

The upper dentition and relationships of the enigmatic Australian Cretaceous mammal *Kollikodon ritchiei*

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Abstract

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Mesozoic mammals from Australia are rare, so far only known from the Early Cretaceous, and most are poorly represented in terms of dentitions much less cranial material. No upper molars of any have been described. *Kollikodon ritchiei* is perhaps the most bizarre of these, originally described on the basis of a dentary fragment with three molars. Here we describe a second specimen of this extremely rare taxon, one that retains extraordinarily specialised upper cheekteeth (last premolar and all four molars). Each molar supports rows of bladeless, rounded cuspsules many of which exhibit apical pits that may be the result of masticating hard items such as shells or chitin. Reanalysis of the phylogenetic position of this taxon suggests, based on a limited number of apparent synapomorphies, that it is an australosphenidan mammal and probably the sister group to Monotremata. This reanalysis also supports the view that within Monotremata, tachyglossids and ornithorhynchids diverged in the early to middle Cenozoic.

Keywords

New South Wales, Mesozoic, Albian, Australosphenida, Monotremata, Ausktribosphenidae.

Introduction

Mesozoic mammals from Australia were unknown until the description in 1985 of the holotype and only known specimen of the monotreme *Steropodon galmani* (Archer et al., 1985), a partial right dentary with all three molars, from the Early Cretaceous (Albian) Griman Creek Formation at Lightning Ridge, New South Wales. This was followed by discovery at Lightning Ridge of *Kollikodon ritchiei* (Flannery et al., 1995), known from a single partial right dentary with three molars *in situ* and alveoli for the posterior two premolars and a fourth molar. Since then, additional Early Cretaceous mammals have been described from sites in southern Victoria and New South Wales. These include: from the Aptian Flat Rocks locality in Victoria, the ausktribosphenids *Ausktribosphenos nyktos* (Rich et al., 1997) and *Bishops whitmorei* (Rich et al., 2001a), the monotreme *Teinolophos trusleri* (Rich et al., 1999, 2001b), and the multituberculate *Corriebaatar marywaltersae* (Rich et al., 2009); from the Albian Dinosaur Cove locality in Victoria, the partial humerus of (the possible monotreme) *Kryoryctes cadburyi* (Pridmore et al., 2005); and from Lightning Ridge in New South Wales a very large, mammal-like isolated tooth (Clemens et al., 2003). Most recent phylogenetic analyses have

placed ausktribosphenids and monotremes within a larger Gondwanan radiation termed Australosphenida (Luo et al., 2001, 2002, 2007a; Martin and Rauhut, 2005; Rougier et al., 2011; Wood and Rougier, 2005), together with the early Jurassic (Toarcian) (Cúneo et al., 2013) South American *Asfaltomylos* (Rauhut et al., 2002) and *Henosferus* (Rougier et al., 2007), and the middle Jurassic (Bathonian) *Ambondro mahabo* (Flynn et al., 1999) from Madagascar. Some authors, however, have questioned the inclusion of monotremes within Australosphenida (Pascual et al., 2002; Rich et al., 2002; Rowe et al., 2008; Woodburne, 2003).

Archer et al. (1985) described *Steropodon galmani* as a plesiomorphic, toothed monotreme in the monotypic family Steropodontidae, an assignment that has been widely accepted (Kielan-Jaworowska et al., 1987; Musser, 2006; Phillips et al., 2009). Inclusion of *Teinolophos trusleri* within Monotremata is also uncontested, despite some debate over placement within the stem or crown group (Phillips et al., 2009; Rich et al., 2001b; Rowe et al., 2008). Flannery et al. (1995) described *Kollikodon ritchiei* as a possible monotreme, placing it in its own monotypic family, the Kollikodontidae. This assignment has proved more controversial, with suggestions that it may be a basal

mammaliaform rather than a monotreme and as such more appropriately placed outside crown-group Mammalia (Musser, 2003). This controversy rejects in part the limited morphological information available on the basis of the previously only known specimen, a partial dentary with three highly autapomorphic, bunodont molars. Discovery of an additional specimen of *K. ritchiei*, a partial maxilla with one premolar and four molars, now provides significant additional information about the structure and likely evolutionary relationships of this enigmatic taxon. This specimen also represents the first maxilla with teeth known for any Australian Mesozoic mammal.

Here we describe this specimen and test the evolutionary relationships of *K. ritchiei* via phylogenetic analysis based on a comprehensive morphological character matrix.

Materials and Methods

Measurements of the specimen were taken to the nearest 0.01 mm using a Leica M205 C microscope and integrated Leica DFC290 camera. Tooth lengths were measured along the long axis of the molar row. Widths were measured from the widest transverse points across the tooth, perpendicular to the long axis.

