

A NEW SPECIES OF *NAMBAROO* (MARSUPIALIA; MACROPODOIDEA) FROM THE MIOCENE CAMFIELD BEDS OF NORTHERN AUSTRALIA WITH OBSERVATIONS ON THE PHYLOGENY OF THE BALBARINAE

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ABSTRACT—*Nambaroo bullockensis* sp. nov. is a structurally primitive macropodoid from the Bullock Creek Local Fauna of the Camfield Beds of the Northern Territory, Australia. This species extends the range of *Nambaroo* from the late Oligocene or early Miocene up to the middle Miocene. Despite its young age, *N. bullockensis* retains many features thought to be plesiomorphic for macropodoids. Cladistic analysis based on characters of m1 for this new species and all other balbarines shows *Nambaroo* to be paraphyletic, but supports the monophyly of *Ganawamaya* and *Balbaroo*.

INTRODUCTION

Bullock Creek in the Northern Territory of Australia is one of only a few Australian localities producing Miocene fossil vertebrates (e.g., Rich, 1991; Woodburne et al., 1985). The Bullock Creek Local Fauna (LF), from freshwater limestone facies of the Camfield Beds (Randal and Brown, 1967; Plane and Gatehouse, 1968; Murray and Megirian, 1992), is a diverse assemblage of invertebrates, fish, amphibians, reptiles, birds, and mammals. A general account of the fauna and its occurrence may be found in Murray and Megirian (1992), with more recent studies by Tyler (1994), Hand et al. (1998), Murray and Megirian (2000), Megirian and Murray (1999), and Murray et al. (2000). The Bullock Creek LF is interpreted to be of middle Miocene age on the basis of marsupial biochronology (e.g., Woodburne et al., 1985; Rich, 1991; Megirian, 1994; Murray et al., 2000).

The Bullock Creek LF is biased towards large animals, and the small-mammal component of the assemblage is not well documented. Although macropodoids are the dominant small mammals, only one species, *Balbaroo camfieldensis* Flannery, Archer, and Plane, 1983, has been described. Here we describe a new species of *Nambaroo* Flannery and Rich, 1986, on the basis of a dentary retaining m1–4, and three isolated teeth. *Nambaroo bullockensis* sp. nov. extends the range of the genus beyond the late Oligocene or early Miocene, the age of all previously described species, and exhibits dental characters that are of phylogenetic interest.

Phylogenetic relationships within macropodoids are not well resolved, especially among the structurally primitive forms of which there are now several genera and numerous species recognized. Balbarinae was erected by Flannery et al. (1983) to accommodate fossil macropodoids in which the m1 protolophid is markedly compressed. Case (1984), Woodburne (1984), and Szalay (1994) disagreed with this analysis and reduced Balbarinae to a tribe within the Macropodinae. Flannery (1989) suggested that balbarines may be a paraphyletic group, ancestral to both macropodines and sthenurines. More recently, Cooke and Kear (1999) and Kear and Cooke (2001) elevated the Balbarinae to family level, considering them a group basal to all other macropodoids.

Flannery (1989) divided the subfamily into two clades, distinguished by the presence or absence of a protostylid on m1. These were the plesiomorphic *Nambaroo* clade, which retains the protostylid, into which Cooke (1997) suggests both *Wururoo* and

Ganawamaya fit, and the derived *Balbaroo* clade. While neither *Wururoo* nor *Ganawamaya* possesses a protostylid, Cooke (1997) argued for their placement here on the basis of other plesiomorphic features. Kear and Cooke (2001), as part of their elevation of Balbarinae to family level, erected a new subfamily, Nambarinae, for *Nambaroo* + *Wururoo* + *Ganawamaya*. They claim Nambarinae are monophyletic on the basis of two synapomorphies, a posteriorly positioned digastric eminence and an i1 occlusal surface that lies below the molar occlusal plane. This subfamily is shown in our analysis to be paraphyletic. While the possibility of the Balbaridae as a sister group to the Macropodidae (Cooke, 1999) is not discounted, this is based on an analysis of cranial and dental characteristics, which, while given a brief synopsis in Wroe et al. (1998) and Kear and Cooke (2001), is currently unpublished. For these reasons, the classification recommended by Kear and Cooke (2001) is not followed here.

