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Revision of Oligo-Miocene kangaroos, *Ganawamaya* and *Nambaroo* (Marsupialia: Macropodiformes, Balbaridae)

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ABSTRACT

The generic and specific status of fossil kangaroo specimens attributed to *Nambaroo* and *Ganawamaya* from the Riversleigh World Heritage Area, Australia, are revised and new material is described. Results indicate that the previously proposed 12 species (eight of *Nambaroo* and four of *Ganawamaya*) represent four species from a single genus (*Ganawamaya*). Previous studies distinguished species of *Ganawamaya* from *Nambaroo* in lacking a protostylid on the lower first molar. However, our analyses indicate that the apparent presence/absence of the protostylid is related to the degree of dental wear, being totally worn in older individuals. Unworn specimens from Riversleigh were previously typically attributed to *Nambaroo*, while worn specimens were most commonly attributed to *Ganawamaya*. With support from phylogenetic analyses, we refer Riversleigh's *N. couperi* and *N. gillespieae* to *Ganawamaya*. The diagnoses of both genera are revised. We also assign undescribed specimens from the Ngapakaldi Quarry and Leaf Locality, South Australia, to *Gan. couperi* comb. nov. and *Gan. acris*, respectively, and describe new material of *Gan. acris* and *Gan. aediculis*.

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INTRODUCTION

The Riversleigh World Heritage Area (WHA), located in northwestern Queensland, Australia, contains numerous macropodiform-bearing fossil deposits dating from the late Oligocene through to the late Miocene (Travouillon et al., 2006; Arena et al., 2015). A biostratigraphic study by Cooke (1997a) found that during the late Oligocene, Balbaridae, an extinct family of kangaroos with hypertrophied canines, was the most diverse macropodiform (kangaroos and allies) family represented in the Riversleigh WHA deposits. Cooke (1997a) suggested that in the middle Miocene, macropodids were the most diverse, and that only a single balbarid species, '*Balbaroo* sp. 4' (now *B. nalima*; Black et al., 2014), was present. Subsequent to publication of Cooke (1997a), several new Riversleigh fossil macropodiform specimens have been recovered, and many additional species have been described (e.g., Kear et al., 2007; Bates et al., 2014; Travouillon et al., 2014; Cooke et al., 2015; Travouillon et al., 2015; Butler et al., 2016).

In order to understand the temporal range, evolution, and extinction of Australia's earliest macropodiforms, it is necessary to have a robust understanding of alpha-level taxonomic diversity throughout the Cenozoic. One group that requires taxonomic revision is the Balbaridae. First erected as a subfamily by Flannery et al. (1982) who proposed that the group was ancestral to Macropodidae, Balbaridae was elevated to family level following a morphology-based phylogenetic analysis by Kear and Cooke (2001). More recent studies suggest that Balbaridae is most closely related to the hypsiprymnodontid subfamily Propleopinae (Wroe et al., 1998; Kear et al., 2007; Kear and Pledge, 2007). Several balbarid genera have been described including *Balbaroo* (Flannery et al., 1982), *Galanarla* (Flannery et al., 1982), *Nambaroo* (Flannery and Rich, 1986), *Ganawamaya* (Cooke, 1992), and *Wururoo* (Cooke, 1997b).

Nambaroo was described to include three species (*N. tarrinyeri*, *N. Saltavus,* and *N. novus*) from the Namba Formation, South Australia (Flannery and Rich, 1986). Two additional species, *N. couperi* Cooke 1997 and *N. gillespieae* Kear et al., 2007, were described from the Riversleigh WHA. *Nambaroo bullockensis*, from the Bullock Creek Local Fauna from the Camfield Beds, Northern Territory, was later described by Schwartz and Megirian (2004). Black et al. (2014) identified *N. bullockensis* as a junior synonym of *Balbaroo camfieldensis* Flannery et al., 1982. *Ganawamaya* was described from Riversleigh by Cooke (1992) to include the three species *Gan. acris*, *Gan. ornata* and *Gan. aediculis*. Cooke (1997a) listed eight morphospecies of *Nambaroo* and four of *Ganawamaya*, all from Riversleigh, although several of these species (six of *Nambaroo* and one of *Ganawamaya*) were not formally described therein. Those species were informally described in a thesis by Cooke (1996).

Black et al. (2014) demonstrated that a remnant protostylid is evident in unworn juvenile molars (those specimens without a fully erupted fourth premolar) of some *Balbaroo* taxa (e.g., *B. fangaroo* and *B. nalima*) and suggested that the lack of a protostylid in adult specimens is most likely the results of a greater degree of dental wear. This suggests that the apparent lack of a protostylid in other balbarid species may similarly be the result of dental wear. *Ganawamaya* was previously distinguished from *Nambaroo* by the lack of a protostylid on m1 (Cooke, 1992). The present study aims to revise the taxonomic status of species attributed to *Ganawamaya* and *Nambaroo* and to assess whether the lack of a protostylid in species of *Ganawamaya* is related to dental wear. Our study is based on a re-examination of previously known material, as well as new specimens that have been recovered since Cooke's (1997a) biostratigraphic study. As part of this revision, we describe new material for *Gan. acris, N. couperi* and *Gan. aediculis* and revise the generic classification of *N. couperi* based on new material. The phylogenetic relationships of *Nambaroo* and *Ganawamaya* within Macropodiformes are also reassessed.

MATERIALS AND METHODS

Terminology

Terminology for dental anatomy follows Archer (1984), Cooke (1997b), and Cooke (1997c). Higher systematic nomenclature follows Prideaux and Warburton (2010) except for subordinal classification (Macropodiformes) which follows Meredith et al. (2009).

Materials and Mensuration

Specimens used in this study were collected from several fossil sites in the Riversleigh WHA and from Ngapakaldi Quarry (Ngapakaldi Local Fauna) and Leaf Locality (Kutjamarpu Local Fauna), Tirari Desert, South Australia. *Ganawamaya* and *Nambaroo* specimens from Riversleigh are housed in the Queensland Museum fossil collection (prefix QM F), Brisbane, Australia. Specimens from South Australia were measured from casts of original specimens made by the University of California Museum of Paleontology (prefix UCMP) at Berkeley USA. These casts are currently stored in the Queensland Museum and the School of Biological, Earth, and Environmental Sciences at the University of New South Wales (UNSW).

Several specimens examined in this study were previously listed as undescribed morphospecies by Cooke (1996). Specimens attributed to *Ganawamaya* sp. 4 by Cooke (1996) include: QM F20365, right dentary with i1, p3, m1–m4. Specimens for *Nambaroo* sp. 2 include: QM F20563, right dentary with m1; QM F57790, right dentary with i1, p3, m1–m4. Specimens attributed to *Nambaroo* sp. 4 include: QM F19899, right dentary with i1, dp3, unerupted p3, m1, m3. Specimens attributed to *Nambaroo* sp. 5 include: QM F13099, right dentary with i1, p3, m1–m4; QM F20036, left dentary with m1–m3; QM F24185, left maxilla with P3, M1; QM F24186, left dentary with p3, m1; QM F57788, left m4; QM F58648, left maxilla with P3, M1–M4; QM F57791, left maxilla with P3, M1–M2. Specimens attributed to *Nambaroo* sp. 6 include: QM F19639, right dentary with p3, m1; QM F19661, right dentary with m1–m2; QM F20292, right dentary with m1–m2; QM F24222, left dentary with m1–m3; QM F57789, right dentary with i1, m1–m3. Specimens attributed to *Nambaroo* sp. 8 include: QM F19878, left dentary with dp3, unerupted p3, m1.

Maximum tooth length and width of the third premolar were measured for each specimen using digital callipers. In addition, maximum tooth length, anterior and posterior widths were measured for all molars. Length measurements were taken at the base of the crown while widths were measured across the base of the anterior and posterior lophs. All dental measurements are presented in Tables 1–7.

Metric Analysis

Metric analyses were conducted using PAST Version 3.01 (Hammer et al., 2001). In order to determine whether the amount of variation within each species is consistent with that expected for a mixed sex mammalian population, coefficients of variation (CVs) were calculated for dental measurements from the revised *Ganawamaya* species (see Systematic Palaeontology). Expected ranges of variation for dental measurements within macropodiforms are from Travouillon et al. (2014) in which ranges of CVs for the extant macropodids *Thylogale stigmatica* (3.54–12.5) and *T. thetis* (4.98–11.16) were calculated. Bivariate plots (length vs. anterior, or posterior, width of all molars and length vs. width of the third premolar) were made. For each molar, either the anterior or posterior width was used for bivariate plots depending on which measurement best distinguished between species. We also conducted Kruskal-Wallis and Mann-Whitney U tests for each dental measurement to determine whether dental measurements differ for each species. *Ganawamaya couperi* comb. nov. could not be included in statistical analysis for the lower fourth molar or upper third and fourth molars as only one specimen for each of these molars was available. A Principal Component Analysis (PCA) using log transformed dental measurements for all molars and premolars was conducted for both upper and lower tooth rows.

Phylogenetic Analysis

A phylogenetic analysis was conducted using a combination of the taxon-character matrices by Kear and Pledge (2007) and Prideaux and Warburton (2010), as integrated in Butler et al. (2016). Characters for *Ganawamaya* were then rescored with specimens classified as outlined in our study (i.e., four species; *Ganawamaya acris*, *Gan. aediculis*, *Gan. gillespieae* comb. nov., and *Gan. couperi* comb. nov.). The total matrix consists of 120 characters (Appendix 1). An additional character (120), not included in previous matrices, was included in the matrix to account for the presence or absence of the interparietal bone. Parsimony analysis was completed using PAUP 4.0b10 (Swofford, 2002). The analysis used a two-stage heuristic search in which the initial search involved 1,000 replicates, saving 10 trees per replicate, followed by a second search within the saved trees. Bootstrap values were then calculated using 1000 replicates. Decay indices were calculated using TreeRot v3.

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA, Linnaeus, 1758
Infraclass MARSUPIALIA Illiger, 1811

Order DIPROTODONTIA Owen, 1866
Suborder MACROPODIFORMES Kirsch, Lapointe and Springer, 1997
Family BALBARIDAE Flannery, Archer and Plane, 1982 sensu Cooke and Kear, 1999
Genus GANAWAMAYA Cooke, 1992

Type Species. *Ganawamaya acris* Cooke, 1992, by original description.

Emended Generic Diagnosis. Species of *Ganawamaya* differ from all other balbarids in having the following unique combination of features: a poorly developed hypocingulid; a lack of a neometaconule and postlink; a short buccally flexed p3 with five cuspids along the occlusal margin; pronounced lingual cingulum on P3; a well-developed posterobuccal transcrista on P3; a rectilinear P3; a poorly developed preprotocrista; a postprotocrista that extends into the interloph valley; a pronounced nuchal crest; and well-developed postorbital processes.

Remarks. While species of *Ganawamaya* and *Balbaroo* all have a pronounced nuchal crest, it is less developed in *Ganawamaya*. However, it is better developed than in several macropodiform groups (e.g., macropodines). Species of *Ganawamaya* also have a more gracile cranium and smaller molars than those of *Balbaroo*. Species of *Ganawamaya* differ from species of *Nambaroo* in having a rectilinear p3 as opposed to a more plagiaulacoid form, a less developed preprotocrista, and a postprotocrista on the M1 that extends into the interloph valley and in lacking a neometaconule and postlink. Herein 'plagiaulacoid' is used in this study to refer to a shorter tooth with a recurved crown and many cuspids and transcristae, while 'rectilinear' refers to a tooth with a straight crown and less cuspids and transcristae than premolars with a plagiaulacoid form. For example, the p3 of NMV P157559, referred to *N. tarrinyeri* by Flannery and Rich (1986), has a recurved crown with seven cuspids with associated transcristae anterior to the large posterior cuspid.

In this study, we also examined the holotype and sole specimen of *Galanarla tessellata,* QM F10644. The distinguishing features of *Gal. tessellata* proposed by Flannery et al. (1982) are shared with species of *Nambaroo* and *Ganawamaya*. Those include: lophodont molars, a convex ventral margin of the dentary, a small buccal opening for the masseteric canal, a p3 flexed buccally out of alignment with the molar row. The holotype of *Gal. tessellata* is a heavily damaged jaw with two very worn molars. It is closest to *Gan. aediculis* in size and morphology. However, because most diagnostic features distinguishing balbarids (those of p3 and m1) are not preserved, its relationship to other balbarid taxa cannot, at present, be determined. However, the type locality for *Gal. tessellata,* Riversleigh's D Site, is no longer accessible for fossil collection. Additionally, more informative specimens may in the future be recovered from other Depositional Phase 1 deposits such as Hiatus and White Hunter Sites (e.g., Arena et al., 2015). We suggest *Gal. tesselata* might be considered as a *nomen dubium* as the holotype specimen cannot be confidently ascribed to a single taxon.

Ganawamaya acris Cooke, 1992
Figures 1–2

v* 1992 *Ganawamaya ornata* Cooke, p. 202, figs. 1, 3.

Holotype. QM F16840, right dentary with i1, p3 and m1–m4 from RSO Site, Riversleigh WHA, northwestern Queensland, Australia (Cooke, 1992).

Referred Specimens. Boid Site: QM F24693, right dentary with p3, m1–m2, broken m3–m4. Camel Sputum Site: QM F58648, left maxilla with P3, M1–M4; QM F16841, right maxilla with P3, M1–M4; QM F19677, left maxilla with M2–M3; QM F19693, right maxilla with broken M1, M2–M4; QM F19862, left maxilla with P3, M1; QM F19901, right dentary with p3, m2–m4; QM F19969, right dentary with m3; QM F19970, left dentary with m2–m4; QM F19981, left maxilla with M2–M3; QM F20161, left maxilla with M1–M4; QM F20286, right maxilla with M3–M4; QM F20523, left maxilla with P3, M1–M4; QM F20617, left maxilla with P3, M1; QM F20618, left maxilla with M1–M4; QM F23476, right maxilla with P3, M1; QM F23485, right maxilla with M2–M3; QM F23485, right maxilla with M2–M3; QM F24189, right maxilla with broken M1, M2, broken M3. Creaser's Ramparts Site: QM F20365, right dentary with i1, p3, m1–m4; QM F30870, left dentary with i1, p2, dp3, m1; QM F23820, right maxilla with M2–M4; QM F30274, right maxilla with P3, M1–4. Gag Site: QM F58649, partial left dentary with m1–m2. Inabeyance Site: QM F58650, right p3; QM F24514, left dentary with i1, p3, broken m1–m2, m3–m4. Judith's Horizontalis Site: QM F58651, left maxilla with P3, M1–M4. Neville's Garden Site: QM F13090, right maxilla with M2–M4; QM F19879, right dentary with m1–m4; QM F19880, left dentary with m3, m4 in crypt; QM F24186, left dentary with p3, m1; QM F24222, left dentary with m1–m3. Price is Right Site: QM F58652, left dentary with i1, p3, m1–m2, m4; QM F58653, left dentary with p3, m1–m4; QM F58654, right dentary with p3, m1–m3; QM F58655, left p3

TABLE 1. Measurements (mm; rounded to one decimal place) of the lower dentition of the type and referred material of *Ganawamaya acris*. L = tooth length, AW= anterior width, PW = posterior width, p = lower premolar, m = lower molar.

Specimen	Locality	p3L	p3W	m1L	m1A W	m1P W	m2L	m2A W	m2P W	m3L	m3A W	m3P W	m4L	m4A W	m4P W
QMF24693	Boid Site	6.0	3.6	6.2	3.7	4.4	7.0	4.6	5.0						
QMF19901	Camel Sputum Site	6.8	4.1				6.3	4.4	4.7	7.0	4.8	4.9	6.8	4.9	4.5
QMF19969	Camel Sputum Site									7.1	4.6	4.6			
QMF19970	Camel Sputum Site						6.6	4.3	4.5	6.8	4.8	4.8	7.1	4.7	4.4
QMF20365	Creaser's Ramparts	6.2	4.4	5.8	3.5	4.2	6.4	4.0	4.7	6.7	4.8	4.5	7.2	4.5	4.1
QMF30870	Creaser's Ramparts			5.0	3.1	3.8									
QMF58649	Gag Site			6.1	3.9	4.0	6.0	4.2	4.2						
QMF24514	Inabeyance Site	6.7	3.7	6.5						6.8	4.6	4.6	6.8	4.5	4.3
QMF58658	Inabeyance Site	7.2	3.9												
QMF19879	Neville's Garden Site			6.6	3.6	4.2	6.7	4.4	4.4	6.8	4.7	4.7	7.5	4.8	4.4
QMF19880	Neville's Garden Site									7.9	5.1	5.2			
QMF24186	Neville's Garden Site	7.0	4.3	7.0	4.0	4.7									
QMF24222	Neville's Garden Site			6.6	3.7	4.4	7.1	4.5	4.9	7.5	5.0	4.9			
QMF58652	Price is Right Site	6.7	4.0	5.9	3.6	4.4	6.0	4.4	4.6				6.7	4.6	4.0
QMF58653	Price is Right Site	5.8	3.5	5.8	3.4	3.9	6.1	4.4	4.5	6.7	4.7	4.5	7.2	4.5	4.2
QMF58654	Price Is Right Site	7.3	4.1	5.7	3.6	4.3	6.0	4.4	4.8	6.9	4.7	4.9			
QMF58655	Price is Right Site	5.7	2.9												
QMF16840	RSO Site	6.7	3.9	5.9	3.4	4.1	6.3	4.0	4.3	6.6	4.6	4.6	6.8	4.7	4.4
QMF20033	RSO Site	6.6								7.4	5.3	5.1			
QMF19625	Upper Site						7.0	4.2	4.4						
QMF19639	Upper Site			6.5	2.9	4.1									
QMF19661	Upper Site			6.2	3.3	4.1	6.0	4.2	4.4						
QMF19665	Upper Site									6.9	4.5	4.8	6.9	4.7	
QMF19944	Upper Site			6.2	3.8	4.5	7.1	4.6	4.8	7.3	5.0	5.0			
QMF20192	Upper Site						7.2	4.7	4.9	7.4	5.1	5.1			
QMF20292	Upper Site			6.6	3.4	4.1									
QMF16839	Wayne's Wok Site	6.7	3.9	6.5	3.8	4.4	6.3	4.2	4.8	6.8	4.7	5.0			
QMF16842	Wayne's Wok Site	6.1	3.4												
QMF19596	Wayne's Wok Site	6.1													
QMF19846	Wayne's Wok Site												7.7	4.9	4.6
QMF19899	Wayne's Wok Site	6.6		5.7	3.5	4.3				7.1	4.7	4.9			
QMF20563	Wayne's Wok Site			6.1	3.4	4.0									
QMF57788	Wayne's Wok Site												7.3	4.6	4.3
QMF57789	Wayne's Wok Site			6.5	3.6	4.3	6.8	4.3	4.7	7.1	4.9	4.8			
QMF57790	Wayne's Wok Site	6.4	3.6	6.1	3.3	4.1	6.5	4.3	4.8	7.3	4.8	4.8	7.3	5.0	4.6
QMF58657	Wayne's Wok Site	6.0	3.5												
QMF58659	Wayne's Wok Site	6.2								6.8	4.8	4.6			
UCMP88204	Kutjamarpu Local Fauna, South Australia	7.0	4.1	6.9	3.8	4.7	7.6	5.1	5.2	7.8	5.4	5.2			

TABLE 2. Measurements (mm; rounded to one decimal place) of the upper dentition of the type and referred material of *Ganawamaya acris*. L = tooth length, AW= anterior width, PW = posterior width, P = upper premolar, M = upper molar.

Specimen	Locality	P3L	P3W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW	M4L	M4AW	M4PW
QMF16841	Camel Sputum Site	6.8	4.3	6.0	5.4	4.9	6.6	6.1	5.2	7.5	6.0	5.2	6.2	5.6	4.2
QMF19677	Camel Sputum Site						6.7	7.0	5.7	7.4	6.5	5.5			
QMF19693	Camel Sputum Site						6.0	5.7	5.2	5.7	5.6	4.6	5.9	5.2	3.7
QMF19862	Camel Sputum Site	6.7	4.9	6.7	5.4	4.8									
QMF19981	Camel Sputum Site						6.9	6.1	5.2	7.4	6.2	5.3			
QMF20161	Camel Sputum Site			6.3	5.7	5.2	6.6	6.0	4.9	6.7	5.6	4.9	7.2	5.7	4.4
QMF20286	Camel Sputum Site									8.1	6.7	5.7	7.1	5.8	4.6
QMF20523	Camel Sputum Site	7.4	5.0	6.8	6.0	5.4	7.3	6.4	5.7	7.9	6.1	5.5	7.3	5.4	4.5
QMF20617	Camel Sputum Site	6.9	4.1	6.7	5.7	5.3									
QMF20618	Camel Sputum Site			6.8	5.7	5.2	6.9	6.2	5.3	7.4	6.0	5.2	7.2	5.4	4.4
QMF23476	Camel Sputum Site	8.0	5.6	7.4	6.1	5.6									
QMF23485	Camel Sputum Site						6.9	6.5	5.3	8.1	6.1	5.1			
QMF24189	Camel Sputum Site					5.6	6.7	6.4	5.3	6.6					
QMF58648	Camel Sputum Site	6.7	4.2	5.9	5.3	4.8	6.4	5.5	4.8	6.7	5.5	4.6	7.3	5.5	3.7
QMF23820	Creaser's Ramparts Site						6.8	5.9	5.3	7.1	6.1	5.4	7.4	5.7	
QMF30274	Creaser's Ramparts Site	7.4	4.8	6.8	5.6	5.4	6.5	6.2	5.4	7.3	6.4	5.2	7.2	5.6	4.3
QMF58651	Judith's Horizontalis Site	7.5	4.5	6.8	5.8	5.2	6.6	6.0	5.3	7.3	6.1	4.9	7.2	5.3	4.5
QMF13090	Neville's Garden Site						7.3	6.6	5.4	7.2	6.3	4.9	7.9	5.7	4.5

cap. RSO: QM F20033, left dentary with dp3, unerupted p3, m3. Upper Site: QM F58656, left maxilla with P3, M1–M4; QM F19618, left maxilla with M2; QM F19625, right m2; QM F19639, right dentary with m1 and unerupted p3 ; QM F19661, right m1 and m2; QM F19665, right dentary with m3–m4; QM F19684, right maxilla with P3, M1; QM F19686, right maxilla with dP3, unerupted P3, M1–M2; QM F19840, palate with left M1–M4 and right M2–M4; QM F19884, right maxilla with M1, QM F19927, left maxilla with M3; QM F19944, right dentary with m1–m3; QM F19946, right M2,;QM F20192, right dentary with m2–m3; QM F20280, right maxilla with M1; QM F20292, right dentary with m1; QM F20296, right maxilla with M2–M4. Wayne's Wok Site: QM F58657, right dentary with p3; QM F57789, right dentary with m1–m3; QM F58659, right dentary with p2, dp3, unerupted p3, m3; QM F16839, right dentary with p3, m1–m3; QM F16842, left dentary with i1, p3; QM F19577, cranium with left P3, M1–M3; QM F19596; right dentary with p2, dp3, unerupted p3; QM F19821, right maxilla with M1–M4; QM F19846, left dentary with m4; QM F19899, right dentary with i1, dp3, unerupted p3, m1, m3; QM F19920, right maxilla with partial M1–M4; QM F19935, right maxilla with M1–M2; QM F20563, right dentary with m1; QM F24192, right maxilla with M2–M4; QM F31461, cranium with left P3, M1–M4 and right M1–M4; QM F36412, right maxilla with P3, M1–M3; QM F57788, left m4; QM F57790, right dentary with i1, p3, m1–m4.

