

# Variation and taxonomy of Asiamerican eutherian mammal *Paranyctoides*

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**Abstract:** A parsimony analysis of the distribution of 408 characters in 73 taxa of Cretaceous eutherians and related taxa places three species of *Paranyctoides*, the Asiatic *P. quadrans* and the North American *P. sternbergi* and *P. maleficus*, into a monophyletic taxon supported by three unambiguous synapomorphies. In this analysis *P. quadrans* has three autapomorphies, but in the analysis using combined terminal taxon for the entire sample of North American *Paranyctoides* two of these autapomorphies (development of styler cusps C and D on upper molars) disappeared because these characters are also variably present in the North American sample. The remaining autapomorphy of *P. quadrans*, m3 shorter than m2, is known from a single specimen and also may be affected by individual variation. The North American sample of *Paranyctoides* cannot be clearly separated into distinct species on morphological or morphometric grounds and is considered as representing a single species, *P. sternbergi* Fox, 1979 (= *P. maleficus* Fox, 1984, syn. nov.). It differs from the Asiatic *P. quadrans* (Nesov, 1993) only in having a sharp lingual ridge on p5 and m3 longer than m2. *Paranyctoides* is the sister taxon to Zhelestidae; this clade is supported by four unambiguous synapomorphies.

**Résumé :** Une analyse de parcimonie de la distribution de 408 caractères parmi 73 taxons d'euthériens et autres taxons apparentés du Crétacé place trois espèces de *Paranyctoides*, *P. quadrans*, une espèce asiatique, ainsi que *P. sternbergi* et *P. maleficus*, des espèces nord-américaines, dans un taxon monophylétique supporté par trois synapomorphies non ambiguës. Dans cette analyse, *P. quadrans* compte trois autapomorphies, mais dans l'analyse faisant appel à un taxon terminal combiné pour l'échantillon entier de *Paranyctoides* nord-américains, deux de ces autapomorphies (développement des cuspidés stylières C et D sur les molaires supérieures) disparaissent puisque ces caractères sont également présents de manière variable dans l'échantillon nord-américain. La troisième autapomorphie de *P. quadrans*, le fait que m3 est plus courte que m2, n'est connue que d'un seul spécimen et pourrait être assujettie à des variations individuelles. L'échantillon nord-américain de *Paranyctoides* ne peut être clairement subdivisé en espèces distinctes sur des bases morphologiques ou morphométriques et est considéré ne représenter qu'une seule espèce, *P. sternbergi* Fox, 1979 (= *P. maleficus* Fox, 1984, syn. nov.), qui se distingue de *P. quadrans* (Nesov, 1993), l'espèce asiatique, seulement par la présence d'une crête linguale acérée sur p5 et le fait que m3 est plus longue que m2. *Paranyctoides* est le taxon-frère des zhelestidés; ce clade est supporté par quatre synapomorphies non ambiguës. [Traduit par la Rédaction]

## Introduction

The rare Late Cretaceous mammal *Paranyctoides* Fox, 1979, was first announced as the oldest eutherian mammal from North America (Fox 1970). Subsequently, two named species, *P. sternbergi* Fox, 1979, and *P. maleficus* Fox, 1984b, and several unnamed species of *Paranyctoides* have been reported from Aquilan, Judithian, and Lancian strata of North America (Fox 1979, 1984a, 1984b; Rigby and Wolberg 1987; Cifelli 1990; Montellano 1992; Kielan-Jaworowska et al. 2004). The genus was identified also from the Turonian Bissekty and Aitym formations of Kyzylkum Desert in Uzbekistan (Nesov 1993; Archibald and Averianov 2001, 2005; Averianov and Archibald 2003, 2013). Originally *Paranyctoides* was placed in the lipotyphlan family Nyctitheriidae (Fox 1979, 1984a, 1984b) but currently it is recognized as a non-placental eutherian mammal (Wible et al. 2007, 2009; Archibald and Averianov 2012; Averianov and Archibald 2013). The Asiatic material of *Paranyctoides* has been recently revised by Averianov and Archibald (2013), who recognized one valid species from the Bissekty Formation, *P. quadrans* (Nesov 1982). However, Montellano-Ballesteros et al. (2013) have questioned the attribution of the Asiatic species to the genus

*Paranyctoides*. These authors described the recognition of *Paranyctoides* in Asia as “surprising” and correctly noted that it is the only genus of Mesozoic eutherians found in both North America and Asia. To stress the unusual nature of this occurrence, they noted that there is only one family-level taxon of therians known to occur in Asia and North America, the Deltatheridiidae. This is not correct because there are two more family-group taxa of Cretaceous eutherians, known from the Late Cretaceous of both North America and Asia, Cimolestidae and Zhelestidae (Wible et al. 2007, 2009; Archibald and Averianov 2012). If other groups of mammals are considered, this situation is even less unusual. The symmetrodontan clade Spalacolestinae is known from the Late Cretaceous of North America and Asia (Cifelli and Gordon 1999; Averianov 2002; Averianov and Archibald 2003). This case is especially interesting because spalacolestine symmetrodontans and *Paranyctoides* coexisted in the Bissekty and Aitym formations of Asia and in the Milk River and Wahweap formations of North America (Fox 1976; Cifelli and Madsen 1986; Kielan-Jaworowska et al. 2004). The North American *Symmetrodontoides* Fox, 1976, is known from the isolated teeth (Fox 1976, 1985; Cifelli and Madsen 1986), whereas the Asiatic *Shalbaatar* Nesov, 1997, is based on edentulous dentary

Received 2 April 2013. Accepted 2 June 2013.

Paper handled by Associate Editor Hans Sues.

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fragments (Nesov 1997; Averianov and Archibald 2003). It would not be surprising if these taxa were found to be synonymous in the future. There is also an Early Cretaceous eutriconodontan, *Gobiconodon Trofimov*, 1978, which was widely distributed in Asia, Europe, North Africa, and North America (Trofimov 1978; Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Rougier et al. 2001; Cuenca-Bescos and Canudo 2003; Li et al. 2003; Sigogneau-Russell 2003; Sweetman 2006). The current rarity of shared genus-level mammalian taxa between Asia and North America largely reflects our poor knowledge of late Mesozoic terrestrial ecosystems.

