Understanding morphological variation in the extant koala as a framework for identification of species boundaries in extinct koalas (Phascolarctidae; Marsupialia)

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Understanding morphological variation in the extant koala as a framework for identification of species boundaries in extinct koalas (Phascolarctidae; Marsupialia)

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We document morphological variation (both geographical and sexual) in the dentition of the extant koala, Phascolarctos cinereus, in order to facilitate discrimination of species boundaries in extinct phascolarctids. Considerable variation is evident in dental structures previously used to diagnose several phascolarctid fossil species. Consistent patterns of morphological variation are not evident between sexes or geographic regions, with variation as great between samples as within them. Metric variation is evident between the sexes in upper molar dimensions with Victorian (southern) males significantly larger than Victorian females, although this is not reflected in lower molar dimensions or in the Queensland (northern) sample. Male koalas from southern populations generally display significantly larger molars than their northern counterparts; however this trend is not evident in female upper molar dimensions. In both males and females, some, but not all, lower molar dimensions are larger in southern populations than northern. In light of these results, a systematic revision of species of Litokoala suggests L. ‘dicktfordi’ is a junior synonym of L. kutjamarpensis, and the poorly known L. thurmerae is regarded to be a nomen dubium. Further, we describe a partial cranium of a new species of koala from Early Miocene sediments in the Riversleigh World Heritage Area, northern Australia. Litokoala dicksmithi sp. nov. is the fifth koala species recorded from the diverse rainforest assemblages of Riversleigh and the third species referred to the Oligo-Miocene genus Litokoala. Aspects of cranial morphology, including a shortened robust rostrum and broad, irregular nasal aperture, confirm placement of Litokoala as sister taxon to the modern genus Phascolarctos. Relatively large orbits and small body size suggest the possibility that L. dicksmithi was nocturnal, had enhanced visual acuity, and was a more agile arboreal species than the relatively sedentary extant koala.


Keywords: intraspecific variation; morphometric; Phascolarctomorphia; rainforest; Miocene; Riversleigh

Introduction

Accurately assessing the number of species in the fossil record is fundamental to understanding evolutionary histories, past biodiversity, and responses of species and palaeocommunities to environmental change. However, determining species boundaries in fossil taxa may be a challenge for palaeontologists who are often confronted by limited fossil samples, poor preservation and the absence of modern analogues. Conspicuous morphological variability within a species may result from geographical effects (with concomitant environmental or climatic influences), biological factors (e.g. sexual dimorphism and ontogeny) or a combination of both (Albrecht et al. 2003). Understanding the nature of such variation within modern analogues is important to assessing the validity of morphological features used in species determinations of extinct groups. Surprisingly, despite the need for such data, there are few comprehensive published accounts of intraspecific variation in either extant or extinct marsupials.

Among extant marsupials, analyses of both qualitative and quantitative dental variation have been investigated in species of Perameles (Peramelidae; e.g. Freedman 1967; Freedman & Joffe 1967a, b), Macropus (Macropodidae; e.g. Bartholomai 1971; Easton 2006), and the Patagonian opossum Lestodelphys halli (Didelphidae; e.g. Martin 2005). Studies of variation in fossil marsupials are few owing to the relative paucity of fossil samples from single localities. Archer & Dawson (1982) analysed a moderate sample (n = 55) of marsupial lion cranial and dental remains referable to the genus Thylacoleo, from Pleistocene deposits of Wellington Caves (NSW). Prideaux (2004) undertook an analysis of craniodental morphological variation among sphenurines as part of a taxonomic review of the macropodid subfamily. Recently, several benchmark studies (e.g. Murray et al. 2000a, b; Price 2008a; Black & Hand 2010; Price & Sobbe

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2011) of diprotodontids (Marsupialia: Diprotodontidae), a relatively abundant and widespread group of Australasian marsupial herbivores, have significantly improved understanding of the expected level of variation within a fossil population.

The diprotodontian infraorder Phascolarctomorphia contains a single living species, the koala *Phascolarctos cinereus* (Goldfuss, 1817), a unique yet iconic representative of Australia’s marsupial fauna. Although the koala family (Phascolarctidae) was once evidently more diverse with seven genera and at least 17 species currently recognized, most taxa are known from scant dental remains. Inevitably, this has presented difficulties for species identification and taxonomic assignment. In particular, the Oligo-Miocene genus *Litokoala*, sister taxon to *Phascolarctos*, has had a controversial (see Louys *et al.* 2007; Pledge 2010), albeit relatively short, taxonomic history. Prior to recent discoveries of partial crania preserving complete tooth rows (e.g. Louys *et al.* 2007; this paper) from the Riversleigh World Heritage Area, north-western Queensland (Fig. 1), the genus was known from a few isolated teeth (see Stirton *et al.* 1967; Springer 1987).

Assessment of species boundaries and intraspecific variation in previous systematic studies of koalas by Black & Archer (1997), Louys *et al.* (2007) and Price (2008b) have been based on unpublished qualitative accounts of variation in *P. cinereus* dentitions by the authors (e.g. unpublished thesis of Black 1992). Bartholomai (1968) documented metric variation in P3–M2 dimensions for a sample of modern Queensland *Phascolarctos cinereus* specimens but restricted discussion of morphological variation to a few aspects of P3. Here we present both qualitative and quantitative assessments of variation in the upper and lower dentitions of *P. cinereus*. We then revisit the taxonomy of *Litokoala*, and describe a new rainforest species from the Riversleigh World Heritage Area, north-western Queensland, Australia.

**Material and methods**

For our qualitative and quantitative analyses of *P. cinereus* we focus on the dental series, specifically upper and lower premolars and molars, rather than other cranial or postcranial characters. The reasons for this are four-fold: (1) for
consistency across other taxonomic studies that focus on cheek teeth; (2) teeth are relatively common elements in the fossil record with most fossil marsupials having been described on the basis of dentitions; (3) teeth are systematically and taxonomically important elements; and (4) all fossil koala species that have been described to date have been based largely on dental characteristics with some known only from isolated teeth.

Modern koala specimens examined were derived from collections of the Queensland Museum (Brisbane), Australian Museum (Sydney), University of New South Wales (Sydney) and Museum Victoria (Melbourne). Fossil material described here is registered in the fossil collection of the Queensland Museum. Reference to Litokoala kutijamarbensis throughout the text is sensu Louys et al. (2007) unless stated otherwise. Higher-level systematic nomenclature follows Aplin & Archer (1987). Molar morphology follows Archer (1978) with revisions by Tedford & Woodburne (1987); such that the metacone is considered homologous to the older term ‘hypocone’, and the cusp between the metacone and ‘true’ metaconule is deemed the ‘neometacunule’). Cheek tooth homology follows Luckett (1993). Biostratigraphic nomenclature follows Travouillon et al. (2006), Woodburne et al. (1993) and Creaser (1997).

Qualitative analysis
A sample of 109 skulls from 55 localities in New South Wales, Victoria and Queensland (Fig. 1) was used to investigate qualitative morphological variation in the dentition of modern Phascolarctos cinereus (see Online Supplementary Material). Ten of these skulls were from unknown localities but were included in the analysis because of their clean, relatively unworn dentitions. Only cheek teeth were examined and both sexes were represented in the sample. It is recognized that P. cinereus exhibits marked sexual dimorphism with males being significantly larger than females (Martin et al. 2008). However, it is unclear whether sexually related differences are exhibited within dental morphology. Thus, an initial assessment of morphological variation in each sex was made to determine whether any morphologies or patterns might be gender specific. Similarly, in order to assess whether morphologies or patterns of morphological variation were evident within and/or between geographical regions, variation in specimens from New South Wales, Victoria and Queensland populations was assessed independently. An example of Phascolarctos cinereus upper and lower dentitions and the dental nomenclature used in this analysis is provided in Figure 2. A representative sample of morphologies for each tooth position is illustrated in Figures 3–12. Figured specimens were selected on the basis of least wear.

Quantitative analyses
Phascolarctos cinereus also exhibits distinctly different body sizes throughout its modern geographical range. For instance, adult individuals within southern, higher latitude populations (e.g. Victoria) typically range in body size from 8.5 to 12 kg. In contrast, individuals from northern, lower latitudes (e.g. Queensland) are significantly smaller, weighing on average from 5.1 to 6.5 kg (Martin et al. 2008). Thus, P. cinereus body size appears to represent a latitudinal morphocline reflecting Bergmann’s rule (e.g. Meiri & Dayan 2003). However, it has never been demonstrated that such latitudinal differences are also reflected in dental morphometrics. Thus, using teeth as a surrogate for body size (following Gould 1975; Myers 2001), we test the following hypotheses: (1) that no significant difference in premolar and molar dimensions exist between koalas from southern (Victorian) and northern (Queensland) populations; and (2) that no significant difference in premolar and molar dimensions exist between male and female individuals from the same geographical region. We test these hypotheses independently for upper and lower dentitions. Understanding such size variation in the modern koala is critical for establishing the significance of morphometric differences between fossil species.

In order to test the hypotheses, we took a series of dental measurements from museum specimens originally sourced from Queensland and Victorian populations. Linear measurements were made for premolars and molars of adult individuals using Mitutoyo digital callipers and included: maximum length, anterior width (maximum width across anterior root) and posterior width (maximum width across posterior root) for premolars, and maximum length, anterior width (maximum width across trigon/trigonid) and posterior width (maximum width across talon/talonid) for molars. This approach is consistent with numerous other morphometric dental studies of not only koalas (e.g. Bartholomai 1968; Price 2008b; Price et al. 2009; Pledge 2010), but marsupials in general (e.g. Freedman 1967; Freedman & Joffe 1967a, b, Bartholomai 1971; Price 2002, 2005, 2008a; Easton 2006; Black & Hand 2010), and allows for direct comparison of results between respective investigations. Both upper (n = 49) and lower (n = 70) dentitions were measured. Analyses were performed using PAST (version 1.51; Hammer et al. 2006) computer software. Univariate statistics for dental measurements are provided in Online Supplementary Material Appendix 1. Multivariate analysis of variance (MANOVA) was used to assess any differences indicated by whole tooth rows, as well as individual teeth. This method enables simultaneous comparisons of all three measurements and, in the case of tooth rows, more than one tooth position at a time. Differences were considered to be significant at the 95% confidence interval. Where significant differences were found in the morphometrics of a particular tooth position, the measurements of that tooth were compared between groups using t-tests. Only significant differences are reported (Tables 1–3).
Figure 2. Occlusal view of *Phascolarctos cinereus* upper (A, B) and lower (C, D) dentitions. A, AR8398, left upper tooth row; B, line drawing of AR8398 indicating major features of the upper tooth row (except crenulations); C, AR6508, left lower tooth row; D, line drawing of AR6508 indicating major features of the lower tooth row (except crenulations). Abbreviations: a, anterior; alf, anterolingual fossa; almcl, anterolingual buttress of metaconule; alpr, anterolingual buttress of protocone; b, buccal; co, cristid obliqua; cstd, columnar stylid; end, entoconid; er, entostylid ridge; estd, entostylid; hyd, hypoconid; lc, lingual cingulum; lcr, lingual cingular ridge; locr, longitudinal crest; lsed, lingual shelf of entoconid; lsmd, lingual shelf of metaconid; mbb, metacone buccal basin; mcl, metaconule; me, metacone; med, metaconid; mestd, metastylid; nmcl, neometacune; pa, paracone; pas, parastyle; pbb, paracone buccal basin; pbc, posterobuccal crest of P3; pbr, posterobuccal ridge of P3; pcl, paraconule; plpc, posterolingual paracrista; poend, postentocristid; pohyd, posthypocristid; pomcl, postmetaconulecrista; pomec, postmetacrista; pomd, postmetacristid; prd, protocristid; prprd, postprotocristid; prprstd, protostylid cristid; prstd, protostylid; StB, stylar cusp B; StC, stylar cusp C; StD, stylar cusp D; StE, stylar cusp E; tv, transverse valley.
Identification of species boundaries in extinct koalas

Table 1. Results of t-tests for differences in upper tooth dimensions of male and female *P. cinereus* between geographical regions. Letters in brackets indicate which population has on average the larger mean. Abbreviations: AW, anterior width; L, length; n.s., not significant; PW, posterior width; Q, Queensland population; V, Victorian population.

