1996) *Paranyctoides* was always the sister taxon to ‘zhelestids.’ More recent analyses (e.g., Archibald & Averianov unpublished data) suggest that the *Paranyctoides* and *Gallolestes* form a clade within a well-supported ‘Zhelestidae’. Some of the character state changes noted within the *Paranyctoides/Gallolestes* clade must be hypothesized for some terminal taxa, as the

Fig. 5. Two phylogenetic scenarios for *Paranyctoides* and *Gallolestes*. The clades shown as solid lines and the characters that unite them in **A** are from a phylogenetic analysis (Archibald and Averianov, unpublished data). The clades shown as dashed lines are possible relationships but are not based upon a phylogenetic analysis. **A**. This scenario assumes the submolariform tooth anterior to m1 in *Gallolestes pachymandibularis* is the ultimate premolar (p5) as is a similar tooth known for *Paranyctoides aralensis*. Note it requires two migration events for the *Gallolestes–Paranyctoides* clade. **B**. This scenario, which we tend to favor, assumes the submolariform tooth anterior to m1 in *G. pachymandibularis* is the ultimate deciduous premolar (dp5) and the similar tooth in *P. aralensis* is an m1. Note it requires one migration event for the *Gallolestes–Paranyctoides* clade.



appropriate part of the dentition is not known. Such changes were not included in the above noted phylogenetic analysis so they are simply hung on the tree, as indicated by the dashed lines.

Within the *Paranyctoides/Gallolestes* clade, possession of stylar cusps ‘c’ and ‘d’ are treated as synapomorphic for the included taxa. The early eutherians *Prokennalestes trofimovi* and *P. minor* (Kielan-Jaworowska & Dashzeveg 1989) have stylar cusps, while *Murtoilestes abramovi* (Averianov & Skutschas 2001) does not. Whether other Late Cretaceous eutherian taxa lost them, while they were retained in the *Paranyctoides/Gallolestes* clade, or they were regained in this clade remains uncertain. Although the evolutionary linkage of characters must be approached with caution, the ancestral retention of a wide stylar shelf in this clade suggests the stylar cusps might also be a retention.

The reportedly less robust cusps in *Paranyctoides maleficus* (and in the very poorly known *P. megakeros* as noted by Lillegraven & McKenna 1986) were regarded by Fox (1984) as an ancestral trait, a very reasonable point of view. We simply chose what appears to be the more parsimonious course and treated this as a derived state rather than viewing the increased dental robusticity in the ‘zhelestids’ and the other members of the *Paranyctoides/Gallolestes* clade as having evolved twice. Cifelli (1990b) noted, however, that he was unable to distinguish molars of *P. sternbergi* and *P. maleficus*, so the degree of difference between these taxa may not be as great as suggested by Fox (1984).

The possible molarization of the p5 trigonid and its possible eruption before m1 or m2 are the major reasons for the scenario in Fig. 5A. Of course these conditions can only be hypothesized for *Paranyctoides aralensis* as no p5 and m1 are known in a single specimen. If this unlikely, but possible pattern of molarization and early eruption of p5 are not true, then the scenario in Fig. 5B is more likely.

Finally, as we have only two upper molars possibly belonging to or at least related to *Paranyctoides aralensis*, and which differ from one another, we cannot make any definitive decisions regarding the upper dentition. We feel most confident that ZIN C.85044 belongs at least to *Paranyctoides* if not to *P. aralensis*. As discussed, CCMGE 7/11758, the type and only specimen of *Sailestes quadrans* is more problematic. *Paranyctoides* resembles metatherians in its wide stylar shelf and variably present cusps ‘c’ and ‘d’. This is also the condition in *Sailestes quadrans*. In addition, however, *Sailestes quadrans* has very weak pre- and postcingula, which are more similar to many metatherians rather than to species of *Paranyctoides* for which uppers are known. Although we include it for completeness, our best guess is that *Sailestes quadrans* is a metatherian.

## Biogeographic and biochronologic considerations

*Paranyctoides* is known from the late Turonian through possibly the Santonian of Middle Asia, while it, along with *Gallolestes* are known from the early and middle Campanian of North America. Turonian-aged therians have been reported from North America (Cifelli 1990b), but nothing referable to *Paranyctoides* or *Gallolestes* has been described. The likely sister taxa to the *Paranyctoides–Gallolestes* clade, mem-

bers of 'Zhelestidae', are also known from the Turonian through Coniacian of Middle Asia and Campanian of Kazakhstan, but first known in North America only in the mid-Campanian. A 'zhelestid' is also reported from the Cenomanian of Japan (Setoguchi *et al.* 1999). Further, there is a hint that in Middle Asia 'zhelestids' or possibly earlier related taxa are known from the Cenomanian (e.g., *Eozhelestes mangit* from Sheikhdzheili, western Uzbekistan, Nesso *et al.* 1997; Nesso *et al.* 1998). This suggests very tentatively that migration is from west to east via Beringia. If this is the case and if the scenario in Fig. 5A is correct, there were three migration events to North America, but only two if the more likely scenario in Fig. 5B is correct.

Finally, it is of interest that to date, neither the *Paranyctoides*–*Gallolestes* clade nor 'Zhelestidae' are definitely known from the rich Campanian sites of the Gobi Desert. Nesso *et al.* (1998) suggested this might well be a result of ecology, as the North American and Uzbekistani sites are low coastal plains while those in the Gobi are more inland.

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