We recognize the Balbarinae as a taxon composed of the following species: from the late Oligocene or early Miocene Tarkarooloo LF, Namba Formation, South Australia, *Nambaroo saltavus*, *N. tarrinyeri*, and *N. novus* Flannery and Rich, 1986; from the late Oligocene or early Miocene beds of the Carl Creek Limestone, northwestern Queensland, *N. couperi*, *Wururoo dayamayi* Cooke, 1997, *Ganawamaya acris*, *G. ornata*, and *G. aediculus* Cooke, 1992, *Balbaroo gregoriensis* Flannery, Archer, and Plane, 1983, and *B. fangaroo* Cooke, 2000; and from the middle Miocene Bullock Creek LF, Camfield Beds, Northern Territory, *B. camfieldensis* Flannery, Archer, and Plane, 1983.

MATERIALS AND METHODS

Molar homology follows Luckett (1993) and Cooke (1997), following Ride (1993). Dental terminology follows Cooke (1997) (Fig. 1). Lower molars are designated by lower case m, and uppers by upper case M.

Institutional Abbreviations—CPC, Commonwealth Paleontological Collection; NMV, National Museum of Victoria; NTM, Northern Territory Museum (Museum and Art Gallery of the Northern Territory); QVM, Queen Victoria Museum, Tasmania; QMF, Queensland Museum fossil vertebrate collection; SAM, South Australian Museum.

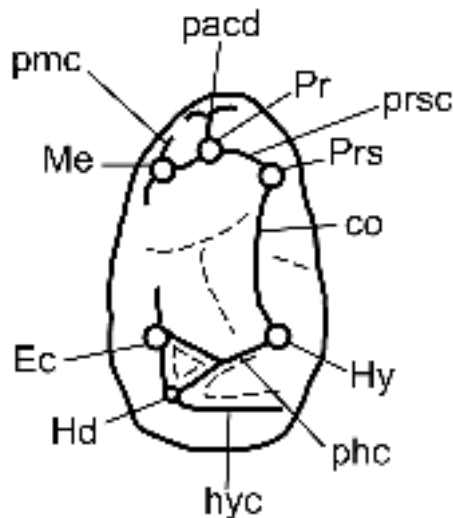


FIGURE 1. Schematic occlusal view of *N. saltavus* m1 illustrating tooth terminology. **Abbreviations:** co, cristid obliqua; Ec, entoconid; Hd, hypoconulid; Hy, hypoconid; Me, metaconid; pacd, paracristid; phc, post-hypocristid; pmc, premetacristid; Pr, protoconid; Prs, protostylid; prsc, protostylid crest.

SYSTEMATIC PALEONTOLOGY

MACROPODIDAE Gray, 1821

BALBARINAE Flannery, Archer, and Plane, 1983

NAMBAROO Flannery and Rich, 1986

NAMBAROO BULLOCKENSIS sp. nov.

Holotype—NTM P991-24, right dentary fragment retaining m1–m4 (Figs. 2, 3A)

Hypodigm—NTM P991-24 (Blast Site); QVM:2000:GFV:18, left m3 (unrecorded quarry); QVM:2000:GFV:67, left m2 (unrecorded quarry); QVM:2000:GFV:69, left m4 trigonid (unrecorded quarry); QVM:2000:GFV:68, left m3 trigonid (unrecorded quarry); NTM P9464-215, left M2 (Top Site); and NTM P87110-26, right M3 (Top Site).

Type Locality and Age—Plane and Gatehouse (1968) named the general area from which they collected fossils from the Camfield Beds the ‘Small Hills Locality.’ Later workers differentiated the various quarries producing the Bullock Creek LF. The holotype of *Nambaroo bullockensis* is from Blast Site. Fossils from Blast Site are the type assemblage of the Bullock Creek LF and estimated to be middle Miocene in age (e.g., Woodburne et al., 1985; Rich, 1991; Murray et al., 2000).