<table>
<thead>
<tr>
<th>Tooth</th>
<th>L</th>
<th>AW</th>
<th>PW</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P3</td>
<td></td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>M1</td>
<td></td>
<td>p = 0.006 (V)</td>
<td>n.s.</td>
</tr>
<tr>
<td>M2</td>
<td></td>
<td>p = 0.007 (V)</td>
<td>p = 0.002 (V)</td>
</tr>
<tr>
<td>M3</td>
<td></td>
<td>p = 0.004 (V)</td>
<td>p = 0.001 (V)</td>
</tr>
<tr>
<td>M4</td>
<td></td>
<td>p &lt; 0.001 (V)</td>
<td>n.s.</td>
</tr>
<tr>
<td>Female</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P3</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>M1</td>
<td>n.s.</td>
<td>n.s.</td>
<td>p &lt; 0.001 (M)</td>
</tr>
<tr>
<td>M2</td>
<td>n.s.</td>
<td>p &lt; 0.001 (M)</td>
<td>p &lt; 0.001 (M)</td>
</tr>
<tr>
<td>M3</td>
<td>n.s.</td>
<td>p = 0.021 (M)</td>
<td>p = 0.003 (M)</td>
</tr>
<tr>
<td>M4</td>
<td>n.s.</td>
<td>p = 0.003 (M)</td>
<td>p &lt; 0.001 (M)</td>
</tr>
</tbody>
</table>

Table 2. Results of t-tests for differences in upper tooth measurements between males and females of Victorian *P. cinereus*. Letters in brackets indicate which sex has on average the larger mean. Abbreviations: AW, anterior width; F, female; L, length; M, male; n.s., not significant; PW, posterior width.

<table>
<thead>
<tr>
<th>Tooth</th>
<th>L</th>
<th>AW</th>
<th>PW</th>
</tr>
</thead>
<tbody>
<tr>
<td>P3</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>M1</td>
<td></td>
<td>p = 0.003 (M)</td>
<td>p &gt; 0.001 (M)</td>
</tr>
<tr>
<td>M2</td>
<td></td>
<td>p = 0.018 (M)</td>
<td>p &lt; 0.001 (M)</td>
</tr>
<tr>
<td>M3</td>
<td></td>
<td>p = 0.021 (M)</td>
<td>p = 0.003 (M)</td>
</tr>
<tr>
<td>M4</td>
<td></td>
<td>p = 0.003 (M)</td>
<td>p &lt; 0.001 (M)</td>
</tr>
</tbody>
</table>

Table 3. Results of t-tests for differences in lower tooth dimensions of male and female *P. cinereus* between geographical regions. Letters in brackets indicate which population has on average the larger mean. Abbreviations: AW, anterior width; L, length; n.s., not significant; PW, posterior width; V, Victorian population.

<table>
<thead>
<tr>
<th>Tooth</th>
<th>L</th>
<th>AW</th>
<th>PW</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P3</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>M1</td>
<td>n.s.</td>
<td>p &lt; 0.001 (V)</td>
<td>p = 0.02 (V)</td>
</tr>
<tr>
<td>M2</td>
<td>n.s.</td>
<td>p = 0.045 (V)</td>
<td>n.s.</td>
</tr>
<tr>
<td>M3</td>
<td>p &lt; 0.001 (V)</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>M4</td>
<td>p &lt; 0.001 (V)</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>Female</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P3</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>M1</td>
<td>n.s.</td>
<td>p &lt; 0.001 (V)</td>
<td>p = 0.02 (V)</td>
</tr>
<tr>
<td>M2</td>
<td>n.s.</td>
<td>p = 0.049 (V)</td>
<td>n.s.</td>
</tr>
<tr>
<td>M3</td>
<td>p &lt; 0.001 (V)</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>M4</td>
<td>p &lt; 0.001 (V)</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
</tbody>
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Institutional abbreviations

Morphological and morphometric variation in *Phascolarctos cinereus*

Description and morphological variation
Aspects of the dental morphology of *Phascolarctos cinereus* have been described by Stirton (1957), Archer (1978) and Lanyon & Sanson (1986). Cheek tooth morphology is redescribed here using current dental terminology (Fig. 2B) and including a discussion of intraspecific variation.

P3. Subovate tooth that is wider posteriorly than anteriorly (Fig. 3A–F). In juvenile unworn specimens (e.g. QM J13278) three distinct apices are positioned anteriorly, medially and posteriorly along a mildly buccally convex longitudinal crest. A posterobuccal ridge is generally associated with the posteriormost cusp (Figs 2B, 3F). Anteriorly, the longitudinal crest bifurcates into short spurs (buccal and
lingual) that fade into the base of the tooth crown (Fig. 3C).

A well-developed, variably cuspate lingual cingular ridge (Figs 2A, B, 3A) meets the longitudinal crest at the posterior tooth margin, forming a trench between them.

Variable features of P3 include: tooth shape; the degree of surface enamel crenulations; the development of lingual and buccal ridges from the longitudinal crest; the extent of bifurcation, both anteriorly and posteriorly, of the longitudinal crest; the degree of inflection of the longitudinal crest; the presence of a posterobuccal cuspule at the base of the crown (Fig. 3A, D); and the degree to which the lingual cingulum extends anteriorly. In Figure 3F, for example, the lingual cingulum is continuous anteriorly with a lingual crest from the longitudinal crest. A unique pocket is formed between these structures and the well-developed lingual crest which extends from the anterior apex of the longitudinal crest. A similar pocket can be formed at the posterolingual (Fig. 3B) or posterobuccal tooth corners (Fig. 3F).

**Figure 4.** Comparison of the left M1 of six individuals of *P. cinereus*. A, QM J13278 (right M1 mirrored); B, AM M5266; C, AR20842; D, AM M7356; E, AM M2185 (right M1 mirrored); F, AR2626. Abbreviations: a, anterior; alf, anterolingual fossa; b, buccal; mcl, metaconule; me, metacone; nmcl, neometaconule; pa, paracone; pas, parastyle; pcl, paraconule; pr, protocone.

M1–4. Molars selenodont; trapezoidal in occlusal view with anterior tooth moiety wider than posterior moiety (Fig. 2A, B). Variation is evident in overall tooth outline, in particular the degree of convexity of the buccal tooth margin of M1–4 (Figs 4–7) and anterior extension of the parastylar corner (M1 only; Fig. 4A–F). Four main pyramidal cusps: anterobuccal paracone, posterobuccal metacone, anterolingual protocone and posterolingual metaconule. Metacone tallest cusp, followed by subequal paracone and metaconule, then protocone. Protocone apex slightly lingually displaced with respect to metaconule apex but may be directly anteriorly opposite in some specimens.

Buccal selene comprised of prominent pre- and postcristae that descend anterobuccally and posterobuc-

**Figure 5.** Comparison of the left M2 of six individuals of *P. cinereus*. A, AM M6806; B, AR8398; C, AM M4841 (right M2 mirrored); D, QM J13278; E, AM M7486; F, AM M12475. Abbreviations: a, anterior; b, buccal; mcl, metaconule; me, metacone; nmcl, neometaconule; pa, paracone; pcl, paraconule; pr, protocone; prst, protostyle.
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Figure 6. Comparison of the left M\textsuperscript{3} of six individuals of *P. cinereus*. A, AM M7356; B, AM M7364; C, AM M12475; D, QM J13278; E, AM M5743; F, AM M7486. Abbreviations: a, anterior; b, buccal; mcl, metaconule; me, metacone; nmcl, neometacolum; pa, paracone; pcl, paraconule; pr, protocone; prst, protostyle.

Figure 7. Comparison of the left M\textsuperscript{4} of six individuals of *P. cinereus*. A, AR1574; B, AM S415; C, AM M5743; D, AM M12475; E, AM M7356; F, AM M7364. Abbreviations: a, anterior; b, buccal; mcl, metaconule; me, metacone; pa, paracone; pr, protocone.

metacone towards the buccal tooth margin (Fig. 2A, B). Resultant buccal surfaces of the paracone and metacone are triangular in occlusal outline. Preparacrista, postparacrista, premetaconule and postmetaconule bifurcate at buccal margin into short anterior and posterior spurs which define stylar cusps B, C, D and E, respectively. The buccal basins of the paracone and metacone are variably open or closed depending on the development of the stylar border and vary greatly in depth. Generally, the metacone buccal basin is open on M\textsuperscript{3-4}. Varying development of stylar cusps consequently affects the degree of concavity of the buccal margin. In some specimens (e.g. AM M7356, AM M 7438, AM M12475, AR2626, QM J19170, P481) supernumerary cusuples (i.e. in addition to stylar cusps A–E) are present on the stylar border of the paracone and metacone and are most noticeable on M\textsuperscript{1-2} (Fig. 4D, F).

On M\textsuperscript{1}, an additional stylar cusp, the parastyle (stylar cusp A), exists as an enlarged, crenulated swelling of the anterobuccal cingulum (Fig. 2A, B). The breadth, degree of crenulation and degree to which the parastyle projects anteriorly are highly variable (contrast Fig. 4A with Fig. 4F). It is sometimes connected to the paraconule (Fig. 4A). In AM M7364 an anterobuccal pocket is formed between the bases of the parastyle, paraconule, preparacrista and anterolingual paracrista.

A posterolingual paracrista is present in all specimens studied, the base of which is variably crenulated. It either terminates at the posterolingual base of the paracone (Fig. 4D) or extends further into the transverse median valley to intersect the buccal spurs from the junction of the postprotocrista and the premetaconulecrista. The latter condition is most apparent in M\textsuperscript{3-4} (Figs 6, 7). A buccal spur off the posterolingual paracrista is variably present and appears to form part of the transversely orientated crenulation pattern found in the transverse valley of some upper molars (Fig. 5A).

The anterolingual paracrista (Figs 4C, 5A), anterolingual metacrista (Figs 6E, 7C, D) and posterolingual metacrista (Fig. 4B) are variably present. When present, these crests may be well developed, extending from the apex of the
The lingual cingulum, which blocks the lingual exit of the transverse valley, is present on M1–3 (Figs 4D, 5E) and metaconule (Figs 5F, 6A, 7C). A well-developed anterolingual buttress of the metaconule (Fig. 4B, F) is variably developed, as are buccal ribs from the apices of the protocone (Figs 4D, 5E) and metaconule (Figs 5F, 6A). A well-developed anterolingual buttress of the metaconule towards the longitudinal tooth valley (Fig. 2A, B). It is generally linear (although bifurcate in some individuals) and, in the more posterior molars, may be poorly distinguishable. The degree to which the neometacuneal extends posteriorly along the longitudinal valley between the metacone and metaconule varies between individuals, as does its anterobuccal extension along the transverse valley. The neometacuneal variably connects to the buccal spurs that extend from the junction of the postprotocrista and premetaconulecrista (Fig. 5A, E).

The protostyle is a short ridge that originates from the preprotocrista at a point just lingual to the longitudinal valley (Fig. 2A, B). It is generally linear (although bifurcate in some individuals) and varies in its extension posteriorly. In general it extends further posteriorly in more posterior molars. In some specimens (e.g. QM J13278) it is indistinguishable from the molar crenulation pattern (Figs 4A, 5D).

A small pocket is formed between the anterior cingulum and an anterior crest from the preparacrista at the anterobuccal corner of M4 of one individual studied (AM M12475, Fig. 7D). The anterior crest of the preparacrista is not evident in any other tooth studied.

Similarly, the left and right M3 of one individual studied (AM M7364, Fig. 7F) are unique in that these teeth are reduced (or malformed) to such an extent that they exist as small rounded structures consisting of a rounded basin bordered by a continuous cingulum on which only the apex of the presumed metacone is evident. Similar abnormal variations have been noted in kangaroos (Archer 1975).

P3. Subovate tooth, wider posteriorly, tapering anteriorly (Fig. 2C, D). Tooth shape varies from elongate and narrow in some individuals (Fig. 8F), to shorter and bulbous in others (Fig. 8E). The buccal and lingual demarcation between the anterior and posterior moieties also varies between individuals, as does the lingual curvature of the tooth with respect to the molar row. There are three main cusps positioned anteriorly, medially and posteriorly along a longitudinal crest which varies in its degree of lingual...
Figure 8. Comparison of the left $P_3$ of six individuals of *P. cinereus*. A, AM M7356; B, AM M7364; C, QM J13278; D, AM M2185; E, AM M7486; F, AM M12475. Abbreviations: a, anterior; l, lingual; locr, longitudinal crest; pbc, posteroconid crest.

deflection. The extent to which the longitudinal crest curves around the lingual tooth margin, both anteriorly and posteriorly, is variable (Fig. 8C, E). Buccal ribs from the apices of the cusps on the longitudinal crest (Fig. 8F) are variably present. A well-developed, variably cuspate, crescentic crest occupies the posteroconid corner of the tooth, the nature of which is not constant between individuals. In general, it extends posteroconidally from the medial cusp apex (Fig. 8B), but it can exist as an isolated crest at the posteroconid tooth corner (Fig. 8C). In some individuals it terminates prior to meeting the posterior tooth margin, resulting in a posteriorly open crescentic trench basal to the longitudinal crest (Fig. 8B). In other individuals the posteroconid crest is highly crescentic and curves towards (and may meet) the posterior apex of the longitudinal crest, resulting in a posteroconid pocket (Fig. 8A, D, E). An additional cuspule occupies this pocket in Figure 8F. The height of the posteroconid crest varies also from sitting relatively high on the crown in some individuals (e.g. AM M7486), to relatively lower in others (e.g. AM M7486, Fig. 8E).

