NEW EVIDENCE ON THE STEM PLACENTAL MAMMAL *PARANYCTOIDES* FROM THE UPPER CRETACEOUS OF UZBEKISTAN

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A newly discovered maxillary fragment (ZIN 102716) of *Paranyctoides quadrans* from the Bissekty Formation (Upper Cretaceous, Turonian) at Dzharakuduk, Uzbekistan shows this species has a P5 about half the labiolingual width of M1 and an infraorbital foramen placed above P4 near the anterior margin of the orbit and below the maxillolacrimal contact. The maxillary foramen, likely posterior to M1, is positioned more posteriorly compared to other stem placental mammals. The infraorbital canal is roofed by a thin plate of maxilla with facets for the lacrimal and jugal above. The posterior part of this roof may be formed entirely by the lacrimal. In *Paranyctoides* the upper posterior premolars (P4–5) and molars were confined to the posterior third of the maxilla below the orbit, as in the stem therian *Eomaia*. In a majority of stem placentals, including Early Cretaceous *Prokennalestes* and *Acristatherium*, the upper posterior premolars and molars occupy the posterior half of the maxilla, with P4–5 placed in front of the orbit. A new phylogenetic analysis places *Paranyctoides* in a polytomy with *Sheikhdzheilia*, *Lainodon*, and Zhelestinae.

Key words: Mammalia, Placentalia, *Paranyctoides*, Upper Cretaceous, Uzbekistan.

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INTRODUCTION

The stem placental mammal *Paranyctoides* is among the rarest mammalian taxa in the Upper Cretaceous of Asia and North America (Fox 1979, 1984; Cifelli 1990; Nessov 1993; Archibald and Averianov 2001; Averianov and Archibald 2003, 2013a). It is one of the few generic-level mammalian taxa known from these two continents. Montellano-Ballesteros *et al.* (2013) argued that these were in fact generically distinct taxa. Subsequently, Averianov and Archibald (2013b) demonstrated much of the argued differences are the result of misinterpretation of morphological characters of the Asiatic taxon and thus at least for now there is no basis to recognize two genera.

Two species are currently recognized, *P. quadrans* in the Turonian–?Coniacian of Asia and *P. sternbergi* in the Campanian–Maastrichtian of North America (Averianov and Archibald 2013a, b). Until recently, our knowledge of *Paranyctoides* was limited to isolated teeth and dentary fragments. Recent phylogenetic analyses placed *Paranyctoides* in a more terminal position to Zhelestidae (Wible *et al.* 2007, 2009) or as sister taxon to Zhelestidae (Archibald and Averianov 2012; Averianov and Archibald 2013b; Manz *et al.* 2015). *Paranyctoides* is clearly distinct from most other Cretaceous stem placental mammals by its transversely unexpanded upper molars (Butler 1990), similar in this respect only to *Bobolestes* (see below). Here, we report on the discovery of the first maxillary fragment of *Paranyctoides*. This specimen (ZIN 102716) was found recently among the thousands of unsorted bones from the CBI-14 locality, Bissekty Formation, Dzharakuduk in Uzbekistan, from where the Asiatic species, *Paranyctoides quadrans*, was previously described (Nessov 1982, 1993; Archibald and Averianov 2001; Averianov and Archibald 2013a). Although incomplete, ZIN 102716 reveals an unusual structure of the infraorbital canal and the posterior part of the maxilla, differentiating *Paranyctoides* from the majority of other Cretaceous stem placental mammals.

Institutional abbreviations. — CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg; ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg.

Measurements. —AW, anterior width; L, length; PW, posterior width. All measurements are in mm.

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SYSTEMATIC PALEONTOLOGY

Mammalia Linnaeus, 1758

Theria Parker *et* Haswell, 1897

Eutheria Gill, 1872

Eutheria *incertae sedis*

Genus ***Paranyctoides*** Fox, 1979

Paranyctoides quadrans (Nessov, 1982)

(Fig. 1)

For synonymy see Averianov and Archibald (2013a, p. 18).

Holotype: CCMGE 7/11758, right M1.

Type locality and horizon: Dzharakuduk, Kyzylkum Desert, Uzbekistan; Bissekty Formation, Upper Cretaceous (middle–upper Turonian)

Referred specimens. — Specimens listed by Averianov and Archibald (2013a, p. 18) and ZIN 102716, left maxillary fragment with M1 and alveoli for P5 and distal root of P4 from the type locality (locality CBI-14, Dzharakuduk).