Diagnosis—Balbarine macropodoid of the genus *Nambaroo* possessing protostylid, protostylid crest, well-developed hypocingulid, and premetacristid on m1; all molars lacking hypoconulid and paraconid; hypocingulid spanning full width of all lower molars; molars increasing in length from m1 to m4; protolophid of m1 and m2 wider than hypolophid, m3 protolophid of equal width, and on m4, hypolophid narrower than protolophid. Largest known species of genus, with molar dimensions an average of 60% larger than any known specimens of the other species (Table 1). Distinguished from *N. novus*, *N. saltavus*, and *N. couperi* in possessing premetacristid on m1; from *N. tarrinyeri* and *N. saltavus* in possessing well-developed hypocingulid; and from *N. couperi* and *N. saltavus* in lacking hypoconulid.

Etymology—bullockensis refers to the type locality.

DESCRIPTION

Holotype

Dentary—The tooth row is straight in dorsal aspect (Fig. 2). The horizontal ramus is twisted slightly such that the long axis of a cross-section below m1 would point ventro-lingually, but below m4 would point ventro-buccally. The deepest point of the dentary is below m1. The majority of the coronoid process is missing, but the base of the anterior margin rises at an angle of approximately 100° to the occlusal plane. Part of the posterior root of p3 is present in its alveolus anterior to m1. The horizontal ramus anterior to this point is missing. The angular process and condyle are also missing. The buccal margin of the masseteric canal is straight, so that the entrance to the masseteric foramen is D-shaped in posterior view. The masseteric canal appears to penetrate at least to the anterior margin of m3. The large masseteric foramen is situated low in the masseteric fossa and in buccal view is hidden by the masseteric crest.

m1—The protolophid is narrower than the hypolophid (Fig. 3A). The precingulid is large, taking up about two thirds of the trigonid width. The paracristid runs straight antero-posteriorly to contact the anterior margin at the midpoint of the tooth. No rudimentary paraconid (sensu Flannery et al., 1983) is present. A short premetacristid is present, running straight to the anterior margin. Swelling buccal to the protoconid is slightly indistinct due to wear but clearly represents the protostylid, joined to the protoconid by a protostylid crest. The cristid obliqua runs antero-lingually from the hypoconid to terminate on the rear face of the protolophid at the base of the protoconid. The entoconid is the tallest cusp, followed by the hypoconid, metaconid, and protoconid, with the protostylid the shortest cusp. The hypocingulid is well developed, extending the full width of the tooth.

m2—This tooth is larger than m1 (Table 1). The protolophid is only slightly narrower than the hypolophid. The protoconid is broken at its tip, but was probably approximately the same height as the hypoconid, and both cusps are smaller than the entoconid and metaconid which also approximate each other in size. The cristid obliqua terminates just lingual of the protoconid, and along with the paracristid, is more strongly developed than on m1. The paracristid is straight and the precingulid takes up only one-third of the area of the anterior margin. A well-developed hypocingulid is present, extending the full width of the tooth.

m3—This is larger than m2. The protolophid and hypolophid are of equal width. The metaconid is the tallest cusp, followed by the entoconid and hypoconid, which are about the same height, and the protoconid is the shortest cusp. The cristid obliqua and the paracristid are more strongly expressed than on m2, probably due to less wear. The cristid obliqua originates at the hypoconid and contacts the protolophid just buccal of its midpoint. The paracristid curves antero-lingually before straightening to contact the anterior margin. The precingulid is similar to that of m2 and the hypocingulid runs the full width of the tooth.

m4—This is larger than m3. The hypolophid is slightly narrower than the protolophid. The metaconid is the tallest cusp, followed by the hypoconid, protoconid, and finally, the entoconid. The cristid obliqua originates at the hypoconid and terminates at the midpoint of the protolophid at its base. The paracristid curves in the manner described above for m3. The hypocingulid is weakly developed, but extends the full width of the tooth.