M1. Morphology of M1 differs to that of M2–4 in its construction of the trigonid which is comprised of three major cuspsids: metaconid, protoconid and protostylid (Fig. 2C, D). The protoconid occupies a more lingual position than on M2–4 with its apex just buccal to that of the anterolingually positioned metaconid to which it is connected by a short transverse crest. The main anterobuccal cusp is a large protostylid. An arcuate preprotostylid cristid extends anterolingually to meet a linear anteriorly directed preprotocristid at the anterior tooth margin. A slight swelling

Figure 9. Comparison of the left M1 of six individuals of *P. cinereus*. A, AM M7486; B, AR1574; C, QM J13278; D, AM M12475; E, AM M7356; F, AM M7364. Abbreviations: a, anterior; end, entoconid; er, entostylid ridge; hyd, hypoconid; l, lingual; med, metaconid; prd, protoconid; pstd, protostylid.

at this point may represent a weak paraconid. The linear postprotostylid cristid descends posteriorly into the median transverse valley, becoming crenulate at its posterior base (Fig. 9D). Generally it bifurcates into lingual and posterior arms, but the extent to which these arms extend lingually and posteriorly, respectively, varies. In Figure 9B, E and F the lingual arm terminates basal to the postprotocristid, whereas it is only weakly developed in Figures 9A and D. The posterior arm either terminates in the transverse valley between the opposing bases of the protostylid and hypoconid (Fig. 9E), or transgresses this valley and meets the anterior base of the hypoconid, consequently blocking the buccal exit of the transverse valley (Fig. 9A). Additionally, the posterior arm of the postprotostylid cristid meets a (variably present) anterobuccal spur from the cristid obliqua, blocking the buccal exit of the transverse valley slightly lingual to the buccal margin (Fig. 9C, D).

The postprotocristid of M1 extends posteriorly (sometimes posteroconidally) into the transverse median valley where it generally meets an elongate anterolingually directed prehypocristid (cristid obliqua) (Fig. 9A, C–F). In some specimens (e.g. AM M7438, AR1574) the postprotocristid terminates before meeting the prehypocristid, the latter extending further lingually and connecting to the
pre-entocristid (Fig. 9B) or terminating basal to the postmetacristid (e.g. AM M7438).

There does not appear to be a premetacristid on M1, although in some specimens a small columnar stylid at the lingual base of the metaconid possesses a short anterior spur (Fig. 9C, E). It is possible that the transverse crest linking the apices of the metaconid and protoconid on M1 may represent a premetacristid. A well-developed columnar stylid is present on the lingual face of the entoconid, giving this cusp the appearance of having a twinned apex (Fig. 9E, F). On M1–4 the postmetacristid extends posterolingually from the metaconid apex and may bifurcate just prior to the lingual tooth margin into short anterolingual and posterolingual spurs (Fig. 10D, F). These spurs (the premetastylid cristid and postmetastylid cristid) define the apex of the metastylid (Fig. 2C, D). The pre-entocristid varies from a linear (Fig. 9A) to highly arcuate crest (Fig. 9D), and is generally continuous with the postmetastylid cristid at the median lingual tooth margin. This feature is often referred to as the metastylid fold (see Black & Archer 1997). In some specimens (e.g. AR1574), however, the pre-entocristid connects to the posterior base of the postmetacristid (Fig. 9B). A similar bifurcation of the postentocristid at the posterobuccal tooth corner into a weak buccal preentostylid cristid and a distinct postentostylid cristid defines the apex of the entostylid (Fig. 2C, D). The postentostylid cristid is continuous with the posterior cingulum which is in turn continuous with the posthypocristid. An entostylid ridge extends anterobuccally from the junction of the postentostylid cristid and posterior cingulum into the talonid basin. The entostylid ridge on M1–3 (generally absent in M4s examined except AM M5266) may exist as a well-developed cuspatate structure (Fig. 9D) or be relatively indistinguishable existing as a series of discontinuous crenulate ridges at the posterobuccal base of the entoconid (Fig. 10E, F). In some specimens it is linear and mirrored by a parallel crest that extends anteriorly from the posthypocristid (Figs 10C, 11A). In some individuals the entostylid ridge extends anterobuccally from the postentostylid cristid and variably connects to the posterior cingulum (AM M7486, AR1574) and a variably present anteriorly directed ridge off the posthypocristid (Fig. 9A, B). It is isolated at the posterobuccal base of the entoconid in others. The above-mentioned variations for the entostylid ridge vary significantly along the tooth row in individual specimens. In some specimens a variably defined crest or lingual rib descends from the hypoconid apex into the
Identification of species boundaries in extinct koalas

longitudinal valley between the hypoconid and entoconid (Fig. 9C, D).

**M2–4.** Subrectangular in occlusal view, longer than wide and much narrower than their corresponding upper molars (Fig. 2C, D). Comprised of four main cusps: an anterolingual metaconid; postero-lingual entoconid; anterobuccal protoconid; and postero-buccal hypoconid. The lingual seione is composed of prominent pre- and postcristids that descend anterolingually and postero-lingually (respectively) from the apices of the metaconid and entoconid towards the lingual tooth margin. The premetacristid is continuous with the anterior cingulum. A slight swelling at their junction has been referred to by some authors (e.g. Pledge 1987) as a parastylid. The construction of the talonid is similar to that described for M1. Again, the pre-entocristid, although generally continuous with the postmetastylid cristid, may terminate at the posterior base of the postmetacristid. This appears to be variable within a single individual. In AR1574 for example, the latter condition is evident on the right M1 and M3 and the left M1–3, whereas the pre-entocristid connects to the postmetastylid cristid on the remaining molars.

The buccal seione is composed of prominent pre- and postcristids that descend anterolingually and postero-lingually (respectively) from the apices of the protoconid and hypoconid towards the median longitudinal valley (Fig. 2C, D). The preprotocristid terminates at the anterior tooth margin and generally abuts the posterior cingulum of the preceding tooth. It may be highly crenulated at its anterior extent (Figs 10F, 11E). On M2–3 of all specimens studied the postprotocristid and cristid obliqua (prehypocristid) join at the longitudinal valley and, in some individuals, a series of variably developed spurs spread lingually from this junction (Fig 10C, 11E). On M4 the cristid obliqua generally meets the postprotocristid (Fig. 12C) and/or the pre-ento-cristid (Fig. 12A, D). A relatively deep buccal valley is created between the posterior and anterior bases of the protoconid and hypoconid, respectively, and the junction of the postprotocristid and cristid obliqua. A buccal cingulum is generally present on M2–4, but it is variably developed, may be crenulated (Fig. 10C), and in some individuals may ascend the anterobuccal face of the hypoconid (Fig. 10A). A small stylar cusp medially positioned on the buccal cingulum at the buccal tip of the valley separating the trigonid and talonid of M2–4 is variably developed.

Columnar stylids are present on both the metaconid and entoconid of M2–4, giving these cuspids a ‘twinned’ appearance (Fig. 2C, D). Their development varies from strongly (Fig. 10D) to poorly developed between individuals and along the tooth row becoming reduced in the more posterior molars (Fig. 12B–D). In some individuals the columnar stylid of the metaconid of M2 is anteroposteriorly broad with well-developed anterior, posterior and transverse accessory crests (Fig. 10F). In others (e.g. AR6071)

Figure 12. Comparison of the left M4 of six individuals of *P. cinereus*. A, AR1574; B, AM M2185; C, AM S415; D, AM M7364; E, AM M7438; F, AM M12475. Abbreviations: a, anterior; cstd, columnar stylid; end, entoconid; hyd, hypoconid; l, lingual; med, metaconid; prd, protoconid.

the columnar stylids are well-developed but irregular structures composed of a series of ribs descending the lingual face of the metaconid and entoconid.

Again, the pattern of enamel crenulations is highly variable and, as a result, the morphology of the postprotostylid cristid (in M1), the cristid obliqua and the entostylid ridge is not constant between individuals. Other features found to vary within the lower molars include: the development of the lingual shelf of the metaconid and entoconid; and the presence or degree of development of lingual ribs from the apices of the protoconid and hypoconid on M2–4, and the hypoconid of M1. In AM M7438 (Fig. 12E) well-developed postero-lingually directed ribs extend from the protoconid apex into the longitudinal valley on M3–4 (absent on M1–2). Tooth shape varied from sub-rectangular (Fig. 10D) to ovate (Fig. 10E), depending on the development of the metastylid, entostylid and columnar stylids on the lingual tooth margin and the degree of reduction of the talonid, particularly in more posterior molars (e.g. contrast Fig. 12C with Fig. 12D).

**Variation along the tooth row.** Upper molars: Molar crenulations may change from a reticular crenulation pattern to a more transverse alignment from M1–4, or vice versa. Some specimens show reduction in crenulations from M1–4 (e.g. AM M12475; contrast Fig. 5F with Fig. 7D). The angle between the premetacrista and postmetacrista at the metacone apex becomes wider from M1–3 with associated
increased length of the metacone buccal margin (Fig. 2A, B). On M3–4 the postmetacrista shortens both absolutely and with respect to the length of the premetacrista (Fig. 2A, B). As a consequence, the buccal margin of the metacone becomes obliquely oriented with respect to the anteroposterior plane of the tooth. The buccal basins/surfaces of the paracone and metacone become progressively shallower from M1–4. This feature is most noticeable on the metacone wherein the stylist shelf is progressively reduced and often absent in M3–4. Generally the paraconule and neometacone become weaker through M1–4 (Fig. 2A, B), becoming indistinguishable from the enamel crenulation pattern in more posterior molars (Fig. 6D), although some specimens (e.g. AR2626) have a paracone on M2 that is as well developed as that of M1. The posterior moiety becomes progressively reduced (buccolingually) with respect to the anterior moiety. This is most pronounced in M4 with often extreme reduction of both the metacone and metaconule (Fig. 7A). The protostyle generally becomes more anteroposteriorly elongate in M2–3 (and sometimes M3) but may be reduced in M4 (although in some specimens the protostyle is progressively reduced from M2–4; e.g. AR2626). The posterolingual paracrista may become more prominent from M1–4. The anterolingual fossette and associated anterolingual buttress from the protocone apex) if present in M1 is generally absent in M2–4 (although it is present in M1–3 of AR8398). M2–4 lack the well-developed parasystylar region of M1 and in most M4 a well-developed anterolingual metacrista is developed (Fig. 7A, C–E) (yet absent in M1–3). The lingual pocket between the posterior base of the protocone, the anterior base of the metaconule and the lingual cingulum is progressively reduced from M1–4 and a lingual cingulum may be absent entirely on M4 (Fig. 2A, B).

Lower molars: The columnar stylids of the metaconid and entoconid become progressively reduced from M2–4, as do the metastylid and entostylid (Fig. 2C, D). Tooth shape generally changes from subcetrangular in M2 to ovate in M4 with more arcuate anterior, lingual and posterior tooth margins. The molars become progressively narrower through M1 to M4. The entostylid ridge is reduced from M1–3 and is absent in all M4s (and some M3s). The buccal valley between the protoconid and hypoconid is reduced in area and depth from M2–M4 (Fig. 2C, D), and the buccal cingulum (including associated crenulations/cusps, if developed) is also reduced in more posterior molars.

Sexual dimorphism and populational morphological variation. Conspicuous patterns of qualitative morphological variation within or between sexes and within or between regions were not evident in the Phascolarctos cinereus sample studied here.

Summary of dental characters useful for distinguishing species. Because significant variation occurs along the molar row with many features becoming progressively reduced, attenuated or absent in the more posterior molars of P. cinereus, morphological features that may be useful in distinguishing phascolarctid species are generally restricted to the premolar and first molar of the upper and lower tooth rows.

Features consistently developed on P3 of P. cinereus include: the presence of a midline longitudinal crest; the number of major cusps (three) developed along this crest and the presence of a lingual cingulum. Consistent features developed on M1 include: the relative height of major cusps; and the presence of a parastylid, protostylid, paraconule, neometacone, posterolingual paracrista and lingual cingulum. All P. cinereus M1s possess enamel crenulations (albeit they vary in degree and pattern of expression). Consistent features developed on P1 include: a midline longitudinal crest with three cusps (anterior, medial and posterior) and the presence of a posterobuccal crest. Consistent features of M1 include: the relative height of major cusps; the development and position of the protostylid; the presence of a metastylid, entostylid and entostylid ridge; the presence of a columnar stylid on the entoconid; and the presence of a transverse crest connecting the apices of the metaconid and protoconid. As in M1, all lower first molars possess enamel crenulations.