TABLE 2 (continued).

Specimen	Locality	P3L	P3W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW	M4L	M4AW	M4PW
QMF19618	Upper Site						7.4	5.7	5.0						
QMF19684	Upper Site	7.6	4.8	7.0	5.7	5.4									
QMF19686	Upper Site	7.1	4.2	6.8	5.6	5.4	7.4	6.0	5.5						
QMF19840	Upper Site			6.0	5.4	5.2	6.8	5.9	5.1	6.9	5.6	5.1	6.5	5.2	3.9
QMF19840	Upper Site						6.4		5.3	7.0	5.8	4.8	6.4	5.3	4.1
QMF19884	Upper Site			7.0	5.8	5.0									
QMF19927	Upper Site									7.1	5.5	4.9			
QMF19946	Upper Site						7.3	6.4	5.5						
QMF20280	Upper Site			6.6	5.6	5.4									
QMF20296	Upper Site						7.4	6.4	5.7	7.8	6.4	5.4	6.5	5.4	4.1
QMF58656	Upper Site	7.2	4.9	6.6	5.8	5.2	7.0	6.3	5.5	7.1	6.2	5.5	7.3	5.7	4.6
QMF19577	Wayne's Wok Site	7.5	4.5	6.8	5.7	5.5	7.4	6.3	5.6	7.9	6.1	5.6			
QMF19821	Wayne's Wok Site			6.4	5.8	5.3	6.6	6.2	5.6	7.2	6.3	5.6	7.3	6.0	4.8
QMF19920	Wayne's Wok Site			6.3			6.6		5.2						
QMF19935	Wayne's Wok Site			6.3	5.2	4.9	6.8	5.8	4.9						
QMF24192	Wayne's Wok Site						7.0	6.2	5.4	7.2	6.1	5.3	7.3	5.3	
QMF31461	Wayne's Wok Site	7.5	5.1	6.4	5.6	5.3	6.4	6.2	5.4	7.6	6.5	5.6	7.7	6.1	4.7
QMF31461	Wayne's Wok Site			6.3	5.8	5.6	7.0	6.4	5.5	7.7	6.6	5.7	7.8	6.1	4.5
QMF36412	Wayne's Wok Site	7.4	4.6	6.3	5.5	5.4	6.9	6.3	5.3	7.1					
UCMP88212	Kutjamarpu Local Fauna, South Australia						7.5	6.1	5.7	7.5	6.2	5.9	8.6	5.9	4.7

The following specimens are referred based on casts of the original specimen: Basal Conglomerate, Leaf Locality, Wipajiri Formation, Tirari Desert, Lake Eyre Basin, South Australia: UCMP 88204, right dentary with p3, m1–m4; UCMP 88212, left maxilla with M2–M3.

Emended species diagnosis. *Ganawamaya acris* differs from all other species of *Ganawamaya* in having the following unique combination of features: masseteric process of the maxilla with small rounded eminence; well-developed sulcus on the anterior extremity of the zygomatic arch; distinct process on the ectotympanic; large zygomatic epitympanic sinus with thin medial wall; large mastoid foramen on mastoid/squamosal suture; well-developed anterior cingulum on M1; less well-defined posthypocristid on m1 and m2 and no posthypocristid on m4; more prominent paraconid on m1; large and sinuous i1 with dorsal and ventral enamel flanges; no marked convexities on the lateral margins of the interloph valley of lower molars; no hypoconulid on lower molars; poorly developed anterior cingulum on M1; stylar cusp C less prominent and connected to postparacrista on M1; and larger molar size; no additional cuspid on the posterior end of the p3 below the occlusal margin.

Description

Cranial morphology described here is based on QM F31461 (Figures 1, 2). This cranium has been transected through the splanchnocranium suggesting that either the anterior portion was

TABLE 3. Measurements (mm; rounded to one decimal place) of the lower dentition of the type and referred material of *Ganawamaya aediculis*. Abbreviations are the same as Table 1.

Specimen	Locality	p3L	p3W	m1L	m1AW	m1PW	m2L	m2AW	m2PW	m3L	m3AW	m3PW	m4L	m4AW	m4PW
QMF30076	Gillespie's Gully Site	5.9	3.4	6.3	3.6	4.1	6.7	4.4	4.8	6.9	4.8	4.8	7.3	4.8	3.8
QMF30298	LSO Site	5.9	3.7	5.8	3.4	3.9				6.5	4.2	4.0	7.0	4.1	3.9
QMF31463	LSO Site	6.2	3.6												
QMF16843	White Hunter Site	6.4	3.9	5.4	3.8	4.2	5.9	4.2	4.3	6.0	4.4	4.5	6.7	4.2	3.9
QMF19584	White Hunter Site	6.1	2.6	6.0	3.3	3.8									
QMF19605	White Hunter Site												6.4	4.1	4.0
QMF19876	White Hunter Site						6.7	4.4	4.6	6.4	4.5	4.8	7.2	4.6	4.4
QMF19878	White Hunter Site	6.0	3.4	5.7	3.4	3.9									
QMF19993	White Hunter Site									5.8	4.2	4.2	-	3.8	
QMF19994	White Hunter Site														
QMF20146	White Hunter Site									6.6	4.3	4.3			
QMF31182	White Hunter Site	5.9	3.7	5.3	3.1	3.7	5.6	3.8	3.9	5.8	4.0	4.0	-	3.8	-
QMF58660	White Hunter Site	6.6	3.6	5.9	3.3	3.8	6.3	4.2	4.3	6.6	4.5	4.3	7.0	4.4	4.2

TABLE 4. Measurements (mm; rounded to one decimal place) of the upper dentition of the type and referred material of *Ganawamaya aediculis*. Abbreviations are the same as Table 2.

Specimen	Locality	P3L	P3W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW	M4L	M4AW	M4PW
QMF58658	LSO Site	6.9	4.3	5.6	5.3	4.5									
QMF58658	LSO Site	6.8	4.0	5.5	5.5	4.6	6.3	5.6	4.6	6.7	5.9	4.6	6.6	4.9	4.0
QMF20633	White Hunter Site						5.9	4.9	4.3	6.1	4.8	4.3	6.4	4.7	3.4
QMF23354	White Hunter Site			5.5	5.0	4.5	6.1	5.3	4.6						
QMF57791	White Hunter Site	6.8	4.6	6.7	5.6	4.8	6.9	5.8	4.9						

TABLE 5. Measurements (mm; rounded to one decimal place) of the lower dentition of the type and referred material of *Ganawamaya gillespieae* comb. nov. Abbreviations are the same as Table 1.

Specimen	Locality	p3L	p3W	m1L	m1AW	m1PW	m2L	m2AW	m2PW	m3L	m3AW	m3PW	m4L	m4AW	m4PW
QMF13099	Dirk's Towers Site	6.6	3.6	6.1	3.1	4.3	6.3	4.2	4.5	6.2	4.7	4.4	6.5	4.6	4.0
QMF20036	Dirk's Towers Site			5.5	3.5	4.3	6.4	4.3	4.5	6.5	4.7	4.5			
QMF29661	Dirk's Towers Site								4.5	6.5	4.7	4.7	6.4	4.4	3.9
QMF30289	Dirk's Towers Site	6.8	4.1	6.3	3.9	4.3	6.6	4.6	4.4	7.4	5.1	4.7	7.4	4.8	4.4
QMF36233	Dirk's Towers Site	6.8	4.0												
QMF36339	Dirk's Towers Site			6.2	3.3	4.0	6.3	4.1	4.5	6.9	4.7	4.7			
QMF35432	Quantum Leap Site	6.2	3.2	5.9	3.4	3.7	6.2	4.3	4.2	6.4	4.6	4.2	6.6	4.7	4.0

TABLE 6. Measurements (mm; rounded to one decimal place) of the upper dentition of the type and referred material of *Ganawamaya gillespieae* comb. nov. Abbreviations are the same as Table 2.

Specimen	Locality	P3L	P3W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW	M4L	M4AW	M4PW
QMF13100	Dirk's Towers Site						6.7	5.8	4.7	6.9	5.8	4.8	6.5	5.6	4.3
QMF16912	Dirk's Towers Site			6.4	5.3	5.1	7.0	5.7	5.1						
QMF24178	Dirk's Towers Site			6.1	6.1	5.2	6.6	5.7	5.0				6.9	5.7	4.3
QMF24180	Dirk's Towers Site						7.0	5.8	4.9	7.0	6.0	4.7			
QMF24185	Dirk's Towers Site	6.9	4.3	6.4	5.5	4.9									
QMF24479	Dirk's Towers Site									7.6	6.2	5.1			
QMF35432	Quantum Leap Site	6.9	4.2	5.9	5.2	4.5	6.9	5.8	4.8	6.9	5.6	4.6	7.0	5.1	4.1
QMF35432	Quantum Leap Site	6.7	4.3	6.0	5.5	4.6	6.2	5.7	4.7	6.8	5.6	4.8	6.7	5.3	4.1

TABLE 7. Measurements (mm; rounded to one decimal place) of the upper and lower dentition of the type and referred material of *Ganawamaya couperi* comb. nov. Abbreviations are the same as Tables 1 and 2.

Specimen	Locality	p3L	p3W	m1L	m1AW	m1PW	m2L	m2AW	m2PW	m3L	m3AW	m3PW	m4L	m4AW	m4PW
QMF30401	White Hunter Site	4.9	3.1	5.1	3.0	3.4	5.1	3.5	3.9	5.4	3.9	4.1	5.6	3.7	3.6
UCMP57334	Ngapakaldi Local Fauna	5.4	3.2	4.6	2.9	3.3	4.7	3.1	3.3	4.6	3.1	3.2			
UCMP10600	Ngapakaldi Local Fauna	4.9	3.2	4.7	3.2	3.2				4.8	3.6	3.4			
Specimen	**Locality**	**P3L**	**P3W**	**M1L**	**M1AW**	**M1PW**	**M2L**	**M2AW**	**M2PW**	**M3L**	**M3AW**	**M3PW**	**M4L**	**M4AW**	**M4PW**
UCMP57340	Ngapakaldi Local Fauna	5.3	3.3	5.2	4.6	4.1	4.7	3.4	4.1	5.0	4.4	3.9	5.1	4.0	3.0
UCMP57337	Ngapakaldi Local Fauna	4.5	3.0	4.0	2.8	2.8	4.4	3.1	3.0						

inadvertently separated in the field at the time of collection or was destroyed during the fossilization process. No specimens examined appear to represent the anterior portion of this cranium.

Maxilla and Palatine. No distinct masseteric process is evident. However, there is a small eminence in place of this process. The maxillopalatine fenestrae are not well preserved. However, the anterior margin is bordered by the maxilla from a point level with the anterior end of M2, and the posterior margin is bordered by the palatine from a point level with the anterior end of M3. The suborbital shelf of the maxilla is flat, narrow and anteriorly tapered. The infraorbital canal is situated in the anterior portion of the suborbital shelf. The infraorbital foramen, positioned dorsal to the anterior end of M1, is elliptical in shape. The sphenopalatine foramen is positioned posterior to the infraorbital canal on the anterior end of the palatine. Both the sphenopalatine foramina are oval in shape. A subrounded maxillary foramen is located posterior to the maxillojugal suture. The sphenorbital fissure is large (approximately 6 mm wide). The foramen rotundum is located posterolateral to the sphenorbital fissure from which it is separated by a thin wall.

Lacrimal. Only the most lateral potion of the lacrimal is preserved. Two small lacrimal foramina occur on the anterior margin of the orbit.

Frontal, parietal, and interparietal. The dorsal anterior portion of the frontal is not preserved. In dorsal view, however, part of a deep sulcus is evident along the posterior portion of the metopic suture. An ethmoidal foramen is positioned at the posteroventral corner of the frontal along the frontal-orbitosphenoid suture. A well-developed sagittal

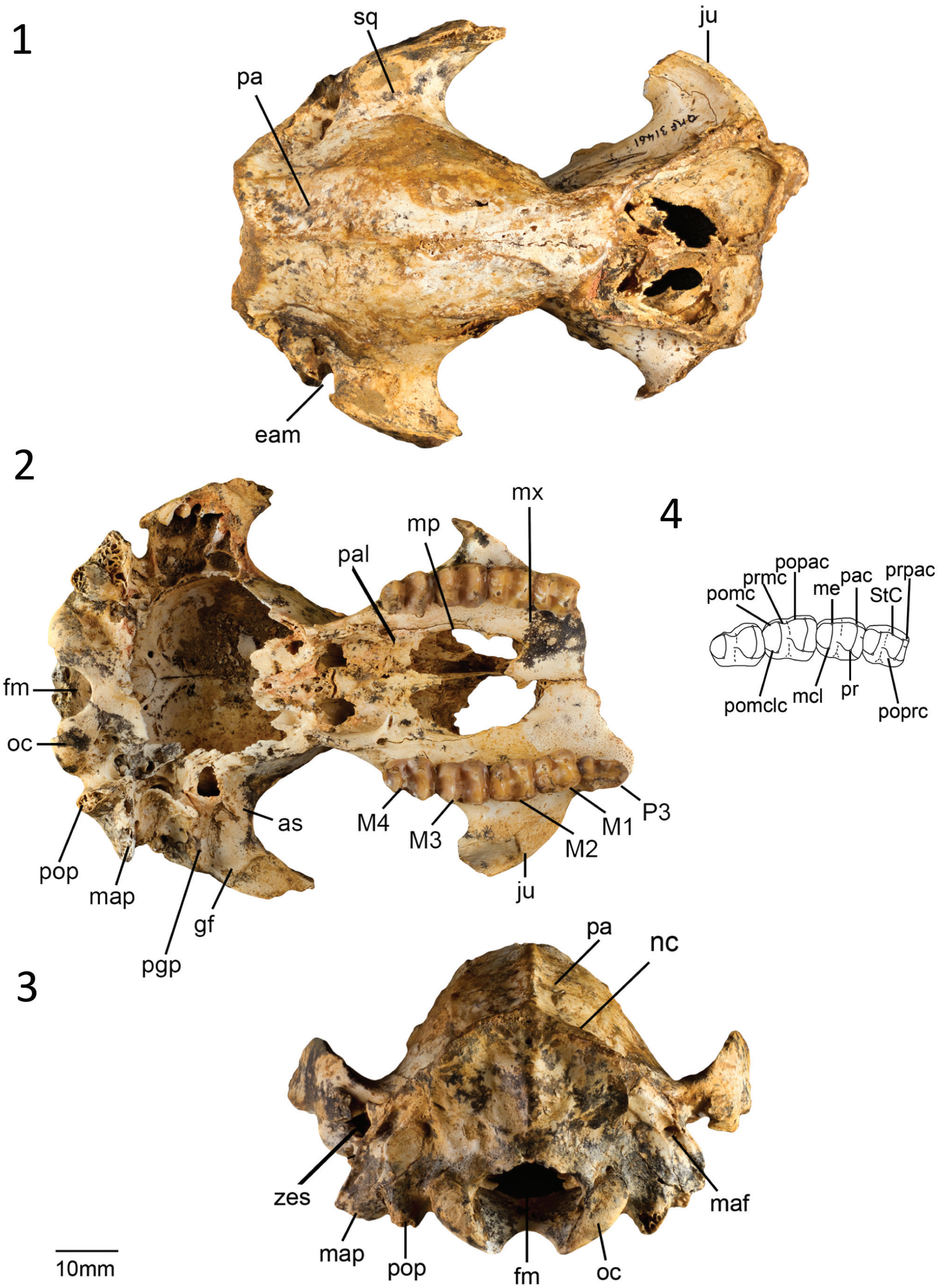

FIGURE 1. *Ganawamaya acris* partial cranium (QM F31461) in dorsal view (**1**); ventral view (**2**); posterior view (**3**); and line drawing of dentition in occlusal view (**4**). Abbreviations: as, alisphenoid; eam, exit of auditory meatus; fm, foramen magnum; gf, glenoid fossa; ju, jugal; M1–M4, upper first to fourth molar; maf, mastoid foramen on the mastoid-squamosal suture; map, mastoid process; mcl, metaconule; me, metacone; mp, maxillopalatine fenestra; mx, maxilla; nc, nuchal crest; oc, occipital; P3, upper third premolar; pa, parietal; pac, paracone; pal, palatine; pgp, postglenoid process; pop, paroccipital process; pomc, postmetacrista; pomclc, postmetaconule crista; popac, postparacrista; poprc, postprotocrista; pr, protocone; prpac, preparacrista; sq, squamosal; StC, stylar cusp C; zes, zygomatic epitympanic sinus.

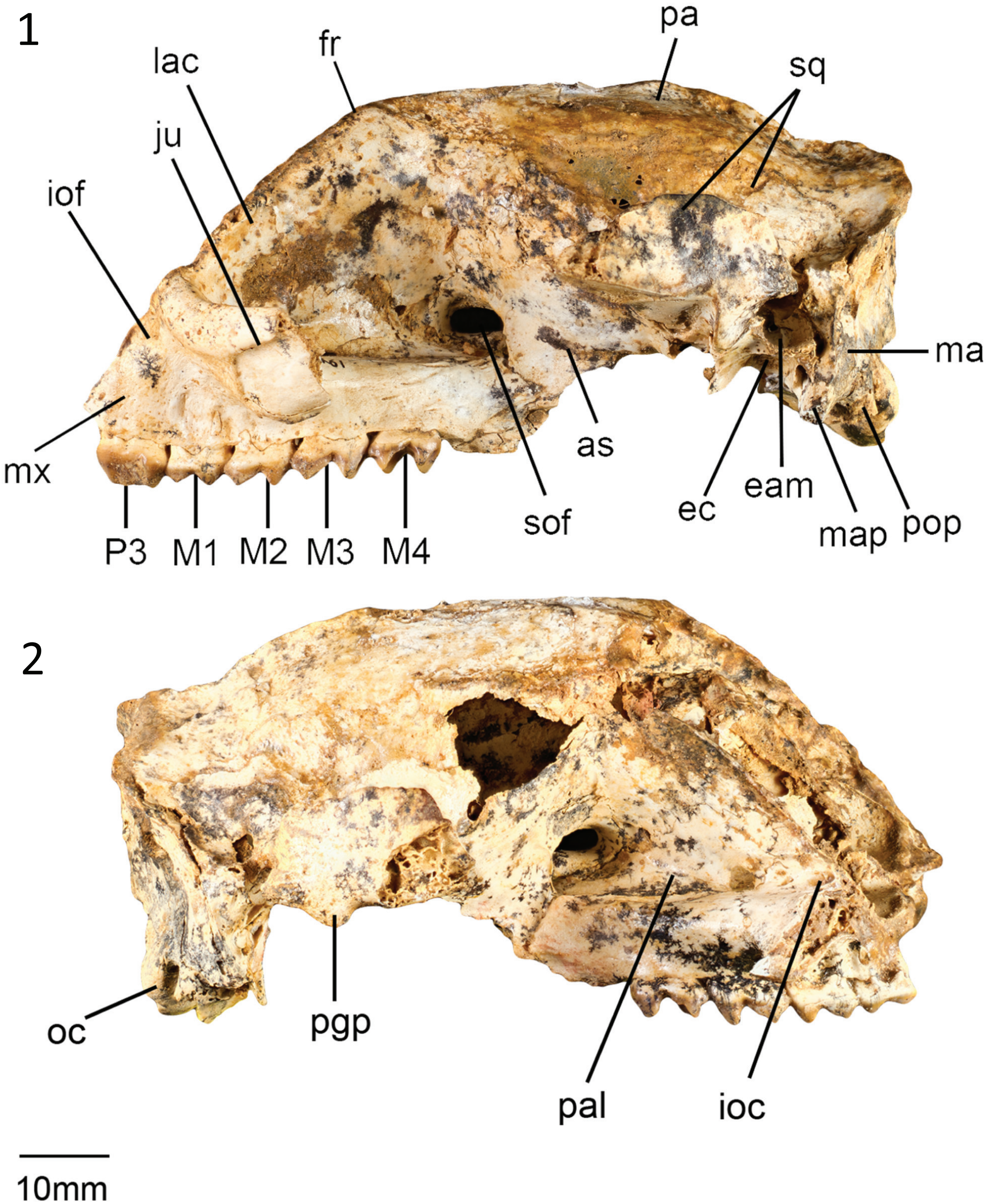

FIGURE 2. *Ganawamaya acris* partial cranium (QM F31461) in left lateral view (**1**) and right lateral view (**2**). Abbreviations: as, alisphenoid; eam, exit of auditory meatus; ec, ectotympanic; fr, frontal; ioc, infraorbital canal; iof, infraorbital foramen; ju, jugal; lac, lacrimal; M1–M4, upper first to fourth molar; ma, mastoid; map, mastoid process; mx, maxilla; oc, occipital; P3, upper third premolar; pa, parietal; pal, palatine; pgp, postglenoid process; pop, paroccipital process; sof, sphenorbital fissure; sq, squamosal.

crest is evident along the parietal-parietal suture. The parietals curve gently to form a well-developed nuchal crest. A wedge between the anterior wings of the parietals is formed by the frontals. The anterior wings of the parietals terminate dorsally where post-orbital constriction of the cranium occurs. A frontal-squamosal contact is evident posterior to postorbital constriction of the cranium. There is no contact between the alisphenoid and the parietals. No interparietal-parietal suture is present, suggesting that these bones have completely fused.

