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Late Cretaceous relatives of rabbits, rodents, and other extant eutherian mammals

J. David Archibald*, **Alexander O. Averianov**† & **Eric G. Ekdale***

* *Department of Biology, San Diego State University, San Diego, California 92182-4614, USA*
† *Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, Saint Petersburg 199034, Russia*

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Extant eutherian mammals and their most recent common ancestor constitute the crown group Placentalia. This taxon, plus all extinct taxa that share a more recent common ancestor with placentals than they do with Metatheria (including marsupials), constitute Eutheria[1]. The oldest well documented eutherian-dominated fauna in the world is Dzharakuduk, Uzbekistan[2]. Among eutherians that it yields is *Kulbeckia*, an 85–90-Myr-old member of Zalambdalestidae (a family of Late Cretaceous Asian eutherians)[3]. This extends Zalambdalestidae back by some 10 million years from sites in the Gobi Desert, Mongolia[4]. A phylogenetic analysis of well described Late Cretaceous eutherians strongly supports Zalambdalestidae, less strongly supports 'Zhelestidae' (a Late Cretaceous clade related to Tertiary ungulates), but does not support Asioryctitheria (a group of Late Cretaceous Asian eutherians). A second analysis incorporating placentals from clades that include rodents (*Tribosphenomys*), lagomorphs (*Mimotona*) and archaic ungulates (*Protungulatum* and *Oxyprimus*) strongly supports Zalambdalestidae in a clade with Glires (rabbits, rodents and extinct relatives) and less strongly 'Zhelestidae' within a clade that includes archaic ungulates ('condylarths'). This argues that some Late Cretaceous eutherians belong within the crown group Placentalia. The ages of these taxa are in line with molecularly based estimates of 64–104 Myr ago (median 84 Myr ago) for the superordinal diversification of some placentals[5], but provide no support for a Late Cretaceous diversification of extant placental orders.

Timing of the origin of major clades of extant placental mammals remains controversial. Some molecular studies place the origin of such clades (orders) far back into the Cretaceous[6]. Most palaeobiologists argue that such clades originated in the Palaeocene or later[7,8]. Others argue that more inclusive extant placental clades (superordinal groupings) may not be discernible even in the Late Cretaceous[9]. Some proposed exceptions are Late Cretaceous representatives of Ungulatomorpha ('Zhelestidae'[10]), lipotyphlans (*Paranyctoides* and *Batodon*[11]) and Glires (Zalambdalestidae[11]). The timing of the origin and relationships of Glires are among the most controversial subjects in studies of mammal evolution.

Glires includes extinct early Tertiary taxa, as well as extant Rodentia (rodents) and Lagomorpha (rabbits and pikas). The monophyly of Glires has been repeatedly upheld[5] but the timing of the origin of Glires is contested; on the basis of molecular studies

one of its members, Rodentia, has been argued to appear over 100 Myr ago[6,12]. This is almost as old as the oldest eutherian fossils[13–15]. The relationships of Glires to other eutherian taxa are also disputed; it has been argued that Glires may share a common ancestry with the Late Cretaceous Zalambdalestidae[11].

We present new data for the oldest known zalambdalestid, *Kulbeckia kulbecke*, from the 85–90-Myr-old Dzharakuduk fauna, Bissekty Formation, Uzbekistan[2]. Until recently, zalambdalestids were known almost exclusively from 75-Myr-old fossils from the Gobi Desert (J. R. Wible, M. J. Novacek & G. W. Rougier, manuscript in preparation; and ref. 16). *Kulbeckia* was named in 1993, on the basis of a few teeth[17]. Possible affinities with zalambdalestids were not recognized until 1997 (ref. 3). During field seasons at Dzharakuduk (1997–2000), over 40 additional specimens were recovered including teeth, dentaries, petrosals, a partial skull, and postcrania (Figs 1, 2). Similarities of zalambdalestids and Glires warrant further consideration.