Montellano-Ballesteros et al. (2013) summarized the characters that they considered diagnostic for *Paranyctoides* and concluded that the Asiatic material is not referable to this taxon. They also revised the North American materials of *Paranyctoides* and recognized six valid species. The arguments and conclusions of these authors are critically evaluated in this paper. Citing more general literature sources, Montellano-Ballesteros et al. (2013) noted the uncertainty in the homologies of teeth in going from five premolars in stem eutherians to four premolars in placentals. More relevant recent literature has established homologies of these teeth in these taxa (Averianov et al. 2010; Archibald and Averianov 2012; O'Leary et al. 2013), with the penultimate premolar being P4/p4 and ultimate premolars being P5/p5. Montellano-Ballesteros et al. (2013) also cast doubt on the referral of edentulous dentary fragments from the Bissekty Formation to *P. quadrans* (Averianov and Archibald 2013) but did not explain their reasons for this concern. Edentulous dentary fragments are the most common mammalian elements in these fluvial Cretaceous deposits. The study of such specimens provided a wealth of information on dental formulae, relative size of incisors, canines, and premolars, position of mental foramina, mandibular symphysis, and other morphological characters important for phylogenetic analysis (Archibald and Averianov 2006, 2012). Such materials referable to *Paranyctoides* are undoubtedly present in the North American collections, and their study by other specialists could considerably promote our understanding of this rare and interesting mammal.

#### Institutional abbreviations

AMNH, American Museum of Natural History, New York; CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; MNA, Museum of Northern Arizona, Flagstaff, Arizona; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; UALVP, University of Alberta, Laboratory for Vertebrate Paleontology, Edmonton, Alberta; UCMP, University of California Museum of Paleontology, Berkeley, California; UMNH VP, Utah Museum of Natural History Vertebrate Paleontology Collection, Salt Lake City, Utah; UNM-B, Bureau of Land Management collections housed at University of New Mexico, Albuquerque, New Mexico; URBAC, Uzbek/Russian/British/American/Canadian Joint Paleontological Expedition, mammal specimens housed in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.; ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

#### Geographic and geologic settings of *Paranyctoides* occurrences in Asia and North America

Remains of *Paranyctoides* have been found in two stratigraphic units in Asia and eight in North America. The information on these units and their mammalian faunas, arranged from the oldest to the youngest, is summarized as follows.

(1) Bissekty Formation. The Bissekty Formation is distributed in the Central Kyzylkum Desert of Uzbekistan and composed of the cross-bedded fluvial sandstones with discontinuous intraformational conglomerates, which represent flooding surfaces resulting from regional changes in depositional regime

following drops in eustatic sea level (Archibald et al. 1998; Nesov et al. 1998; Redman and Leighton 2009). The continental Bissekty Formation is intercalated between the marine or near-shore marine Kendyktube and Aitym formations which produced remains of orthostratigraphically useful invertebrates, allowing precise dating of the Bissekty Formation as middle-late Turonian (Pyatkov et al. 1967; C. King, personal communication). The Bissekty Formation produces one of the richest Cretaceous mammalian faunas known to date, which is notable for the predominance of eutherian mammals (Archibald and Averianov 2005). In addition to the eutherian *Paranyctoides*, this fauna includes a spalacotheriid symmetrodontan, a multituberculata, a metatherian, and several taxa of asioryctitherian, zalambdalestid, and zhelestid eutherians (Archibald and Averianov 2003, 2006, 2012; Averianov and Archibald 2003, 2006, 2013; Averianov et al. 2010).

- (2) Aitym Formation. This is stratigraphic unit overlying the Bissekty Formation in the Central Kyzylkum Desert, Uzbekistan. The unit is formed by sandstones deposited in a marginal marine environment and is rich in the remains of marine invertebrates and sharks of late Turonian to possibly early Coniacian age (Archibald et al. 1998; Nesov et al. 1998). A few terrestrial vertebrates have been found in this unit, including some mammal specimens. The mammalian fauna appears to be very similar to that of the Bissekty Formation and includes the same or closely related species (Averianov 1999; Averianov and Archibald 2003, 2013; Archibald and Averianov 2005, 2012).
- (3) Milk River Formation. The Milk River Formation is exposed along the Milk River in southern Alberta, Canada. It is divided into a marine lower and a terrestrial upper member; the latter is composed of argillaceous sandstones and has produced a diverse vertebrate fauna of late Santonian to early Campanian age (Leahy and Lerbekmo 1995; Gao and Fox 1996; Braman 2001). The Aquilan, the oldest of the North American Late Cretaceous land-mammal ages, is defined on the basis of the mammalian fauna from the upper Milk River Formation (Cifelli et al. 2004; Kielan-Jaworowska et al. 2004). This fauna is notable for the first appearance of Eutheria in North America, represented by *Paranyctoides*. The purported Early Cretaceous North American eutherian *Montanalestes* is a stem marsupial (Averianov et al. 2010). Other mammals of from the upper Milk River Formation include the last eutriconodontans and spalacotheriid symmetrodontans known in the fossil record and diverse multituberculates and metatherians (Fox 1969, 1970, 1971a, 1971b, 1972, 1976, 1980, 1982, 1984a, 1984b, 1985; Kielan-Jaworowska et al. 2004).
- (4) Judithian age occurrences in North America. *Paranyctoides* becomes widely distributed in North America during the next land-mammal age, the Judithian, which is equivalent to the late Campanian (Cifelli et al. 2004; Kielan-Jaworowska et al. 2004). This age it is represented by the Dinosaur Park Formation in southern Alberta, Canada, the Wahweap and Kaiparovits formations in Utah, USA, the Judith River Formation in Montana, USA, and the Kirtland Shale in New Mexico, USA (Fox 1979, 2005; Rigby and Wolberg 1987; Cifelli 1990; Montellano 1992; Montellano-Ballesteros et al. 2013). The mammalian fauna of the Judithian age is dominated by diverse multituberculates and metatherians; eutherians are represented by zhelestids, *Cimolestes*, *Gypsonictops*, and *Paranyctoides*; and there are also some tribosphenic taxa of uncertain affinities (Cifelli et al. 2004; Kielan-Jaworowska et al. 2004; Archibald and Averianov 2012).
- (5) Lancian age occurrences in North America. The late Maastriichtian Lancian mammal fauna of North America is the best-sampled and -studied Mesozoic mammalian fauna in the world, known from numerous localities and large numbers of specimens (Cifelli et al. 2004; Kielan-Jaworowska et al. 2004).

*Paranyctoides* is a rare element in this fauna and is known from mostly unpublished materials (Hunter and Archibald 2002; Montellano-Ballesteros et al. 2013). The only published specimen is a lower molar from the Lance Formation of Wyoming, USA (Clemens 1973: figs. 28e–28g). Similar to the Judithian fauna, the Lancian mammalian fauna is dominated by multituberculates and metatherians but also has a greater diversity of eutherians (Cifelli et al. 2004; Kielan-Jaworowska et al. 2004).