Zygomatic arch. The majority of the zygomatic arch is not preserved. The jugal extends anteriorly to the ventral portion of the lacrimal. There is a distinct, well-developed sulcus on the anterior extremity of the zygomatic arch. This sulcus appears to be related to the attachment of the superficial masseter muscle (Warburton, 2009). As in other balbarids, the zygomatic arch transitions smoothly into the facial region as opposed to being separated by a sulcus. The glenoid fossa is generally flat and merges smoothly into the ventral surface of the jugal. A prominent postglenoid process is present.

Neurocranium. The neurocranium is slightly domed. The frontal and parietals form most of the roof of the neurocranium. The ventral walls of the neurocranium are formed laterally by the dorsal wing of the squamosal. The ventral portion of the neurocranium is not preserved.

Basicranium. Small foramina are evident on the occipital condyle with short canals that open posteriorly into the foramen magnum. A hypoglossal foramen is situated medial to these foramina. The paroccipital and mastoid processes are partly broken. However, both appear to project below the level of the occipital condyle. The mastoid process appears more massive than the paroccipital process. A large mastoid foramen occurs on the mastoid-squamosal suture. The occipital condyles are small. The posterior lacerate foramen is only partially preserved but it appears to have been large.

The tympanic wing of the alisphenoid is flat. The external auditory meatus is bordered ventrally by the ectotympanic and dorsally by the squamosal. The ectotympanic has a straight posterior border, concave lateral border, and convex anterior and medial border. The ventral wall of the postglenoid process is contributed to by the ectotympanic. A distinct process is evident on the anteromedial-most corner of the ectotympanic. The zygomatic epitympanic sinus is large with a thin mesial wall. The basioccipital is not preserved.

Upper dentition. The upper dentition for *Ganawamaya acris* is described in Cooke (1992) except for the dP3, which is preserved in QM F19686. In occlusal view, the dP3 is trapezoidal in outline with a longer buccal margin compared to the lingual one. The paracone and metacone are subequal in height and taller than the protocone and metaconule. The protocone is large and taller than the metaconule. The paracone and protocone are not connected by a protoloph. A weak crest extends lingually from the paracone to meet the preparacrista. The postprotocrista extends posteriorly from the protocone to meet a short, very poorly developed premetaconule crista. A small stylar cusp C (StC) is present buccal to the paracone. A well-developed stylar cusp A (StA) is evident anterobuccal to the paracone. A poorly developed preparacrista extends from the paracone to the base of the StA. A well-defined postparacrista extends posteriorly into the interloph valley where it meets a poorly developed premetacrista. A postmetacrista extends posteriorly from the metacone but it is unclear where it terminates because part of the back of the tooth is obscured by a small piece of unprocessed limestone matrix.

Lower dentition. The lower dentition for *Ganawamaya acris* is described in Cooke (1992) except for p2 and dp3 which are preserved in QM F30870 and QM F19596.

The p2 is a short, tear-shaped tooth in occlusal view with steeply sloping buccal and lingual faces. Two prominent cuspids are evident on the tooth each with faint associated transcristids. The main crest departs in a posterior direction from the anteriormost cuspid posteriorly and terminates at the posterior end of the tooth. In buccal view the occlusal surface appears slightly convex.

The dp3 is triangular in occlusal outline and tapers anteriorly. Anteriorly, it abuts with the posterior end of p2. The protoconid is centrally positioned on the trigonid and is the tallest cusp on the tooth. A paracristid descends anteriorly from the protoconid to contact a well-developed paraconid. In QM F19596, a small cusp is present anterolingual to the protoconid and is connected to the paracristid by a short crest. A distinct protostylid is present buccal to the protoconid. The metaconid is well developed. The protoconid, paraconid, and metaconid are laterally compressed. A postmetacristid descends posteriorly into the interlophid valley where it meets a preentocristid. The cristid obliqua extends anterolingually from the hypoconid to the interlophid valley. The hypolophid is formed buccally by the posthypocristid and lingually by a buccal crest from the entoconid. The posthypocristid continues along the posterior flank of the hypolophid and meets the postentocristid at the posterolingual end of the tooth, encircling a small hypocingulid (a cingulid around the posterior base of the hypolophid). The postentocristid is well developed and continues vertically down the entoconid.

Additional morphological variation observed compared to the description by Cooke (1992) in the lower dentition includes the following: a protostylid is present on m1 in all juvenile specimens that have unworn molars (e.g., QM F19899, 57790, 57789); complex enamel ridges on the i1 of some juvenile specimens such as QM F19899 and QM F16842 (the holotype of *Gan. ornata*); the paracristid is straight in worn specimens (e.g., holotype of *Gan. acris* QM F16840 and 57790) but sinuous in juvenile and unworn specimens (e.g., QM F19899 and 57789); five cuspids are present on the occlusal surface of p3 on specimens such as QM F16842, 19899 and 57790, but in the holotype, QM F16840, the fifth cuspid appears to be obscured by wear. A malformation of the bone is evident on the anterior ventral border of the dentary of QM F57789, and was previously noted in an unpublished thesis by Cooke (1996).

Remarks. A remnant protostylid is evident in unworn juvenile specimens of *Balbaroo* (e.g., *B. fangaroo* and *B. nalima*) but is absent in worn adult specimens (Black et al., 2014). In the description of *Gan. acris* by Cooke (1992), *Ganawamaya* is distinguished from species of *Nambaroo* by the lack of a protostylid on m1. The holotype of *Gan. acris* is however significantly worn and has a distinct wear facet where the protostylid was most likely present. Juvenile specimens, such as those attributed to '*Nambaroo* sp. 4' by Cooke (1997a) and the holotype of *Gan. ornata* Cooke, 1992, and some unworn adult specimens (Figure 3), retain features such as complex enamel ridges on molars, a sinuous paracristid, and a protostylid on the m1. The holotype of *Gan. ornata* is missing m1, and therefore lacks sufficient diagnostic morphological features to separate it from *Gan. acris*. Other previously unpublished *Ganawamaya* specimens identified from Wayne's Wok, the type locality for *Gan. ornata*, are also consistent with *Gan. acris*. The dp3 and p3 of QM F2003 from the type locality of *Gan. acris* (RSO Site) is also identical to the holotype of *Gan. ornata* and specimens of *Gan. acris.* We therefore propose that specimens attributed to undescribed *Ganawamaya* and *Nambaroo* species (*Ganawamaya* sp. 4, *Nambaroo* sp. 2, *Nambaroo* sp. 4, *Nambaroo* sp. 5 and *Nambaroo* sp. 6) from Faunal Zone B by Cooke (1997a), in addition to the holotype of *Gan. ornata* (QM F16842), be referred to *Gan. acris*. One specimen, QM F58649, is from Faunal Zone C, unlike the majority of *Gan. acris* specimens, which suggests that the species spanned the early to middle Miocene.

Age and distribution. The holotype of *Gan. acris,* QM F16840, is from RSO Site, Riversleigh WHA, northwestern Queensland. The RSO Site is interpreted as to be part of Riversleigh's Faunal Zone B (Archer et al., 1989, 1997; Travouillon et al., 2006, 2011; Arena et al., 2015) with radiometric dates by Woodhead et al. (2016) supporting an early Miocene age for RSO Site (16.55 ± 0.29 Ma). The RSO Site is interpreted by Arena et al. (2015) to belong to interval B3 within Faunal Zone B. Other referred specimens are from sites also considered to be part of interval B3 of Faunal Zone B: Camel Sputum Site, Inabeyance Site, Judith's Horizontalis Site, Neville's Garden Site, Upper Site and Wayne's Wok Site (Arena et al., 2015). Several referred specimens from Boid Site and Creaser's Ramparts Site, are interpreted as Faunal Zone B, intervals B2 or B3 (Arena et al., 2015). Radiometric dates reported by Woodhead et al. (2016) for Camel Sputum Site (17.75 ± 0.78 Ma) and Neville's Garden Site (17.85 ± 0.13 Ma) support the interpretation that these are early Miocene in age. The Price Is Right Site has been interpreted to represent Faunal Zone B (Travouillon et al., 2006, 2011). Arena et al. (2015) found that its biostratigraphy was inconclusive, and it was as likely to be in either interval B2, B3, or C1. One specimen, QM F58649, is from Gag Site, which is interpreted to represent intervals C1 or C2 of Faunal Zone C, and thus middle Miocene in age (Archer et al., 1989, 1997; Travouillon et al., 2006, 2011; Arena et al., 2015). One specimen from the Wipajiri Formation, South Australia, is attributed to *Gan. acris* in our study. The Wipajiri Formation appears to be early or middle Miocene in age based on biocorrelation with Riversleigh deposits (Archer et al., 1997; Travouillon et al., 2006; Black et al., 2012).

Ganawamaya aediculis Cooke, 1992
Figure 4

Holotype. QM F16843, right dentary with p3, m1–m4 from White Hunter Site, Riversleigh WHA, northwestern Queensland, Australia (Cooke, 1992).

Referred specimens. Gillespie's Gully Site: QM F30076, right dentary with i1, p3, m1–m4. LSO Site: QM F58658, right maxilla with P3, M1–M4; QM F30298, right dentary with p3, m1–m4; QM F31463, left dentary with p3. White Hunter Site:

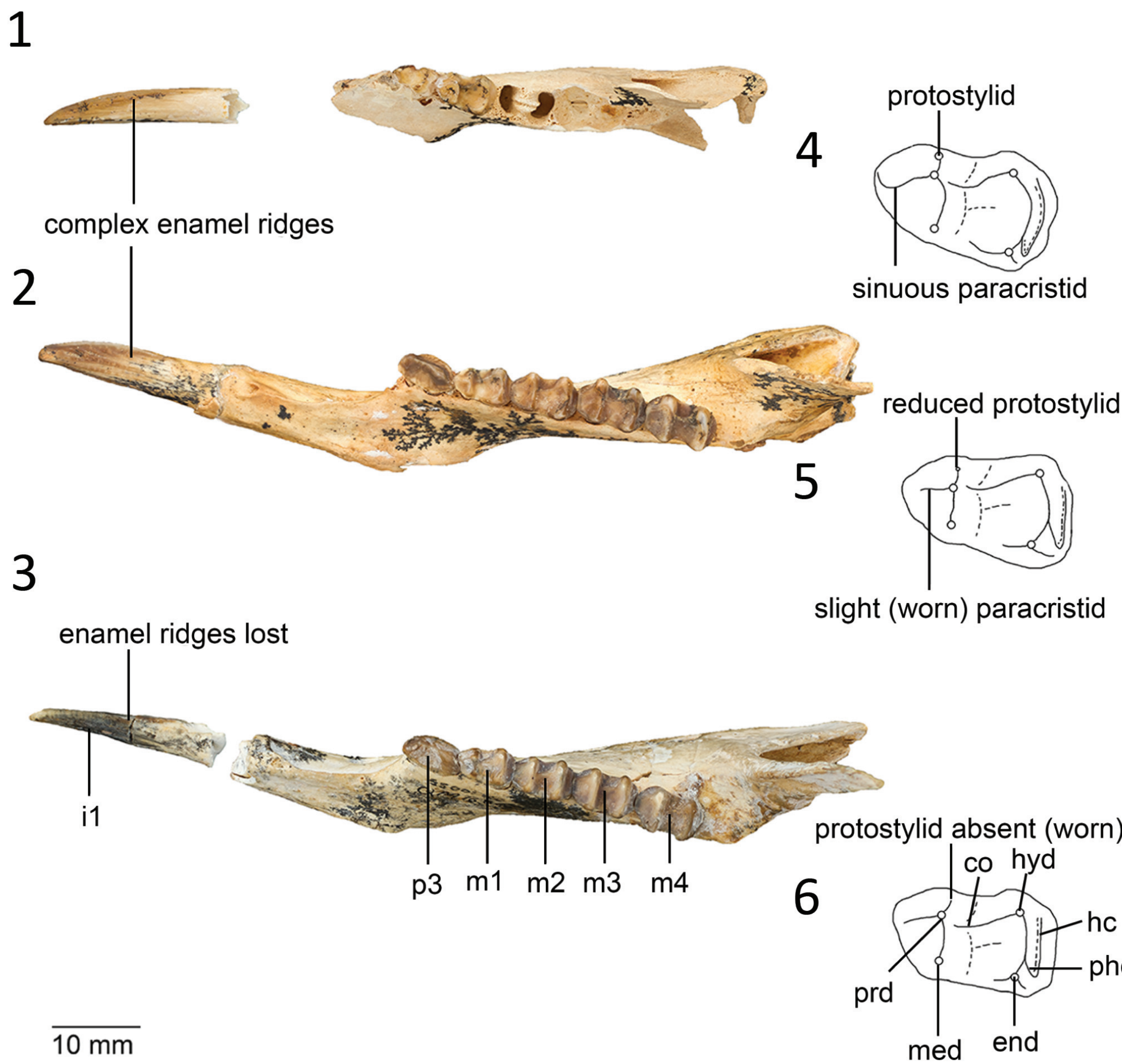

FIGURE 3. Occlusal view of lower dentary and line drawing of first molar for juvenile (**1**), adult (**2**), worn adult (**3**) specimens of a single species from Faunal Zone B; and line drawings for juvenile m1 (**4**), adult m1 (**5**), and worn adult m1 (**6**). The specimens were previously attributed to **1**, *Nambaroo* sp. 4; **2**, *Nambaroo* sp. 2 by Cooke (1997c) and **3**, *Ganawamaya acris* Cooke (1992). Abbreviations: co, cristid obliqua; end, entoconid; hc, hypocingulid; hyd, hypoconid; i1, lower incisor; p3, third premolar; m1–m4, lower molars one to four; med, metaconid; phc, posthypocristid, prd, protoconid.

QM F58660, left dentary with p3, m1–m4; QM F58661, isolated m2–m3; QM F58662, isolated p3; QM F19584, left dentary with p3, m1, m3 in crypt; QM F19605, right dentary with m4; QM F19876, left dentary with m2–m4; QM F19878, left dentary with dp3, unerupted p3, m1; QM F19993, right dentary with m3, broken m4; QM F19994, left dentary with m3 in crypt; QM F20146, right isolated broken m2, m3; QM F20633, Left maxilla with m2–m4; QM F23354, left maxilla with M1–M2, broken M3; QM F31182, left dentary with p3, m1–m3, broken m4; QM F57791, left maxilla with P3, M1–M2.

Emended species diagnosis. *Ganawamaya aediculis* differs from all other species of *Ganawamaya* in having the following unique combination of features: long and sinuous i1 with dorsal and ventral flanges; additional cuspid on posterior end of p3 below the occlusal margin; linear occlusal edge on p3; inclined ridge from the anteriormost cuspid on p3; prominent hypocristid on m1 and m2; reduced

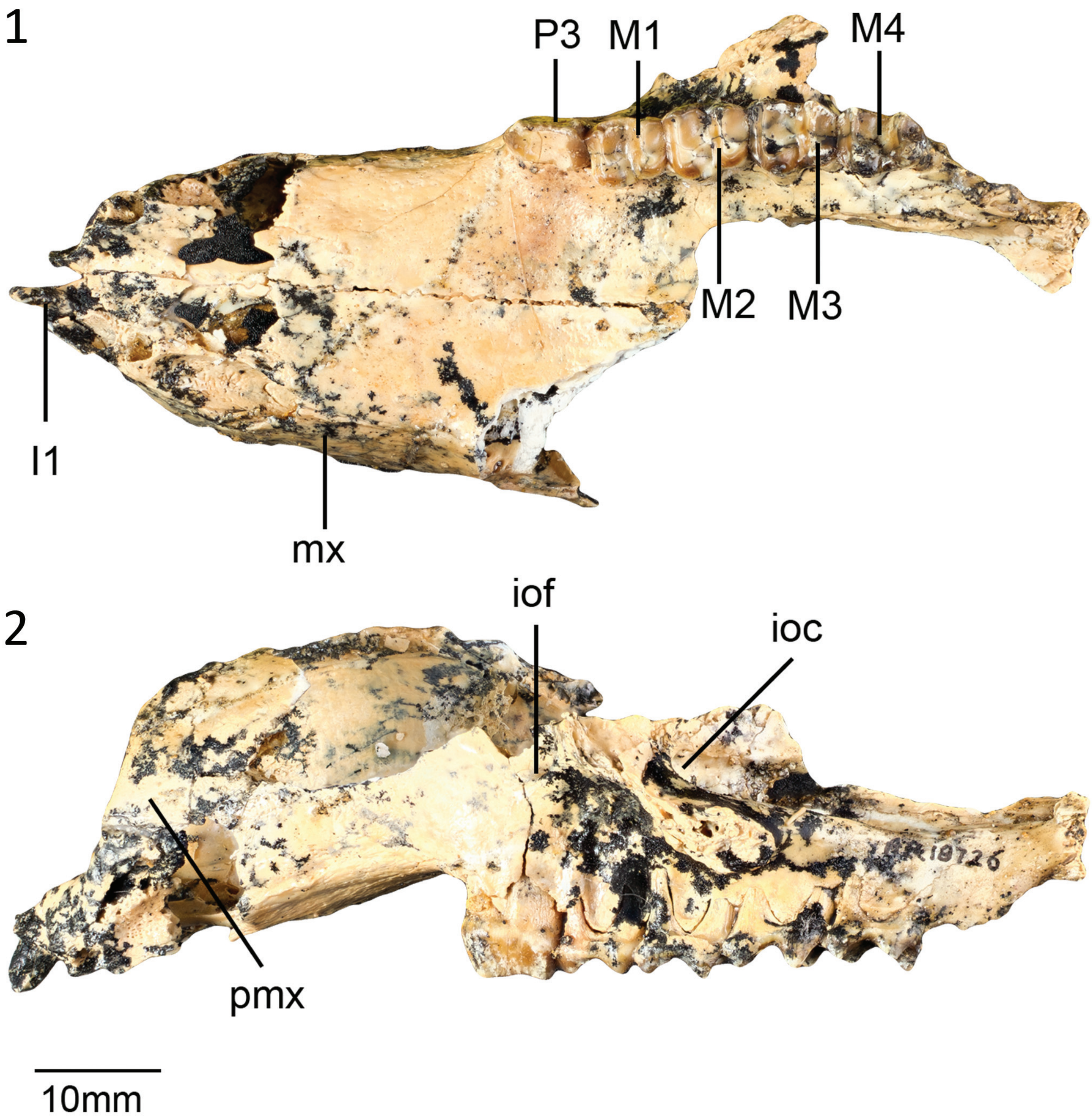

FIGURE 4. *Ganawamaya aediculis* partial cranium (QM F58658) in ventral view (**1**) and left lateral view (**2**). Abbreviations: I1, first upper incisor; ioc, infraorbital canal; iof, infraorbital foramen; M1–M4, upper first to fourth molar; mx, maxilla; P3, upper third premolar; pmx, premaxilla.

paraconid on m1; no hypoconulid; no marked convexities on the lateral margins of the interloph valley of the lower molars; m1 anterior cingulid not extending from paracristid right across to buccal surface of the tooth; poorly developed anterior cingulum of M1; poorly developed anterior cingulum on M1; stylar cusp C on M1 reduced and connected to the postparacrista.

Description

Description follows Cooke (1992) but we note the following additional features.

Premaxilla. In lateral view, the maxillary-premaxillary suture extends ventrally to the posterior margin of the canine alveolus.

Maxilla and palatine. The infraorbital canal is tube-like and positioned at the anterior extremity of the suborbital shelf. The sphenopalatine foramen is oval in shape, anteriorly positioned on the palatine, posterior to the infraorbital canal.

Upper dentition. Description of the upper dentition of *Gan. aediculis* is based on QM F58658 and 20633. In ventral view (Figure 4) the canine alveolus is larger than each of the three incisor alveoli. The I1 is preserved, lightly recurved and antero-ventrally directed. The size of the incisor alveoli may indicate that I2 is the largest incisor, followed by I1 and then I3. The left and right I1 alveoli are separated by a wide diastema. In occlusal view, I1 is long, elongate and laterally compressed. I1 is slightly recurved in lateral view. No I2, I3 or C1 are preserved, however their presence is indicated by alveoli.

The P3 is flexed anterobuccally such that is not in line with the molar row. The tooth is roughly rectangular in occlusal outline but is tapered anteriorly. Five cuspules are visible with the posteriormost cusp being the largest. Each cuspule has an associated transcrista. A prominent posterior lingual cuspule is present from which a well-developed lingual cingulum extends. In lateral view, the occlusal margin of the P3 is slightly concave.

In occlusal view, the M1 is roughly rectangular in outline. The protoloph and metaloph are roughly equal in height, however, the metaloph is narrower than the protoloph. The paracone is shorter but more massive than the protocone. A short, well-developed preparacrista extends from the paracone connecting to a well-developed anterior cingulum at the anterior end of the tooth. The anterior cingulum is bordered lingually by a faint forelink, representing a remnant preprotocrista. No precingulum is present. On the face of the paracone and lingual to the preprotocrista, a shallow concavity is present. The postparacrista is prominent and extends towards the interloph valley from the paracone. The postparacrista on M1 extends posteriorly to meet a small but distinct cusp. This cusp is interpreted to represent stylar cusp C in *N. gillespieae* by Kear et al. (2007). A poorly developed postprotocrista extends posteriorly to the interloph valley where it forms a midlink. The metacone is slightly taller than the metaconule. A premetacrista extends anteriorly to meet the postparacrista in the interloph valley. A prominent postmetacrista extends from the metacone to meet the postmetaconule crista. Both the neometaconule and postlink are absent.

The M2 is similar in morphology to M1 except as follows: it is slightly larger; the preparacrista is more buccally positioned; the anterior cingulum is wider; a precingulum is present lingual to the very faint forelink and borders the anterolingual margin of the tooth; the postparacrista is straighter anteriorly but meets the premetacrista more lingually in the interloph valley; the premetacrista is less developed; StC is present as a distinct cusp on the postparacrista only on QM F20633 where it is, however, poorly defined.

The M3 is similar in morphology to the M2 except as follows: StC is absent; the premetacrista, postprotocrista, and midlink are reduced.

The M4 is similar in morphology to the M3 except as follows: the metaloph is markedly narrower than the protoloph; the postparacrista and premetacrista are reduced; the forelink is more lingually situated.

Lower dentition. The description in Cooke (1992) is sufficient except for as follows: The protostylid on the m1 is present on unworn adult specimens e.g., QM F31181; and there are five cuspids on p3.