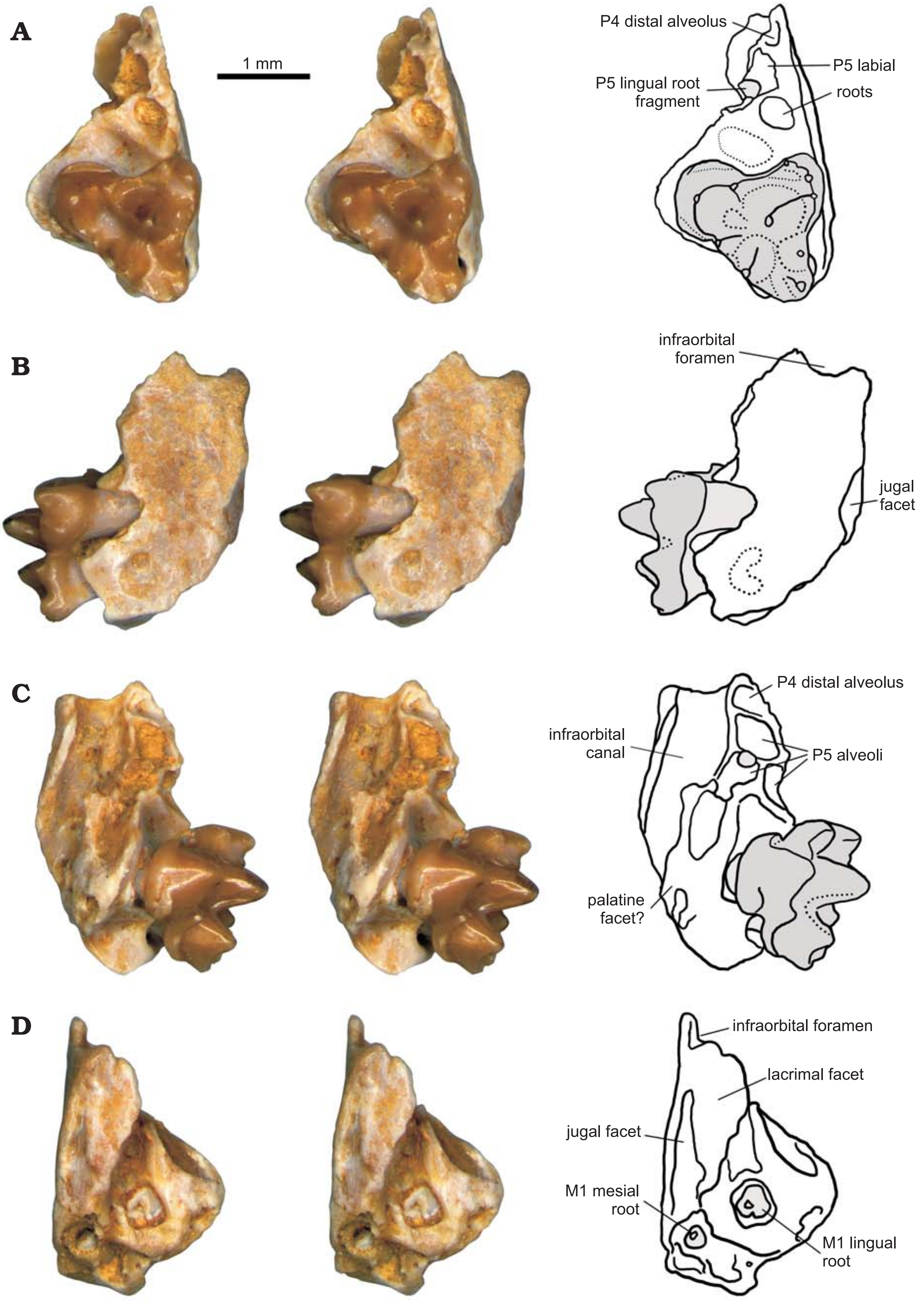

Fig. 1. *Paranyctoides quadrans*, ZIN 102716, left maxillary fragment with M1 and alveoli for P5 and P4, Dzharakuduk, Uzbekistan, Bissekty Formation, Upper Cretaceous (Turonian), in occlusal (**A**), labial (**B**), lingual (**C**), and dorsal (**D**) views. Photographic stereo-pairs and explanatory drawings.

