ORIGINAL PAPER

Were There Miocene Meridiolestidans? Assessing the Phylogenetic Placement of *Necrolestes patagonensis* and the Presence of a 40 Million Year Meridiolestidan Ghost Lineage

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Abstract The enigmatic mammal *Necrolestes patagonensis* from the Miocene of Patagonia possesses a highly apomorphic osteological form that has confounded phylogenetic interpretation for over a century. In this time it has been affiliated with both eutherians and metatherians; however, a recent study by Rougier et al. (Proc Natl Acad Sci USA 109:19871–19872, 2012) raises the intriguing possibility that *Necrolestes* is a relictual member of a clade of South American non-therian dryolestoids, the Meridiolestida. This group is known chiefly from the Cretaceous of South America and assignment of *Necrolestes* to Meridiolestida implies a ghost lineage of about 40 million years. Such a lengthy ghost lineage requires strong evidence, which minimizes potentially circular assumptions of anatomical homology. Here, we vary the coding of cusp homologies in *Necrolestes,* previously assumed to diverge from the metatherian pattern*,* and add zalambdodont and incipiently zalambdodont metatherian taxa to the analyses, in order to assess the effects of non-independent characters and taxon sampling on the original topology. The results of both maximum parsimony and Bayesian analysis using the Mk model show that these possible sources of bias have little effect on the topology and ultimately increase confidence in the placement of *Necrolestes* in Meridiolestida and its concomitant 40 million year ghost lineage. Additionally, our Bayesian analysis resolves Australosphenida in a trichotomy with *Peramus* and *Vincelestes* + Boreosphenida. This contrasts with the majority of existing topologies, and raises interesting questions regarding both the evolution of tribosphenY and the use of the Mk model with paleontological datasets.

Introduction

The enigmatic and highly apomorphic mammal *Necrolestes patagonensis*, from the Miocene Santa Cruz Formation of Patagonia, has been compared with a multitude of mammalian taxa. The title of the most recent redescription of the species, "Neither a Rodent nor a Platypus" (Asher et al. 2007) neatly encapsulates the level of uncertainty over its phylogenetic position throughout its taxonomic history. Its zalambdodont dentition and adaptations for parasagittal fossoriality suggest affinities primarily with golden moles (Chrysochloridae) or marsupial moles (Notoryctidae). The earliest investigations into this taxon focused closely on these similarities, with both Ameghino (1891) and Scott (1905) in favor of chrysochlorid affinities. Patterson (1958), for example, favored affinities with metatherians, an idea supported by some recent investigators (e.g., Ladevéze et al. 2008), but not others (e.g., Goin et al. 2007). Recently, Rougier et al. (2012) and Chimento et al. (2012) suggested that *Necrolestes* represents a relictual descendant of the meridiolestidans, a clade of non-therian South American dryolestoids otherwise known primarily from the Mesozoic. This placement of *Necrolestes* was repeated using an independent dataset by Averianov et al. (2013),

Rachel N. O'Meara and Richard S. Thompson contributed equally to this work, and consider this a joint first-authorship manuscript.

Electronic supplementary material The online version of this article (doi:10.1007/s10914-013-9252-3) contains supplementary material, which is available to authorized users.

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though they found Meridiolestida to be the sister group of Spalacotheriidae. Regardless, this placement of *Necrolestes* extends the record of Meridiolestida by approximately 40 million years (see Supplementary Material).

Affinities between dryolestoids and *Necrolestes* were first suggested as "conceivable" by Van Valen in 1988, but had never previously been tested cladistically. The lack of attention to Van Valen's hypothesis may have been due to the large temporal disjunction between Meridiolestida and the Miocene *Necrolestes*. It was only with the discovery of *Peligrotherium* (Gelfo and Pascual 2001), from the early Paleocene of Patagonia, that the survival of Meridiolestida across the K-Pg boundary became widely accepted, providing a more favorable context for the interpretation of *Necrolestes* as a meridiolestidan relict.

Rougier et al.'s (2012) placement is based on further preparation of the best preserved material of *Necrolestes* from the collections of the Yale Peabody Museum, which reveals a series of new characters of the basicranium. They also noticed a striking similarity between the dentitions of *Necrolestes* and the recently described meridiolestidan *Cronopio dentiacutus* (Rougier et al. 2011). Both taxa possess three single-rooted, hypsodont molars with a relatively simple triangular morphology, as well as a double-rooted anterior premolar. By adding *Necrolestes* to their earlier phylogenetic analysis of the Mesozoic mammaliaform radiation (Rougier et al. 2011, 2012) supported a hypothesis of close relatedness between *Cronopio* and *Necrolestes*, resolving them as sister taxa within Meridiolestida. This striking finding extends the record of meridiolestidans by about 40 million years.

Rougier et al.'s (2012) assignment of *Necrolestes* to Meridiolestida is certainly exciting and consistent with biogeographic evidence, but entailed several a priori methodological assumptions that could potentially bias its placement. An example of such a bias can be found in their treatment of zalambdodonty in *Necrolestes*. Zalambdodont mammals have high crested, "lambda"-shaped molars, where the primary lingual cusp is not the protocone, as seen in most tribosphenic taxa, but either the paracone or metacone (Asher and Sánchez-Villagra 2005). In most zalambdodont eutherians, such as tenrecs, the primary lingual cusp is inferred to be the paracone based on its occlusion in the hypoflexid of the corresponding lower molar. Further evidence for this is provided by the tenrec *Potamogale* which retains both a small metacone and a large paracone (Asher and Sánchez-Villagra 2005). Molecular phylogenies resolve Potamogalinae as the sister-group to all other tenrecs (Asher et al. 2010) providing independent support for paracone zalambdodonty in the wider clade. However, in metatherians (e.g., *Notoryctes*, *Yalkaparidon*) the same dental pattern has been hypothesized to have evolved by the elaboration of the metacone with concomitant paracone reduction (Archer et al. 1988). This pattern has been demonstrated by the discovery of *Naraboryctes* (Archer et al. 2011), a Miocene,

incipiently zalambdodont metatherian with an enlarged metacone and greatly reduced paracone, believed to be a relative of *Notoryctes*. While this relationship cannot be corroborated by molecular evidence, further support for the hypothesized metacone zalambdodonty of *Notoryctes* is provided by its occasional retention of a vestigial paracone (Murray and Megirian 2006).

