Middle Miocene origins for tough-browse dietary specialisations in the koala (Marsupialia, Phascolarctidae) evolutionary tree: description of a new genus and species from the Riversleigh World Heritage Area

Karen H. Black

Palaeontology, Geobiology and Earth Archives (PANGEA) Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia, 2052 (k.black@unsw.edu.au)

Abstract   Black, K.H. 2016. Middle Miocene origins for tough-browse dietary specialisations in the koala (Marsupialia, Phascolarctidae) evolutionary tree: description of a new genus and species from the Riversleigh World Heritage Area. *Memoirs of Museum Victoria* 74: 255–262.

   Stelakoala riversleighensis gen. et sp. nov. is described on the basis of an isolated M_1 from the middle Miocene Jim's Jaw Site of the Riversleigh World Heritage Area, northwestern Queensland. The new genus shares affinities, particularly in its possession of a metastylid fold, with a specialised clade of phascolarctids that includes species of *Litokoala* and the modern genus *Phascolarctos*. Dental specialisations of *Stelakoala riversleighensis* include a high molar crown, the presence of large accessory blades and cuspids, and the development of lingual ribs on the entoconid and metaconid. These features effectively increase both the number and available surface area of the molar cutting blades. Of particular note is the reinforcement of the primary cutting blade through the development of ribs on the lingual cuspids. These structures foreshadow the condition found in *Phascolarctos,* and may represent an early stage in the transition to a more fibrous, highly specialised diet in the evolutionary history of koalas.

Keywords   Miocene, Vombatiformes, Phascolarctomorphia, Cainozoic, diet.

Introduction

The Miocene deposits of the Riversleigh World Heritage Area (Fig. 1) display the greatest abundance and highest taxonomic diversity of extinct koalas from any single region in Australia. Currently, five genera (*Litokoala*, *Nimiokoala*, *Priscakoala*, Encore gen. nov and *Stelakoala* gen. nov) and seven species have been identified (Black et al., 2014b; this analysis) from deposits spanning the early Miocene to early late Miocene. Included amongst these is the most dentally generalised species known, *Priscakoala lucyturnbullae* Black, Archer and Hand, 2012a, although the geologically oldest koalas derive from the late Oligocene Namba and Etadunna Formations of South Australia (e.g., *Madakoala devisi* Woodburne, Tedford, Archer and Pledge, 1987; *M. wellsi* Woodburne, Tedford, Archer and Pledge, 1987; *Perikoala palankarinnica*, Stirton, 1957; *Perikoala robustus* Woodburne, Tedford, Archer and Pledge, 1987; *Litokoala kutjamarpensis* Stirton, Tedford and Woodburne, 1967; and *Nimiokoala* sp.[Black and Archer, 1997]). As yet, no phascolarctids have been identified in Riversleigh's late Oligocene (Faunal Zone A) faunas.

   While Riversleigh's Miocene (Faunal Zones B–D) deposits have yielded arguably the most exceptionally well-preserved koala fossil cranial material known (e.g., for

Nimiokoala greystanesi Black and Archer, 1997, *Litokoala kutjamarpensis* and *Litokoala dicksmithi* Black, Louys and Price, 2014a), most specimens comprise isolated teeth or, at best, partial dentitions. *Stelakoala riversleighensis* gen. et sp. nov. is described here on the basis of a single first lower molar (M_1) from a middle Miocene deposit, Jim's Jaw Site. Despite the relative scarcity of material, M_1 has previously been demonstrated to hold considerable taxonomic and phylogenetic significance within Phascolarctidae (Black et al., 2012a, 2014a, 2014b). Consequently, *Stelakoala riversleighensis* is shown here to represent a significant stage in the evolution of this iconic and once diverse group of Australian marsupials.

Terminology

Systematic nomenclature follows Aplin and Archer (1987). Taxonomically valid phascolarctid species are those identified by Black et al. (2014b). Reference to *Litokoala kutjamarpensis* is sensu Louys et al. (2007) and Black et al. (2014a). Biostratigraphic nomenclature follows Archer et al. (1994, 1997b), Creaser 1997 and Travouillon et al. (2006). Molar morphology follows Archer (1978).
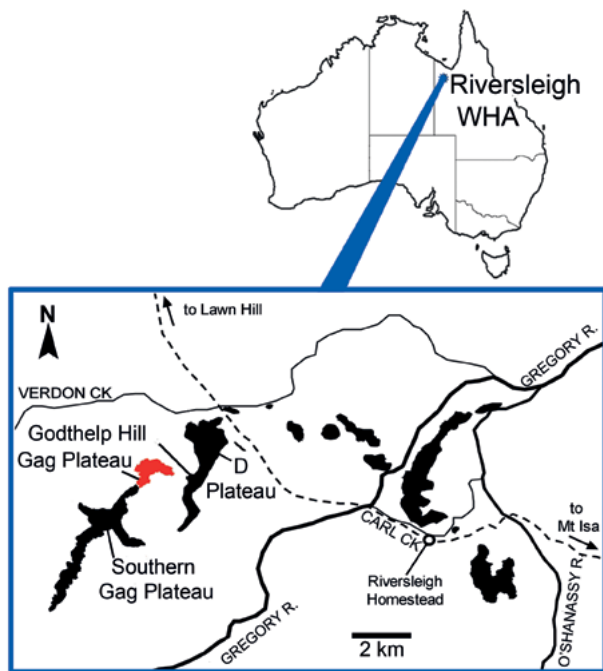
Figure 1. Map and regional schematic of the Riversleigh World Heritage Area (After Arena, 2005, and Megirian, 1992). The Type locality of *Stelakoala riversleighensis* gen. et sp. nov., Jim's Jaw Site, is located on the northern Gag Plateau (highlighted red).

Institutional abbreviations

AM , Australian Museum, Sydney; AR, University of New South Wales, Sydney; QM, Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide.

