

Evolutionary transition of dental formula in Late Cretaceous eutherian mammals

Alexander O. Averianov^{1,2} · J. David Archibald³

Received: 17 June 2015 / Revised: 1 August 2015 / Accepted: 19 August 2015
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Abstract *Kulbeckia kulbecke*, stem placentar mammal from the Late Cretaceous of Uzbekistan, shows a transitional stage of evolution in the dental formula from five to four premolars. A non-replaced dP3/dp3 may occur as individual variation. In other specimens, the lower premolars are crowded with no space for development of dp3. As is evident from the CT scanning of one juvenile specimen, the development of dp3 started in a late ontogenetic stage and was confined to the pulp cavity of the developing p2. This dp3 would have been reabsorbed in a later ontogenetic stage, as the roots of p2 formed. The initial stage of reduction of the third premolar can be traced to stem therians (*Juramaia* and *Eomaia*), which have both dP3 and P3 present in the adult dentition. Further delay in the development of dP3/dp3 led to the loss of the permanent P3/p3 (a possible synapomorphy for Eutheria). The dP3/dp3 was present during most of the adult stages in the Late Cretaceous stem placentals Zhelestidae and *Gypsonictops*. This tooth is totally absent in basal taxa of Placentalia, which normally have at most four premolars.

Keywords Dentition · Dental · Replacement · Evolution · Mammals · Eutheria · Cretaceous

Introduction

For over 150 years, the postcanine dental formula of four premolars and three molars, found in some Recent and Paleogene “insectivorans” and other plesiomorphic placentar mammals, was considered ancestral for Eutheria (Owen 1845; Gregory 1910; Ziegler 1971; Bown and Kraus 1979; Westergaard 1980, 1983; Novacek 1986). McKenna (1975) challenged this view by proposing that the initial eutherian dental formula included five premolars and three molars. According to McKenna, eutherians achieved the dental formula with four premolars and three molars independently in various eutherian clades, either by loss of one anterior premolar, most likely in the third position (superclade Emotheria), or by loss of the last molar and non-replacement of the fifth premolar (superclade Tokotheria). This hypothesis was based on observations of the Late Cretaceous eutherian *Gypsonictops* from North America (Lillegraven 1969; Clemens 1973; Fox 1979) and then unpublished data on the Early Cretaceous eutherian *Prokennalestes* from Asia (Kielan-Jaworowska and Dashzeveg 1989; Sigogneau-Russell et al. 1992), all of which have five lower premolars. Luckett and Maier (1982) and Luckett (1993) criticized this view noting that one of these five premolars could be a temporarily retained deciduous premolar. Since then, a number of other Cretaceous eutherians with five premolars have been discovered (Nesov et al. 1998; Ji et al. 2002; Averianov and Archibald 2005, 2013a; Zan et al. 2006; Wible et al. 2007, 2009; Hu et al. 2010; Archibald and Averianov 2012; Averianov et al. 2014). The view of Luckett was partially supported because, as discussed below, in some stem therians (*Juramaia*, *Eomaia*), the milk tooth (dP3) can be

Communicated by: Sven Thatje

Electronic supplementary material The online version of this article (doi:10.1007/s00114-015-1308-1) contains supplementary material, which is available to authorized users.

✉ Alexander O. Averianov
dzharakuduk@mail.ru

- ¹ Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia
- ² Department of Sedimentary Geology, Geological Faculty, Saint Petersburg State University, Saint Petersburg, Russia
- ³ Department of Biology, San Diego State University, San Diego, CA, USA

present for some time in the adult dentition along with the permanent P3. The current consensus, as reviewed by O’Leary et al. (2013), is that the postcanine formula with five premolars and three molars is the plesiomorphic therian condition. Eutherians lost the third permanent premolar whereas metatherians lost replacement in the fifth premolar locus and lost one of the anterior premolars, third (O’Leary et al. 2013) or first (Averianov et al. 2010), acquiring a dental formula with three premolars and four molars.