Molar Gradients—Along the tooth row from m1 to m4, the contact point of the cristid obliqua with the rear face of the protolophid is progressively more lingual. The paracristid, which contacts the anterior margin on m1 at the midpoint of the tooth, is a little more buccally situated on m2 and more so on m3 so that only one third of the anterior margin is buccal to the paracristid. This trend does not continue on m4, where the paracristid is again more lingually situated. The molars increase in length

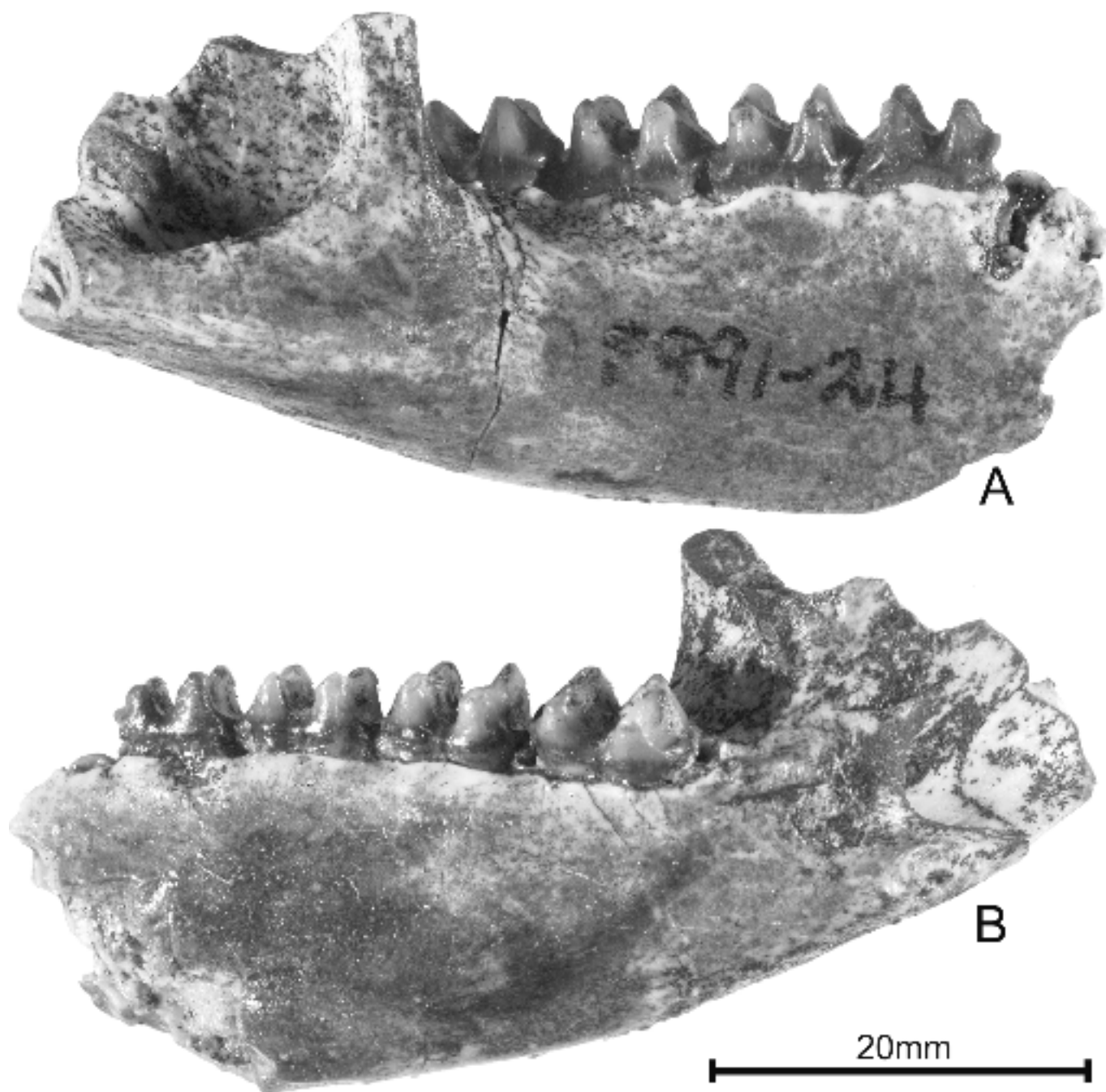


FIGURE 2. Right mandible with m1 to m4. **A**, buccal view of *N. bullockensis* sp. nov., holotype, NTM P991-24. **B**, lingual view of holotype.

