

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

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4 **Understanding morphological variation in the extant koala as a framework**
5 **for identification of species boundaries in extinct koalas (Phascolarctidae;**
6 **Marsupialia)**
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4 We document morphological variation (both geographical and sexual) in the dentition of the
5 extant koala, *Phascolarctos cinereus*, in order to facilitate discrimination of species
6 boundaries in extinct phascolarctids. Considerable variation is evident in dental structures
7 previously used to diagnose several phascolarctid fossil species. Consistent patterns of
8 morphological variation are not evident between sexes or geographic regions, with variation
9 as great between samples as within them. Metric variation is evident between the sexes in
10 upper molar dimensions with Victorian (southern) males significantly larger than Victorian
11 females, although this is not reflected in lower molar dimensions or in the Queensland
12 (northern) sample. Male koalas from southern populations generally display significantly
13 larger molars than their northern counterparts; however this trend is not evident in female
14 upper molar dimensions. In both males and females, some, but not all, lower molar
15 dimensions are larger in southern populations than northern. In light of these results, a
16 systematic revision of species of *Litokoala* suggests *L. 'dicktedfordi'* is a junior synonym of
17 *L. kutjamarpensis*, and the poorly known *L. thurmerae* is regarded to be a *nomen dubium*.
18 Further, we describe a partial cranium of a new species of koala from early Miocene
19 sediments in the Riversleigh World Heritage Area, northern Australia. *Litokoala dicksmithi* n.
20 sp. is the fifth koala species recorded from the diverse rainforest assemblages of Riversleigh
21 and the third species referred to the Oligo-Miocene genus *Litokoala*. Aspects of cranial
22 morphology, including a shortened robust rostrum and broad, irregular nasal aperture,
23 confirm placement of *Litokoala* as sister-taxon to the modern genus *Phascolarctos*.
24 Relatively large orbits and small body size suggest the possibility that *L. dicksmithi* was
25 nocturnal, had enhanced visual acuity, and was a more agile arboreal species than the
26 relatively sedentary extant koala.
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44 **Keywords:** intraspecific variation, morphometric, Phascolarctomorpha, rainforest, Miocene,
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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, 1967b), *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 sthenurines as part of a taxonomic review of the macropodid subfamily. Recently, several benchmark studies (e.g., Murray et al. 2000a, 2000b; Price 2008a; Black & Hand 2010; Price & Sobbe 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 Phascolarctomorpha 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 recognised, most taxa are known from scant dental remains. Inevitably, this has presented difficulties for species

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4 identification and taxonomic assignment. In particular, the Oligo-Miocene genus *Litokoala*,
5 sister-taxon to *Phascolarctos*, has had a controversial (see Louys et al. 2007; Pledge 2010),
6 albeit relatively short, taxonomic history. Prior to recent discoveries of partial crania
7 preserving complete tooth rows (e.g., Louys et al. 2007; this paper) from the Riversleigh
8 World Heritage Area, northwestern Queensland (Figure 1), the genus was known from a few
9 isolated teeth (see Stirton et al. 1967; Springer 1987).

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14 Assessment of species boundaries and intraspecific variation in previous systematic
15 studies of koalas by Black & Archer (1997), Louys et al. (2007) and Price (2008b) have been
16 based on unpublished qualitative accounts of variation in *P. cinereus* dentitions by the
17 authors (e.g., unpublished thesis of Black [1992]). Bartholomai (1968) documented metric
18 variation in P^3 - M^2 dimensions for a sample of modern Queensland *Phascolarctos cinereus*
19 specimens but restricted discussion of morphological variation to a few aspects of P^3 . Here
20 we present both qualitative and quantitative assessments of variation in the upper and lower
21 dentitions of *P. cinereus*. We then revisit the taxonomy of *Litokoala*, and describe a new
22 rainforest species from the Riversleigh World Heritage Area, northwestern Queensland,
23 Australia.

24 25 26 27 28 29 30 31 32 **Materials and methods**

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

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49 Modern koala specimens examined were derived from collections of the Queensland
50 Museum (Brisbane), Australian Museum (Sydney), University of New South Wales (Sydney)
51 and Museum Victoria (Melbourne). Fossil material described here is registered in the fossil
52 collection of the Queensland Museum. Reference to *Litokoala kutjampensis* throughout the
53 text is *sensu* Louys et al. (2007) unless stated otherwise. Higher-level systematic
54 nomenclature follows Aplin & Archer (1987). Molar morphology follows Archer (1978) with
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4 revisions by Tedford & Woodburne (1987; such that the metaconule is considered
5 homologous to the older term 'hypocone', and the cusp between the metacone and 'true'
6 metaconule is deemed the 'neometaconule'). Cheek tooth homology follows Luckett (1993).
7 Biostratigraphic nomenclature follows Travouillon et al. (2006), Woodburne et al. (1993) and
8 Creaser (1997).
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12 13 14 **Qualitative analysis**

15 A sample of 109 skulls from 55 localities in New South Wales, Victoria and Queensland
16 (Figure 1), was used to investigate qualitative morphological variation in the dentition of
17 modern *Phascolarctos cinereus* (see online supplementary data). Ten of these skulls were
18 from unknown localities, but were included in the analysis because of their clean, relatively
19 unworn dentitions. Only cheek teeth were examined and both sexes were represented in the
20 sample. It is recognised that *P. cinereus* exhibits marked sexual dimorphism with males being
21 significantly larger than females (Martin et al. 2008). However, it is unclear whether sexually
22 related differences are exhibited within dental morphology. Thus, an initial assessment of
23 morphological variation in each sex was made to determine whether any morphologies or
24 patterns might be gender specific. Similarly, in order to assess whether morphologies or
25 patterns of morphological variation were evident within and/or between geographical regions,
26 variation in specimens from New South Wales, Victoria and Queensland populations was
27 assessed independently. An example of *Phascolarctos cinereus* upper and lower dentitions
28 and the dental nomenclature used in this analysis are provided in Figure 2. A representative
29 sample of morphologies for each tooth position is illustrated in Figs 3-12. Figured specimens
30 were selected on the basis of least wear.
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44 **Quantitative analyses**

45 *Phascolarctos cinereus* also exhibits distinctly different body sizes throughout its modern
46 geographic range. For instance, adult individuals within southern, higher latitude populations
47 (e.g., Victoria) typically range in body size from 8.5 to 12 kg. In contrast, individuals from
48 northern, lower latitudes (e.g., Queensland) are significantly smaller, weighing on average
49 from 5.1 to 6.5 kg (Martin et al. 2008). Thus, *P. cinereus* body size appears to represent a
50 latitudinal morphocline reflecting Bergmann's Rule (e.g., Meiri & Dayan 2003). However, it
51 has never been demonstrated that such latitudinal differences are also reflected in dental
52 morphometrics. Thus, using teeth as a surrogate for body size (following Gould 1975 and
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4 Myers 2001), we test the following hypotheses: 1) that no significant difference in premolar
5 and molar dimensions exist between koalas from southern (Victorian) and northern
6 (Queensland) populations; and 2) that no significant difference in premolar and molar
7 dimensions exist between male and female individuals from the same geographic region. We
8 test these hypotheses independently for upper and lower dentitions. Understanding such size
9 variation in the modern koala is critical for establishing the significance of morphometric
10 differences between fossil species.
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16 In order to test the hypotheses, we took a series of dental measurements from museum
17 specimens originally sourced from Queensland and Victorian populations. Linear
18 measurements were made for premolars and molars of adult individuals using Mitutoyo
19 digital calipers and included: maximum length, anterior width (maximum width across
20 anterior root) and posterior width (maximum width across posterior root) for premolars, and
21 maximum length, anterior width (maximum width across trigon/trigonid) and posterior width
22 (maximum width across talon/ talonid) for molars. This approach is consistent with numerous
23 other morphometric dental studies of not only koalas (e.g., Bartholomai 1968; Price 2008b;
24 Price et al. 2009; Pledge 2010), but marsupials in general (e.g., Freedman 1967; Freedman &
25 Joffe 1967a, 1967b; Bartholomai 1971; Price 2002, 2005, 2008a; Easton 2006; Black & Hand
26 2010) and allows for direct comparison of results between respective investigations. Both
27 upper (n = 49) and lower (n = 70) dentitions were measured. Analyses were performed using
28 PAST (version 1.51; Hammer et al. 2006) computer software. Univariate statistics for dental
29 measurements are provided in Appendix 1. Multivariate Analysis of Variance (MANOVA)
30 was used to assess any differences indicated by whole tooth rows, as well as individual teeth.
31 This method enables simultaneous comparisons of all three measurements and, in the case of
32 tooth rows, more than one tooth position at a time. Differences were considered to be
33 significant at the 95% confidence interval. Where significant differences were found in the
34 morphometrics of a particular tooth position, the measurements of that tooth were compared
35 between groups using t-tests. Only significant differences are reported (Tables 1-3).
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50 **Institutional abbreviations**

51 AM M, AM P and AM S, Australian Museum mammal collection; AR, specimens
52 temporarily held in collections at the University of New South Wales; QM F, Queensland
53 Museum Fossil collection; QM J and QJM Queensland Museum Mammal collection; NMV
54 C, Museum Victoria Mammal collection; NMV P, Museum Victoria Palaeontology
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4 collection; SAM P, South Australian Museum Palaeontological collection; UCR, University
5 of California, Riverside Palaeontology collection.
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11 12 13 14 **Morphological and morphometric variation in *Phascolarctos cinereus***

15 16 17 **Description and morphological variation**

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19 Aspects of the dental morphology of *Phascolarctos cinereus* have been described by
20 Stirton (1957), Archer (1978) and Lanyon & Sanson (1986). Cheek tooth morphology is re-
21 described here using current dental terminology (Fig. 2B) and including a discussion of
22 intraspecific variation.
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25 **P³**. Subovate tooth that is wider posteriorly than anteriorly (Figs 3A-F). In juvenile unworn
26 specimens (e.g., QM J13278) three distinct apices are positioned anteriorly, medially and
27 posteriorly along a mildly buccally convex longitudinal crest. A posterobuccal ridge is
28 generally associated with the posterior-most cusp (Figs 2B, 3F). Anteriorly, the longitudinal
29 crest bifurcates into short spurs (buccal and lingual) that fade into the base of the tooth crown
30 (Fig. 3C). A well developed, variably cusped lingual cingular ridge (Figs 2A-B, 3A) meets
31 the longitudinal crest at the posterior tooth margin, forming a trench between them.
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37 Variable features of P³ include: tooth shape; the degree of surface enamel crenulations; the
38 development of lingual and buccal ridges from the longitudinal crest; the extent of
39 bifurcation, both anteriorly and posteriorly, of the longitudinal crest; the degree of inflection
40 of the longitudinal crest; the presence of a posterobuccal cuspule at the base of the crown
41 (Figs 3A, 3D); and the degree to which the lingual cingulum extends anteriorly. In Fig. 3F,
42 for example, the lingual cingulum is continuous anteriorly with a lingual crest from the
43 longitudinal crest. A unique pocket is formed between these structures and the well
44 developed lingual crest which extends from the anterior apex of the longitudinal crest. A
45 similar pocket can be formed at the posterolingual (Fig. 3B) or posterobuccal tooth corners
46 (Fig. 3F).
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53 **M¹⁻⁴**. Molars selenodont; trapezoidal in occlusal view with anterior tooth moiety wider than
54 posterior moiety (Figs 2A-B). Variation is evident in overall tooth outline, in particular the
55 degree of convexity of the buccal tooth margin of M¹⁻⁴ (Figs 4-7) and anterior extension of
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4 the parastylar corner (M^1 only; Figs 4A-F). Four main pyramidal cusps: anterobuccal
5 paracone, posterobuccal metacone, anterolingual protocone and posterolingual metaconule.
6 Metacone tallest cusp, followed by subequal paracone and metaconule, then protocone.
7 Protocone generally taller than metaconule on M^{3-4} . Protocone lies lingually opposite
8 paracone, and metaconule lies lingually opposite metacone. Protocone apex slightly lingually
9 displaced with respect to metaconule apex but may be directly anteriorly opposite in some
10 specimens.
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16 Buccal selene comprised of prominent pre- and postcristae that descend anterobuccally
17 and posterobuccally (respectively) from the apices of the paracone and metacone towards the
18 buccal tooth margin (Figs 2A-B). Resultant buccal surfaces of the paracone and metacone are
19 triangular in occlusal outline. Preparacrista, postparacrista, premetacrista and postmetacrista
20 bifurcate at buccal margin into short anterior and posterior spurs which define stylar cusps B,
21 C, D and E, respectively. The buccal basins of the paracone and metacone are variably open
22 or closed depending on the development of the stylar border and vary greatly in depth.
23 Generally, the metacone buccal basin is open on M^{3-4} . Varying development of stylar cusps
24 consequently affect the degree of concavity of the buccal margin. In some specimens (e.g.,
25 AM M7356, AM M 7438, AM M12475, AR2626, QM J19170, P481) supernumerary
26 cuspules (i.e., in addition to stylar cusps A-E) are present on the stylar border of the paracone
27 and metacone and are most noticeable on M^{1-2} (Figs 4D, 4F)
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36 On M^1 , an additional stylar cusp, the parastyle (stylar cusp A), exists as an enlarged,
37 crenulated swelling of the anterobuccal cingulum (Figs 2A-B). The breadth, degree of
38 crenulation and degree to which the parastyle projects anteriorly is highly variable (contrast
39 Fig. 4A with Fig. 4F). It is sometimes connected to the paraconule (Fig. 4A). In AM M7364
40 an anterobuccal pocket is formed between the bases of the parastyle, paraconule,
41 preparacrista and anterolingual paracrista.
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46 A posterolingual paracrista is present in all specimens studied, the base of which is
47 variably crenulated. It either terminates at the posterolingual base of the paracone (Fig. 4D)
48 or extends further into the transverse median valley to intersect the buccal spurs from the
49 junction of the postprotocrista and the premetaconulecrista. The latter condition is most
50 apparent in M^{3-4} (Figs 6-7). A buccal spur off the posterolingual paracrista is variably present
51 and appears to form part of the transversely orientated crenulation pattern found in the
52 transverse valley of some upper molars (Fig. 5A).
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4 The anterolingual paracrista (Figs 4C, 5A), anterolingual metacrista (Figs 6E, 7C-D) and
5 posterolingual metacrista (Fig. 4B) are variably present. When present, these crests may be
6 well developed, extending from the apex of the paracone and metacone, or less defined,
7 extending basal to the apices of these cusps.
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11 The lingual selene is comprised of prominent pre- and postcristae that descend
12 anterobuccally and posterobuccally (respectively) from the apices of the protocone and
13 metaconule towards the longitudinal tooth valley (Figs 2A-B). The preprotocrista and
14 postmetaconulecrista are continuous with the anterior and posterior cingula, respectively.
15 The postprotocrista and premetaconulecrista meet lingual of the longitudinal valley and
16 radiate at their juncture into a series of enamel crenulations (Figs 4A, 4C). The
17 postprotocrista often bifurcates before its junction with the premetaconulecrista into a well-
18 developed posterolingual arm that extends into the valley between the protocone and
19 metaconule (Figs 4B-C). A well-developed anterolingual buttress of the metaconule (Figs 4B,
20 4F) is variably developed as are buccal ribs from the apices of the protocone (Figs 4D, 5E)
21 and metaconule (Figs 5F, 6A, 7C).
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29 A variably cusped lingual cingulum, which blocks the lingual exit of the transverse valley,
30 is present on M^{1-3} (Figs 4E-F, 5E) and sometimes M^4 (Fig. 7A). It is continuous with the
31 anterolingual buttress of the metaconule and the posterolingual arm of the postprotocrista
32 (generally on M^1) in individuals in which these ridges are present (Figs 4B-C,) and may be
33 highly crenulated (Fig. 4B). In AM M2185 (Fig. 4E), the lingual cingulum is cusped and
34 projects lingually well beyond the bases of the protocone and metaconule. In AM M5266
35 (Fig. 4B) it is similarly developed to the neomorphic cuspules characteristic of *L.*
36 *kutjamarpensis* and *L. garyjohnstoni*. An anterolingual buttress of the protocone (Figs 4B,
37 4D) is variably present as is the development of an anterolingual fossette. The latter structure
38 appears as a well developed, often crenulated pocket at the anterolingual base of the
39 protocone, bounded by the anterolingual cingulum, the anterolingual buttress of the
40 protocone and the preprotocrista (Figs 2A-B). It is well developed on M^1 of QM J13278 (Fig.
41 4A) and AR2626 (Fig. 4F) but generally absent on M^{2-4} ; except in QM J13278 (Fig. 5D)
42 where it is developed but to a lesser extent, on M^2 also.
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52 Molars are generally crenulated, although the degree of expression and pattern of surface
53 enamel crenulations are not constant between individuals. Most notably, in the transverse
54 valley of M^{1-4} enamel crenulations vary from a highly reticulate pattern in some individuals
55 (Fig. 4A) to well developed transverse parallel ridges which extend lingually from the
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4 postparacrista and the premetacrista (Figs 4D-E) in others. This feature also varies along the
5 tooth row within an individual specimen. The M^1 may exhibit a reticular crenulation pattern
6 whereas M^4 in the same individual exhibits well developed transverse ridges, or vice versa.
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9 As a result of variation in enamel crenulations, the structures of the parastyle, paraconule,
10 neometaconule and protostyle exhibit considerable intraspecific variation. These structures
11 vary not only in size and shape, but also in their orientation and connection to surrounding
12 structures.
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15 The paraconule is situated at the anterolingual base of the paracone with its long axis
16 variably running parallel to the preparacrista (Figs 4D, 5C) or more anteriorly directed in
17 some individuals (Figs 4B-C). It is either isolated at this point (Figs 4D-E) or connected to
18 the lingual base of the paracone and/or parastyle (M^1 only; Fig. 4C) and/or anterior cingulum
19 (Figs 5B, 5D). The paraconule varies from being a bulbous cuspsate structure (Figs 5C, 7B,
20 7D) to a relatively linear structure or, depending on the degree of crenulation, in some
21 individuals it is represented by a number of bifurcate arms that are relatively
22 indistinguishable from the enamel crenulations on the rest of the crown (Figs 5B, 5D).
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29 The neometaconule is situated at the anterolingual base of the metacone (Figs 2A-B) and
30 may be isolated at this point (Fig. 4D), or connected to the base of the metacone (Fig. 4A) or
31 anterolingual metacrista (Fig. 6E). It may be arcuate or relatively linear and is generally
32 highly crenulated. It is variably developed in individuals and, in the more posterior molars,
33 may be poorly distinguishable. The degree to which the neometaconule extends posteriorly
34 along the longitudinal valley between the metacone and metaconule varies between
35 individuals as does its anterobuccal extension along the transverse valley. The neometaconule
36 variably connects to the buccal spurs that extend from the junction of the postprotocrista and
37 premetaconulecrista (Figs 5A, 5E).
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44 The protostyle is a short ridge that originates from the preprotocrista at a point just lingual
45 to the longitudinal valley (Figs 2A-B). It is generally linear (although bifurcate in some
46 individuals) and varies in its extension posteriorly. In general it extends further posteriorly in
47 more posterior molars. In some specimens (e.g., QM J13278) it is indistinguishable from the
48 molar crenulation pattern (Figs 4A, 5D).
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52 A small pocket is formed between the anterior cingulum and an anterior crest from the
53 preparacrista at the anterobuccal corner of M^4 of one individual studied (AM M12475, Fig.
54 7D). The anterior crest of the preparacrista is not evident in any other tooth studied.
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4 Similarly, the left and right M^4 of one individual studied (AM M7364, Fig. 7F) are unique
5 in that these teeth are reduced (or malformed) to such an extent that they exist as small
6 rounded structures consisting of a rounded basin bordered by a continuous cingulum on
7 which only the apex of the presumed metacone is evident. Similar abnormal variations have
8 been noted in kangaroos (Archer 1975).

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12 **P₃**. Subovate tooth, wider posteriorly, tapering anteriorly (Figs 2C-D). Tooth shape varies
13 from elongate and narrow in some individuals (Fig. 8F) to shorter and bulbous in others (Fig.
14 8E). The buccal and lingual demarcation between the anterior and posterior moieties also
15 varies between individuals as does the lingual curvature of the tooth with respect to the molar
16 row. There are three main cusps positioned anteriorly, medially and posteriorly along a
17 longitudinal crest which varies in its degree of lingual deflection. The extent to which the
18 longitudinal crest curves around the lingual tooth margin, both anteriorly and posteriorly, is
19 variable (Figs 8C, 8E). Buccal ribs from the apices of the cusps on the longitudinal crest (Fig.
20 8F) are variably present. A well developed, variably cusped, crescentic crest occupies the
21 posterobuccal corner of the tooth, the nature of which is not constant between individuals. In
22 general, it extends posterobuccally from the medial cusp apex (Fig. 8B), but it can exist as an
23 isolated crest at the posterobuccal tooth corner (Fig. 8C). In some individuals it terminates
24 prior to meeting the posterior tooth margin, resulting in a posteriorly open crescentic trench
25 basal to the longitudinal crest (Fig. 8B). In other individuals the posterobuccal crest is highly
26 crescentic and curves towards (and may meet) the posterior apex of the longitudinal crest
27 resulting in a posterobuccal pocket (Figs 8A, 8D-E). An additional cusplule occupies this
28 pocket in Figure 8F. The height of the posterobuccal crest varies also from sitting relatively
29 high on the crown in some individuals (e.g., AR1574) to relatively lower in others (e.g., AM
30 M7486, Fig. 8E).