A detailed picture of the evolutionary transition from five to four premolars in eutherians is unclear. In the Early Cretaceous stem therians *Eomaia* and *Acristatherium*, the third premolar is unreduced and larger than the p2 (Ji, Luo et al. 2002; Hu, Meng et al. 2010). In the Early Cretaceous *Prokennalestes*, a possible stem placental, the third premolar (dP3/dp3) is significantly reduced compared with the adjacent premolars (unpublished data of AA). Surprisingly, this tooth is totally lost in another Early Cretaceous stem placental, *Sasayamamylos* (Kusuhashi, Tsutsumi et al. 2013). In the Cenomanian stem placental *Bobolestes*, the Cenomanian zhelestid *Eozhelestes*, and the early Turonian zhelestid *Borisodon*, the third premolar is somewhat smaller than p2 (Averianov and Archibald 2005; Archibald and Averianov 2012). In the Cenomanian large Zhelestidae indet. sp. A, the late Turonian zhelestids from Uzbekistan, and in the Santonian zhelestid *Zhalmouzia* from Kazakhstan, the third premolars, most likely an unreplaced dP3 and dp3, are distinctly smaller than the adjacent premolars, but each retains two roots. This tooth is present in most individuals but was shed in at least some older individuals in which the alveoli are plugged by bone (Averianov and Archibald 2005; Archibald and Averianov 2012; Averianov, Archibald et al. 2014). The third premolar (likely an unreplaced dP3 and dp3) is also smaller than the second in *Paranyctoides*, the sister taxon for the Zhelestidae (Averianov and Archibald 2013a). In the Late Cretaceous Zalambdalestidae (except *Zhangolestes*) and Asioryctitheria, the third premolar locus is absent (Kielan-Jaworowska 1984; Novacek, Rougier et al. 1997; Wible, Novacek et al. 2004; Archibald and Averianov 2006; Zan, Wood et al. 2006). In one juvenile specimen of the Campanian asioryctitherian *Kennalestes* from Mongolia in which dP5 has not yet been replaced and M3 not yet erupted, the DP3 is present on one side but absent from the other (Kielan-Jaworowska 1981). In the Campanian–Maastrichtian North American leptictid *Gypsonictops*, a tooth in the upper third premolar position might be present in a few instances whereas a small, probably deciduous lower p3 is usually present (Lillegraven 1969; Clemens 1973; Fox 1977, 1979). Here, we report on the discovery of the third premolar locus in some specimens of the Turonian zalambdalestid *Kulbeckia kulbecke* from Uzbekistan. Previously, this taxon was considered as having only four upper and lower premolars (Archibald,

Averianov et al. 2001; Archibald and Averianov 2003). These new data provide the first insight into dental ontogeny of this taxon and, moreover, provide important information pertaining to the evolutionary steps that led to the transformation of the dental formula in eutherian and placental mammals.

Materials and methods

The specimens of *K. kulbecke* described herein were collected by L.A. Nesov and his colleagues in 1977–1994 and by the Uzbekistan/Russian/British/American/Canadian (URBAC) joint paleontological expeditions in 1997–2006 in the late Turonian Bissekty Formation at Dzharakuduk, central Kyzylkum Desert, Uzbekistan (Archibald et al. 1998; Nesov et al. 1998). At Dzharakuduk, the Bissekty Formation is exposed along an escarpment that extends from about 42° 06′ 22.60″ N and 62° 37′ 09.00″ E to 42° 05′ 44.22″ N and 62° 41′ 06.49″ E. The Bissekty Formation comprises an up to 80-m-thick succession of medium-grained, poorly lithified, cross-bedded fluvial sandstones and clast-supported, well-cemented intraformational conglomerates (Redman and Leighton 2009). The geological age is bracketed using invertebrate fossils from marine units overlying and underlying the Bissekty Formation, as well as by the comparison with the Late Cretaceous vertebrate complexes of Central Asia (Averianov and Sues 2012). The unit is assigned a late Turonian age, approximately 90.4–88.6 Ma (Gradstein et al. 2004). The described material is housed in the National Museum of Natural History (USNM), Smithsonian Institution, Washington DC, USA, and Zoological Institute (ZIN), Russian Academy of Sciences, Saint Petersburg, Russia.