along the molar row (Table 1). The protolophid is narrower than the hypolophid on both m1 and m2; on m3 they are approximately the same width, and on m4 the hypolophid is slightly narrower than the protolophid. The hypocingulid is well developed on all molars except m4, although tooth wear may be responsible for its absence. The trigonid basin, as enclosed by the premetacristid and paracristid, becomes lower and broader posteriorly and its length increases.

Referred Lower Molars

Material—QVM:2000:GFV:18, left m3; QVM:2000:GFV:67, left m2 lacking hypoconid and with damaged entoconid; QVM:

2000:GFV:69, left m4 trigonid; QVM:2000:GFV:68 left m3 trigonid. All are from unrecorded quarries.

Description—QVM:2000:GFV:69 and QVM:2000:GFV:68 are interpreted as being, respectively, m4 and m3 on the basis of comparison with the holotype. These isolated lower molars differ from the holotype only in the following: on QVM:2000:GFV:18 (Fig. 3B) a weak pre-entocristid is present on the anterior face of the entoconid and on QVM:2000:GFV:67 the lingual curvature of the metacristid coincides with a slight bulge in the enamel.

Referred Upper Molars

Material—NTM P9464-215, left M2 (Top Site); NTM P87110-26, right M3 (Top Site).

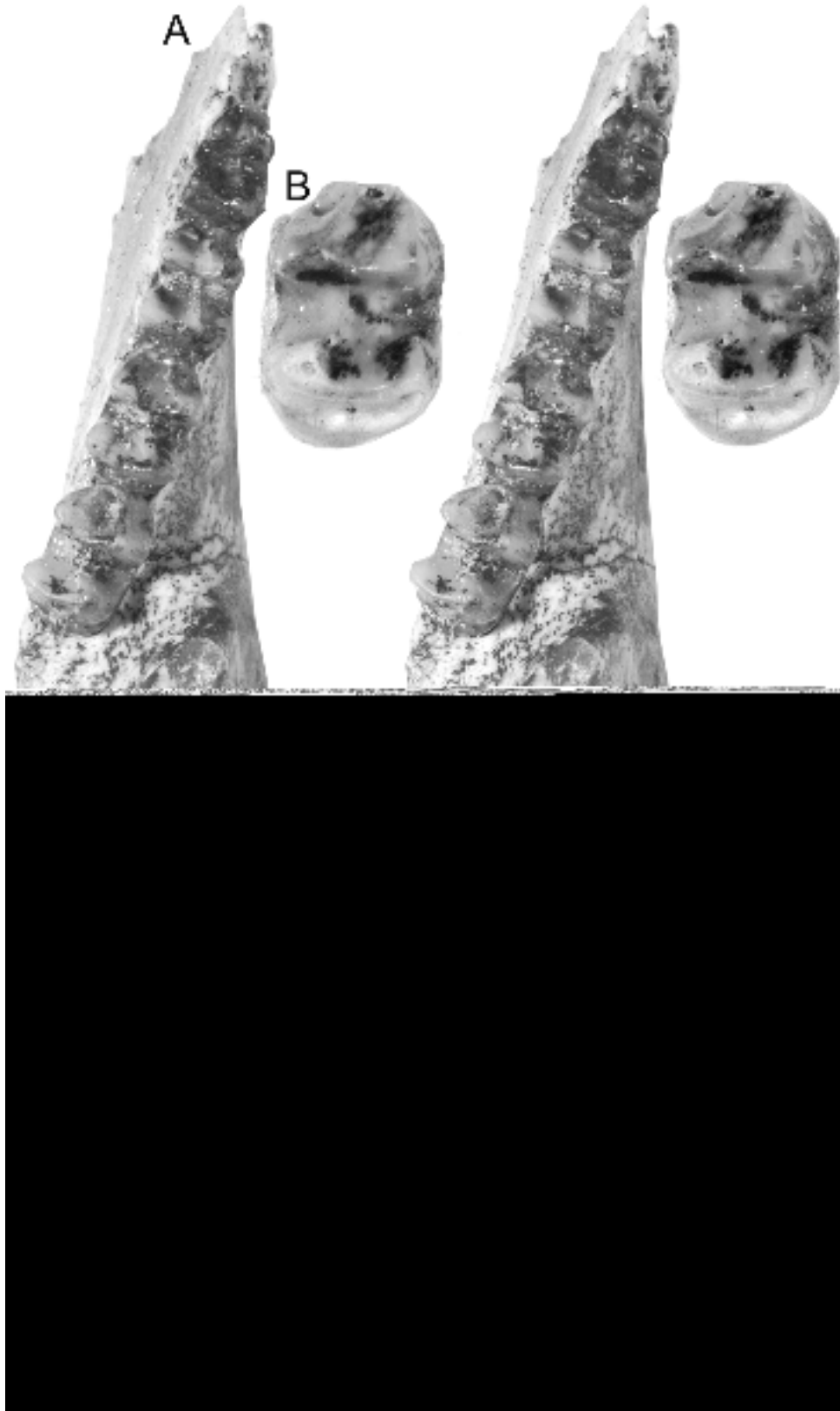


FIGURE 3. **A**, stereopair of occlusal view of *N. bullockensis* sp. nov., holotype, NTM P991-24, Rm1—m4. **B**, stereopair of occlusal view of QVM:2000:GFV:18, Lm3. **C**, stereopair of occlusal view of NTM P9464-215, LM2. **D**, stereopair of occlusal view of NTM P87110-26, RM3.