In a review of the dentally zalambdodont Mammalia, Asher and Sánchez-Villagra (2005) suggested that the occlusal pattern of *Necrolestes* supported the identification of the primary lingual cusp as a metacone. They based this claim on YPM-PU 15699, a skull of *Necrolestes* that preserves upper and lower teeth in occlusion. This shows that the primary lingual cusp of the upper molar occludes more closely to the paracristid of the more posterior lower molar, than to the hypoflexid of the corresponding lower tooth. Rougier et al. (2012) acknowledged this interpretation, but argued that as the basicranium and braincase of *Necrolestes* indicate non-therian ancestry, the primary lingual cusp homology of *Necrolestes* should be interpreted in the comparative framework of nontherian mammals. They thus code its upper primary lingual cusp as the paracone seen throughout the dryolestoids. Similarity of the dryolestoid paracone with the primary lingual cusp of *Necrolestes* may justify postulating primary (conjectural) homology for these two characters, based on Hennig's auxiliary principle. This states that in the absence of evidence to the contrary, homology based on similarity of characters may be assumed (Hennig 1966; de Pinna 1991). However, where there are alternative interpretations of similarity, such assumptions of primary homology must be made with care, so as not to bias phylogenetic analysis against the competing interpretations. Thus, assuming that *Necrolestes* is a paracone zalambdodont may bias phylogenetic analysis against its being resolved as a metatherian metacone zalambdodont. Further, secondary homology statements (legitimated statements of primary homology) can only be made after testing by congruence against the pattern of other primary homologies (de Pinna 1991) in a phylogenetic analysis. If the initial statement of primary homology is based, not solely on similarity, but also on other statements of primary homology, this non-independence of character coding can bias the outcome of phylogenetic analysis, and hence statements of secondary homology.

The taxon sample of Rougier et al.'s (2012) study could also bias the phylogenetic position of *Necrolestes*. The cladistic matrix used by Rougier et al. (2011) was originally compiled to assess the phylogenetic affinities of an unusual radiation of South American dryolestoids, and as such, samples heavily from Mesozoic taxa. Rougier et al. (2012) claim that their hypothesis of the dryolestoid affinities of *Necrolestes* "is supported by a morphological phylogenetic analysis that includes a broad sampling of therian and non-therian taxa". While their non-therian sample is indeed large, both eutherian and metatherian clades are poorly represented, with their

sample including only three eutherians (*Prokennalestes*, *Asioryctes,* and *Erinaceus*) and five metatherians (*Deltatheridium, Asiatherium, Kokopellia, Pucadelphys,* and *Didelphis*), each including a single extant form. It is reasonable to assume that the low sample of eutherian and metatherian diversity increased the likelihood of resolving *Necrolestes* as a dryolestoid, and did not test the previously articulated possibility that *Necrolestes* is a zalambdodont metatherian.

Here, we attempt to reduce some of these biases by reanalyzing a number of variants of Rougier et al.'s (2012) dataset. First we explore the influence of primary lingual cusp homology in *Necrolestes* by recoding dental characters to reflect both uncertain zalambdodonty (as assumed by Averianov et al. 2013) and metacone zalambdodonty. Second, we increase the taxon sample of metatherians, adding three zalambdodont or incipiently zalambdodont metatherian taxa (*Notoryctes, Naraboryctes,* and *Yalkaparidon*) in order to test more explicitly the major alternative hypothesis of metatherian relationships for *Necrolestes* (Ladevéze et al. 2008). To supplement these analyses, we vary the tooth cusp homologies of *Cronopio*, the sister-taxon of *Necrolestes*, which were neither investigated nor justified in its recent description (Rougier et al. 2011). By varying the cusp homologies of *Cronopio* in conjunction with *Necrolestes,* we can test whether they drive the placement of *Cronopio* in Meridiolestida. In addition, alternative analyses from which *Cronopio* is excluded allow us to assess the extent to which the dental similarities between *Cronopio* and *Necrolestes* drive the latter's placement in the meridiolestidan clade.

We use both parsimony and Bayesian analyses to assess the position of *Necrolestes* in our modified dataset. Bayesian methods have only been applied to the radiation of Mesozoic mammaliaforms once before (Gurovich and Beck 2009) based on an earlier iteration of the Rougier et al. (2012) matrix (Rougier et al. 2007). This analysis recovered an unusual placement of Australosphenida, in a surprisingly close relationship to Boreosphenida. This placement leads to a novel interpretation of the evolution of tribospheny, though this was not discussed in the original paper (Gurovich and Beck 2009). We investigate whether the modifications to the matrix since Rougier et al. (2007) alter the position of Australosphenida when analyzed under a Bayesian framework, and discuss the implications for the evolution of tribospheny. Furthermore, Bayesian analyses permit the use of Bayes factors to explicitly test the likelihood of *Necrolestes* having metatherian affinities. These analyses are coupled with maximum parsimony Templeton tests, which specifically test the metatherian position of *Necrolestes* (in contrast to those investigating its therian position in Rougier et al. 2012). This will provide the most robust test to date of the presence of a 40 million year ghost lineage of meridiolestidan mammals in South America.

Methodology

Tooth Cusp Homologies

We identified 11 characters of the upper dentition that were affected by the identification of the primary lingual cusp of *Necrolestes* and *Cronopio* as a paracone or metacone. The characters of the lower dentition remained unaffected, as the lingual-most cusp in the lower molars of a zalambdodont remains the protoconid. Changes to the upper dentition characters included the addition of new character states (character 147), redefinition of the character statement (character 115), and recoding of variation (characters 58, 102, 122, 125, 126, 127, 129 130 and 131; see Supplementary Material for details). We recoded characters in two ways: firstly we assumed uncertainty about the identity of the primary lingual cusp ("uncertain zalambdodonty") and secondly we defined this cusp as the metacone ("metacone zalambdodonty"). Four of the characters that required recoding relate to the identity of the stylar cusps. These are clearly defined for paracone zalambdodonts, with the mesial cusp being the stylocone and posterior cusp the metastyle; however, there appears to be no consensus on stylar cusp homologies for metacone zalambdodonts. Hence these characters are all recoded as uncertain in both treatments. Definitions and justifications for changes to each of these 11 characters can be found in the Supplementary Material. Two additional character states (character 2: position of the posteriormost mental foramen, and character 285: maximum vertical depth of zygomatic arch relative to length of skull) were altered to accommodate the dental and zygomatic conditions of *Notoryctes* and *Yalkaparidon*.

Increased Taxon Sample

In order to partly address the potential taxon bias of the Rougier et al. (2012) study, we included three additional metatherian taxa in the character matrix: the zalambdodonts *Notoryctes typhlops* and *Yalkaparidon* spp. (Archer et al. 1988; coded as a composite of *Y. coheni* and *Y. jonesi*), and the incipiently zalambdodont *Naraboryctes philcreaseri*. Here, *Notoryctes* is coded as a metacone zalambdodont, based primarily on reports of a vestigial paracone in some individuals (Murray and Megirian 2006). *Yalkaparidon* is coded as a metacone zalambdodont unless otherwise noted, based on a tentative analysis of its occlusal relationships (Beck et al. 2013), though an alternative "uncertain zalambdodont" coding is also assessed.

Notoryctes was coded from two specimens (UMZC A5.1/1 and UMZC A5.1/5) and from animated 3D renderings and 'dynamic cutaway' views of specimen AMNH 202107 from the Digital Morphology website, University of Texas, Austin (Rodgers 2008). *Naraboryctes* was coded

from figures and text of Archer et al. (2011), and *Yalkaparidon* was coded from figures and text of Archer et al. (1988) and Beck (2009). Wherever possible we have followed the coding strategy of Rougier et al. (2012). We also present two alternative interpretations of *Yalkaparidon*, based on Beck et al. (2013), which are analyzed independently (see Supplementary Material for details of these analyses). Additional sources of information for coding these specimens are detailed in the Supplementary Material, as well as a nexus file of the complete character matrix used in this study, including recoded characters and additional metatherian taxa.