Remarks. Cooke 1992 described the holotype of *Gan. aediculis* (QM F16843) as having six cuspids on p3 with five associated transcristids. However, upon further inspection we clarify that like in other *Ganawamaya* species, only five cuspids and four transcristids appear to be present on the occlusal surface (Figure 5). However, an additional in *Gan. aediculis*, previously interpreted a sixth cuspid at the posterior of the p3 on the holotype, is present below the occlusal margin. The presence of a posterior cuspid on the p3 bellow the occlusal margin may be a distinguishing feature of *Gan. aediculis* (Figure 5). We propose that all *Ganamwaya* have five cuspids along the occlusal row of the p3 while *Gan. aediculis* has an additional posterior cuspid below the occlusal row. On a number of specimens attributed here to *Gan. aediculis*, the presence of this cuspid cannot be confirmed as the posterior end of the p3 has been obscured and worn by a slightly overlapping m1, making it difficult to determine whether this additional cusp is diagnostic of all *Gan. aediculis*. All specimens referable to species of *Ganawamaya* (and some previously referred to *Nambaroo*) from Faunal Zone A, also exhibit variation in apparent cuspid morphology that can be attributed to differences in inter-proximal dental wear similar to that of specimens reassigned to *Gan. acris*. These variations include the presence, or apparent absence, of the protostylid on m1, the shape of the paracristid on m1 and the complexity of enamel ridges on i1. However, specimens from Faunal Zone A assemblages differ from those in Faunal Zone B in having a better defined posthypocristid on m1 and m2. Specimens previously attributed to 'N. sp. 8' (Cooke, 1996, 1997a)

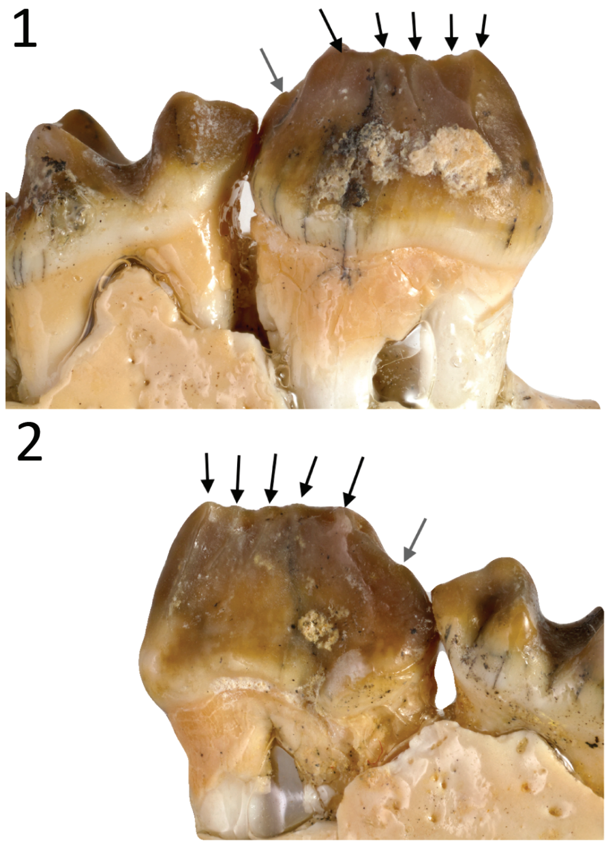

FIGURE 5. Lower third premolar of *Ganawamaya aediculis* holotype (QM F16843) in buccal view (**1**) and lingual view (**2**). Black arrows indicate each cuspid along the occlusal surface of the p3. Grey arrows indicate the additional sixth cuspid present below the occlusal margin.

are referred here to *Gan. aediculis* because they lack features that would warrant separation as a distinct taxon.

Age and distribution. The holotype of *Gan. aediculis* is from White Hunter Site, Riversleigh WHA, northwestern Queensland. The White Hunter Site is interpreted to be part of Faunal Zone A, which is interpreted to be late Oligocene in age (Archer et al., 1989, 1997; Myers and Archer 1997; Travouillon et al., 2006, 2011; Arena et al., 2015). Several other referred specimens are also from sites considered to belong to Faunal Zone A: Gillespie's Gully and LSO Site (Travouillon et al., 2006, 2011).

Ganawamaya gillespieae comb. nov.

v* 2007 *Nambaroo gillespieae*; Kear, Cooke, Archer, and Flannery, p. 1147, figs. 1–10.

Holotype. QM F35432, cranium, left dentary and postcranial material from Quantum Leap Site, Riversleigh WHA, northwestern Queensland, Australia (Kear et al., 2007).

Referred specimens. Dirk's Tower Site: QM F13099, right dentary with p3, m1–m4; QM F13100, left maxilla with M2–M4; QM F16912, right maxilla with M1–M2; QM F20036, left dentary with m1–m3; QM F24178, right maxilla with M1–M2, M4; QM F24180, right maxilla with M2–M3; QM F24185, left maxilla with P3 and M1; QM F24479, left maxilla with broken M2, M3; QM F29661, right dentary with m2–m4; QM F30289, left dentary with p3, m1–m4; QM F36233, left dentary with i1, p3; QM F36339, left dentary with i1, dp2, unerupted p3, m1–m3.

Emended species diagnosis. *Ganawamaya gillespieae* comb nov. differs from all other species of *Ganawamaya* in having the following unique combination of features: no distinct masseteric process; poorly-developed sulcus on anterior extremity of zygomatic arch; a large zygomatic epitympanic sinus with a thick mesial wall; a small mastoid foramen on the mastoid/squamosal suture; prominent hypocristid on m1 and m2; reduced paraconidon m1; long and sinuous i1 with dorsal and ventral flanges; no hypoconulid; no marked convexities on lateral margins of interlophid valley of lower molars; poorly developed anterior cingulum of M1; stylar cusp C on M1 reduced and connected to postparacrista; no additional cuspid on the posterior of p3 below the occlusal margin; m1 anterior cingulid extends from the paracristid right across to buccal surface of tooth; curved occlusal edge on p3; no inclined ridge from the anteriormost cuspid on p3.

Description

The lower dentition resembles that described by Kear et al. (2007) other than as follows: The p2 (preserved in QM F36339) is a very short but broad tooth with steeply sloping buccal and lingual faces. Two prominent cuspids are evident along the blade of the tooth, each with associated transcristae. In buccal view the occlusal surface is slightly convex.

Remarks. Specimens here referred to species of *Ganawamaya* (and some previously referred to *Nambaroo*) from Quantum Leap and Dirk's Tower also exhibit cusp morphology variation that can be attributed to differences in dental wear similar to that of specimens reassigned to *Gan. acris* and *Gan. aediculis*. These variations include the presence, or apparent absence, of the protostylid on m1, the shape of the paracristid on m1 and the complexity of enamel ridges on i1. Both QM F13099 and 20036 for example have no protostylid but are otherwise similar to the holotype of *Gan. gillespieae* comb. nov. A second specimen referred

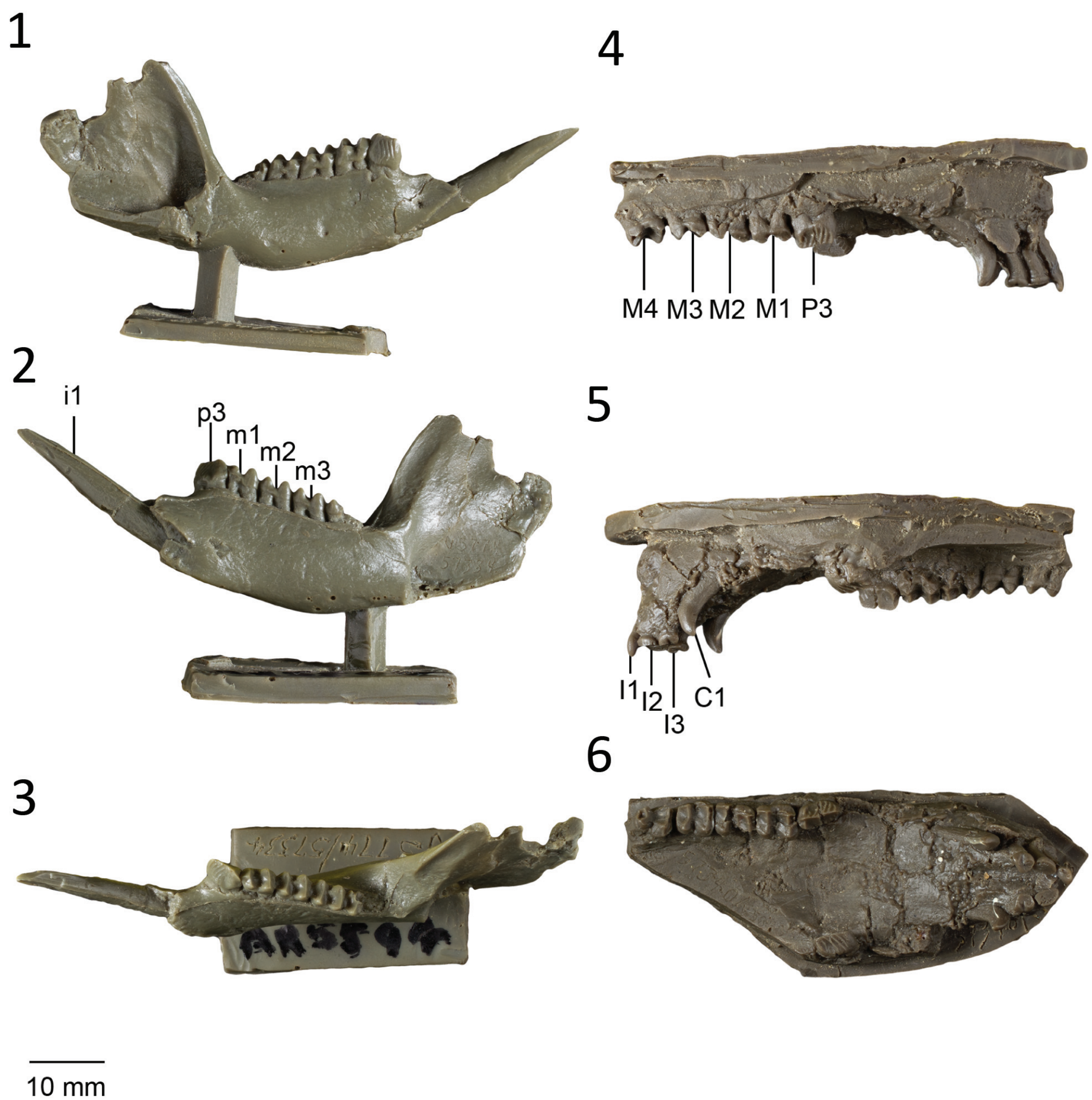

FIGURE 6. Cast of lower dentition of *Ganawamaya couperi* comb. nov. (UCMP 57334) (**1-3**) and cast of upper dentition of *Gan. couperi* comb. nov. (UCMP 57340) (**4-6**) from the Ngapakaldi Local Fauna, South Australia. Right lateral view (**1** and **4**), left lateral view (**2** and **5**), and occlusal view (**3** and **6**). Abbreviations: C, canine, I1, first upper incisor; i1, first lower incisor, M1–M4, upper first to fourth molar; m1–m3, lower first to third molar, P3, upper third premolar; p3, lower third premolar.

to *N. gillespieae* from Wayne's Wok Site (AR 12829) by Kear et al. (2007) could not be located for the present study. This specimen is therefore not included in the revised specimen list of *Gan. aediculis*.

Age and distribution. The holotype of *Ganawamaya gillespieae* comb. nov. is from Quantum Leap Site, Riversleigh WHA, northwestern Queensland. The Quantum Site was initially interpreted to be part of Faunal Zone A (Travouillon et al., 2006, 2011). However, recent studies indicate that it is part of intervals B2 or B3 of Faunal Zone B (Travouillon et al., 2010, 2013; Arena et al., 2015). Other referred specimens from Dirk's Tower Site are interpreted to represent part of interval B1 of Faunal Zone B by Arena et al. (2015).

Ganawamaya couperi comb. nov.
Figure 6

v* 1997 *Nambaroo couperi*; Cooke, p. 270, figs. 1, 2.

Holotype. QM F30401, right dentary with p3 and m1–m4 from White Hunter Site, Riversleigh WHA, northwestern Queensland, Australia (Cooke, 1997b).

Referred specimens. The following specimens are referred based on casts of the original specimens. Ngapakaldi Local Fauna, South Australia: UCMP 57340, left maxilla with P3, M1–M4; UCMP 57337 right M1–M2 and right p3, m1–m3; UCMP 57334, right dentary with p3, m1–m3.

Emended species diagnosis. *Ganawamaya couperi* comb. nov. differs from all other species of *Ganawamaya* in having the following combination of features: i1 long and narrow with no ventral flange; a hypoconulid present posterior to the entoconid on the buccal side of the m1; prominent posthypocristid on the m1–m4; marked convexities on the lateral margins of m1–m4; anterior cingulum on M1 is well developed; stylar cusp C is a prominent blade-like convexity buccal to the postparacrista; generally smaller molar size; no additional cuspid on the posterior end of the p3 below the occlusal margin; a poorly developed posterolingual cusp on the P3.

Description

Upper dentition. Description of the upper dentition of *Gan. couperi* comb. nov. is based on casts of UCMP 57340 (Figure 6) and 57337. In occlusal view, I1 is large, elongate, and laterally compressed. In lateral view, I1 is slightly recurved, with a low but distinct posterobuccal cusp present. The crown of I1 sits much higher than that of I2 and I3. In occlusal view, I2 is oval in shape but much longer than it is wide. The crown is completely flat from wear. I3 is shorter but wider than I2. I3 is distinctly bilobed buccally, with the anterior lobe being larger than the posterior lob. Lingually, the crown has been flattened by wear.

The canines sit directly posterior to the incisors with no intervening diastemata. They are tall and reach a height equal to that of the crowns of I2-3. They are recurved and are slightly laterally inclined. A large diastema separates C1 from P3.

In occlusal view, the occlusal margin of P3 is anterobuccally flexed and is out of alignment with M1. The P3 is blade-like, elliptical in shape, and tapered anteriorly. Six cuspules, each with associated lingual and buccal transcristae, are present along the occlusal margin. The posteriormost lingual and buccal transcristae are well developed as lateral blades, with a poorly developed posterolingual cusp.

The M1 is bilophodont, low crowned and roughly rectangular in outline. The metaloph is narrower than the protoloph. However, both are subequal in height. The paracone is shorter but more massive than the protocone. A short, well-developed preparacrista extends from the paracone to the anterior end of the tooth where it meets a reduced anterior cingulum. The anterior cingulum is bordered lingually by the forelink (remnant of the preprotocrista). No precingulum is present. A shallow concavity is present on the anterior face of the paracone lingual to the preparacrista. The postparacrista extends from the paracone posteriorly towards the interloph valley on UCMP 57340. The postparacrista is less developed on UCMP 57337. A prominent blade-like convexity is evident buccal to the postparacrista which is interpreted as stylar cusp C. The postprotocrista is weakly developed but extends posteriorly to the interloph valley where it forms a midlink. The metacone is taller than the metaconule. A prominent premetacrista extends into the interloph valley where it meets the postparacrista. A well-developed postmetacrista extends posteriorly from the metacone to meet the postmetaconule crista. The neometaconule and postlink are absent.

The M2 is similar in morphology to the M1 except as follows: it is larger; its protocone is taller; a long precingulum borders the anterior flank of the tooth from the forelink to the lingual side of the tooth; the premetacrista is less well developed; the postprotocrista and midlink are reduced on UCMP 57337.

The M3 is similar in morphology to the M2 except as follows: the preparacrista is more buccally situated; the postparacrista, premetacrista, postprotocrista, and midlink are reduced.

The M4 is similar in morphology to M3 except as follows: the metaloph is markedly shorter than the protoloph; the postparacrista is reduced; StC is absent; the postprotocrista and midlink are reduced; the forelink is more lingually situated, equalling the size of the anterior cingulum and precingulum.

Lower dentition. The description of *Ganawamaya couperi* comb. nov. is as stated by Cooke (1997b) except as follows: the i1, which is preserved in UCMP 57334, is long and narrow and rises to the level of the molar row. A dorsal enamel flange is present but there is no ventral flange.

The protostylid of the m1is tall in UCMP 10600, a juvenile specimen, and is also present although more worn on the holotype and UCMP 57337. The portion of the missing protostylid is represented by a flat wear facet on UCMP 57334, which represents an even older individual.

Remarks. Flannery and Rich (1986) diagnosed species of the genus *Nambaroo* as exhibiting the following features: well-developed lophs and lophids, m1 with a markedly compressed trigonid, a protostylid, posthypocristid on m1, and absence of a well-developed posterior cingulid on the lower molars. Our study demonstrates, in particular, that the protostylid is present in species of *Ganawamaya* as well as *Nambaroo*. *Ganawamaya couperi* comb. nov. differs from species of *Nambaroo* in having a rectilinear rather than a third premolar with a plagiaulacoid form, a less developed preprotocrista and a postprotocrista that extends into the interloph valley on M1. These features are present in the specimen previously attributed by Cooke (1997b) to *N. couperi* (QMF30401) and for this reason we contend that *Gan. couperi* comb.nov. is a species of *Ganawamaya* rather than *Nambaroo.* It is currently unclear whether the protostylid is lost due to wear in other species of *Nambaroo*. Large upper canines are also preserved in UCMP 57340. Although canine alveoli have been described for *Nambaroo* (Kear et al. 2007) and *Ganawamaya* in our study, this specimen is the first to be described in which the canines are preserved.

Age and distribution. The holotype is from White Hunter Site, Riversleigh WHA, northwestern Queensland, Australia. This site is part of Riversleigh's Depositional Phase 1 and contains species interpreted to represent Faunal Zone A assemblages which have been interpreted to be late Oligocene in age (Archer et al., 1989, 1997; Myers and Archer 1997; Travouillon et al., 2006, 2011; Arena et al., 2015). The referred specimens are from the Ngapakaldi Quarry of the Etadunna Formation is interpreted to be late Oligocene (24.6 Ma) in age (Woodburne et al., 1993).

Genus NAMBAROO Flannery and Rich, 1986

Type Species. *Nambaroo tarrinyeri* Flannery and Rich, 1986, by original description.

Emended generic diagnosis. Species of *Nambaroo* differ from all other balbarids in having the following combination of features: a short buccally flexed p3 with six to eight cuspids; a more plagiaulacoid p3 form; a poorly developed hypocingulid on the m1; a pronounced lingual cingulum on P3; possession of a neometaconule and postlink; a well-developed postprotocrista that does not extend into the interloph valley on M1.

Remarks. *Nambaroo* was first described by Flannery and Rich (1986) to accommodate three species characterised as differing from other balbarids (*Ganawamaya* was not described at the time) by having a protostylid on m1, lacking a well-developed posterior cingulid on lower molars, and possessing a posthypocristid on the m1. Species of *Nambaroo* differ from *Balbaroo* in having noticeably smaller molars, a poorly developed midlink, and in lacking a well-developed hypocingulid on all lower molars. As previously discussed, our study demonstrates that the protostylid, a defining character in the generic diagnosis of *Nambaroo* (Flannery and Rich, 1986) is present in species of *Ganawamaya* as well as *Nambaroo*. However, *Nambaroo* species do differ from *Ganawamaya* species in having a more plagiaulacoid molar form as opposed to rectilinear, a more developed preprotocrista and postprotocrista, and possession of a postlink and neometaconule.

MORPHOMETRIC AND PHYLOGENETIC ANALYSES

Coefficients of Variation

Coefficients of variation for lower molars range from 3.7 to 14.2 for the revised *Ganawamaya aediculis* list of specimens (Appendix 2), 1.1 to 9.2 for *Gan. gillespieae* comb. nov. (Appendix 3) and 3.5 to 9.8 for *Gan. acris* (Appendix 4). For the upper dentition, coefficients of variation range from 0.1 to 11.4 for *Gan. aediculis*, 0.8 to 6.4 for *Gan. gillespieae* comb. nov. and from 3.9 to 8.9 for *Gan. acris*. The sample size for *Gan. couperi* comb. nov. was too small for statistical analysis. With the exception of variation in the length of P3 (0.8) and upper molars of *Gan. gillespieae* comb. nov., CVs are generally consistent with those for the extant macropodid species *Thylogale thetis* (4.98–11.16) and *T. stigmatica* (3.54–12.5); see Travouillon et al. (2014). While these results indicate that the range of dental measurements for *Ganawamaya* specimens are consistent with, or less diverse, than that evident in *Thylogale* species, we acknowledge that these results should be taken with caution as the expected variation in this study is based solely on two extant taxa. We propose that further study of intraspecific variation in the dentition of modern macropodids should be completed in the future.

Bivariate Plots and Statistical Analysis

Bivariate plots for lower dentition using the revised taxonomic classifications from this study are presented in Figure 7. The lower dentition of *Ganawamaya acris, Gan. gillespieae* comb. nov. and *Gan. aediculis* cannot be distinguished using bivariate plots. *Ganawamaya couperi* comb. nov.