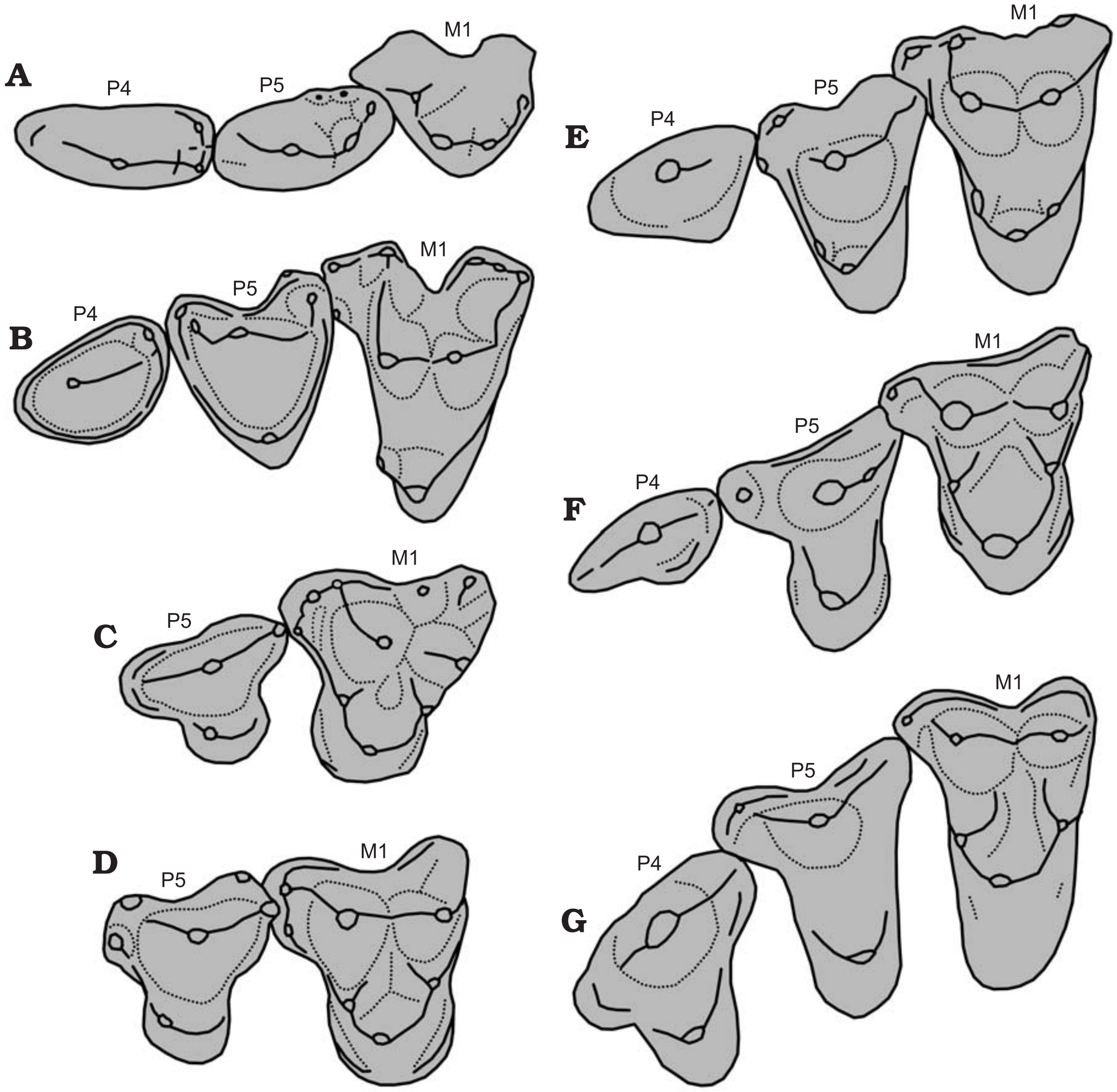

Fig. 2. Posterior premolars and M1 in selected stem therian and stem placental mammals in occlusal view. **A**. *Peramus tenuirostris*, after Clemens and Mills (1971, pl. 1). **B**. *Juramaia sinensis*, after Luo *et al.* (2011, fig. 2). **C**. *Paranyctoides quadrans*, based on ZIN 102716 with P5 hypothetically reconstructed. **D**. *Paranyctoides sternbergi*, after Montellano (1992, fig. 28a) and Montellano-Ballesteros *et al.* (2013, fig. 1J). **E**. *Prokennalestes trofimovi*, after Kielan-Jaworowska and Dashzeveg (1989, fig. 1A). **F**. *Aspanlestes aptap*, after Archibald and Averianov (2005, fig. 1E). **G**. *Kulbeckia kulbecke*, after Archibald and Averianov (2005, fig. 1G). Not to scale.

DESCRIPTION

ZIN 102716 is a left maxillary fragment with M1 and alveoli for P5 and the distal root of P4 (Fig. 1). The anterior margin of the palatal process is broken anterior to the level of M1 protocone. Posterior to this level a flattened area might represent the palatine facet (Fig. 1C). There are three alveoli for P5, two labial and one lingual. There is only a remnant of the lingual root (Fig. 1A, C). It is not complete lingually but because about two-thirds of its circumference is preserved it is likely not to have been much larger than what is present. The reconstructed labiolingual width of P5 is about half that of M1 (Fig. 2C). There are no diastemata between P4–5 and P5–M1. The height of the maxilla between the alveolar surface and the infraorbital canal is very small at P5, suggesting that this tooth had very short roots. The posterolateral edge of the infraorbital foramen is preserved above the distal alveolus of P4 (Fig. 1B, D). Two of three roots of M1 are exposed in the floor of infraorbital canal (Fig. 1D), in contrast with the other stem placental mammals, which have the roots of M1 exposed in orbit floor, posterior to the maxillary foramen (posterior opening of the infraorbital canal). This suggests a more posterior position of the maxillary foramen in *Paranyctoides*, possibly between M1 and M2, or above M2. The infraorbital canal is roofed dorsolaterally by a thin maxillary plate with a flattened dorsal surface (Fig. 1D). On this surface there is a depressed triangular area posterolaterally that likely is the jugal facet (Fig. 1B, D). The second distinct facet on the dorsal surface of infraorbital canal roof, a flat surface anteromedial to the jugal facet, is likely a facet for the lacrimal (Fig. 1D). The medial margin of the maxillary plate above the infraorbital canal is intact with the lacrimal likely forming the dorsomedial roof of the infraorbital canal. The lacrimal component of the infraorbital canal roof apparently increased in width posteriorly. It is unclear if lacrimal participated in the roof of the infraorbital foramen. Most likely the foramen was entirely within the maxilla as in all known stem therian and placental mammals.