In general, the shape, extent and degree of development of many structures on P. cinereus teeth were found to be highly variable. Consequently, as a general rule, the presence or absence of a structure (as opposed to its shape or relative development) appears more useful in discriminating species boundaries in phascolarctids. Nevertheless, the relative development of a structure may fall outside the expected range of variation for a species and, as such, may still be a useful diagnostic feature. Nimbiokoola greystanesi M1s for example exhibit consistently large, pyramidal parastyles and large, bicuspid neometacanules that are diagnostic for the species (Black & Archer 1997).

Morphometric analysis

Upper dentition. MANOVA of upper tooth dimensions of male P. cinereus showed significant differences between northern (Queensland) and southern (Victorian) populations (F = 3.225, df = 15, 11, p = 0.028). Likewise significant differences in upper tooth dimensions between females from Queensland and Victoria were observed (F = 7.451, df = 15, 9, p = 0.002). For both male and female koalas, significant differences between geographical regions existed for each tooth position. (Male: P3: F = 5.064, df = 3, 23, p = 0.008; M1: F = 3.661, df = 3, 23, p = 0.027; M2: F = 4.817, df = 3, 23, p = 0.01; M3: F = 4.732, df = 3, 23, p = 0.01; M4: F = 5.376, df = 3, 23, p = 0.006. Female: P3: F = 3.973, df = 3, 21, p = 0.022; M1: F = 5.404, df = 3, 21, p = 0.006; M2: F = 3.742, df = 3, 21, p = 0.027; M3: F = 7.113, df = 3, 21, p = 0.002; M4: F = 3.219, df = 3, 21, p = 0.044.) Analysis of individual tooth measurements suggests that the Victorian male population has on average
greater lengths of both premolars and molars, and larger anterior widths of molars (M$^3$–M$^4$) than Queensland males. Only the M$^2$ showed significantly different posterior widths (Table 1). For females, very few of the individual tooth measurements were significantly different between regions, the notable exception being the posterior widths of P$^3$, M$^1$ and M$^2$ which were larger for Queensland koalas (Table 1).

MANOVA of upper tooth dimensions between male and female koalas from Queensland showed no significant differences between the sexes ($F = 1.267, df = 15, 13, p = 0.338$), yet significant differences were evident in the Victorian sample ($F = 5.405, df = 15, 7, p = 0.0157$). Male and female premolars did not differ significantly; only molars showed significant differences between the sexes (M$^1$: $F = 7.309, df = 3, 19, p = 0.002$; M$^2$: $F = 10.64, df = 3, 19, p < 0.001$; M$^3$: $F = 4.48, df = 3, 19, p = 0.0154$; M$^4$: $F = 9.752, df = 3, 19, p < 0.001$). Analysis of individual tooth measurements showed that Victorian male koalas have significantly bigger molars in all dimensions with respect to females, except for the posterior width of M$^4$ (Table 2).

**Lower dentition.** MANOVA of lower tooth dimensions of male *P. cinereus* showed significant differences between northern (Queensland) and southern (Victorian) populations ($F = 13.5, df = 15, 14, p < 0.001$). With respect to individual teeth, both premolars and molars of males from northern and southern populations differed significantly in dimensions (P$^3$: $F = 5.661, df = 3, 26, p = 0.004$; M$^1$: $F = 10.57, df = 3, 26, p < 0.001$; M$^2$: $F = 7.956, df = 3, 26, p < 0.001$; M$^3$: $F = 7.121, df = 3, 26, p = 0.001$; M$^4$: $F = 6.973, df = 3, 26, p = 0.001$). MANOVA of lower tooth dimensions of female *P. cinereus* showed significant differences between northern (Queensland) and southern (Victorian) populations ($F = 5.621, df = 15, 24, p < 0.001$). With respect to individual teeth positions, premolars did not show any significant differences in dimensions measured ($F = 0.6496, df = 3, 36, p = 0.6$); however, molars from northern and southern populations differed significantly (M$^1$: $F = 7.568, df = 3, 36, p = 0.0004$; M$^2$: $F = 4.01, df = 3, 36, p = 0.015$; M$^3$: $F = 5.356, df = 3, 36, p = 0.004$; M$^4$: $F = 4.746, df = 3, 36, p = 0.007$). Analysis of the individual tooth measurements showed that for both male and female koalas, Victorian specimens were significantly larger than Queensland specimens in the following dimensions: M$^3$ and M$^4$ length, M$^1$ and M$^2$ anterior width, and M$^1$ posterior width (Table 3). MANOVA of lower tooth dimensions between male and female koalas from Victoria and between male and female koalas from Queensland showed no differences existing along the tooth row (Queensland: $F = 1.41, df = 15, 31, p = 0.2035$; Victoria: $F = 2.359, df = 15, 7, p = 0.1275$).

**Systematic palaeontology**

Class **Marsupialia** Illiger, 1811
Order **Diprotodonta** Owen, 1866

Suborder **Vombatiformes** Woodburne, 1984
Infraorder **Phascolarctomorpha** Aplin & Archer, 1987
Family **Phascolarctidae** Owen, 1839
Genus **Litokoala** Stirton et al., 1967

**Type species.** *Litokoala kutjamarpensis* Stirton et al., 1967.

**Additional species.** *L. garyjohnstoni* Louys et al., 2007; *Litokoala dicksmithi* sp. nov.

**Diagnosis.** In addition to the dental (e.g. Black & Archer 1997; Louys et al. 2007) and cranial features (Louys et al. 2009) described elsewhere, species of *Litokoala* differ from all other phascolarctids in having a twinned or secondary infraorbital foramen, a prominent masseteric process composed entirely of maxilla, an almost vertically oriented premaxillomaxilla suture on the lateral face of the rostrum, and a large, anteriorly extensive lacrimal.

*Litokoala* species differ from *Phascolarctos* species in having proportionately larger orbits, a less constricted rostrum anteriorly at the level of the incisor arcade, a shallow maxillolabial fossa, and a zygomatic arch that projects posterolaterally (as opposed to laterally) from the face. *Litokoala* species differ from *Nimikokala* species in having a relatively shorter, broader, deeper rostrum, a broader maxillary palate, and a larger, broader narial aperture with an irregular border (as in *Phascolarctos*). Louys et al. (2007, p. 100) differentiated *Litokoala* species from other phascolarctids by possession of “...a well-developed neomorphic cuspule at the anterolingual base of the metaconule of M$^1$ (with the exception of species of *Phascolarctos* de Blainville, 1816 where it is variably present)”. Because this feature is variably present in *Phascolarctos*, absent in *Litokoala dicksmithi* and unknown for *L.thurmerae* (known only from M$^3$), we do not regard it to be diagnostic for the genus.

*Litokoala kutjamarpensis* Stirton et al., 1967
1987 *Litokoala kanunkaensis* Springer; 320, figs 1, 2.
2010 *Litokoala dickedfordi* Pledge; 81, fig. 5.

**Holotype.** SAM P13845, right M$^1$.

**Material.** From Kanunka North Site: SAM P32397, a right M$^2$; UCR21945, a right M$^4$; UCR21980, a metacone of a right M$^3$; UCR21979, a metacone of a left M$^1$. From Riverleigh: QM F30500, right P$^3$, QM F13079, right dentary fragment with posterior half of P$^3$, M$^3$-2, QM F30502, right M$^3$, Henks Hollow Local Fauna; QM F30501, right M$^1$, Gag Site; QM F30503, M$^9$ fragment containing paracone and buccal half of protocone, Gotham Site; QM F51382, a partial skull with left and right P$^3$, M$^3$-4, Jim’s Carousel Site; QM F20809, right M$^1$, JC9 Site.

**Occurrence.** The holotype is from the Kutjamarpur Local Fauna, Leaf Locality, Lake Ngapakaldi, Wipajiri Formation, South Australia, which is interpreted to be Early Miocene in age (Woodburne et al. 1993). Kanunka North
Site (Zone E of the Etadunna Formation) is located on the west side of Lake Kanuka, South Australia. This deposit is Late Oligocene in age (Woodburne et al. 1993). The Henk’s Hollow, Gag, Gotham, Jim’s Carousel and JC9 Sites from the Riversleigh World Heritage Area, Lawn Hill National Park, north-western Queensland, are Faunal Zone C deposits which are interpreted to be Middle Miocene in age (Creaser 1997; Arena 2005; Travouillon et al. 2006).

Remarks. Dental descriptions of *L. kutjamarpensis* are provided in Stirton et al. (1967), Black & Archer (1997; as *L. kanunkaensis*) and Louys et al. (2007), and a description of the cranium is given by Louys et al. (2009). Arguments for subsuming *L. kanunkaensis* into *L. kutjamarpensis* can be found in Louys et al. (2007) and are recounted in the discussion below. Arguments for synonymizing *L. `dicksmithi'* with *L. kutjamarpensis* are also given below.

**Litokoala garyjohnstoni** Louys et al., 2007  
**Holotype.** QM F51405, left partial maxilla with P3, M1–3.  
**Material.** Paratype, QM F51406, left M4.  
**Occurrence.** Outasite, Godthelp Hill, Riversleigh World Heritage Area, Lawn Hill National Park, north-western Queensland. Outasite is a Faunal Zone B deposit and is interpreted to be Early Miocene in age (Creaser 1997; Travouillon et al. 2006).

Remarks. *Litokoala garyjohnstoni* is described in Louys et al. (2007).

**Litokoala dicksmithi** sp. nov  
(Figs 13, 14)  
**Diagnosis.** Rostrum short with twinned infraorbital foramen; narial aperture broad with irregular border. Differs from other *Litokoala* spp. in: its deeper transverse and longitudinal valleys in the upper molars; its larger, broader protocone in the upper molars; lacking a neomorphic cuspule at the anterolingual base of the metaconule on M1; protocone in the upper molars; lacking a neomorphic longitudinal valleys in the upper molars; its larger, broader metaconule at the anterolingual base of the metaconule on M1 (unknown for *L. thurmerae*); and P3 lacking a lingual cingulum with narrower, shallow lingual valley (unknown for *L. thurmerae*). Differs from *L. garyjohnstoni* in: its longer, more prominent masseteric process; P3 with reduced medial and posterior lingual cusps and reduced anterobuccal crest from medial midline cusp; reduced molar crenulations; and posteriorly narrow upper molars across the metacone and metaconule. Differs from *L. kutjamarpensis* in: its less linear arrangement of midline cusps and crests on P3; and lacking an anterolingual metacrista on upper molars.

**Derivation of name.** The specific name honours Dick Smith, Australian aviator, adventurer and philanthropist for his long-term financial support of Australian scientific endeavour and in particular fossil research at Riversleigh.

**Holotype.** QM F54567, partial anterior skull with left I1, P3, M1, partial M2; right P3, M1–4.

**Occurrence.** Ross Scott Orr (RSO) Site, Faunal Zone B (Travouillon et al. 2006), Riversleigh World Heritage Area, north-western Queensland; Early Miocene.

**Description**  
Adult skull with right P3–M4, Li1, LP3–M2. Approximately the same size as *Litokoala kutjamarpensis* skull (QM F51382) judging by width of the palate and length of tooth row, and slightly shorter than *Nimiokoala*. We estimate the total length of the skull (based on overlap with QM F51382) to have been approximately 76 mm, which is suggestive of a relatively short, broad skull. Right side preserves nasal, premaxilla, maxilla, lacrimal, part of the frontal, orbitosphenoid, endocranial portion of the alisphenoid, anterior jugal and partial palatine (Fig. 13A). Left side is largely missing, preserving only the premaxilla, nasal and partial maxilla. Cranial and dental measurements are given in Tables 4 and 5, respectively. The description is restricted to the right hand side. Comparisons are made throughout with *Phascolarctos cinereus* (hereafter *Phascolarctos*) and *Nimiokoala greystanesi* (hereafter *Nimiokoala*), the only two koala species with which there is considerable overlap with the skull portion preserved.