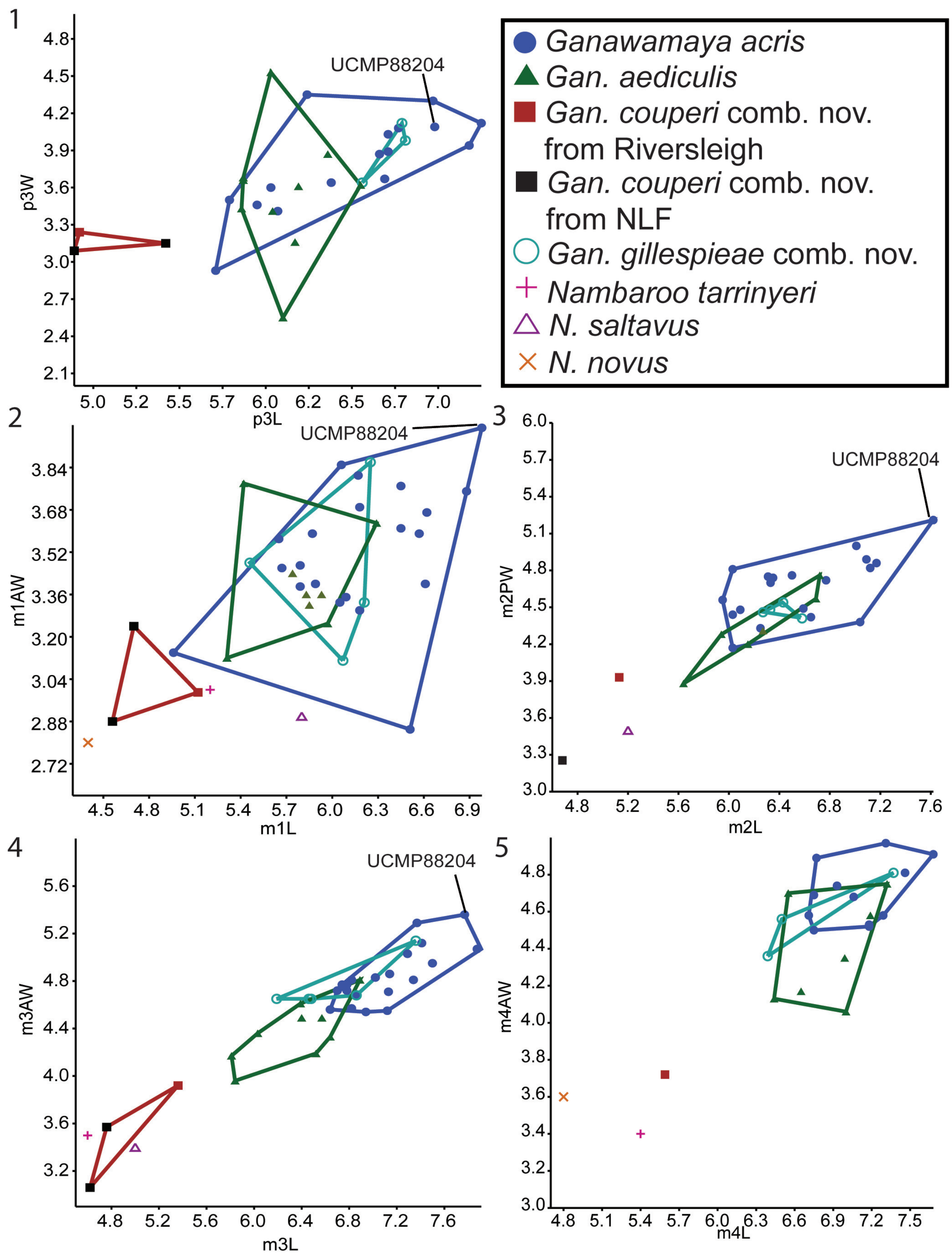

FIGURE 7. Bivariate plots of lower teeth: the third premolar (**1**) and the first to fourth molars (**2-5**) for specimens of *Ganawamaya acris*, *Gan. couperi* comb. nov.*, Gan. aediculis*, *Gan. gillespieae* comb. nov., *Nambaroo tarrinyeri*, *N. novus* and *N. saltavus* from the Riversleigh World Heritage Area and the Ngapakaldi Local Fauna (NLF). Black squares represent specimens of *Gan. couperi* comb. nov. from NLF. Abbreviations: L, length; AW, anterior width; PW, posterior width; M1–M4, upper first to four premolar, P3, upper third premolar.

can be distinguished from other *Ganawamaya* species at Riversleigh in having a shorter premolar and smaller molars. Specimens of *Gan. couperi* comb. nov. from South Australia (Ngapakaldi Local Fauna) are similar in molar size to the holotype from Riversleigh. Species of *Nambaroo* (*N. tarrinyeri*, *N. novus* and *N. saltavus*) cannot be distinguished from species of *Ganawamaya* based on molar size. The *Gan. acris* specimen from Leaf Locality (UCMP 88204) clusters with larger *Gan. acris* specimens from Riversleigh. These results also reflect those for the upper dentition (Figure 8). The results of Kruskal-Wallis tests (Appendix 5) indicate that dental measurements for each species differ significantly ($p < 0.05$) for lower premolar length and width, lower first molar length and anterior width, lower second molar posterior width, lower third molar length and widths, lower fourth molar anterior width, upper third premolar length and width and upper first, second and third molar length and widths. Mann-Whitney U tests (Appendix 6) suggest that *Gan, couperi* comb. nov. is generally significant smaller than other *Ganawamaya* species ($p < 0.05$). *Ganawamaya gillespieae* comb. nov. is generally similar to *Gan. acris* in size but is significantly smaller ($p < 0.05$) in terms of third lower and upper molar posterior width, first upper molar posterior width, and second upper molar anterior and posterior widths (Appendix 6). *Ganawamaya aediculis* differs from other species significantly in terms of lower third premolar length, lower first and second molar posterior width, and lower third premolar length and width ($p < 0.05$; Appendix 6).

Principal Component Analysis (PCA)

In the PCA of log transformed lower tooth measurements (Appendix 7), PC (Principal Component) 1 accounts for 62.7% of variance while PC2 accounts for 10.0% (Figure 9.1). The length of the premolar, length of the molars and the anterior, and posterior, widths of the m3 appear to have the most significant effect on PC1 (Appendix 7). PC2 is driven primarily by length and width of the lower third premolar. There is some overlap between *Ganawamaya acris* and *Gan. aediculis*. *Ganawamaya acris* and *Gan. gillespieae* comb. nov. overlap entirely. However, *Gan. couperi* comb. nov. falls outside the size range of other *Ganawamaya* species. In the PCA of log transformed upper tooth measurements (Appendix 8), PC1 accounts for 63.8% of the variance while PC2 accounts for 17.7% (Figure 9.2). Loadings for PC1 are highest for the length and width of the upper first and second molars as well as the length of the P3 (Appendix 8). The length and width of the upper fourth and third molars also have high loadings. Loadings for PC2 are highest for the length and width of the upper third and fourth molars. While there is some separation of *Gan. acris* (PC1: -0.4–2.56) and *Gan. aediculis* (PC1: -1.8–0.5) specimens in terms of principal components, both can be distinguished from *Gan. couperi* comb. nov., which has lower PC2 values (Figure 9.2). There is significant overlap between *Gan. acris* and *Gan. gillespieae* comb. nov. Sample sizes for *Nambaroo* species (*N. tarrinyeri*, *N. novus*, and *N. saltavus*) were not sufficient to include in the PCA.

Phylogenetic Analysis

Our analysis resulted in 1580 most parsimonious trees (tree length = 578, consistency index = 0.36, retention index = 0.79). The trees are summarised in a strict consensus tree in Figure 10. Hypsiprymnodontidae is unresolved at the base of the macropodiform clade. However, Propleopinae is recovered as a distinct group and as a sister taxon to Balbaridae but with low support. Within Balbaridae, *Nambaroo saltavus* and *N. tarrinyeri* are recovered at the base of the balbarid clade. *Ganawamaya* species form a distinct clade to the exclusion of *Nambaroo* species from South Australia (*N. saltavus* and *N. tarrinyeri*) with moderate support (Bootstrap = 79). *Ganawamaya aediculis* and *Gan. gillespieae* comb. nov. cluster together to the exclusion of *Gan. acris* and *Gan. couperi* comb. nov. with low support (Bootstrap = 61). *Ganawamaya* forms a sister clade to *Balbaroo* and *Wururoo*. Macropodidae is recovered as a clade distinct from Hypsiprymnodontidae and Balbaridae with high support (Bootstrap = 85). Our matrix includes those characters uniting Balbaridae as a family in Kear and Cooke (2001), and the strict consensus tree supports its placement as a distinct group.

Within Macropodidae, extant species of Potoroinae (*Potorous tridactylus, Bettongia penicillata*, and *Aepyprymnus rufescens*) are recovered as a monophyletic clade but with low support from bootstrap analysis. Specimens previously referred as fossil potoroines do not form a clade with the extant species and instead appear to be an outgroup to all other macropodids. This suggests that these species are most likely not potoroines but stem macropodids. However, missing data for fossil specimens may affect the positioning of these species within the phylogenetic tree. Species of *Ganguroo* and *Wabularoo* are unresolved at the base of the clade that includes lagostrophines,

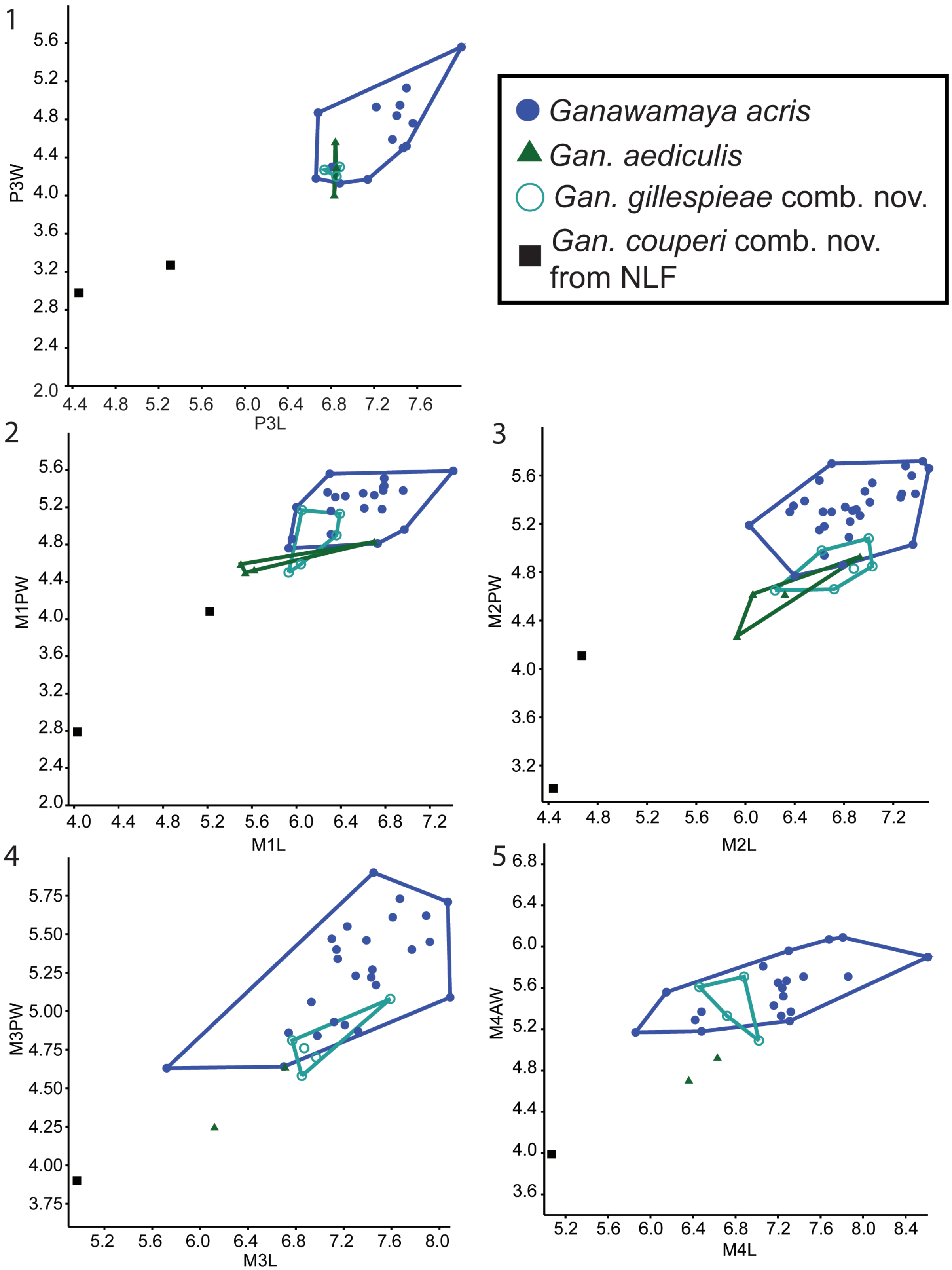

FIGURE 8. Bivariate plots of upper teeth: the third premolar (**1**) and the first to fourth molars (**2-5**) for specimens of *Ganawamaya acris*, *Gan. aediculis*, *Gan. gillespieae* comb. nov. and *Gan. couperi* comb. nov. from the Riversleigh World Heritage Area and the Ngapakaldi Local Fauna (NLF). Black squares represent specimens from NLF. Abbreviations: L, length; AW, anterior width; PW, posterior width; M1–M4, upper first to four premolar; P3, upper third premolar.

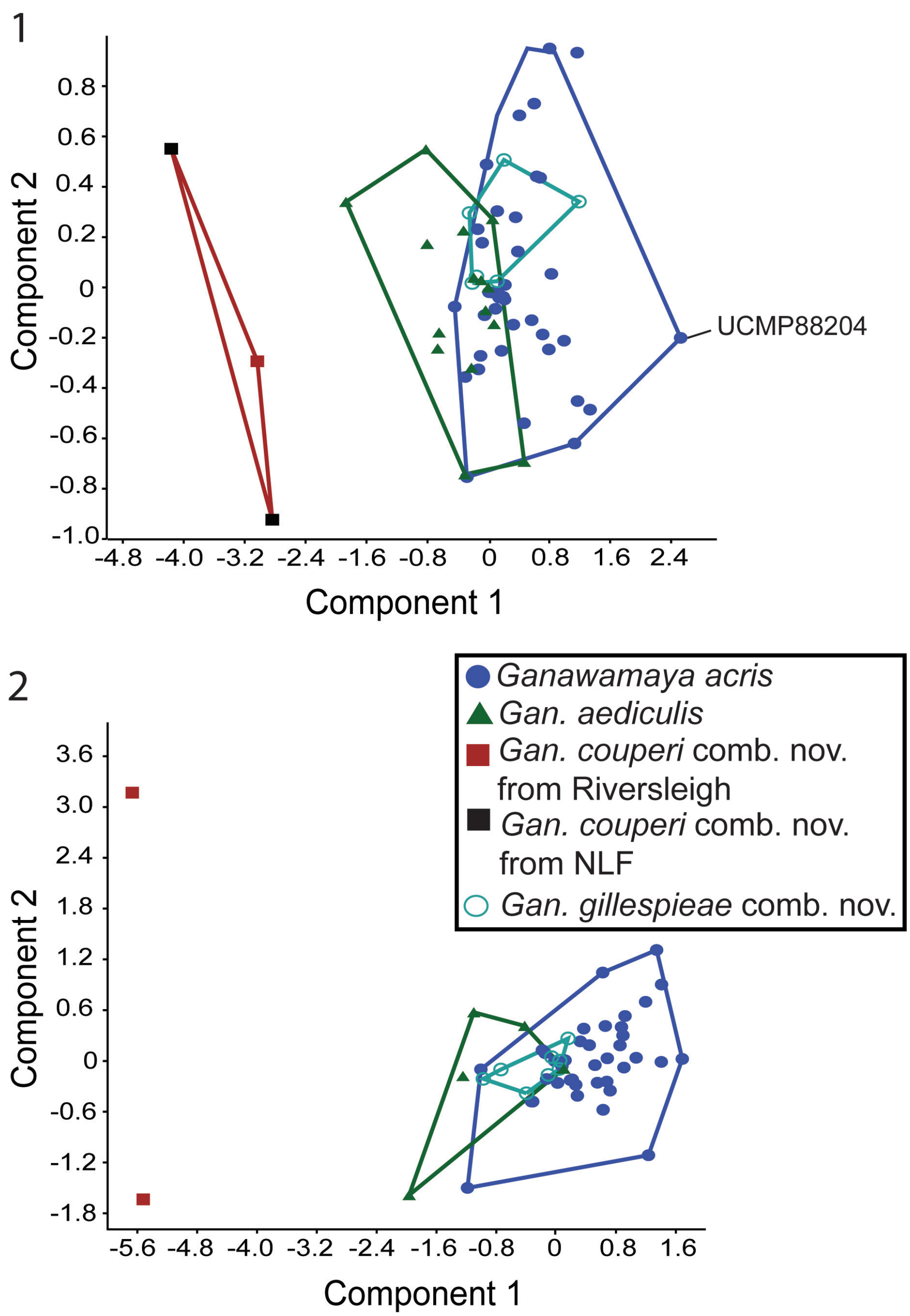

FIGURE 9. Principal Component Analysis with convex hulls of log transformed measurements for upper (**1**) and lower (**2**) tooth measurements for *Ganawamaya acris*, *Gan. couperi* comb. nov., *Gan. gillespieae* comb. nov. and *Gan. aediculis* from the Riversleigh World Heritage Area and the Ngapakaldi Local Fauna (NLF)".

sthenurines, and macropodines. In analyses of previous iterations of the matrix, the interrelationships of Lagostrophinae, Sthenurinae, and Macropodidae were also unresolved (e.g., Butler et al., 2016). We believe that the inclusion of the genus *Cookeroo* in Butler et al. (2016) resulted in the collapse of these clades because the genus shares a number of characters with specimens from each of the three clades. As such we did not include *Cookeroo* in this analysis. This also indicates that macropodiform phylogeny requires significant further study and, as suggested by Butler et al.

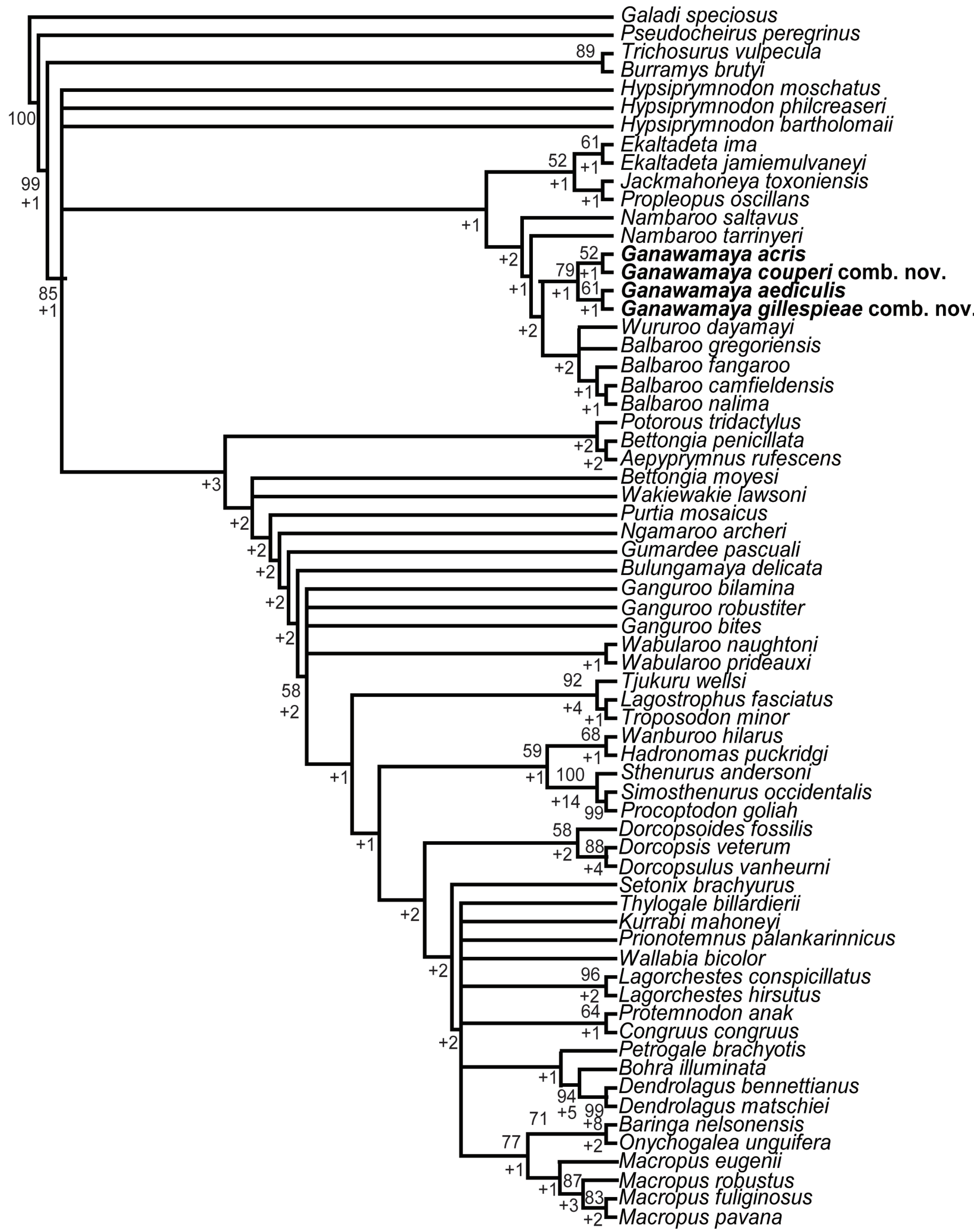

FIGURE 10. Strict consensus of 1580 most parsimonious trees (tree length = 578, consistency index = 0.36, retention index = 0.79) from parsimony analysis of the matrix containing 66 taxa and 120 characters, assessing the phylogenetic relationship of revised *Ganawamaya* (highlighted in bold). Numbers above represent bootstrap values while numbers below represent decay indices. Decay indices are prefaced with a plus sign.

(2016), the inclusion of additional postcranial material, if suitable specimens are recovered, may resolve the issue.

In the present study, Lagostrophinae is recovered as a clade with high support (Bootstrap = 92), and as a sister taxon to Sthenurinae and Macropodinae but with low support, supporting the results of Prideaux and Warburton (2010). Sthenurinae (including *Wanburoo hilarus* and *Hadronomas puckridgi*) is recovered as a clade with low support (Bootstrap = 59) and as a sister taxon to Macropodinae but with low support. Macropodinae is recovered as a clade with low support. The clade composed of members of the genus *Dorcopsoides* is recovered as a sister taxon to all other macropodines. The relationships of clades within Macropodinae are unresolved.

DISCUSSION

Of the features distinguishing *Nambaroo* (see remarks), which were described by Flannery and Rich (1986), only the protostylid differs from descriptions of *Ganawamaya* by Cooke (1992). Of the states listed in the descriptions of *Gan. couperi* comb. nov. (*N. couperi* in Cooke, 1997b) and *Gan. gillespieae* comb. nov. (*N. gillespieae* in Kear et al., 2007), the presence of a protostylid on m1 appears to be the primary distinguishing feature from *Ganawamaya*. In our study, however, the lack of a protostylid on m1 appears to be the result of dental wear and not a diagnostic feature for distinguishing *Nambaroo* and *Ganawamaya*. The protostylid is present in juvenile and relatively little-worn teeth but absent in most adult specimens because of wear. Kear et al. (2007) noted that in *Gan. gillespieae* comb. nov. there is a concavity (wear facet) on the anterobuccal face of the paracone, lingual to the preparacrista on M1, which received the m1 protostylid. This wear facet is also present on *Gan. aediculis* as described in our study, and on the referred specimen of *Gan. acris* described by Cooke (1992) but was not recognised to be the consequence of occlusion between the protostylid of m1 and the upper molar. The presence of this wear facet suggests that a protostylid was likely present in juveniles of *Ganawamaya/Nambaroo* species. However, we interpret that this interaction between the protostylid of the m1 and upper molar only occurs when the jaw is at rest and does not account for the wearing of the protostylid. For *Gan. gillespieae* comb. nov., during occlusion, the protostylid on the m1 slides between blade of the P3 and the P3's posterolateral cusp thus wearing the protostylid slowly. The presence of a protostylid in juveniles but absence in adults is also similar to findings in other balbarid taxa such as *Balbaroo fangaroo* and *B. nalima* (Black et al., 2014) although the protostylid appears to wear slower in *Ganawamaya* than in *Balbaroo*. In species of *Balbaroo* the P3 posterolateral cusp sits directly in front of the protostylid such that as the jaw moves forward it would be expected that the posterolateral cusp would wear down the protostylid much quicker than in *Ganawamaya*.