## Re-evaluation of distinctions between Asiatic and North American species of *Paranyctoides*

Describing differences between the Asiatic and North American species of *Paranyctoides*, Montellano-Ballesteros et al. (2013) separately compared CCMGE 77/11758 (M1) and URBAC 04-347 (M2) with the entire sample of upper molars from North America. This method of comparison confounds differences between tooth positions, exaggerating the differences between the two samples, because the North American sample consists of both M1s and M2s and some of the observed differences are caused by positional variation between M1 and M2. In the following, we evaluate the proposed differences between *P. quadrans* and North American taxa.

### Upper molars

According to Montellano-Ballesteros et al. (2013), M1 of *P. quadrans* differs from M1–2 of North American species by having (1) nearly quadrate outline, (2) narrow stylar shelf, (3) no ectoflexus, (4) a large and distinct stylar cusp C, (5) a distinct stylar cusp D, (6) protocone distinctly lower than the paracone, (7) protocone mesiodistally expanded, (8) parastylar lobe extended mesially, and (9) paraconule closer to protocone.

The M1 of *P. quadrans* is somewhat rectangular but not quadrate (character 1 from the list in the preceding text), its crown width is some 20% greater than the crown length. The squarish crown shape is characteristic for M1s. The M1 (UALVP 5520) from the Milk River Formation (Fox 1970: fig. 1; 1984b: figs. 4e, 4f; Montellano-Ballesteros et al. 2013: figs. 1F–1J) has the crown width with 16% greater than the crown length, which is similar to the M1 of *P. quadrans*. The definite M1 (OMNH 21977) from the Kaiparowits Formation (Cifelli 1990: figs. 4K–4M) is even more squarish, having the crown width only 6% greater than the crown length.

The width of the stylar shelf also varies between M1s and M2s, being narrower in M1s. In the M1 of *P. quadrans* the stylar shelf is narrower than in the M1 from the Kaiparowits Formation (OMNH 21977), but is comparable to the M1 from the Milk River Formation (UALVP 5520) in which the width of the stylar shelf is the same.

The M1 of *P. quadrans* (CCMGE 77/117) has an ectoflexus, *contra* Montellano-Ballesteros et al. (2013), although it is not as pronounced as in the North American M1s (UALVP 5520 and OMNH 21977). On the M2s, the ectoflexus appears much deeper compared with M1 because the parastylar lobe is more labially directed.

The small stylar “cusps” C and D, which are merely crown crenulations in CCMGE 77/117 (M1 of *P. quadrans*), have also been described for M1 (OMNH 21977) from the Kaiparowits Formation (Cifelli 1990: 352): “The stylar shelf is broad and bears two marginal cusps in addition to the stylocone, one at the posterior margin of the ectoflexus, and another, larger cusp posterior to that, in the position of cusp D.” The only difference from the condition in *P. quadrans* is that the cusp C is larger in the former. Distinct enamel crenulations, exactly as in CCMGE 77/117, can be seen along the stylar shelf of M1 (UALVP 16180) from the Milk River Formation (Fox 1984b: figs. 4a, 4b; Montellano-Ballesteros et al. 2013: figs. 1A–1E).

We found no systematic differences between *P. quadrans* and the North American species in the height of the protocone relative to the paracone. The height of the protocone, measured along

the mesial side from the base of the crown, is 78% of the paracone height in CCMGE 77/117, whereas in the North American M1s it varied from 72% in UALVP 16180 to 81% in UALVP 5520.

There is no difference in the mesiodistal expansion of the protocone in M1 of *P. quadrans* compared with the M1s from North America. In CCMGE 77/117 the mesiodistal width of the protocone is 54% of the mesiodistal length of the crown. In North American M1s it is 57% (UALVP 5520), 55% (UALVP 16180), or 50% (OMNH 21977).

In CCMGE 77/117 the parastylar lobe is extended mesially. In Cretaceous eutherians this is a characteristic feature of M1 compared to M2 in which the parastylar lobe is extended mesiolabially. The mesial lobe is similarly mesially extended in the M1s from North America (UALVP 5520, 16180, OMNH 21977).

Montellano-Ballesteros et al. (2013) claim that the paraconule is closer to the protocone in the North American sample of M1s, but not in *P. quadrans*. In CCMGE 77/117 the distance between the paraconule and protocone apices, measured along the straight line, is 76% of the distance between the protocone and metaconule apices. In the North American M1s it is 61% (OMNH 21977), 63% (UALVP 16180), or 68% (UALVP 5520).

The M2 of *P. quadrans* differs from M1–2 of the North American species according to Montellano-Ballesteros et al. (2013) in having (1) a large stylar cusp C, (2) a small stylar cusp D, (3) paracone and metacone relatively low and separated by a deep groove, (4) paraconule closer to the protocone, and (5) prominent protocone, approaching the height of the major labial cusps.

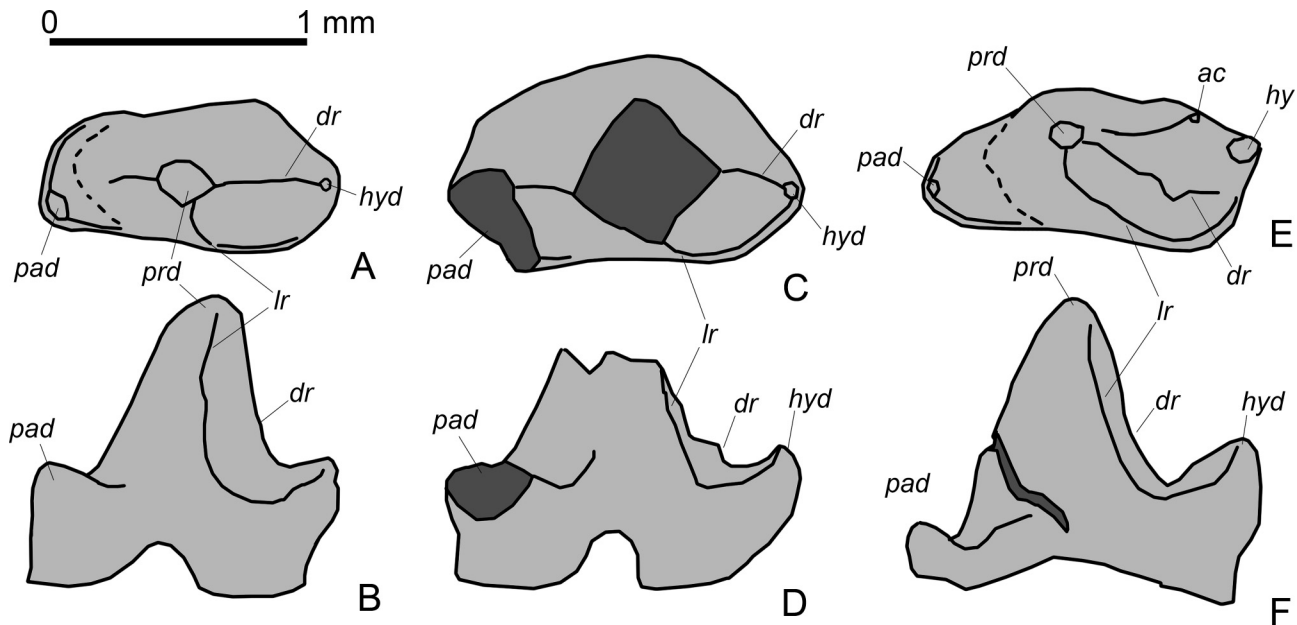
A single M2 of *P. quadrans* (URBAC 04-347) has a large stylar cusp C and a much smaller but still distinct cusp D (Averianov and Archibald 2013: fig. 1A). The development of the stylar cusps C and D is highly variable in the sample of M2s from North America. In the sample from the Milk River Formation stylar cusps are absent in UALVP 16173 (Fox 1984b: figs. 4c, 4d); in UALVP 16169 (Fox 1984b: figs. 3a–3c) there is a small enamel crenulation in the place of cusp D; and in UALVP 16172 (Montellano-Ballesteros et al. 2013: figs. 1K–1O) there are several small enamel crenulations along the ectoflexus margin. In TMP 2004.021.0002 from the Dinosaur Park Formation (Montellano-Ballesteros et al. 2013: figs. 2A–2E), cusp C is lacking but there is a distinct cusp D, of the same size and position as in URBAC 04-347. Among two M2s from the Judith River Formation the stylar cusps are lacking in UCMP 144822 (personal observation by A.A.) but UCMP 118603 (Montellano 1992: fig. 28b; personal observation by A.A.) has a large stylar cusp C and a minute stylar cusp D, exactly as in URBAC 04-347. The variation in the ectoflexus cuspules was previously mentioned for the sample from the Milk River Formation by Fox (1984b: 14), who did not find them “taxonomically significant”.