**Facial region.** Rostrum short and relatively deep (17.9 mm at C1 alveoli), tapers slightly anteriorly. Shorter and deeper than *Nimiokoala* and similarly proportioned to *Phascolarctos*. Slight inflation of premaxilla portion of rostrum dorsolaterally, but not to the extent as seen in *Phascolarctos* in which the rostrum in anterior view is distinctly keyhole-shaped (i.e. broad dorsally, narrow ventrally). In *L. dicksmithi* and *Nimiokoala*, the rostrum is slightly broader ventrally than dorsally and not constricted as in *Phascolarctos*. Nasals are wide posteriorly, taper anteriorly and flare slightly at their anterior extremity (Fig. 13C). Although the nasals are broken anteriorly it appears that their anterior border was quite irregular, as in *Phascolarctos* which has numerous short anterior projections. This is unlike the condition found in most other diprotodontians (possibly including *Nimiokoala*) in which the anterior border of the nasals is well defined and medially tapering. The nasals are dorsally flattened as in *Nimiokoala* and unlike in *Phascolarctos* where they are mildly convex and inflated. Nasofrontal suture is broad (11.1 mm) and transversely orientated (Fig. 13C). The nasals are slightly inflated laterally at this suture and the frontals more inflated dorsally than in *Nimiokoala*, indicating a slightly deeper skull for *L. dicksmithi*. Nasal aperture (Fig. 13D) broader (12.91 mm) than high (10.15 mm), larger than *Nimiokoala* (8.47 mm wide, 7.42 mm high), and similarly proportioned to *Phascolarctos*. Premaxilla short, premaxillomaxilla suture vertically orientated in lateral view terminating dorsally at its junction with the nasals at a point vertically in line with the infraorbital foramina (Fig. 13A). This is unlike the condition in *Nimiokoala* and *Phascolarctos* where it runs...
Figure 13. QM F54567, Litokoala dicksmithi sp. nov. partial skull. A, right lateral view; B, occlusal view; C, dorsal view; D, anterior view. Abbreviations: als, alisphenoid; C1, canine; fr, frontal; I1, first upper incisor; I1a, first upper incisor alveolus; I2, second upper incisor; I3, third upper incisor; if, interincisive foramen; iof1, primary infraorbital foramen; iof2, secondary infraorbital foramen; jg, jugal; lac, lacrimal; lacf, lacrimal foramen; lt, lacrimal tuberosity; max, maxilla; mp, masseteric process; mr, masseteric ridge; ns, nasal; off, orbitosphenoid-frontal (ethmoidal) foramen; or, orbital ridge; os, orbitosphenoid; P3, upper premolar; pal, palatine; pmx, premaxilla; pv, palatal vacuity lateral border; sos, suborbital shelf.
Table 4. Cranial measurements (mm) of *Litokoala* spp. and *Nimiokoala greystanesi*. Abbreviations: DL, diastema length (between I3 and P3); DZP, depth of zygomatic process through masseteric process; HPOP, height of cranium at postorbital process; NAH, narial aperture height; NAW, narial aperture width; NL, nasal length; NW, maximum width of nasals; PMD, premaxilla depth; PW, posterior width; PWC1, palate width at anterior of C1 alveoli; PWI3, palate width at I3; PWM1, palate width at anterior root M1; RD, rostrum depth (at C1 alveoli); RW, rostrum width (at C1 alveoli); TRL, tooth row length.

<table>
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<th></th>
<th><em>L. dicksmithi</em></th>
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</table>

Right nasal measured and doubled.

Figure 14. QM F54567, *Litokoala dicksmithi* sp. nov. upper right P3, M1-4 in occlusal view. A, stereopair of right P3, M1-4; B, line drawing showing major features of P3, M1-4. Abbreviations: a, anterior; ac, anterior cingulum; antc, anterior cusp of P3; b, buccal; mcl, metaconule; me, metacone; medc, medial cusp of P3; nmcl, neometaconule; pa, paracone; pas, parastyle; pcl, paraconule; plc, posterolinguinal cusp of P3; postc, posterior cusp of P3; pr, protocone; stB, stylar cusp B; stC, stylar cusp C.
diagonally (posterodorsally) across the lateral side of rostrum and terminates dorsally at its junction with the nasals at a point vertically in line with P3. In lateral view, the premaxillomaxilla suture originates at the anterior base of the canine as it does in *Phascolarctos*, extending through the canine alveoli to emerge on the palatal surface at the postero medial base of the canine (Fig. 13B). Interincisive foramina mostly contained within the premaxilla, yet bordered posteriorly and posterolaterally by maxilla (Fig. 13B). The interincisive foramina are larger than in *Nimiokoala* and relatively and absolutely larger than most *Phascolarctos*. Incisor arcade U-shaped, wider and shallower than *Nimiokoala*, much shallower than the deep premaxillary palate of *Phascolarctos*. Distance between incisors and canine is short (2.2 mm), and proportionately more similar to *Phascolarctos* than to *Nimiokoala* (4.2 mm). The maxillary palate is broad, as in *L. kutjamarpensis*, and flat, as in *Nimiokoala*, unlike the arched palate of *Phascolarctos*. The maxillary palate is preserved to the level of M2 on the left side; on the right side it is mostly complete except for a triangular wedge of bone opposite M1–2 (Fig. 13B). Much of the palatal portion of the palatine bones is not preserved except for a narrow lateral sliver of the right palate which extends anteriorly to the level of the M2/M3 boundary as it does in *L. kutjamarpensis* and *Phascolarctos*. Large posterior palatal vacuities are present and appear to have been restricted to the palatines, terminating at or just posterior to the maxillopalatine suture. In *L. kutjamarpensis* the condition is unclear because the area is poorly preserved. Although Louys et al. (2009, p. 984) in their description of *L. kutjamarpensis* referred to the posterior palatal vacuities as “maxillary-palatine vacuities” and stated “The maxillary-palatine vacuity is large and extends from the posterior margin of M2 to just behind the anterior margin of M4…” they did not indicate where the maxillopalatine suture is positioned relative to M2, and hence did not indicate whether the vacuities extend into the maxilla or terminate at the maxillopalatine suture. In *Phascolarctos* they are restricted to the palatines, falling well short of the maxillopalatine suture (condition unknown for *Nimiokoala*). The ridged ventral surface of the vomer is exposed through the palatal vacuities. A small, ovate infraorbital foramen is 2.0 mm anterior to and 3.9 mm above P1. A smaller, secondary infraorbital foramen lies ventral and slightly posterior to the primary infraorbital foramen, 1.93 mm above the alveolar margin (Fig. 13A). Both foramina are confluent with the infraorbital canal. In *Phascolarctos* and *Nimiokoala* there is a single infraorbital foramen. It is similarly positioned in *Nimiokoala* to the primary foramen of *L. dicksmithi*. In *Phascolarctos* the infraorbital foramen is proportionately smaller and positioned high on the rostrum near the orbit at a point above P1 or M1. Black & Hand (2010) have shown the presence of a secondary infraorbital foramen to be a variable feature within the diprotodontid *Nimbodon lavarackorum*. Its presence in *L. dicksmithi* may also be variable; however, this cannot be determined on the basis of a single known specimen.

The maxilla does not deepen above the molars like it does in *Phascolarctos*, and the suborbital shelf sits quite low in the orbit, close to the tooth row. Unlike *Phascolarctos*, *Nimiokoala* and *L. garyjohnstoni*, *L. dicksmithi* has a prominent masseteric process that extends ventrally to below the alveolar margin (Fig. 13A, D). A similar process appears to have been present in *L. kutjamarpensis* (QM 51382) but the extent to which it extends ventrally is unknown. In *L. garyjohnstoni* the masseteric process is significantly less pronounced, remaining 1.71 mm above the alveolar margin. In all *Litokoala* species, the masseteric process is composed entirely of maxilla. The zygomatic arch is deep anteriorly, deeper than in *Nimiokoala*, with a well-defined masseteric ridge (Fig. 13A) and sulcus indicating the site of attachment for the masseter lateralis profundus. Anteriorly, the zygomatic arch projects posterolaterally from the face, unlike *Phascolarctos* in which it projects more laterally. In *L. dicksmithi* the anterior jugal portion of the zygomatic arch is relatively deeply concave compared with both *Nimiokoala* and *Phascolarctos*.

**Sphenorbital region.** The orbit is large, similar in size to *Nimiokoala* yet proportionately larger than *Phascolarctos*. A small but prominent ridge-like postorbital process is positioned on the frontal at the dorsal border of the orbit 10.2 mm posterior to the anterior preorbital ridge. The lacrimal is roughly circular; it extends 4.75 mm beyond the preorbital ridge where it contacts the maxilla on the rostrum. It is absolutely and proportionately larger than in either *Phascolarctos* or *Nimiokoala*. It is bound posterodorsally by the frontal, posteriorly by the palatine and ventrally by the maxilla and jugal. The preorbital ridge is complete and not as well defined as in *Nimiokoala*. A distinct lacrimal

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**Table 5.** Dental measurements (mm) of *Litokoala dicksmithi*. Abbreviations: AW, anterior width; L, length; PW, posterior width.

<table>
<thead>
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<th>Specimen</th>
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<th>W</th>
<th>M¹</th>
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foramen is situated just anterior and outside the orbit (Fig. 13A). A smaller foramen is positioned 3.65 mm dorso-posteriorly to the lacrimal foramen and perforates the preorbital ridge just dorsal to a weak lacrimal tuberosity. Three small foramina pierce the lacrimal close to its ventral suture with the maxilla. Below these foramina on the lacrimojugal suture is a small unperforated yet deep ovate depression.

A well-defined infraorbital canal perforates the maxilla just below this suture line; like *Nimiokoala* it is situated at the anterior end of a well-developed sulcus. Posterior to the infraorbital canal and within the infraorbital sulcus lies the sphenopalatine foramen. Again as in *Nimiokoala* it lies on the maxillopalatine suture. The dorsal margin of the palate is preserved; it interdigitates with the maxilla ventrally and anteriorly, makes contact with the lacrimal anterodorsally, interdigitates with the frontal dorsally and makes contact with the orbitosphenoid at its posterior-most preserved point (Fig. 13A). The orbital portion of the maxilla is roughly ovate, its anteriormost point being coincident with the lacrimojugal suture, and is entirely bound dorsally by the palate. The orbitosphenoid is present as a roughly circular bone at the posteroventral corner of the specimen preserved; it contacts the palate anterovertrally and the frontal anteriodorally and dorsally (Fig. 13A). At the suture between the orbitosphenoid and the frontal lies the ethmoidal foramen; this foramen is also present in *Nimiokoala* which it lies on the maxillopalatine suture. The dorsal margin of the palate is preserved; it interdigitates with the maxilla ventrally and anteriorly, makes contact with the lacrimal anterodorsally, interdigitates with the frontal dorsally and makes contact with the orbitosphenoid at its posterior-most preserved point (Fig. 13A). The orbital portion of the maxilla is roughly ovate, its anteriormost point being coincident with the lacrimojugal suture, and is entirely bound dorsally by the palate. The orbitosphenoid is present as a roughly circular bone at the posteroventral corner of the specimen preserved; it contacts the palate anterovertrally and the frontal anteriodorally and dorsally (Fig. 13A). At the suture between the orbitosphenoid and the frontal lies the ethmoidal foramen; this foramen is also present in *Phascolarctos*. Posteriorly it is bound by the alisphenoid, but the suture between these two bones is difficult to discern. At the posteroventral margin of the orbitosphenoid, the anterodorsal rim of the sphenorbital fissure can be seen. The alisphenoid is almost only preserved as an endocranial lamina, its suture line with the frontal is however discernable. The frontal makes a large ventral contribution to the sphenorbital region; on the cranial roof it is preserved only as a triangular wedge (Fig. 13C).

**Dentition.** (Fig. 14A, B). QM F54567 preserves the L1, LP3-M2 and RP3-M4. The adult upper tooth formula would be I1–3, C1, P1, M1–4. The alveolus for I2 is larger than I1, the latter being similar in size to the alveolus of C1 (Fig. 13B). In basic dimensions the alveoli for I2–3 and C1 are comparable with *Nimiokoala*. As in other species of *Litokoala*, the premolar is positioned more in line with the molar row (Fig. 14A, B) and less divergent anteromedially as in *Nimiokoala*.

**P1.** Left I1 preserved. Short, gracile tooth with enamel on all surfaces and a small ovate wear facet on the posterior surface of its tip. Relatively blunt tip but this may be partially attributed to abrasion. Projects anterovertrally and would have converged medially on tip of right I1 (Fig. 13D). Less robust, more protracted and less ventrally extensive than I1 of *Nimiokoala* or *Phascolarctos* (the only other phascolarctids for which a first upper incisor is known) and in this regard is more reminiscent of an I1 of the latter taxa than an I1.

**P3.** Bulbous P3 with four main cusps, three of which are positioned anteriordorsally, medially, and posteriorly along the longitudinal tooth midline (Fig. 14A, B). The fourth and smallest cusp is positioned at the posterolingual tooth margin. The P3 is widest posteriordorsally at the level of the posterolingual cusp and tapers in width to the anterior tooth margin. There is significant wear on the posterolingual face of the anterior cusp, the apices of the medial and posterolingual cusps and the posterior blade of the posterior cusp. A small ovate wear facet that probably represented a small lingual cuspule is positioned at the anterior base of the posterolingual cusp along the lingual tooth margin in the same position as the small lingual cusp in *L. garyjohnstoni* and the small cuspule in *L. kutjamarpensis* (QM F51382). The relative heights of the major cusps are difficult to discern as a result of wear. The anterior cusp is situated approximately 0.95 mm from the anterior margin. Anterior, buccal and lingual crests extend from its apex and fade towards the base of the crown. The buccal crest is not as extensive, nor prominent as in *L. garyjohnstoni* in which it meets a well-developed anterobuccally directed crest from the apex of the medial cusp. In L. *dicksmithi* the buccal crest of the medial cusp is weak and fades out midway to the base of the crown. A better-developed yet worn lingual crest extends from the apex of the medial cusp and terminates at the base of the crown at the small ovate wear facet (mentioned above) resembling the condition found in *L. garyjohnstoni*. In *L. kutjamarpensis* (QM F51382) the lingual crest of the medial cusp terminates abruptly before meeting the small lingual cuspule.