The hallmark of Glires is its enlarged, medially placed pair of incisors, which are procumbent, have enamel restricted to the more ventro- or dorsolabial margin of the tooth, are open-rooted, ever-growing, and have Hunter–Schreger bands[18]. Other mammals possess incisors that have some of these traits, but only Glires has all six character states. In the lower incisors, the zalambdalestid *Kulbeckia* possesses the first four of these states, although the enamel encompasses a greater circumference of the crown, which is a slightly more ancestral condition (Fig. 2c). We cannot demonstrate that the open-rooted lower incisor was ever-growing and scanning electron micrographs (SEMs) of the surface of the lower incisor did not reveal Hunter–Schreger bands. Although suggestive, these character states alone are not strong evidence for a phylogenetic relationship, because other eutherians possess some of these traits. When a suite of other comparisons is added, the zalambdalestid–Glires link becomes more plausible.

The two larger, anterior upper incisors and much smaller third upper incisor known for *Kulbeckia* are preserved only as roots; thus, the disposition of enamel is unknown. One (or two) smaller, more medial incisor(s) may have been present (Fig. 2a, b). Rodents possess one upper incisor on each side while lagomorphs possess two, and thus the condition in *Kulbeckia* could have been ancestral to both of these orders. *Kulbeckia* and other zalambdalestids (*Zalambdalestes* and *Barunlestes*) warrant further comparison with Glires, especially with more basal members. All have narrow, elongate snouts (Figs 1a and 2b). *Zalambdalestes* and *Barunlestes* fall between the ancestral condition in which most of the elongation is within the maxilla and the derived condition in Glires in which half or more of the elongation is in the premaxilla. Although it shows some premaxillary elongation, *Kulbeckia* is close to the ancestral condition. In the morphocline *Kulbeckia* to *Zalambdalestes* to *Barunlestes* to Glires, we see a reduction of incisors from 3, 4, or 5/4 (5 in the upper jaw, 4 in the lower jaw) to 2/3 or 3/3 to 2/3 to 1/1 or 2/1. Homologies of the four lower incisors are open to interpretation. *Kulbeckia* may retain the ancestral therian condition of four incisor sites seen in some early eutherians. In these taxa, however, the incisors are of nearly equal size, while in *Kulbeckia* the most medial incisor is six times longer and perhaps as much wider than the three following teeth. In Glires embryological evidence suggests that the medial, enlarged lower tooth is the second, lower, deciduous incisor[19]. Unfortunately, embryological evidence does not help in determining homologies in available fossils, and thus without ontogenetic information we use the overall anatomy of the dentitions to support the view that the medial pair of lower incisors in zalambdalestids and Glires are homologous.

In the same taxa, canines are never large, ranging from two roots above (in the upper jaw) and below (in the lower jaw) to one above and below to no canines. In *Kulbeckia* there are 4/4 premolars while later zalambdalestids have 3/4 or 4/4, and among some Glires, 3/3 are retained. Upper molars of both *Kulbeckia* and early Glires such as

Tribosphenomys and *Mimotona* have transversely expanded crowns, a metacingulum where the postmetaconular crista continues onto the metastylar lobe, and a narrower metastylar lobe on the second upper molar[20,31] (Fig. 1b, c). In illustrations, molar conules in *Zalambdalestes* and *Barunlestes* are shown as labial nearer the paracone and metacone and at least in the former taxon are characterized as 'incipient' and 'very indistinct'[16]. This is unlike the more lingual condition in *Kulbeckia* and early Glires. All published specimens of *Zalambdalestes* and *Barunlestes* are worn and thus the conular positions are subject to interpretation.