The paracone and metacone in URBAC 04-347 are heavily worn and were considered by Montellano-Ballesteros et al. (2013) as “relatively low”. The groove between the paracone and metacone in URBAC 04-347 has the same depth, as in, for example, TMP 2004.021.0002. Interestingly, a deep valley between a widely separated paracone and metacone was cited as a character diagnostic for *Paranyctoides* (Fox 1979: 122). Consequently, this character, “paracone and metacone well separated”, was included in the revised diagnosis of *Paranyctoides* by Montellano-Ballesteros et al. (2013). Nevertheless, these authors consider that “paracone and metacone separated by deep groove” would differentiate *P. quadrans* from North American species. As noted earlier in the text, this is not the case.

In URBAC 04-347 the distance between the protocone and paracone is 68% of the distance between the protocone and metaconule, which is in the range of variation for the North American sample of M2s: 57% (TMP 2004.021.0002), 67% (UALVP 16172), 81% (UCMP 118603).

As noted earlier, the paracone and metacone in URBAC 04-347 are heavily worn, which gives the incorrect impression that the protocone is prominent and approaching the height of the major

**Fig. 1.** Variation of p5 in *Paranyctoides*: URBAC 03-204 from the Bissekty Formation in occlusal (A) and lingual (B) views; UALVP 16174 from the Milk River Formation in occlusal (C) and lingual (D) views (reversed); UALVP 14822 from the Dinosaur Park Formation in occlusal (E) and lingual (F) views. C–F modified from Montellano-Ballesteros et al. (2013). Abbreviations: ac, additional cusp; dr, distal ridge; hyd, hypoconid; lr, lingual ridge; pad, paraconid; prd, protoconid. The broken parts of the crown are marked by dark grey.



labial cusps. The claim that protocone is prominent and approaching the height of the major labial cusps in M2 of *P. quadrans*, made by Montellano-Ballesteros et al. (2013), also contradicts their claim that in M1 of the same species the “protocone distinctly lower than the paracone”.

#### Ultimate lower premolar

Montellano-Ballesteros et al. (2013) noted two characters distinguishing p5 of *P. quadrans* (URBAC 03-204; Averianov and Archibald 2013: fig. 2) from the sample of North American p5s: (1) the sharp ridges that descend posteriorly from the apex of the protoconid are lacking, and (2) the talonid is not bicuspid. The latter character was considered of great importance. There are three p5s in the North American sample: UALVP 16174 from the Milk River Formation (Fox 1984b: figs. 1a–1c; Montellano-Ballesteros et al. 2013: figs. 1P–1T) and UALVP 14822 (Fox 1979: figs. 2a–2c; Montellano-Ballesteros et al. 2013: figs. 2K–2O) and UALVP 14823 from the Dinosaur Park Formation. The latter specimen was mentioned by Fox (1979) and Montellano-Ballesteros et al. (2013) but was never figured or described.

The structure of the premolariform p5 in *P. quadrans* is very similar to that in basal zhelestids, which have no metaconid or metaconid swelling, as in *Borisodon kara* (Nesov, 1993) (Archibald and Averianov 2012). In basal zhelestids, as well as in *Paranyctoides*, there are two ridges extending down the crown from the protoconid apex and delimiting labially and lingually a concave area on the distolingual face of the protoconid (Figs. 1A, 1B). UALVP 14822 and UALVP 16174 differ from this condition only in that the lingual ridge is sharp and more pronounced. Development of this ridge is highly variable in zhelestids (Archibald and Averianov 2012) and has no taxonomic importance.

In the “bicuspid” talonid in UALVP 14822, one cusp is minute, merely an enamel crenulation, along the distal cingulid labial to the talonid cusp (= hypoconid; Fig. 1E) (Montellano-Ballesteros et al. 2013: fig. 2K). Fox (1979: 119) previously described this cusp in this specimen as a possible entoconid. However, in the other p5 from North America (UALVP 16174), with a completely preserved talonid, this cusp is absent and the talonid is unicuspid (Fig. 1C).

#### Lower molars

Montellano-Ballesteros et al. (2013) note the following “important” characters differentiating *P. quadrans* from the North American sample of lower molars: (1) the trigonid is less than twice the height of the talonid; (2) the talonid basin is broader; (3) the hypoflexid notch is remarkably deep; (4) the paraconid is placed more anteriorly; (5) the last molar is smaller than the preceding; (6) the hypoconid is placed lingually with a slight approximation to the entoconid; (7) the shape of the crown is more nearly quadrate; and (8) the cusps are more rounded.

Unfortunately, all known lower molars from the Bissekty Formation are variably worn and not suitable for precise measurement of cusp height. In ZIN 85294 from the Aitym Formation (Averianov and Archibald 2003: figs. 7d, 7e) the hypoconid height, measured along the labial side, is 78% of the protoconid height. In the unworn UALVP 14822 from the Dinosaur Park Formation this ratio is 59%.