The apex of the medial cusp is positioned 2.39 mm posterior to the anterior tooth margin. Short anterior and posterior crests link the apices of the medial and anterior cusps (respectively) in a shallow valley which defines the anterior and posterior tooth moieties (Fig. 14A, B). A short posterolingually directed crest links the apices of the medial and posterior cusps. The apex of the posterior cusp is positioned 3.04 mm posterior to the anterior tooth margin. The posterolingual placement of the posterior cusp with respect to the medial cusp is also found in *L. garyjohnstoni* and less so in *L. kutjamarpensis*. Both *L. dicksmithi* and *L. garyjohnstoni* lack the lingual crest of the posterior cusp found in *L. kutjamarpensis*. A prominent posteriorly directed crest connects the posterior cusp apex to the anterior cingulum of M1. The posterolingual cusp is small and similarly developed to that of *L. kutjamarpensis* but weaker with respect to *L. garyjohnstoni*. Short weak anterior and posterior crests extend from its apex. The anterior crest is heavily worn but appears to have been connected to the small lingual cuspule represented by an ovate wear facet. In *L. dicksmithi* the well-developed crest found in both *L. garyjohnstoni* and *L. kutjamarpensis* that links the small lingual cuspule anteriorly with the lingual crest of the anterior cusp is absent. The resultant effect is a less trenchant, more bulbous looking premolar overall.
**M1.** Description based on LM1 because enamel is missing from the lingual face of metaconule on RM1. The enamel is moderately crenulated although less apparent due to wear. Crenulations are evident in the transverse valley, on the anterior bases of the paracone, metacone, paraconule and neometacune, the posterior bases of the parastyle, paracone and metacone, the buccal base of the protocone, and the anterior cingulum. M1 is longer (across the buccal margin) than it is wide. The buccal margin is convex and the anterior margin slopes posterolingually. The tooth is markedly wider anteriorly (i.e. across the paracone and protocone) than posteriorly (across the metacone and metacune) and in this regard resembles the M3 of *Nimiokoala* more so than either *L. garyjohnstoni* or *L. kutjamarpensis*. This is in part due to the absence of the ‘neomorphic cuspule’ *(sensu* Stirton *et al.* 1967) located at the anterolinguval base of the metacune in other *Litokoala* species. The apices of the paracone and metacone slightly overhang their lingual bases as they do in *L. kutjamarpensis* and contra *L. garyjohnstoni*. The buccal surface of the paracone is reduced relative to the metacone as it is in *L. garyjohnstoni*. The respective heights of the major cusps are difficult to discern due to moderate wear with dentine exposed on all apices; however, the metacone appears to have been taller than the paracone. The metacune is the most worn of the major cusps. Dentine is also exposed on the apex of the parastyle, the neometacune, the buccal end of the metacune crist and the lingual end of the posterolinguval parastyle. The parastyle is a large (although very worn), pyramidal cusp which occupies the anterobuccal corner of the tooth and is similarly developed as in *L. garyjohnstoni* and slightly larger than in *L. kutjamarpensis*. The degree and pattern of wear is similar to that found in the holotype of *L. kutjamarpensis* (SAM P13845), the worn posterior base of the parastyle appearing as a buccal ridge connecting the paracone and buccal cingulum. The tooth is slightly higher crowned and the transverse and longitudinal valleys are slightly deeper than in other *Litokoala* spp. Stylar cusps are weakly developed, similar to *L. kutjamarpensis*, and reduced relative to *L. garyjohnstoni*. Unlike other *Litokoala* spp., stylar cusps B and C do not form a continuous ridge that effectively closes off the paracone buccal basin along the buccal tooth margin. The preparastyle is short, heavily worn and bifurcates at the buccal tooth margin into a short anterior spur that terminates just prior to meeting the posterobuccal base of the parastyle, and a short posterior ridge that represents a poorly developed stylar cusp B. The postparastyle is linear, longer and less worn than the preparastyle and similarly bifurcates at the buccal tooth margin into a short anterior ridge representing stylar cusp C, and a short posterobuccal arm that meets the premetacune at the buccal margin, effectively closing off the buccal end of the transverse valley. Both the postparastyle and premetacune meet a series of short, transversely oriented ridges (that form part of the molar crenulation pattern) at this point. The premetacune is moderately worn, elongate, anterobuccally directed (running in a parallel plane to the preparastyle) and branches before its junction with the postparastyle to a short posterior ridge that represents stylar cusp D. The postmetacune is more heavily worn than the premetacune (having dentine exposed at the metacone apex) and is directed slightly more posteriorly than the postparastyle, terminating ventral to the anterior cingulum of M2 at the anterobuccal tooth corner. A slight swelling at this point represents stylar cusp E. A large crescentic paracune is situated at the anterolinguval base of the parastyle. A more elongate, slightly crescentic posterior crest curves around the base of the paracone to meet a well-developed and moderately worn posterolinguval parastyle as it does in other species of *Litokoala*. A third posterolinguvally directed crest extends from the paracone apex and terminates at the buccal base of the protocone. In the RM1, this crest is anterolinguvally directed and meets a short posterior spur from the anterior cingulum, the latter representing a weakly developed protostyle (Fig. 14A, B). A large crescentic neometacune occupies the longitudinal valley between the metacone and metacune, its apex positioned at the anterolinguval base of the metacune. A well-developed anterior neometacune crest extends anterobuccally into the transverse valley, becoming part of the crenulation pattern. A posterior neometacune crest extends posteriorly, curving slightly buccally at the posterolinguval base of the metacune where it meets a weakly developed posterolinguval metacune. A linear and slightly worn preprotostyle is continuous with the anterior cingulum anteriorly. A crescentic postprotostyle meets a bifurcate premetacune crist in the transverse valley well buccal to the lingual margin. A weak anterolinguvally directed crest extends down the lingual face of the protocone, becoming more prominent towards the base of the crown. It is more prominent in RM1 and becomes progressively better developed in M2–4 and originates from the protocone apex (Fig. 14A, B). This crest is well developed in M1–4 of *L. kutjamarpensis* but weakly expressed in *L. garyjohnstoni*. The lingual face of the protocone slopes less steeply towards its base and consequently projects further lingually than that of the metacune. A crescentic postmetacune crist extends posteriorly from the metacune apex becoming continuous with the posterior cingulum, at which point it abuts and extends ventral to the anterior cingulum of M2. The valley between the posterior base of the protocone and the anterior base of the metacune is narrow in comparison with other *Litokoala* spp. and is an artefact of the absence of a neomorphic cuspule at the anterolinguval base of the metacune.

**M2.** Similar in most respects to M1 except for the following features: a large pyramidal parastyle is absent and
consequently the anterior tooth margin is linear and oriented in the buccolingual plane; enamel crenulations are reduced and restricted to the transverse valley and the anterior base of the paracone and metacone; the buccal surface of the paracone is larger and the metacuneal buccal margin is less convex and slopes posterolingually; stylar cusps B and C are larger; the lingual face of the protocone more steeply slopes towards its base and consequently is less lingually projecting; the anterior paraconule crest connects to the anterior cingulum; the posterior paraconule crest is continuous with the anteriormost of the transverse ridges at the buccal end of the transverse valley; the anterolingual crest of the paracone is reduced; a protostyle is absent; the premetacuneal valley of the transverse ridge; preparacrista overhangs the anterior base of the paracone and metacone; the buccal surface of the paracone and metacone are reduced; the buccal surface of the paracone is larger and the metacone buccal margin is less convex and slopes posterolingually; stylar cusps B and C are smaller in size and posteriorly attenuated. The metacone is reduced and more steeply sloping; the anterobuccal protocone crest is more distinct and originates from the protocone apex.

\[ \text{M}^1 \] Similar to \[ \text{M}^2 \] but differs in the following features: smaller size; buccal surfaces of the paracone and metacone more elongate anteroposteriorly, narrower buccolingually and more steeply sloping; protocone, metacone, metaconule, paracone, and neometacuneal reduced; enamel crenulations restricted to the buccal end of the transverse valley; preparacrista overhangs the anterior base of the paracone and anterobuccal protocone crest more distinct and originates from the protocone apex.

\[ \text{M}^4 \] As in other \textit{Litokoala} spp., \[ \text{M}^4 \] is significantly smaller in size and posteriorly attenuated. The metacone and metacuneole are significantly reduced and non-cusplike, their apices incorporated into the posterobuccal and posterolingual cingulae, respectively. A fine network of ridges/crenulations radiate from the posterobuccal, anteroposterior, and posterior lingual tooth margins towards the transverse median valley. The neometacuneole is indistinct from the crenulation pattern. Anteriorly, the tooth resembles \[ \text{M}^3 \] but the following differences are noted: the paracone, protocone, and paraconule are reduced; the buccal surface of the paracone is reduced and more steeply sloping; the anterobuccal protocone crest is more distinct; a posterobuccal protocone crest is developed; stylar cusps C and D are reduced; a valley separating the posterior and anterior bases of the protocone and metacone, respectively, is absent; and the postprotocrista is less arcuate, more posterobuccally directed and continuous with the posterolingual cingula that incorporates the metacone apex.

**Discussion**

\textit{Litokoala dicksmithi} sp. nov. is known from an exceptionally well-preserved partial cranium. It is the first cranial material for the genus that preserves the rostrum. Overall, the facial region of \textit{L. dicksmithi} resembles the modern koala more so than does \textit{Nimiokoala greystanesi}, the only other extinct phascolarctid for which comparable cranial material is known. Louys \textit{et al.} (2009) found the rostral morphology of \textit{N. greystanesi} to be most similar to a generalized phalangerid, such as the extant common brushtail possum (\textit{Trichosurus vulpecula}), than to the modern koala. \textit{Litokoala dicksmithi} is more ‘koala-like’ and resembles \textit{Phascolarctos} (contra \textit{Nimiokoala}) in having a shorter, more robust rostrum with a broad nasal aperture that has an irregular anterior border. The latter feature appears to be a cranial synapomorphy for the \textit{Litokoala–Phascolarctos} clade, a grouping previously well-supported by dental apomorphies (see Woodburne \textit{et al.} 1987; Black & Archer 1997; Black \textit{et al.} 2012). In contrast to \textit{Phascolarctos}, however, and like \textit{Nimiokoala}, \textit{L. dicksmithi} shows a lack of facial flexion or deepening of the maxilla with respect to the tooth row, features which probably evolved in the modern koala in response to a more specialized diet (Louys \textit{et al.} 2009).

Features in which \textit{L. dicksmithi} more closely resembles \textit{N. greystanesi} than \textit{P. cinereus} include: the general shape of the rostrum in anterior view (i.e. broader ventrally than dorsally); a broad maxillary palate; and proportionately larger orbits. Features unique to \textit{L. dicksmithi} among phascolarctids include: well-developed and ventrally extensive masseteric processes; ‘twinned’ infraorbital foramina; a broad, shallow premaxillary palate and correspondingly broad U-shaped incisor arcade; large interincisive foramina (anterolateral palate) and proportionately larger and anteriorly extensive lacrimals (Fig. 13A–D).

In some aspects of dental morphology \textit{L. dicksmithi} resembles \textit{N. greystanesi} in features that have previously (e.g. Woodburne \textit{et al.} 1987; Black & Archer 1997) been found to be plesiomorphic with respect to the \textit{Litokoala–Phascolarctos} clade. These features include the absence of the neomorphic cuspule at the base of the metacone of \[ \text{M}^1 \] that is present in both \textit{L. kutjamarpensis} and \textit{L. garyjohnstoni} (unknown for \textit{L. thurmerae}), and the absence of a ‘trenchant’ premolar characterized by a well-developed lingual cingulum and mediolingual cusp on \[ \text{P}^3 \]. Development of the ‘trenchant’ premolar characteristic of \textit{L. garyjohnstoni}, \textit{L. kutjamarpensis} and species of \textit{Phascolarctos} could be achieved through enlargement of the small mediolingual cuspule found in \textit{L. dicksmithi} and its associated anterior and posterior apical crests, to form a continuous lingual cingulum. The presence of a trenchant premolar in some but not all species of \textit{Litokoala} and in species of \textit{Phascolarctos} suggests this feature may have evolved independently in these lineages and may not, as previously indicated (e.g. Woodburne \textit{et al.} 1987; Black & Archer 1997), be a synapomorphy for a \textit{Litokoala–Phascolarctos} clade. This result was supported by a recent analysis of phascolarctid phylogeny by Black \textit{et al.} (2012) who did not find a trenchant premolar to be an unambiguous synapomorphy uniting the \textit{Litokoala–Phascolarctos} clade.
Palaeoecology of Litokoala

Litokoala dicksmithi from Faunal Zone B (Early Miocene) is the third Litokoala species described from the rainforest assemblages of the Riversleigh World Heritage Area, northwestern Queensland. We also recognize L. kutjamarpensis (sensu Louys et al. 2007) from numerous Faunal Zone C (Middle Miocene) local faunas and L. garyjohnstoni from the Faunal Zone B Outsite Local Fauna. Although L. dicksmithi and L. garyjohnstoni may have been sympatric they do not appear to have been sympatric. Known from single specimens, both taxa are rare components of Riversleigh’s Early Miocene faunal assemblages.