Systematic Palaeontology

Marsupialia Illiger, 1811

Diprotodontia Owen, 1866

Vombatiformes Woodburne, 1984

Phascolarctidae Owen, 1839

Stelakoala **gen. nov.**

Type and only species. Stelakoala riversleighensis gen. et sp. nov.

Generic diagnosis. High crowned M_1 with: large protostylid; strong pre- and postprotostylid cristids; large entostylid ridge with well-developed buccal spur; twinned lingual ribs on the entoconid and a single rib on the metaconid; a metastylid fold wherein the postmetastylid cristid is continuous with the preentocristid; a metaconid positioned close to the lingual tooth margin. *Stelakoala* is unique among phascolarctids in having the following features: a greater separation between the metaconid and protoconid apices with respect to trigonid width;

possession of a strong premetacristid; and an incipiently cuspate, short, crescentic preprotostylid cristid that is not continuous with an anterior cingulum. Among known koalas it is most similar to species of *Phascolarctos* and *Litokoala*, particularly with respect to the development of the protostylid and entostylid and in its apomorphic possession of a metastylid fold.

Remarks. The Jim's Jaw Site M_1 was previously regarded to be a new species of *Litokoala* in an unpublished thesis by Black (1992) (see also *Litokoala* new sp. 1 of Archer et al., 2006). This assignment was based on overall similarities in molar morphology to that of *Litokoala kutjamarpensis* (sensu Louys et al., 2007; previously *L. kanunkaensis* Springer, 1987), although Black (1992) did also note similarities to *Phascolarctos* spp. in the shared presence of twinned lingual ribs on the entoconid. The M_1 is recognized here as a new genus and species of koala because it possesses a combination of derived features found in *Litokoala* and/or *Phascolarctos*, as well as autapomorphic features that preclude its assignment to either genus.

Etymology. Stela is the latin word for 'a pillar or support bearing markings' in reference to the buttressing of the lingual faces of the entoconid and metaconid by the development of lingual ribs.

Stelakoala riversleighensis **sp. nov.**

(Figures 2–3; Table 1)

Holotype. QM F57737, isolated right M_1.

Type locality. Jim's Jaw Site, northern section of the Gag Plateau (Fig. 1), Riversleigh World Heritage Area, northwestern Queensland.

Age. Faunal Zone C deposit; middle Miocene (Archer et al., 1989, 1991; Arena, 2005; Travouillon et al., 2006; Woodhead et al., 2016).

Specific diagnosis. The species diagnosis is that for the genus until other species are known.

Specific etymology. In reference to the Riversleigh World Heritage Area where this taxon has been found.

Description. Robust M_1 (length 6.0 mm; anterior width 3.6 mm; posterior width 4.2 mm) with five major cuspids (metaconid, protoconid, and protostylid on the trigonid; and entoconid and hypoconid on the talonid) and four smaller cuspids (anterior paraconid, lingual metastylid, posterolingual entostylid, and cuspate entostylid ridge). The protoconid, protostylid and hypoconid are the most heavily worn of the cuspids, with the entoconid and metaconid enamel only slightly breached at their apices. This pattern of greater wear on the buccal conids relative to the lingual conids is also found in *P. cinereus*.

The cristid obliqua, the anterobuccal base of the entoconid, the posterobuccal base of the metaconid and the base of the posterior arm of the protostylid are strongly crenulated with large ridge-like crenulations (Fig. 2). A well-developed paraconid occupies the anterolingual corner of the tooth, and is connected to the protoconid by the preprotocristid. There is no connection between the apices of the protoconid and

Table 1. Dimensions (in mm) and proportional relationships of M_1 trigonid cuspids in fossil and extant koalas for which an M_1 is known (see Figure 3 for an explanation of the measurements taken). Percentages in brackets represent percentage of trigonid width. For species known from multiple M_1s (e.g., *N. greystanesi*, *L. kutjamarpensis*, *Phascolarctos cinereus* and *Phascolarctos yorkenis* [Pledge, 1992]), only the least worn specimens were measured. Previously published measurements of trigonid width for extinct koalas (e.g., Woodburne et al., 1987) were not used in order to reduce measurer error and maintain consistency. With respect to *P. yorkensis* which is known from two M_1s, wear and damage to the lingual tooth margin of the M_1 of the holotype (Pledge, 1992; p. 121) excluded this specimen from the analysis, and AM F98886 (an isolated right M_1) was unavailable for study. Consequently, measurements for *Phascolarctos yorkensis* were taken from Archer et al. (1997a, table 3, figure 2).

	Specimen	Metaconid-lingual margin	Metaconid-protoconid	Protoconid-protostylid	Protostylid-buccal margin	Trigonid width
Priscakoala lucyturnbullae	QM F16914	0.77 (21%)	0.81 (22%)	1.12 (31%)	0.93 (26%)	3.63
Madakoala wellsi	SAM P24793	1.22 (24%)	1.12 (22%)	1.30 (26%)	1.39 (28%)	5.03
Madakoala devisi	SAM P24792	1.08 (24%)	1.11 (25%)	1.09 (24%)	1.24 (27%)	4.52
Perikoala robustus	SAM P26552	1.27 (29%)	0.98 (22%)	0.95 (22%)	1.17 (27%)	4.37
Perikoala palankarinnica	QM F14693	0.90 (26%)	0.84 (24%)	---	---	3.52
Nimiokoala greystanesi	QM F30493	0.62 (19%)	0.87 (26%)	1.24 (38%)	0.57 (17%)	3.30
	QM F30488	0.87 (24%)	0.87 (24%)	1.36 (38%)	0.49 (14%)	3.59
	QM F57891	0.73 (22%)	0.74 (22%)	1.34 (40%)	0.55 (16%)	3.36
	Mean	0.74 (22%)	0.83 (24%)	1.31 (38%)	0.54 (16%)	3.42
Litokoala kutjamarpensis	QM F30501	0.34 (12%)	0.58 (20%)	1.25 (43%)	0.72 (25%)	2.89
Phascolarctos cinereus	AR6508	0.80 (19%)	0.95 (23%)	1.65 (39%)	0.78 (19%)	4.18
	AR1574	0.64 (15%)	0.86 (20%)	1.78 (42%)	0.95 (23%)	4.23
	QM J13278	0.68 (16%)	0.85 (21%)	1.85 (45%)	0.70 (18%)	4.08
	Mean	0.71 (17%)	0.89 (21%)	1.76 (42%)	0.81 (20%)	4.16
Phascolarctos yorkensis	AM F98886	0.83 (13%)	1.23 (19%)	2.87 (44%)	1.57 (24%)	6.50
Stelakoala riversleighensis	QM F57737	0.44 (12%)	1.23 (34%)	0.94 (26%)	0.99 (28%)	3.60