Phylogenetic Analyses

To test the impact of the assumption of paracone zalambdodonty in *Necrolestes* and *Cronopio*, two parsimony analyses were performed: the first assumed "uncertain zalambdodonty," the second "metacone zalambdodonty." These analyses were repeated with and without the additional metatherian taxa. These analyses were also repeated with *Cronopio* removed, acting as a more stringent test of the attraction of *Necrolestes* to the meridiolestidan clade.

Parsimony analyses were carried out in PAUP*v4.0 (Swofford 2002). All analyses used the heuristic search algorithm with 1,000 replications and a random addition sequence. Branch supports (Bremer 1988, 1994) were calculated in PAUP*, using 1,000 replications and a random addition sequence coupled with reverse constraints to calculate support for each node. Bootstrap supports were calculated in PAUP*, with ten random addition sequences per 1,000 bootstrap pseudoreplicates. Character optimizations were performed in Winclada v1 (Nixon 1999-2002). In order to statistically assess the competing phylogenetic hypothesis that *Necrolestes* is a metatherian, two-tailed Templeton tests (Templeton 1983) were performed to compare all most parsimonious trees (MPTs) from a dataset constrained topologically to resolve *Necrolestes* as a metatherian, with the unconstrained MPTs, using "Pscores" in PAUP*.

Bayesian analyses were performed in MrBayes 3.2.2 (Ronquist et al. 2012) using the Mk model of morphological evolution (Lewis 2001) with the coding parameter set to 'inf', to ensure that the model only accepted informative characters (in line with the dataset's construction). We added a gamma parameter to model among character rate variation, which was found to be strongly preferable to an 'equal rates' model based on Bayes factor analyses. The Bayes factor is essentially the ratio of the likelihoods (the probability of the model given the data) of each model. This provides an estimate of how much more appropriate one model is than another: a high Bayes factor provides stronger support for the model with the highest likelihood

(Kass and Raftery 1995; Yang and Rannala 1997; Nylander et al. 2004). The marginal likelihood is used to calculate the Bayes factor, but is notoriously difficult to estimate accurately. The harmonic mean has traditionally been used for such estimations (Nylander et al. 2004), but this value is exceptionally inconsistent (Fan et al. 2011; Xie et al. 2011; Baele et al. 2012). Subsequently, recent studies have employed stepping stone analyses, which have been shown to more accurately and consistently estimate the marginal likelihood (Fan et al. 2011; Xie et al. 2011; Baele et al. 2012). We present Bayes factor estimates using this newer method. Kass and Raftery (1995) suggest that any Bayes factor (expressed as twice the natural logarithm) over 10 would be classed as very strong evidence to accept the more probable model, though the stringency of this criterion is open to debate (Brandley et al. 2005). The comparison of the analyses with and without a gamma parameter yielded a mean Bayes factor (expressed as twice the natural logarithm) of 148, strongly favoring the gamma parameter.

Each Bayesian analysis ran for five million generations, sampling trees every 500 generations. The first 25 % were discarded as burnin. To ensure successful convergence the temperature (a property of the Metropolis coupling implemented in MrBayes; see Ronquist et al. 2009) had to be raised to 0.25, though all other settings used the default values in MrBayes 3.2.2. All new taxa were included in the Bayesian analysis, while *Cronopio*, *Necrolestes,* and *Yalkaparidon* were considered metacone zalambdodonts. This taxon sample and coding strategy represents our most stringent test of the placement of *Necrolestes* in the Meridiolestida, as both *Cronopio* and *Necrolestes* were assumed to share a dental pattern with that of metatherian zalambdodonts. The standard deviation of split frequencies (<0.05) and PRSF value (approximately 1.00: Ronquist et al. 2009) were used to assess convergence between the two independent runs, while estimated sample sizes (> 200) and Tracer v1.5 (Rambaut and Drummond 2007) plots helped to assess the quality of mixing within each run. In order to compare competing phylogenetic hypotheses, a second Bayesian analysis was conducted under the same conditions while constraining *Necrolestes* to form a clade with the Metatheria. In order to compare the two hypotheses, the most likely sampled tree from each Bayesian analysis (found in the treeprobs file) was used as a fixed topology for a stepping stone analysis (see Supplementary Material for details). This allowed the calculation of two comparable marginal likelihood values for a Bayes factor analysis (Kass and Raftery 1995; Yang and Rannala 1997; Nylander et al. 2004). Finally, ancestral state reconstructions were carried out on the Bayesian topology in Mesquite (Maddison and Maddison 2010), using the MK model.

Results

Parsimony Analyses

The results of the parsimony analyses are consistent regardless of either the coding of dental characters or the addition of the newly-coded metatherian taxa. All parsimony based analyses produce topologies compatible with those of Rougier et al. (2012), as demonstrated in Fig. 1. In all analyses that did not include the three additional metatherian taxa, tree length was shorter than that recovered by Rougier et al. (2012), likely caused by the introduction of more uncertain character states. *Necrolestes* is always recovered as the sister taxon to *Cronopio* within Meridiolestida. The exclusion of *Cronopio* from the analyses does not affect the placement of *Necrolestes*, which is resolved as the sister group of the meridiolestidan *Leonardus* in all such treatments. The three additional metatherian taxa are recovered as a monophyletic group in a sister clade to *Didelphis* (Fig. 1: node 51) with a high branch support of 9 in all analyses. This relationship is maintained regardless of the coding of the primary lingual cusp of *Yalkaparidon*. The metacone-zalambdodont + *Didelphis* clade (Fig. 1: node 50) has low branch support of 1 in all analyses, and this node collapses to form a polytomy, along with node 49, when coding *Yalkaparidon* following Beck et al. (2013). *Yalkaparidon* and *Notoryctes* are recovered as sister taxa, to the exclusion of the early notoryctemorphian *Naraboryctes*. This clade has high support in all analyses, though based on our character optimisations nine of the 11 characters uniting *Yalkaparidon* and *Notoryctes* are linked to their lack of a talonid basin (suggestive of contingent character coding in the Rougier et al. 2012 matrix).

The clade supports for a subset of the meridiolestidan clades under different treatments are summarized in Fig. 2. With *Cronopio* included in the analyses, the Total Branch Support (Thompson et al. 2012) for these clades is identical under all treatments ("metacone zalambdodonty," "uncertain zalambdodonty," with and without new taxa) and identical to the Total Branch Support assuming "paracone zalambdodonty." Although Total Branch Support does not vary with treatment, branch supports for the individual nodes differ depending on whether "metacone zalambdodonty" or "uncertain zalambdodonty" is assumed. For example, if "metacone zalambdodonty" is assumed, there is increased branch support for node D (the *Necrolestes-Cronopio* clade), but correspondingly lower branch support for the deeper node B (the meridiolestidan clade). The addition of the newly-coded metatherian taxa does not alter the branch supports at each meridiolestidan node for any condition of zalambdodonty. In addition, under an assumption of "metacone zalambdodonty," bootstrap supports for nodes B, C, and D are either unchanged or show a small increase relative to the bootstrap analyses of the Rougier et al. (2012) data. This small increase in support is

surprising, but may be due to the removal of character conflict within Meridiolestida. Support for nodes A to D is reduced in analyses in which *Cronopio* is excluded in comparison with those treatments in which it was included. In particular, the sister group relationship between *Necrolestes* and *Leonardus* has slightly reduced clade support relative to comparable nodes. These findings suggest that the placement of *Necrolestes* in Meridiolestida is independent of primary lingual cusp identity, and not solely driven by the other dental characters it shares with *Cronopio*.