Body size estimates for L. dicksmithi based on the predictive regression equations of Myers (2001) range between 3.1 kg (based on M\(^3\) length) and 4.2 kg (based on M\(^3\) width), making the species comparable in size to the possum Trichosurus vulpecula (1.5–4.5 kg; Strahan 2004). Body size estimates based on the same dental variables (M\(^3\)L and M\(^3\)W, respectively) gave size ranges of 2.4–4.5 kg for L. garyjohnstoni, 2.7–4.6 kg for L. kutjamarpensis and 2.6–4.1 kg for N. greystanesi. These fossil phascolarctids represent the smallest vombatiforms presently known. As such, they contradict recent hypotheses (e.g. Phillips & Pratt 2008) of long-term ecological niche differentiation between the diprotodontian suborders Vombatiformes and Phalangerida, which suggest that the former is characterized by large-bodied (>7 kg) forms that subsist on lower quality forage relative to members of the latter. The relatively small and similar body size of these koalas may reflect the optimum body size for a phascolarctid specializing on nutrient-rich plants in Australia’s Early to Middle Miocene rainforests. At all other times during their evolutionary history, koalas have been comparable in size to (e.g. late Oligocene species of Madakoaola and Perikoala, and Pleistocene Invictokoala), if not larger than (e.g. Pliocene to Pleistocene Phascolarctos spp.), the modern species (4.1–13.5 kg; Martin et al. 2008).

One exception is a new plesiomorphic genus and species of koala, Priscakoala lucytwinbulla, described by Black et al. (2012) from Early to Middle Miocene deposits at Riversleigh. This rare species was similar in size to the modern koala and sympatric with Nimikoala greystanesi in two Early to Middle Miocene assemblages at Riversleigh (Black et al. 2012). Priscakoala lucytwinbulla possessed simple, uncrenulated selodont molars that are suggestive of a diet of relatively softer leaves than those of the smaller coeval species of Litokoala and Nimikoala, which are characterized by relatively complex dentitions (Black et al. 2012). Interestingly, another probable rainforest koala, Invictokoala monticola Price & Hocknull, 2011, from Pleistocene deposits of Mt Etna, Queensland, also exhibits a relatively simple selendont dentition reminiscent of that of the similarly sized plesiomorphic Priscakoala lucytwinbulla.

The proportionately larger size of the orbits in Litokoala species suggests the intriguing possibility that these koalas were nocturnal and may have possessed greater visual acuity than the modern species. Orbit size has been shown to be strongly correlated with activity pattern in primates, with nocturnal species having proportionately larger orbits than diurnal species (Kay & Cartmill 1977; Kay & Kirk 2000). Among mammals, relatively large eyes are also associated with increased visual acuity (Kiltie 2000). Taken in conjunction with their small body size, this may suggest that species of Litokoala were more agile arboreal folivores than the relatively sedentary sloth-like living species.

Species identification in extinct marsupials

In extant ecosystems, biologists identify species using a combination of criteria including morphological and genetic distinction, reproductive isolation, and geographical distribution. Palaeontologists, however, are generally restricted to morphological criteria as a means of determining species boundaries in the fossil record. Further, while a range of morphological criteria can be addressed in the diagnosis of extant species (e.g. external morphology, soft anatomy and skeletal anatomy; see Voss & Jansa 2009), palaeontologists are further restricted to a subset of these features, notably dental and/or skeletal remains. In the case of marsupials (and mammals in general), most extinct taxa are described on the basis of teeth and here we restrict our discussion to studies involving dentitions.

Archer & Dawson’s (1982) analysis of craniodental remains referable to the marsupial lion genus Thylacoleo from Wellington Caves, New South Wales indicated conservative tooth dimensions and morphologies suggesting only a single species was represented in the sample (T. carnifex). Extreme size variation was evident in cranial morphology, however, which may have been sexually dimorphic in nature.

Prideaux’s (2004) systematic review of the macropodid subfamily Sthenurinae indicated significant intraspecific variation in dental morphology, particularly in species with broad geographical ranges (e.g. Simosthenurus occidentalis, S. maddocki, S. pales and Procoptodon browneorum). Simosthenurus occidentalis was found to be one of the most variable sthenurines, yet the level of morphological variation found between regional samples was no greater than that found within samples. Geographical differences in size were evident, however, with molars of individuals from the south-western extent of S. occidentalis’s range being up to 19% smaller than those from south-eastern populations (Prideaux 2004).

Murray et al. (2000a, b) and Black & Hand (2010) have demonstrated significant craniodental morphological variation within populations of the Miocene diprotodontids Neohelos stirtoni and Nimbadon lavarackorum, respectively, including apparent sexual dimorphism in cranial morphology and broadscale variation in tooth morphology (but not dimensions). Consequently, Black & Hand (2010) synonymized Nimbadon whitelawi with the type species
$N. lavarackorum$, the morphological differences between the species being encompassed in the range of variation exhibited by $N. lavarackorum$.

Price (2008a) characterized interpopulational variation in the Pleistocene diprotodontid genus $Diprotodon$ by analysing a sample of > 1000 teeth from localities across its range. Prior to that study more than eight species of $Diprotodon$ had been described (Mahoney & Ride 1975). Price’s (2008a) morphometric analysis indicated the presence of only a single, wide-ranging, highly variable and sexually dimorphic species ($Diprotodon optatum$). Price & Sobbe (2011) documented asymmetry in premolar morphology within a single individual of $Diprotodon optatum$ that encompassed the extremes of variation recorded for the morphospecies as a whole.

Our study of variation in $P. cinereus$ dentitions highlights the need for caution when interpreting the significance of certain dental structures in determining species boundaries within selenodont marsupials. Our qualitative analysis indicates that a relatively high degree of intraspecific variation characterizes the dentition of the modern koala. Features found to be highly variable across all teeth examined include tooth shape and the expression and pattern of enamel crenulations, the developmental and orientation of cristae associated with the paraconule, neometaconule, protostyle and parastyle; the variation include: the development and orientation of the talonid on M3–4. Highly variable features of the lower molars (Figs 4–7), structures subject to a high degree of variation include: the development and orientation of the paracone, neomeatacone, protostyle and parastyle; the development and orientation of cristae associated with the major cusps; the development of the anterolinguinal fossa and lingual cingulum; the development of the stylar cusps; the depth and degree of closure of the buccal basins of the paracone and metacone; and the degree of reduction of the posterior moiety of M4. Highly variable features of the lower dentition (Figs 8–12) include: the construction of the longitudinal and posterobuccal crest of P3; the degree of development of the columnar stylids, entostylid ridge and buccal cingulum on the lower molars; the junction of the pre-entocristid with either the postmetacristid or postmetastylid cristid; the junction of the postprotocristid and cristid obliqua; and the degree of reduction of the talonid on M3–4.

Although significant differences in upper molar dimensions were apparent between the sexes of the Victorian population, there was no evidence of gender-specific morphometric differences in premolar or lower molar dimensions, or in individual tooth dimensions of Queensland specimens, nor did we observe qualitative morphological variation between male and female $P. cinereus$. Comparable results have been found in other studies of dental variation in extant marsupials. Freedman (1967) found no evidence of gender based morphological variation in the dentition of the modern long-nosed bandicoot $Perameles nasuta$, except for canine morphology; although metric differences were apparent (Freedman & Joffe 1967a). Similarly, Aplin et al. (2010) found considerable sexual dimorphism in upper and lower third premolar size in the bandicoot $Peroryctes broadbenti$, yet found no morphological differences between the sexes. Bartholomai (1971) found considerable morphological variation in dental morphology in both the eastern grey kangaroo $Macropus giganteus$ and agile wallaby $M. agilis$, while only the larger species, $M. giganteus$, exhibited significant sexual dimorphism in dental dimensions. In smaller species of $Perameles$ (e.g. $P. bougainville$), sexual dimorphism in skull and tooth size was not evident and morphological variation was not assessed (Freedman & Joffe 1967b). Aplin et al. (2010) noted similar patterns in the expression of sexual dimorphism in New Guinean bandicoots, with larger species being more strongly dimorphic (in features such as body weight, premolar dimensions and canine length and robustness) than smaller species.

**Geographical differences**

$Phascolarctos cinereus$ today occurs naturally in all states of Australia except Tasmania, Western Australia and the Northern Territory (Fig. 1). Koalas from southern populations (e.g. Victoria) are on average significantly larger than their northern (e.g. Queensland) counterparts and also display differences in pelage colour and thickness, and muzzle shape (Lee & Martin 1988). To reflect these morphological differences, early taxonomists recognized three subspecies: $P. cinereus victor$ (Troughton, 1935) from Victoria; $P. c. cinereus$ (Goldfuss, 1817) from New South Wales; and $P. c. adustus$ (Thomas, 1923) from Queensland. However, the distribution of these subspecies has never been adequately defined and was arbitrarily delineated by state borders rather than definitive geographical boundaries (Lee & Martin 1988; Sherwin et al. 2000; Strahan 2004). Genetic studies (e.g. Takami et al. 1998; Houlden et al. 1999) do not support subspecies distinction. Morphological differences between northern and southern populations may represent the ends of a gradual latitudinal cline (Sherwin et al. 2000; Strahan 2004); an apparent reflection of Bergmann’s rule (Mayr 1956).

Our morphometric analysis showed significant differences in some (but not all) tooth dimensions between northern and southern koala populations, yet results were not consistent across the sexes and did not always reflect Bergmann’s rule. Significant differences in upper molar dimensions were evident between northern and southern male populations, with molars and premolars of Victorian males consistently larger than those of Queensland males in all significantly different dimensions measured. Conversely, female upper tooth dimensions show very few significant differences between regions; those observed, with one exception, all showed Queensland specimens to be larger than Victorian specimens. Similarly, Bartholomai (1968) did not find any significant differences in $P. cinereus$ upper ($P^1–M^3$) tooth dimensions between Victorian and
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Queensland specimens, although his analysis did not include $M^3$ or the lower dentition. Our analysis of lower dentitions showed that significant differences in premolar dimensions were not evident between northern and southern populations. With regard to lower molars, some (but not all) molar dimensions showed significant differences and, of those, Victorian specimens were found to be consistently larger than Queensland specimens. Compared with upper dentitions, lower dentitions showed a greater consistency in which individual dimensions were found to be significantly different between males and females (Table 3).

Because $P. \text{cinereus}$ has a relatively wide geographical range it may be argued that the degree of morphological variation found in the present study represents the maximum level of variation expected for a species and may not be indicative of that found within a more geographically restricted fossil population. However, we found no evidence of any consistent differences or patterns in dental morphology between individuals from northern and southern regions. Further, variation within localities was as great as that found between regions.

Martin (2005) found similarly high morphological variation in cranial and dental features of the monotypic Patagonian opossum $Lestodelphys halli$ across its range, but could not identify significant differences between localities. Prideaux (2004) also found this to be the case for sthenurine species with broad geographical ranges (see above), albeit the distinction of these fossil species cannot be supported by molecular data as in the extant $L. halli$. Further, morphological variation in dentitions of extinct diprotodontids (e.g. $Neohelos stirtoni$, $Diprotodon optatum$ and $Nimbadon laversackorum$) from single localities indicate comparably high levels of variation (Murray et al. 2000b; Price & Piper 2009; Black & Hand 2010; Price & Sobbe 2011) as that found for $P. \text{cinereus}$.

**Taxonomy of Litokoala**

*Litokoala* Stirton et al., 1967 is sister taxon to the modern genus *Phascolarctos* (Black & Archer 1997; Black 1999; Black et al. 2012). Species have been identified from deposits within South Australia (Wipajiri and Etadunna Formations) and Queensland (Riversleigh World Heritage Area) spanning the Late Oligocene to Middle Miocene. However, the taxonomic distinction of several of these species (e.g. *L. kanunkaensis*, *L. dicktedfordi*) has been questioned (e.g. Louys et al. 2007; Pledge 2010) and stems from the lack of comparable material between taxa and poor preservation of the type material for both *L. kutjamarpensis* Stirton, Telford & Woodburne, 1967 and *L. kanunkaensis* Springer, 1987, the holotypes of which are single, isolated molars ($M^1$ and $M^2$, respectively).