The above suite of characters in *Kulbeckia*, other zalambdalestids, and Glires is suggestive of a possible phylogenetic relationship. To test this we performed phylogenetic analyses using MacClade[21] and PAUP*[22], beginning with better represented Late Cretaceous eutherians. We used 70 characters including those from previous studies (J. R. Wible, M. J. Novacek & G. W. Rougier, manuscript in preparation and refs 1, 10, 23, 24) based upon upper and lower dentitions, anterior skull, dentary and petrosal (see the Supplementary Information). Only multistate characters forming a morphocline were coded as ordered: all characters were unweighted; and the branch and bound search option was used. Results for this analysis indicate a well supported (bootstrap value over 70) Zalambdalestidae. Although Zhelestidae is also supported, it is not as well supported and may include *Pavanyctoides* and *Gallolestes* (Fig. 3a). Asioryctitheria (*Asioryctes* and *Kennalestes*) is not supported, but neither is there evidence against it. The third published asioryctithere, *Ukhaatherium*, was not included, as it was not separately coded in earlier analyses[1].

In the next analysis we added early Tertiary placental taxa belonging to clades that are argued to be linked to Late Cretaceous eutherians[10,11] (Fig. 3b). These taxa were chosen because they are widely accepted basal members of superordinal clades within the crown taxon Placentalia, yet they retain some ancestral eutherian character states. These included two taxa from Glires, *Tribosphenomys* and *Mimotona*, and two archaic ungulates, *Protungulatum* and *Oxyprimus*. *Tribosphenomys* is a very basal taxon within Simplicidentata, which also includes Rodentia[20]. *Mimotona* is a well known member of Mimotonidae, which along with Lagomorpha[25] comprise Duplicidentata. *Protungulatum* is a basal taxon within Ungulata or within Arctocyonidae. The latter taxon has been argued to be basal to other archaic ungulates as well as Artiodactyla and Cetacea[26]. *Oxyprimus* is a basal ungulate regarded as either an arctocyonid or hyopsodontid[26].

Results for this analysis yield a well supported (bootstrap values over 70) 'gliriform' clade including zalambdalestids as well as a Glires clade composed of *Tribosophenomys* and *Mimotona* (Fig. 3b). Formal taxonomic revisions are beyond the scope of this work, but we note that if the relationship among zalambdalestids, *Tribosphenomys* and *Mimotona* are supported by further analyses, Zalambdalestidae is rendered paraphyletic. The same concern has been expressed for 'Zhelestidae' and hence the placement of this taxon within quotes[23]. Asian 'Zhelestidae' remain monophyletic and along with other 'zhelestids' and archaic ungulates form a polytomy with *Paranyctoides* and *Gallolestes* (Fig. 3b). *Paranyctoides* and *Gallolestes* are not referred to 'Zhelestidae', but they may belong with this clade (dashed lines in Fig. 3b). Among 'zhelestids', *Alostera* groups with archaic ungulates. *Alostera* is based on isolated teeth, but does possess features of archaic ungulates not seen in other 'zhelestids', raising the possibility that it is either an archaic ungulate or the nearest sister taxon.

We follow recent taxonomic usage that defines Placentalia as the clade formed by the most recent common ancestor of living eutherians, plus all its descendants[1]. Eutheria is the clade that includes Placentalia (crown group) and all taxa that share a more
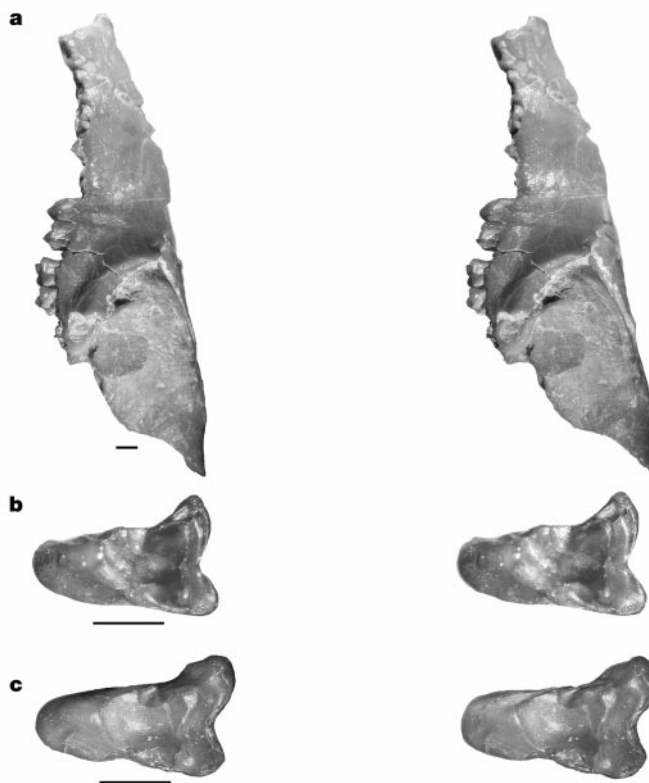