metaconid, yet weak ridges (ribs) on their lingual and buccal faces, respectively, meet in the deep longitudinal valley separating these cuspids. A short, arcuate valley is developed between the posterior base of the paraconid, the preprotocristid and the anterobuccal base of the metaconid. The apex of the protoconid is positioned slightly buccal of the tooth midline (Fig. 2B, 3). The postprotocristid runs posteriorly and slightly lingually into the central basin where it joins the cristid obliqua along the transverse axis. The metastylid and entostylid are moderately developed. The premetacristid is a short linear crest which fades into the anterior base of the metaconid. The postmetacristid extends posterolingually from the metaconid apex to the lingual margin, swelling at this point to form the metastylid. If not for the tooth being broken at this point, the short buccal postmetastylid cristid would meet the preentocristid slightly buccal to the top of the transverse valley forming a 'metastylid fold' (Fig. 2B).

The protostylid is moderately developed and its base occupies one third the width of the trigonid. The valley separating the protoconid and protostylid is very narrow, unlike that seen in *Litokoala kutjamarpensis* and *Phascolarctos* species. The posterior ridge of the protostylid terminates in the transverse valley between the protostylid and

hypoconid becoming slightly crenulous at its tip. A relatively deep pocket is formed between the posterior protostylid ridge, the cristid obliqua, the postprotocristid and the bases of the protoconid and protostylid. The short anterior ridge of the protostylid extends anteriorly, then curves anterolingually, terminating at the anterobuccal base of the protoconid. It does not extend from the protostylid apex but from the anterior base of the protostylid and when viewed buccally, appears as a small cuspule at the anterior base of the protostylid (Fig. 2D). An anterior cingulum is not developed. Short buccal ribs extend from the apex of the metaconid, protoconid and entoconid. Lingual ribs are present on all major cusps. The lingual rib of the entoconid bifurcates, one arm continuing lingually, the other anterolingually fading down the lingual tooth margin (Fig. 2B–C), giving the appearance of a 'twinned' entoconid similar to that found in *Phascolarctos*. Also as in *Phascolarctos* spp., moderate depressions occupy the lingual face of the entoconid between the lingual ribs and the preentocristid (anterolingually) and postentocristid (posterolingually) (see entoconid lingual shelf of Black et al. 2014a; fig. 2).The preentocristid is a relatively short, crescentic crest extending anterobuccally then curving anterolingually where it bifurcates, a short ridge continuing anterolingually to
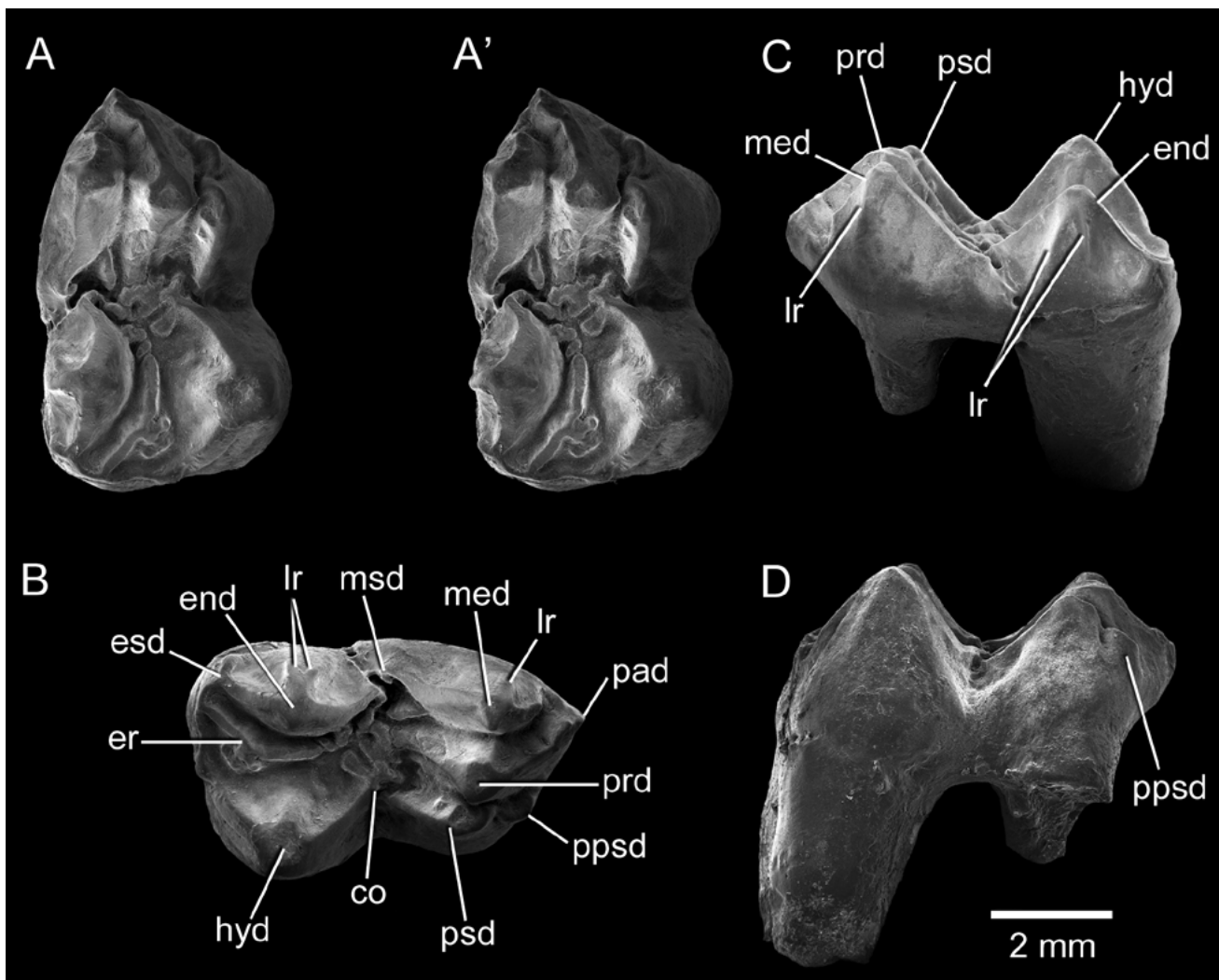
Figure 2. *Stelakoala riversleighensis* gen. et sp. nov. holotype (QM F57737) from Jim's Jaw Site, Riversleigh World Heritage Area, Qld. A-A', Occlusal stereopair; B, labelled occlusal view; C, lingual view; D, buccal view. Abbreviations: co, cristid obliqua; end, entoconid; esd, entostylid; er, entostylid ridge; hyd, hypoconid; lr, lingual ribs; med, metaconid; msd, metastylid; pad, paraconid; ppsd, preprotostylid cristid; prd, protoconid; psd, protostylid.