Our phylogenetic analysis also indicates that species of *Ganawamaya* and species previously attributed to *Nambaroo* from Riversleigh form a distinct clade to the exclusion of *Nambaroo saltavus* and *N. tarrinyeri* (Figure 10). Specimens of *Ganawamaya* from Riversleigh differ from *N. tarrinyeri* and *N. saltavus* in having a more rectilinear rather than plagiaulacoid-like p3 in addition to a less developed preprotocrista and a postprotocrista that extends into the interloph valley in M1 and in lacking a postlink and neometaconule on upper molars, although they are similar in molar size to smaller *Gan. couperi* comb. nov. (Figure 7). These results indicate that Riversleigh species previously attributed to *Nambaroo* and *Ganawamaya* are referrable to a single genus, *Ganawamaya*, and that the assigned species differ from those of *Nambaroo* from South Australia. Specimens previously attributed to *N. couperi* and *N. gillespieae* are here referred to *Ganawamaya*. Thus, the geographic range of *Nambaroo* is restricted only to South Australia.

The previously proposed 12 species for *Ganawamaya* (previously *Ganawamaya* and *Nambaroo*) at Riversleigh (Cooke, 1996, 1997a) were distinguished on the combination of the complexity of enamel ridges on the m1, shape of the paracristid, number of cusps on P3 and the presence of a hypoconulid on lower molars (Cooke, 1992, 1996, 1997b). Variation in the complexity of enamel ridges and shape of the paracristid appear to relate to stages of dental wear (see Figure 3). Juvenile or less worn adult specimens have a longer more sinuous paracristid, while adult specimens can have a shorter paracristid resulting from wear of the anterior portion of the paracristid. Complex enamel ridges are generally evident in juvenile specimens, such as that of the holotype of *Gan. ornata*. The combination of a sinuous versus straight paracristid, and the presence or absence of complex enamel ridges, are therefore evidently not taxonomically informative characters for distinguishing species of *Ganawamaya* (and previously *Nambaroo*).

The results of our phylogenetic analysis are consistent with previous phylogenetic analyses (Kear et al., 2007; Kear and Pledge, 2007; Travouillon et al., 2014) in that Propleopinae (*Ekaltadeta, Jackamhoneya, Propleopus*) comes out as the sister taxon of Balbaridae, although support for this relationship is weak. *Nambaroo saltavus* and *N. tarrinyeri* appear to be relatively plesiomorphic members of the balbarid clade, with species of *Ganawamaya* (including *Gan. couperi* comb. nov.) forming a distinct clade. *Ganawamaya* species are recovered as the sister taxon to a group including species of *Balbaroo* and *Wururoo*. The interrelationships of *Balbaroo* species in our analyses are consistent with the results of Black et al. (2014), although there is relatively low bootstrap support for this relationship. Here, an additional phylogenetic character, the presence or absence of an interparietal, was included in the analysis. No interparietal was evident in either of the propleopine or balbarid crania available for study, and the absence of an interparietal appears to be a synapomorphy uniting the two clades in our analysis. If this is the case, Propleopinae could be a subfamily of Balbaridae, rather than Hypsiprymnodontidae. However, it should be noted that an interparietal suture on a balbarid was described and figured by Kear (2003) on a *Balbaroo* endocranial cast. However, because this specimen and the undescribed but associated fragmentary cranium referred to by Kear (2003) could not be located for our present study, we cannot confirm the existence of this feature in balbarids.

In terms of Riversleigh biostratigraphy, *Gan. couperi* comb. nov. is known only in Faunal Zone A assemblages. *Ganawamaya couperi* comb. nov. appears to be more plesiomorphic than *Gan. aediculis* in that it retains a hypoconulid similar to that seen in species of *Nambaroo* from the late Oligocene Namba Formation (Flannery and Rich, 1986). However, *Gan. couperi* comb. nov. groups phologentically with *Ganawamaya* from Riversleigh as opposed to *Nambaroo*. *Ganawamaya couperi* comb. nov. can also be distinguished from other species of *Ganawamaya* in having marked convexities on the lateral margins of the m1–m4 (Cooke, 1997b) and by its significantly smaller molar size as evident in bivariate plots (Figure 8, 9). *Ganawamaya aediculis* is only present in Fauna Zone A assemblages at Riversleigh. It has features that appear to be ancestral to those of *Gan. acris*, such as the presence of a more pronounced posthypocristid on m1 and a poorly developed anterior cingulid, a strongly developed postprotocrista on M1, a less developed sulcus on the anterior extremity of the zygomatic arch, a distinct process on the ectotympanic, and smaller mastoid foramen on the mastoid/squamosal suture. Additionally, the presence of *Gan. aediculis* primarily in late Oligocene (Faunal Zone A) deposits suggests that it may be ancestral to *Gan. acris,* which occurs primarily in Miocene assemblages (Faunal Zone B, intervals B2 and B3, and Faunal Zone C, interval C1). This relationship was not resolved in phylogenetic analyses (Figure 10), which indicate that *Gan. gillespieae* comb. nov. and *Gan. aediculis* cluster together to the exclusion of *Gan. acris* and *Gan. couperi* comb. nov. However, we believe that this is because there are no characters distinguishing *Gan. gillespieae* comb. nov. and *Gan. aediculis* in the phylogenetic matrix. Despite this, examination of characters not included in the matrix but noted in our species diagnoses suggests that *Gan. gillespieae* comb. nov. retains an m1 anterior cingulid which extends from the paracristid right across to the buccal surface of the tooth, a more curved occlusal edge on p3 and no inclined ridge from the anteriormost cuspid on p3. It is therefore possible that *Gan. aediculis*, *Gan. gillespieae* comb. nov., and *Gan. acris* form a continuous evolutionary lineage and may be chronospecies.

A presence/absence table for *Ganawamaya* species is provided in Table 8. Specimens from Dirk's Tower are interpreted as belonging to Faunal Zone B by Travouillon et al. (2010) and interval B1 by Arena et al. (2015). Specimens from Quantum Leap Site interpreted as a Faunal Zone B assemblage by Travouillon et al. (2010) and interval B2 or B3 by Arena et al. (2015), are referred to *Gan. gillespieae* comb. nov. The presence of *Gan. gillespieae* comb. nov. alone and absence of *Gan. acris* in Quantum Leap Sites suggest that the deposit may be older than other Faunal Zone B, interval B2 sites. One specimen attributed to *Gan. acris* in this study is from Gag Site which is interpreted as a Faunal Zone C assemblage, interval C1 or C2 by Arena et al. (2015). This extends the temporal range of *Ganawamaya* into the middle Miocene. This specimen is currently the only *Ganawamaya* specimen known from Faunal Zone C. As a result two balbarid species (*Gan. acris* and *Balbaroo nalima*) are present in Faunal Zone C assemblages at Riversleigh.

A previous biostratigraphic study has indicated the presence of undescribed species of *Nambaroo* in the Ngapakaldi Quarry and Leaf Locality deposits (Woodburne et al., 1993). Examination of four specimens from the Ngapakaldi

TABLE 8. Presence/absence table for species of *Ganawamaya* throughout Australia. Numbers represent the number of specimens. Abbreviations are: B, Boid Site; CR, Creaser's Ramparts Site; CS, Camel Sputum Site; D, D Site; DT, Dirk's Towers Site; G, Gag Site; GG, Gillespie's Gully Site; LSO, LSO Site; NG, Neville's Garden Site; PIR, Price Is Right Site; RSO, RSO Site; U, Upper Site; WH, White Hunter Site; WW, Wayne's Wok Site.

Series/Epoch	late Oligocene				early Miocene												middle Miocene
Faunal Zone	FZA				FZB											FZB/C	FZC
Interval	A				B1	B2/B3			B3							B2/B3/C1	C2/C3
Site (Queensland)	D	WH	GG	LSO	DT	QL	B	CR	CS	I	JH	NG	RSO	U	WW	PIR	G
Gan. aediculis		15	1	3													
Gan. couperi comb. nov.		1															
Gan. gillespieae comb. nov.					12	1											
Gan. acris							1	4	19	2	1	5	2	17	18	4	1
Site (South Australia)	Ngapakaldi															Wipajiri	
Gan. couperi comb. nov.	3																
Gan. acris																2	

Quarry, South Australia (UCMP 10600, 57340, 57337 and 57334) indicates that these specimens differ from *Nambaroo tarrinyeri, N. novus,* and *N. saltavus* from the Namba Formation, South Australia. Each specimen exhibits morphological features that characterise *Gan. couperi* comb. nov. including a more rectilinear (rather than plagiaulacoid) p3, less developed preprotocrista, a postprotocrista that extends into the interloph valley, a posthypocristid evident on m4, and marked convexities on the lateral margins of the m1–m4. The associated upper dentition (UCMP 57340) indicates that in *Gan. couperi* comb. nov., StC is present buccal to the postparacrista, which is not the case in other *Ganawamaya* species where StC is connected to the preparacrista. Two specimens from the Leaf Locality, South Australia (UCMP 88212 and 88204), are identified in the present study as *Gan. acris*. The presence of species of *Ganawamaya* in South Australia significantly extends the geographic range of this genus, and further supports the correlation between the Leaf Locality of the Wipajiri Formation and early Miocene assemblages (e.g., Faunal Zone B) at Riversleigh (e.g., Archer et al., 1997; Travouillon et al., 2006).

After revising Riversleigh specimens referred to *Ganawamaya* or previously attributed to *Nambaroo*, we recognise a total of four species, all referable to *Ganawamaya*: *Gan. acris, Gan. aediculis*, *Gan. couperi* comb. nov., and *Gan. gillespieae* comb. nov. Postcranial material, QM F35432, from Riversleigh previously referred to *N. gillespieae* (Kear et al., 2007) is now referred to *Ganawamaya*. This postcranial material has been interpreted to imply a quadrupedal gait for *Nambaroo* and other balbarid species (Kear et al., 2007; Black et al., 2014). Alternatively, analysis of macropodiform calcaneal measurements by Janis et al. (2016) indicates that balbarids postcranial material is more consistent with generalized hoppers such as those of the genus *Thylogale* (pademelons). Further analysis is required in order to resolve the conflicting results for proposed locomotor ability of balbarids at Riversleigh.

Species of *Ganawamaya* also exhibit lophodont dentitions, consistent with a browsing herbivorous diet, and a mesowear profile of sharp and tall cusps, consistent with mesowear profiles of extant browsing kangaroo species recorded by Butler et al. (2014). Analysis of the relationship between macropodiform craniodental measurements and diet suggests that the diets of balbarids such as *Balbaroo* species and *Gan. aediculis* are generally consistent with extant folivorous browsing kangaroos. Species of *Nambaroo* fall either in the browsing/omnivore category or close to folivorous browsers (Janis et al., 2016). Analyses by Janis et al. (2016) suggest that macropodid species from the same Riversleigh Faunal Zones were also folivorous browsers.

The similar diets of balbarids such as *Ganawamaya* and macropodid species (Janis et al., 2016) may suggest that extinction of Balbaridae during the middle Miocene, as proposed by Cooke (1997a), was driven by competition between these clades. If macropodids exhibited a greater deal of dietary plasticity this may have put balbarids at a selective disadvantage at a time when global cooling (e.g., McGowran and Li, 1994) and changes in environment at Riversleigh from rainforest to open woodland during the mid to late Miocene occurred (Travouillon et al., 2009). Such changes in environment at the time are supported by analyses from Travouillon et al. (2009). However, further study comparing diets of these species using dietary proxies known to reflect diet of kangaroos on ecological time scales such as mesowear analysis (e.g., Butler et al., 2014) or stable isotope analysis (Montanari et al., 2013) are required in order to test these hypotheses further. Recent analyses of trends in macropodiform species diversity and trends in body mass through time (Butler et al., 2017) made use of the revised classifications of *Ganawamaya* specimens presented in this study. The results suggested that balbarids were less abundant than macropodids during the Late Oligocene and most of the Miocene (Butler et al., 2017).

CONCLUSION

The revision of *Nambaroo* and *Ganawamaya* results in a significant reduction in apparent diversity of late Oligocene to early Miocene balbarids from 12 proposed species down to just four. In addition, the temporal range of *Ganawamaya* is extended into the middle Miocene of Riversleigh. Recent description, and revision, of balbarids from Riversleigh (e.g., Kear et al., 2007; Bates et al., 2014; Black et al., 2014; Travouillon et al., 2014, 2015; Cooke et al., 2015; Butler et al., 2016) suggest that the current understanding of balbarid and macropodid diversity and their temporal ranges will benefit from continued reassessment of existing, as well as rapidly accumulating new fossils from Oligo-Miocene sites throughout Australia.

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APPENDIX 1.

Nexus formatted character matrix for taxa included in the phylogenetic analysis using revised species classifications for *Ganawamaya* and *Nambaroo* from this study. Outgroup species: *Pseudocheirus peregrinus, Trichosurus vulpecula, Galadi speciosus*, and *Burramys brutyi*. ? = missing data.
Revision of Oligo-Miocene kangaroos, *Ganawamaya* and *Nambaroo* (Marsupialia: Macropodiformes, Balbaridae)
Kaylene Butler, Kenny J. Travouillon, Gilbert J. Price, Michael Archer, and Suzanne J. Hand
Palaeontologia Electronica

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#NEXUS

[ File saved by NDE version 0.5.0, Fri Sep 09 10:09:50 2016 ]

BEGIN TAXA;
DIMENSIONS NTAX=66;
TAXLABELS
'Galadi speciosus'
'Trichosurus vulpecula'
'Pseudocheirus peregrinus'
'Burramys brutyi'
'Nambaroo tarrinyeri'
'Nambaroo saltavus'
'Wururoo dayamayi'
'Balbaroo gregoriensis'
'Balbaroo fangaroo'
'Balbaroo camfieldensis'
'Balbaroo nalima'
'Hypsiprymnodon moschatus'
'Hypsiprymnodon bartholomaii'
'Hypsiprymnodon philcreaseri'
'Ekaltadeta ima'
'Ekaltadeta jamiemulvaneyi'
'Jackmahoneya toxoniensis'
'Propleopus oscillans'
'Bettongia moyesi'
'Bettongia penicillata'
'Aepyprymnus rufescens'
'Potorous tridactylus'
'Purtia mosaicus'
'Wakiewakie lawsoni'
'Ngamaroo archeri'
'Lagostrophus fasciatus'
'Tjukuru wellsi'
'Troposodon minor'
'Gumardee pascuali'
'Bulungamaya delicata'
'Ganguroo bilamina'
'Ganguroo bites'
'Ganguroo robustiter'
'Wabularoo naughtoni'
'Wabularoo prideauxi'
'Wanburoo hilarus'
```

```
'Hadronomas puckridgi'
'Sthenurus andersoni'
'Simosthenurus occidentalis'
'Procoptodon goliah'
'Dorcopsoides fossilis'
'Dorcopsis veterum'
'Dorcopsulus vanheurni'
'Setonix brachyurus'
'Thylogale billardierii'
'Petrogale brachyotis'
'Bohra illuminata'
'Dendrolagus bennettianus'
'Dendrolagus matschiei'
'Protemnodon anak'
'Congruus congruus'
'Wallabia bicolor'
'Prionotemnus palankarinnicus'
'Kurrabi mahoneyi'
'Lagorchestes conspicillatus'
'Lagorchestes hirsutus'
'Baringa nelsonensis'
'Onychogalea unguifera'
'Macropus eugenii'
'Macropus fuliginosus'
'Macropus pavana'
'Macropus robustus'
'Ganawamaya acris'
'Ganawamaya aediculis'
'Ganawamaya couperi'
'Ganawamaya gillespieae'
;
ENDBLOCK;