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34 **M₁**. Morphology of M_1 differs to that of M_{2-4} in its construction of the trigonid which is
35 comprised of three major cuspids: metaconid, protoconid and protostylid (Figs 2C-D). The
36 protoconid occupies a more lingual position than on M_{2-4} with its apex just buccal to that of
37 the anterolingually positioned metaconid to which it is connected by a short transverse crest.
38 The main anterobuccal cuspid is a large protostylid. An arcuate preprotostylid cristid extends
39 anterolingually to meet a linear anteriorly directed preprotocristid at the anterior tooth
40 margin. A slight swelling at this point may represent a weak paraconid. The linear
41 postprotostylid cristid descends posteriorly into the median transverse valley becoming
42 crenulate at its posterior base (Fig. 9D). Generally it bifurcates into lingual and posterior
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4 arms, but the extent to which these arms extend lingually and posteriorly, respectively, varies.
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6 In Figures 9B, 9E and 9F the lingual arm terminates basal to the postprotocristid, whereas it
7
8 is only weakly developed in Figures 9A and 9D. The posterior arm either terminates in the
9
10 transverse valley between the opposing bases of the protostylid and hypoconid (Fig. 9E), or
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12 transgresses this valley and meets the anterior base of the hypoconid, consequently blocking
13
14 the buccal exit of the transverse valley (Fig. 9A). Additionally, the posterior arm of the
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16 postprotostylid cristid meets a (variably present) anterobuccal spur from the cristid obliqua,
17
18 blocking the buccal exit of the transverse valley slightly lingual to the buccal margin (Figs
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20 9C-D).

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22 The postprotocristid of M_1 extends posteriorly (sometimes posterolingually) into the
23
24 transverse median valley where it generally meets an elongate anterolingually directed
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26 prehypocristid (cristid obliqua) (Figs 9A, 9C-F). In some specimens (e.g., AM M7438,
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28 AR1574) the postprotocristid terminates before meeting the prehypocristid, the latter
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30 extending further lingually and connecting to the preentocristid (Fig. 9B) or terminating basal
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32 to the postmetacristid (e.g., AM M7438).

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34 There does not appear to be a premetacristid on M_1 , although in some specimens a small
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36 columnar stylid at the lingual base of the metaconid possesses a short anterior spur (Figs 9C,
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38 9E). It is possible that the transverse crest linking the apices of the metaconid and protoconid
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40 on M_1 may represent a premetacristid. A well-developed columnar stylid is present on the
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42 lingual face of the entoconid, giving this cusp the appearance of having a twinned apex (Figs
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44 9E-F). On M_{1-4} the postmetacristid extends posterolingually from the metaconid apex and
45
46 may bifurcate just prior to the lingual tooth margin into short anterolingual and posterolingual
47
48 spurs (Figs 10D, 10F). These spurs (the premetastylid cristid and postmetastylid cristid)
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50 define the apex of the metastylid (Figs 2C-D). The preentocristid varies from a linear (Fig.
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52 9A) to highly arcuate crest (Fig. 9D), and is generally continuous with the postmetastylid
53
54 cristid at the median lingual tooth margin. This feature is often referred to as the metastylid
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56 fold (see Black & Archer 1997). In some specimens (e.g., AR1574), however, the
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58 preentocristid connects to the posterior base of the postmetacristid (Fig. 9B). A similar
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60 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
(Figs 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

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4 entostylid ridge on M_{1-3} (generally absent in M_{4s} examined except AM M5266) may exist as
5 a well developed cusped structure (Fig. 9D) or be relatively indistinguishable existing as a
6 series of discontinuous crenulate ridges at the posterobuccal base of the entoconid (Figs 10E-
7 F). In some specimens it is linear and mirrored by a parallel crest that extends anteriorly from
8 the posthypocristid (Figs 10C, 11A). In some individuals the entostylid ridge extends
9 anterobuccally from the postentostylid cristid and variably connects to the posterior cingulum
10 (AM M7486, AR1574) and a variably present anteriorly directed ridge off the posthypocristid
11 (Figs 9A-B). It is isolated at the posterobuccal base of the entoconid in others. The above-
12 mentioned variations for the entostylid ridge vary significantly along the tooth row in
13 individual specimens. In some specimens a variably defined crest or lingual rib descends
14 from the hypoconid apex into the longitudinal valley between the hypoconid and entoconid
15 (Figs 9C-D).

16
17 **$M_{2.4}$.** Subrectangular in occlusal view, longer than wide and much narrower than their
18 corresponding upper molars (Figs 2C-D). Comprised of four main cusps: an anterolingual
19 metaconid; posterolingual entoconid; anterobuccal protoconid; and posterobuccal hypoconid.
20 The lingual selene is composed of prominent pre- and postcristids that descend
21 anterolingually and posterolingually (respectively) from the apices of the metaconid and
22 entoconid towards the lingual tooth margin. The premetacristid is continuous with the
23 anterior cingulum. A slight swelling at their junction has been referred to by some authors
24 (e.g., Pledge 1987) as a parastylid. The construction of the talonid is similar to that described
25 for M_1 . Again, the preentocristid, although generally continuous with the postmetastylid
26 cristid, may terminate at the posterior base of the postmetacristid. This appears to be variable
27 within a single individual. In AR1574 for example, the latter condition is evident on the right
28 M_1 and M_3 and the left M_{1-3} , whereas the preentocristid connects to the postmetastylid cristid
29 on the remaining molars.

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31 The buccal selene is composed of prominent pre- and postcristids that descend
32 anterolingually and posterolingually (respectively) from the apices of the protoconid and
33 hypoconid towards the median longitudinal valley (Figs 2C-D). The preprotocristid
34 terminates at the anterior tooth margin and generally abuts the posterior cingulum of the
35 preceding tooth. It may be highly crenulated at its anterior extent (Figs 10F, 11E). On M_{2-3} of
36 all specimens studied the postprotocristid and cristid obliqua (prehypocristid) join at the
37 longitudinal valley and, in some individuals, a series of variably developed spurs spread
38 lingually from this junction (Fig 10C, 11E). On M_4 the cristid obliqua generally meets the
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4 postprotocristid (Fig. 12C) and/or the preentocristid (Figs 12A, 12D). A relatively deep
5 buccal valley is created between the posterior and anterior bases of the protoconid and
6 hypoconid, respectively, and the junction of the postprotocristid and cristid obliqua. A buccal
7 cingulum is generally present on M_{2-4} , but it is variably developed, may be crenulated (Fig.
8 10C), and in some individuals may ascend the anterobuccal face of the hypoconid (Fig. 10A).
9 A small styler cusp medially positioned on the buccal cingulum at the buccal tip of the valley
10 separating the trigonid and talonid of M_{2-4} is variably developed.

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16 Columnar stylids are present on both the metaconid and entoconid of M_{2-4} giving these
17 cusps a 'twinned' appearance (Figs 2C-D). Their development varies from strongly (Fig.
18 10D) to poorly developed between individuals and along the tooth row becoming reduced in
19 the more posterior molars (Figs 12B-D). In some individuals the columnar stylid of the
20 metaconid of M_2 is antero-posteriorly broad with well developed anterior, posterior and
21 transverse accessory crests (Fig. 10F). In others (e.g., AR6071) the columnar stylids are well-
22 developed but irregular structures composed of a series of ribs descending the lingual face of
23 the metaconid and entoconid.

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29 Again, the pattern of enamel crenulations is highly variable and, as a result, the
30 morphology of the postprotostylid cristid (in M_1), the cristid obliqua and the entostylid ridge
31 are not constant between individuals. Other features found to vary within the lower molars
32 include: the development of the lingual shelf of the metaconid and entoconid; and the
33 presence or degree of development of lingual ribs from the apices of the protoconid and
34 hypoconid on M_{2-4} , and the hypoconid of M_1 . In AM M7438 (Fig. 12E) well developed
35 posterolingually directed ribs extend from the protoconid apex into the longitudinal valley on
36 M_{3-4} (absent on M_{1-2}). Tooth shape varied from sub-rectangular (Fig. 10D) to ovate (Fig. 10E)
37 depending on the development of the metastylid, entostylid and columnar stylids on the
38 lingual tooth margin and the degree of reduction of the talonid, particularly in more posterior
39 molars (e.g., contrast Fig. 12C with Fig. 12D).

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47 **Variation along the tooth row.** Upper molars: Molar crenulations may change from a
48 reticular crenulation pattern to more transverse alignment from M^{1-4} , or vice versa. Some
49 specimens show reduction in crenulations from M^{1-4} (e.g., AM M12475; contrast Fig. 5F with
50 Fig. 7D). The angle between the premetacrista and postmetacrista at the metacone apex
51 becomes wider from M^{1-3} with associated increased length of the metacone buccal margin
52 (Figs 2A-B). On M^{3-4} the postmetacrista shortens both absolutely and with respect to the
53 length of the premetacrista (Figs 2A-B). As a consequence, the buccal margin of the
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metacone becomes obliquely oriented with respect to the antero-posterior plane of the tooth. The buccal basins/surfaces of the paracone and metacone become progressively shallower from M^{1-4} . This feature is most noticeable on the metacone wherein the styler shelf is progressively reduced and often absent in M^{3-4} . Generally the paraconule and neometaconule become weaker through M^{1-4} (Figs 2A-B) becoming indistinguishable from the enamel crenulation pattern in more posterior molars (Fig. 6D), although, some specimens (e.g., AR2626) have a paraconule on M^2 that is as well-developed as that of M^1 . The posterior moiety becomes progressively reduced (bucco-lingually) with respect to the anterior moiety. This is most pronounced in M^4 with often extreme reduction of both the metacone and metaconule (Fig. 7A). The protostyle generally becomes more antero-posteriorly elongate in M^{2-3} (and sometimes M^4) but may be reduced in M^4 (although in some specimens the protostyle is progressively reduced from M^{2-4} ; e.g., AR2626). The posterolingual paracrista may become more prominent from M^{1-4} . The anterolingual fossette (and associated anterolingual buttress from the protocone apex) if present in M^1 , is generally absent in M^{2-4} (although it is present in M^{1-3} of AR8398). M^{2-4} lack the well-developed parastylar region of M^1 and in most M^4 a well-developed anterolingual metacrista is developed (Figs 7A, 7C-E) (yet absent in M^{1-3}). The lingual pocket between the posterior base of the protocone, the anterior base of the metaconule and the lingual cingulum is progressively reduced from M^{1-4} and a lingual cingulum may be absent entirely on M^4 (Figs 2A-B).

Lower molars: The columnar stylids of the metaconid and entoconid become progressively reduced from M_{2-4} as do the metastylid and entostylid (Figs 2C-D). Tooth shape generally changes from subrectangular in M_2 to ovate in M_4 with more arcuate anterior, lingual and posterior tooth margins. The molars become progressively narrower through M_1 to M_4 . The entostylid ridge is reduced from M_{1-3} and is absent in all M_4 s (and some M_3 s). The buccal valley between the protoconid and hypoconid is reduced in area and depth from M_2 - M_4 (Figs 2C-D), and the buccal cingulum (including associated crenulations/cuspids, 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

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4 may be useful in distinguishing phascolarctid species are generally restricted to the premolar
5 and first molar of the upper and lower tooth rows.
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8 Features consistently developed on P^3 of *P. cinereus* include: the presence of a midline
9 longitudinal crest; the number of major cusps (three) developed along this crest and the
10 presence of a lingual cingulum. Consistent features developed on M^1 include: the relative
11 height of major cusps; the presence of a parastyle, protostyle, paraconule, neometconule,
12 posterolingual paracrista, and lingual cingulum. All *P. cinereus* M^1 s possess enamel
13 crenulations (albeit they vary in degree and pattern of expression). Consistent features
14 developed on P_3 include: a midline longitudinal crest with three cusps (anterior, medial and
15 posterior) and the presence of a posterobuccal crest. Consistent features of M_1 include: the
16 relative height of major cusps; the development and position of the protostylid; the
17 presence of a metastylid, entostylid and entostylid ridge; the presence of a columnar stylid on
18 the entoconid; and the presence of a transverse crest connecting the apices of the metaconid
19 and protoconid. As in M^1 , all lower first molars possess enamel crenulations.
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23 In general, the shape, extent and degree of development of many structures on *P. cinereus*
24 teeth were found to be highly variable. Consequently, as a general rule, the presence or
25 absence of a structure (as opposed to its shape or relative development) appears more useful
26 in discriminating species boundaries in phascolarctids. Nevertheless, the relative
27 development of a structure may fall outside the expected range of variation for a species and
28 as such, may still be a useful diagnostic feature. *Nimiokoala greystanesi* M^1 s for example
29 exhibit consistently large, pyramidal parastyles and large, bicuspid neometaconules that are
30 diagnostic for the species (Black & Archer 1997).
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45 **Morphometric analysis**

46 **Upper dentition.** MANOVA of upper tooth dimensions of male *P. cinereus* showed
47 significant differences between northern (Queensland) and southern (Victorian) populations
48 ($F = 3.225$, d.f. = 15, 11, $p = 0.028$). Likewise significant differences in upper tooth
49 dimensions between females from Queensland and Victoria were observed ($F = 7.451$, d.f. =
50 15, 9, $p = 0.002$). For both male and female koalas, significant differences between
51 geographic regions existed for each tooth position (Male: P^3 : $F = 5.064$, d.f. = 3, 23, $p =$
52 0.008; M^1 : $F = 3.661$, d.f. = 3, 23, $p = 0.027$; M^2 : $F = 4.817$, d.f. = 3, 23, $p = 0.01$; M^3 : $F =$
53 4.732, d.f. = 3, 23, $p = 0.01$; M^4 : $F = 5.376$, d.f. = 3, 23, $p = 0.006$. Female: P^3 : $F = 3.973$, d.f.
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4 = 3, 21, $p = 0.022$; M^1 : $F = 5.404$, d.f. = 3, 21, $p = 0.006$; M^2 : $F = 3.742$, d.f. = 3, 21, $p =$
5 0.027; M^3 : $F = 7.113$, d.f. = 3, 21, $p = 0.002$; M^4 : $F = 3.219$, d.f. = 3, 21, $p = 0.044$). Analysis
6 of individual tooth measurements suggests that the Victorian male population has on average
7 greater lengths of both premolars and molars, and larger anterior widths of molars (M^1 - M^3)
8 than Queensland males. Only the M^2 showed significantly different posterior widths (Table
9 1). For females, very few of the individual tooth measurements were significantly different
10 between regions, the notable exception being the posterior widths of P^3 , M^1 and M^2 which
11 were larger for Queensland koalas (Table 1).
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18 MANOVA of upper tooth dimensions between male and female koalas from Queensland
19 showed no significant differences between the sexes ($F = 1.267$, d.f. = 15, 13, $p = 0.338$), yet
20 significant differences were evident in the Victorian sample ($F = 5.405$, d.f. = 15, 7, $p =$
21 0.0157). Male and female premolars did not differ significantly; only molars showed
22 significant differences between the sexes (M^1 : $F = 7.309$, d.f. = 3, 19, $p = 0.002$; M^2 : $F =$
23 10.64, d.f. = 3, 19, $p < 0.001$; M^3 : $F = 4.48$, d.f. = 3, 19, $p = 0.0154$; M^4 : $F = 9.752$, d.f. = 3,
24 19, $p < 0.001$). Analysis of individual tooth measurements showed that Victorian male koalas
25 have significantly bigger molars in all dimensions with respect to females, except for the
26 posterior width of M^4 (Table 2).
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32 **Lower dentition.** MANOVA of lower tooth dimensions of male *P. cinereus* showed
33 significant differences between northern (Queensland) and southern (Victorian) populations
34 ($F = 13.5$, d.f. = 15, 14, $p < 0.001$). With respect to individual teeth, both premolars and
35 molars of males from northern and southern populations differed significantly in dimensions
36 (P_3 : $F = 5.661$, d.f. = 3, 26, $p = 0.004$; M_1 : $F = 10.57$, d.f. = 3, 26, $p < 0.001$; M_2 : $F = 7.956$,
37 d.f. = 3, 26, $p < 0.001$; M_3 : $F = 7.121$, d.f. = 3, 26, $p = 0.001$; M_4 : $F = 6.973$, d.f. = 3, 26, $p =$
38 0.001). MANOVA of lower tooth dimensions of female *P. cinereus* showed significant
39 differences between northern (Queensland) and southern (Victorian) populations ($F = 5.621$,
40 d.f. = 15, 24, $p < 0.001$). With respect to individual teeth positions, premolars did not show
41 any significant differences in dimensions measured ($F = 0.6496$, d.f. = 3, 36, $p = 0.6$),
42 however molars from northern and southern populations differed significantly (M_1 : $F =$
43 7.568, d.f. = 3, 36, $p = 0.0004$; M_2 : $F = 4.01$, d.f. = 3, 36, $p = 0.015$; M_3 : $F = 5.356$, d.f. = 3,
44 36, $p = 0.004$; M_4 : $F = 4.746$, d.f. = 3, 36, $p = 0.007$). Analysis of the individual tooth
45 measurements showed that for both male and female koalas, Victorian specimens were
46 significantly larger than Queensland specimens in the following dimensions: M_3 and M_4
47 length, M_1 and M_2 anterior width, and M_1 posterior width (Table 3). MANOVA of lower
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4 tooth dimensions between male and female koalas from Victoria and between male and
5 female koalas from Queensland showed no differences existing along the tooth row
6 (Queensland: $F = 1.41$, d.f. = 15, 31, $p = 0.2035$; Victoria: $F = 2.359$, d.f. = 15, 7, $p =$
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8 0.1275).
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14 Systematic Palaeontology

17 Class **Marsupialia** Illiger, 1811

18 Order **Diprotodontia** Owen, 1866

19 Suborder **Vombatiformes** Woodburne, 1984

20 Infraorder **Phascolarctomorpha** Aplin & Archer, 1987

21 Family **Phascolarctidae** Owen, 1839

22 Genus ***Litokoala*** Stirton, Tedford & Woodburne 1967
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29 **Type species.** *Litokoala kutjamarpensis* Stirton, Tedford & Woodburne, 1967

30 **Additional species.** *L. garyjohnstoni* Louys, Black, Archer, Hand & Godthelp, 2007;

31 *Litokoala dicksmithi* sp. nov.
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34 **Diagnosis.** In addition to the dental (e.g., Black & Archer 1997; Louys et al. 2007) and
35 cranial features (Louys et al. 2009) described elsewhere, species of *Litokoala* differ from all
36 other phascolarctids in having a twinned or secondary infraorbital foramen, a prominent
37 masseteric process composed entirely of maxilla, an almost vertically-oriented premaxilla-
38 maxilla suture on the lateral face of the rostrum and a large, anteriorly extensive lacrimal.
39 *Litokoala* species differ from *Phascolarctos* species in having proportionately larger orbits, a
40 less constricted rostrum anteriorly at the level of the incisor arcade, a shallow maxillo-labial
41 fossa, and a zygomatic arch that projects posterolaterally (as opposed to laterally) from the
42 face. *Litokoala* species differ from *Nimiokoala* species in having a relatively shorter, broader,
43 deeper rostrum, a broader maxillary palate, and a larger, broader narial aperture with an
44 irregular border (as in *Phascolarctos*). Louys et al. (2007, p.100) differentiated *Litokoala*
45 species from other phascolarctids by possession of "... a well-developed neomorphic cuspule
46 at the anterolingual base of the metaconule of M^1 (with the exception of species of
47 *Phascolarctos* de Blainville, 1816 where it is variably present)". Because this feature is
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4 variably present in *Phascolarctos*, absent in *Litokoala dicksmithi* and unknown for *L.*
5 *thurmerae* (known only from M³) we do not regard it to be diagnostic for the genus.
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9 *Litokoala kutjampensis* Stirton, Tedford & Woodburne 1967
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12 1987 *Litokoala kanunkaensis* Springer; 320-323, figs 1-2
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14 2010 *Litokoala dicktedfordi* Pledge; 81-82, fig. 5
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17 **Holotype.** SAM P13845, right M¹
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19 **Material.** From Kanunka North Site: SAM P32397, a right M₂; UCR21945, a right M₄;
20 UCR21980, a metacone of a right M³; UCR21979, a metacone of a left M¹. From
21 Riversleigh: QM F30500, right P₃, QM F13079, right dentary fragment with posterior half of
22 P₃, M₁₋₂, QM F30502, right M³, Henks Hollow Local Fauna; QM F30501, right M₁, Gag
23 Site; QM F30503, M^x fragment containing paracone and buccal half of protocone, Gotham
24 Site; QM F51382, a partial skull with left and right P³, M¹⁻⁴, Jim's Carousel Site; QM
25 F20809, right M₃, JC9 Site.
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30 **Occurrence.** The Holotype is from the Kutjamparu Local Fauna, Leaf Locality, Lake
31 Ngapakaldi, Wipajiri Formation, South Australia which is interpreted to be early to Miocene
32 in age (Woodburne et al. 1993; Travouillon et al. 2006). Kanunka North Site (Zone E of the
33 Etadunna Formation) is located on the west side of Lake Kanunka, South Australia. This
34 deposit is late Oligocene in age (Woodburne et al. 1993). The Henk's Hollow, Gag, Gotham,
35 Jim's Carousel and JC9 Sites from the Riversleigh World Heritage Area, Lawn Hill National
36 Park, northwestern Queensland, are Faunal Zone C deposits which are interpreted to be
37 middle Miocene in age (Creaser 1997; Arena 2005; Travouillon et al. 2006).
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44 **Remarks.** Dental descriptions of *L. kutjampensis* are provided in Stirton et al. (1967),
45 Black & Archer (1997; as *L. kanunkaensis*) and Louys et al. (2007), and description of the
46 cranium is given by Louys et al. (2009). Arguments for subsuming *L. kanunkaensis* into *L.*
47 *kutjampensis* can be found in Louys et al. (2007) and are recounted in the discussion
48 below. Arguments for synonymising *L. 'dicktedfordi'* with *L. kutjampensis* are also given
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55 *Litokoala garyjohnstoni* Louys, Black, Archer, Hand, & Godthelp 2007
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57 **Holotype.** QM F51405, left partial maxilla with P³, M¹⁻³
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4 **Material.** Paratype, QM F51406, left M⁴

5 **Occurrence.** Outasite, Godthelp Hill, Riversleigh World Heritage Area, Lawn Hill National
6 Park, northwestern Queensland. Outasite is a Faunal Zone B deposit and is interpreted to be
7 early Miocene in age (Creaser 1997; Travouillon et al. 2006).
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9 **Remarks.** *Litokoala garyjohnstoni* is described in Louys et al. (2007).
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14 *Litokoala dicksmithi*, sp. nov.