The talonid width (TAW) in the sample of m1–2s from the Bissekty and Aitym formations is 100% of trigonid width (TRW) (CCMGE 67/12455), 109% (URBAC 03-215), or 110% (ZIN 85294) (Averianov and Archibald 2013). In the m3s from the Bissekty Formation this ratio is 91% (ZIN 82588) or 93% (CCMGE 67/12455). In the sample from the Milk River Formation the TAW/TRW ratio is 110%–129%,  $M = 114.8\% \pm 3.58\%$  ( $n = 5$ ;  $n =$  number of samples) for m1, 109% for m2, and 82%–91% ( $n = 2$ ) for m3 (Fox 1984b: table 1). In the sample from the Dinosaur Park Formation TAW/TRW ratio is 111%–125% for m1 ( $n = 2$ ) and 82%–90% for m2 ( $n = 2$ ) (Fox 1979: table 1). Thus it is the small sample of m2s from the Dinosaur Park Formation rather than the Bissekty sample that is significantly narrower than all other Asian or North American m1s or m2s.

The depth of the hypoflexid correlates to the point at which the oblique cristid contacts the trigonid. In all adequately preserved and figured lower molars from both Asiatic and North American samples the oblique cristid terminates at the protocristid notch. It is interesting that a “deep hypoflexid notch” was cited in the original diagnosis of *Paranyctoides* (Fox 1979: 119); Montellano-Ballesteros et al. (2013) now think that presence of this character in *P. quadrans* differentiates it from North American *Paranyctoides*.

The paraconid is placed slightly more mesially in m1 compared with m2 and m3 in the majority of Cretaceous eutherians. We cannot determine upon which molars [Montellano-Ballesteros et al. \(2013\)](#) based their observation that in *P. quadrans* the paraconid is more mesially placed.

There are only two specimens with m2–3 with published measurements: CCMGE 67/12455 from the Bissekty Formation and UALVP 5573 from the Milk River Formation ([Fox 1984b](#); [Averianov and Archibald 2013](#)). The length of m3 to the length of m2 ratio is 94% in the former and 100% in the latter. For comparison, in the sample of *Parazhelestes mynbulakensis* ([Nesov 1985b](#)) from the Bissekty Formation there are three specimens with m2–3. The Lm3/Lm2 ratio in these specimens is 92%, 98%, and 100%, respectively ([Archibald and Averianov 2012](#): appendix 3). Thus, a difference in this parameter of 8% in one sample suggests that a 6% difference between different species of *Paranyctoides* is of no significance. The hypoconulid in the lower molars of both Asiatic and North American samples is slightly closer but not twinned with the entoconid on m1–2 and almost equidistant from the entoconid and hypoconid in m3. There is some variation in the position of the entoconid in m1–2 within both samples, and there are specimens with exactly the same position of the hypoconulid in *P. quadrans* (e.g., CCMGE 67/12455) and North American taxa (UALVP 5573, TMP 1999.008.0007).

The shape of the lower molar crown is somewhat more squared in m2 compared with m1 and 3. The teeth of the same tooth loci do not differ significantly in the crown shape between Asiatic and North American samples.

Regarding the more rounded cusps noted earlier in the text, most of the lower molars of *Paranyctoides* from the Bissekty Formation are somewhat worn. This gives the impression that they have “more rounded cusps”.

Based on the analysis presented earlier, we can confirm only two of 24 alleged differences between *P. quadrans* and the North American sample of *Paranyctoides* proposed by [Montellano-Ballesteros et al. \(2013\)](#). These are the sharp lingual ridge on p5 and the relative height of the talonid and trigonid on lower molars. The taxonomic significance of these two characters is not certain; both may be affected by individual variation and wear. The other characters are based on incorrect observations, or incorrect interpretation of positional variation between tooth loci, or individual variation.

### Phylogenetic analysis of Asiatic and North American *Paranyctoides*

[Montellano-Ballesteros et al. \(2013\)](#) scored for the North American *Paranyctoides* 63 of 127 dental characters used in the phylogenetic analysis by [Archibald and Averianov \(2012\)](#) and found eight differences. These differences are discussed in the following text. The character numbers correspond to those in the matrix of [Wible et al. \(2009\)](#) and [Archibald and Averianov \(2012\)](#).

Character 42: Ultimate upper premolar, para- and metastylar lobes development. The P5 is actually not known for the Asiatic taxon, and coding of this character in [Archibald and Averianov \(2012\)](#) was based on the American material. Thus this “difference” is a subjective interpretation of the same material and not relevant for distinguishing between the American and Asiatic taxa.

Character 58: Ultimate lower premolar, number of talonid cusps. As was noted earlier, a “bicuspid” talonid is present only in one of two known p5s (UALVP 14822), whereas in the other p5 (UALVP 16174) the talonid is unicuspid, as in URBAC 03-204. The North American sample should be coded as polymorphic for this character (0 + 1). The presence of an additional minute cusp in UALVP 14822 is likely individual variation with no taxonomic importance.

Character 62: Size of the lower molar series. This character has three states: (0) molars subequal; (1) posterior increase

(m1 < m2 < m3); (2) posterior decrease (m1 > m2 > m3). In *P. quadrans* m1 = m2 > m3, while in the North American sample m1 = m2 = m3. The relative length of m2 to m3 is known from a single specimen in each sample and the size difference is only 6%. This is well within the limits of individual variation. Both the Asiatic and American samples should be coded as plesiomorphic (0) for this character.

Character 73: Upper molars, stylar cusp D, confused with the metastyle (= cusp E) by [Montellano-Ballesteros et al. \(2013\)](#). As was described earlier, the stylar cusp D is variably present in the North American sample, which should be coded as a polymorphic state (0 + 1) for this character. It may well be polymorphic in *P. quadrans*, where only two upper molars are currently known.

Character 108: Lower molars, paraconid on lingual margin. [Archibald and Averianov \(2012\)](#) coded *Paranyctoides* as having the paraconid on the lingual margin (state 1). After reconsideration of all available specimens we found this coding to be incorrect. None of the specimens shows extreme lingual position of the paraconid as, for example, in *Avitotherium utahensis* [Cifelli, 1990](#) ([Cifelli 1990](#): fig. 6D). Both the North American and Asiatic samples should be coded as plesiomorphic (0) for this character.

Character 117: Lower molars, trigonid height relative to the talonid height. As noted earlier, this character can be clearly assessed only for two unworn specimens (ZIN 85294 and UALVP 14822). The height of the hypoconid is 78% of the protoconid in the former specimen and 59% in the latter specimen. However, the primitive state (trigonid twice or higher than the talonid) requires this ratio to be less than 50%. Thus both the North American and Asiatic specimens should be coded as derived for this character.