The M1 is little worn and agrees in morphology and size (Figs 1, 2C; L = 1.6; AW = 1.6; PW = 1.7) with an isolated M1, the holotype of *P. quadrans* (CCMGE 7/11758; L = 1.5; AW = 1.6; PW = 1.7). The outline of the crown approximates the shape of an isosceles triangle, with the mesial and distal sides of similar length. The labial margin is concave with a shallow ectoflexus. The parastylar lobe is protruding mostly mesially. The metastylar lobe is directed distolabially. There is a distinct ectocingulum labial to the paracone and connected to the parastyle. A small stylocone is on this ectocingulum. Distal to the stylocone there are two stylar cusps, C and D, the first of which is somewhat larger. Both of these cusps are present on the holotype of *P. quadrans*, although they are less developed there. There is a short ridge directed from cusp D towards the metacone but not reaching the base of the latter. The stylar shelf, a flattened area between the bases of the labial cusps and ectocingulum or stylar cusps, is absent labial to the paracone and narrow labial to the metacone. The metacone is distinctly smaller and lower than the paracone. The centrocrista is straight. The preparacrista is directed mesiolabially and connects to the stylocone. The postmetacrista is distally convex and connected to stylar cusp D. There is no metastyle. The postmetacrista is moderately worn, while the preprotocrista is unworn. The same is characteristic of the holotype of *P. quadrans*. On the parastylar lobe there are a large parastyle and much smaller preparastyle. The parastylar lobe is separated from the base of the paracone by a distinctly worn parastylar groove (= protoconid notch). The crown is distinctly constricted between the trigon and labial part. The trigon is narrower labiolingually compared with the labial part, in contrast with the majority of other Late Cretaceous stem placentals that have the trigon labiolingually wider than the labial part (Fig. 2). The protocone is large and is somewhat taller than the metacone. Its apex is situated opposite the paracone. The conules are well developed and winged, located about midway between the protocone and labial cusps (the paraconule is a slightly closer to the protocone than is the metaconule). The conules project well above the pre- and postprotocrista. The internal conular cristae extend labially towards the bases of their respective labial cusps. The trigon basin is deepest between conular internal cristae and the centrocrista. The preparacrista (= preparaconule crista) extends labially towards the preparastyle. The postparacrista (= postmetaconule crista) extends labial to the metacone apex but does not reach the labial margin. The precingulum and postcingulum are much better developed compared with the holotype of *P. quadrans*. The postcingulum is somewhat shorter. The protoconal cingula extend labially towards the area dorsal to the conules and are well separated lingually.

PHYLOGENETIC ANALYSIS

For the phylogenetic analysis we used the data matrix created by Wible *et al.* (2009) and consisting of 408 characters as modified by Archibald and Averianov (2012) and Averianov and Archibald (2013b). Additional postcranial characters 409–415, scorings of several additional taxa, and scoring corrections of the previously included taxa has been adopted from Goswami *et al.* (2011) and Manz *et al.* (2015). A new cranial character 416 is introduced and discussed herein. The newly-recovered maxillary fragment ZIN 102716 allows coding of the following five morphological characters whose state was previously unknown for *Paranyctoides*.

46(0): Ultimate upper premolar size (occlusal surface) relative to first upper molar: smaller or subequal. This character in its current formulation has little phylogenetic value for the analyzed taxa, as the derived state, ultimate upper premolar larger than M1 in occlusal surface, occurs sporadically in few terminal taxa within different clades. However, *Paranyctoides* is clearly different from other Cretaceous stem placental