15 (Figs 13-14)

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17 **Diagnosis.** Rostrum short with twinned infraorbital foramen; narial aperture broad with
18 irregular border. Differs from other *Litokoala* spp. in: its deeper transverse and longitudinal
19 valleys in the upper molars; its larger, broader protocone in the upper molars; lacking a
20 neomorphic cuspule at the anterolingual base of the metaconule on M¹ (unknown for *L.*
21 *thurmerae*); and P³ lacking a lingual cingulum with narrower, shallow lingual valley
22 (unknown for *L. thurmerae*). Differs from *L. garyjohnstoni* in: its longer, more prominent
23 masseteric process; P³ with reduced medial and posterior lingual cusps and reduced
24 anterobuccal crest from medial midline cusp; reduced molar crenulations; and posteriorly
25 narrow upper molars across the metacone and metaconule. Differs from *L. kutjampensis* in:
26 its less linear arrangement of midline cusps and crests on P³; and lacking an anterolingual
27 metacrista on upper molars.
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30 **Derivation of name.** The specific name honours Dick Smith, Australian aviator, adventurer
31 and philanthropist for his long-term financial support of Australian scientific endeavour and
32 in particular fossil research at Riversleigh.
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35 **Holotype.** QM F54567, partial anterior skull with left I¹, P³, M¹, partial M²; right P³, M¹⁻⁴.
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37 **Occurrence.** Ross Scott Orr (RSO) Site, Faunal Zone B (Travouillon et al. 2006),
38 Riversleigh World Heritage Area, northwestern Queensland; early Miocene.
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40 **Description.** Adult skull with right P³-M⁴, LI¹, LP³-M². Approximately the same size as
41 *Litokoala kutjampensis* skull (QM F51382) judging by width of the palate and length of
42 tooth row, and slightly shorter than *Nimiokoala*. We estimate the total length of the skull
43 (based on overlap with QM F51382) to have been approximately 76 mm which is suggestive
44 of a relatively short, broad skull. Right side preserves nasal, premaxilla, maxilla, lacrimal,
45 part of the frontal, orbitosphenoid, endocranial portion of the alisphenoid, anterior jugal,
46 partial palatine (Fig. 13A). Left side is largely missing, preserving only the premaxilla, nasal,
47 and partial maxilla. Cranial and dental measurements are given in Tables 4-5, respectively.
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4 The description is restricted to the right hand side. Comparisons are made throughout with
5 *Phascolarctos cinereus* (hereafter *Phascolarctos*) and *Nimiokoala greystanesi* (hereafter
6 *Nimiokoala*), the only two koala species with which there is considerable overlap with the
7 skull portion preserved.
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10 Facial region. Rostrum short and relatively deep (17.9 mm at C¹ alveoli), tapers slightly
11 anteriorly. Shorter and deeper than *Nimiokoala* and similarly proportioned to *Phascolarctos*.
12 Slight inflation of premaxilla portion of rostrum dorsolaterally, but not to the extent as seen in
13 *Phascolarctos* in which the rostrum in anterior view is distinctly keyhole-shaped (i.e., broad
14 dorsally, narrow ventrally). In *L. dicksmithi* and *Nimiokoala*, the rostrum is slightly broader
15 ventrally than dorsally and not constricted as in *Phascolarctos*. Nasals are wide posteriorly,
16 taper anteriorly and flare slightly at their anterior extremity (Fig. 13C). Although the nasals
17 are broken anteriorly it appears that their anterior border was quite irregular as in
18 *Phascolarctos* which has numerous short anterior projections. This is unlike the condition
19 found in most other diprotodontians (possibly including *Nimiokoala*) in which the anterior
20 border of the nasals is well defined and medially tapering. The nasals are dorsally flattened as
21 in *Nimiokoala* and unlike in *Phascolarctos* where they are mildly convex and inflated. Naso-
22 frontal suture is broad (11.1 mm) and transversely orientated (Fig. 13C). The nasals are
23 slightly inflated laterally at this suture and the frontals more inflated dorsally than in
24 *Nimiokoala*, indicating a slightly deeper skull for *L. dicksmithi*. Nasal aperture (Fig. 13D)
25 broader (12.91 mm) than high (10.15 mm), larger than *Nimiokoala* (8.47mm wide, 7.42mm
26 high), and similarly proportioned to *Phascolarctos*. Premaxilla short, premaxilla-maxilla
27 suture vertically orientated in lateral view terminating dorsally at its junction with the nasals
28 at a point vertically in line with the infraorbital foramina (Fig. 13A). This is unlike the
29 condition in *Nimiokoala* and *Phascolarctos* where it runs diagonally (posterodorsally) across
30 the lateral side of rostrum and terminates dorsally at its junction with the nasals at a point
31 vertically in line with P³. In lateral view, the premaxilla-maxilla suture originates at the
32 anterior base of the canine as it does in *Phascolarctos*, extending through the canine alveoli
33 to emerge on palatal surface at the posteromedial base of the canine (Fig. 13B). Interincisive
34 foramina mostly contained within the premaxilla, yet bordered posteriorly and
35 posterolaterally by maxilla (Fig. 13B). The interincisive foramina are larger than in
36 *Nimiokoala* and relatively and absolutely larger than most *Phascolarctos*. Incisor arcade U-
37 shaped, wider and shallower than *Nimiokoala*, much shallower than the deep premaxillary
38 palate of *Phascolarctos*. Distance between incisors and canine is short (2.2 mm), and
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4 proportionately more similar to *Phascolarctos* than to *Nimiokoala* (4.2 mm). The maxillary
5 palate is broad as in *L. kutjampensis* and flat as in *Nimiokoala*; unlike the arched palate of
6 *Phascolarctos*. The maxillary palate is preserved to the level of M² on the left side; on the
7 right side it is mostly complete except for a triangular wedge of bone opposite M¹⁻² (Fig.
8 13B). Much of the palatal portion of the palatine bones are not preserved except for a narrow
9 lateral sliver of the right palatine which extends anteriorly to the level of the M²/M³ boundary
10 as it does in *L. kutjampensis* and *Phascolarctos*. Large posterior palatal vacuities are
11 present and appear to have been restricted to the palatines terminating at or just posterior to
12 the maxilla-palatine suture. In *L. kutjampensis* the condition is unclear because the area is
13 poorly preserved. Although Louys et al. (2009, p.984), in their description of *L.*
14 *kutjampensis*, refer to the posterior palatal vacuities as 'maxillary-palatine vacuities' and
15 state "The maxillary-palatine vacuity is large and extends from the posterior margin of M2 to
16 just behind the anterior margin of M4...", they do not indicate where the maxilla-palatine
17 suture is positioned relative to M2, and hence do not indicate whether the vacuities extend
18 into the maxilla or terminate at the maxillo-palatine suture. In *Phascolarctos* they are
19 restricted to the palatines falling well short of the maxilla-palatine suture (condition unknown
20 for *Nimiokoala*). The ridged ventral surface of the vomer is exposed through the palatal
21 vacuities. A small, ovate infraorbital foramen is 2.0 mm anterior to and 3.9 mm above P³. A
22 smaller, secondary infraorbital foramen lies ventral and slightly posterior to the primary
23 infraorbital foramen, 1.93mm above the alveolar margin (Fig. 13A). Both foramina are
24 confluent with the infraorbital canal. In *Phascolarctos* and *Nimiokoala* there is a single
25 infraorbital foramen. It is similarly positioned in *Nimiokoala* to the primary foramen of *L.*
26 *dicksmithi*. In *Phascolarctos* the infraorbital foramen is proportionately smaller and
27 positioned high on the rostrum near the orbit at a point above P³ or M¹. Black and Hand
28 (2010) have shown the presence of a secondary infraorbital foramen to be a variable feature
29 within the diprotodontid *Nimbadon lavarackorum*. Its presence in *L. dicksmithi* may also be
30 variable, however, this cannot be determined on the basis of a single known specimen.

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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 (Figs 13A, 13D). A similar process appears to
have been present in *L. kutjampensis* (QMF 51382) but the extent to which it extends
ventrally is unknown. In *L. garyjohnstoni* the masseteric process is significantly less

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4 pronounced, remaining 1.71mm above the alveolar margin. In all *Litokoala* species, the
5 masseteric process is composed entirely of maxilla. The zygomatic arch is deep anteriorly,
6 deeper than in *Nimiokoala*, with a well defined masseteric ridge (Fig. 13A) and sulcus
7 indicating the site of attachment for the masseter lateralis profundus. Anteriorly, the
8 zygomatic arch projects posterolaterally from the face, unlike *Phascolarctos* in which it
9 projects more laterally. In *L. dicksmithi* the anterior jugal portion of the zygomatic arch is
10 relatively deeply concave compared with both *Nimiokoala* and *Phascolarctos*.

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16 Sphenorbital region. The orbit is large, similar in size to *Nimiokoala* yet proportionately
17 larger than *Phascolarctos*. A small but prominent ridge-like postorbital process is positioned
18 on the frontal at the dorsal border of the orbit 10.2 mm posterior to the anterior preorbital
19 ridge. The lacrimal is roughly circular, it extends 4.75 mm beyond the preorbital ridge where
20 it contacts the maxilla on the rostrum. It is absolutely and proportionately larger than in either
21 *Phascolarctos* or *Nimiokoala*. It is bound posterodorsally by the frontal, posteriorly by the
22 palatine and ventrally by the maxilla and jugal. The preorbital ridge is complete and not as
23 well defined as in *Nimiokoala*. A distinct lacrimal foramen is situated just anterior and
24 outside the orbit (Fig. 13A). A smaller foramen is positioned 3.65 mm dorso-posteriorly to
25 the lacrimal foramen and perforates the preorbital ridge just dorsal to a weak lacrimal
26 tuberosity. Three small foramina pierce the lacrimal close to its ventral suture with the
27 maxilla. Below these foramina on the lachrimo-jugal suture is a small unperforated yet deep
28 ovate depression. A well defined infraorbital canal perforates the maxilla just below this
29 suture line; like *Nimiokoala* it is situated at the anterior end of a well developed sulcus.
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Posterior to the infraorbital canal and within the infraorbital sulcus lies the sphenopalatine
foramen. Again as in *Nimiokoala* it lies on the maxilla-palatine suture. The dorsal margin of
the palatine 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 anterior most point being coincident with the
jugal-lacrimal suture, and is entirely bound dorsally by the palatine. The orbitosphenoid is
present as a roughly circular bone at the posteroventral corner of the specimen preserved; it
contacts the palatine anteroventrally and the frontal anteriorly 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

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4 orbitosphenoid, the anterodorsal rim of the sphenorbital fissure can be seen. The alisphenoid
5 is almost only preserved as an endocranial lamina, its suture line with the frontal is however
6 discernable. The frontal makes a large ventral contribution to the sphenorbital region; on the
7 cranial roof it is preserved only as a triangular wedge (Fig. 13C).
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10 Dentition (Figs 14A-B). QM F54567 preserves the LI^1 , LP^3 - M^2 and RP^3 - M^4 . The adult
11 upper tooth formula would be I^{1-3} , C^1 , P^3 , M^{1-4} . The alveolus for I^2 is larger than I^3 , the latter
12 being similar in size to the alveolus of C^1 (Fig. 13B). In basic dimensions the alveoli for I^{2-3}
13 and C^1 are comparable with *Nimiokoala*. As in other species of *Litokoala*, the premolar is
14 positioned more in-line with the molar row (Figs 14A-B) and less divergent anteromedially
15 as in *Nimiokoala*.
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18 I^1 . Left I^1 preserved. Short, gracile tooth with enamel on all surfaces and a small ovate
19 wear facet on the posterior surface of its tip. Relatively blunt tip but this may be partially
20 attributed to abrasion. Projects anteroventrally and would have converged medially on tip of
21 right I^1 (Fig. 13D). Less robust, more protracted and less ventrally extensive than I^1 of
22 *Nimiokoala* or *Phascolarctos* (the only other phascolarctids for which a first upper incisor is
23 known) and in this regard is more reminiscent of an I^3 of the latter taxa than an I^1 .
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26 P^3 . Bulbous P^3 with four main cusps, three of which are positioned anteriorly, medially,
27 and posteriorly along the longitudinal tooth midline (Fig. 14A-B). The fourth and smallest
28 cusp is positioned at the posterolingual tooth margin. The P^3 is widest posteriorly at the level
29 of the posterolingual cusp and tapers in width to the anterior tooth margin. There is
30 significant wear on the posterolingual face of the anterior cusp, the apices of the medial and
31 posterolingual cusps and the posterior blade of the posterior cusp. A small ovate wear facet
32 that probably represented a small lingual cuspule is positioned at the anterior base of the
33 posterolingual cusp along the lingual tooth margin in the same position as the small lingual
34 cusp in *L. garyjohnstoni* and the small cuspule in *L. kutjamarpensisi* (QM F51382). The
35 relative heights of the major cusps are difficult to discern as a result of wear. The anterior
36 cusp is situated approximately 0.95 mm from the anterior margin. Anterior, buccal and
37 lingual crests extend from its apex and fade towards the base of the crown. The buccal crest is
38 not as extensive, nor prominent as in *L. garyjohnstoni* in which it meets a well developed
39 anterobuccally directed crest from the apex of the medial cusp. In *L. dicksmithi* the buccal
40 crest of the medial cusp is weak and fades out midway to the base of the crown. A better
41 developed yet worn lingual crest extends from the apex of the medial cusp and terminates at
42 the base of the crown at the small ovate wear facet (mentioned above) resembling the
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4 condition found in *L. garyjohnstoni*. In *L. kutjamarpensis* (QM F51382) the lingual crest of
5 the medial cusp terminates abruptly before meeting the small lingual cuspule.
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7 The apex of the medial cusp is positioned 2.39 mm posterior to the anterior tooth margin.
8 Short anterior and posterior crests link the apices of the medial and anterior cusps
9 (respectively) in a shallow valley which defines the anterior and posterior tooth moieties
10 (Figs 14A-B). A short posterolingually directed crest links the apices of the medial and
11 posterior cusps. The apex of the posterior cusp is positioned 3.04 mm posterior to the
12 anterior tooth margin. The posterolingual placement of the posterior cusp with respect to the
13 medial cusp is also found in *L. garyjohnstoni* and less so in *L. kutjamarpensis*. Both *L.*
14 *dicksmithi* and *L. garyjohnstoni* lack the lingual crest of the posterior cusp found in *L.*
15 *kutjamarpensis*. A prominent posteriorly-directed crest connects the posterior cusp apex to
16 the anterior cingulum of M¹. The posterolingual cusp is small and similarly developed to that
17 of *L. kutjamarpensis* but weaker with respect to *L. garyjohnstoni*. Short weak anterior and
18 posterior crests extend from its apex. The anterior crest is heavily worn small ovate wear
19 facet. In *L. dicksmithi* the well developed crest found in but is continuous with the both *L.*
20 *garyjohnstoni* and *L. kutjamarpensis* that links the small lingual cuspule anteriorly with the
21 lingual crest of the anterior cusp is absent. The resultant effect is a less trenchant, more
22 bulbous looking premolar overall.
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24 M¹. Description based on LM¹ because enamel is missing from the lingual face of
25 metaconule on RM¹. The enamel is moderately crenulated although less apparent due to
26 wear. Crenulations are evident in the transverse valley, on the anterior bases of the paracone,
27 metacone, paraconule and neometaconule, the posterior bases of the parastyle, paracone and
28 metacone, the buccal base of the protocone, and the anterior cingulum. M¹ is longer (across
29 the buccal margin) than it is wide. The buccal margin is convex and the anterior margin
30 slopes posterolingually. The tooth is markedly wider anteriorly (i.e., across the paracone and
31 protocone) than posteriorly (across the metacone and metaconule) and in this regard
32 resembles the M¹ of *Nimiokoala* more so than either *L. garyjohnstoni* or *L. kutjamarpensis*.
33 This is in part due to the absence of the "neomorphic cuspule" (sensu Stirton, Tedford and
34 Woodburne, 1967) located at the anterolingual base of the metaconule in other *Litokoala*
35 species. The apices of the paracone and metacone slightly overhang their lingual bases as
36 they do in *L. kutjamarpensis* and contra *L. garyjohnstoni*. The buccal surface of the paracone
37 is reduced relative to the metacone as it is in *L. garyjohnstoni*. The respective heights of the
38 major cusps are difficult to discern due to moderate wear with dentine exposed on all apices;
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4 however, the metacone appears to have been taller than the paracone. The metaconule is the
5 most worn of the major cusps. Dentine is also exposed on the apex of the parastyle, the
6 neometaconule, the buccal end of the premetaconule crista and the lingual end of the
7 posterolingual paracrista. The parastyle is a large (albeit very worn), pyramidal cusp which
8 occupies the anterobuccal corner of the tooth and is similarly developed as in *L.*
9 *garyjohnstoni* and slightly larger than in *L. kutjamarpensis*. The degree and pattern of wear is
10 similar to that found in the holotype of *L. kutjamarpensis* (SAM P13845), the worn posterior
11 base of the parastyle appearing as a buccal ridge connecting the paraconule and buccal
12 cingulum. The tooth is slightly higher crowned and the transverse and longitudinal valleys are
13 slightly deeper than in other *Litokoala* spp. Styler cusps are weakly developed and so similar
14 to *L. kutjamarpensis* and reduced relative to *L. garyjohnstoni*. Unlike other *Litokoala* spp.,
15 styler cusps B and C do not form a continuous ridge that effectively closes off the paracone
16 buccal basin along the buccal tooth margin. The preparacrista is short, heavily worn and
17 bifurcates at the buccal tooth margin into a short anterior spur that terminates just prior to
18 meeting the posterobuccal base of the parastyle, and a short posterior ridge that represents a
19 poorly developed styler cusp B. The postparacrista is linear, longer and less worn than the
20 preparacrista and similarly bifurcates at the buccal tooth margin into a short anterior ridge
21 representing styler cusp C, and a short posterobuccal arm that meets the premetacrista at the
22 buccal margin, effectively closing off the buccal end of the transverse valley. Both the
23 postparacrista and premetacrista meet a series of short, transversely oriented ridges (that form
24 part of the molar crenulation pattern) at this point. The premetacrista is moderately worn,
25 elongate, anterobuccally directed (running in a parallel plane to the preparacrista) and
26 branches before its junction with the postparacrista into a short posterior ridge that represents
27 styler cusp D. The postmetacrista is more heavily worn than the premetacrista (having
28 dentine exposed at the metacone apex) and is directed slightly more posteriorly than the
29 postparacrista, terminating ventral to the anterior cingulum of M² at the anterobuccal tooth
30 corner. A slight swelling at this point represents styler cusp E. A large crescentic paraconule
31 is situated at the anterolingual base of the paracone. A short, linear crest extends anteriorly
32 from the paraconule apex and terminates at the lingual base of the parastyle. A more
33 elongate, slightly crescentic posterior crest curves around the base of the paracone to meet a
34 well-developed and moderately worn posterolingual paracrista as it does in other species of
35 *Litokoala*. A third posterolingually directed crest extends from the paraconule apex and
36 terminates at the buccal base of the protocone. In the RM¹, this crest is anterolingually
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4 directed and meets a short posterior spur from the anterior cingulum, the latter representing a
5 weakly developed protostyle (Figs 14A-B). A large crescentic neometaconule occupies the
6 longitudinal valley between the metacone and metaconule, its apex positioned at the
7 anterolingual base of the metacone. A well developed anterior neometaconule crest extends
8 anterobuccally into the transverse valley, becoming part of the crenulation pattern. A
9 posterior neometaconule crest extends posteriorly, curving slightly buccally at the
10 posterolingual base of the metacone where it meets a weakly developed posterolingual
11 metacrista. A linear and slightly worn preprotocrista is continuous with the anterior cingulum
12 anteriorly. A crescentic postprotocrista meets a bifurcate premetaconule crista in the
13 transverse valley well buccal to the lingual margin. A weak anterolingually-directed crest
14 extends down the lingual face of the protocone becoming more prominent towards the base of
15 the crown. It is more prominent in RM^1 and becomes progressively better developed in M^{2-4}
16 and originates from the protocone apex (Figs 14A-B). This crest is well developed in M^{1-4} of
17 *L. kutjamarpensis* but weakly expressed in *L. garyjohnstoni*. The lingual face of the
18 protocone slopes less steeply towards its base and consequently projects further lingually than
19 that of the metaconule. A crescentic postmetaconule crista extends posteriorly from the
20 metaconule apex becoming continuous with the posterior cingulum at which point it abuts
21 and extends ventral to, the anterior cingulum of M^2 . The valley between the posterior base of
22 the protocone and the anterior base of the metaconule is narrow in comparison with other
23 *Litokoala* spp. and is an artefact of the absence of a neomorphic cusplule at the anterolingual
24 base of the metaconule.