meet the postmetacristid at the lingual margin. A second ridge extends anterobuccally and becomes part of the crenulation pattern, terminating in the transverse valley. The postentocristid, a more linear crest, runs posterolingually to the apex of the entostylid at the posterolingual corner of the tooth. A short lingual ridge fades down the lingual margin from the entostylid apex. A short posterobuccal ridge extends from the entostylid apex and is continuous with the posterior cingulum (which continues buccally to meet the posthypocristid). From the junction of the posterobuccal ridge of the entostylid and the posterior cingulum the well-developed, slightly crescentic entostylid ridge extends anterobuccally along the longitudinal valley between the entoconid and hypoconid and is cuspate at the posterobuccal base of the entoconid. A short posterobuccally directed ridge

from the apex of the entostylid ridge spreads into three buccally directed spurs which terminate at the posterolingual base of the hypoconid (Fig. 2B). The cristid obliqua extends anterolingually from the hypoconid apex to meet the postprotocristid in the central basin slightly lingual to the longitudinal axis in the transverse valley.

Discussion

Stelakoala riversleighensis gen. et sp. nov. is among the most rarely recorded of extinct koalas, known solely from an isolated M_1. It represents the seventh koala species recorded from the Oligo-Miocene fossil deposits of the Riversleigh World Heritage Area (Black et al., 2014b) and among these, is the only species restricted to the middle Miocene. Original

assessment of the M_1 led Black (1992) in her unpublished Honours thesis (and later Archer et al., 2006), to establish the specimen as a new species of *Litokoala*, the most common and taxonomically diverse genus of extinct koalas. However, recognition here of apomorphies shared with both *Litokoala* and/or *Phascolarctos* combined with several autapomorphic features, indicates the M_1 represents a new genus and species of koala.

Phylogenetic relationships. A phylogenetic analysis of phascolarctid intrafamilial relationships was not performed here because of the limited data for *Stelakoala riversleighensis* and because only eight of the other 15 koala species currently considered taxonomically valid (see Black et al., 2014b, table 1) are known from comparable M_1 material. Nevertheless, *Stelakoala* appears to hold a relatively crownward position within the family. In the most recent phylogenetic analysis of phascolarctid intrafamilial relationships by Black et al. (2012a), eight unambiguous synapomorphies were found to unite a *Nimiokoala/Litokoala/Phascolarctos* clade. Four of these pertain to M_1 and three are shared by *Stelakoala* including the presence of an entostylid ridge, large protostylid, and a well-developed cristid obliqua that meets the postprotocristid lingual to the horizontal tooth midline (Fig. 2B).

Morphologically, the *S. riversleighensis* M_1 is most similar to that of *Litokoala kutjamarpensis* and *Phascolarctos* spp., especially in the presence of a metastylid fold; a synapomorphy found to unite *Litokoala* and *Phascolarctos* to the exclusion of *Nimiokoala* (Black et al., 2012a). Like *Litokoala*, and contra all other koala species, *Stelakoala* exhibits a more lingually positioned metaconid on M_1 (Fig. 3), yet appears more specialised in its possession of a large, cuspate entostylid ridge, and ribs buttressing the lingual faces of the entoconid and metaconid. The latter features were previously considered autapomorphic for *Phascolarctos*.

Unlike species of *Litokoala*, *Nimiokoala* and *Phascolarctos*, however, which exhibit a significantly greater separation of the protostylid from the protoconid (between 38% and 45% of trigonid width; Fig. 3, Table 1), *Stelakoala* shows similar values to more basal forms such as species of *Madakoala* and *Perikoala*. While the modern species *P. cinereus* indicates a moderate level of intraspecific variation in these dimensions (e.g., between 39% and 45% of trigonid width), the value for *Stelakoala* (26% of trigonid width; Table 1) remains lower than expected for such a seemingly advanced species.

Stelakoala is unique among phascolarctids in exhibiting a greater separation between the protoconid and metaconid on M_1 (Fig. 3). Understanding the functional implications of this morphology and *Stelakoala*'s position within Phascolarctidae requires discovery of additional material for the species. On the basis of M_1 morphology alone, *Stelakoala* most likely forms a clade with species of *Litokoala* and *Phascolarctos*. However, an as yet undescribed new genus and species of koala from the early late Miocene Encore Local Fauna of Riversleigh may share closer affinities with *Phascolarctos* than either *Stelakoala* or *Litokoala* (Black et al., 2014b).