Character 120: Lower molars, hypoconulid position. As was discussed earlier, both the North American and Asiatic samples of *Paranyctoides* do not differ in the relative position of the hypoconulid and should be similarly coded as state 1 (hypoconulid in posteromedial position).

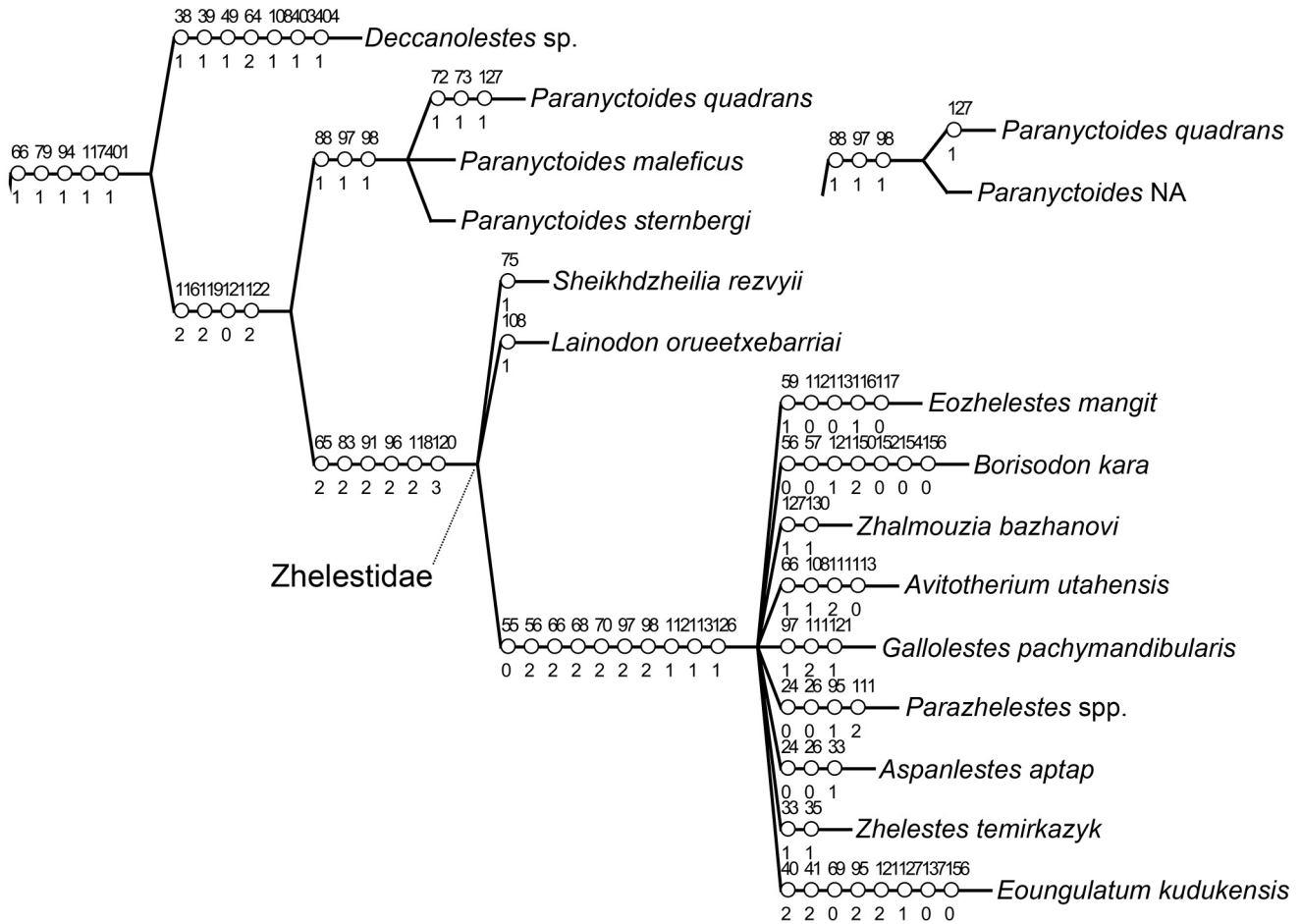
Character 127: Ultimate lower molar size relative to penultimate lower molar. See character 62 earlier. The size of m3 relative to m2 may vary significantly in the paleopopulation and currently the known sample of specimens with both m2 and m3 (only one such specimen is known for either sample) is not large enough to interpret this taxonomically.

The review in the preceding text shows that there are no phylogenetically significant characters that distinguish the Asiatic and North American samples of *Paranyctoides*. To assess the relationships between the Asiatic and North American species of *Paranyctoides* in a broader phylogenetic context we performed a parsimony analysis using the character–taxon matrix of [Wible et al. \(2009\)](#) as modified by [Archibald and Averianov \(2012\)](#). In the latter analysis the terminal taxon *Paranyctoides* was scored on the materials from both Asia and North America. Here we performed two separate analyses.

The first analysis contains three terminal taxa for *Paranyctoides*: *P. quadrans* based on the sample from the Bissekty Formation, *P. maleficus* (Milk River Formation), and *P. sternbergi* (Dinosaur Park Formation). The data matrix consisting of 73 taxa and 408 characters was analyzed by a tree-search maximum parsimony ratchet algorithm using the TNT version 1.1 ([Goloboff et al. 2003](#)) run with Winclada version 1.00.08 interface ([Nixon 1999](#)). All characters are non-additive. Five most parsimonious trees have been produced with tree length 2235 steps, consistency index 0.26, and retention index 0.57. The fragment of the strict consensus of these trees showing interrelationships within *Paranyctoides* and adjacent taxa is illustrated in [Fig. 2](#). In this analysis two North American species, *P. maleficus* and *P. sternbergi*, form a trichotomy with *P. quadrans*.

In the second analysis all samples of the North American *Paranyctoides* were combined in a single terminal taxon. In particular, this differs from the previous analysis by the scoring of P5 characters. The P5 is not known for *P. quadrans*. It is present in the

**Fig. 2.** Fragment of five most parsimonious trees produced by TNT ratchet algorithm using the data set presented in Archibald and Averianov (2012) with separate scoring of *P. maleficus* and *P. sternbergi* (left variant of branch) or combined terminal taxon for the North American *Paranyctoides* (right variant of branch). Only unambiguous characters are shown (white circles are homoplasies). The numbers at the circles are characters (above) and states (below).



sample from the Milk River Formation (Montellano 1992; Montellano-Ballesteros et al. 2013), but this specimen was never described and figured. Consequently, *P. maleficus* cannot be scored for the P5 characters. There are four published P5 of *Paranyctoides* from North America: OMNH 21982 and OMNH 21978 from the Kaiparowits Formation of Utah (Cifelli 1990: figs. 4B–4D, 4H–4I), UNM-B1735 from the Kirtland Shale of New Mexico (Rigby and Wolberg 1987: pl. 2, figs. G–I), and UCMP 131243 from the Judith River Formation of Montana (Montellano 1992: fig. 28a). These specimens are generally similar in overall morphology and all except OMNH 21978 lack the metacone. Thus North American *Paranyctoides* is coded as polymorphic for development of the metacone on P5. The development of the metacone on P5 is also variable in the zhelestid *Parazhelestes mynbulakensis* (Archibald and Averianov 2012: 379). Only one specimen of P4 has been attributed to *Paranyctoides*, OMNH 20180 from the Kaiparowits Formation (Cifelli 1990: figs. 4E–4G). Thus the P4 characters are scored only for the combined North American terminal taxon of *Paranyctoides*.