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39 M^2 . Similar in most respects to M^1 except for the following features: a large pyramidal
40 parastyle is absent and consequently the anterior tooth margin is linear and oriented in the
41 buccal-lingual plane; enamel crenulations are reduced and restricted to the transverse valley
42 and the anterior base of the paracone and metacone; the buccal surface of the paracone is
43 larger and the metacone buccal margin is less convex and slopes posterolingually; stylar
44 cusps B and C are larger; the lingual face of the protocone more steeply slopes towards its
45 base and consequently is less lingually projecting; the anterior paraconule crest connects to
46 the anterior cingulum; the posterior paraconule crest is continuous with the anterior-most of
47 the transverse ridges at the buccal end of the transverse valley; the anterolingual crest of the
48 paraconule is reduced; a protostyle is absent; the premetaconule crista slightly overhangs the
49 transverse valley between the lingual bases of the protocone and metaconule; the posterior
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4 crest of the neometaconule is more linear, less arcuate; and the posterolingual metacrista is
5 further reduced to a short spur at the posterolingual base of the metacone.
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7 M^3 . Similar to M^2 but differs in the following features: smaller size; buccal surfaces of the
8 paracone and metacone more elongate antero-posteriorly, narrower bucco-lingually and more
9 steeply sloping; protocone, metacone metaconule, paraconule and neometaconule reduced;
10 enamel crenulations restricted to the buccal end of the transverse valley; preparacrista
11 overhangs the anterior base of the paracone; and anterobuccal protocone crest more distinct
12 and originates from the protocone apex.
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15 M^4 . As in other *Litokoala* spp. M^4 is significantly smaller in size and posteriorly
16 attenuated. The metacone and metaconule are significantly reduced and non cusp-like, their
17 apices incorporated into the posterobuccal and posterolingual cingulae, respectively. A fine
18 network of ridges/crenulations radiate from the posterobuccal, posterior and posterolingual
19 tooth margins towards the transverse median valley. The neometaconule is indistinct from the
20 crenulation pattern. Anteriorly, the tooth resembles M^3 but the following differences are
21 noted: the paracone, protocone and paraconule are reduced; the buccal surface of the
22 paracone is reduced and more steeply sloping; the anterobuccal protocone crest is more
23 distinct; a posterobuccal protocone crest is developed; stylar cusps C and D are reduced; a
24 valley separating the posterior and anterior bases of the protocone and metaconule,
25 respectively, is absent; and the postprotocrista is less arcuate, more posterobuccally directed
26 and continuous with the posterolingual cingula that incorporates the metaconule apex.
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41 Discussion

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45 *Litokoala dicksmithi* n. sp. is known from an exceptionally well preserved partial cranium.
46 It is the first cranial material for the genus that preserves the rostrum. Overall, the facial
47 region of *L. dicksmithi* resembles the modern koala more so than does *Nimiokoala*
48 *greystanesi*, the only other extinct phascolarctid for which comparable cranial material is
49 known. Louys et al. (2009) found the rostral morphology of *N. greystanesi* to be most similar
50 to a generalised phalangerid, such as the extant common brushtail possum (*Trichosurus*
51 *vulpecula*), than to the modern koala. *Litokoala dicksmithi* is more "koala-like" and
52 resembles *Phascolarctos* (contra *Nimiokoala*) in having a shorter, more robust rostrum with a
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4 broad nasal aperture that has an irregular anterior border. The latter feature appears to be a
5 cranial synapomorphy for the *Litokoala-Phascolarctos* clade, a grouping previously well-
6 supported by dental apomorphies (see Woodburne et al. 1987, Black & Archer 1997, Black et
7 al. 2012). In contrast to *Phascolarctos*, however, and like *Nimiokoala*, *L. dicksmithi* shows a
8 lack of facial flexion or deepening of the maxilla with respect to the tooth row, features
9 which probably evolved in the modern koala in response to a more specialised diet (Louys et
10 al. 2009).

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16 Features in which *L. dicksmithi* more closely resembles *N. greystanesi* than *P. cinereus*
17 include: the general shape of the rostrum in anterior view (i.e., broader ventrally than
18 dorsally); a broad maxillary palate; and proportionately larger orbits. Features unique to *L.*
19 *dicksmithi* among phascolarctids include: well developed and ventrally extensive masseteric
20 processes; "twinned" infraorbital foramina; a broad, shallow premaxillary palate and
21 correspondingly broad U-shaped incisor arcade; large interincisive foramina (anterior palatal
22 fenestrae); and proportionately larger and anteriorly extensive lacrimals (Figs 13A-D).

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28 In some aspects of dental morphology *L. dicksmithi* resembles *N. greystanesi* in features
29 that have previously (e.g., Woodburne et al. 1987; Black & Archer 1997) been found to be
30 plesiomorphic with respect to the *Litokoala-Phascolarctos* clade. These features include the
31 absence of the neomorphic cuspule at the base of the metaconule of M¹ that is present in both
32 *L. kutjampensis* and *L. garyjohnstoni* (unknown for *L. thurmerae*), and the absence of a
33 "trenchant" premolar characterised by a well-developed lingual cingulum and medial lingual
34 cusp on P³. Development of the "trenchant" premolar characteristic of *L. garyjohnstoni*, *L.*
35 *kutjampensis* and species of *Phascolarctos* could be achieved through enlargement of the
36 small medial lingual cuspule found in *L. dicksmithi* and its associated anterior and posterior
37 apical crests, to form a continuous lingual cingulum. The presence of a trenchant premolar in
38 some but not all species of *Litokoala* and in species of *Phascolarctos* suggests this feature
39 may have evolved independently in these lineages and may not, as previously indicated (e.g.
40 Woodburne et al. 1987; Black & Archer 1997), be a synapomorphy for a *Litokoala-*
41 *Phascolarctos* clade. This result was supported by a recent analysis of phascolarctid
42 phylogeny by Black et al. (2012) who did not find a trenchant premolar to be an
43 unambiguous synapomorphy uniting the *Litokoala-Phascolarctos* clade.
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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 recognise *L. kutjamarpensis* (*sensu* Louys et al. 2007) from numerous Faunal Zone C (middle Miocene) local faunas and *L. garyjohnstoni* from the Faunal Zone B Outasite Local Fauna. Although *L. dicksmithi* and *L. garyjohnstoni* may have been syntopic 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^3L and M^3W , 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 characterised 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 specialising 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 *Madakoala* 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 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 *Nimiokoala greystanesi* in two early to middle Miocene assemblages at Riversleigh (Black et al. 2012). The plesiomorphic Riversleigh species possessed simple, uncrenulated selenodont molars that are suggestive of a diet of relatively softer leaves than those of the smaller coeval species of *Litokoala* and *Nimiokoala*, which are characterised by relatively complex dentitions (Black et al. 2012). Interestingly, another probable rainforest koala, *Invictokoala monticola* Price and Hocknull, 2011, from

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4 Pleistocene deposits of Mt Etna, Queensland, also exhibits a relatively simple selenodont
5 dentition reminiscent of that of the similarly sized plesiomorphic Riversleigh taxon.
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7 The proportionately larger size of the orbits in *Litokoala* species suggests the intriguing
8 possibility that these koalas were nocturnal and may have possessed greater visual acuity than
9 the modern species. Orbit size has been shown to be strongly correlated with activity pattern
10 in primates with nocturnal species having proportionately larger orbits than diurnal species
11 (Kay & Cartmill 1977, Kay & Kirk 2000). Among mammals, relatively large eyes are also
12 associated with increased visual acuity (Kiltie 2000). Taken in conjunction with their small
13 body size, this may suggest that species of *Litokoala* were more agile arboreal folivores than
14 the relatively sedentary sloth-like living species.
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25 **Species identification in extinct marsupials**

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28 In extant ecosystems, biologists identify species using a combination of criteria including
29 morphologic and genetic distinction, reproductive isolation, and geographic distribution.
30 Palaeontologists, however, are generally restricted to morphological criteria as a means of
31 determining species boundaries in the fossil record. Further, while a range of morphological
32 criteria can be addressed in the diagnosis of extant species (e.g. external morphology, soft
33 anatomy and skeletal anatomy; see Voss and Jansa 2009), palaeontologists are further
34 restricted to a subset of these features, notably dental and/or skeletal remains. In the case of
35 marsupials (and mammals in general), most extinct taxa are described on the basis of teeth
36 and here we restrict our discussion to studies involving dentitions.
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43 Archer & Dawson's (1982) analysis of cranio-dental remains referable to the marsupial
44 lion genus *Thylacoleo* from Wellington Caves, New South Wales indicated conservative
45 tooth dimensions and morphologies suggesting only a single species was represented in the
46 sample (*T. carnifex*). Extreme size variation was evident in cranial morphology, however,
47 which may have been sexually dimorphic in nature.
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51 Prideaux's (2004) systematic review of the macropodid subfamily Sthenurinae indicated
52 significant intraspecific variation in dental morphology, particularly in species with broad
53 geographic ranges (e.g., *Simosthenurus occidentalis*, *S. maddocki*, *S. pales*, *Procoptodon*
54 *browneorum*). *Simosthenurus occidentalis* was found to be one of the most variable
55 sthenurines yet the level of morphological variation found between regional samples was no
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4 greater than that found within samples. Geographic differences in size were evident,
5 however, with molars of individuals from the south-western extent of *S. occidentalis*'s range
6 being up to 19% smaller than those from south-eastern populations (Prideaux 2004).
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9 Murray et al. (2000a, b) and Black & Hand (2010) have demonstrated significant cranio-
10 dental morphological variation within populations of the Miocene diprotodontids *Neohelos*
11 *stirtoni* and *Nimbadon lavarackorum*, respectively, including apparent sexual dimorphism in
12 cranial morphology and broad-scale variation in tooth morphology (but not dimensions).
13 Consequently, Black & Hand (2010) synonymised *Nimbadon whitelawi* with the type species
14 *Ni. lavarackorum*, the morphological differences between the species being encompassed in
15 the range of variation exhibited by *Ni. lavarackorum*.
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20 Price (2008) characterised interpopulational variation in the Pleistocene diprotodontid
21 genus *Diprotodon* by analysing a sample of >1000 teeth from localities across its range. Prior
22 to that study more than eight species of *Diprotodon* had been described (Mahoney & Ride
23 1975). Price's (2008) morphometric analysis indicated the presence of only a single, wide-
24 ranging, highly-variable and sexually dimorphic species (*Diprotodon optatum*). Price &
25 Sobbe (2011) documented asymmetry in premolar morphology within a single individual of
26 *Diprotodon optatum* that encompassed the extremes of variation recorded for the
27 morphospecies as a whole.
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34 Our study of variation in *P. cinereus* dentitions highlights the need for caution when
35 interpreting the significance of certain dental structures in determining species boundaries
36 within selenodont marsupials. Our qualitative analysis indicates that a relatively high degree
37 of intraspecific variation characterises the dentition of the modern koala. Features found to be
38 highly variable across all teeth examined include tooth shape and the expression and pattern
39 of enamel crenulations. On P³, the construction of the longitudinal crest and lingual cingulum
40 were highly variable as was the presence of a posterobuccal cuspule (Figs 3A-F). In the upper
41 molars (Figs 4-7), structures subject to a high degree of variation include: the development
42 and orientation of the paraconule, neometaconule, protostyle and parastyle; the development
43 and orientation of cristae associated with the major cusps; the development of the
44 anterolingual fossa and lingual cingulum; the development of the styler cusps; the depth and
45 degree of closure of the buccal basins of the paracone and metacone; and the degree of
46 reduction of the posterior moiety of M⁴. Highly variable features of the lower dentition (Figs
47 8-12) include: the construction of the longitudinal and posterobuccal crest of P₃; the degree of
48 development of the columnar stylids, entostylid ridge and buccal cingulum on the lower
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4 molars; the junction of the preentocristid with either the postmetacristid or postmetastylid
5 cristid; the junction of the postprotocristid and cristid obliqua; and the degree of reduction of
6 the talonid on M₃₋₄.
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9 Although significant differences in upper molar dimensions were apparent between the
10 sexes of the Victorian population, there was no evidence of gender-specific morphometric
11 differences in premolar or lower molar dimensions or in individual tooth dimensions of
12 Queensland specimens, nor did we observe qualitative morphological variation between male
13 and female *P. cinereus*. Comparable results have been found in other studies of dental
14 variation in extant marsupials. Freedman (1967) found no evidence of gender based
15 morphological variation in the dentition of the modern long-nosed bandicoot *Perameles*
16 *nasuta*, except for canine morphology, although metric differences were apparent (Freedman
17 & Joffe, 1967a). Similarly, Aplin et al. (2010) found considerable sexual dimorphism in
18 upper and lower third premolar size in the bandicoot *Peroryctes broadbenti* yet found no
19 morphological differences between the sexes. Bartholomai (1971) found considerable
20 morphological variation in dental morphology in both the eastern grey kangaroo *Macropus*
21 *giganteus* and agile wallaby *M. agilis*, while only the larger species, *M. giganteus*, exhibited
22 significant sexual dimorphism in dental dimensions. In smaller species of *Perameles* (e.g., *P.*
23 *bougainville*), sexual dimorphism in skull and tooth size was not evident and morphological
24 variation was not assessed (Freedman and Joffe, 1967b). Aplin et al. (2010) noted similar
25 patterns in the expression of sexual dimorphism in New Guinean bandicoots with larger
26 species being more strongly dimorphic (in features such as body weight, premolar
27 dimensions and canine length and robustness) than smaller species.
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42 **Geographical differences.** *Phascolarctos cinereus* today occurs naturally in all states of
43 Australia except Tasmania, Western Australia and the Northern Territory (Figure 1). Koalas
44 from southern populations (e.g., Victoria) are on average significantly larger than their
45 northern (e.g., Queensland) counterparts and also display differences in pelage colour and
46 thickness, and muzzle shape (Lee & Martin 1988). To reflect these morphological
47 differences, early taxonomists recognised three subspecies: *P. cinereus victor* (Troughton
48 1935) from Victoria; *P. c. cinereus* (Goldfuss 1817) from New South Wales; and *P. c.*
49 *adustus* (Thomas 1923) from Queensland. However, the distribution of these subspecies has
50 never been adequately defined and was arbitrarily delineated by state borders rather than
51 definitive geographical boundaries (Lee & Martin 1988; Strahan 2004; Sherwin et al. 2000).
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4 Genetic studies (e.g., Takami et al. 1998, Houlden et al. 1999) do not support subspecies
5 distinction. Morphological differences between northern and southern populations may
6 represent the ends of a gradual latitudinal cline (Strahan 2004; Sherwin et al. 2000) - an
7 apparent reflection of Bergmann's Rule (Mayr 1956).
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10 Our morphometric analysis showed significant differences in some (but not all) tooth
11 dimensions between northern and southern koala populations yet results were not consistent
12 across the sexes and did not always reflect Bergmann's Rule. Significant differences in upper
13 molar dimensions were evident between northern and southern male populations, with molars
14 and premolars of Victorian males consistently larger than those of Queensland males in all
15 significantly different dimensions measured. Conversely, female upper tooth dimensions
16 show very few significant differences between regions; those observed, with one exception,
17 all showed Queensland specimens larger than Victorian specimens. Similarly, Bartholomai
18 (1968) did not find any significant differences in *P. cinereus* upper (P^3 - M^2) tooth dimensions
19 between Victorian and Queensland specimens, although his analysis did not include M^{3-4} or
20 the lower dentition. Our analysis of lower dentitions showed that significant differences in
21 premolar dimensions were not evident between northern and southern populations. With
22 regard to lower molars, some (but not all) molar dimensions showed significant differences
23 and of those, Victorian specimens were found to be consistently larger than Queensland
24 specimens. Compared with upper dentitions, lower dentitions showed a greater consistency in
25 which individual dimensions were found to be significantly different between males and
26 females (Table 3).
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39 Because *P. cinereus* has a relatively widespread geographic range it may be argued that
40 the degree of morphological variation found in the present study represents the maximum
41 level of variation expected for a species and may not be indicative of that found within a
42 more geographically restricted fossil population. However, we found no evidence of any
43 consistent differences or patterns in dental morphology between individuals from northern
44 and southern regions. Further, variation within localities was as great as that found between
45 regions.
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50 Martin (2005) found similarly high morphological variation in cranial and dental features
51 of the monotypic Patagonian opossum *Lestodelphys halli* across its range, but could not
52 identify significant differences between localities. Prideaux (2004) also found this to be the
53 case for sthenurine species with broad geographic ranges (see above) albeit, the distinction of
54 these fossil species cannot be supported by molecular data as in the extant *L. halli*. Further,
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4 morphological variation in dentitions of extinct diprotodontids (e.g., *Neohelos stirtoni*,
5 *Diprotodon optatum* and *Nimbadon lavarackorum*) from single localities indicate comparably
6 high levels of variation (Murray et al. 2000b; Price & Piper 2009; Price & Sobbe 2011; Black
7 & Hand 2010) as that found for *P. cinereus*.
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10 11 12 **Taxonomy of *Litokoala***

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14 *Litokoala* Stirton, 1967 is sister taxon to the modern genus *Phascolarctos* (Black & Archer
15 1997; Black 1999; Black et al. 2012). Species have been identified from deposits within
16 South Australia (Wipajiri and Etadunna Formations) and Queensland (Riversleigh World
17 Heritage Area) spanning the late Oligocene to middle Miocene. However, the taxonomic
18 distinction of several of these species (e.g., *L. kanunkaensis*, *L. dicktedfordi*) has been
19 questioned (e.g., Louys et al. 2007; Pledge 2010) and stems from the lack of comparable
20 material between taxa and poor preservation of the type material for both *L. kutjampensis*
21 Stirton, Tedford & Woodburne, 1967 and *L. kanunkaensis* Springer, 1987, the holotypes of
22 which are single, isolated molars (M¹ and M₂, respectively).
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26 Black & Archer (1997) referred six specimens from Riversleigh's Faunal Zone C
27 assemblages (Henk's Hollow, Gag, Gotham, Jim's Carousel Local Faunas) to *L.*
28 *kanunkaensis* including the first P₃, M₁, M₃, upper molar (M³) and partial dentary (containing
29 P₃-M₂) for the species. This referral was based on clear similarities between M₂ of the partial
30 dentary (from the Henk's Hollow Local Fauna) and the South Australian holotype. Some
31 differences were noted (Black & Archer 1997, p.220), but they did not fall outside the
32 expected range of intraspecific variation gauged from comparing dentitions of the modern
33 koala (see above). The P₃ and M³, also from Henk's Hollow Local Fauna, were referred on
34 the basis of equable size, morphology and locality. More recently, Louys et al. (2007)
35 described the complete cheek tooth row of a partial skull from Jim's Carousel Site,
36 Riversleigh, and referred it to *L. kanunkaensis*. The complete tooth row allowed Louys et al.
37 (2007) to not only assess morphological changes along the molar row, but also facilitated
38 comparison of M¹ of *L. kutjampensis* with M³ of *L. kanunkaensis*. Louys et al. (2007)
39 found that the differences noted by Springer (1987) and Black & Archer (1997) as separating
40 these species could be accounted for by both variation along the tooth row of a single
41 individual and normal expected variation within a species. Consequently, Louys et al. (2007)
42 made *L. kanunkaensis* a junior synonym of *L. kutjampensis*.
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4 Recently Pledge (2010) provided an alternative interpretation to Black & Archer's (1997)
5 and Louys et al.'s (2007) assignment of the Riversleigh *Litokoala* material to *L. kanunkaensis*
6 and Louys et al.'s (2007) synonymy of the species with *L. kutjampensis*. Instead, Pledge
7 (2010) established a new species for the Riversleigh material, *Litokoala dicktedfordi* Pledge,
8 2010, and suggested that the upper molar material for *L. kanunkaensis* was too fragmentary to
9 be of taxonomic use.