Fossils were recovered by surface collecting at the richest sites in 1977–1994 with subsequent dry and wet screening of 300 t of matrix between 1997 and 2006, which produced approximately 1500 mammalian specimens (Archibald and Averianov 2005). The computed tomography data were collected by utilizing the high-resolution micro CT SkyScan 1172 (at 59 kV and a voxel size of 2.97 μm) in the Resource Center “Geomodel” of Saint Petersburg University. The CT scans were processed using CTvox 2.7.0 and Avizo 8.1 software. 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 have been adopted from Goswami et al. (2011) and Manzi et al. (2015). The character-taxon matrix, consisting of 416 characters and 91 taxa, was analyzed using parsimony ratchet analysis using PAUP (PRAP) (Müller 2007) and PAUP* 4.0b10 (Swofford 2002). The equal-weight analysis with 10,000 ratchet replications produced 6799 most parsimonious trees with tree length

of 2766 steps, consistency index of 0.220, and retention index of 0.570. 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 (RC) indices, and a heuristic search with 10,000 random sequence addition replicates, and tree bisection and reconnection (TBR) 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. The last run resulted in 15 most parsimonious trees with tree length of 334.7 steps, consistency index of 0.381, and retention index of 0.678.

Results

We identify a total of 38 dentary specimens of *K. kulbecke*, 17 of which (44.7 %) belong to sub-adult individuals with teeth erupting and/or being replaced. There is a similarly high proportion of juvenile specimens for asioryctitherians and zhelestids from the Bissekty Formation at Dzharakuduk (Archibald and Averianov 2006, 2012). This apparently reflects either a high mortality rate at these ontogenetic stages or longer postnatal development compared with the modern placentals or, most likely, both. The eruption sequence of the lower dentition, reconstructed from these specimens, is similar to that in Zhelestidae (Archibald and Averianov 2012), with two exceptions. The permanent canine in *K. kulbecke* erupts at an earlier ontogenetic stage, at the same time that the p2 is erupting. In Zhelestidae, the permanent canine erupts at the same time as p4. The other more significant difference is that dp3 does not erupt in a majority of the specimens in *K. kulbecke*. If this tooth does erupt, it is much delayed and occurs, most likely, between the eruption of p2 and p4. In Zhelestidae, dp3 is fully erupted before eruption of m1 (Archibald and Averianov 2012). In Zhelestidae, the first and third premolar loci were likely monophyodont, with dp1 and dp3 not replaced by permanent teeth (Archibald and Averianov 2012). In the crown group placentals, the first premolar is functionally monophyodont, with very few exceptions, and there are four premolars, with dp3 lacking (Novacek 1986; Luckett 1993).

K. kulbecke previously was considered as having only four premolars (Archibald et al. 2001; Archibald and Averianov 2003). Subsequent study of additional specimens shows that the small double-rooted dp3 is present in two of ten specimens preserving this region of dentary (Fig. 1d, e). The edentulous specimen USNM 594413 (=URBAC 98-10) is referred to *K. kulbecke* based on size similarity and having an enlarged lower incisor, extending back to between p3 and p4. In other specimens, the postcanine alveoli are crowded without any diastema between the p2 and p4 (Fig. 1c). The dp3, when