Figure 1 Stereo pairs of *Kulbeckia kulbecke*, Dzharakuduk fauna, Bissekty Formation. **a**, Left lateral view of anterior skull (URBAC 99-53); **b**, occlusal view left M1, type (CCMGE 52/12455); **c**, occlusal view left M2 (ZIN C.82565). CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg; URBAC, Uzbekistanian/Russian/ British/American/Canadian Joint Paleontological Expedition specimens in the Institute of Zoology, Tashkent, and the Royal Ontario Museum, Toronto; ZIN C., Systematic Collections, Zoological Institute, Russian Academy of Sciences, Saint Petersburg. Scale bars equal 1 mm.

recent common ancestor with it (stem eutherians) than they do with Metatheria (including the crown group Marsupialia). Metatheria is the sister taxon of Eutheria. As described above, our analysis argues that some Late Cretaceous eutherians belong within the crown group Placentalia. This view has been challenged by studies that suggest Placentalia possesses apomorphies not seen in Late Cretaceous eutherians[27]. These derived characters are: upper incisors four or fewer, nasals not posteriorly expanded, lacrimal without well developed facial process, jugal not posteriorly extensive in the zygoma, and epipubics absent. These five characters remain poorly known for most eutherians. For example, we observed a well developed facial process of the lacrimal among both extinct and extant Artiodactyla and Perissodactyla, and extinct archaic ungulates, all of which are placentals and yet retain the argued ancestral eutherian condition. Although less common, the nasals are posteriorly expanded in various clades in the above taxa,

in some cases contacting the lacrimals. Also, the reduction or loss of epipubics[28,29] and the reduction in number of upper incisors to four or fewer occurred in at least three different clades of metatherians[30]. Such reductions and losses also very probably occurred many times in eutherians and thus we question their reliability for uniting all Placentalia. On the basis of our phylogenetic analyses we feel that current evidence supports a crown group, Placentalia, that includes some Late Cretaceous eutherians. More specifically, these results support a superordinal clade including zalambdalestids and Glires. A zhelestid and ungulate superordinal clade also continues to be supported.

Finally, our analysis provides corroborating evidence concerning the timing of superordinal diversification. Both zalambdalestids and zhelestids occur in the 85–90-Myr-old faunas at Dzharakuduk[2].
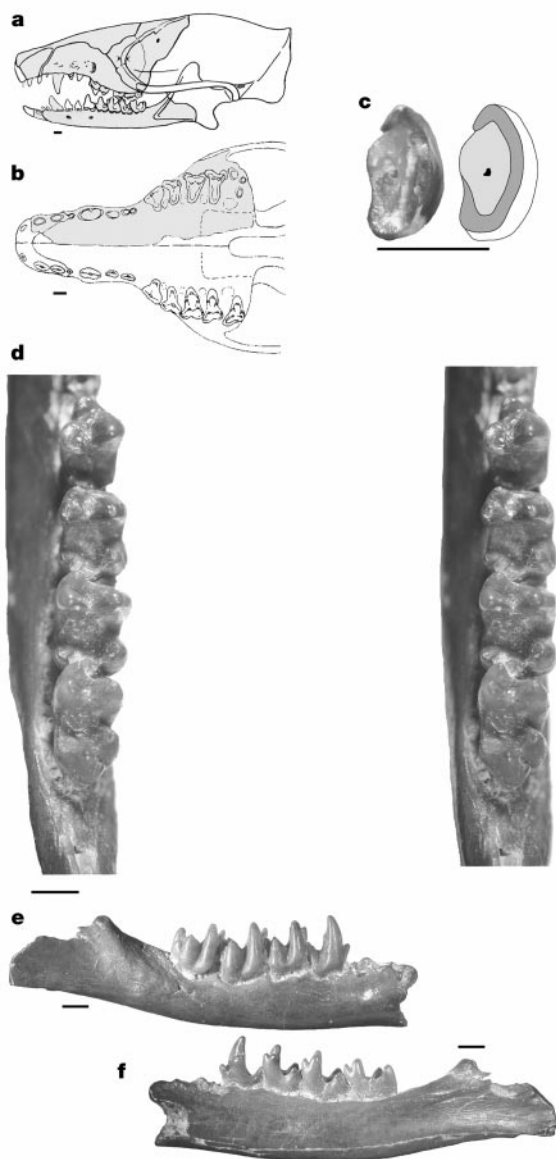