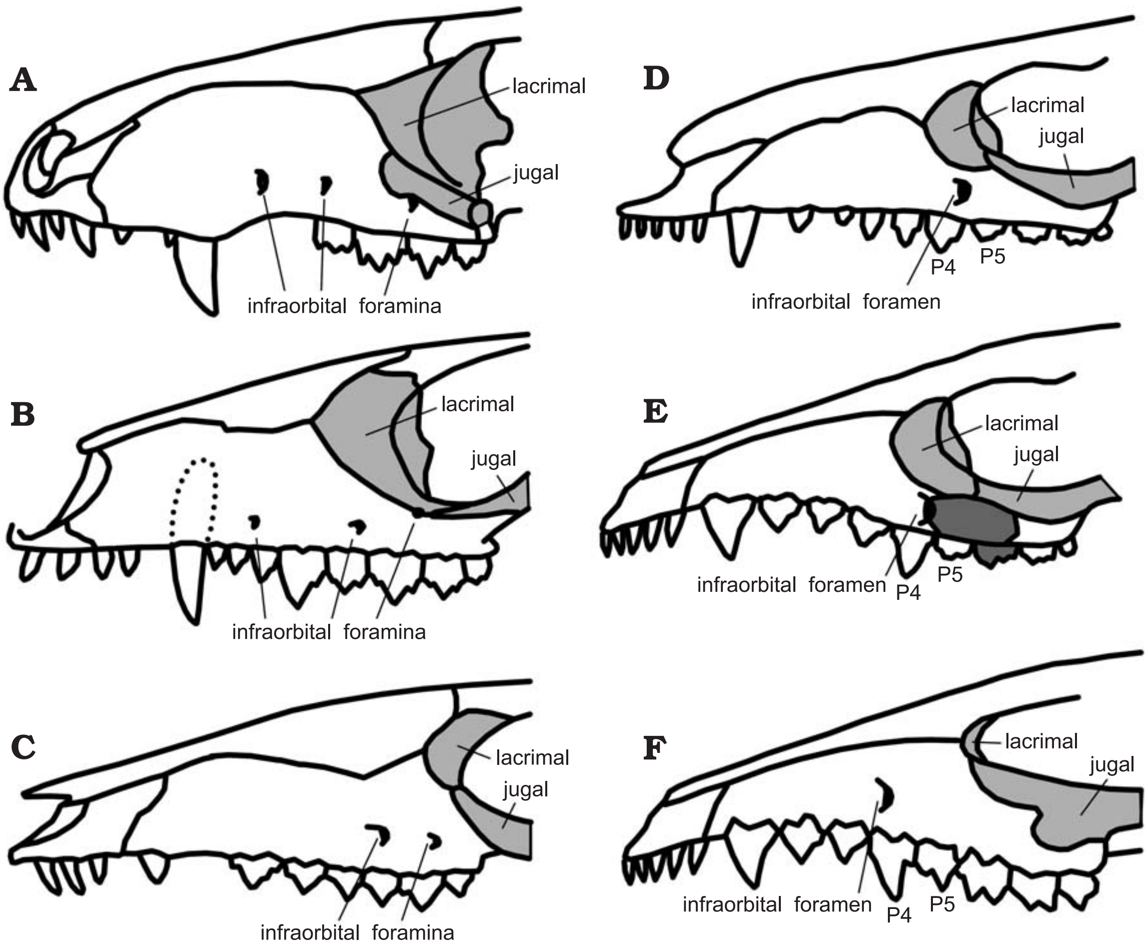

Fig. 3. Anterior part of the skull in lateral view of selected stem mammals (A, B), stem therians (C, D), and stem placentals (E, F). **A**. *Sinoconodon* sp., after Crompton and Luo (1993, fig. 4.9). **B**. *Morganucodon watsoni*, after Kermack *et al.* (1981, fig. 99A). **C**. *Maotherium sinense*, after Rougier *et al.* (2003, fig. 2A). **D**. *Eomaia scansoria*, after Ji *et al.* (2002, fig. 1c). **E**. *Paranyctoides quadrans*, hypothetical reconstruction based on maxillary fragment ZIN 102716, shown in dark grey. **F**. *Asioryctes nemegtensis*, based on Wible *et al.* (2009, fig. 35). Lacrimal and jugal are shown in light grey. Not to scale.

mammals, including *Prokennalestes*, in having P5 distinctly narrower labiolingually compared with M1 (Fig. 2). In this *Paranyctoides* approaches the condition of the stem therian *Juramaia* (Fig. 2B). It is not clear, however, if this is a retention of the plesiomorphic state or a neomorphic character correlated with distinct labiolingual narrowing of upper molars in *Paranyctoides*.

164(1): Exit(s) of infraorbital canal: single. Although the maxilla is incompletely known for *Paranyctoides*, a large infraorbital foramen placed above P4 is a typical condition for the Cretaceous stem placental mammals, suggesting that the infraorbital canal had a single anterior exit as in those taxa. In more basal mammals with multiple exits of the infraorbital canal (state 0) the posterior infraorbital foramen is distinctly smaller (Fig. 3). The single infraorbital foramen is characteristic for *Peramus* and more derived stem therian mammals.

165(1): Infraorbital foramen position: dorsal to penultimate premolar or more anterior. This state is characteristic for *Peramus* and more derived stem and crown therian mammals. A more derived state, infraorbital foramen placed dorsal to the first molar or more posterior [165(2)], is acquired independently in some clades of crown group placentals.

166(0): Infraorbital canal length: long (more than one molar length). A plesiomorphic state that is found in all stem therian and stem placental mammals. The infraorbital canal is shortened [166(1)] in Glires and some Primates and some insectivorous mammals.

New character 416: Infraorbital canal position: near the anterior margin of orbit, below lacrimal or jugal (0), or well anterior to the anterior margin of orbit (1). For the taxa with multiple exits of the infraorbital canal the larger anterior foramen is considered. As was discussed by Krause *et al.* (2014), the posterior infraorbital foramen that is at the maxillojugal or maxillolacrimal suture (Fig. 3A, B) is for the lacrimal branch of the infraorbital nerve. In the stem therian *Maotherium* the posterior infraorbital foramen is placed entirely within the maxilla but still near the anterior end of the orbit (Fig. 3C). In *Maotherium* most of the cheek teeth are placed anterior to this infraorbital foramen. In the stem therian *Eomaia* the single infraorbital foramen is placed above P4 and below the anterior margin of the orbit and the maxillolacrimal suture (Fig. 3D).

The single known specimen of *Eomaia scansoria* was originally interpreted as being a basal eutherian with five premolars and P5 placed below the infraorbital foramen (Ji *et al.* 2002). Averianov *et al.* (2010) suggested instead that on this specimen there are six premolars including one delayed deciduous premolar, and P4 is placed below the infraorital foramen. O'Leary *et al.* (2013) found that *Eomaia* is a stem therian. Luo *et al.* (2011) described *Juramaia sinensis* as a basal eutherian identifying it as having six premolars including delayed dP3, and P4 below the infraorbital foramen, which supports the interpretation of dental formula in *Eomaia* proposed by Averianov *et al.* (2010). In the data matrix by Wible *et al.* (2009) *Eomaia* is coded as having P4, not P5 below the infraorbital foramen, which follows our interpretation of this taxon. What seems most likely is that *Eomaia* and *Juramaia* are both stem therians and both retain a delayed dP3.