The second analysis, using the same settings as in the first analysis, produced seven most parsimonious trees with the same statistics. The combined terminal taxon for North American *Paranyctoides* was found as a sister taxon for *P. quadrans* (Fig. 2).

In both analyses the grouping of Asiatic and North American species of *Paranyctoides* is supported by three synapomorphies:

Character 88(1): upper molars, paraconule prominent, closer to protocone;

Character 97(1): upper molars, precingulum present but not reaching labially past the paraconule or paraconule position;

Character 98(1): upper molars, postcingulum present but not reaching labially past the metaconule or metaconule position.

In the first analysis *P. quadrans* has three autapomorphies:

Character 72(1): upper molars, styler cusp C present;

Character 73(1): upper molars, styler cusp D present;

Character 127(1): ultimate lower molar smaller than penultimate molar.

In the second analysis only the last character remains as an autapomorphy of *P. quadrans* (Fig. 2) because the styler cusps C and D are polymorphically present in the combined North American sample of *Paranyctoides*. As was noted earlier in the text, character 127(1) was assessed for *P. quadrans* on the basis of a single specimen. As this character is subject to individual variation, discovery of additional materials on *P. quadrans* may invalidate this apparent autapomorphy.

The genus *Paranyctoides* Fox, 1979, is defined here as a stem-based taxon comprising all taxa that are closer to *Paranyctoides sternbergi* Fox, 1979, than to *Zhelestes temirkazyk* Nesov, 1985a. By this phylogenetic definition, *Paranyctoides quadrans* (Nesov, 1982) clearly belongs to this genus.

## Taxonomic composition of *Paranyctoides* in North America

The original diagnosis of *Paranyctoides* Fox, 1979, based on the type species *P. sternbergi* Fox, 1979, from the Dinosaur Park Formation of Alberta, Canada (Fox 1979), included a combination of primitive and derived characters widely distributed among other Cretaceous eutherians. Among these characters, bicuspid talonid of p5 should be excluded from the generic diagnosis. It is known for a single specimen (UALVP 14822), the holotype of *P. sternbergi*, which is possibly aberrant in this respect, because this small additional talonid cusp is not known in other Cretaceous eutherians. In the second specimen of p5 from North America (UALVP 16174) this character is lacking (see preceding text.). The original generic diagnosis was confined to characters of the lower dentition because no upper molars were referred to *P. sternbergi* at the time. However, in the same paper Fox (1979: 122) noted a closely related species from the Milk River Formation with an upper molar (Fox 1970). This species was subsequently described as *P. maleficus* Fox, 1984b. However, Fox 1984b did not provide a revised diagnosis for the genus that would incorporate characters from the upper dentition. The next revised diagnosis of *Paranyctoides*, based on upper and lower dentition, was provided by Kielan-Jaworowska et al. (2004: 506). Montellano-Ballesteros et al. (2013) further modified the diagnosis of the genus, restricted to the North American taxa. The most striking character of *Paranyctoides*, “the upper molars are not very transverse”, was cited only in the latter diagnosis. This is possibly the only autapomorphy of the genus present in both the North American and Asiatic species (Butler 1990: 541). Unfortunately, this character was never unambiguously and quantitatively defined and thus was not included in the current phylogenetic analyses.

Fox (1984b: 10) provided the following diagnosis for the second species of *Paranyctoides*, *P. maleficus*: (1) more robust crowns of lower teeth; (2) upper molars not very transverse; (3) wide stylar shelf; (4) strong parastylar lobe; (5) weak stylocone; (6) separate paracone and metacone; (7) robust conules; and (8) pre- and post-protoconid cingula, with incipient hypocone on at least some teeth. Seven of eight characters in this diagnosis pertain to the upper molars although the upper molars were not reported for the type species at that time. It is now clear that these characters of the upper dentition are diagnostic at the generic rather than species level and cannot differentiate *P. maleficus* from *P. sternbergi*. The single remaining diagnostic character, “more robust construction of crowns”, is so vague as to be of no real help for delimiting the species. This recognition of the species from Alberta was the main reason that subsequent finds of *Paranyctoides* in other parts of North America have gone unnamed: Wahweap sp. A, Wahweap sp. B., Kaiparowits sp. A., Kaiparowits sp. B., *Paranyctoides* cf. *P. sternbergi*, *Paranyctoides* cf. *P. maleficus* (Rigby and Wolberg 1987; Cifelli 1990; Montellano 1992). According to the taxonomic assessment provided by Montellano-Ballesteros et al. (2013) the genus consists of six valid species: *P. sternbergi*, *P. maleficus*, and four unnamed species from Utah. It is unclear where they would place *Paranyctoides* from the Judith River Formation of Montana.

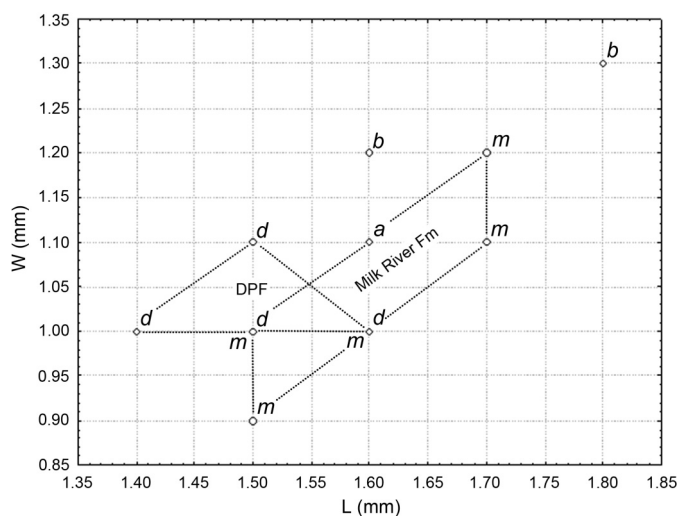
Valid species are those that can be unambiguously distinguished from other species by a differential diagnosis. Such a diagnosis was provided for none of the species considered valid by Montellano-Ballesteros et al. (2013). If the validity of the species is claimed, it should not remain unnamed as done by Montellano-Ballesteros et al. (2013). Currently, there is no evidence that the sample of *Paranyctoides* from North America represents more than a single species. All the known specimens of *Paranyctoides* from North America and Asia are very similar in size, as evident from the most commonly found lower molars, m1 and m2 (Table 1; Fig. 3). Based on this, we consider all North American specimens of *Paranyctoides* attributable to a single species, *P. sternbergi* Fox, 1979. The current taxonomic revision of *Paranyctoides* is provided as follows.