Kollikodon ritchiei was added to a revised version of the character matrix of Luo et al. (2011), which is in itself a modified version of earlier matrices (Luo et al., 2001, 2002, 2007b; Luo & Wible, 2005). Revisions to the matrix were made on the basis of corrections and criticisms by Woodburne et al. (2003), Rougier et al. (2007), Rowe et al. (2008) and Phillips et al. (2009). The final matrix included 104 taxa and 438 characters. 62 multistate characters representing plausible morphoclines were ordered. The topologies of the consensus trees derived through the ordered and unordered analyses were very similar, and as such only the ordered analyses are included here (Wiens, 2001).

Maximum parsimony analyses were conducted using the computer program PAUP* (Phylogenetic Analysis Using Parsimony and Other Methods) version 4.0b10 (Swofford, 2002). 1,000 heuristic replicates were initially carried out, saving 10 trees per replicate, followed by a second heuristic search within the trees obtained from the first search. Zero-length branches were then collapsed. Strict and 50% majority-rule consensus trees were derived from the most parsimonious trees recovered for each analysis. Bootstrap analysis was used to assess nodal support. To calculate bootstrap values, 250 bootstrap replicates were run, with a time limit of 60 seconds per replicate.

Bayesian analyses were conducted using Lewis's (2001) Mk likelihood model for discrete morphological data in the program MrBayes 3.2.1 (Ronquist et al., 2012). Applied assumptions included scoring of only parsimony informative characters and gamma distribution that permits rate variation across different characters. Two independent runs of four Monte Carlo Markov chains (one cold and three heated) were run for 5,000,000 generations with trees sampled every 500 generations. Convergence was confirmed by average standard deviation of split frequencies of less than 0.05. The first 25% of samples were discarded as "burn-in" and remaining samples used to construct the 50% majority-consensus.

Systematic Palaeontology

Mammalia Linnaeus, 1758

Australosphenida Luo, Cifelli and Kielan-Jaworowska, 2001

Kollikodontidae Flannery, Archer, Rich and Jones, 1995

Kollikodon Flannery, Archer, Rich and Jones, 1995

Kollikodon ritchiei Flannery, Archer, Rich and Jones, 1995

Holotype. AM F96602 (Australian Museum Palaeontological Collection, Sydney, Australia.), right dentary fragment preserving m1-3 and alveoli for two premolars and m4.

Referred specimen. Opalised right skull fragment preserving part of the maxilla, which retains the posterior premolar (possibly P4) and M1-4, and possibly also part of the palatine (Figs 1–2). A 35 µm voxel Xradia microCT data file of the specimen has been lodged with the Museum of Victoria in Melbourne. Detailed 3D prints of this specimen can be made from the scan data. Solid casts taken from a mould of the complete upper dentition are also available; one (AM F140201) is registered in the collections of the Australian Museum. Although the original specimen, which is a natural glass cast without internal structure of any kind, is less informative than the microCT scan data (given that it reveals structures in undercut areas not visible via conventional microscopy) and no more informative than 3D prints and hard casts, this specimen is available for further examination as part of the National Opal Collection, on application to its Director, Andrew Cody (andrew@codyopal.com).

Locality and age. Griman Creek Formation; Early Cretaceous (Middle Albian) (Flannery et al., 1995). The type locality is claim 30226, Moonshine area of the Cocoran opal field, Lightning Ridge, New South Wales, Australia (Flannery et al., 1995). The new skull fragment described here comes from an unnamed mine on the Cocoran opal field.

New diagnosis of clade containing Kollikodon and monotremes. *Kollikodon ritchiei* and definitive monotremes (ornithorhynchids, tachyglossids, *Steropodon* and *Teinolophos*) differ from other groups variously regarded as australosphenidans (ausktribosphenids, *Ambondro*, *Asfaltomylos* and shuotheriids), in so far as they are known, in having no paraconid on the first lower molar, an extremely abrupt discontinuity in size between the ultimate premolar and the first molar in the upper and lower dentitions, and in the presence of an enlarged dentary canal.

Revised specific diagnosis. *Kollikodon ritchiei* is a large (by Mesozoic standards) mammal (estimated body mass approximately 1935 g based on m1 area (Legendre, 1986)) that differs from definitive monotremes that retain a functional dentition in exhibiting the following combination of features: bunodont molars with no vertical blades (lophs or crests) of any kind; broadly crescentic upper molars with unique cusp arrangement; reduced or absent posterior cingula/cingulids on all molars; markedly convex curve of the buccal edge of the upper and (to a lesser extent) lower molar rows.