TABLE 1. Comparative tooth measurements for balbarine lower molars. **Abbreviations:** **Aw**, anterior width as measured across the protolophid; **Pw**, posterior width as measured across the hypolophid; **L**, length, as measured along the midline of the tooth. Measurements in millimeters.

Taxon	Specimen number	m1			m2			m3			m4			Source
		L	Aw	Pw	L	Aw	Pw	L	Aw	Pw	L	Aw	Pw	
<i>Nambaroo bullockensis</i>	NTM P991-24	7.6	4.0	5.0	7.8	5.1	5.6	8.1	5.7	5.8	9.3	5.9	5.7	This work
sp. nov.	QVM:2000:GFV:18	—	—	—	—	—	—	7.5	5.1	5.2	—	—	—	This work
<i>Nambaroo tarrinyeri</i>	SAM P24245	5.8	2.9	3.1	—	—	—	—	—	—	—	—	—	Flannery and Rich (1986)
	NMV P157569	—	—	—	5.2	3.0	3.5	—	—	—	—	—	—	Flannery and Rich (1986)
	NMV P157556	—	—	—	—	—	—	5.0	3.4	3.5	—	—	—	Flannery and Rich (1986)
<i>Nambaroo novus</i>	SAM P24244	4.4	2.8	3.0	—	—	—	—	—	—	—	—	—	Flannery and Rich (1986)
	NMV P157557	—	—	—	—	—	—	—	—	—	4.8	3.6	3.9	Flannery and Rich (1986)
<i>Nambaroo saltavus</i>	SAM P24242	5.2	3.0	3.4	—	—	—	—	—	—	—	—	—	Flannery and Rich (1986)
	NMV P157581	—	—	—	—	—	—	—	—	—	5.4	3.4	3.3	Flannery and Rich (1986)
	NMV P157555	—	—	—	—	—	—	4.6	3.5	3.3	—	—	—	Flannery and Rich (1986)
<i>Nambaroo couperi</i>	QMF 30401	5.2	2.6	3.3	5.4	3.5	3.9	5.6	3.9	4.1	5.4	3.8	3.6	Cooke (1997)
<i>Wururoo dayamayi</i>	QMF 19820	5.9	4.1	4.2	6.5	4.8	4.5	6.9	5.1	4.7	6.7	4.3	4.1	Cooke (1997)
<i>Ganawamaya acris</i>	QMF 16840	6.0	3.3	3.7	6.3	4.1	4.3	6.6	4.5	4.5	6.7	4.8	4.5	Cooke (1992)
<i>Ganawamaya aediculis</i>	QMF 16843	6.1	3.4	3.9	6.7	4.0	4.2	6.6	4.4	4.2	6.4	4.1	3.8	Cooke (1992)
<i>Balbaroo gregoriensis</i>	CPC 22186	7.3	4.2	4.3	—	—	—	—	—	—	—	—	—	Flannery et al. (1983)
<i>Balbaroo camfieldensis</i>	CPC 22179	7.1	3.6	5.0	7.7	4.9	5.4	8.9	5.4	5.4	8.4	5.5	—	Flannery et al. (1983)
	NMV P165000	—	—	—	8.2	—	—	8.6	5.6	—	—	5.8	5.5	Flannery et al. (1983)