As a consequence of the data presented here (Fig. 3, Table 1) it is evident that the position of the protoconid on M_1, a
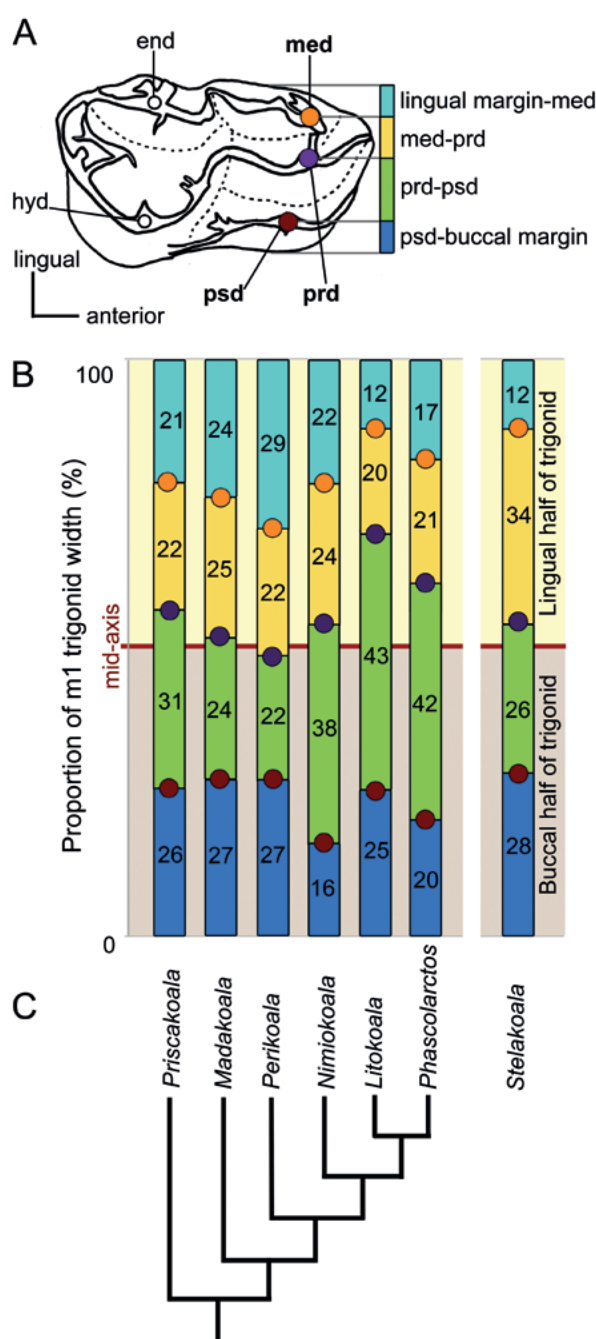

Figure 3. The evolution of primary M_1 trigonid cuspids (metaconid, protoconid and protostylid) in phascolarctids. A, Schematic diagram of a phascolarctid right M_1 illustrating how dimensions and percentages represented in Table 1 were obtained (adapted from Black et al., 2014a); B, Graphical representation of the relative positions and distance between the primary M_1 trigonid cuspids as a percentage of trigonid width; C, phylogenetic relationships of phascolarctids (from Black et al., 2012a). Abbreviations: end, entoconid; hyd, hypoconid; med, metaconid, prd, protoconid; psd, protostylid. Data for *Madakoala*, *Perikoala*, *Litokoala*, *Nimiokoala* and *Phascolarctos*, is based on *M. devisi*, *Pe. robustus*, *L. kutjamarpensis*, *N. greystanesi* and *P. cinereus*, respectively, with mean values used for the latter two species (Table 1).

character commonly used in previous analyses of phascolarctid intrafamilial relationships (e.g., Woodburne et al., 1987; Black and Archer, 1997; Black et al., 2012a), is uninformative with respect to delimiting koala relationships. Consequently, in future analyses, inclusion of a character that defines the relative separation of major trigonid cuspids on M_1 with respect to trigonid width, may be more useful for clarifying relationships within the family.

Age and Biostratigraphy. The morphologically derived nature of *Stelakoala* agrees with the suggested middle Miocene (Faunal Zone C) age for the Jim's Jaw Site Type Locality which was previously based on lithostratigraphic relationships and biocorrelation of its contained fauna (Creaser, 1997; Travouillon et al., 2006; Black et al., 2013; Gillespie et al., 2014). Further evidence for a middle Miocene age comes from recently obtained U-Pb radiometric ages of spatially related deposits on Riversleigh's Gag Plateau. Woodhead et al. (2016) found that all of the Riversleigh deposits that produced radiometric dates of middle Miocene age were geographically restricted to the Gag Plateau. Jim's Jaw Site is located on the northern section of the Gag Plateau (Fig. 1) in a sequence of horizontally bedded sediments, topographically four meters below Ringtail Site (Creaser, 1997) which has been radiometrically dated at 13.56 ± 0.67 Ma (Woodhead et al., 2016). Jim's Jaw Site contains a large chronomorph (Black et al., 2013; fig. 7, table B) of the zygomaturine diprotodontid *Neohelos tirarensis* Stirton, 1967, a form antecedent to *Neohelos stirtoni* Murray et al., 2000. The latter species is known from AL90 Site (Black et al., 2013; Arena et al., 2014), a palaeocave deposit located on the southern section of the Gag Plateau (Arena et al., 2014), that has been radiometrically dated at between 14.17 and 15.11 Ma (Woodhead et al., 2016). Most recently, Arena et al. (2016) have further temporally subdivided Riversleigh's middle Miocene Faunal Zones C assemblages on the basis of species successions in nine contemporaneous marsupial lineages. The stage-of-evolution of representatives of three of these lineages in the Jim's Jaw LF (e.g., *Neohelos tirarensis*, *Wakaleo oldfieldi* Clemens and Plane, 1974, and *Ganguroo* sp. 2), indicate this fauna represents a relatively older time interval within Faunal Zone C.