We further evaluated the strength of the meridiolestidan (Rougier et al. 2012) vs. metatherian (Patterson 1958; Ladevéze et al. 2008) hypotheses using two tailed Templeton tests (Templeton 1983). We used the dataset including the three additional metatherian taxa and coding *Necrolestes* and *Cronopio* as metacone zalambdodonts. The test compared all 37 MPTs from this analysis with the 173 MPTs produced from an analysis constrained to resolve *Necrolestes* as a metatherian. We found a significant difference between the two hypotheses ($P<0.005$ in all comparisons, with a mean value of 0.0014), with the constrained (metatherian) topology having a tree length 33 steps greater than the unconstrained MPT (length=1,275). This finding is similar to the Templeton test of Rougier et al. (2012), who used this methodology to assess the probability of placing *Necrolestes* in Theria. They found significant evidence to reject this hypothesis, also recovering a constrained tree 33 steps longer than their most parsimonious hypothesis. Clearly, the additional metatherian taxa do not act to weaken *Necrolestes*' placement in Meridiolestida.

Bayesian Analyses

The results of the Bayesian analysis are summarized in Fig. 3. The additional metatherian taxa are recovered in a sister group relationship to *Didelphis*, as in the parsimony analysis. Meridiolestida is recovered with strong support ($P=0.99$), again confirming the placement of *Necrolestes* in this clade regardless of its zalambdodont cusp homologies. By constraining the Bayesian analysis to resolve *Necrolestes* within Metatheria, the probability of the two resultant models could be compared using Bayes Factors. Comparisons of each analysis yielded Bayes Factors (expressed as twice their natural logarithm) of 479. This provides very strong evidence to favor the original Bayesian topology, suggesting that *Necrolestes* is e^{479} (e is the base of the natural logarithm and equal to roughly 2.718) times more likely to be placed in Meridiolestida than Metatheria. Any result over 10 would be classed as very strong evidence against the metatherian hypothesis, according to Kass and Raftery (1995), and while the actual threshold for significance has been debated (Brandley et al. 2005), the magnitude of our Bayes factor seems
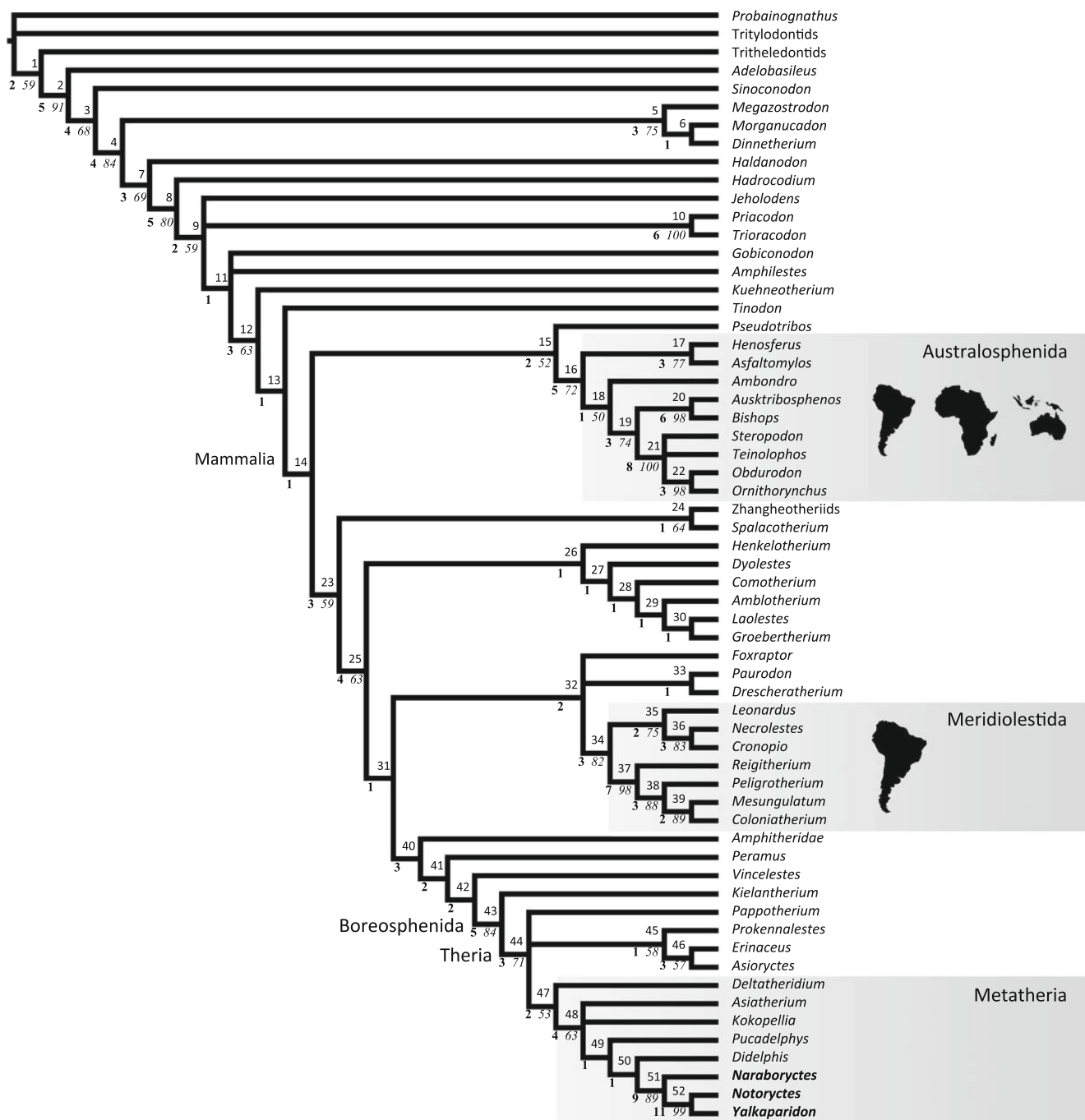
Fig. 1 Strict consensus topology based on the 37 most parsimonious trees (MPTs, length=1,242) from the reanalysis of Rougier et al.'s (2012) dataset, including the three additional metatherian taxa (shown in **bold**), and describing both *Necrolestes* and *Cronopio* as metacone zalambdodonts. This topology is consistent across other analyses regardless of the inclusion of 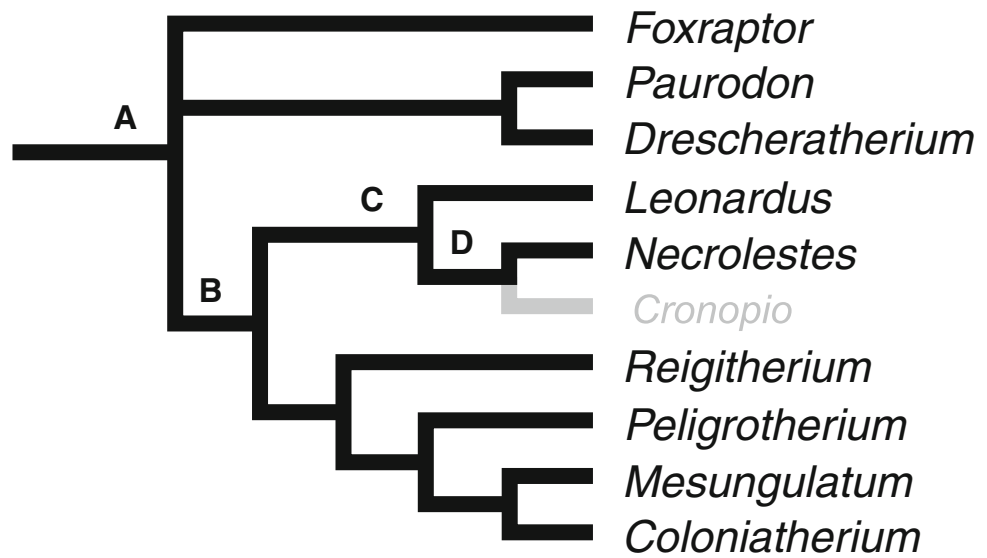zalambdodont and incipiently zalambdodont metatherians, *Cronopio,* or the recoding of cusp homology characters. Numbers above the branches identify clades discussed in the text and in Fig. 2; numbers below are support values. **Bold** values are branch supports (Bremer 1988, 1994); *italics* indicates bootstraps. Tree lengths for all other parsimony analyses can be found in the Supplementary Material