In *Eomaia* the posterior premolars (P4–5) and all molars are confined to the posterior half of the maxilla below the lacrimal and jugal. A similar condition is found in the stem therian *Peramus* (Clemens and Mills 1971, pl. 1). Among the stem placental mammals this primitive condition has been retained only in *Paranyctoides*, while in other stem placentals, including the Early Cretaceous *Prokennalestes* and *Acristatherium* (Hu *et al.* 2010), the infraorbital foramen is placed well anterior to the orbit and P4–5 and M1–3 occupythe larger portion of the maxilla (Fig. 3F).

The character-taxon matrix (Supplementary Online Material available at http://www.palaeontologia.pan.pl/SOM/pp67-Averianov_and_Archibald_SOM.txt), consisting of 416 characters and 91 taxa, was analyzed using PRAP, parsimony ratchet analysis using PAUP (Müller 2007), and PAUP* 4.0b10 (Swofford 2002). The equal-weight analysis with 10,000 ratchet replications produced 6799 most parsimonious trees with the tree statistics shown in Table 1. The strict consensus tree shows little resolution among Zhelestidae. To increase resolution and recover a clearer phylogenetic signal, a successive weighting analysis (Farris 1969) was conducted. Using PAUP, the characters were reweighted by the maximum value of rescaled consistency indices (RC), and a heuristic search with 10,000 random sequence addition replicates and TBR (tree bisection and reconnection) branch swapping was performed. During reweighting 367 characters (88.2%) received a weight of less than 1. Tree statistics stabilized after three successive runs of the reweight analysis (Table 1). The fragment of the strict consensus tree of 15 most parsimonious trees recovered in the last analysis, relevant to the phylogenetic position of *Paranyctoides*, is shown on Fig. 4.

The current phylogenetic hypothesis is different in a number of details from the previously published cladogram (Averianov and Archibald 2013b, fig. 2). *Deccanolestes*, which was previously the sister taxon for the clade *Paranyctoides* + Zhelestidae, is clustered with *Afrodon* (Adapisoriculidae) and moved to the insectivorous lineage within the crown-group placentals. *Bobolestes* is the sister taxon for the clade comprised of two clades, *Paranyctoides* + Zhelestidae and a clade containing the remaining stem and crown-group placentals. The taxa mentioned above are not included within the segment of the phylogeny that is figured on Fig. 4. In the previous analysis *Paranyctoides* was the sister taxon for the Zhelestidae. Now *Eozhelestes* is the sister taxon for the remaining taxa of this clade and *Paranyctoides* is nested in a polytomy with *Sheikhdzheilia*, *Lainodon*, and Zhelestinae (Fig. 4). Uncertain and basal positions for *Eozhelestes*, *Sheikhdzheilia*, and *Lainodon* can be affected, however, by the fragmentary nature of these taxa. The upper molars are not known for *Eozhelestes* and only one fragmentary upper molar is known

Table 1. Statistics for equal weight (PRAP and PAUP) and reweight (PAUP) analyses.

Parameters	Equal weight analysis	Reweight analysis 1	Reweight analysis 2	Reweight analysis 3
Number of trees (N)	6799	15	15	15
Tree length (L)	2766	337.1	334.7	334.7
Consistency index (CI)	0.220	0.378	0.381	0.381
Retention index (RI)	0.570	0.676	0.678	0.678
Rescaled consistency index (RC)	0.125	0.256	0.258	0.258
Homoplasy index (HI)	0.780	0.622	0.619	0.619