Description—NTM P9464-215 (Fig. 3C) and NTM P87110-26 (Fig. 3D) are interpreted as M2 and M3 and referred to *N. bullockensis* by analogy with an undescribed Riversleigh *Nambaroo*. This specimen, QMF 34352, has an associated skull and dentary in which the upper molars are slightly shorter than the lowers, more fully lophodont, have fewer strong cristae, and poorly developed metacingulae. The differences between upper and lower molars seen in this specimen are similar to those differences observed between the holotype of *N. bullockensis* and the referred upper teeth. It is therefore considered probable that the uppers described here belong to *Nambaroo bullockensis*. Variation seen between these upper molars, where the M3 does not possess a forelink, is considered attributable to variation along the molar row. Other balbarine species that possess forelinks, such as *Balbaroo fangaroo*, also show variation in this feature along the molar row (L.R.S.S. pers. obs.).

A weak midlink is present on both teeth, and buccal cusps are higher than lingual cusps. There is no posterior shelf; the post-hypocrista descends postero-buccally across the metaloph and ends abruptly at the base of the crown. On NTM P9464-215, a small swelling is present in the interloph valley on the lingual side, and is thought to be a possible remnant of the lingual cingulum. Also on this tooth a small preprotocrista ('forelink') on the anterior face of the protoloph, buccal to the paracone, connects the crest of the loph to the anterior edge of the tooth, creating a small pocket in front of the paracone. NTM P87110-26 is 7.6 mm long, measured along the midline of the tooth, the protoloph is 4.9 mm wide, and the metaloph is 4.7 mm wide. NTM P9464-215 is the same length and 4.8 mm across at the protoloph, but is only 4.5 mm wide across the metaloph. NTM P87110-26 shows no remnant lingual cingulum in the interloph valley, and no preprotocrista. The area between the centrocrista and the midlink is slightly broader than in NTM P9464-215.

CHARACTER ANALYSIS

The phylogenetic relationships of Balbarinae were analysed using the characters of m1, which is known for all species except *Ganawamaya ornata*. The following is a list of characters used in this analysis. Character polarity for each species is shown in Table 2.

1. The protostylid. Archer (1978), Archer and Flannery (1985), and Flannery and Rich (1986) recognized the homology of the protostylid in macropodoids and phalangeridans. *Nambaroo* species all possess a protostylid (0) (Flannery and Rich, 1986;

Cooke, 1997), while the other balbarine genera have lost this cusp (1) (Flannery et al., 1983; Cooke, 1992, 1997, 1999).