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14 Further, Pledge (2010) questioned the taxonomic value of marsupial lower molars in
15 general. However, within Phascolarctidae, lower molars are actually the most comparable
16 element across species. In fact, the nominated holotypes of seven fossil phascolarctid species
17 (e.g., *Perikoala palankarinnica* Stirton, 1957; *Perikoala robustus* Woodburne et al., 1987;
18 *Madakoala devisi* Woodburne et al., 1987; *Madakoala wellsi* Woodburne et al., 1987;
19 *Litokoala kanunkaensis*; *Phascolarctos yorkensis* Pledge, 1992; *Phascolarctos maris* Pledge,
20 1987) are lower dentitions and/or dentaries, with only four taxa known exclusively from
21 upper dentitions. Thus, this extensive past usage demonstrates that the lower molars, at least
22 within phascolarctids, do have substantial taxonomic utility.

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

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

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

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29 Although Pledge (2010) regarded *L. kanunkaensis* to be possibly a *nomen dubium* due to
30 the paucity of material known from the type locality, he named a new species of *Litokoala*, *L.*
31 *thurmerae*, on the basis of a single isolated M³ (SAM P30159) from the Ngama Local Fauna
32 of the Etadunna Formation, South Australia, that he described as being "somewhat damaged"
33 and "well worn with all four principal cusps deeply eroded/corroded" (Pledge 2010, p. 82).

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Pledge (2010) distinguishes *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; neometaconule development; degree of convexity of the
buccal tooth margin; and the presence of a cuspsule 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., stelar cusp development, buccal cingulum
development, angle enclosed by pre- and postmetacristae) 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.*

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4 *cinereus* dentitions indicates their extent and pattern to be highly variable. This is also the
5 case within species of *Litokoala*. For example, *L. garyjohnstoni* shows a progressive
6 reduction and change in pattern of molar crenulations from M^1 to M^3 . Although Pledge
7 (2010) uses the absence of enamel crenulations in *L. thurmerae* as diagnostic for the species,
8 he also calls their validity into question (Pledge 2010; p.85, "The worn and thegosed nature
9 of the crown of the tooth may make statements about the enamel surface ornament
10 suspect...").
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16 With regard to size, Pledge (2010; p.82-83) notes in his description of *L. thurmerae* that
17 the tooth is damaged at the anterobuccal corner and lingual face of the protocone. It is also
18 evident that the anterobuccal and lingual borders of the tooth are incomplete (Pledge 2010,
19 fig. 1), but incompleteness of the specimen does not appear to have been accounted for (ibid,
20 tables 1-2) where the measurements given are not estimates. This suggests that the length and
21 anterior width of the specimen have been underestimated, and hence the suggestion that *L.*
22 *thurmerae* is 20-25% smaller than other *Litokoala* species is inaccurate and excessive. It
23 should be noted that two different measurements for the length of the *L. thurmerae* M^3 are
24 given by Pledge (2010, tables 1-2) but this may be a typographical error. Further, Pledge
25 (2010) states that *L. thurmerae* is 25% smaller than *L. kutjamarpenis*, yet this value was
26 calculated by comparing the length of M^3 with that of M^1 . In all koalas, molar length
27 decreases from M^1 to M^3 . In the holotype of *L. garyjohnstoni*, for example, M^1 is 17% longer
28 than M^3 . Further, comparisons between modern koala M^1 lengths show a difference of almost
29 30% between the largest (8.73 mm) and smallest (6.75 mm) individuals measured, while a
30 size difference of 10% is evident between the posterior widths of the left (4.37 mm) and right
31 (4.86 mm) M^3 in a single individual of *L. kutjamarpenis* (Louys et al. 2007).
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43 Pledge (2010) also suggested that the small size and more southerly location of *L.*
44 *thurmerae* with respect to *L. 'dicktedfordi'* provided independent support for its taxonomic
45 distinction. However, our results demonstrate Bergmann's Rule is not uniformly reflected in
46 dental dimensions of the modern koala, *Phascolarctos cinereus*, and thus geographically-
47 related size differences are not reliable indicators of taxonomic distinction. Further, although
48 as a general trend, mammalian body size has been shown to be correlated with both
49 geography (e.g. Bergmann's Rule) and time (e.g. Cope's Rule), many factors affect the
50 optimum body size for a species, including resource availability and distribution, habitat
51 structure, temperature, rainfall, and interspecific competition (see Price & Piper 2009;
52 McNab 2010).
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4 For these reasons, we regard the holotype (and only specimen) to be of limited diagnostic
5 value. Until more complete and diagnostic material (e.g., P³, M¹ or M₁) is recovered from the
6 Mammalon Hill type locality, we regard *Litokoala thurmerae* to be a *nomen dubium*.
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10 11 12 **Chronology of *Litokoala***

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14 Species of *Litokoala* have a temporal range spanning the late Oligocene to the middle
15 Miocene. *Litokoala kutjampensis*, the most abundant species, spans this time period and
16 also has the largest geographic range (South Australia and Queensland). *Litokoala*
17 *kutjampensis* has been recorded from Faunal Zone E of the Etadunna Formation, South
18 Australia (24.1- 24.0 Ma; Megirian et al. 2010), the Kutjamarpu Local Fauna of the Wipajiri
19 Formation, South Australia (23.4 Ma, Megirian et al. 2010), and Riversleigh's middle
20 Miocene Faunal Zone C assemblages (Queensland). Both Louys et al. (2007) and Pledge
21 (2010) have noted the apparent age disparity between these deposits. The maximum age of
22 the Kutjamarpu Local Fauna has most recently been estimated to be 23.4 Ma (late Oligocene)
23 based on biostratigraphy of the Wipajiri Formation relative to the underlying
24 magnetostratigraphically dated Etadunna Formation, with an age range of 23.4 Ma to 17.6
25 Ma (Megirian et al. 2010). This range is in general agreement with Archer et al.'s (1997)
26 suggestion of an early or middle Miocene age for the Kutjamarpu Local Fauna based on
27 biocorrelation with Riversleigh's Faunal Zone B and Faunal Zone C (formerly System B-C)
28 assemblages.
29

30
31 In addition to *L. kutjampensis*, taxa shared between the Kutjamarpu Local Fauna and
32 Riversleigh's Faunal Zone C assemblages include: the diprotodontid *Neohelos tirarensis*
33 (Black 1997; Murray et al. 2000a); the thylacoleonid *Wakaleo oldfieldi* (Gillespie 2007); and
34 the pseudocheirids *Marlu kutjampensis*, *Marlu ampelos*, *Marlu syke* (Roberts et al. 2009)
35 and *Paljara tirarensae* (Roberts et al. 2008). In fact, *Marlu kutjampensis* is recorded from
36 three Riversleigh sites known to contain *L. kutjampensis* (e.g. Gag, Henk's Hollow and
37 Jim's Carousel Sites; Roberts et al. 2009). Multivariate analyses (Travouillon et al. 2006) of
38 species presence data could not resolve whether the Kutjamarpu Local Fauna grouped most
39 closely with Riversleigh Faunal Zone B or C deposits because of a large degree of overlap in
40 taxa between the respective assemblages.
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42
43 *Litokoala thurmerae* is known from a single molar from the Ngama Local Fauna of the
44 Etadunna Formation, while both *L. garyjohnstoni* and *L. dicksmithi* are known from isolated
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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 (24.6Ma, Faunal Zone C; Megirian et al. 2010) and Ngama (24.1Ma; Faunal Zone D; Megirian et al. 2010) Local Faunas of the Etadunna Formation based on the shared presence of *Ngapakaldia bonythoni* (Black 2010) and *Kuterintja ngama* (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. kanunkaensis*, a taxon since synonymised 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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Figure captions

Figure 1. Map of Australia indicating main study sites (closed circles, modern; open circles, fossil) and geographic distribution (grey shading) of the modern koala, *Phascolarctos cinereus*. Abbreviations: NSW, New South Wales; NT, Northern Territory; QLD, Queensland; SA, South Australia; TAS, Tasmania; VIC, Victoria; WA, Western Australia.

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, neometaconule; 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; pomed, postmetacristid; popac, postparacrista; pomcl, postmetaconulecrista; poprc, postprotocrista; poprd, postprotocristid; pr, protocone; prd, protoconid; prend, preentocristid; prmcl, premetaconulecrista; prmec, premetacrista; prpac, preparacrista; prprc, preprotocrista; prprd, preprotocristid; prst, protostyle; prpstd, preprotostylid cristid; pstd, protostylid; StB, stylar cusp B; StC, stylar cusp C; StD, stylar cusp D; StE, stylar cusp E; tv, transverse valley.

Figure 3. Comparison of the left P³ of six individuals of *P. cinereus*. **A**, AM M4841; **B**, AM M12475; **C**, AM M7364; **D**, QM J13278; **E**, AM M7486; **F**, AM P481. Abbreviations: a, anterior; b, buccal; lcr, lingual cingular ridge; locr, longitudinal crest.

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,

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4 metaconule; me, metacone; nmcl, neometaconule; pa, paracone; pas, parastyle; pcl,
5 paraconule; pr, protocone.
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9 **Figure 5.** Comparison of the left M^2 of six individuals of *P. cinereus*. **A**, AM M6806; **B**,
10 AR8398; **C**, AM M4841 (right M^1 mirrored); **D**, QM J13278; **E**, AM M7486; **F**, AM
11 M12475. Abbreviations: a, anterior; b, buccal; mcl, metaconule; me, metacone; nmcl,
12 neometaconule; pa, paracone; pcl, paraconule; pr, protocone; prst, protostyle.
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17 **Figure 6.** Comparison of the left M^3 of six individuals of *P. cinereus*. **A**, AM M7356; **B**, AM
18 M7364; **C**, AM M12475; **D**, QM J13278; **E**, AM M5743; **F**, AM M7486. Abbreviations: a,
19 anterior; b, buccal; mcl, metaconule; me, metacone; nmcl, neometaconule; pa, paracone; pcl,
20 paraconule; pr, protocone; prst, protostyle.
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25 **Figure 7.** Comparison of the left M^4 of six individuals of *P. cinereus*. **A**, AR1574; **B**, AM
26 S415; **C**, AM M5743; **D**, AM M12475; **E**, AM M7356; **F**, AM M7364. Abbreviations: a,
27 anterior; b, buccal; mcl, metaconule; me, metacone; pa, paracone; pr, protocone.
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32 **Figure 8.** Comparison of the left P_3 of six individuals of *P. cinereus*. **A**, AM M7356; **B**, AM
33 M7364; **C**, QM J13278; **D**, AM M2185; **E**, AM M7486; **F**, AM M12475. Abbreviations: a,
34 anterior; l, lingual; locr, longitudinal crest; pbc, posterobuccal crest.
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39 **Figure 9.** Comparison of the left M_1 of six individuals of *P. cinereus*. **A**, AM M7486; **B**,
40 AR1574; **C**, QM J13278; **D**, AM M12475; **E**, AM M7356; **F**, AM M7364. Abbreviations: a,
41 anterior; end, entoconid; er, entostylid ridge; hyd, hypoconid; l, lingual; med, metaconid; prd,
42 protoconid; pstd, protostylid.
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47 **Figure 10.** Comparison of the left M_2 of six individuals of *P. cinereus*. **A**, AM M5266; **B**,
48 AM M5743; **C**, AM M12475; **D**, AM M6582; **E**, QM J13278; **F**, AM M7356. Abbreviations:
49 a, anterior; cstd, columnar stylid; end, entoconid; er, entostylid ridge; hyd, hypoconid; l,
50 lingual; lsed, lingual shelf of entoconid; lsmd, lingual shelf of metaconid; med, metaconid;
51 prd, protoconid.
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4 **Figure 11.** Comparison of the left M₃ of six individuals of *P. cinereus*. **A**, AM M7356; **B**,
5 AM S415; **C**, AM M2185; **D**, AM M5743; **E**, AM M12475; **F**, AM M7486. Abbreviations:
6 a, anterior; cstd, columnar stylid; end, entoconid; er, entostylid ridge; hyd, hypoconid; l,
7 lingual; lsed, lingual shelf of entoconid; lsm, lingual shelf of metaconid; med, metaconid;
8 prd, protoconid.
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14 **Figure 12.** Comparison of the left M₄ of six individuals of *P. cinereus*. **A**, AR1574; **B**, AM
15 M2185; **C**, AM S415; **D**, AM M7364; **E**, AM M7438; **F**, AM M12475. Abbreviations: a,
16 anterior; cstd, columnar stylid; end, entoconid; hyd, hypoconid; l, lingual; med, metaconid;
17 prd, protoconid.
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23 **Figure 13.** QM F54567, *Litokoala dicksmithi* n. sp. partial skull. **A**, right lateral view; **B**,
24 occlusal view view; **C**, dorsal view; **D**, anterior view. Abbreviations: als, alisphenoid; C1,
25 canine; fr, frontal; I1, first upper incisor; I1a, first upper incisor alveolus; I2, second upper
26 incisor; I3, third upper incisor; if, interincisive foramen; iof1, primary infraorbital foramen;
27 iof2, secondary infraorbital foramen; jg, jugal; lac, lacrimal; lacf, lacrimal foramen; lt,
28 lacrimal tuberosity; max, maxilla; mp, masseteric process; mr, masseteric ridge; ns, nasal;
29 off, orbitosphenoid-frontal foramen; or, orbital ridge; os, orbitosphenoid; P3, upper premolar;
30 pal, palatine; pmx, premaxilla; pv, palatal vacuity lateral border; sos, suborbital shelf.
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37 **Figure 14.** QM F54567, *Litokoala dicksmithi* n. sp. upper right P³, M¹⁻⁴ in occlusal view. **A**,
38 stereopair of right P³, M¹⁻⁴; **B**, line drawing showing major features of P³, M¹⁻⁴.
39 Abbreviations: a, anterior; ac, anterior cingulum; antc, anterior cusp of P³; b, buccal; mcl,
40 metaconule; me, metacone; medc, medial cusp of P³; nmcl, neometaconule; pa, paracone;
41 pas, parastyle; pcl, paraconule; plc, posterolingual cusp of P³; postc, posterior cusp of P³; pr,
42 protocone; stB, stylar cusp B; stC, stylar cusp C.
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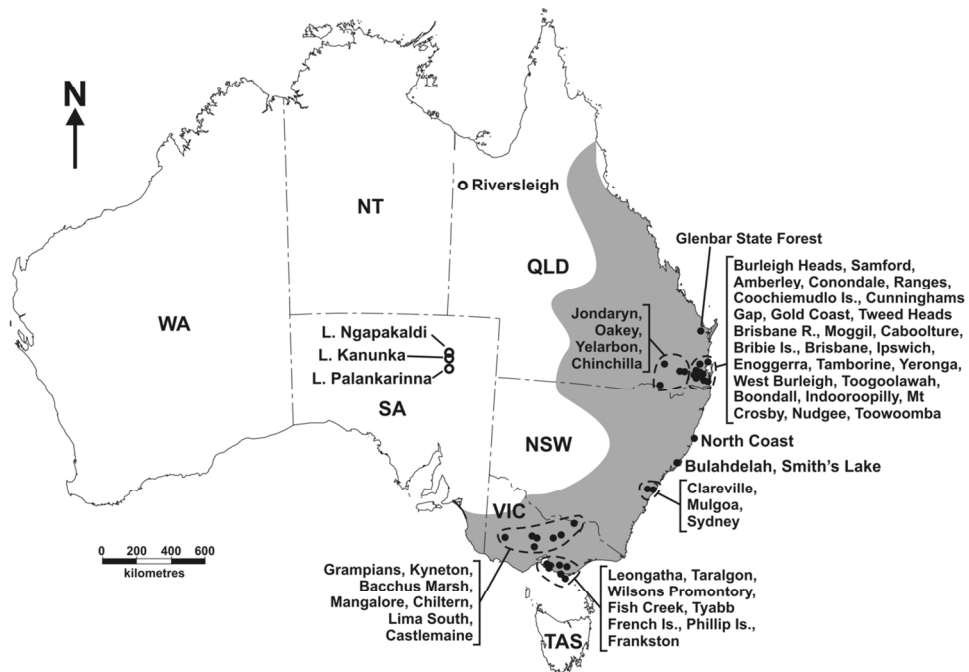
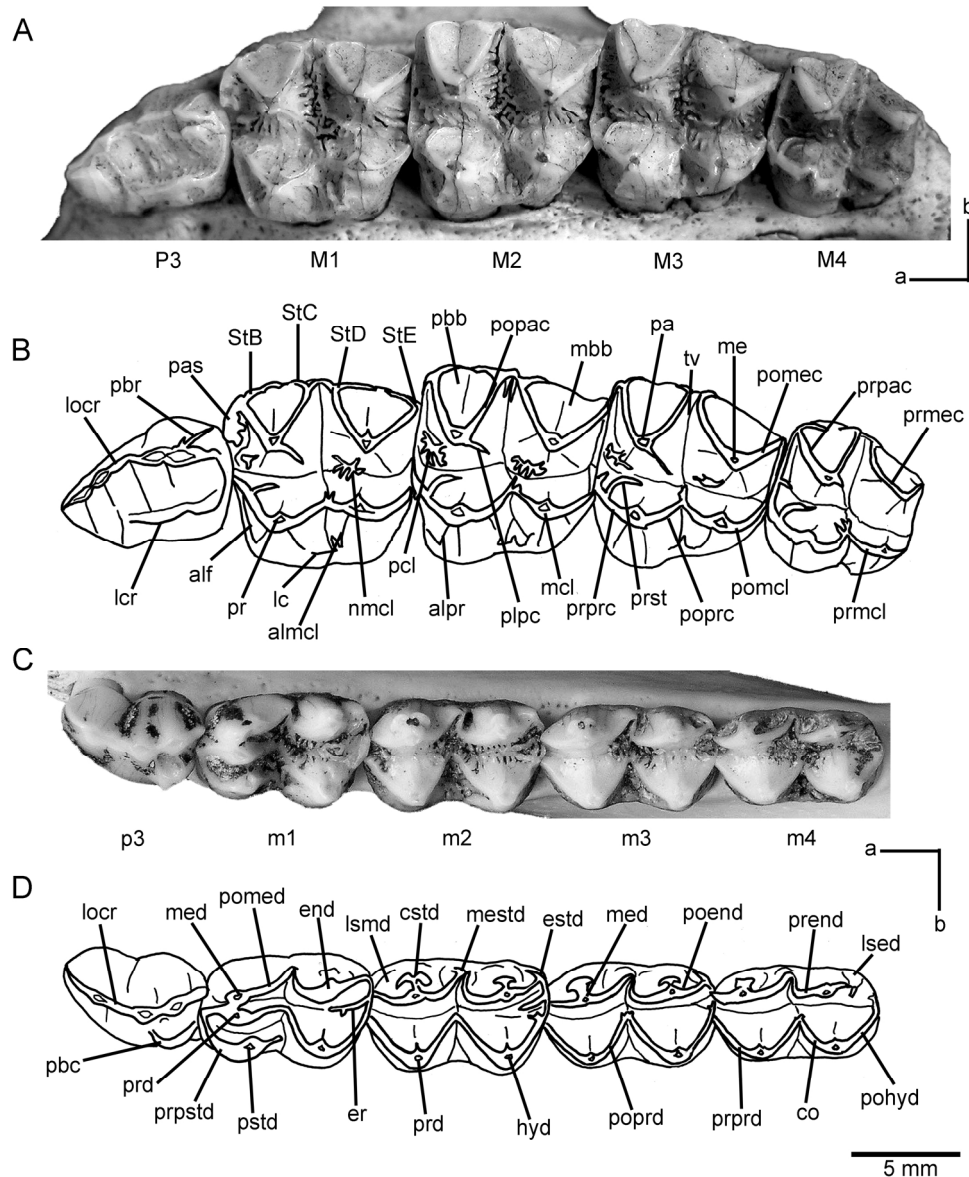


Figure 1. Map of Australia indicating main study sites (closed circles, modern; open circles, fossil) and geographic distribution (grey shading) of the modern koala, *Phascolarctos cinereus*. Abbreviations: NSW, New South Wales; NT, Northern Territory; QLD, Queensland; SA, South Australia; TAS, Tasmania; VIC, Victoria; WA, Western Australia.
121x85mm (300 x 300 DPI)