Collectively, these data suggest that the type locality of *Stelakoala riversleighensis* predates both Ringtail and AL90 sites and is likely around 15-16 Ma.

Palaeoecology. Using Myers' (2001; table 5) predictive regression equations that correlate dental dimensions (in this case first lower molar area) with marsupial body mass, *Stelakoala riversleighensis* is estimated to have weighed 6.2 kg. This value falls at the lower end of the range for modern *P. cinereus* (4.1-13.5 kg; Strahan, 2004) and makes *S. riversleighensis* the largest koala species currently described from the region. Aside from *Stelakoala* and the archaic early Miocene *Priscakoala lucyturnbullae* (5.1 kg; Black et al., 2014b), most koala species that inhabited the early-middle Miocene rainforests of Riversleigh (e.g., species of *Litokoala* and *Nimiokoala*) were characteristically small forms weighing between 2.6 and 3.7 kg (Black et al., 2014b). Two such species were potentially coeval with *S. riversleighensis* during the

middle Miocene: the possum-like early to middle Miocene *Nimiokoala greystanesi* and the late Oligocene to middle Miocene *Litokoala kutjamarpensis* (Black et al., 2014b).

In terms of dental morphology, *Stelakoala riversleighensis* exhibits features, such as the development of ribs on the entoconid and metaconid, which foreshadow the condition found in *P. cinereus*. Buttressing of the lingual cuspids is consistently present in *P. cinereus* lower molars, however, it varies in expression from weak ribs to strongly developed columnar stylids such that in some individuals the metaconid and entoconid apices may appear double-cusped (see Black et al., 2014a, fig. 2). Analyses of jaw mechanics, occlusion and microwear in *P. cinereus* indicate that during the power stroke of the masticatory cycle, the lingual cuspids and their associated pre- and postcristids are the major surfaces of leaf segmentation (Lanyon and Sanson, 1986; Young and Robson, 1987). Consequently, reinforcement of this area through the development of ribs or columnar stylids may function to delay the effects of wear and/or provide additional cutting edges (Lanyon and Sanson, 1986) for processing a highly fibrous diet of eucalypt leaves.

The development of lingual buttressing on the entoconid and metaconid in *Stelakoala*, combined with its high-crowned molars, large accessory cuspids (e.g., protostylid and cuspate entostylid ridge) and the extension of the lingual cutting blade through the development of a strong premetacristid, may also be interpreted as adaptations to a diet of more fibrous browse.

Nine fossil species have so far been identified from Jim's Jaw Site although the functional ecology (excepting diet) of these taxa is largely undetermined. Nonetheless, the presence of six browsing marsupial species (three arboreal, three terrestrial) suggests a relatively diverse, forested palaeoenvironment. In addition to *Stelakoala*, these include: two, as yet, unnamed pseudocheirid species (*Pildra* sp. 2 and Pseudocheirid new genus 2, sp.2); the diprotodontid *Neohelos tirarensis*; the bulungamayine kangaroo *Wanburoo hilarus* Cooke, 1999; and the macropodid *Ganguroo* sp. 2. The omnivorous pygmy possum *Burramys brutyi* Brammall and Archer, 1997, is also present as are the carnivorous dasyurid *Barinya wangala* Wroe, 1999 and thylacoleonid *Wakaleo oldfieldi* (Gillespie et al., 2014; Travouillon et al., 2015; Arena et al., 2016).

Evidence for extensive rainforest habitats at Riversleigh has been well documented, at least until the end of the middle Miocene Climatic Optimum (Archer et al., 1994, 1997b; Travouillon et al., 2009, 2012; Black et al., 2012b, 2012c; Arena et al., 2014; Woodhead et al., 2016). After this time (circa 15–13 Ma), palaeotemperatures dropped by as much as 7°C (Shevenell et al., 2004; Billups and Scheiderich, 2010) resulting in the regional collapse of rainforests and the expansion of sclerophyll communities, with *Eucalyptus*-dominated forests becoming widespread by late Miocene times (Martin, 2006). Nevertheless, palynological evidence indicates *Eucalyptus* was present in the late Oligocene to early Miocene of central Australia (Martin, 2006). Archer and Hand (1987) hypothesized that an association between koalas and eucalypts may have developed during this time, with koalas potentially specializing on eucalypts within or at the

fringes of wet forest communities. The relatively generalised masticatory system of *L. kutjamarpensis* compared with the highly specialised cranio-mandibular morphology of *P. cinereus*, led Louys et al. (2009) to suggest this association developed after the divergence of the *Litokoala* and *Phascolarctos* lineages. Consequently, the derived dental specializations evident in the middle Miocene *Stelakoala riversleighensis* may signal the beginnings of such a transition to a more fibrous, highly specialised diet, ultimately culminating in the dependence of the extant koala on a diet of predominantly eucalypt leaves.

Acknowledgements

References

Aplin, K.P., and Archer, M. 1987. Recent advances in marsupial systematics with a new syncretic classification Pp. xv–lxxii in: Archer, M. (ed), *Possums and Opossums: Studies in Evolution*. Surrey Beatty and Sons Pty Ltd, Chipping Norton.

Archer, M. 1978. The nature of the molar-premolar boundary in marsupials and a reinterpretation of the homology of marsupial cheek teeth. *Memoirs of the Queensland Museum* 18: 157–164.

Archer, M., and Hand, S.J. 1987. Evolutionary considerations Pp. 79–106 in: Cronin, L. (ed), *Koala: Australia's Endearing Marsupial*. Reed Books, Sydney.

Archer, M., Godthelp, H., Hand, S., and Megirian, D. 1989. Fossil mammals of Riversleigh, northwestern Queensland: preliminary overview of biostratigraphy, correlation and environmental change. *Australian Zoologist* 25: 29–65.