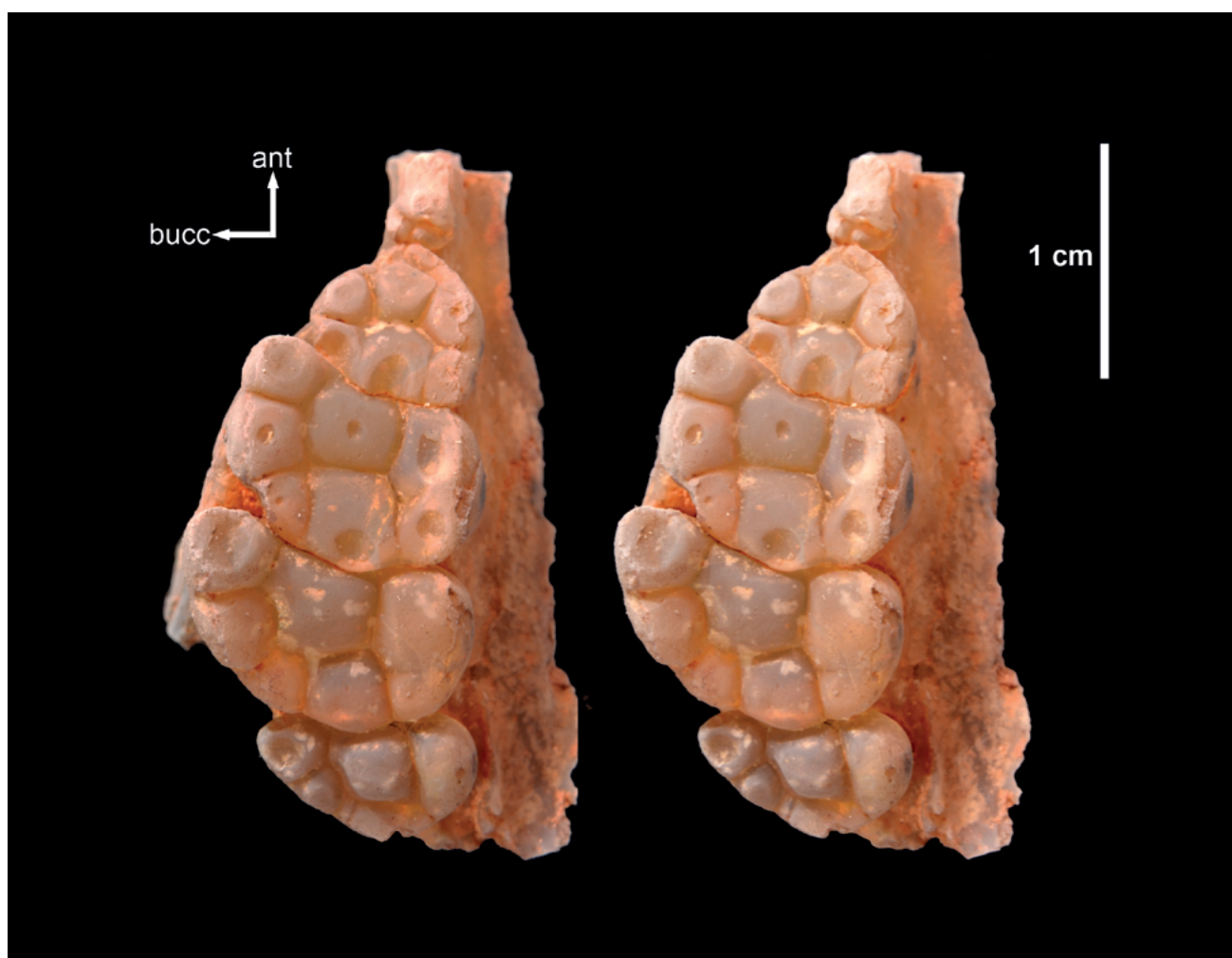


Figure 1. *Kollikodon ritchiei* right maxillary fragment and molar row preserving Px, M1, M2, M3 and RM4. Stereopair occlusal view. ant, anterior; bucc, buccal.

Description of the upper dentition and cranial fragment

The new specimen is a right cranial fragment comprising part of the maxilla and possibly part of the palatine (Figs 1–2). The maxilla preserves the root of the zygomatic arch and part of the palatal shelf. The palatine may form part of the posterior section of this shelf, although no sutures are evident. The infraorbital canal is exposed on the anterodorsal edge of the broken maxilla. No complete edges can be identified around the preserved portion of the palate.