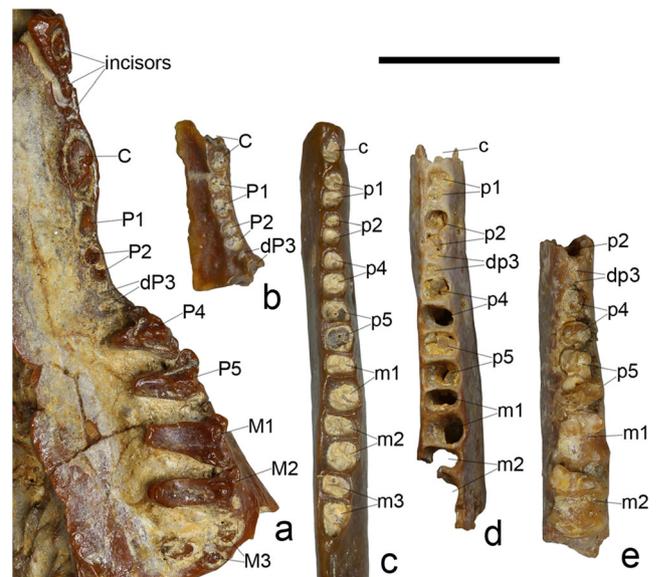


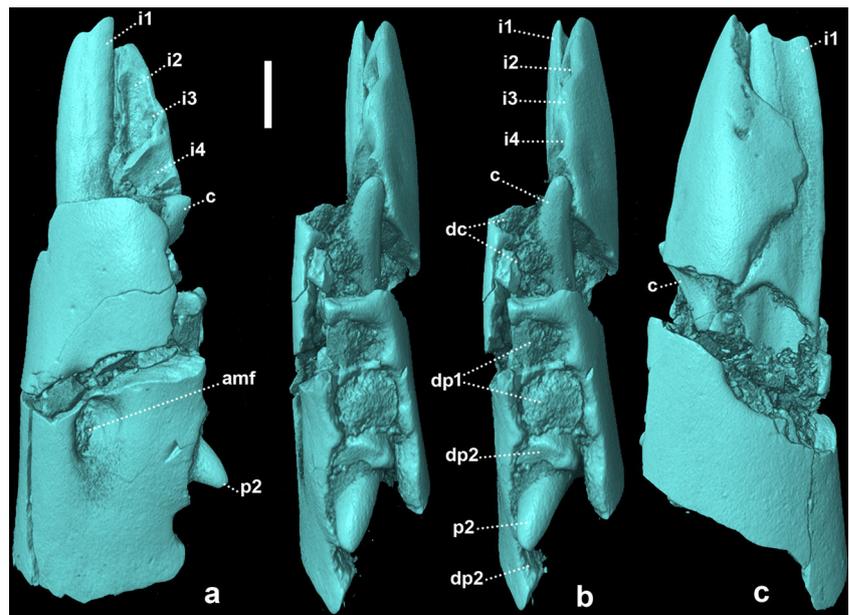
Fig. 1 Specimens of *Kulbeckia kulbecke* showing variation in premolars. **a** Left side skull fragment USNM 594400 (=URBAC 99-53) with dp3 shed and its alveoli plugged by bone. **b** Left maxillary fragment ZIN 88896 with alveoli for small dp3. **c** Right dentary fragment USNM 594414 (=URBAC 98-4) with typical premolar formula lacking dp3. **d** Right dentary fragment USNM 594413 (=URBAC 98-10) with alveoli for small dp3. **e** Right dentary fragment USNM 594447 (=URBAC 99-64) with alveoli for small dp3. Scale bar=5 mm

present, is the smallest lower premolar. There are only two specimens of *K. kulbecke* preserving the region of the upper premolars. In one specimen belonging to an old individual with a heavily worn dentition, the double-rooted dp3 was shed and its alveoli are plugged by bone, producing a large diastema between P2 and P4 (Fig. 1a). In another, likely a younger individual, a small double-rooted dp3 is partially preserved (Fig. 1b).

Data on development of dp3 comes from a juvenile specimen with an erupting anterior dentition, USNM 594415 (=URBAC 98-3; Fig. 2). The external morphology of this specimen was described previously (Archibald and Averianov 2003). This specimen preserves a broken ever-growing first incisor (i1), alveoli for posterior incisors (i2-4), alveoli for a deciduous canine (dc), an erupting canine (c), alveoli for dp1, partially resorbed mesial root of dp2 and alveolus for the distal dp2 root, and p2 erupting between the two dp2 alveoli. One of the small precanine alveoli could be for a deciduous incisor, so the number of the permanent incisors in *K. kulbecke* cannot be established definitively.