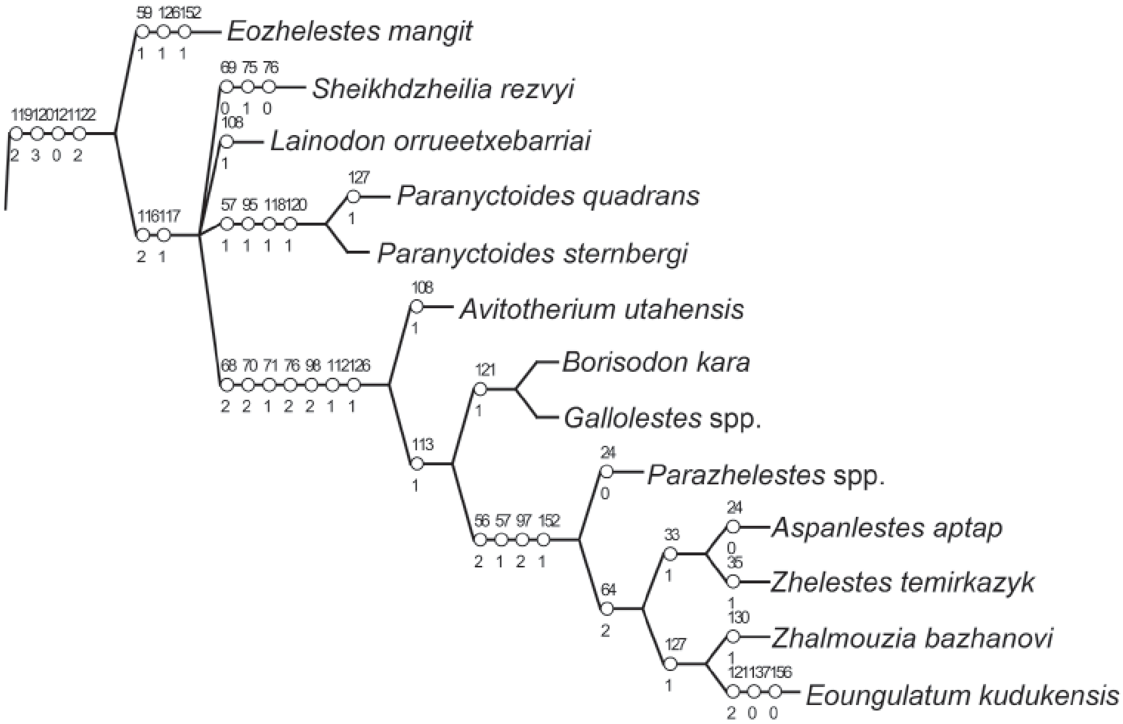

Fig. 4. Fragment of strict consensus tree of 15 most parsimonious trees produced by PAUP reweight analysis showing interrelationships within Zhelestidae and *Paranyctoides*. Only unambiguous characters are shown (white circles are homoplasies). The numbers at the circles are characters (above) and states (below).

for *Lainodon* (Averianov and Archibald 2005; Archibald and Averianov 2012; Gheerbrant and Astibia 2012). In *Sheikhdzheilia* the upper molars are as wide labiolingually as in other zhelestids (Averianov and Archibald 2005). The only stem placental mammal, which has the upper molars as narrow labiolingually as in *Paranyctoides*, is the Cenomanian *Bobolestes* (Averianov and Archibald 2005). However, both taxa cannot be closely related because *Bobolestes* has a molariform p5 whereas the available evidence in *Paranyctoides* suggests this tooth was likely a simpler, premolariform tooth (Averianov and Archibald 2005, 2013b).

REFERENCES

Archibald, J.D. and Averianov, A.O. 2001. *Paranyctoides* and allies from the Late Cretaceous of North America and Asia. *Acta Palaeontologica Polonica* **46**, 533–551.

Archibald, J.D. and Averianov, A.O. 2005. Mammalian faunal succession in the Cretaceous of the Kyzylkum Desert. *Journal of Mammalian Evolution* **12**, 9–22.

Archibald, J.D. and Averianov, A.O. 2012. Phylogenetic analysis, taxonomic revision, and dental ontogeny of the Cretaceous Zhelestidae (Mammalia: Eutheria). *Zoological Journal of the Linnean Society* **164**, 361–426.

Averianov, A.O. and Archibald, J.D. 2003. Mammals from the Upper Cretaceous Aitym Formation, Kyzylkum Desert, Uzbekistan. *Cretaceous Research* **24**, 171–191.

Averianov, A.O. and Archibald, J.D. 2005. Mammals from the mid-Cretaceous Khodzhakul Formation, Kyzylkum Desert, Uzbekistan. *Cretaceous Research* **26**, 593–608.

Averianov, A.O. and Archibald, J.D. 2013a. New material and reinterpretation of the Late Cretaceous eutherian mammal *Paranyctoides* from Uzbekistan. *Acta Palaeontologica Polonica* **58**, 17–23.

Averianov, A.O. and Archibald, J.D. 2013b. Variation and taxonomy of Asiamerican eutherian mammal *Paranyctoides*. *Canadian Journal of Earth Sciences* **50**, 895–903.

Averianov, A.O., Archibald, J.D., and Ekdale, E.G. 2010. New material of the Late Cretaceous deltatheroidan mammal *Sulestes* from Uzbekistan and phylogenetic reassessment of the metatherian-eutherian dichotomy. *Journal of Systematic Palaeontology* **8**, 301–330.

Butler, P.M. 1990. Early trends in the evolution of tribosphenic molars. *Biological Reviews* **65**, 529–552.

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

Clemens, W.A. and Mills, J.R.E. 1971. Review of *Peramus tenuirostris* Owen (Eupantotheria, Mammalia). *Bulletin of the British Museum of Natural History (Geology)* **20**, 89–113.

Crompton, A.W. and Luo, Z.-X. 1993. Relationships of the Liassic mammals, *Sinoconodon*, *Morganucodon oehleri*, and *Dinnetherium*. *In*: F.S. Szalay, M.J. Novacek, and M.C. McKenna (eds) *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials, Volume 1*, 30–44. Springer Verlag, New York.

Farris, J.S. 1969. A successive approximations approach to character weighting. *Systematic Zoology* **18**, 374–385.

Fox, R.C. 1979. Mammals from the Upper Cretaceous Oldman Formation, Alberta. III. Eutheria. *Canadian Journal of Earth Sciences* **16**, 114–125.