Within the maxilla, the posterior premolar (actual homology with other mammalian premolars is unknown) and all four upper molars, M1–4, are preserved in situ. No inference can be made about teeth anterior to the posterior premolar because the maxilla is missing anterior to that point. As in the lower dentition, there is a stark discontinuity in size between the premolar and the molar row. The double-rooted, comparatively simple premolar aligns with the median row of cusps on the molars. The four fully bunodont molars are

characterized by rows of low, rounded, dome-like cusps that are separated from each other by arcuate grooves of varying depth. None of the cusps is subtended by blades although the enamel edges of pits in the apices of many of the cusps may have provided horizontal arcuate blades that assisted in segmenting food during transverse mastication.

The occlusal plane of the upper molar row is anteroposteriorly convex, corresponding to the concavity of the occlusal plane of the lower molar row. Although the lingual margin of the upper tooth row is more or less rectilinear, the buccal margin is strongly convex, reflecting differences in the width of the individual molars, with M2–3 being the widest. When the holotype is placed in centric occlusion with the upper dentition, the buccal margins of the upper molars markedly overhang the buccal margin of the lower molars, resulting in a strongly anisodontic bite. Considering the molars, M3 has the largest total occlusal surface followed in descending order by M2, M4 and M1 (Table 1).

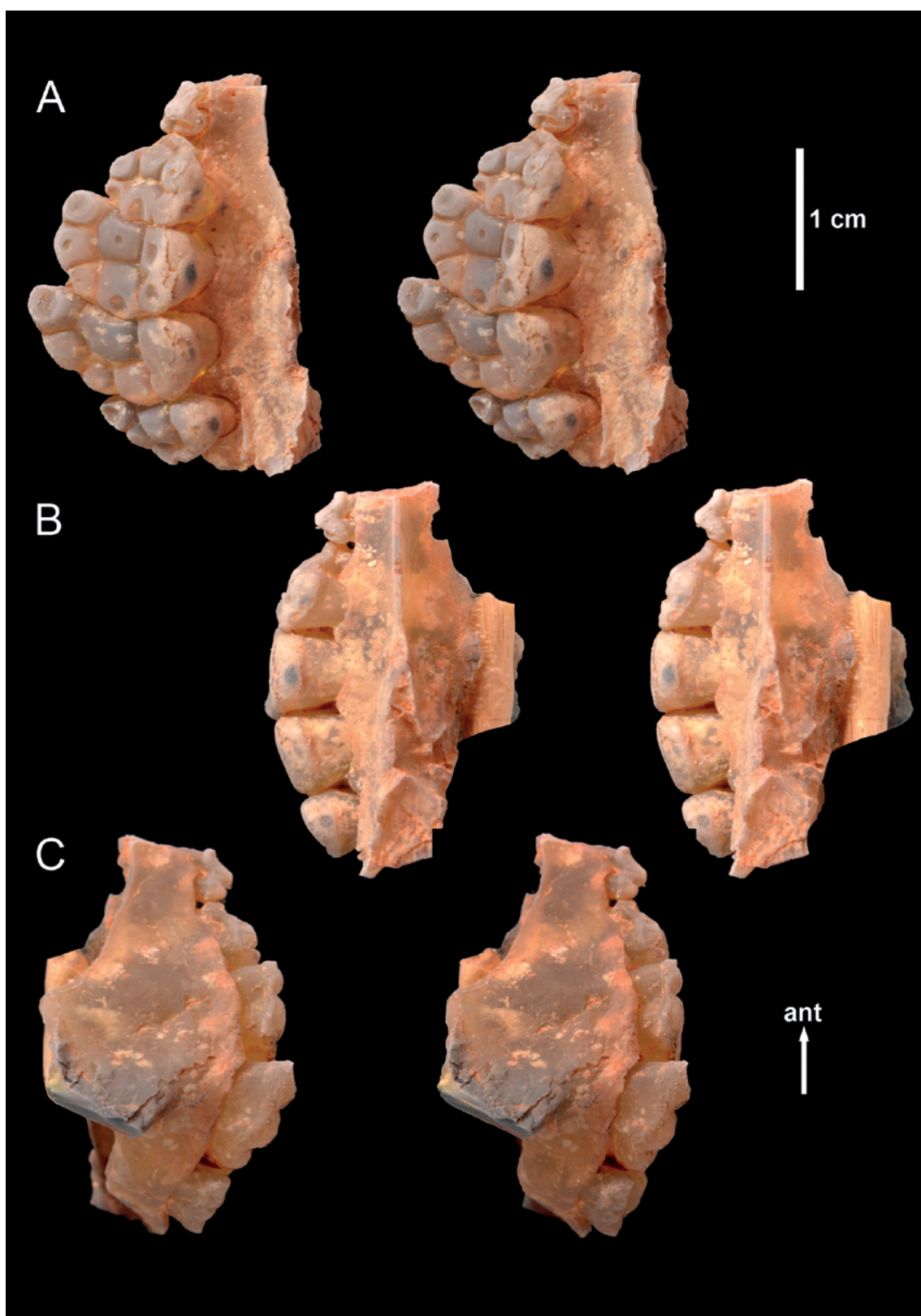


Figure 2. *Kollikodon ritchiei* right maxillary fragment and molar row preserving Px, M1, M2, M3 and M4. (A) Stereopair oblique-occlusal view. (B) Stereopair lingual view. (C) Stereopair buccal view. ant, anterior.