The CT scan of this specimen reveals a tooth germ in the pulp cavity of the p2 (Figs. 3 and 4). The p2 is clearly a permanent tooth that is in the process of replacing dp2. The specimen preserves the mesial root of the dp2, which is resorbed on its distal side, mesial to the erupting crown of p2. The crown of p2 is just emerging above the dentary alveolar plane (Figs. 3 and 4), which means that its roots were only starting to form at the time of death. The small tooth in the

Fig. 2 CT micrograph of left dentary fragment USNM 594415 of *Kulbeckia kulbecke*. **a** Labial view. **b** Occlusal view, stereopair. **c** Lingual view. *amf* anterior mental foramen. Scale bar=0.5 mm



pulp cavity cannot be a replacement tooth because no more than two tooth generations of premolars are known for Eutheria. It is interpreted as a germ of dp3, which when present is usually not replaced in eutherians, and is traditionally designated as p3. This tooth has an anomalous crown morphology, with a groove along the distal side, flanked by two ridges, and a pulp cavity open on the occlusal side.

An alternative interpretation of the object inside the p2 pulp cavity, proposed by one of the reviewers, is that it is the root fragment of dp2. There are several problems with this interpretation. First, it is not clear how this root could come to be inside a closed space of the p2 pulp cavity with intact walls (supplementary Fig. 1). Second, the complex morphology of this object does not correspond with the simple round or oval in cross section premolar roots. Third, the mesial root of dp2 is still present and resorbed from the inner (distal) side to give space for the erupting p2 crown. The same morphology is

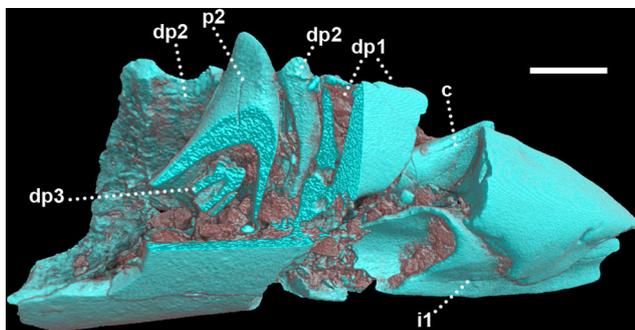


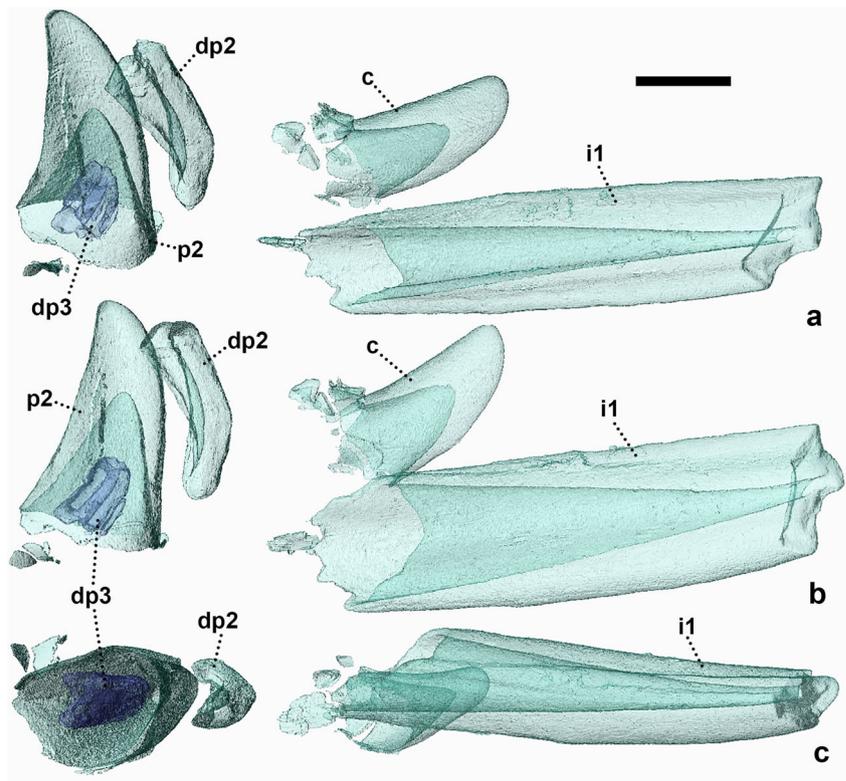
Fig. 3 CT micrograph of left dentary fragment USNM 594415 of *Kulbeckia kulbecke*. The specimen is in lingual and somewhat posterior view. The part of dentary and teeth is digitally cut off to see the cryptic dp3 in the pulp cavity of p2. The low-density clay particles are contrasted by red color. The bone and teeth tissues have a similar density and are shown in blue. Scale bar=0.5 mm