compelling evidence to reject the metatherian hypothesis given this dataset.

The majority of differences between the Bayesian and parsimony topologies are a consequence of a loss of resolution occurring at a node which is poorly supported in the parsimony analysis (e.g., the collapse of Fig. 1: node 26 in the Bayesian analysis), an increase in resolution of such nodes (e.g., Fig. 1: node 9, is a polytomy, but is fully resolved in the Bayesian topology), or a rearrangement of a poorly supported node. The former can be considered an advantage of the Bayesian

Fig. 2 A summary of the support indices for four nodes key to the placement of *Necrolestes* within Meridiolestida. The root of the phylogeny (**A**) corresponds to node 32 in Fig. 1, **B** to node 34, **C** to node 35, and **D** to node 36. The table shows the support values (*Boot* bootstrap support, *BS* branch support, *Char.* number of unambiguous synapomorphies) across each of these nodes, and their total (**T**) under a range of different treatments of zalambdodonty and taxon samples


	Node	Rougier et al. 2012 Paracone			Original Taxa Metacone			Original Taxa Uncertain			New Taxa Metacone			New Taxa Uncertain		
		Boot	BS	Char.	Boot	BS	Char.	Boot	BS	Char.	Boot	BS	Char.	Boot	BS	Char.
With *Cronopio*	A	< 50	2	5	< 50	2	5	< 50	2	5	< 50	2	5	< 50	2	5
	B	82	4	14	82	3	13	86	4	14	82	3	13	84	4	14
	C	67	2	4	72	2	4	84	3	4	75	2	4	84	3	4
	D	67	2	3	85	3	4	62	1	2	83	3	4	62	1	2
	T	-	10	26	-	10	26	-	10	25	-	10	26	-	10	25
Without *Cronopio*	A				< 50	3	5	< 50	3	5	< 50	3	5	< 50	3	5
	B		N/A		75	2	10	81	3	11	75	2	10	81	3	11
	C				57	1	4	72	2	4	58	1	4	70	1	4
	T				-	6	19	-	8		-	6	19	-	7	20

approach, highlighting the uncertainty within the dataset; the last two, which represent alternative hypotheses, are generally poorly supported and thus should be treated with caution. However, there is one major topological difference between the two analyses: the Bayesian topology recovers the australosphenidans (excluding *Pseudotribos*) in a trichotomy with *Peramus* and *Vincelestes* + Boreosphenida (Boreosphenida is equivalent to Tribosphenida of McKenna 1975). This finding is poorly supported ($P=0.72$), though this could still be considered surprisingly high for such an unusual finding, and given the level of missing data in a paleontological dataset.

The recovery of this more traditional placement of the monotremes closer to the therian crown, rather than separated from therians by a long stem lineage of eutriconodont, spalacotheroid, and dryolestoid taxa, is particularly striking given that both topologies are based on the same dataset. In order to test the robusticity of this finding, we performed a second constrained Bayesian analysis, this time constraining the tree to the parsimony topology. This was again compared to the unconstrained Bayesian topology using Bayes factors. Comparisons of both independent runs of each analysis yielded Bayes Factors (expressed as twice their natural logarithm) of 402 providing strong evidence in favor of the unconstrained Bayesian topology.