Although each molar is distinctly different from the others, there are common features and meristic trends that progress posteriorly along the molar row. The molars are transversely wide. Many of the cusps have pits or depressions at their apices. The arrangement of cusps on each molar could be interpreted as forming either a series of two arcuate transverse rows of cusps, three variably-longitudinal rows of cusps, or two central anteromedial cusps ringed by a perimeter of 2 to 3 buccal cusps and 1 to 2 lingual cusps. Given the morphological distinctiveness of each molar, none of these interpretations applies equally well to all of the individual teeth.

On M2-4 the anterobuccal and anterolingual corner cusps are anteriorly displaced compared to the anteromedial cusp, resulting in a concave anterior margin and a convex posterior margin of the crown. In contrast, M1 has convex margins on both the anterior and posterior sides of the crown making it unlike the otherwise crescentic M2-4. The distinction between the lingual cusps becomes less evident posteriorly such that in M4 only one anteroposteriorly elongate lingual cusp is apparent. M1 is the only molar that exhibits a basal anterior cingulum. In contrast to the holotype in which it can be clearly seen that each lower molar is double-rooted, the number of roots for each upper molar and the internal structure of the maxilla are unclear. There appears to be no preservation of any anatomical feature within the glass structure of the maxilla.

The apical pits invite speculation that these may have originally been areas of thin or even absent enamel that, once breached to expose softer dentine, served to increase the transverse cutting capacity of the otherwise blade-less molars. Functionally they would have acted as entrapment devices to help immobilize items being transversely sheared. Unfortunately, the amorphous glass constituency of the crowns does not enable differentiation of enamel and dentine hence this possibility cannot be tested. Alternatively the pits may be the result of apical concussive pressure caused by compression against wide, flat, hardened surfaces such as mollusc shells or crustacean chitin. If the result of compression, it is perhaps surprising that all except two (the hemicircular pits in the posterobuccal and posteromedial cusps of M1) are nearly circular even at the extreme buccal edge of the dentition such as the anterobuccal cusp of M4. If the two hemicircular pits at the posterior margin of M1 were also originally circular, interproximal wear could have removed the posterior halves of these pits. However, if this is the explanation for the hemicircularity, the lack of corresponding loss of tooth material from the anterior flank of M2 as well as the lack of posterior wear on the posterior premolar invite a more detailed analysis of potentially unique occlusal mechanics in this strange group of mammals.

Phylogenetic Analysis

Maximum parsimony analysis of our morphological character matrix, with selected multistate characters ordered, recovered 6048 most parsimonious trees (tree length = 2339; consistency index = 0.35). A simplified 50% majority-rule consensus is given in Fig. 3A, with dotted lines indicating nodes that collapse in the strict consensus. In the 50% majority-rule consensus tree, *Kollikodon ritchiei* is placed within Australosphenida, forming a

Table 1. Dimensions of the upper right dentition of the original specimen of *Kollikodon ritchiei* represented by AM F140201 (in mm).

Tooth	Length	Width
Px	4.49	3.58
M1	6.86	8.77
M2	8.33	13.24
M3	7.74	15.20
M4	5.74	12.01

polytomy with the monotreme *Teinolophos trusleri* and another monotreme clade comprising *Steropodon galmani*, *Tachyglossus aculeatus*, *Obdurodon dicksoni* and *Ornithorhynchus anatinus*. The *K. ritchiei*/monotreme clade is weakly supported, with a bootstrap value of 53% and it collapses in the strict consensus. There is, however, strong support (bootstrap value 80%) for the clade comprising *S. galmani*, *Ta. aculeatus*, *Ob. dicksoni* and *Or. anatinus*. Under strict consensus the australosphenidan clade collapses, as does the clade placing *K. ritchiei* and *Te. trusleri* with the other monotremes. When *K. ritchiei* is excluded from analyses, however, Australosphenida is retained in the strict consensus and is reasonably well supported compared to other higher-level clades, with a bootstrap value of 69%; monophyly of the monotremes is also strongly supported, with a bootstrap value of 86%.