46 Figure 2. Occlusal view of *Phascolarctos cinereus* upper (A-B) and lower (C-D) dentitions. A, AR8398, left
 47 upper tooth row; B, line drawing of AR8398 indicating major features of the upper tooth row (except
 48 crenulations); C, AR6508, left lower tooth row; D, line drawing of AR6508 indicating major features of the
 49 lower tooth row (except crenulations). Abbreviations: a, anterior; alf, anterolingual fossa; almcl,
 50 anterolingual buttress of metaconule; alpr, anterolingual buttress of protocone; b, buccal; co, cristid
 51 obliqua; cstdd, columnar stylid; end, entoconid; er, entostylid ridge; estd, entostylid; hyd, hypoconid; lc,
 52 lingual cingulum; lcr, lingual cingular ridge; locr, longitudinal crest; lsed, lingual shelf of entoconid; lsmd,
 53 lingual shelf of metaconid; mbb, metacone buccal basin; mcl, metaconule; me, metacone; med, metaconid;
 54 mestd, metastylid; nmcl, neometaconule; pa, paracone; pas, parastyle; pbb, paracone buccal basin; pbc,
 55 posterobuccal crest of P3; pbr, posterobuccal ridge of P3; pcl, paraconule; plpc, posterolingual paracrista;
 56 poend, postentocristid; pohyd, posthypoconid; pomcl, postmetaconulecrista; pomec, postmetacrista;
 57 pomed, postmetacristid; popac, postparacrista; pomcl, postmetaconulecrista; poprd, postprotocristid;
 58 pr, protocone; prd, protoconid; prend, preentocristid; prmcl, premetaconulecrista; prmec,
 59 premetacrista; prpac, preparacrista; prprc, preprotocrista; prprd, preprotocristid; prstd, preprotocristid;

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preprotostylid cristid; pstd, protostylid; StB, stylar cusp B; StC, stylar cusp C; StD, stylar cusp D; StE, stylar cusp E; tv, transverse valley.
189x224mm (300 x 300 DPI)

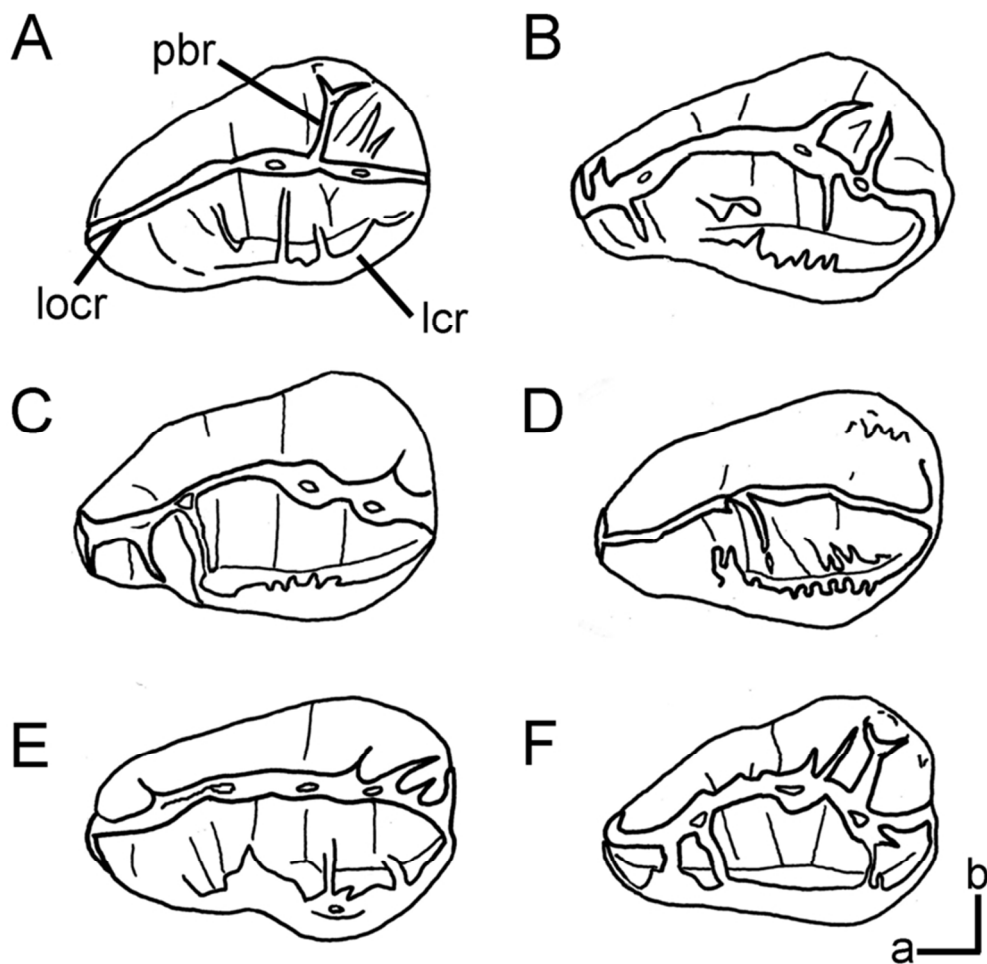


Figure 3. Comparison of the left P3 of six individuals of *P. cinereus*. A, AM M4841; B, AM M12475; C, AM M7364; D, QM J13278; E, AM M7486; F, AM P481. Abbreviations: a, anterior; b, buccal; lcr, lingual cingular ridge; lo cr, longitudinal crest.
75x73mm (300 x 300 DPI)

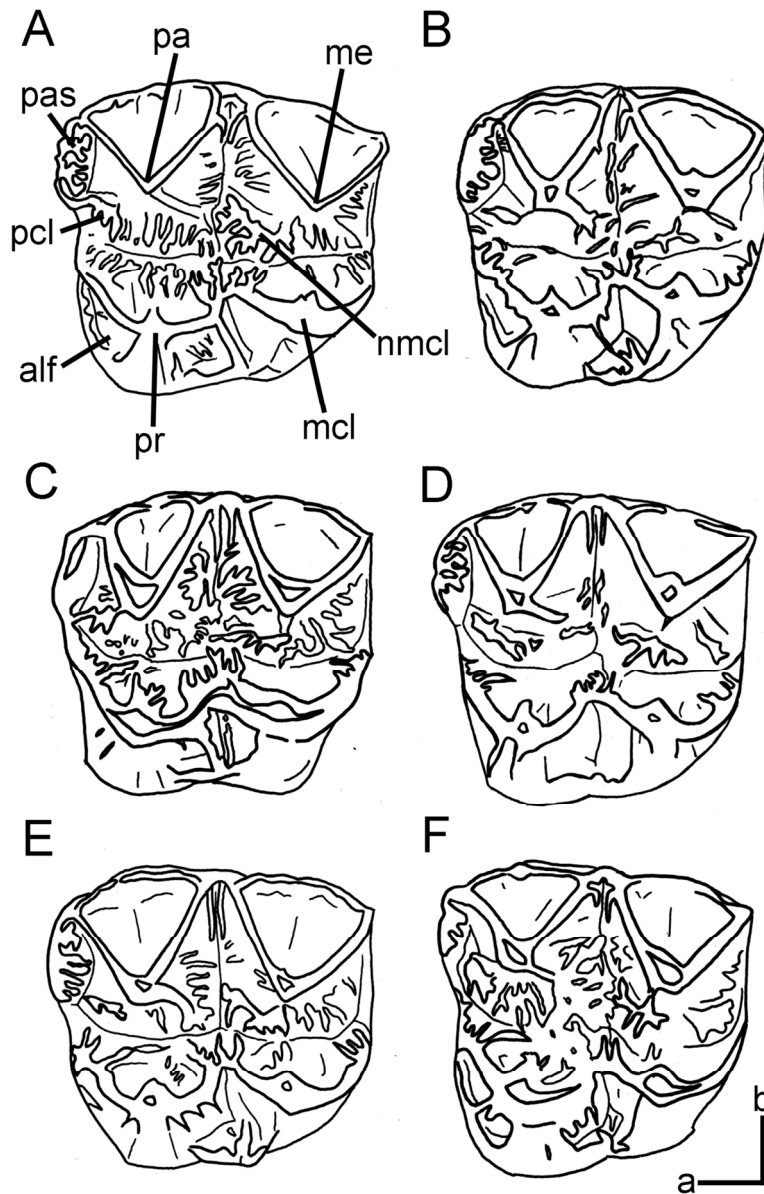


Figure 4. Comparison of the left M1 of six individuals of *P. cinereus*. A, QM J13278 (right M1 mirrored) ; B, AM M5266; C, AR20842; D, AM M7356; E, AM M2185 (right M1 mirrored); F, AR2626. Abbreviations: a, anterior; alf, anterolingual fossa; b, buccal; mcl, metaconule; me, metacone; nmcl, neometaconule; pa, paracone; pas, parastyle; pcl, paraconule; pr, protocone.
119x182mm (300 x 300 DPI)

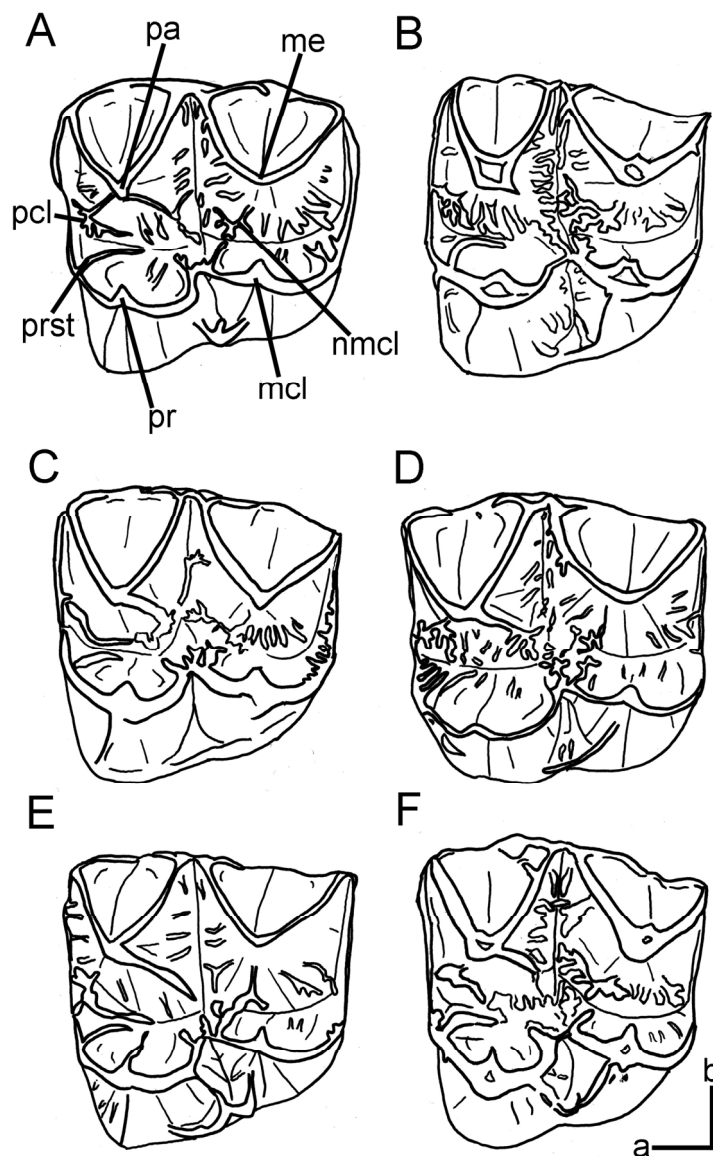


Figure 5. Comparison of the left M2 of six individuals of *P. cinereus*. A, AM M6806; B, AR8398; C, AM M4841 (right M1 mirrored); D, QM J13278; E, AM M7486; F, AM M12475. Abbreviations: a, anterior; b, buccal; mcl, metaconule; me, metacone; nmcl, neometaconule; pa, paracone; pcl, paraconule; pr, protocone; prst, protostyle.

129x213mm (300 x 300 DPI)

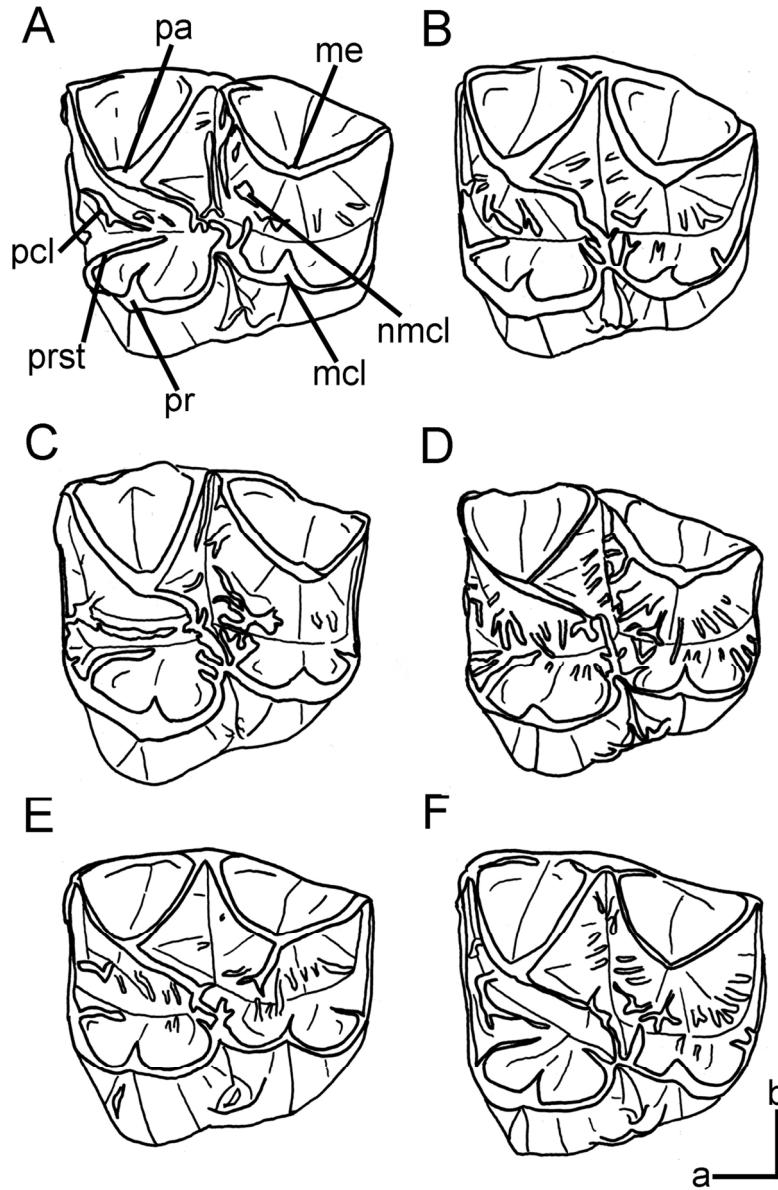


Figure 6. Comparison of the left M3 of six individuals of *P. cinereus*. A, AM M7356; B, AM M7364; C, AM M12475; D, QM J13278; E, AM M5743; F, AM M7486. Abbreviations: a, anterior; b, buccal; mcl, metaconule; me, metacone; nmcl, neometaconule; pa, paracone; pcl, paraconule; pr, protocone; prst, protostyle.

119x182mm (300 x 300 DPI)

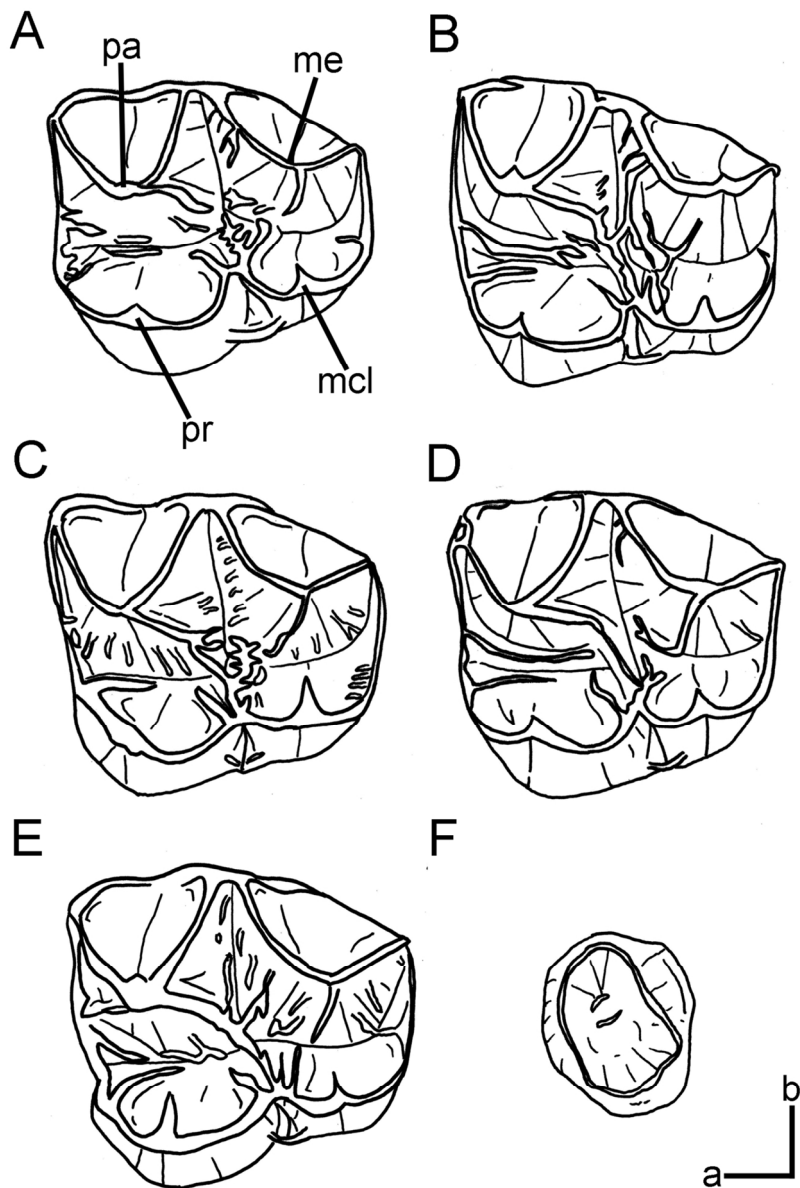


Figure 7. Comparison of the left M4 of six individuals of *P. cinereus*. A, AR1574; B, AM S415; C, AM M5743; D, AM M12475; E, AM M7356; F, AM M7364. Abbreviations: a, anterior; b, buccal; mcl, metaconule; me, metacone; pa, paracone; pr, protocone.
114x167mm (300 x 300 DPI)

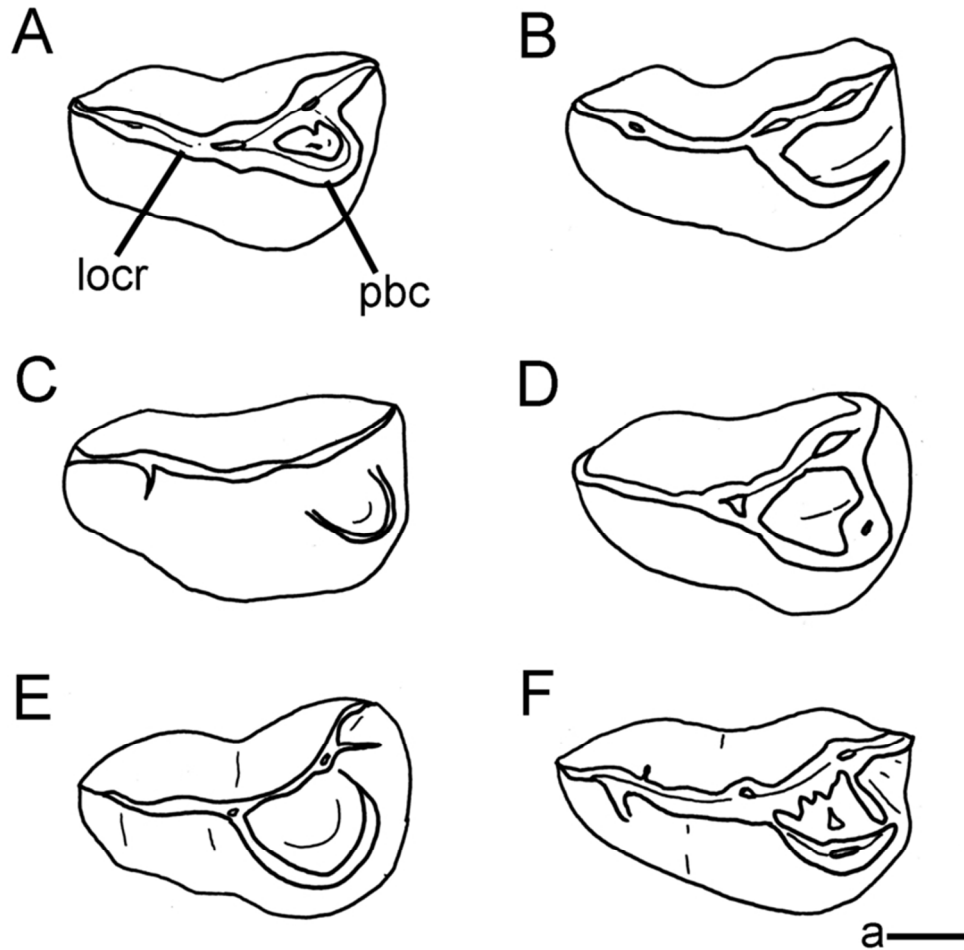


Figure 8. Comparison of the left P3 of six individuals of *P. cinereus*. A, AM M7356; B, AM M7364; C, QM J13278; D, AM M2185; E, AM M7486; F, AM M12475. Abbreviations: a, anterior; l, lingual; locr, longitudinal crest; pbc, posterobuccal crest.
75x71mm (300 x 300 DPI)