Figure 2 *Kulbeckia kulbecke*, Dzharakuduk fauna, Bissekty Formation. **a**, **b**, Left lateral and palatal reconstructions, with parts known shown in grey; **c**, broken tip of lower left incisor showing restriction of enamel (medium grey) to dorsal, labial and ventral surfaces (URBAC 98-3); **d**, stereo occlusal view, p5, m1-3 (URBAC 98-2); **e**, **f**, labial and lingual views of the same specimen. For institutional abbreviations see Fig. 1. Scale bars equal 1 mm.
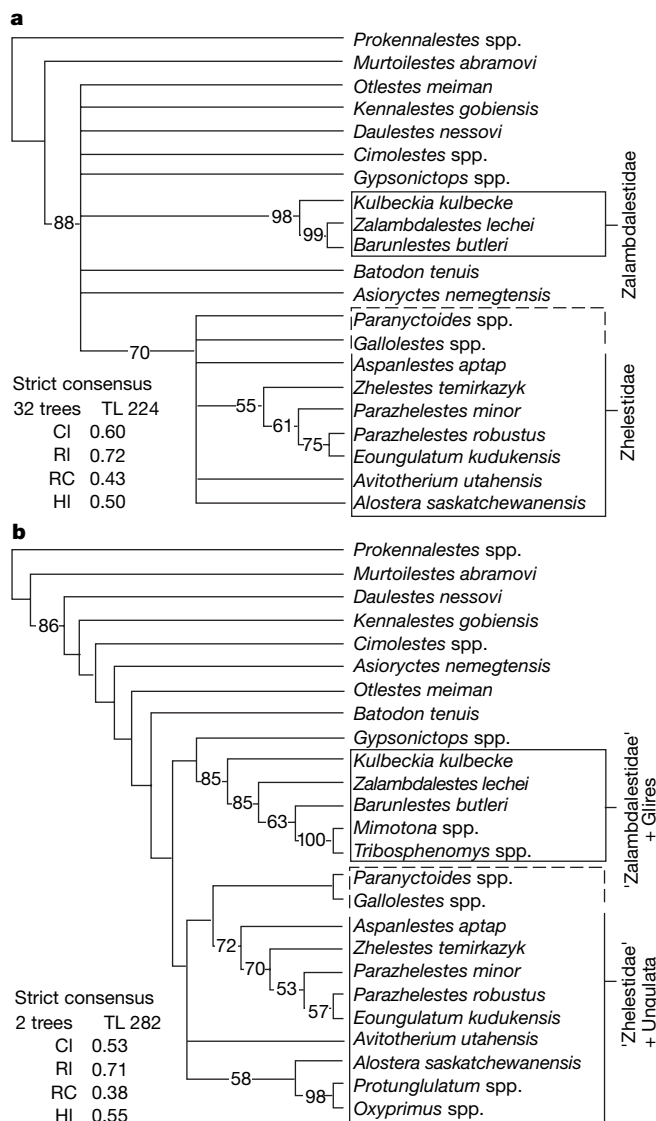