expected for the distal root of dp2: it should be resorbed from the inner (mesial) side, which is not true for the object inside p2 pulp cavity.

Discussion

The scenario creating the unusual development of the dp3 tooth germ inside the pulp cavity of the developing p2 is outlined on Fig. 5. During the normal mode of tooth development, which would lead to eruption of dp3, there is enough space between dp2/p2 and dp4/p4 for eruption of this tooth (double-headed arrow on Fig. 5a). The dp3 erupts and functions for some time in adult dentition (Fig. 5a). In abnormal development, the interstitial growth of the dentary slows or stops at an earlier ontogenetic stage. This results in the absence of space between dp2 and dp4 (Fig. 5b). This slowing of dentary growth leads to a change in spatial configuration of the tooth germs. In particular, the tooth germs posterior to the second premolar position shift somewhat anteriorly (arrow on Fig. 5b). The tooth germ of the much delayed dp3 occurs below but posterior to the p2 tooth germ during normal ontogenesis (Fig. 5a), but with the anterior shift of the tooth germ of dp3, it now rests directly below the tooth germ of p2 (Fig. 5b). During subsequent development of the p2 tooth germ, the dp3 tooth germ can come to lie below the pulp cavity of p2 (Figs. 3 and 4). The dp3 tooth germ would be resorbed in a later ontogenetic stage as the roots of p2 fully formed. This resorption was likely already started at the time of death of USNM 594415 as the pulp cavity of dp3 is open dorsally. Developing beneath the pulp cavity of p2, dp3 had no possibility of erupting. This would result in the absence of dp3 in the adult dentition (Fig. 5b). Other similarly abnormal

Fig. 4 Digitally extracted dentition of left dentary fragment USNM 594415 of *Kulbeckia kulbecke*. **a** Occluso-lingual view. **b** Lingual view. **c** Ventral view. Scale bar=0.5 mm



conditions of tooth eruption were likely in this species resulting in dp3 commonly not erupting.

The normal mode of tooth development, with a small dp3 present in the adult dentition, was characteristic for the majority of the Cretaceous stem placental taxa (state b on Fig. 6). The replacement in the third premolar locus is documented for the upper dentition of the stem therians *Juramaia* and *Eomaia* (Ji, Luo et al. 2002; Luo, Yuan et al. 2011; O’Leary et al.

2013). In these taxa, dp3 is present together with reduced in size P3 in the adult dentition (see Averianov, Archibald et al. (2010) for interpretation of the postcanine dentition in *Eomaia*). When the third premolar is unreduced in size, i.e., larger than the second premolar and smaller than the fourth premolar, as in the stem therian *Acristatherium* (Hu, Meng et al. 2010), this tooth is most likely the permanent molar, which replaced the deciduous predecessor. Loss of the

Fig. 5 Developmental scenario of normal (a) and abnormal (b) tooth development in the Cretaceous stem placental mammals. dp1 and dp3 are non-replacing deciduous teeth (green). dc, dp2, dp4, and dp5 are replacing deciduous teeth (blue). c, p2, p4, p5, and m1 are permanent teeth (yellow). A double-headed arrow in a represents space on dentary available for eruption of dp3. In a slowdown of dentary growth, this space is not available and the tooth germ of dp3 becomes in more anterior position (arrow in b)