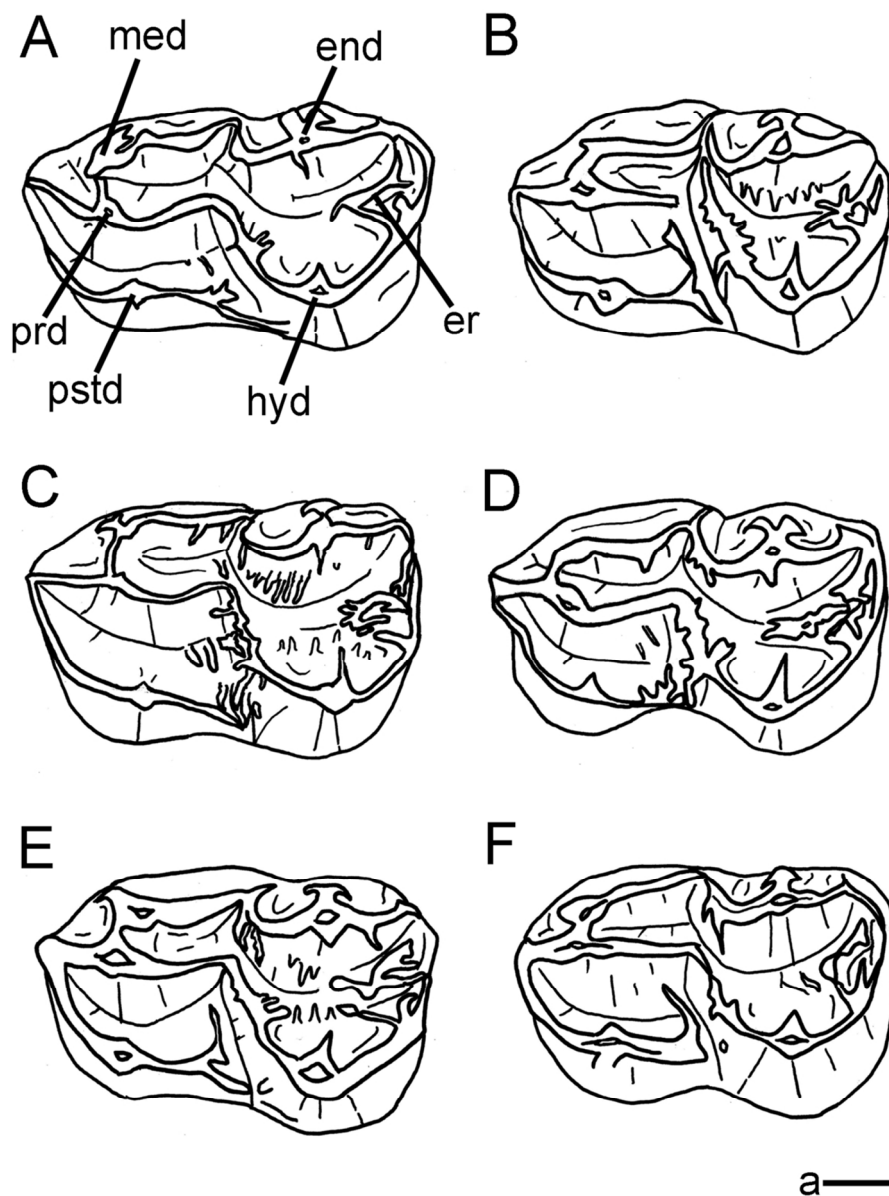


Figure 9. Comparison of the left M1 of six individuals of *P. cinereus*. A, AM M7486; B, AR1574; C, QM J13278; D, AM M12475; E, AM M7356; F, AM M7364. Abbreviations: a, anterior; end, entoconid; er, entostylid ridge; hyd, hypoconid; l, lingual; med, metaconid; prd, protoconid; pstd, protostylid.
102x134mm (300 x 300 DPI)

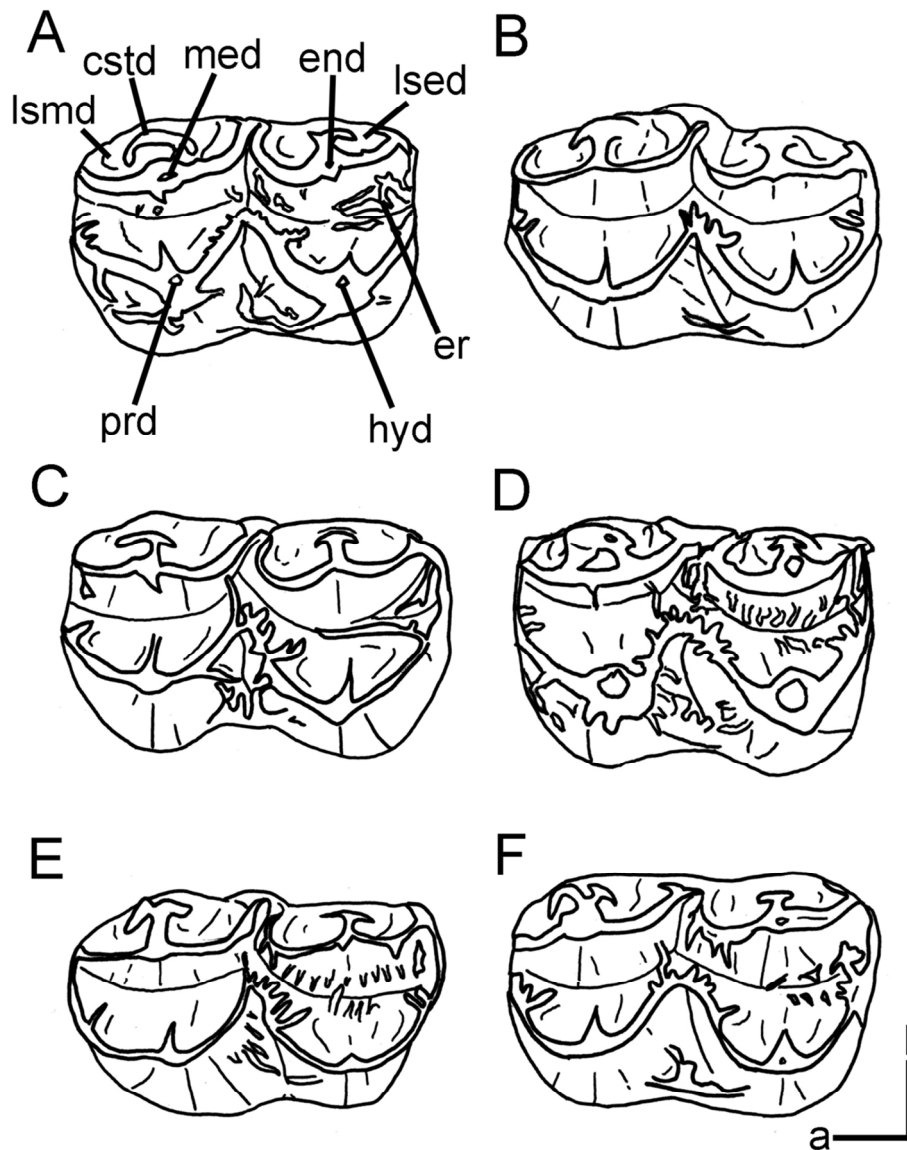


Figure 10. Comparison of the left M2 of six individuals of *P. cinereus*. A, AM M5266; B, AM M5743; C, AM M12475; D, AM M6582; E, QM J13278; F, AM M7356. Abbreviations: a, anterior; cstd, columnar stylid; end, entoconid; er, entostylid ridge; hyd, hypoconid; l, lingual; l sed, lingual shelf of entoconid; l smd, lingual shelf of metaconid; med, metaconid; prd, protoconid.

102x134mm (300 x 300 DPI)

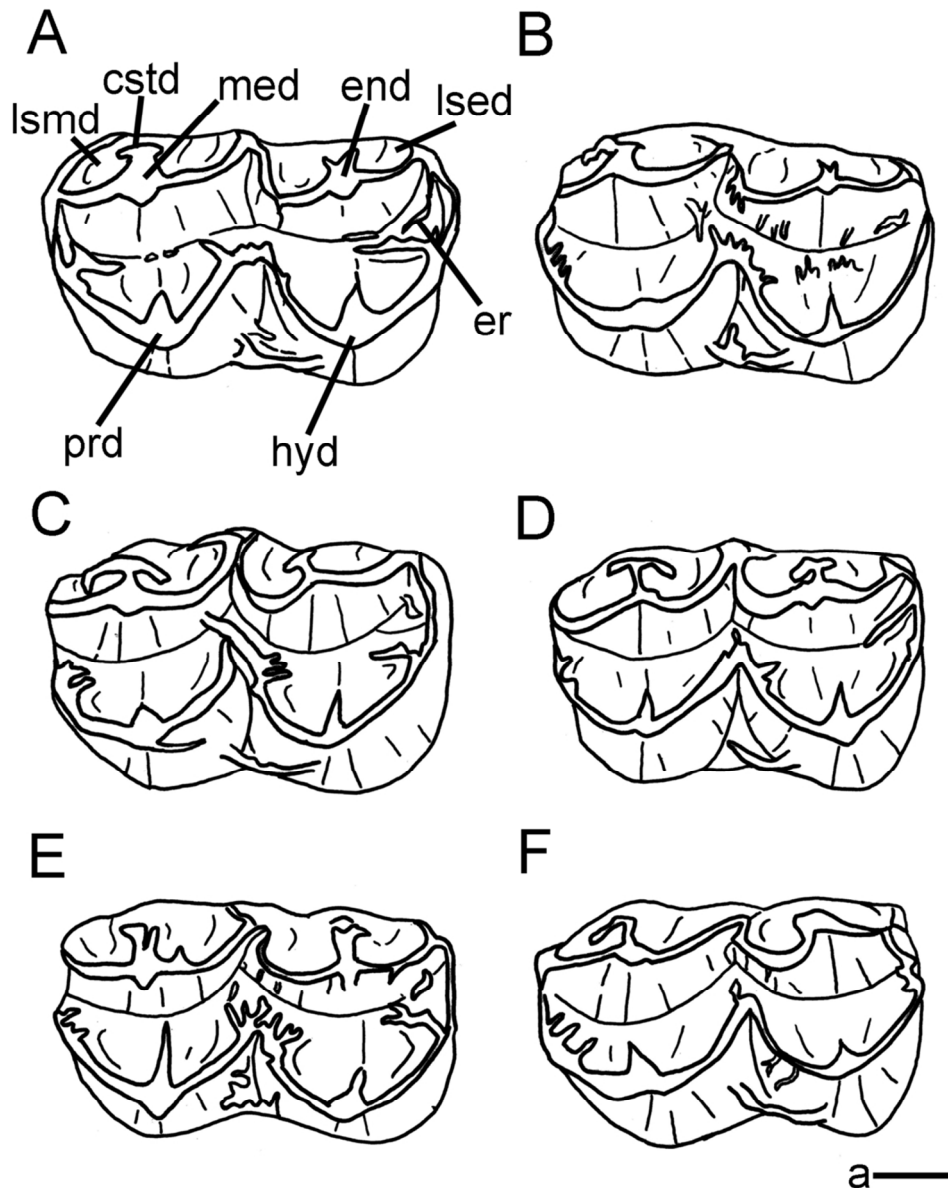


Figure 11. Comparison of the left M3 of six individuals of *P. cinereus*. A, AM M7356; B, AM S415; C, AM M2185; D, AM M5743; E, AM M12475; F, AM M7486. Abbreviations: a, anterior; cstd, columnar stylid; end, entoconid; er, entostylid ridge; hyd, hypoconid; l, lingual; lscd, lingual shelf of entoconid; lsmc, lingual shelf of metaconid; med, metaconid; prc, protoconid.

97x121mm (300 x 300 DPI)

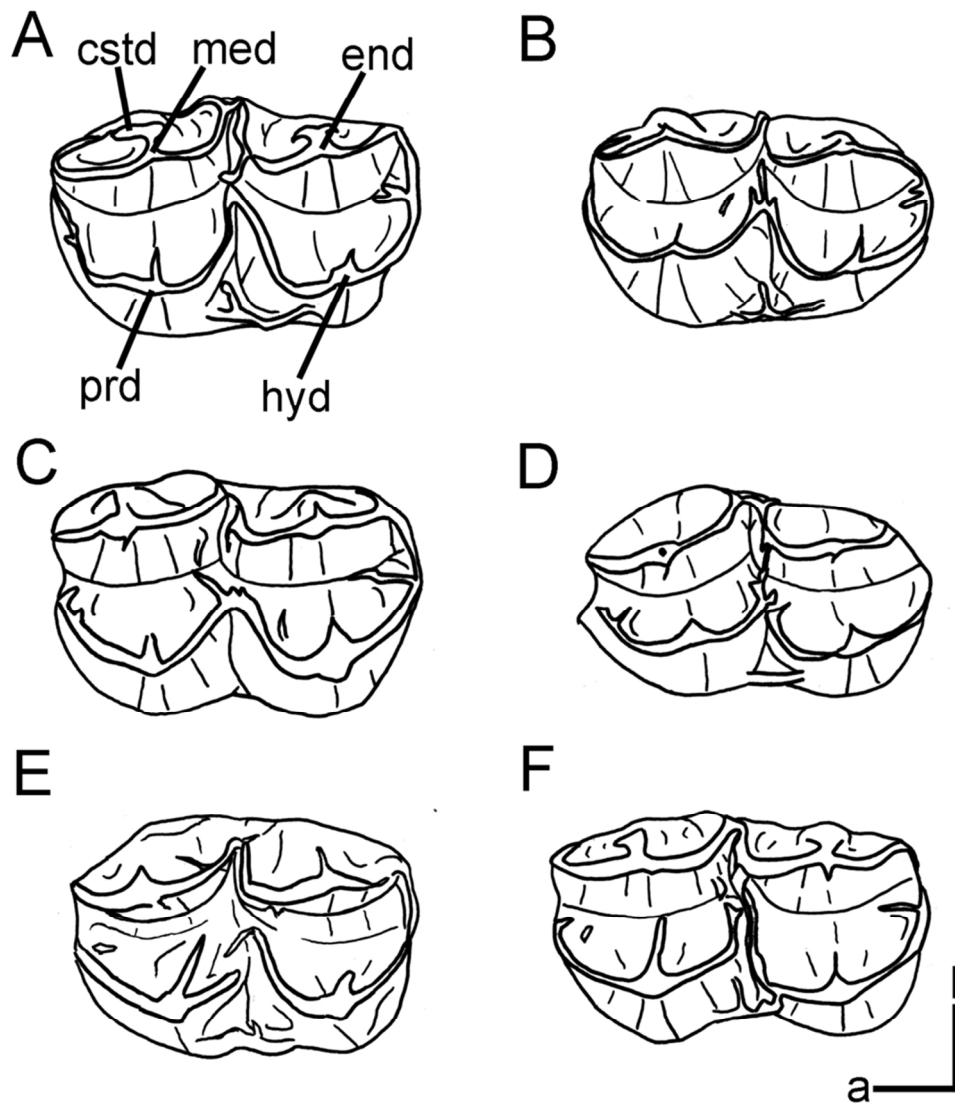


Figure 12. Comparison of the left M4 of six individuals of *P. cinereus*. A, AR1574; B, AM M2185; C, AM S415; D, AM M7364; E, AM M7438; F, AM M12475. Abbreviations: a, anterior; cstd, columnar stylid; end, entoconid; hyd, hypoconid; l, lingual; med, metaconid; prd, protoconid.
88x100mm (300 x 300 DPI)

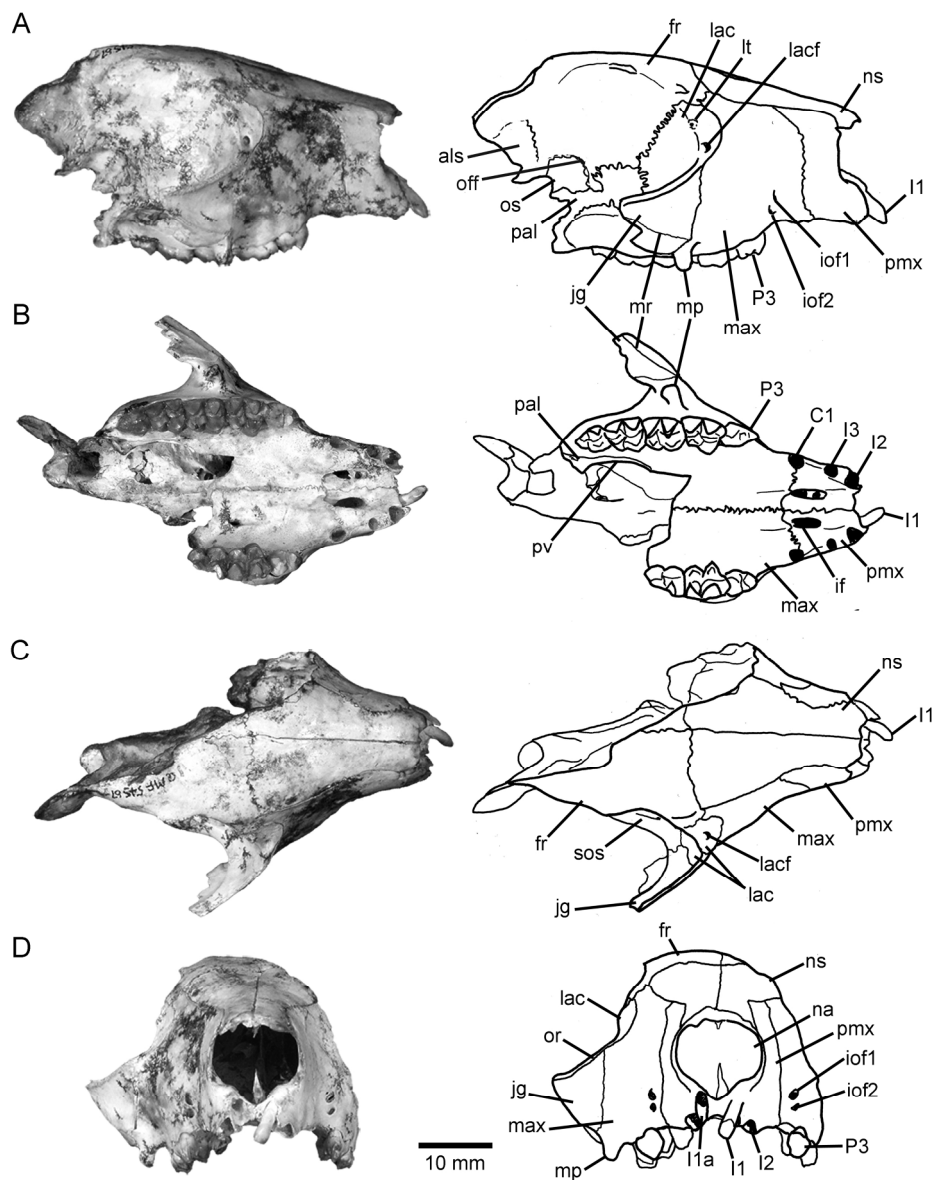


Figure 13. QM F54567, *Litokoala dicksmithi* n. sp. partial skull. A, right lateral view; B, occlusal view view; C, dorsal view; D, anterior view. Abbreviations: als, alisphenoid; C1, canine; fr, frontal; I1, first upper incisor; I1a, first upper incisor alveolus; I2, second upper incisor; I3, third 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 foramen; or, orbital ridge; os, orbitosphenoid; P3, upper premolar; pal, palatine; pmx, premaxilla; pv, palatal vacuity lateral border; sos, suborbital shelf.