We also conducted Templeton tests (under a parsimony framework) to compare the topology of the 37 unconstrained MPTs with the 54 MPTs produced by a parsimony analysis constrained to resolve the Bayesian topology. This aimed to test the close relationship between Australosphenida and Boreosphenida from a parsimony perspective as a complement to calculating the Bayes Factors. The Templeton tests found that the two topologies are significantly different ($P<0.006$ for all comparisons, with a mean P value of 0.0044) with the constrained topology having a total length (length=1,276) that exceeds that of the unconstrained MPT (length=1,242) by 34 steps. Hence, while MP and Bayesian optimality criteria converge overall on a very similar topology (Figs. 1 and 3), a fact underscored by the approximately 7×10^{98} possible rooted, bifurcating trees for 61 terminal taxa (Felsenstein 1978), they differ significantly in terms of their placement of Australosphenida. Clearly, therefore, the possibility that Australosphenida have a close relationship with Boreosphenida requires further analysis and investigation of additional character sets.
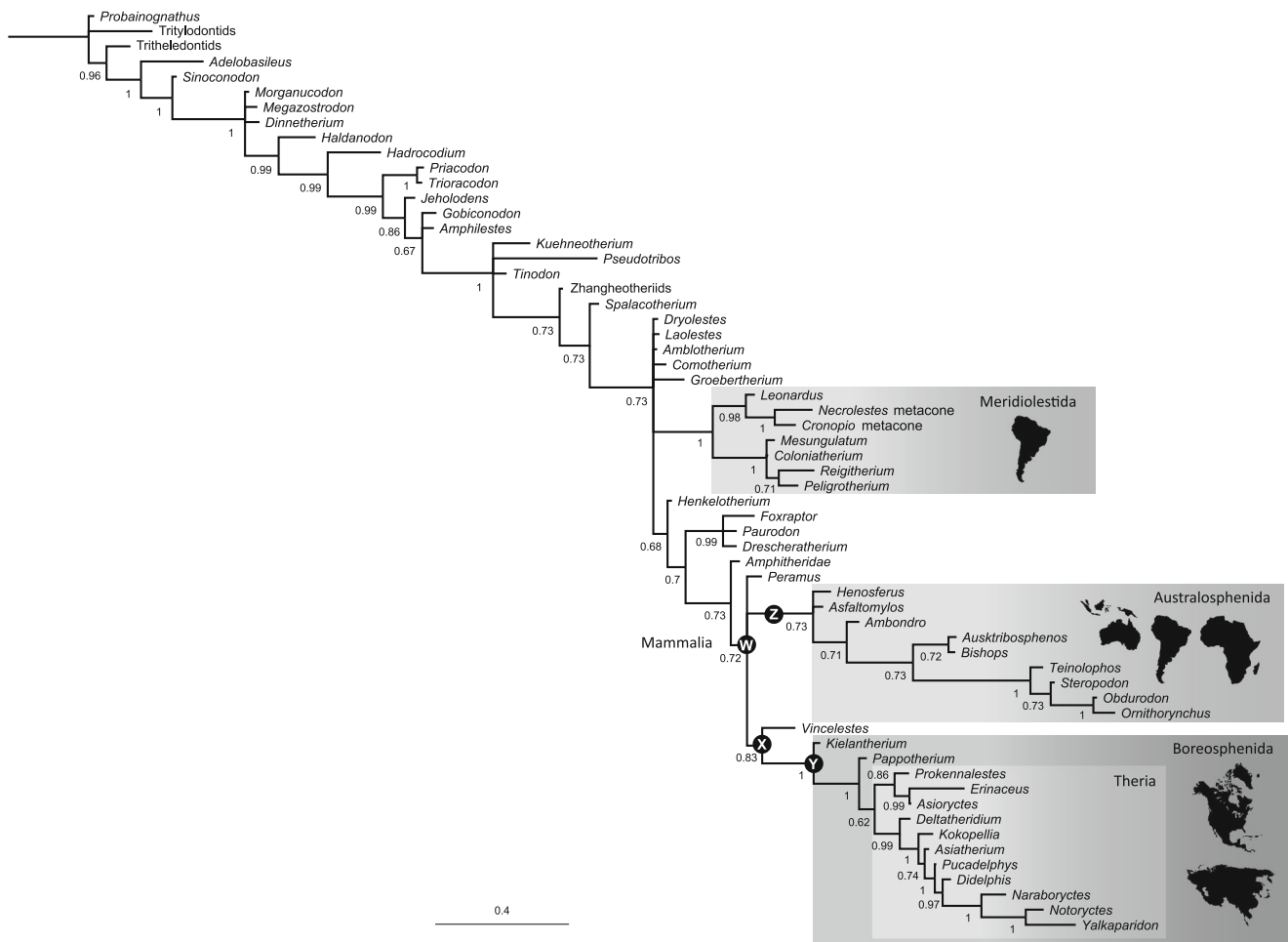
Fig. 3 Bayesian phylogeny based on Rougier et al.'s (2012) dataset including the expanded taxon sample and treating both *Necrolestes* and *Cronopio* as metacone zalambdodonts. Data were analyzed using the Mk model with a gamma parameter in MrBayes v3.2.2 for five million generations. Numbers on the branches are posterior probabilities. Letters identify four key nodes used for ancestral states reconstructions. The mean log (ln) likelihood for this topology is −4752.388

Discussion

By testing alternate coding strategies for the zalambdodonty of *Necrolestes,* and including three metatherians, we robustly assessed the placement of *Necrolestes* in Meridiolestida. All of our analyses strongly support Rougier et al.'s (2012) placement of *Necrolestes* as the sister of *Cronopio*, nested within Meridiolestida. Furthermore, the differing results of the parsimony and Bayesian analyses raise interesting questions regarding the phylogenetic position of Australosphenida and the role of Bayesian inference in paleontological datasets.

The Phylogenetic Position of *Necrolestes*

Throughout our parsimony analyses, we always recovered topologies consistent with the MPTs figured by Rougier et al. (2012), regardless of the coding of zalambdodonty or the inclusion of the additional metatherian taxa (Fig. 1). *Necrolestes* was even recovered as a meridiolestidan when its sister taxon, *Cronopio*, was excluded. MP branch support indices suggest that the addition of new metatherian taxa does not weaken support for a meridiolestidan clade, or the inclusion of *Necrolestes* and *Cronopio* within this clade. A Bayesian analysis reached the same conclusion (Fig. 3) with strong support for the position of *Necrolestes* as the sister taxon of *Cronopio* (P=0.99), and for their inclusion in Meridiolestida (P=0.98). Both Templeton tests (used in a parsimony framework) and Bayes factor analyses (in the Bayesian framework) strongly reject the alternative hypothesis that *Necrolestes* is a metatherian. The resistance of this dataset to perturbation, combined with the rejection of one of the most widely argued alternative hypotheses (Patterson 1958; Ladevéze et al. 2008) underscores the strength of phylogenetic signal uniting *Necrolestes* with the Meridiolestida in the Rougier et al. (2012) dataset, and shows the limited influence of dental cusp homology in this region of the tree. Finally, character optimization across the meridiolestidan clade of the parsimony topology that assumes "uncertain

zalambdodonty" in *Necrolestes* and *Cronopio* suggests that the primary lingual cusp in both these taxa is the paracone (Supplementary Material). This acts as an a posteriori corroboration of the original assumption made by Rougier et al. (2012).

The Role of Lingual Cusp Characters

Character optimizations highlight the limited influence of lingual cusp characters on the dataset. In the analysis that included the additional metatherians and assumed metacone zalambdodonty, 22 of the 26 character states that unambiguously optimize at nodes A, B, C, and D (Fig. 2) are dental. Of these dental characters, only four are dependent on the identity of the primary lingual cusp, and only one on the presence or absence of the talonid basin. A further 15 characters cannot be unambiguously optimized to a particular node, but always optimize across nodes A, B, C, or D (Fig. 2). Of these 15 characters, nine are dental, but only one is affected by lingual cusp homology, and none by the presence or absence of the talonid basin (see Supplementary Material for details). Optimization across the topology therefore supports the conclusion that the phylogenetic position of *Necrolestes* is not influenced by its zalambdodonty. Our branch support analyses (Fig. 2) support the same conclusion, finding stable levels of total support for the meridiolestidan clades (with the inclusion of *Cronopio*), regardless of treatment. Clearly, the identity of the primary lingual cusp is not important in influencing the phylogenetic position of *Necrolestes* as a meridiolestidan.

This is a reassuring finding, as the homology of the primary lingual cusp in *Necrolestes* is not the only problematic statement of cusp homology in Mesozoic mammals; for example, the identities of talonid basin cusps (e.g., cusp d) of non-tribosphenic trechnotherians remain controversial (Davis 2011) while many cusp homologies of docodonts (Luo and Martin 2007) and pseudotribosphenic mammals are unclear (Chow and Rich 1982; Luo et al. 2007; Rich and Vickers-Rich 2010). As highly functional elements, cusp morphology may be particularly prone to convergence; cusp form across the dentition is known to be controlled by a limited number of developmental genes that can vary substantially between closely related species (Kangas et al. 2004). While dental characters remain undoubtedly important, the fact that a priori assignment of cusp homology in *Necrolestes* does not necessarily affect phylogenetic hypotheses permits greater confidence in topologies derived from this dataset. Of course, our examination has been limited to features relevant to zalambdodonty in *Necrolestes*. One obvious extension of this could be to test the assumption of paracone zalambdodonty throughout the dryolestoid radiation. However, such an analysis would ideally examine the available evidence for cusp homologies on a taxon by taxon basis, and be included within a more thorough investigation into the impact of cusp homology decisions across all Mesozoic mammals. Such an investigation is clearly of immense value, but beyond the scope of this study.