Bayesian analysis of the same matrix using the Mk model and a gamma distribution to model rate heterogeneity between characters (Fig. 3B) resulted in a similar topology to the maximum parsimony analysis; specifically, *K. ritchiei* is placed within Australosphenida as sister to monotremes. Bayesian posterior probability (BPP) support for a monotreme/*Kollikodon* clade was moderate at 0.83. Support for Australosphenida was considerably stronger, with a BPP of 0.95. Unlike in the maximum parsimony analysis, the position of *Te. trusleri* was retained in the Bayesian analysis, with a support value of 0.75. Strikingly, in contrast to the maximum parsimony tree, *Or. anatinus* and *Ta. aculeatus* were sister-taxa to the exclusion of *Ob. dicksoni*, with relatively high BPP of 0.94.

The monotreme/*Kollikodon* clade (as resolved in the maximum parsimony analysis) is supported by a single synapomorphy that can be scored for *K. ritchiei*: the abrupt disjunction in size between premolars and molars, with the molars being significantly larger than the premolars in both groups (character 448: 0 => 1). This character state change optimizes as a synapomorphy of this clade regardless of whether accelerated or delayed transformation is assumed, and occurs along no other branch on the tree (i.e. it has a consistency index of 1).

Comparisons with other putative australosphenidans are equally difficult because the molar morphology of *K. ritchiei* is so autapomorphic with no resemblance to any of the tribosphenic or pseudotribosphenic morphologies exhibited by species of *Ambondro*, *Henosferus*, *Asfaltomylos*, *Ausktribosphenos*, *Bishops*, *Pseudotribos* or *Shuotherium*. On the other hand, features noted above that appear to group *K.*