Archer M., Hand, S.J., Godthelp, H., and Attenborough, D. 1991. *Riversleigh: the story of animals in ancient rainforests of inland Australia*: Reed Books Pty Ltd: Sydney.

Archer, M., Hand, S.J., and Godthelp, H. 1994. *Riversleigh*. Reed Books Pty Ltd: Sydney. 264 pp.

Archer, M., Black, K., and Nettle, K. 1997a. Giant ringtail possums (Marsupialia, Pseudocheiridae) and giant koalas (Phascolarctidae) from the late Cainozoic of Australia. *Proceedings of the Linnean Society of New South Wales* 117: 3–15.

Archer, M., Hand, S.J., Godthelp, H., and Creaser, P. 1997b. Correlation of the Cainozoic sediments of the Riversleigh World Heritage Fossil Property, Queensland, Australia. Pp. 131–152 in: Aguilar, J-P., Legendre, S., and Michaux, J. (eds), *Actes du Congres BiocroM'97. Memoirs et Traveaux Ecole Pratique des Hautes Etudes*. Institut de Montpellier: Montpellier.

Archer, M., Arena, D.A., Bassarova, M., Beck, R.M.D., Black, K., Boles, W.E., Brewer, P., Cooke, B.N., Crosby, K., Gillespie, A., Godthelp, H., Hand, S.J., Kear, B.P., Louys, J., Morrell, A., Muirhead, J., Roberts, K.K., Scanlon, J.D., Travouillon, K.J., and Wroe, S. 2006. Current status of species-level representation in faunas from selected fossil localities in the Riversleigh World Heritage Area, northwestern Queensland. *Alcheringa: An Australasian Journal of Palaeontology* 30:1–17.

Arena, D.A. 2005. *The geological history and development of the terrain at the Riversleigh World Heritage Area during the middle Tertiary*. Unpublished Ph. D. Thesis, University of New South Wales, Sydney. 275 pp.

Arena, D.A., Black, K.H., Archer, M., Hand, S.J., Godthelp, H., and Creaser, P. 2014. Reconstructing a Miocene pitfall trap: recognition and interpretation of fossiliferous Cenozoic palaeokarst, *Sedimentary Geology* doi: 10.1016/j.sedgeo.2014.01.005.

Arena, D.A., Travouillon, K.J., Beck, R.M.D., Black, K.H., Gillespie, A.K., Myers, T.J., Archer, M., and Hand, S.J. (2016). Mammalian lineages and the biostratigraphy and biochronology of Cenozoic faunas from the Riversleigh World Heritage Area, Australia. *Lethaia* 49:43–60.

Billups, K., and Scheiderich, K. 2010. A synthesis of Late Oligocene through Miocene deep sea temperatures as inferred from foraminiferal Mg/Ca ratios. *International Association of Sedimentologists Special Publication* 42: 1–16.

Black, K. 1992. *Systematics and palaeobiology of fossil phascolarctids from Riversleigh*. Unpublished Honours thesis, University of New South Wales, Sydney. 63 pp.

Black, K., and Archer, M. 1997. *Nimiokoala* gen. nov. (Marsupialia, Phascolarctidae) from Riversleigh, northwestern Queensland, with a revision of *Litokoala*. *Memoirs of the Queensland Museum* 41: 209–228.

Black, K.H., Archer, M., and Hand, S.J. 2012a. New Tertiary koala (Marsupialia, Phascolarctidae) from Riversleigh, Australia, with a revision of phascolarctid phylogenetics, paleoecology, and paleobiodiversity. *Journal of Vertebrate Paleontology* 32: 125–138.

Black, K.H., Archer, M., Hand, S.J., and Godthelp, H. 2012b. The rise of Australian marsupials: a synopsis of biostratigraphic, phylogenetic, palaeoecological and palaeobiogeographic understanding. Pp. 983–1078 in: Talent, J.A. (ed), *Earth and Life: Global Biodiversity, Extinction Intervals and Biogeographic Perturbations through Time*. Springer Verlag, Dordrecht.

Black, K.H., Camens, A.B., Archer, M., and Hand, S.J. 2012c. Herds overhead: *Nimbadon lavarackorum* (Diprotodontidae), Heavyweight marsupial herbivores in the Miocene forests of Australia. *PLoS ONE* 7, e48213. doi:10.1371/journal.pone.0048213.

Black, K.H., Archer, M., Hand, S.J., and Godthelp, H. 2013. Revision in the marsupial diprotodontid genus *Neohelos*: systematics and biostratigraphy. *Acta Palaeontologica Polonica* 58: 679–706.

Black, K.H., Louys, J., and Price, G.J. 2014a. Understanding morphologic and morphometric variation in the extant koala as a framework for identification of species boundaries in extinct koalas (Phascolarctidae; Marsupialia). *Journal of Systematic Palaeontology* 12: 237–264.

Black, K.H., Price, G.J., Archer, M., and Hand, S.J. 2014b. Bearing up well? Understanding the past, present and future of Australia's koalas. *Gondwana Research* 25: 1186–1201.

Brammall, J. and Archer, M. 1997. A new Oligocene-Miocene species of *Burramys* (Marsupialia, Burramyidae) from Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41: 247–268.

Clemens, W.A. and Plane, M. 1974. Mid-Tertiary Thylacoleonidae (Marsupialia, Mammalia). *Journal of Paleontology* 48: 652–660.

Cooke, B.N. 1999. *Wanburoo hilarus* gen. et sp. nov., a lophodont bulungamayine kangaroo (Marsupialia: Macropodoidea: Bulungamayinae) from the Miocene deposits of Riversleigh, northwestern Queensland. *Records of the Western Australian Museum* Supplement 57: 239–253.

Creaser, P. 1997. Oligocene-Miocene sediments of Riversleigh: the potential significance of topography. *Memoirs of the Queensland Museum* 41: 303–314.