**Table 1.** Measurements of the lower molars m1–2 of *Paranyctoides* (after Fox 1979, 1984b; Averianov and Archibald 2013).

Specimen	Formation	L (mm)	W (mm)
ZIN 85294 (m1)	Aitym	1.6	1.1
CCMGE 67/12455 (m2)	Bissekty	1.8	1.3
URBAC 03-215 (m1)	Bissekty	1.6	1.2
UA 14822 (m1)	Dinosaur Park	1.5	1
UA 4271 (m2)	Dinosaur Park	1.6	1
UA 6998 (m1)	Dinosaur Park	1.4	1
UA 6998 (m2)	Dinosaur Park	1.5	1.1
UA 16168 (m1)	Milk River	1.6	1
UA 16170 (m1)	Milk River	1.5	0.9
UA 16171 (m1)	Milk River	1.5	0.9
UA 16173 (m1)	Milk River	1.7	1.1
UA 16175 (m1)	Milk River	1.5	1
UA 16181 (m1)	Milk River	1.6	1
UA 5573 (m2)	Milk River	1.7	1.2

Note: L, maximum length; W, maximum width.

**Fig. 3.** Length (L) to width (W) ratio of lower molars (m1 and m2) of *Paranyctoides* specimens based on measurements present in Table 1. Abbreviations: a, Aitym Formation; b, Bissekty Formation; d, Dinosaur Park Formation (DPF); m, Milk River Formation.



## Systematic paleontology

Genus *Paranyctoides* Fox, 1979

*Paranyctoides*. Fox 1979: 119.

*Sailestes*. Nesov 1982: 237.

TYPE SPECIES: *Paranyctoides sternbergi* Fox, 1979.

REVISED DIAGNOSIS: Similar to Zhelestidae and differing from other Cretaceous eutherians in having the following combination of characters of lower molars: oblique cristid complete, attached to or near notch in protocristid; talonid subequal or wider than trigonid; hypoconulid on m3 short and erect; entoconid subequal to hypoconid and hypoconulid. Differs from Zhelestidae by the following characters of upper molars: paracone prominent, closer to protocone; precingulum present but not reaching labially past the paracone or paracone position; postcingulum present but not reaching labially past the metacone or metacone position. Additionally differs from all other Cretaceous eutherians by having relatively unexpanded transversely upper molars.

COMPOSITION: Type species and *P. quadrans* (Nesov, 1982).

DISTRIBUTION: Asia, North America; Late Cretaceous.

*Paranyctooides sternbergi* Fox, 1979

Eutheria [indet.]: Fox 1970: 630, fig. 1.

*Paranyctooides sternbergi*: Fox 1979: 119, figs. 2, 3, 4c; Montellano-Ballesteros et al. (2013: fig. 2); Fox (2005 : fig. 22.1 (11, 12)).

*Paranyctooides maleficus*, syn. nov.: Fox 1984b: 9, figs. 1–4; Montellano-Ballesteros et al. (2013): fig. 1.

*Paranyctooides* cf. *P. sternbergi*: Rigby and Wolberg 1987: 75, pl. 2, figs G–L.

*Paranyctooides* Wahweap sp. A: Cifelli 1990: 349, figs. 3A–3C.

*Paranyctooides* Wahweap sp. B: Cifelli 1990: 349, figs. 3D–3F.

*Paranyctooides* Kaiparowits sp. A: Cifelli 1990: 349, figs. 4B–4D.

*Paranyctooides* Kaiparowits sp. B: Cifelli 1990: 349, figs. 4E–4M.

*Paranyctooides* cf. *P. maleficus*: Montellano 1992: 84, fig. 28.

DIAGNOSIS: Differs from *P. quadrans* by having a sharp lingual ridge on p5 and m3 longer than m2.

DISTRIBUTION: North America (Canada and USA); Late Cretaceous (Campanian–Maastrichtian).

*Paranyctooides quadrans* (Nesov, 1982)

For full synonymy see Averianov and Archibald (2013: 18).

DIAGNOSIS: Differs from the type species by lacking a sharp lingual ridge on p5 and m3 shorter than m2.

DISTRIBUTION: Central Asia (Uzbekistan); Late Cretaceous (Turonian and possible Coniacian).

## Conclusions

The oldest remains of *Paranyctooides* come from the middle–late Turonian Bissekty Formation of Central Asia, which was the westernmost point of the Asian landmass separated by the Turgai Strait from Europe in the Cretaceous. The middle Turonian was a time of global marine regression and climatic optimum (Eaton et al. 1997; Hasegawa 2003), which likely promoted faunal interchange between Asia and western North America across Beringia. The spalacotheriid symmetrodontans and ornithopod and ceratopsian dinosaurs were particularly involved in this interchange (Head and Kobayashi 2001; Averianov and Archibald 2003; Sues and Averianov 2009a, 2009b). It is not clear if *Paranyctooides* dispersed to North America during this favorable event or later. The oldest North American record of *Paranyctooides* is from the late Santonian – lower Campanian Milk River Formation of Alberta, Canada. The next eutherian groups arriving in North America from Asia were the zhelestids and cimolestids (Nesov et al. 1998; Wible et al. 2007, 2009; Archibald and Averianov 2012). These are first known in North America from the late Campanian Judithian faunas, although there is a questionable record of zhelestid in the upper Santonian Eutaw Formation of Mississippi, USA (Emry et al. 1981; Nesov et al. 1998). In North America *Paranyctooides* was always a rare element of the mammalian faunas. In Judithian it has the widest distribution, from southern Alberta to New Mexico. During the Lancian *Paranyctooides* is known from few records in Montana and Wyoming. Apparently this taxon did not survive the Cretaceous–Paleogene extinction.

## Acknowledgements

We thank Thomas Martin and an anonymous reviewer for reading the manuscript and providing useful suggestions. A.A. is grateful to W.A. Clemens for access to the specimens in the UCMP collection. The work of A.A. was supported by the Russian Foundation for Basic Research (projects 13-04-01401 and 13-04-00525).

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