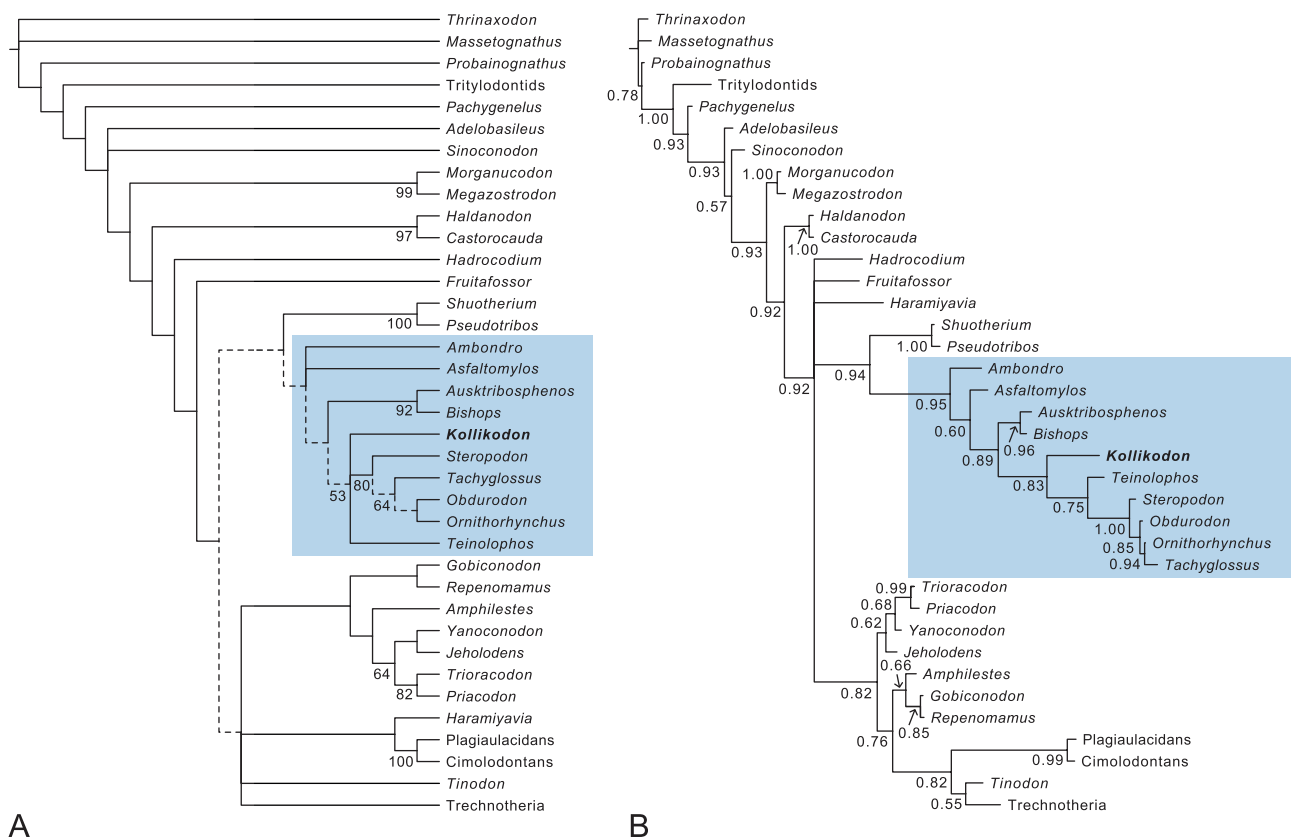


Figure 3. Results of phylogenetic analyses of 104 taxa and 438 characters, including 62 ordered characters. *Kollikodon ritchiei* is highlighted in bold, Australosphenida is indicated by blue shading. 68 taxa are collapsed in the clade Trechnotheria. (A) Maximum parsimony analysis 50% majority-rule consensus. Dashed lines indicate nodes that collapse under strict consensus of 6048 most parsimonious trees, each with a tree length of 2336 and consistency index (CI) of 0.35. Numbers below branches indicate bootstrap values (only those above 50% reported). (B) Bayesian analysis 50% majority-rule consensus of the post burn-in trees. Nodal support values indicate Bayesian posterior probabilities above 50%.

ritchiei with monotremes are not shared with species in these other australosphenidan taxa.

Discussion

The specimen described here represents the first maxillary dentition of any Australian Mesozoic mammal. It can be confidently referred to *Kollikodon ritchiei* on the basis of similarities in the bunodont dentition and other aspects of molar crown morphology, compatible size, and a close occlusal fit with the holotype. This specimen confirms that *K. ritchiei* is highly autapomorphic and in fact even more unusual than originally appreciated, with the crescent-shaped upper molars and cusp arrangement being unique among mammaliaforms known to date. The original description suggested that *K. ritchiei* had at least four lower molars (Flannery et al., 1995). Based on the presence of four molars in the upper dentition, four molars were probably also present in the lower dentition.

The numerous apical pits present on the upper molars combined with the highly bunodont morphology, curvature of the cusp rows on each crown and marked convexity of the molar row as a whole suggest an unusual form of occlusion.

None of the cusps is subtended by primary blades, suggesting that whatever food was eaten was probably crushed although the circular pits, however they were formed, may have helped immobilize hard food items that were being masticated in whichever direction comminution took place.

The known material of *K. ritchiei* preserves very few features that are phylogenetically informative and this taxon is therefore scored for only 26 of 438 characters in our matrix. The upper and lower cheektooth dentition is well preserved, as are some aspects of mandibular morphology, but the material composition of the maxilla (transparent glass with no internal features preserved) and its missing margins have resulted in retention of very little additional information about cranial morphology. Many dental characters in the modified matrix of Luo et al. (2011) relate to the presence or absence of specific cusps, as well as their relative position and sizes (if present). The majority of these characters cannot be scored for *K. ritchiei* because the homologies of most of the cusps (particularly on the upper molars) are unclear. The difficulties of applying tribosphenic terminology to even tribosphenic-like monotreme teeth is also an ongoing point of contention (Woodburne, 2003). A further stumbling block is the limited

fossil record of other Mesozoic australosphenidans, because no upper dentitions or maxillae have yet been published. Nevertheless maximum parsimony and Bayesian methods of phylogenetic analysis support the inclusion of *K. ritchiei* within crown-group Mammalia, in contrast to recent suggestions that it may have been a stem-mammaliaform (Musser, 2003). Both methods also place *K. ritchiei* as sister group to definitive monotremes within Australosphenida, albeit with varying degrees of support.

It should be emphasized that only one feature was recovered as synapomorphic for a *Kollikodon*/monotreme clade in all analyses: the marked disjunction in size between the posterior premolar and the first molar. This feature occurs in all toothed monotremes that are represented by adequate fossils, i.e. *Steropodon galmani* (Archer et al., 1985) and the Miocene ornithorhynchid *Obdurodon dicksoni* (Archer et al., 1992), in addition to *K. ritchiei*. As such it appears to be an unambiguous, uncontradicted synapomorphy for this clade. The same condition appears to be present in the extant platypus *Ornithorhynchus anatinus* (Green, 1937) but, because of significant uncertainties about its vestigial dentition, it was scored as unknown in our matrix. Presence of an enlarged mandibular canal was also identified in the original description of *K. ritchiei* (Flannery et al., 1995) as an apomorphy linking this taxon with definitive monotremes, possibly indicating sensory elaboration at the front of the face such as occurs in ornithorhynchids which have many electroreceptors in the dermis covering the bill.