Gillespie, A., Archer, M., Hand, S.J., Black, K.H. 2014. New material referable to *Wakaleo* (Marsupialia: Thylacoleonidae) from the Riversleigh World Heritage Area, northwestern Queensland: revising species boundaries and distributions in Oligo/Miocene marsupial lions. *Alcheringa: An Australasian Journal of Palaeontology* 38: 513–527.

Illiger, C., 1811. *Prodromus systematis mammalium et avium additis terminis zoographicis utriudque classis. C.* Salfeld: Berlin.

Lanyon, J.M., Sanson, G.D. 1986. Koala (*Phascolarctos cinereus*) dentition and nutrition. I. Morphology and occlusion of cheekteeth. *Journal of Zoology* 209: 155–168.

Louys, J., Black, K., Archer, M., Hand, S.J., and Godthelp, H. 2007. Descriptions of koala fossils from the Miocene of Riversleigh, northwestern Queensland and implications for *Litokoala* (Marsupialia, Phascolarctidae). *Alcheringa: An Australasian Journal of Palaeontology* 31: 99–110.

Louys, J., Aplin, K., Beck, R.M.D., and Archer, M. 2009. Cranial anatomy of Oligo-Miocene koalas (Diprotodontia: Phascolarctidae): stages in the evolution of an extreme leaf-eating specialization. *Journal of Vertebrate Paleontology* 29: 981–992.

Martin, H.A. 2006. Cenozoic climatic change and the development of the arid vegetation in Australia. *Journal of Arid Environments* 66: 533–63.

Megirian, D. 1992. Interpretation of the Miocene Carl Creek Limestone, northwestern Queensland. *The Beagle: Records of the Museums and Art Galleries of the Northern Territory* 9: 219–248.

Murray, P., Megirian, D., Rich, T., Plane, M., and Vickers-Rich, P. 2000. *Neohelos stirtoni*, a new species of Zygomaturinae (Diprotodontidae: Marsupialia) from the mid-Tertiary of northern Australia. *Memoirs of the Queen Victoria Museum* 105: 1–47.

Owen, R. 1839. Outlines of a classification of the Marsupialia. *Proceedings of the Zoological Society of London* 7: 5–19.

Owen, R. 1866. *On the Anatomy of Vertebrates*. Longmans Green: London.

Pledge, N.S. 1992. The Curramulka local fauna: a new late Tertiary fossil assemblage from Yorke Peninsula, South Australia. *Beagle: Records of the Museums and Art Galleries of the Northern Territory* 9: 115–142.

Shevenell, A.E., Kennett, J.P., and Lea, D.W. 2004. Middle Miocene southern ocean cooling and Antarctic cryosphere expansion. *Science* 305: 1766–1770.

Springer, M.S. 1987. Lower molars of *Litokoala* (Marsupialia: Phascolarctidae) and their bearing on phascolarctid evolution. Pp. 319–325 in: Archer, M. (ed), *Possums and Opossums: Studies in Evolution*. Surrey Beatty and Sons Pty Ltd, Chipping Norton.

Stirton, R.A. 1957. A new koala from the Pliocene Palankarinna fauna of South Australia. *Records of the South Australian Museum* 13: 71–87.

Stirton, R. 1967. A diprotodontid from the Miocene Kutjamarpu Fauna, South Australia. *Bureau of Mineral Resources, Geology and Geophysics Bulletin* 85: 45–51.

Stirton, R.A., Tedford, R.H., and Woodburne, M.O. 1967. A new Tertiary formation and fauna from the Tirari Desert, South Australia. *Records of the South Australian Museum* 15: 427–462.

Strahan, R. 2004. *The Mammals of Australia*. New Holland Publishers, Sydney.

Travouillon, K.J., Archer, M., Hand, S.J., and Godthelp, H. 2006. Multivariate analyses of Cenozoic mammalian faunas from Riversleigh, northwestern Queensland. *Alcheringa: An Australasian Journal of Palaeontology* 30: 323–349.

Travouillon, K.J., Legendre, S., Archer, M., and Hand, S.J. 2009. Palaeoecological analyses of Riversleigh's Oligo-Miocene sites: Implications for Oligo-Miocene climate change in Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 276: 24–37.

Travouillon, K.J., Escarguel, G., Legendre, S., Archer, M., Hand, S.J., 2011. The use of MSR (Minimum Sample Richness) for sample assemblage comparisons. *Paleobiology* 37: 696–709.

Travouillon, K.J., Archer, M., and Hand, S.J. 2012. Early to middle Miocene monsoon climate in Australia: COMMENT. *Geology* 40: e273.69.

Woodburne, M.O. 1984. Families of marsupials: relationships, evolution and biogeography. Pp. 48–71 in: Broadhead, T.W. (ed), *Mammals: Notes for a Short Course*. University of Tennessee Department of Geological Sciences, Studies in Geology: Tennessee.

Woodburne, M., Tedford, R., Archer, M., and Pledge, N. 1987. *Madakoala*, a new genus and two species of Miocene koalas (Marsupialia: Phascolarctidae) from South Australia and a new species of *Perikoala*. Pp. 293–317 in: Archer, M. (ed), *Possums and Opossums: Studies in Evolution*. Surrey Beatty and Sons Pty Ltd, Chipping Norton.

Woodhead, J., Hand, S.J., Archer, M., Graham, I., Sniderman, K., Arena, D.A., Black, K.H., Godthelp, H., Creaser, P., and Price, L. 2016. Developing a radiometrically-dated chronologic sequence for Neogene biotic change in Australia, from the Riversleigh World Heritage Area of Queensland. *Gondwana Research* 29:153–167.

Wroe, S. 1999. The geologically oldest dasyurid (Marsupialia), from the Miocene of Riversleigh, northwestern Queensland. *Palaeontology* 42: 1–27.

Young, W.G. and Robson, S.K. 1987. Jaw movements from microwear on the molar teeth of *Phascolarctos cinereus*. *Journal of Zoology* 213: 51–61.