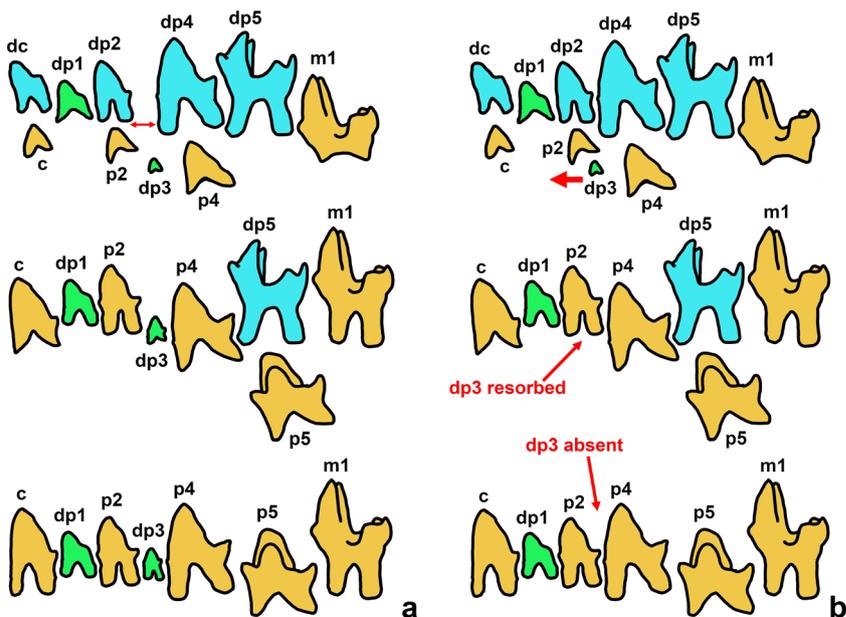
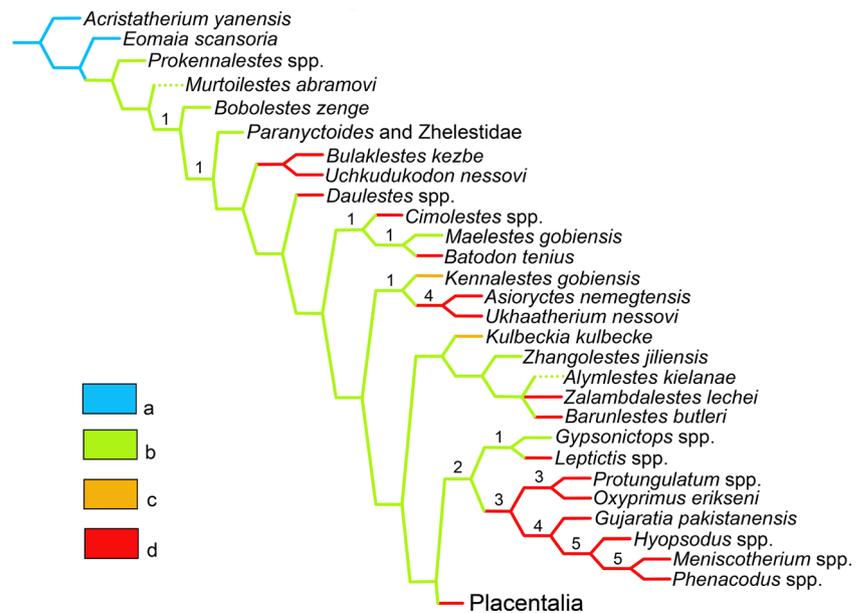


Fig. 6 Evolutionary pattern of reduction of dP3/dp3 in eutherian mammals based on a simplified strict consensus tree of 15 most parsimonious trees produced by PAUP reweight analysis. *a* Dp3/dp3 present and unreduced in size; *b*, dP3/dp3 present and reduced in size; *c*, dP3/dp3 reduced in size and might be present as an individual variation; and *d*, dP3/dp3 absent. The character states are optimized for delayed transformation which favored parallelisms rather than reversals. Dotted line represents unknown state for a terminal taxon. Numbers above the nodes are Bremer support values calculated by TNT



permanent P3/p3 might be an important synapomorphy for Eutheria (state b on Fig. 6).