In contrast to the autapomorphic and extremely bunodont *K. ritchiei*, all known toothed monotremes show remarkable similarity in molar morphology spanning a significant period of time from the Early Cretaceous *S. galmani* and *T. trusleri* to the Paleocene *Monotrematum sudamericanum* and the three Oligocene/Miocene species of *Obdurodon* (Musser, 2006; Pascual et al., 2002; Pian et al., 2013). The only molar features that have been identified as characteristic of monotremes that are also present in *K. ritchiei* include the presence of very large and wide talonids, and absence of a cusp in the paraconid position on the first lower molar (Long et al., 2002). Definitive monotremes that retain an adult dentition share a number of additional dental apomorphies, including prominent shelf-like anterior and posterior cingulids on the lower molars and high transverse, loph-like blades on the trigonids and talonids present as either a single blade or as a V-shaped blade. In definitive monotremes for which the upper dentition is known, this pattern is mimicked on the upper molars with transverse V-shaped blades. Although the dentition of *Or. anatinus* is vestigial and deciduous, the same pattern appears to be present in the molar remnants found in juveniles (Green, 1937; Woodburne & Tedford, 1975).

In contrast, *Kollikodon ritchiei* lacks any traces of vertical transverse blades, cingula or cingulids. Furthermore, although the cusps of the lower molars of *K. ritchiei* can be tentatively homologised with those of toothed monotremes (Flannery et al., 1995), we are unable to do this with any confidence for the cusps of the upper molars. However, it is possible that the bunodont form of the molars in *K. ritchiei* evolved from a relatively more plesiomorphic transverse blade system of the

kind seen in species of *Steropodon*, *Teinolophus*, *Monotrematum* and *Obdurodon*. Based on the results of our formal phylogenetic analyses and pending discovery of morphologically annectant taxa, we suggest the most parsimonious hypothesis is that *K. ritchiei* is a highly autapomorphic sister-taxon to definitive monotremes.

While in both the maximum parsimony and Bayesian analyses, *Kollikodon* fell outside crown-group Monotremata, it was closer to definitive monotremes than other australosphenidans. Whether *Kollikodon* itself should be considered a monotreme is ultimately dependent on how the clade Monotremata is defined. A *Kollikodon* plus definitive monotreme clade is supported by the following apomorphies: presence of a partially enlarged mandibular canal, the marked disjunction in size between the last premolar and the first molar, large and wide talonids, and absence of a cusp in the position of a paraconid on the first lower molar. Tentatively we suggest that, despite these potential synapomorphies, the otherwise highly autapomorphic and character-ambiguous *Kollikodon* should be regarded as a sister group of Monotremata.

One striking difference between our maximum parsimony and Bayesian analyses is the relationships suggested between the living platypus *Ornithorhynchus anatinus*, the fossil platypus species of *Obdurodon*, and the living short-beaked echidna *Tachyglossus aculeatus*. The maximum parsimony analysis weakly supported an *Ornithorhynchus* plus *Obdurodon* clade to the exclusion of *Tachyglossus*, whereas the Bayesian analysis recovered a strongly supported *Ornithorhynchus* plus *Tachyglossus* clade to the exclusion of *Obdurodon*. The latter topology implies that tachyglossids evolved from a semi-aquatic, billed platypus-like ancestor, potentially relatively late in the Cenozoic. Further evidence in support of this hypothesis comes from molecular-based divergence dates, which estimate that *Ornithorhynchus* and tachyglossids diverged 19–48 million years ago (Meredith et al., 2011; Phillips et al., 2009), and also from estimates of myoglobin net surface charge in *T. aculeatus* which suggest an amphibious ancestry (Mirceta et al., 2013). To date, the fossil record has provided little additional data bearing on this issue because all known fossil tachyglossids are edentulous and obviously ‘echidna-like’. There are no pre-Pleistocene cranial remains of tachyglossids known with the exception of *Megalibgwilia robustus* (also known as “*Zaglossus*” *robustus*; see Flannery and Groves, 1998; Griffiths et al., 1991; Musser, 2006). The single specimen of *M. robustus* is commonly presumed to be Miocene in age. However, there is significant uncertainty about this dating and a Pliocene age may be more likely (Musser, 2006). If the latter is the case, there are no pre-Pliocene tachyglossids known. The phylogenetic analyses presented here also support this hypothesis in that *Obdurodon*, *Tachyglossus* and *Ornithorhynchus* form a clade to the exclusion of *Steropodon* and *Teinolophos*, although the precise relationships within this clade differ depending on the method of analysis. No support was found for the recent hypothesis (Rowe et al., 2008) that *T. trusleri* and *S. galmani* are crown-group monotremes closer to *Ornithorhynchus* than to tachyglossids.

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