Characters Uniting *Necrolestes* with Meridiolestida

As the identity of the primary lingual cusp has such little impact on the placement of *Necrolestes*, it is clear that this topology is driven by other characteristics. Rougier et al. (2012) identified possession of three single-rooted, hypsodont molars as a synapomorphy of *Necrolestes* and *Cronopio*. Indeed, two of the four unambiguously optimized characters uniting *Necrolestes* and *Cronopio* relate to this root pattern. Nevertheless, even in the absence of *Cronopio*, *Necrolestes* remains a meridiolestidan. This suggests that this unusual synapomorphic molar root pattern is not fundamental to the placement of *Necrolestes* in this clade. Twenty-two of 26 character states that unambiguously optimize at these nodes are dental, 14 of which suggest that transversely wide post-canines, with a relatively simple, triangular arrangement of cusps unite the group (see Supplementary Material). Therefore, it appears that the general form of the molar teeth is of greater importance than specific cusp identity in the Rougier et al. (2012) matrix.

As discussed by Rougier et al. (2012), assignment of the Miocene *Necrolestes* to Meridiolestida extends the fossil record of this group by approximately 40 million years, producing a very substantial ghost lineage that begins in the Paleocene (Selandian) (Gelfo and Pascual 2001; Gelfo et al. 2009), lasting through the entire Paleogene. Such a lengthy ghost lineage rightfully warrants careful scrutiny. Our assessment of alternative phylogenetic hypotheses, and consideration of additional taxa, tree reconstruction methods, and statistical treatments, increases confidence in the meridiolestidan affinities of *Necrolestes*. We therefore support the existence of a 40 million year ghost lineage implicit in this novel result.

Moreover, this hypothesis is supported by biogeographic evidence. The Meridiolestida are, to date, known only from South America and this is compatible with the South American distribution of *Necrolestes*. In addition, several authors (e.g., Rougier et al. 2012; Woodburne et al. 2013) have noted that the Late Cretaceous South American fauna does not mirror the abrupt discontinuity observed in northern mammalian faunas at the end-Cretaceous extinction event, with at least three Gondwanan Mesozoic lineages also known from the Cenozoic of South America (*Monotrematum*, gondwanatherians, and *Peligrotherium*). This observation supports the idea that *Necrolestes* may also have extended the meridiolestidan lineage into the Cenozoic as part of a diverse South American fauna comprising eutherian, metatherian, and non-therian mammals.

The Additional Metatherian Taxa

Notoryctes, *Naraboryctes,* and *Yalkaparidon* form a sister group to *Didelphis* in the parsimony analyses. This clade has a high bootstrap value and very strong branch support (Fig. 1), regardless of the interpretation of *Yalkaparidon*. However, Notoryctemorphia appear as a paraphyletic group, with *Yalkaparidon* in a sister-group relationship with *Notoryctes* that excludes *Naraboryctes*. This placement of *Yalkaparidon* within Metatheria should be treated with caution, due to the small sample of metatherian diversity. Archer et al. (1988) did not consider *Yalkaparidon* to be a notoryctemorphian and argued that its metacone zalambdodonty was acquired convergently with that of *Notoryctes*, while Beck et al. (2013) analyses of its phylogenetic affinities were inconclusive. Branch support for the *Notoryctes-Yalkaparidon* clade is very strong, but may be explained by the retention of a talonid basin in the incipiently zalambdodont dentition of *Naraboryctes*. The fully zalambdodont molars of *Notoryctes* and *Yalkaparidon* lack a talonid basin, causing these two taxa to be attracted to each other. Unambiguous optimization of characters across this topology supports this idea: of the 11 characters uniting *Yalkaparidon* and *Notoryctes*, nine of them relate to the absence of features associated with the talonid basin. This suggests character correlation is present in Rougier et al.'s (2012) coding strategy (followed here), by independently scoring the absence of the talonid cusps, the absence of the talonid basin itself is given greater significance in the analysis. The taxonomic scope of the matrix makes such correlations difficult to avoid; however, the issue would need to be addressed and additional marsupial taxa included to produce a more accurate representation of the relationships of *Yalkaparidon* and Notoryctemorphia.

The Placement of Australosphenida

In general, the topology of the unconstrained Bayesian analysis is very similar to that of the parsimony analysis. However, one major difference between the two analyses is the position of Australosphenida (excluding *Pseudotribos*). The phylogenetic position of this group has been a source of controversy since the proposal of the taxon by Luo et al. (2001). The traditional view of dental evolution in Mesozoic mammals had been that tribosphasphy evolved once in the Early Cretaceous (Bown and Kraus 1979), and was followed by diversification of therian mammals in Laurasian continents (Lillegraven 1974). Luo et al. (2001) argued instead that there had been two separate origins of the tribosphenic molar: once in a Gondwanan lineage, which is today represented by monotremes, and once in a lineage of the northern continents, which is today represented by therian mammals. These groups were referred to as Australosphenida and Boreosphenida, respectively.

Luo et al. (2001) proposed this dual origin hypothesis following the description of the Jurassic, tribosphenic *Ambondro* (Flynn et al. 1999). Comparisons of *Ambondro* with the only other Gondwanan Mesozoic mammals known at that time (*Ausktribosphenos* and *Steropodon*) showed that the tribosphenic molars of the Gondwanan mammals shared certain unique features to the exclusion of northern tribosphenic mammals. The dual origin hypothesis has been supported by phylogenetic analyses that place several non-tribosphenic groups, including Dryolestoidea, on the boreosphenidan stem (Luo et al. 2001, 2002; Kielan-Jaworowska et al. 2004). Further phylogenetic studies have reinforced the hypothesis, and additional taxa have since been attributed to Australosphenida, including *Bishops* (Luo et al. 2002), *Asfaltomylos* (Rauhut et al. 2002; Martin and Rauhut 2005), and *Henosferus* (Rougier et al. 2007).

However, the dual-origin hypothesis has been disputed by several authors (Sigogneau-Russell et al. 2001; Rich et al. 2002; Woodburne 2003; Woodburne et al. 2003; Rowe et al. 2008) who argue that some or all of the extinct Gondwanan tribosphenic taxa are more closely related to northern tribosphenic mammals than to monotremes. Woodburne et al. (2003) performed a phylogenetic analysis that supports this more traditional view, resolving *Bishops*, *Ausktribosphenos, Ambondro,* and *Asfaltomylos* as eutherians, while monotremes are found to be the sister-group of a clade comprising therian mammals, dryolestoids, spalacotheroids, and allotherians. The dual-origin hypothesis remains controversial.