Figure 3 Phylogenetic analyses discussed in the text. Numbers refer to bootstrap values over 50. Matrix of taxa, characters, and states are defined in Supplementary Information. **a**, Cladogram of all better described Late Cretaceous eutherians with Early Cretaceous *Prokennalestes* and *Murtoilestes* as outgroup taxa, showing monophyly of Zalambdalestidae and Zhelestidae. **b**, Cladogram of same taxa but including two Tertiary members of Glires, *Mimotona* and *Tribosphenomys*, and two Tertiary members of Ungulata, *Protungulatum* and *Oxyprimus*, showing a gliriform clade including 'Zalambdalestidae' and Glires and an ungulatomorph clade including 'Zhelestidae' and Ungulata. TL, treelength; CI, consistency index; RI retention index; RC, rescaled consistency index; HI, homoplasy index.

The presence of zalambdalestids argues that the superordinal clade including Glires had separated from other superordinal placental clades by this time. This is also applicable for zhelestids, thus suggesting that some ungulate clades had separated from other superordinal placental clades by this time. The dates of these fossil taxa are concordant with molecularly based estimates of 64–104 Myr ago (median 84 Myr ago) for the superordinal diversification of placentals[5]. No members of extant placental orders, however, are known from the Late Cretaceous (with the possible exception of some insectivores). Subsequent diversification of living placental orders within these Late Cretaceous placental superordinal groups did not begin until about 65 Myr ago, after dinosaur extinction[7,8]. ☐

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Rapid responses of British butterflies to opposing forces of climate and habitat change

M. S. Warren*, J. K. Hill†‡, J. A. Thomas§, J. Asher*, R. Fox*, B. Huntley‡, D. B. Roy‖, M. G. Telfer‖, S. Jeffcoate*, P. Harding‖, G. Jeffcoate*, S. G. Willis‡, J. N. Greatorex-Davies‖, D. Moss‖ & C. D. Thomas¶

* *Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset BH20 5QP, UK*
† *Department of Biology, University of York, PO Box 373, York YO10 5YW, UK*
‡ *Environmental Research Centre, Department of Biological Sciences, University of Durham, Durham DH1 3LE, UK*
§ *Centre for Ecology and Hydrology, Dorset Laboratory, Winfrith Technology Centre, Dorchester, DT2 8ZD, UK*
‖ *Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire PE28 2LS, UK*
¶ *Centre for Biodiversity and Conservation, School of Biology, University of Leeds, Leeds LS2 9JT, UK*

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Habitat degradation and climate change are thought to be altering the distributions and abundances of animals and plants throughout the world, but their combined impacts have not been assessed for any species assemblage[1–4]. Here we evaluated changes in the distribution sizes and abundances of 46 species of butterflies that approach their northern climatic range margins in Britain—where changes in climate and habitat are opposing forces. These insects might be expected to have responded positively to climate warming over the past 30 years, yet three-quarters of them declined: negative responses to habitat loss have outweighed positive responses to climate warming. Half of the species that were mobile and habitat generalists increased their distribution sites over this period (consistent with a climate explanation), whereas the other generalists and 89% of the habitat specialists declined in distribution size (consistent with habitat limitation). Changes in population abundances closely matched changes in distributions. The dual forces of habitat modification and climate change are likely to cause specialists to decline, leaving biological communities with reduced numbers of species and dominated by mobile and widespread habitat generalists.

We studied all 46 non-migratory British butterfly species that reach their northern margins in Britain, where the summer–spring climate has warmed by approximately 1–1.5 °C in the past 25 years[5,6]. Many of these butterflies are restricted to warm local environments in Britain and have faster larval growth rates, earlier flight periods and increased abundances at higher temperatures (within the British temperature range)[1,7–9]. Range expansions have