Black & Archer (1997) referred six specimens from Riversleigh’s Faunal Zone C assemblages (Henk’s Hollow, Gag, Gotham, Jim’s Carousel Local Faunas) to *L. kanunkaensis*, including the first $P_3$, $M_1$, $M_3$, upper molar ($M^3$) and partial dentary (containing $P_3$–$M_2$) for the species. This referral was based on clear similarities between $M_2$ of the partial dentary (from the Henk’s Hollow Local Fauna) and the South Australian holotype. Some differences were noted (Black & Archer 1997, p. 220), but they did not fall outside the expected range of intraspecific variation gauged from comparing dentitions of the modern koala (see above). The $P_3$ and $M_3$, also from Henk’s Hollow Local Fauna, were referred on the basis of equitable size, morphology and locality. More recently, Louys et al. (2007) described the complete cheek tooth row of a partial skull from Jim’s Carousel Site, Riversleigh, and referred it to *L. kanunkaensis*. The complete tooth row allowed Louys et al. (2007) not only to assess morphological changes along the molar row, but also facilitated comparison of $M^1$ of *L. kutjamarpensis* with $M^1$ of *L. kanunkaensis*. Louys et al. (2007) found that the differences noted by Springer (1987) and Black & Archer (1997) as separating these species could be accounted for by both variation along the tooth row of a single individual and normal expected variation within a species. Consequently, Louys et al. (2007) made *L. kanunkaensis* a junior synonym of *L. kutjamarpensis*.


Further, Pledge (2010) questioned the taxonomic value of marsupial lower molars in general. However, within Phascolarctidae, lower molars are actually the most comparable element across species. In fact, the nominated holotypes of seven fossil phascolarctid species (e.g. *Perikoala palankarinnica* Stirton, 1957; *Perikoala robustus* Woodburne et al., 1987; *Madakoala devisi* Woodburne et al., 1987; *Madakoala wellsi* Woodburne et al., 1987; *Litokoala kanunkaensis*; *Phascolarctos yorkensis* Pledge, 1992; *Phascolarctos maris* Pledge, 1987) are lower dentitions and/or dentaries, with only four taxa known exclusively from upper dentitions. Thus, this extensive past usage demonstrates that the lower molars, at least within phascolarctids, do have substantial taxonomic utility.

By discounting the taxonomic value of lower dentitions, Pledge (2010) overlooked the numerous morphological similarities between the *L. kanunkaensis* holotype and the Riversleigh lower molar material originally described by Black & Archer (1997). Instead, Pledge (2010) referred all of the Riversleigh *Litokoala* lower dentitions to *L. dicktedfordi*. Although Pledge (2010) considered *L. dicktedfordi* to be represented by both upper and lower dentitions, in the specific diagnosis, comparisons with *L. kanunkaensis*...
were made using only the latter’s fragmentary upper molar material, and not the M₂ holotype.

Pledge (2010) identified the following features that apparently distinguish L. ‘dicktedfordi’ from L. kutjamarpensis: large size of M₁; larger, more angular parastyle; a sharper, more angular paracone and neomeataconule; and much younger geological age. In regard to the latter, geological age is an extrinsic feature of a species and, in itself, is of no value in determining species boundaries. It is noteworthy, however, that there is no evidence of a significant difference in age; biocorrelation of Riversleigh’s Faunal Zone C assemblages with the Kutjamarpu Local Fauna is well documented (e.g. Archer et al. 1997; Black 1997; Murray et al. 2000a; Travouillon et al. 2006; Gillespie 2007; Roberts et al. 2008, 2009), with at least seven shared taxa identified (see next section).

In terms of size, while the length of the L. ‘dicktedfordi’ M₁ is greater than that of L. kutjamarpensis, it is only about 8% bigger. On the basis of our above investigation of morphometric variation in the extant koala, such a minimal size difference is actually within the bounds of intraspecific size variation. The anterior and posterior widths of the L. ‘dicktedfordi’ M₁ are also smaller than that of L. kutjamarpensis. Louys et al. (2007) attributed differences between the L. kutjamarpensis holotype and QM F51382 (L. ‘dicktedfordi’ holotype) to differences in wear between the specimens and to the normal expected level of variation within a fossil species based on an unpublished qualitative analysis of variation in the modern koala by Black (1992). Such an interpretation is supported by our current study of the morphological and morphometrical variation in the modern koala, P. cinereus. Our findings indicate the features used by Pledge (2010) to distinguish L. ‘dicktedfordi’ from L. kutjamarpensis and L. kanunkaensis are highly variable within the modern species (see Figs 4–7). By extrapolating those findings, we would argue for a similar range of variation in the closely related genus, Litokoala. Our data indicate that such differences do not warrant specific distinction and further support Louys et al.’s (2007) interpretation of this material as referable to L. kutjamarpensis following synonymy of L. kanunkaensis with kutjamarpensis.

Although Pledge (2010) regarded L. kanunkaensis to be possibly a nomen dubium due to the paucity of material known from the type locality, he named a new species of Litokoala, L. thurmerae, on the basis of a single isolated M₁ (SAM P30159) from the Ngama Local Fauna of the Etadunna Formation, South Australia, that he described as being “somewhat damaged” and “well worn with all four principal cusps deeply eroded/corroded” (Pledge 2010, p. 82).

Pledge (2010) distinguished L. thurmerae from other species of Litokoala on the basis of its smaller size, the absence of enamel crenulations, and a small number of morphological differences including: cusp height; neomeataconule development; degree of convexity of the buccal tooth margin; and the presence of a cuspule on the buccal margin of the metacone. Unfortunately, most of the above features are not reliable diagnostic characters of species within Phascolarctidae because they are encompassed by the range of variation seen in L. kutjamarpensis (sensu Louys et al. 2007), and are highly variable in the modern koala, and thus likely also variable characters of fossil Litokoala. Other features identified by Pledge (2010) as distinguishing L. thurmerae (e.g. stylar cusp development, buccal cingulum development, angle enclosed by pre- and postmetaconules) were found to vary along the tooth row within individuals of both L. kutjamarpensis and P. cinereus.

With regard to enamel crenulations, while the presence or absence of enamel crenulations appears to be a valid distinguishing feature between species, our morphological analysis of P. cinereus dentitions indicates their extent and pattern to be highly variable. This is also the case within species of Litokoala. For example, L. garyjohnstoni shows a progressive reduction and change in pattern of molar crenulations from M₁ to M₃. Although Pledge (2010) used the absence of enamel crenulations in L. thurmerae as diagnostic for the species, he also called their validity into question (Pledge 2010, p. 85: “The worn and thegosed nature of the crown of the tooth may make statements about the enamel surface ornament suspect . . .”).

With regard to size, Pledge (2010, pp. 82–83) noted in his description of L. thurmerae that the tooth is damaged at the anterobuccal corner and lingual face of the protocone. It is also evident that the anterobuccal and lingual borders of the tooth are incomplete (Pledge 2010, fig. 1), but incompleteness of the specimen does not appear to have been accounted for (Pledge 2010, tables 1, 2), where the measurements given are not estimates. This suggests that the length and anterior width of the specimen have been underestimated, and hence the suggestion that L. thurmerae is 20–25% smaller than other Litokoala species is inaccurate and excessive. It should be noted that two different measurements for the length of the L. thurmerae M₁ were given by Pledge (2010, tables 1, 2) but this may be a typographical error. Further, Pledge (2010) stated that L. thurmerae is 25% smaller than L. kutjamarpensis, yet this value was calculated by comparing the length of M₃ with that of M₁. In all koalas, molar length decreases from M₁ to M₃. In the holotype of L. garyjohnstoni, for example, M₁ is 17% longer than M₃. Further, comparisons between modern koala M₁ lengths show a difference of almost 30% between the largest (8.73 mm) and smallest (6.75 mm) individuals measured, while a size difference of 10% is evident between the posterior widths of the left (4.37 mm) and right (4.86 mm) M₃ in a single individual of L. kutjamarpensis (Louys et al. 2007).

Pledge (2010) also suggested that the small size and more southerly location of L. thurmerae with respect to L. ‘dicktedfordi’ provided independent support for its taxonomic distinction. However, our results demonstrate Bergmann’s
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rule is not uniformly reflected in dental dimensions of the modern koala, *Phascolarctos cinereus*, and thus geographically related size differences are not reliable indicators of taxonomic distinction. Further, although as a general trend mammalian body size has been shown to be correlated with both geography (e.g. Bergmann’s rule) and time (e.g. Cope’s rule), many factors affect the optimum body size for a species, including resource availability and distribution, habitat structure, temperature, rainfall, and interspecific competition (see Price & Piper 2009; McNab 2010).

For these reasons, we regard the holotype (and only specimen, SAM P30159) to be of limited diagnostic value. Until more complete and diagnostic material (e.g. P3, M1 or M2) is recovered from the Mammal Hill type locality, we regard *Litokoala thurmerae* to be a *nomen dubium*.

**Chronology of *Litokoala***

Species of *Litokoala* have a temporal range spanning the Late Oligocene to the Middle Miocene. *Litokoala kutjamarpensis*, the most abundant species, spans this time period and also has the largest geographical range (South Australia and Queensland). *Litokoala kutjamarpensis* has been recorded from Faunal Zone E of the Etadunna Formation, South Australia (24.1–24.0 Ma; Megirian *et al.* 2010), the Kutjamarpu Local Fauna of the Wipajiri Formation, South Australia (23.4 Ma, Megirian *et al.* 2010), and Riversleigh’s Middle Miocene Faunal Zone C assemblages (Queensland). Both Louys *et al.* (2007) and Pledge (2010) have noted the apparent age disparity between these deposits. The maximum age of the Kutjamarpu Local Fauna has most recently been estimated to be 23.4 Ma (Late Oligocene) based on biostratigraphy of the Wipajiri Formation relative to the underlying magnetostratigraphically dated Etadunna Formation, with an age range of 23.4 Ma to 17.6 Ma (Megirian *et al.* 2010). This range is in general agreement with Archer *et al.*’s (1997) suggestion of an Early or Middle Miocene age for the Kutjamarpu Local Fauna based on biocorrelation with Riversleigh’s Faunal Zone B and Faunal Zone C (formerly System B–C) assemblages.

In addition to *L. kutjamarpensis*, taxa shared between the Kutjamarpu Local Fauna and Riversleigh’s Faunal Zone C assemblages include: the diprotodontid *Neohelos tirarensis* (Black 1997; Murray *et al.* 2000a; Black *et al.* in press); the thylacoleonid *Wakaleo oldfieldi* (see Gillespie 2007); and the pseudocheirids *Marlu kutjamarpensis, Marlu ampeles, Marlu syke* (see Roberts *et al.* 2009) and *Puljara tirarensae* (see Roberts *et al.* 2008). In fact, *Marlu kutjamarpensis* is recorded from three Riversleigh sites known to contain *L. kutjamarpensis* (i.e. Gag, Henk’s Hollow and Jim’s Carousel Sites; Roberts *et al.* 2009). Multivariate analyses (Travouillon *et al.* 2006) of species presence data could not resolve whether the Kutjamarpu Local Fauna grouped most closely with Riversleigh Faunal Zone B or C deposits because of a large degree of overlap in taxa between the respective assemblages.

*Litokoala thurmerae* is known from a single molar from the Ngama Local Fauna of the Etadunna Formation, while both *L. garyjohnstoni* and *L. dicksmithi* are known from isolated specimens from separate Early Miocene Faunal Zone B deposits at Riversleigh. Riversleigh’s Faunal Zone A assemblages have been shown to correlate with the Late Oligocene Ngapakaldi (24.6 Ma, Faunal Zone C; Megirian *et al.* 2010) and Ngama (24.1 Ma; Faunal Zone D; Megirian *et al.* 2010) Local Faunas of the Etadunna Formation based on the shared presence of *Ngapakaldia bonythoni* (see Black 2010) and *Kuterintja ngama* (see Myers & Archer 1997) respectively. Black (2010) has also recorded the presence of *Ngapakaldia bonythoni* in several of Riversleigh’s Faunal Zone B assemblages. Within the Etadunna Formation, Faunal Zones C and D are stratigraphically older than Faunal Zone E (24.0 Ma; Megirian *et al.*, 2010), which includes the type locality of *L. kamunkaensis*, a taxon since synonymized with *L. kutjamarpensis*. Hence, it is possible that some of Riversleigh’s Faunal Zone A and B assemblages may predate those of the Etadunna Formation.

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**Supplementary material**

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**References**


Identification of species boundaries in extinct koalas