Our parsimony topology is similar to that of Luo et al. (2001) and clearly supports the dual origin hypothesis. Character optimization across this topology shows that no character states associated with tribosphenic molars optimize basal to the Australosphenida-Boreosphenida divergence, consistent with the independent acquisition of tribosphasphy in these two lineages (see Supplementary Material for detailed character optimizations). Our Bayesian analysis resolves a monophyletic Australosphenida (excluding *Pseudotribos*) in a trichotomy with *Peramus* and Boreosphenida + *Vincelestes*. This result is similar to an earlier Bayesian analysis by Gurovich and Beck (2009), despite the characters added to the Rougier et al. (2007, 2011, 2012) matrices in this time. In the Luo et al. (2002) topology, a paraphyletic assemblage of eutriconodont, spalacotheroid, and dryolestoid groups occupies the therian stem, separating the Australosphenida from the Boreosphenida. According to our Bayesian analysis, the only pre-tribosphenic taxon on the therian stem, separating boreosphenidans from the australosphenidans is *Vincelestes*, with the position of the pre-tribosphenic *Peramus* being ambiguous.

The position of the australosphenidan clade in our Bayesian tree is not strongly supported. A posterior probability of 0.95 is often seen as robust in a Bayesian framework, although

even Bayes supports of 1.0 can be misleading (Suzuki et al. 2002). Our value of 0.72 is much lower, but suggestive, particularly given the high quantity of missing data in the dataset. The large magnitude of the Bayes factors produced in our comparison of the unconstrained Bayesian topology with our parsimony topology clearly indicates lack of support for the latter in a Bayesian context. However, although the optimal Bayesian and MP topologies are quite similar overall, we recover the opposite, statistically significant result in favor of the parsimony topology, and placement of the Australosphenida far from Boreosphenida in a parsimony context (Fig. 1). Therefore, our reanalysis of the Rougier et al. (2012) dataset does not enable firm conclusions regarding the phylogenetic position of Australosphenida.

The interpretation of the pre-tribosphenic taxa *Vincelestes* and *Peramus* is crucial to the understanding of the evolution of tribosphery under our Bayesian phylogeny. Ancestral state reconstructions of the last common ancestor of Australosphenida and Boreosphenida (Fig. 3: node W; see Supplementary Material for complete table of relevant character states) suggest that it possessed a partially expanded talonid region with at least one, and possibly two, functional talonid cusps (hypoconulid and hypoconid) and a well-developed hypoflexid. However, this ancestor is reconstructed as having no functional lingual protocone and an unbasined talonid region, suggesting that the principal occlusal relationship in the distal portion of its pre-tribosphenic tooth would be between the paracone and the hypoflexid. This tooth form would resemble that seen in *Peramus* (Crompton 1971; Clemens and Mills 1971). The last common ancestor of Boreosphenida + *Vincelestes* (Fig. 3: node X) is reconstructed with a functional lingual protocone, while acquisition of a truly tribosphenic basined talonid occurred in more derived members of the boreosphenidan clade (Fig. 3: node Y). The last common ancestor of all australosphenidans (Fig. 3: node Z) is independently reconstructed as having a fully basined talonid. However, presence of a functional lingual protocone is reconstructed as equivocal due to the majority of Australosphenida being known only from their lower dentitions. It is likely that a functional lingual protocone was present in these animals, as inferred from the presence of a basined talonid, but this cannot be regarded as certain.

This ancestral reconstruction suggests the independent evolution of the functional tribosphenic tooth complex in Australosphenida and Boreosphenida, derived from a shared ancestral set of distal lower molar cusps. This derivation of the tribosphenic molar is consistent with hypotheses of its evolution within stem Boreosphenida (Crompton 1971; Bown and Kraus 1979; Davis 2011), but suggests that the tribosphenic precursor predates the divergence from Australosphenida. This model is also consistent with the idea of plasticity of tooth form in Mesozoic mammals, with a shearing-grinding dentition evolving convergently in different lineages, in response to similar functional demands of the organisms (Luo et al. 2007). Such 'protocone-like' structures clearly evolved convergently in multiple Mesozoic mammal lineages, including pseudotribosphenic mammals (Luo et al. 2007), docodonts (Sigogneau-Russell 2003), and tinodontids (Averianov and Lopatin 2008). Finally it is worth noting that this interpretation could change depending on the resolution of the trichotomy at node W (Fig. 3), as well as the interpretation of *Vincelestes*, which was recently recovered not as a stem boreosphenidan but as a basal member of the Dryolestida by Averianov et al. (2013).

Though the Bayesian analysis presents an exciting and novel interpretation for the evolution of tribosphery, it remains surprising that the two different methodologies produce such different phylogenetic hypotheses from the same dataset. It is possible that the variation of evolutionary rates across characters in the Bayesian framework has resulted in this topological difference. This ability to apply among character rate variation to a morphological phylogeny, in tandem with explicit branch lengths, is a potential strength of this analytical approach (Lee and Worthy 2012). The different manner in which Bayesian and parsimony methods handle inapplicable data could also be responsible for the topological differences recovered here (M. R. Smith pers. comm.), though neither methodology is immune to errors caused by uncertain or inapplicable character states (Maddison 1993; Simmons 2012a, b; though see Wiens and Morrill 2011). Critics of a probabilistic approach to morphological evolution argue that the use of an explicit (and overly simple) model of morphological evolution is unjustifiable, and the assumptions inherent to the model are responsible for the topological differences (Spencer and Wilberg 2013; Xu and Pol 2013). While we agree that caution is required in their use, the need for improved methods for the combined analysis of morphological and molecular data is likely to drive the use of such model-based approaches in the future. Investigating their behavior in a morphology only context is crucial to ensure their improvement. Further investigation into the behavior of morphological data in a Bayesian framework is clearly required to explain our different placements of Australosphenida. Regardless, these differences highlight the potential of Bayesian and parsimony analysis comparisons to explore the uncertainty within a dataset, thus directing future morphological study.

Summary

Rougier et al. (2012) code the zalambdodont dentition of *Necrolestes* based more on a priori perception of its phylogenetic affinities and less on intrinsic features of the dentition itself. However, Hennig's auxilliary principle, that similarity justifies the assumption of homology in the absence of other evidence, is equally applicable to both interpretations of

zalambdodonty in *Necrolestes*. The definitive test for secondary homology is congruence (de Pinna 1991). This requires construction of a phylogenetic tree using multiple independent characters, which then permits evaluation of secondary homology (de Pinna 1991). To code features of the dentition on the basis of perceived primary homologies of cranial characters is to make a priori assumptions that weaken any subsequent tests based on congruence and cast doubt on the validity of resulting phylogenetic trees.

By undertaking more rigorous homology assessments and by including metacone zalambdodont taxa, we have addressed the possible bias caused by non-independent coding of characters. The fact that, after applying statistical tests under two different methodologies (parsimony and Bayesian analysis), *Necrolestes* is always recovered as a meridiolestidan is stronger support for the conclusions of Rougier et al. (2012) than they themselves presented. Further, the inclusion of additional metatherian taxa permits assessment of a common alternative hypothesis of the phylogenetic position of *Necrolestes*. Templeton and Bayes factor tests show that constraining *Necrolestes* to the Metatheria produces topologies that are much less likely than those in which *Necrolestes* resolves as a meridiolestidan. We therefore accept the hypothesis that meridiolestidans exhibit an approximately 40 million year ghost lineage between the Paleocene and early Miocene.

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