212x267mm (300 x 300 DPI)

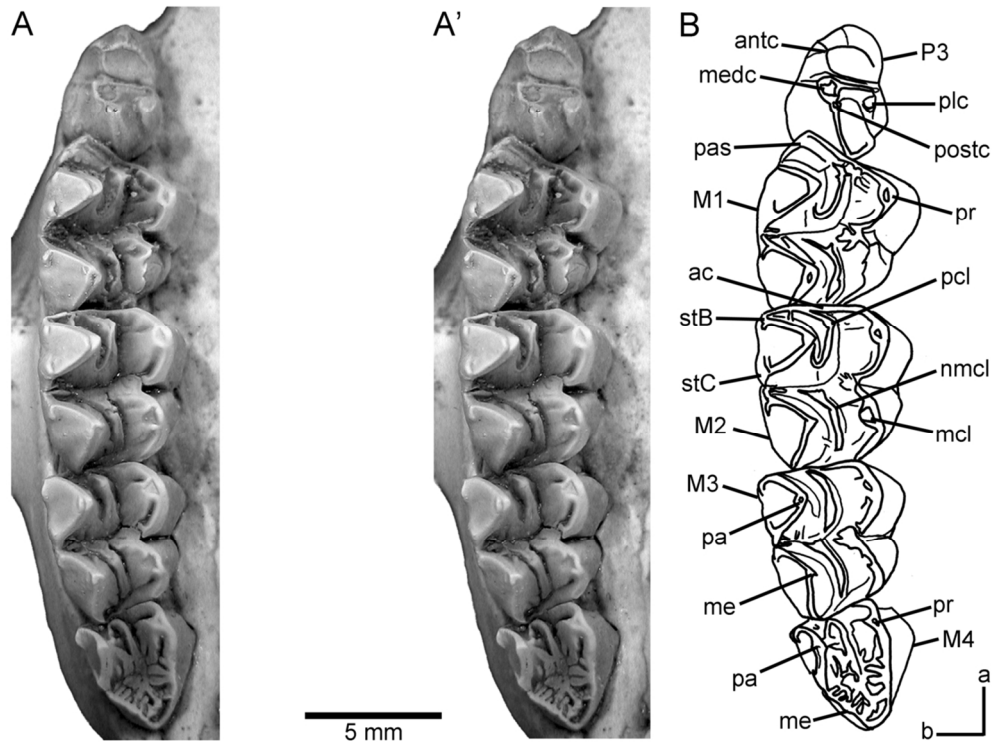


Figure 14. QM F54567, *Litokoala dicksmithi* n. sp. upper right P3, M1-4 in occlusal view. A, stereopair of right P3, M1-4; B, line drawing showing major features of P3, M1-4. Abbreviations: a, anterior; ac, anterior cingulum; antc, anterior cusp of P3; b, buccal; mcl, metaconule; me, metacone; medc, medial cusp of P3; nmcl, neometaconule; pa, paracone; pas, parastyle; pcl, paraconule; plc, posterolingual cusp of P3; postc, posterior cusp of P3; pr, protocone; stB, stylar cusp B; stC, stylar cusp C.
112x83mm (300 x 300 DPI)

Table 1. Results of t-tests for differences in upper tooth dimensions of male and female *P. cinereus* between geographic 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.

Tooth	L	AW	PW
Male			
P ³	$p = 0.006$ (V)	n.s.	n.s.
M ¹	$p = 0.03$ (V)	$p = 0.008$ (V)	n.s.
M ²	$p = 0.007$ (V)	$p = 0.002$ (V)	$p = 0.03$ (V)
M ³	$p = 0.004$ (V)	$p = 0.001$ (V)	n.s.
M ⁴	$p < 0.001$ (V)	n.s.	n.s.
Female			
P ³	n.s.	n.s.	$p = 0.05$ (Q)
M ¹	n.s.	n.s.	$p = 0.002$ (Q)
M ²	n.s.	n.s.	$p = 0.011$ (Q)
M ³	n.s.	n.s.	$p = 0.008$ (V)
M ⁴	n.s.	n.s.	n.s.

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.

Tooth	L	AW	PW
P ³	n.s.	n.s.	n.s.
M ¹	$p = 0.003$ (M)	$p > 0.001$ (M)	$p = 0.002$ (M)
M ²	$p = 0.018$ (M)	$p < 0.001$ (M)	$p < 0.001$ (M)
M ³	$p = 0.021$ (M)	$p = 0.003$ (M)	$p = 0.029$ (M)
M ⁴	$p = 0.003$ (M)	$p < 0.001$ (M)	n.s.

Table 3. Results of t-tests for differences in lower tooth dimensions of male and female *P. cinereus* between geographic 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.

Tooth	L	AW	PW
Male			
P ₃	n.s.	n.s.	n.s.
M ₁	n.s.	$p < 0.001$ (V)	$p = 0.02$ (V)
M ₂	n.s.	$p = 0.045$ (V)	n.s.
M ₃	$p < 0.001$ (V)	n.s.	n.s.
M ₄	$p < 0.001$ (V)	n.s.	n.s.
Female			
P ₃	n.s.	n.s.	n.s.
M ₁	n.s.	$p < 0.001$ (V)	$p = 0.02$ (V)
M ₂	n.s.	$p = 0.049$ (V)	n.s.
M ₃	$p < 0.001$ (V)	n.s.	n.s.
M ₄	$p < 0.001$ (V)	n.s.	n.s.

Table 1. 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.

	<i>L. dicksmithi</i>	<i>L. kutjamarpensis</i>	<i>L. garyjohnstoni</i>	<i>N. greystanesi</i>	
	QM F 54567	QM F51382	QM F51405	QM F30483	QM F30482
			QM F51406		
DL	10.5	---	---	12.2	---
DZP	11.4	---	---	---	---
HPOP	28.25	---	---	---	---
NAH	10.15	---	---	7.42	---
NAW	12.91	---	---	8.47	---
NL	26.4	---	---	27.25	---
NW	23.1#	---	---	---	---
PMD	16.0	---	---	14.4	---
PWC1	10.3	---	---	9.0	---
PWI3	7.2	---	---	7.0	---
PWM1	15.25	14.6	---	14.5	11.30
RD	17.9	---	---	16.3	---
RW	16.2	---	---	14.85	---
TRL	25.2	25.0	24.2	---	---

right nasal measured and doubled

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Table 2. Dental measurements (mm) of *Litokoala dicksmithi*. Abbreviations: AW, anterior width; L, length; PW, posterior width.

Specimen	P ³			M ¹			M ²			M ³			M ⁴		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	
QM F54567															
Left	5.40	3.68	6.60	5.70	4.94	---	---	---	---	---	---	---	---	---	
QM F54567															
Right	5.30	3.64	6.64	5.73	---	5.53	5.48	4.79	5.51	5.18	4.23	4.43	3.79	2.58	

Appendix 1. Univariate statistics for *Phascolarctos cinereus* dentitions from Queensland and Victoria. Abbreviations: AW, anterior width; L, length; PW, posterior width.

Queensland males

	P ³ L	P ³ AW	P ³ PW	M ¹ L	M ¹ AW	M ¹ PW	M ² L	M ² AW	M ² PW	M ³ L	M ³ AW	M ³ PW	M ⁴ L	M ⁴ AW	M ⁴ PW
N	16	16	16	16	16	16	17	17	17	16	16	16	16	16	16
Min	6.5	3.3	4.7	7.0	7.2	7.0	6.9	7.5	6.4	6.6	6.7	5.9	6.4	5.6	4.5
Max	7.6	4.6	5.4	8.5	8.3	7.9	8.4	8.8	7.8	7.9	8.1	7.4	7.5	7.5	6.2
Mean	7.1	3.9	5.1	7.8	7.8	7.5	7.6	8.0	7.2	7.2	7.5	6.6	6.8	6.6	5.4
SE	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2
Var	0.1	0.2	0.1	0.2	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.2	0.1	0.3	0.4
SD	0.3	0.4	0.2	0.4	0.3	0.3	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.5	0.6
CV	4.6	10.1	3.9	5.4	4.3	3.3	5.1	4.6	5.3	5.3	4.9	6.4	5.3	8.1	10.9

	P ₃ L	P ₃ AW	P ₃ PW	M ₁ L	M ₁ AW	M ₁ PW	M ₂ L	M ₂ AW	M ₂ PW	M ₃ L	M ₃ AW	M ₃ PW	M ₄ L	M ₄ AW	M ₄ PW
N	18	18	18	20	20	20	20	20	20	20	20	20	20	20	20
Min	5.4	2.8	3.6	6.7	4.3	4.8	7.0	4.6	4.8	6.9	4.5	4.5	6.1	4.2	4.1
Max	7.7	3.4	4.4	8.2	5.1	5.7	8.4	5.7	5.7	8.0	5.6	5.5	8.0	5.4	5.1
Mean	6.1	3.1	3.9	7.4	4.7	5.2	7.5	5.2	5.2	7.4	5.0	4.9	7.4	4.9	4.5
SE	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Var	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1

SD	0.5	0.2	0.2	0.4	0.2	0.3	0.3	0.3	0.2	0.3	0.3	0.3	0.4	0.3	0.3
CV	7.9	6.2	5.7	5.0	4.9	4.9	4.3	5.2	4.6	3.8	5.5	5.2	5.4	6.1	6.2

 Queensland females

	P ³ L	P ³ AW	P ³ PW	M ¹ L	M ¹ AW	M ¹ PW	M ² L	M ² AW	M ² PW	M ³ L	M ³ AW	M ³ PW	M ⁴ L	M ⁴ AW	M ⁴ PW
N	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
Min	6.4	3.4	4.6	7.0	6.7	6.9	7.1	7.5	6.8	7.0	6.7	6.3	6.3	5.9	5.1
Max	7.6	4.5	8.8	8.5	8.4	7.9	8.0	8.3	7.7	8.0	7.6	7.2	7.4	8.4	6.6
Mean	7.0	3.9	5.4	7.8	7.6	7.4	7.5	8.0	7.2	7.3	7.3	6.7	6.7	6.7	5.5
SE	0.1	0.	0.3	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1
Var	0.2	0.1	1.2	0.3	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.4	0.2
SD	0.4	0.3	1.1	0.5	0.5	0.3	0.2	0.3	0.3	0.3	0.3	0.3	0.3	0.7	0.4
CV	5.6	8.7	20.1	6.6	6.7	4.2	3.2	3.5	3.4	4.1	3.8	3.7	4.8	9.8	7.4

	P ₃ L	P ₃ AW	P ₃ PW	M ₁ L	M ₁ AW	M ₁ PW	M ₂ L	M ₂ AW	M ₂ PW	M ₃ L	M ₃ AW	M ₃ PW	M ₄ L	M ₄ AW	M ₄ PW
N	25	25	25	27	27	27	27	27	27	27	27	27	27	27	27
Min	5.2	2.3	3.1	6.7	3.9	4.4	6.9	4.1	4.4	6.8	4.5	4.1	6.	4.3	3.9
Max	6.7	3.	4.4	7.9	5.0	5.6	8.2	5.6	5.7	8.0	5.6	5.5	8.2	5.4	5.6
Mean	5.9	3.1	3.8	7.3	4.5	5.0	7.4	5.0	5.0	7.3	4.9	4.8	7.4	4.8	4.5
SE	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.8

Var	0.2	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1
SD	0.4	0.3	0.4	0.3	0.3	0.3	0.3	0.3	0.3	0.4	0.3	0.3	0.3	0.4	0.3	0.4
CV	6.6	11.1	10.3	4.5	6.0	5.7	4.5	5.9	5.1	5.2	5.0	6.7	5.3	5.5	8.3	

Victorian males

	P ³ L	P ³ AW	P ³ PW	M ¹ L	M ¹ AW	M ¹ PW	M ² L	M ² AW	M ² PW	M ³ L	M ³ AW	M ³ PW	M ⁴ L	M ⁴ AW	M ⁴ PW
N	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Min	6.9	3.2	4.5	7.4	7.9	7.0	7.6	7.9	7.1	7.2	7.5	6.4	6.9	6.5	5.2
Max	8.1	4.4	5.5	8.4	8.5	7.7	8.2	8.9	7.9	8.3	8.6	7.1	7.8	7.4	6.4
Mean	7.6	3.9	5.0	8.1	8.2	7.5	8.0	8.5	7.5	7.7	8.0	6.6	7.4	6.9	5.6
SE	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Var	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.2
SD	0.4	0.4	0.3	0.3	0.2	0.2	0.2	0.3	0.3	0.4	0.4	0.3	0.3	0.3	0.4
CV	5.5	9.6	6.0	3.8	2.6	2.7	2.8	3.5	3.4	4.7	5.2	3.9	4.1	4.2	7.7

	P ₃ L	P ₃ AW	P ₃ PW	M ₁ L	M ₁ AW	M ₁ PW	M ₂ L	M ₂ AW	M ₂ PW	M ₃ L	M ₃ AW	M ₃ PW	M ₄ L	M ₄ AW	M ₄ PW
N	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Min	5.4	3.1	3.3	7.1	4.7	5.2	7.7	4.8	5.0	7.6	5.0	4.6	7.3	4.9	4.4
Max	6.6	3.4	4.2	8.2	5.4	5.9	8.6	5.9	5.8	8.4	5.8	5.6	8.5	6.1	5.2
Mean	6.0	3.3	4.0	7.6	5.2	5.4	8.1	5.5	5.3	7.9	5.4	5.1	8.1	5.3	4.7

SE	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Var	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.1
SD	0.3	0.1	0.3	0.4	0.2	0.2	0.3	0.4	0.3	0.3	0.3	0.3	0.3	0.4	0.4	0.3
CV	5.6	2.6	7.2	5.2	4.4	3.6	3.6	6.3	5.4	3.4	4.9	5.9	5.0	8.1	5.9	

Victorian females

	P ³ L	P ³ AW	P ³ PW	M ¹ L	M ¹ AW	M ¹ PW	M ² L	M ² AW	M ² PW	M ³ L	M ³ AW	M ³ PW	M ⁴ L	M ⁴ AW	M ⁴ PW
N	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Min	5.4	3.1	3.3	7.1	4.7	5.2	7.7	4.8	5.0	7.6	5.0	4.6	7.3	4.9	4.4
Max	6.6	3.4	4.2	8.2	5.4	5.9	8.6	5.9	5.8	8.4	5.8	5.6	8.5	6.1	5.2
Mean	6.0	3.3	4.0	7.6	5.2	5.4	8.1	5.5	5.3	7.9	5.4	5.1	8.1	5.3	4.7
SE	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Var	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1
SD	0.3	0.1	0.3	0.4	0.2	0.2	0.3	0.4	0.3	0.3	0.3	0.3	0.4	0.4	0.3
CV	5.6	2.6	7.2	5.2	4.4	3.6	3.6	6.3	5.4	3.4	4.9	5.9	5.0	8.1	5.9

	P ₃ L	P ₃ AW	P ₃ PW	M ₁ L	M ₁ AW	M ₁ PW	M ₂ L	M ₂ AW	M ₂ PW	M ₃ L	M ₃ AW	M ₃ PW	M ₄ L	M ₄ AW	M ₄ PW
N	13	13	13	13	13	13	13	13	13	13	13	13	13	13	13
Min	5.4	2.9	3.1	6.6	4.5	4.8	7.3	4.8	4.7	7.4	4.5	4.6	7.4	4.2	4.2
Max	6.3	3.5	4.6	7.9	5.2	5.6	8.1	5.5	5.5	8.0	5.6	5.2	8.6	5.5	5.0

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Mean	5.8	3.1	3.7	7.3	4.8	5.2	7.6	5.2	5.0	7.8	5.1	4.9	7.9	4.9	4.5
SE	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Var	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
SD	0.3	0.2	0.4	0.4	0.2	0.2	0.2	0.2	0.2	0.2	0.3	0.2	0.4	0.3	0.2
CV	5.0	6.2	9.3	5.6	3.8	3.9	2.8	3.8	4.8	2.4	5.3	3.4	4.7	6.4	4.6

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3 **Supplementary data 1**
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7 Supplementary data for 'Understanding morphological variation in the extant koala as a
8 framework for identification of species boundaries in extinct koalas (*Phascolarctidae*;
9 *Marsupialia*)' by Karen H. Black, Julien Louys, Gilbert J. Price.
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16 Specimens used in the morphological and morphometric variation study of *Phascolarctos*
17 *cinereus*. Abbreviations: AM M, AM P and AM S, Australian Museum mammal
18 collection; AR, specimens temporarily held in collections at the University of New South
19 Wales; QM J and QJM Queensland Museum Mammal collection; NMV C, Museum
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Specimen	Sex	Locality
AM M2185	Male	No data
AM M4841	Male	French Island, Vic
AM M5266	Male	Enoggerra, Qld
AM M5743	Male	North coast, NSW
AM M6582	Male	Clareville, NSW
AM M 6806	No data	No data
AM M7356	Male	NSW
AM M7364	Male	NSW
AM M7438	Female	No data
AM M7486	Male	NSW
AM M12475	No data	Bulahdelah, NSW
AM P481	No data	Mulgoa, NSW
AM S415	No data	No data
AM S1570	No data	Sydney, NSW
AR1574	No data	No data
AR2626	No data	Smith's Lake, NSW
AR6071	No data	No data

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3	AR6509	No data	No data
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5	AR8398	No data	No data
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7	AR8403	No data	No data
8			
9	AR20842	No data	No data
10			
11	NMV C18606	Female	Lima south, Vic
12	NMV C19006	Male	Fyans Creek, Grampians, Vic
13			
14	NMV C20502	Male	Kyneton, Vic
15			
16	NMV C20504	Male	Frankston, Vic
17			
18	NMV C23049	Female	Chiltern, Vic
19			
20	NMV C26518	Male	Mangalore, Vic
21	NMV C2831	Female	Bowen, Qld
22			
23	NMV C2992	Male	Castlemaine, Vic
24			
25	NMV C31175	Male	Victoria
26			
27	NMV C35907	Male	Mardan (nr. Leongatha), Vic
28			
29	NMV C5776	Female	Taralgon south, Vic
30	NMV C6178	Female	Taralgon, Vic
31			
32	NMV C6253	Female	Red Bull Ck., French Island, Vic
33			
34	NMV C6669	Male	Wilson's Promontory, Vic
35			
36	NMV C6728	Female	Wilson's Promontory, Vic
37			
38	NMV C6741	Female	Bacchus Marsh, Vic
39			
40	NMV C6743	Female	Wilson's Promontory, Vic
41			
42	NMV C6745	Female	Bacchus Marsh, Vic
43			
44	NMV C6757	Female	Tyabb, Vic
45			
46	NMV C6758	Male	Fish Ck., Vic
47			
48	NMV C8588	Female	Phillip Is., Vic
49			
50	NMV C8601	Female	Phillip Is., Vic
51			
52	NMV C8626	Female	Frankston, Vic
53			
54	NMV C8628	Male	Leongatha, Vic
55			
56	QM J992	Male	10mls W of Ipswich, Qld
57			
58	QM J2296	Male	Fleays Sanctuary, Gold Coast, Qld
59			
60	QM J3793	Male	Brisbane River, Bellvue, Qld

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QM J3856	Male	Samford Scrub, Qld
QM J4668	Male	Caboolture, Qld
QM J5749	Male	Range near Brisbane, Qld
QM J5835	Female	West Burleigh, Qld
QM J7118	Female	Camp Mountain, Samford, Qld
QM J7309	Female	Coochiemudlo Island, Qld
QM J8119	Male	Yeronga, Qld
QM J8199	Female	Nudgee, Qld
QM J8742	Male	Conondale Ranges, Qld
QM J8811	Male	Toogoolawah, Qld
QM J10034	Female	Moggil, Qld
QM J10462	Male	Boondall, Qld
QM J11253	Female	Ormiston, Brisbane, Qld
QM J12120	Female	Glenbar State Forest, Qld
QM J13375	Female	Burleigh Heads, Qld
QM J13610	male	Yelarbon, 100mls W of Warwick, Qld
QM J14982	Female	Mt Tamborine, Qld
QM J14983	Male	Toowoomba Range Escarpment, Qld
QM J15023	Female	Mt Crosby, Qld
QM J15074	Female	Indooroopilly, Qld
QM J16453	Female	Tweed Heads, Qld
QM J18526	Male	Oakey, Qld
QM J18530	Female	Oakey, Qld
QM J18533	Male	Oakey, Qld
QM J18606	Female	Oakey, Qld
QM J18606	Female	Oakey, Qld
QM J18610	Male	Oakey, Qld
QM J18613	Male	Oakey, Qld
QM J18616	Female	Oakey, Qld
QM J18619	Male	Oakey, Qld
QM J18620	Female	Oakey, Qld

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3	QM J18623	Male	Oakey, Qld
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5	QM J18624	Male	Oakey, Qld
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7	QM J18627	Female	Oakey, Qld
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9	QM J18887	Female	Oakey, Qld
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11	QM J18888	Female	Oakey, Qld
12			
13	QM J18890	Male	Oakey, Qld
14			
15	QM J18897	Female	Oakey, Qld
16			
17	QM J18898	Female	Oakey, Qld
18			
19	QM J19170	Male	Oakey, Qld
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21	QM J19175	Male	Oakey, Qld
22			
23	QM J19178	Male	Oakey, Qld
24			
25	QM J19187	Female	Oakey, Qld
26			
27	QM J19189	Female	Oakey, Qld
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29	QM J19370	Female	Oakey, Qld
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31	QM J19375	Male	Oakey, Qld
32			
33	QM J19394	Male	Oakey, Qld
34			
35	QM J19395	Male	Oakey, Qld
36			
37	QM J19419	Male	Oakey, Qld
38			
39	QM J19422	Male	Oakey, Qld
40			
41	QM J19426	Female	Oakey, Qld
42			
43	QM J19429	Female	Oakey, Qld
44			
45	QM J19430	Female	Oakey, Qld
46			
47	QM J19433	Male	Oakey, Qld
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49	QM J19434	Female	Oakey, Qld
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51	QM J19435	Male	Oakey, Qld
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53	QM J19436	Male	Oakey, Qld
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55	QM J19438	Female	Oakey, Qld
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57	QM J19438	Female	Oakey, Qld
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59	QM J19726	Female	Helmsley Station, Oakey region, Qld
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	QM J20262	Female	Cunningham's Gap, Qld

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