BEGIN CHARACTERS;
DIMENSIONS NCHAR=120;
FORMAT DATATYPE=STANDARD MISSING=? GAP=- SYMBOLS="012345";
CHARLABELS
[1] 'Rostrum depth relative to posterior (neurocranial)portion of cranium'
[2] 'Marked cranial foreshortening (brachycephaly)'
[3] 'Level of basicranial plane relative to palatal plane'
[4] 'Splanchnocranium anteroventral deflection'
[5] 'Superficial masseter origin on jugal'
[6] 'Large ectoglenoid process'
[7] 'Postglenoid process'
[8] 'Neurocranium element contact'
[9] 'Ectotympanic proportions'
[10] 'Maximum occiput breadth relative to height'
[11] 'Foramen magnum size relative to occiput size'
[12] 'V-shaped squamosal inflation between occiput and posterior end of zygomatic arch'
[13] 'Relative anteroposterior length of upper incisors'
[14] 'I1 shape'
[15] 'I3 anterobuccal crest'
[16] 'I3 lingual surface'
[17] 'Number of cuspules/ridgelets on P3/p3 anterior to large posterior cusp'
```

[18] 'Deep cleft on main crest of P3 and p3 immediately posterior to anterior most cuspule'
[19] 'P3 lingual cingulum'
[20] 'P3 lateral constriction immediately anterior to posterolingual cusp'
[21] 'Upper cheek tooth row shape in transverse plane'
[22] 'Molar progression'
[23] 'Molar morphology'
[24] 'Preprotocrista development'
[25] 'Postprotocrista orientation'
[26] 'Postprotocrista development'
[27] 'Postprotocrista division'
[28] 'Postparacrista development'
[29] 'Postmetacrista/postmetaconulecrista development'
[30] 'Morphology of symphyseal plate of dentary'
[31] 'Buccinator sulcus on dentary'
[32] 'Anterior extent of masseteric canal'
[33] 'Insertion area for middle masseter muscle'
[34] 'Mandibular condyle shape'
[35] 'Position of i1 occlusal surface during incisor occlusion'
[36] 'i1 morphology'
[37] 'Enamel distribution on i1'
[38] 'p3 morphology'
[39] 'Buccal side of p3'
[40] 'Cheek tooth row shape in dorsoventral plane'
[41] 'Molar crown height index'
[42] 'Premetacristid development'
[43] 'Slight postmetacristid'
[44] 'Postprotocristid development'
[45] 'Cristid obliqua form'
[46] 'Paracristid and cristid obliqua division'
[47] 'Development of postentocristid and posthypocristid'
[48] 'Lophid enamel crenulations'
[49] 'Tuber calcanei posteromedial expansion'
[50] 'Relative length of talus articular region on calcaneus'
[51] 'Step of calcaneus–cuboid articulation'
[52] 'Ventromedian facet of cuboid articulation on calcaneus'
[53] 'Relative breadth of calcaneus–talus articulation'
[54] 'Distinctness of medial and lateral talar facetson calcaneus'
[55] 'Shape of lateral talar facet on calcaneus'
[56] 'Medial projection of sustentaculum tali of calcaneus beyond edge of medial talar facet'
[57] 'Shape of sustentaculum tali of calcaneus'
[58] 'Posterior extent of sustentaculum tali'
[59] 'Orientation of talar trochlear crests'
[60] 'Height of medial trochlear crest on talus relativeto lateral crest'
[61] 'Medial malleolar process/fossa on talus'
[62] 'Metatarsal IV length relative to calcaneus length'
[63] 'Metatarsal IV relative breadth'
[64] 'Metatarsal IV distal epiphysis breadth'
[65] 'Metatarsal V relative breadth'
[66] 'Metatarsal V plantar ridge'
[67] 'Relative length of fibular articular facet on tibia'
[68] 'Relative length of anterior tibial crest'
[69] 'Shape of anterior tibial crest'
[70] 'Length of tibia relative to that of femur'
[71] 'Development of greater trochanter crest of femur'

[72] 'Angle of ilium to ischium'
[73] 'Position of rectus femoris origin on ilium'
[74] 'Iliopubic process at junction of ilium and pubis'
[75] 'Relative length of ischium to ilium'
[76] 'Area of supraspinous fossa relative to infraspinousfossa of scapula'
[77] 'Scapula acromion shape'
[78] 'Displacement of acromion relative to glenoid fossa on scapula'
[79] 'Relative size of medial tuberosity to lateral tuberosity on humerus'
[80] 'Development of deltoid tuberosity vs. pectoralcrests on humerus'
[81] 'Relative width of trochlear notch posterior margin on ulna'
[82] 'Olecranon length/shape relative to length of ulna'
[83] 'Radius cross-section depth (mid-length) to width of the diaphysis, measured at the mid-length ofthe diaphysis from between the epiphyseal plates'
[84] 'Basioccipital and basisphenoid'
[85] 'Frontal region'
[86] 'Frontal sinuses'
[87] 'Postorbital constriction of skull'
[88] 'Masseteric process'
[89] 'Cheek region of skull'
[90] 'Alisphenoid contribution to paroccipital process'
[91] 'Mastoid process'
[92] 'Inflated alisphenoid forming auditory bulla'
[93] 'Digastric eminence'
[94] 'Mandibular canal'
[95] 'Posterior mental foramen'
[96] 'i1 occlusal surface'
[97] 'Presence of i2'
[98] p2
[99] C1
[100] p3
[101] 'p3/P3'
[102] 'm4 length'
[103] P3
[104] 'm1 protoconid'
[105] 'm1 protoconid'
[106] 'Trigonid basin on m1'
[107] 'm1 protostylid'
[108] 'hypocingulid on lower molars'
[109] 'M1 StC'
[110] 'M1 StD'
[111] 'M1 anterolingual cingulum'
[112] 'M1 neometaconule and postlink'
[113] 'Internal carotid foramen'
[114] 'Ventral margin of mandible'
[115] Postentocristid
[116] 'Height of p3/P3'
[117] 'Palatal vacuities'
[118] 'p3 main crest'
[119] 'p3 occlusal outline'
[120] Interparietal
;
STATELABELS
1
shallow

intermediate
deep,
2
absent
present,
3
'same plane or slightly higher'
'markedly higher',
4
marked
intermediate
minimal,
5
shallow
'deep, with distinct orbital rim',
6
absent
present,
7
absent
small
large,
8
'frontal-squamosal'
'parietal-alisphenoid',
9
small
'thick, wide, rugose, ventrally keeled',
10
'deeper than broad'
'broader than deep',
11
small
large,
12
absent
present,
13
'I2 and/or I3 not reduced relative to I1'
'I2 distinctly shorter than I1 and I3'
'I2 and I3 distinctly shorter than I1',
14
subcylindrical
'slightly broadened'
'markedly broadened',
15
'absent or very small, restricted to anterior end'
distinct,
16
'no anterolingual crest or lingual shelf'
'anterolingual crest present, no lingual shelf'
'anterolingual crest and small lingual shelf present',
17
'Transcristae absent'

'Less than 3'
Three
Four
'between 5 and 10'
'10 or more',
18
absent
present,
19
'absent or very low, fine'
'low, narrow to moderately broad, tapered anteriorly'
'broad, not raised into crest along lingual edge, with or without cuspules'
'broad, raised into low crest along lingual edge'
'raised into high crest along lingual edge',
20
absent
present,
21
straight
'bowed laterally',
22
absent
present,
23
Other
Bunodont
'Bunolophodont '
Lophodont
Bilophodont,
24
'strongly developed, confluent with precingulum'
'small but distinct'
absent,
25
'restricted to lingual side of tooth'
'extends into interloph valley near to tooth midline',
26
'short, thick'
'fine, low'
intermediate
'high, thick, strongly developed',
27
absent
'incipiently or completely divided into two components',
28
present
'absent or very fine and low',
29
'both distinct'
'postmetaconulecrista enlarged, postmetacrista absent or very weak',
30
'shallow, smooth or very slightly rugose'
'deep, rugose'
'deep, very rugose, and anteriorly expanded',

31
absent
'narrow, shallow'
'narrow, deep'
'broad, deep concavity',
32
'Masseteric canal not developped'
'to below anterior cheek teeth'
'to below posterior cheek teeth'
'posterior to m4 (near vertical)',
33
'small to moderately proportioned'
'broad and concave'
'large, terminates ventrally at distinct ridge',
34
'barrel shaped, not tapered medially'
'oval or circular'
'barrel shaped, tapered medially'
'Oval with anteromedial expansion',
35
'i1 rests on crowns of I2 and I3, and posteriorfacet of I1'
'i1 rests on palate, bordered by I2 and I3',
36
'procumbent, thin and elongate'
'procumbent blade with thick enamel flanges'
'slightly robust with thin enamel flanges'
'markedly upturned and robust',
37
'principally buccal side'
'buccal enamel layer extended to completely encircle crown '
'separate lingual enamel layer present',
38
'No transcristae'
Plagiaulacoid
Sectorial,
39
'lacks eminence, cingulid, or crest'
'bears posterobuccal eminence'
'bears welldeveloped buccal cingulid or crest',
40
Concave
'flat or very slightly convex'
'markedly convex dorsally',
41
'low (< 0.45)'
'intermediate (0.45-0.75)'
'high (> 0.75)',
42
'well developed, confluent with paracristid'
'moderately developed'
'weakly developed or absent',
43
present
absent,

44
distinct
'slight or absent',
45
'restricted to buccal side of tooth'
'straight or slightly curved, terminates near tooth midline low on posterior face of protolophid'
'distinctly kinked, terminates near tooth midline low on posterior face of protolophid',
46
absent
present,
47
'postentocristid distinct, meets large posthypocristid'
'both crests fine or absent'
'posthypocristid present, adjacent to distinct central groove',
48
absent
present,
49
absent
present,
50
'long (> 0.43)'
'intermediate (0.43–0.35)'
'short (< 0.35)',
51
incipient
'markedly stepped or slightly bevelled'
'slightly smoothed, oblique'
smoothed,
52
absent
'continuous with dorsolateralfacet'
'separate, distinct, well-developed'
'reduced, confluent with dorsomedial facet',
53
'intermediate (0.40-0.45)'
'narrow (< 0.40)'
'broad (> 0.45)',
54
'confluent, smoothly continuousanteriorly'
'continuous anteriorly, but facetcontours distinct'
'distinct, separate facets',
55
'untapered or marginally tapered medially'
'slightly or moderately tapered medially'
'markedly tapered medially',
56
'absent or very slight'
marked,
57
'straight (anteroventrally oriented) or veryslightly curved'
rounded
square,
58

'roughly in line with fibular facet'
intermediate
'significantly posteriorly placed from fibular facet',
59
'oblique (anterolaterally oriented)'
'anteroposteriorly oriented',
60
'subequal in height (trochleagroove shallow)'
'medial crest slightly higher'
'medial crest distinctly higher, with trochleargroove deep',
61
'fossa intermediate, no distinct process'
'fossa intermediate, process small, slightly mediallyextended'
'fossa broad/shallow, process largeand medially extended'
'fossa narrow/deep,process small, slightly medially extended',
62
'intermediate (1.5-2.4)'
'long (> 2.4) '
'short (< 1.5)',
63
'narrow (< 0.12)'
'intermediate (0.12-0.16)'
'broad (> 0.16)',
64
'narrow relative to ligament attachments'
'distinctly broad relative to shaft width, minimum development of ligament attachments',
65
'intermediate (0.07-0.13)'
'narrow (< 0.07)'
'wide (> 0.13)'
'highly to extremely reduced',
66
'small, posteriorly restricted'
absent
'elongate, well developed',
67
'short (< 0.62)'
'long (> 0.62)',
68
'intermediate (0.20-0.26)'
'long (> 0.26)'
'short (< 0.20)',
69
'stepped-in distally'
'not stepped distally, curves smoothly intodiaphysis',
70
'intermediate (1.10-1.45)'
'short (< 1.10)'
'long (> 1.45)',
71
'distally flared or intermediate'
'distally narrowed'

'distally flared and markedly broadened',
72
'slight angle'
'aligned in same plane'
'large angle',
73
'distinctly separate from acetabular rim'
intermediate
'adjacent to acetabular rim',
74
'very small, pointed'
'long, well-developed, square in outline'
'short, broad'
'very large',
75
'long (> 0.7)'
'short (< 0.7)',
76
'roughly equal'
'supraspinous fossa roughly half area'
'supraspinous fossa roughly one-third area'
'supraspinous fossa much smaller than infraspinous fossa',
77
'anterodorsally curved'
straight,
78
'caudal to the cranial margin ofthe glenoid fossa'
'cranially displaced',
79
'slightly smaller'
'distinctly smaller'
subequal,
80
'deltoid insertion poorly developed'
'intermediate, small deltoid tuberosity connected by oblique ridge'
'large deltoid tuberosity separated from pectoral crest by sulcus',
81
wide
narrow,
82
'long, deep'
intermediate
reduced,
83
'intermediate (1.3-1.5)'
'shallow (< 1.3)'
'deep (1.5-2.0)'
'very deep (> 2.0)',
84
coplanar
angled,
85
'Not flat'
Flat,
86

'Not markedly inflated'
'Markedly inflated',
87
Absent
'Slight constriction'
'Marked constriction',
88
'Not extending below alveolar margin'
'Extending below alveolar margin',
89
'Smooth transition of zygoma to cheek'
'With sulcus anterior to zygoma',
90
'Does not contribute'
'contribute to anterior face',
91
'Small (<paroccipital process)'
'Hypertrophied (>paroccipital process)',
92
Uninflated
'Lightly inflated'
'Highly inflated',
93
Undisctinct
Distinct,
94
'Single mandibular canal'
'Mandibular canal confluent with masseteric canal'
'Mandibular canal length reduced, foramina overlap'
'Mandibular canal lost, single mandibular foramen',
95
Present
Absent,
96
'Reaching to level of molar occlusal plane'
'Below molar occlusal plane',
97
Present
Absent,
98
'persists after p3 eruption'
'displaced by p3 eruption',
99
'Present and large'
'Present and small'
Absent,
100
'Buccally flexed'
'Aligned with molar row',
101
'Very short (P3L/M1 <1)'
'Short (P3L/M1 <1-1.299)'
'Medium (P3L/M1 1.3-1.599)'
'Long (P3L/M1 1.6-1.99)'

'Very long (P3L/M1 >2)',
102
'Smaller than m3'
'Subequal to m3'
'Larger than m3',
103
'Lacking posterolingual cusp or ridge'
'With posterolingual cusp or ridge',
104
Central
Buccal,
105
'Dominates trigonid'
'Subequal to metaconid',
106
'Not developed'
'Narrow transversely'
'Broad transversely',
107
Absent
'Present as enamel ridge'
'Present as cuspid',
108
'Hypocingulid present between low posthypocristid and entoconid'
'Hypocingulid present posterior to posthypocristid'
Absent,
109
Present
'Reduced to stylar crest'
Absent,
110
Present
'Reduced to stylar crest'
Absent,
111
Absent
Present,
112
Absent
Present,
113
'Anterior to basioccipital/basisphenoid suture'
'Close to or posterior to basioccipital/basisphenoid suture',
114
'Convex (anterior of mandible steeply inclined)'
'Straight (anterior of mandible shallowly inclined)',
115
absent
'Present and connects to posthypocristid'
'Present. connected to hypocingulid',
116
'Extends above the level of m1/M1'
'Levels with m1/M1',
117

Present
Absent,
118
'Straight '
Curved
'L-shaped',
119
'Short and wide'
'Short and narrow'
'Long and narrow'
'Long and wide',
120
absent
present,
;
MATRIX
'Galadi speciosus' 0000002101 00????0010 0000000000 0000???001 ?21110-0?? ??????????
?????????? ?????????? ???0001010 0100100001 0201000000 000000000?
'Trichosurus vulpecula' 0001001101 0000000000 0020000000 0000000000 0201000011
0020100000 0220220101 0000100002 0030002100 0100100110 0200001012 0000110001
'Pseudocheirus peregrinus' 0001001101 0000000110 0000000000 0000000000 0001100002
0020000000 0220220101 0000100002 0030001000 0100010011 0000002000 0000111001
'Burramys brutyi' ?????????? ??????4000 0010000000 000??00100 00010000?? ??????????
?????????? ?????????? ???????00? ??000000?0 2000000022 00?0100031
'Nambaroo tarrinyeri' ?????????? ??????4000 ??4001000? ???????10? 02110000??
?????????? ?????????? ?????????? ?????????? ?????????? 0110002(01)22 01??20?00?
'Nambaroo saltavus' ?????????? ??????40?? ??4??????? ???????10? 02010000??
?????????? ?????????? ?????????? ?????????? ?????????? 1??0102(01)?? ????(12)0?00?
'Wururoo dayamayi' ?????????? ??????30?? ?04??????0 11?????100 02111010??
?????????? ?????????? ?????????? ?????????? ??0?0??1?1 21?00111?? ???020?03?
'Balbaroo gregoriensis' ?????????? ?????????? ??4??????? ?????????? 02111010??
?????????? ?????????? ?????????? ?????????? ?????????? ???00101?? ????2?????
'Balbaroo fangaroo' 0001001000 0000004000 0041110000 1100?10201 01111010?? ??????????
?????????? ?????????? ???0011000 1001000101 211011(01)112 0110210130
'Balbaroo camfieldensis' ?????????? ?????????? ?04??????? 110??????1 02111010??
?????????? ?????????? ?????????? ?????????? ??011????? ?1?11101?? ???12?????
'Balbaroo nalima' 0001002000 0000??4000 0041110000 1200?10201 0(01)11101001
22220000?? ?????????? 0????????? 0??0011000 1001001101 211112(012)112 0111210130
'Hypsiprymnodon moschatus' 0000000000 0000004000 0010000000 0100000101 0201000000
0000000000 0000000000 0000000000 0000100000 0101100110 2000002022 0000100031
'Hypsiprymnodon bartholomaii' 0000000100 00????4000 001000000? ???????1?? 0?????????
?????????? ?????????? ?????????? ???????000 01???????0 300?????22 001?100030
'Hypsiprymnodon philcreaseri' ?????????? ??????4000 0010000000 010??00101 02010000??
?????????? ?????????? ?????????? ???????00? ??011001?0 3000002022 00?010?03?
'Ekaltadeta ima' 0000001000 00????4000 0020000000 010?000101 01010000?? ??????????
?????????? ?????????? ???001200? 1001100?0 3000002022 0010100030
'Ekaltadeta jamiemulvaneyi' ?????????? ??????40?? ?02??????? 01?????101 01010000??
?????????? ?????????? ?????????? ?????????? ??0?1??0?0 3??00020?? ???010?03?
'Jackmahoneya toxoniensis' ?????????? ??????4000 ?020100000 0100???101 01010000??
?????????? ?????????? ?????????? ?????????? ??0?10?1?0 3000002002 10?010?03?
'Propleopus oscillans' ?????????? ??????4000 0020000000 01???00101 01010000??
?????????? ?????????? ?????????? ???????01? ??0?100110 2000002022 10?010?03?
'Bettongia moyesi' 10010001?? ??10005000 1010000000 0?0?000200 00000000?? ??????????
?????????? ?????????? ????10100? ????100111 4001120002 10??110021

'Bettongia penicillata' 1001001000 0010005000 1010000000 0100000200 0000000001 1101000000 0000110200 0001110000 0030100000 0203101111 3001120022 1010110021
'Aepyprymnus rufescens' 1001002000 0010004000 1020000000 1100000200 0000000001 1121000001 1100110200 0001120000 0030110001 1103101111 3001120022 0010111021
'Potorous tridactylus' 0001000000 0010004100 1010000000 0100010200 0000000001 1101000000 0010010200 0001100001 0030100000 0101101111 2001120022 0010110121
'Purtia mosaicus' ?????????? ??????50?? ?03??????0 0??????200 00000000?? ?????????? ?????????? ?????????? ?????????? ?????0?1?1 3??11200?? ???011?02?
'Wakiewakie lawsoni' ?????????? ??????50?? ?02??????? 010????200 00000000?? ?????????? ?????????? ?????????? ?????????? ??010??1?1 40?11200?? ???011?02?
'Ngamaroo archeri' ?????????? ??????50?? ?03??????0 010????200 0100000000 21?10001?? ?010??0000 ????????00 0????????? ??011??1?1 3??11200?? ???011?12?
'Lagostrophus fasciatus' 0000002100 0000002010 1040120001 3311001201 1201101001 1101002101 0010021200 1001110001 001?100111 0203111121 1111120222 1110010211
'Tjukuru wellsi' ?????????? ??????10?? ?04??????1 32??????01 12111010?? ?????????? ?????????? ?????????? ?????????? ??0?0??1?1 11?11202?? ???001?21?
'Troposodon minor' ?????????? ???0?02010 0040120001 3211001201 12112010?? ?????????? ?????????? ?????????? ???????11? ??03111?1 1111120122 11?001?21?
'Gumardee pascuali' ?????????? ??????5011 103011000? 11?????200 0???0000?? ?????????? ?????????? ?????????? ?????????? ??0?0??1?1 301112?002 11?011012?
'Bulungamaya delicata' ?????????? ??????4000 0030110000 1201?00201 01000000?? ?????????? ?????????? ?????????? ???????00? ??010001?1 2101120002 11?011?13?
'Ganguroo bilamina' 0001001100 0000004010 0041110000 1201000201 01111010?? ?????????? ?????????? ?????????? ???1101000 1111010111 2111120201 1111010131