Retention of dP3/dp3 is plesiomorphic for therians occurring as an individual variation in *K. kulbecke*. The majority of specimens of *K. kulbecke* had a more derived mode of tooth development (Fig. 5b), which resulted in the loss of dp3 during the ontogeny. This derived development became the norm in the paleopopulation of *K. kulbecke* from the Bissekty Formation. A similar derived tooth development was likely the norm for the Late Cretaceous stem placental (asioryctitherian) mammal *Kennalestes gobiensis*. This species has four premolars in the adult dentition, but one juvenile specimen has an atypical non-replacing dP3 on one side (Kielan-Jaworowska 1981).

The evolutionary transformation of dental formula from five to four premolars occurred in a complex pattern and in different ways in the Cretaceous stem placentals (Fig. 6). Most taxa had a small dP3/dp3 in the adult dentition but no P3/p3, the former sometimes being lost in older individuals (*Prokennalestes*, *Paranyctoides*, *Zhelestidae*, *Maelestes*, *Zhangolestes*, and *Gypsonictops*; state b on Fig. 6). In other taxa (*Kulbeckia*, *Kennalestes*), dP3/dp3 may be present in the adult dentition as an individual variation, when the heterochronic growth of the dentary allowed enough space for eruption of this tooth. In other individuals, development of dP3/dp3 terminated during ontogenesis. In some Late Cretaceous stem placental mammals (*Asioryctitheria*, derived *Zalambdalestidae* and *Cimolestidae*), there are only four or fewer premolars. The development of dP3/dp3 was either completely suppressed in these taxa, or the plesiomorphic condition was retained in a few specimens. The phylogeny in Fig. 6 suggests that the third premolar locus was lost

independently in several clades of stem and crown placental mammals. Our analysis included extant placentals as well as many Late Cretaceous eutherians not found in some recent studies (O'Leary, Bloch et al. 2013). Perhaps, this is the reason that unlike in these studies, *Leptictis* and *Protungulatum* clustered with other extinct taxa rather than nesting within Placentalia. Whichever analysis proves correct regarding the status of these as well as other taxa in the same clade, it is clear that, at or shortly before the appearance of Placentalia, the P3/p3 tooth site was totally lost (Fig. 6). It also possible that this occurred earlier within Eutheria with a few clades regaining this tooth site. Although this cannot be dismissed, we regard the loss of the P3/p3 tooth site multiple times to be the biologically more likely scenario.

Acknowledgments AA is grateful to H.-D. Sues for loan of the USNM specimens of *Kulbeckia* and to S. Nilov for the CT scanning. Fieldwork in Uzbekistan was facilitated by and conducted in cooperation with the Zoological Institute of the National Academy of Sciences of Uzbekistan, particularly D.A. Azimov and Y.A. Chikin. For their efforts in the field, scientific expertise, and camaraderie, we thank A.V. Abramov, G.O. Cherepanov, I.G. Danilov, S. Dominguez, C. King, N. Morris, C.M. Redman, A.S. Resvyi, C. Skrabec, P.P. Skutschas, E.V. Syromyatnikova, and D.J. Ward. The field work in 1997–2006 was funded by the National Science Foundation (EAR-9804771 and EAR-0207004 to J.D. Archibald and H.-D. Sues), the National Geographic Society (#5901-97 and #6281-98 to J.D. Archibald and H.-D. Sues), and the Navoi Mining and Metallurgy Combinat. The laboratory work of AA was supported by the Russian Foundation for Basic Research (project 13-04-00525) and in by the Russian Science Foundation (project 14-14-00015). We thank three anonymous reviewers for reading the manuscript and providing useful comments that improved the paper.

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