Fox, R.C. 1984. *Paranyctoides maleficus* (new species), an early eutherian mammal from the Cretaceous of Alberta. *In*: M.R. Dawson (ed.), Papers in Vertebrate Paleontology Honoring Robert Warren Wilson. *Carnegie Museum of Natural History, Special Publication* 9, 9–20.

Gheerbrant, E. and Astibia, H. 2012. Addition to the Late Cretaceous Laño mammal faunule (Spain) and to the knowledge of European "Zhelestidae" (Lainodontinae nov.). *Bulletin de la Société géologique de France* **183**, 537–546.

Gill, T. 1872. Arrangement of the families of mammals. With analytical tables. *Smithsonian Miscellaneous Collections* **11**, 1–98.

Goswami, A., Prasad, G.V.R., Upchurch, P., Boyer, D.M., Seiffert, E.R., Verma, O., Gheerbrant, E., and Flynn, J.J. 2011. A radiation of arboreal basal eutherian mammals beginning in the Late Cretaceous of India. *Proceedings of the National Academy of Sciences USA* **27**, 16333–16338.

Hu, Y., Meng, J., Li, C., and Wang, Y. 2010. New basal eutherian mammal from the Early Cretaceous Jehol biota, Liaoning, China. *Proceedings of the Royal Society B: Biological Sciences* **277**, 229–236.

Ji, Q., Luo, Z.-X., Yuan, C.-X., Wible, J.R., Zhang, J.-P., and Georg, J.A. 2002. The earliest known eutherian mammal. *Nature* **416**, 816–822.

Kermack, K.A., Mussett, F., and Rigney, H.W. 1981. The skull of *Morganucodon*. *Zoological Journal of the Linnean Society* **71**, 1–158.

Kielan-Jaworowska, Z. and Dashzeveg, D. 1989. Eutherian mammals from the Early Cretaceous of Mongolia. *Zoologica Scripta* **18**, 347–355.

Krause, D.W., Wible, J.R., Hoffmann, S., Groenke, J.R., O'Connor, P.M., Holloway, W.L., and Rossie, J.B. 2014. Craniofacial morphology of *Vintana sertichi* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* **34** (Supplement 1), 14–109.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1: Regnum animale. Editio decima, reformata*. 824 pp. Laurentii Salvii, Stockholm.

Luo, Z.-X., Yuan, C.-X., Meng, Q.-J., and Ji, Q. 2011. A Jurassic eutherian mammal and divergence of marsupials and placentals. *Nature* **476**, 442–445.

Manz, C.L., Chester, S.G.B., Bloch, J.I., Silcox, M.T., and Sargis, E.J. 2015. New partial skeletons of Palaeocene Nyctitheriidae and evaluation of proposed euarchontan affinities. *Biology Letters* **11**, 20140911.

Montellano, M. 1992. Mammalian fauna of the Judith River Formation (Late Cretaceous, Judithian), northcentral Montana. *University of California Publications in Geological Sciences* **136**, 1–115.

Montellano-Ballesteros, M., Fox, R.C., and Scott, C.S. 2013. Species composition of the Late Cretaceous eutherian mammal *Paranyctoides* Fox. *Canadian Journal of Earth Sciences* **50**, 693–700.

Müller, K.F. 2007. *PRAP, Parsimony Ratchet Analysis using PAUP*. Version 2.0b3*. [updated at http://systevol.nees.unibonn.de/software/PRAP].

Nessov, L.A. [Несов, Л.А.] 1982. Древнейшие млекопитающие СССР [The most ancient mammals of the USSR]. *Ежегодник Всесоюзного Палеонтологического Общества* **25**, 228–242.

Nessov, L.A. [Несов, Л.А.] 1993. Новые млекопитающие мезозоя Средней Азии и Казахстана и замечания по эволюции териофаун приморских низменностей мела древней Азии [New Mesozoic mammals of Middle Asia and Kazakhstan and comments about evolution of theriofaunas of Cretaceous coastal plains of Asia]. *Труды Зоологического Института РАН* **249**, 105–133.

O'Leary, M.A., Bloch, J.I., Flynn, J.J., Gaudin, T.J., Giallombardo, A., Giannini, N.P., Goldberg, S.L., Kraatz, B.P., Luo, Z.-X., Meng, J., *et al.* 2013. The placental mammal ancestor and the post-K–Pg radiation of placentals. *Science* **339**, 662–667.

Parker, T.J. and Haswell, W.A. 1897. *A Text-book of Zoology. Volume 2*. 683 pp. MacMillan and Company, London.

Rougier, G.W., Ji, Q., and Novacek, M.J. 2003. A new symmetrodont mammal with fur impressions from the Mesozoic of China. *Acta Geologica Sinica* **77**, 7–14.

Swofford, D.L. 2002. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0*. Sunderland, Sinauer Associates.

Wible, J.R., Rougier, G.W., Novacek, M.J., and Asher, R.J. 2007. Cretaceous eutherians and Laurasian origin for placental mammals near the K/T boundary. *Nature* **447**, 1003–1006.

Wible, J.R., Rougier, G.W., Novacek, M.J., and Asher, R.J. 2009. The eutherian mammal *Maelestes gobiensis* from the Late Cretaceous of Mongolia and the phylogeny of Cretaceous Eutheria. *Bulletin of the American Museum of Natural History* **327**, 1–123.