'Ganguroo bites' ?????????? ??????40?? ?04??????0 1201???201 01111010?? ?????????? ?????????? ?????????? ?????????? ??010??1?1 3??11202?? ???001?12?
'Ganguroo robustiter' 0001001100 0000004010 0041110000 1201000201 01111010?? ?????????? ?????????0 ??0??11010 02?1100000 110101?111 3111120201 1111010131
'Wabularoo naughtoni' ?????????? ??????4000 004111(01)000 2??????201 01111010?? ?????????? ?????????? ?????????? ?????????? ??1?0??1?1 2??1120202 11?101?13?
'Wabularoo prideauxi' ?????????? ??????4020 004111(01)000 220????201 01111010?? ?????????? ?????????? ?????????? ?????????? ??010??1?1 211112020? 11?101?13?
'Wanburoo hilarus' ?????????? ??00014020 0042110000 2201?10211 01111010?? ?????????? ?????????? ?????????? ????????0? ??0201?111 2111120212 11?101013?
'Hadronomas puckridgi' 2002012111 0010014020 0042110000 2201012221 0111101001 1201000111 101102001? ?013?210?? 12?101000? ?012111?1 1111120211 1011010131
'Sthenurus andersoni' 2002012111 0012013040 1042110002 2302032221 1211111101 1201002212 0011310212 2013???112 1221000111 0003001121 2111120222 1010010131
'Simosthenurus occidentalis' 2112012111 0010013040 1042111002 2302032221 1211111101 1221002212 0011310012 2213031112 122100111? 0003001121 2111120222 1010010131
'Procoptodon goliah' 2112012111 0010013040 1042111002 2302032221 1211110101 1201002212 0011310012 2213031?2 1221012111 0003001121 0211120222 1110110101
'Dorcopsoides fossilis' 0000001100 00?110(34)001 0042110000 110?112201 1211101001 1201110101 101002?002 01011????0 010????0?? 1?0?1??1?1 2111120101 10?101012?
'Dorcopsis veterum' 0000001100 0001103001 0042110000 1101100201 1111101001 1202110001 1010020000 0011121010 0101001111 0003111111 4211120212 1011010121
'Dorcopsulus vanheurni' 0000001100 100110(34)001 0042110000 1101100201 11111010?? ???21???01 1?????0000 0111121010 0101101111 0002111111 2211120222 1011010121
'Setonix brachyurus' 0000002100 0002103010 1042120000 1201110201 1211101001 1202100001 1210000000 0102121000 0111001111 0213111121 3111120222 1011010121
'Thylogale billardierii' 0000002100 0002102010 1042120000 1301110201 1211101001 1202100000 1010000000 0101111011 0111101111 0001111121 1111120222 1011010021
'Petrogale brachyotis' 0000002101 1102122010 1042120000 1301120201 1211101001 2202100001 1010000000 0101021011 0101101111 0103(01)11121 1?11120222 1011010021

'Bohra illuminata' 1000002101 1101122010 1042110000 1301120211 1211101010 3322100001 201020000? ?112??10?1 0??1101111 00021??121 2111120222 101?01113?
'Dendrolagus bennettianus' 1000002101 1101121120 1042110000 1201120211 0211101010 3322210000 2220200101 0122021020 0110100111 0002(01)11111 3111120222 1011011131
'Dendrolagus matschiei' 1000002101 1101122120 1042110000 1201120211 0211101010 3322200000 2220201101 0122021021 0110011111 0002111111 3111120222 1010011131
'Protemnodon anak' 1000002101 100210(23)030 1042120000 1301110201 2211101001 1222000201 2211200102 1002121012 0111?01111 0?0?111121 3211120122 101101002?
'Congruus congruus' 1000002101 1002102030 104212000? ?????????? 2????????? ?????????? ?????????? ?????????? ???0101011 00??????21 121?????22 101??11?1?
'Wallabia bicolor' 0000002100 0002102030 1042120000 1303110201 2211101002 1212001201 3010020002 1101121012 0121101111 0003111121 1211120222 1011010021
'Prionotemnus palankarinnicus' ????0????? ???2102010 1042130100 130?110?01 12111010?? ?????????? ?????????? ?????????? ????????1? ??021??1?1 1111120122 10?101001?
'Kurrabi mahoneyi' ?????????? ??????2010 1042130110 130??10?01 22111010?? ?????????? ?????????? ?????????? ???????11? ??0?1111?1 3211120222 10?101?12?
'Lagorchestes conspicillatus' 0000002100 0002102010 1042120000 1301110201 2211101002 1212001001 -100121200 1101121011 0021001111 0202(01)11111 1111120222 1011010101
'Lagorchestes hirsutus' 0000002100 0002102010 1042120000 1301110201 2211101001 1212001001 3100121200 1101121001 0021001111 0202(01)11111 1111120222 1011010101
'Baringa nelsonensis' ?0??1????? ???22??2000 1042130110 132?110?02 22111010?? ?????????? ?????????? ?????????? ?????????? ??0?1111?1 0??1120212 10?101?01?
'Onychogalea unguifera' 0000102100 0022101000 1042130000 1323100202 2211201002 1212001201 3000121202 1001111011 0021101111 0203111111 0211120222 1011010011
'Macropus eugenii' 0000002100 0002101010 1042130110 1301110202 2211201001 1212000101 3000020002 1001111011 0021001111 0103111121 0211120222 1011010011
'Macropus fuliginosus' 0000002100 0002101000 1141130110 1301110202 2211202002 1212000201 1000121202 1001111011 0121001111 0103111121 0211120222 1011011011
'Macropus pavana' ?????????? ??????1000 1141130110 130??????2 22112020?? ?????????? ?????????? ?????????? ?????????? ??0?1??1?? 0211120222 10??01?011
'Macropus robustus' 0000002100 0002101010 1142130110 1301110202 2211202002 1212000201 3010121202 1101111111 0121001111 0103111121 0211120222 1011011011
'Ganawamaya acris' ??0?001000 00????(23)010 0041110000 110??10201 02111010?? ?????????? ?????????? ?????????? ??????2000 100100?1?0 111000(02)122 10?0210100
'Ganawamaya aediculis' ?????????? ???0??4010 0041110000 11?????201 02111010?? ?????????? ?????????? ?????????? ????????0? ??010??100 111000(02)102 00?021010?
'Ganawamaya couperi' ?????????? ??????30?? ?04??????0 1101???201 02111000?? ?????????? ?????????? ?????????? ?????????? ??010??1?0 11?000(02)(01)?? ???021?10?
'Ganawamaya gillespieae' 0001001000 00????(34)010 0041110000 1101?10201 0211101001 2222010000 002000??1? 000110000? 0??0012000 1001000100 111000(02)102 0010210100
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OPTIONS DEFTYPE=UNORD POLYTCOUNT=MINSTEPS;
ENDBLOCK;

BEGIN NOTES;
[Taxon comments]

[Character comments]

[Character state comments]

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[Attribute comments]

[Taxon pictures]

[Character pictures]

[Character state pictures]

[Attribute pictures]
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BEGIN PAUP;

Outgroup 'Galadi speciosus' 'Trichosurus vulpecula' 'Pseudocheirus peregrinus' 'Burramys brutyi';
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set root=outgroup outroot=monophyl criterion=parsimony;

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TYPESET *mytypes = IRREV.UP: 23 38 116;


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APPENDIX 2.

Univariate statistics for teeth of *Ganawamaya aediculis*. Rounded to one decimal place. Measurements are in mm. Abbreviations: N, number of specimens; Min, minimum measurement; Max, maximum measurement; L, tooth length; AW, anterior width; PW, posterior width; P, upper premolar; p, lower premolar; M, upper molar; m, lower molar.

	N	Min	Max	Mean	SE	VA	SD	CV
p3L	10	5.9	6.6	6.1	0.1	0.1	0.2	3.7
p3W	10	2.6	4.5	3.6	0.2	0.3	0.5	14.2
m1L	8	5.3	6.3	5.8	0.1	0.1	0.3	5.4
m1AW	8	3.1	3.8	3.4	0.1	0.0	0.2	6.2
m1PW	8	3.7	4.2	3.9	0.1	0.0	0.2	4.2
m2L	6	5.6	6.7	6.2	0.2	0.2	0.4	6.8
m2AW	6	3.8	4.4	4.2	0.1	0.1	0.2	5.8
m2PW	6	3.9	4.8	4.3	0.1	0.1	0.3	7.0
m3L	9	5.8	6.9	6.3	0.1	0.1	0.4	5.9
m3AW	9	4.0	4.8	4.4	0.1	0.1	0.3	5.8
m3PW	9	4.0	4.8	4.3	0.1	0.1	0.3	6.9
m4L	7	6.4	7.3	6.9	0.1	0.1	0.3	4.9
m4AW	9	3.8	4.8	4.3	0.1	0.1	0.4	8.4
m4PW	7	3.8	4.4	4.0	0.1	0.0	0.2	5.2
P3L	3	6.8	6.9	6.8	0.0	0.0	0.0	0.1
P3W	3	4.0	4.6	4.3	0.2	0.1	0.3	6.5
M1L	4	5.5	6.7	5.8	0.3	0.3	0.6	9.9
M1AW	4	5.0	5.6	5.3	0.1	0.1	0.3	4.8
M1PW	4	4.5	4.8	4.6	0.1	0.0	0.1	3.2
M2L	4	5.9	6.9	6.3	0.2	0.2	0.4	7.0
M2AW	4	4.9	5.8	5.4	0.2	0.2	0.4	7.7
M2PW	4	4.3	4.9	4.6	0.1	0.1	0.3	5.9
M3L	2	6.1	6.7	6.4	0.3	0.2	0.4	6.5
M3AW	2	4.8	5.9	5.3	0.6	0.6	0.8	14.7
M3PW	2	4.3	4.6	4.4	0.2	0.1	0.3	6.2
M4L	2	6.4	6.6	6.5	0.1	0.0	0.2	2.9
M4AW	2	4.7	4.9	4.8	0.1	0.0	0.2	3.2
M4PW	2	3.4	4.0	3.7	0.3	0.2	0.4	11.4

APPENDIX 3.

Univariate statistics for teeth of *Ganawamaya gillespieae* comb. nov. Rounded to one decimal place. Measurements are in mm. Abbreviations are the same as Appendix 2.

	N	Min	Max	Mean	SE	VA	SD	CV
p3L	3	6.6	6.8	6.7	0.1	0.0	0.1	2.1
p3W	3	3.6	4.1	3.9	0.1	0.1	0.2	6.3
m1L	4	5.5	6.3	6.0	0.2	0.1	0.4	6.1
m1AW	4	3.1	3.9	3.4	0.2	0.1	0.3	9.2
m1PW	4	4.0	4.3	4.2	0.1	0.0	0.2	3.9
m2L	4	6.3	6.6	6.4	0.1	0.0	0.1	2.1
m2AW	4	4.1	4.6	4.3	0.1	0.0	0.2	5.1
m2PW	5	4.4	4.5	4.5	0.0	0.0	0.1	1.1
m3L	5	6.2	7.4	6.7	0.2	0.2	0.5	6.8
m3AW	5	4.7	5.1	4.8	0.1	0.0	0.2	4.5
m3PW	5	4.4	4.7	4.6	0.1	0.0	0.1	2.7
m4L	3	6.4	7.4	6.8	0.3	0.3	0.5	7.9
m4AW	3	4.4	4.8	4.6	0.1	0.1	0.2	4.9
m4PW	3	3.9	4.4	4.1	0.1	0.1	0.2	5.7
P3L	3	6.7	6.9	6.8	0.0	0.0	0.1	1.1
P3W	3	4.2	4.3	4.3	0.0	0.0	0.1	1.2
M1L	5	5.9	6.4	6.2	0.1	0.0	0.2	3.4
M1AW	5	5.2	6.1	5.5	0.2	0.1	0.4	6.4
M1PW	5	4.5	5.2	4.9	0.1	0.1	0.3	6.3
M2L	6	6.2	7.0	6.7	0.1	0.1	0.3	4.4
M2AW	6	5.7	5.8	5.7	0.0	0.0	0.0	0.8
M2PW	6	4.7	5.1	4.8	0.1	0.0	0.2	3.5
M3L	5	6.8	7.6	7.0	0.1	0.1	0.3	4.7
M3AW	5	5.6	6.2	5.8	0.1	0.1	0.2	4.2
M3PW	5	4.6	5.1	4.8	0.1	0.0	0.2	3.9
M4L	4	6.5	7.0	6.8	0.1	0.1	0.2	3.5
M4AW	4	5.1	5.7	5.4	0.1	0.1	0.3	5.2
M4PW	4	4.1	4.3	4.2	0.1	0.0	0.1	3.0

APPENDIX 4.

Univariate statistics for teeth of *Ganawamaya acris*. Rounded to one decimal place. Measurements are in mm. Abbreviations are the same as Appendix 2.

	N	Min	Max	Mean	SE	VA	SE	CV
p3L	20	5.7	7.3	6.5	0.1	0.2	0.5	7.0
p3W	16	2.9	4.4	3.8	0.1	0.1	0.4	9.8
m1L	22	5.0	7.0	6.2	0.1	0.2	0.5	7.6
m1AW	21	2.9	4.0	3.5	0.1	0.1	0.3	7.4
m1PW	21	3.8	4.7	4.2	0.1	0.1	0.2	5.8
m2L	19	6.0	7.6	6.6	0.1	0.2	0.5	7.4
m2AW	19	4.0	5.1	4.4	0.1	0.1	0.2	5.5
m2PW	19	4.2	5.2	4.7	0.1	0.1	0.3	5.5
m3L	21	6.6	7.9	7.1	0.1	0.1	0.4	5.1
m3AW	21	4.5	5.4	4.8	0.1	0.1	0.2	4.8
m3PW	21	4.5	5.2	4.8	0.0	0.0	0.2	4.5
m4L	12	6.7	7.7	7.1	0.1	0.1	0.3	4.4
m4AW	12	4.5	5.0	4.7	0.0	0.0	0.2	3.5
m4PW	11	4.0	4.6	4.3	0.1	0.0	0.2	4.4
P3L	14	6.7	8.0	7.3	0.1	0.1	0.4	5.3
P3W	14	4.1	5.6	4.7	0.1	0.2	0.4	8.8
M1L	23	5.9	7.4	6.6	0.1	0.1	0.4	5.5
M1AW	22	5.2	6.1	5.7	0.0	0.0	0.2	3.9
M1PW	23	4.8	5.6	5.2	0.1	0.1	0.2	4.6
M2L	30	6.0	7.5	6.9	0.1	0.1	0.4	5.4
M2AW	28	5.5	7.0	6.2	0.1	0.1	0.3	5.0
M2PW	30	4.8	5.7	5.3	0.0	0.1	0.2	4.5
M3L	27	5.7	8.1	7.3	0.1	0.3	0.5	6.9
M3AW	25	5.5	6.7	6.1	0.1	0.1	0.3	5.6
M3PW	25	4.6	5.9	5.3	0.1	0.1	0.3	6.6
M4L	20	5.9	8.6	7.2	0.1	0.4	0.6	8.9
M4AW	20	5.2	6.1	5.6	0.1	0.1	0.3	5.1
M4PW	18	3.7	4.8	4.3	0.1	0.1	0.3	7.6

APPENDIX 5.

Results of Kruskal-Wallis test comparing each of the four *Ganawamaya* species for each dental measurement. Bold indicates statistical significance. H = test statistic for Kruskal-Wallis test.

Measurement	P value	H (X^2)
p3L	**1.87×10^{-03}**	14.92
p3W	**0.03**	8.60
m1L	**7.79×10^{-03}**	11.83
m1AW	0.05	7.76
m1PW	**5.73×10^{-04}**	17.43
m2L	0.06	7.24
m2AW	0.09	6.24
m2PW	**0.01**	10.28
m3L	**8.74×10^{-05}**	21.38
m3AW	**1.63×10^{-04}**	20.06
m3PW	**2.18×10^{-04}**	19.47
m4L	0.32	2.27
m4AW	**0.03**	3.89
m4PW	0.31	2.35
P3L	**0.03**	8.62
P3W	**0.04**	8.22
M1L	**5.19×10^{-03}**	12.74
M1AW	0.01	10.55
M1PW	**4.62×10^{-03}**	17.88
M2L	**0.02**	9.77
M2AW	**2.65×10^{-04}**	19.06
M2PW	**4.02×10^{-05}**	23
M3L	**0.04**	6.33
M3AW	0.07	5.29
M3PW	**3.78×10^{-03}**	11.15
M4L	0.09	4.78
M4AW	0.05	5.89
M4PW	0.07	5.31

APPENDIX 6.

Results of Mann-Whitney U tests for each molar comparing measurements for each species. Rounded to two decimal places. P values lower than 0.01 are listed as '<0.01'. Bold numbers represent species which differ significantly ($p < 0.05$).

	G. acris	***G. gillespieae* comb. nov.**	***G. aediculis***	***G. couperi* comb. nov.**
p3 length				
G. acris		0.32	**0.02**	**0.01**
G. gillespieae comb. nov.	0.32		**0.01**	0.08
G. aediculis	**0.02**	0.01		**0.01**
G. couperi comb. nov.	**0.01**	0.08	**0.01**	
p3 width				
G. acris		0.61	0.13	**0.02**
G. gillespieae comb. nov.	0.61		0.15	0.08
G. aediculis	0.13	0.15		**0.08**
G. couperi comb. nov.	**0.02**	0.08	**0.08**	
m1 length				
G. acris		0.59	**0.03**	**0.01**
G. gillespieae comb. nov.	0.59		0.27	0.05
G. aediculis	**0.03**	0.27		**0.02**
G. couperi comb. nov.	**0.01**	0.05	**0.02**	
m1 anterior width				
G. acris		0.60	0.18	**0.02**
G. gillespieae comb. nov.	0.60		0.93	0.11
G. aediculis	0.18	0.93		**0.03**
G. couperi comb. nov.	**0.02**	0.11	**0.03**	
m1 posterior width				
G. acris		0.88	**<0.01**	**0.01**
G. gillespieae comb. nov.	0.88		**0.02**	0.05
G. aediculis	**<0.01**	**0.02**		**0.02**
G. couperi comb. nov.	**0.01**	0.05	**0.02**	
m2 length				
G. acris		0.68	0.17	**0.03**
G. gillespieae comb. nov.	0.68		0.52	0.11
G. aediculis	0.17	0.52		0.07
G. couperi comb. nov.	**0.03**	0.11	0.07	
m2 anterior width				
G. acris		0.66	0.32	**0.03**
G. gillespieae comb. nov.	0.66		0.83	0.11
G. aediculis	0.32	0.83		0.07
G. couperi comb. nov.	**0.03**	0.11	0.07	
m2 posterior width				
G. acris		0.17	0.04	0.03
G. gillespieae comb. nov.	**0.17**		0.41	0.08
G. aediculis	**0.04**	0.41		0.13
G. couperi comb. nov.	**0.03**	0.08	0.13	

	G. acris	***G. gillespieae* comb. nov.**	***G. aediculis***	***G. couperi* comb. nov.**
m3 length				
G. acris		0.07	**<0.01**	**0.01**
G. gillespieae comb. nov.	0.07		0.35	**0.04**
G. aediculis	**<0.01**	0.35		**0.02**
G. couperi comb. nov.	**0.01**	**0.04**	**0.02**	
m3 anterior width				
G. acris		0.28	**<0.01**	**0.01**
G. gillespieae comb. nov.	0.28		**0.02**	**0.03**
G. aediculis	**<0.01**	**0.02**		**0.02**
G. couperi comb. nov.	**0.01**	**0.03**	**0.02**	
m3 posterior width				
G. acris		0.05	**<0.01**	**0.01**
G. gillespieae comb. nov.	0.05		0.14	**0.04**
G. aediculis	**<0.01**	0.14		**0.04**
G. couperi comb. nov.	**0.01**	**0.04**	**0.04**	
m4 length				
G. acris		0.28	0.25	
G. gillespieae comb. nov.	0.28		0.65	
G. aediculis	0.25	0.65		
m4 anterior width				
G. acris		0.39	**0.01**	
G. gillespieae comb. nov.	0.39		0.20	
G. aediculis	**0.01**	0.20		
m4 posterior width				
G. acris		0.19	0.25	
G. gillespieae comb. nov.	0.19		0.93	
G. aediculis	0.25	0.93		
P3 length				
G. acris		0.13	0.15	**0.03**
G. gillespieae comb. nov.	0.13		0.82	0.15
G. aediculis	0.15	0.82		0.15
G. couperi comb. nov.	**0.03**	**0.15**	**0.15**	
P3 width				
G. acris		0.17	0.17	**0.03**
G. gillespieae comb. nov.	0.17		0.82	0.15
G. aediculis	0.17	0.82		0.15
G. couperi comb. nov.	**0.03**	0.15	0.15	
M1 length				
G. acris		0.05	**0.02**	**0.02**
G. gillespieae comb. nov.	0.05		0.27	0.08
G. aediculis	**0.02**	0.27		0.11
G. couperi comb. nov.	**0.02**	0.08	0.11	
M1 anterior width				
G. acris		0.18	**0.03**	**0.02**

	G. acris	***G. gillespieae* comb. nov.**	***G. aediculis***	***G. couperi* comb. nov.**
G. gillespieae comb. nov.	0.18		0.90	0.08
G. aediculis	**0.03**	0.90		0.11
G. couperi comb. nov.	**0.02**	0.08	0.11	
M1 posterior width				
G. acris		**0.01**	**<0.01**	**0.02**
G. gillespieae comb. nov.	**0.01**		0.27	0.08
G. aediculis	**<0.01**	0.27		0.11
G. couperi comb. nov.	**0.02**	0.08	0.11	
M2 length				
G. acris		0.64	**0.04**	**0.02**
G. gillespieae comb. nov.	0.64		0.17	0.07
G. aediculis	**0.04**	0.17		0.11
G. couperi comb. nov.	**0.02**	0.07	0.11	
M2 anterior width				
G. acris		**<0.01**	**<0.01**	**0.02**
G. gillespieae comb. nov.	**<0.01**		0.24	0.07
G. aediculis	**<0.01**	0.24		0.11
G. couperi comb. nov.	**0.02**	0.07	0.11	
M2 posterior width				
G. acris		**<0.01**	**<0.01**	**0.02**
G. gillespieae comb. nov.	**<0.01**		0.11	0.07
G. aediculis	**<0.01**	0.11		0.10
G. couperi comb. nov.	**0.02**	0.07	0.10	
M3 length				
G. acris		0.12	0.05	
G. gillespieae	0.12		0.08	
G. aediculis	0.05	0.08		
M3 anterior width				
G. acris		0.11	0.09	
G. gillespieae comb. nov.	0.11		0.56	
G. aediculis	0.09	0.56		
M3 posterior width				
G. acris		**0.01**	**0.03**	
G. gillespieae comb. nov.	**0.01**		0.18	
G. aediculis	**0.03**	0.18		
M4 length				
G. acris		0.10	0.15	
G. gillespieae comb. nov.	0.10		0.25	
G. aediculis	0.15	0.25		
M4 anterior width				
G. acris		0.44	0.03	
G. gillespieae comb. nov.	0.44		0.11	
G. aediculis	0.03	0.11		
M4 posterior width				
G. acris		0.20	0.07	

	G. acris	***G. gillespieae* comb. nov.**	***G. aediculis***	***G. couperi* comb. nov.**
G. gillespieae comb. nov.	0.20		0.11	
G. aediculis	0.07	0.11		

APPENDIX 7.

Summary statistics of principal component analysis of lower tooth measurements for *Ganawamaya acris*, *G. aediculis*, *G. gillespieae* comb. nov. and *G. couperi* comb. nov. (rounded to one decimal place).

PC	Eigen value	% variance		Loadings													
				PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9	PC 10	PC 11	PC 12	PC 13	PC 14
1	1.0	62.7	p3L	0.3	0.7	0.0	0.1	0.0	-0.6	0.0	-0.2	0.0	-0.1	0.0	0.0	-0.2	0.0
2	0.2	10.0	p3W	0.2	0.5	0.2	-0.1	0.3	0.6	-0.3	0.2	-0.1	0.0	0.1	0.1	0.0	-0.1
3	0.1	6.5	m1L	0.3	0.0	0.1	-0.5	-0.8	0.1	-0.2	0.1	0.0	-0.1	0.1	0.1	-0.1	0.0
4	0.1	6.2	m1AW	0.1	0.1	0.1	-0.1	0.1	0.2	0.8	-0.1	-0.4	0.0	0.0	0.3	-0.2	0.2
5	0.1	4.8	m1PW	0.2	0.2	0.1	-0.2	0.0	0.1	0.3	0.0	0.3	0.3	-0.3	-0.5	0.4	-0.1
6	0.0	2.7	m2L	0.3	-0.4	0.4	-0.2	0.3	-0.2	-0.3	-0.1	-0.4	0.4	-0.1	-0.1	-0.2	-0.0
7	0.0	1.7	m2AW	0.2	-0.2	0.2	-0.1	0.2	-0.2	0.1	0.0	0.0	-0.5	0.3	0.2	0.4	-0.5
8	0.0	1.5	m2PW	0.2	-0.2	0.1	-0.1	0.3	-0.1	0.0	0.2	0.6	-0.3	-0.2	0.2	-0.2	0.4
9	0.0	1.0	m3L	0.5	-0.1	-0.4	0.3	0.0	0.2	-0.1	-0.3	-0.2	-0.3	-0.4	0.0	0.1	-0.0
10	0.0	0.8	m3AW	0.3	-0.1	-0.2	0.1	0.1	0.0	0.1	0.2	-0.1	0.0	0.6	-0.4	0.1	0.5
11	0.0	0.7	m3PW	0.3	0.0	-0.3	0.1	0.1	0.0	0.1	0.1	0.3	0.5	0.2	0.3	-0.2	-0.4
12	0.0	0.6	m4L	0.1	-0.1	0.5	0.5	-0.2	0.2	0.1	-0.4	0.3	0.0	0.2	-0.2	-0.2	-0.1
13	0.01	0.4	m4AW	0.1	-0.0	0.2	0.4	-0.2	-0.2	0.2	0.7	-0.2	-0.1	-0.2	-0.1	-0.1	-0.1
14	0.00	0.3	m4PW	0.1	0.0	0.2	0.29	-0.1	-0.1	-0.1	0.0	0.0	0.3	0.0	0.5	0.6	0.3

APPENDIX 8.

Summary statistics of principal component analysis of upper tooth measurements for *Ganawamaya acris*, *G. aediculis* and *G. gillespieae* comb. nov. (rounded to two decimal places).

				Loadings													
PC	**Eigen value**	**% variance**		**PC 1**	**PC 2**	**PC 3**	**PC 4**	**PC 5**	**PC 6**	**PC 7**	**PC 8**	**PC 9**	**PC 10**	**PC 11**	**PC 12**	**PC 13**	**PC 14**
1	1.8	63.8	P3L	0.3	-0.3	0.2	0.1	-0.1	-0.5	-0.1	0.3	0.1	-0.2	0.3	0.3	0.1	-0.4
2	0.5	17.7	P3W	0.2	-0.1	0.3	0.2	0.0	-0.3	-0.4	0.0	0.3	0.3	-0.3	-0.2	0.0	0.4
3	0.1	4.8	M1L	0.3	-0.3	0.3	0.1	-0.3	0.5	-0.2	-0.5	-0.1	-0.1	0.0	0.0	0.0	-0.2
4	0.1	3.7	M1AW	0.3	-0.3	0.1	0.0	0.1	0.0	0.5	0.0	-0.3	0.6	0.2	-0.3	-0.1	-0.0
5	0.1	2.6	M1PW	0.3	-0.3	0.1	0.0	0.1	0.3	0.3	0.3	0.0	-0.6	-0.2	0.0	-0.2	0.4
6	0.1	1.9	M2L	0.4	0.0	-0.4	-0.4	-0.5	0.0	0.1	0.0	0.5	0.1	0.1	-0.1	0.0	0.1
7	0.0	1.2	M2AW	0.4	0.0	-0.4	-0.1	0.3	-0.3	-0.1	-0.4	-0.2	-0.2	-0.3	0.0	-0.3	-0.2
8	0.0	1.1	M2PW	0.3	-0.1	-0.3	0.0	0.3	0.3	-0.3	0.3	-0.2	0.2	0.1	0.2	0.5	0.2
9	0.0	1.0	M3L	0.3	0.4	-0.1	0.5	-0.5	-0.1	0.2	0.1	-0.4	0.0	-0.2	0.0	0.1	0.1
10	0.0	0.7	M3AW	0.2	0.3	0.0	0.3	0.2	0.0	-0.1	-0.2	0.1	-0.2	0.7	-0.4	0.0	0.2
11	0.0	0.6	M3PW	0.2	0.3	0.0	0.2	0.2	0.4	-0.1	0.4	0.3	0.2	-0.1	0.0	-0.5	-0.4
12	0.0	0.4	M4L	0.2	0.4	0.4	-0.6	0.0	0.0	-0.2	0.1	-0.3	-0.1	0.0	-0.1	0.0	0.0
13	0.01	0.3	M4AW	0.2	0.3	0.2	-0.0	0.24	-0.0	0.4	-0.2	0.4	-0.1	-0.4	-0.1	0.5	-0.3
14	0.01	0.3	M4PW	0.2	0.2	0.1	0.0	0.11	-0.0	0.2	-0.3	0.1	0.2	0.2	0.7	-0.2	0.3