2. The hypoconulid. Cooke (1997) described the presence of a hypoconulid on the posterior, lingual face of the hypolophid on *N. couperi*, interpreting its presence as a plesiomorphic state for all macropodoids (0). An examination of *N. saltavus* (SAM P24242) in the course of this study revealed a small cusp, of similar dimension and position to that on *N. couperi*. A hypoconulid is not present on any other species of balbarine (1) (Flannery et al., 1983; Flannery and Rich, 1986; Cooke, 1992, 1997, 1999).
3. The protostylid crest. In balbarines retaining the protostylid, a small crest is often present, linking the protostylid to the protoconid (0). In most of those balbarines without a protostylid, no crest is present (1). There are two species that suggest that the presence or absence of the protostylid crest is not necessarily linked to the presence of the protostylid. These are *N. tarrinyeri*, which possesses a protostylid but no crest (Flannery and Rich, 1986), and *W. dayamayi*, which possesses a remnant of the protostylid crest joined to the cristid obliqua, but does not possess a protostylid (Cooke, 1997).
4. The cristid obliqua. The contact point of the cristid obliqua on m1 varies among balbarines. The most primitive position appears to be that displayed by *N. saltavus* (Flannery and Rich, 1986), where the cristid obliqua contacts the protostylid (0). In *N. tarrinyeri*, the cristid obliqua bifurcates to contact both the protostylid and the protoconid (1), while in *W. dayamayi* it contacts just the protostylid crest (2). In all species of *Bal-*

TABLE 2. Data matrix of characters of m1 in species of Balbarinae. 0 = plesiomorphic state; 1 = apomorphic state; 2 = apomorphic state independent of 1; 3 = apomorphic state independent of 1 and 2

Taxon	Characters				
	1	2	3	4	5
<i>Ganawamaya aediculis</i>	1	1	1	4	2
<i>Ganawamaya acris</i>	1	1	1	4	2
<i>Balbaroo fangaroo</i>	1	1	1	3	2
<i>Balbaroo gregoriensis</i>	1	1	1	3	2
<i>Balbaroo camfieldensis</i>	1	1	1	3	2
<i>Nambaroo novus</i>	0	1	0	3	2
<i>Nambaroo bullockensis</i>	0	1	0	3	2
<i>Nambaroo couperi</i>	0	0	0	0	0
<i>Nambaroo tarrinyeri</i>	0	1	1	1	1
<i>Nambaroo saltavus</i>	0	0	0	0	0
<i>Wururoo dayamayi</i>	1	1	0	2	1

baroo and in *N. novus*, the cristid obliqua contacts the protoconid (3) while in species of *Ganawamaya*, it contacts the protolophid just lingual of the protoconid (4). We follow Flannery and Rich (1986) and Cooke (1997), and so for the purposes of this analysis, this character was considered as an ordered character.

5. Hypolophid development. Development of the hypolophid in balbarines is well documented (Flannery and Rich, 1986; Cooke, 1997), and so this is also considered an ordered character. The most primitive morphology is that displayed by *N. saltavus* and *N. couperi* in which the posthypocristid descends buccally from the hypoconid to contact the hypoconulid (0). In the next evolutionary stage the hypolophid appears complete, but for the presence of a triangular fossette on the rear face of the entoconid (1), which is eventually lost (2), producing a complete hypolophid such as that seen in *Balbaroo camfieldensis* (Flannery and Rich, 1986; Cooke, 1997).

MacClade 4 (Maddison and Maddison, 2001) was used for cladistic analysis of m1 dental characters. A single-most parsimonious tree was produced (Fig. 4), with Treelength = 11, Consistency Index = 0.82 and Retention Index = 0.90, indicating that there is little homoplasy within the cladogram.

Nambaroo bullockensis is referred to *Nambaroo* on the basis of the possession of a protostylid on m1. Other characters, such as the cristid obliqua contacting the base of the protoconid, and the fully developed hypolophid, are synapomorphies within the genus that unite this species with *N. novus*.

Nambaroo saltavus has all of the features Cooke (1997) suggested were representative of the balbarine ancestral condition. *Nambaroo couperi* is here symplesiomorphic with *N. saltavus*, although it can be diagnosed as a distinct species by the autapomorphic loss of the hypocingulid and the postentocristid (Cooke, 1997). Thus, in this analysis, *N. saltavus* and *N. couperi* form the outgroup to all other balbarines.

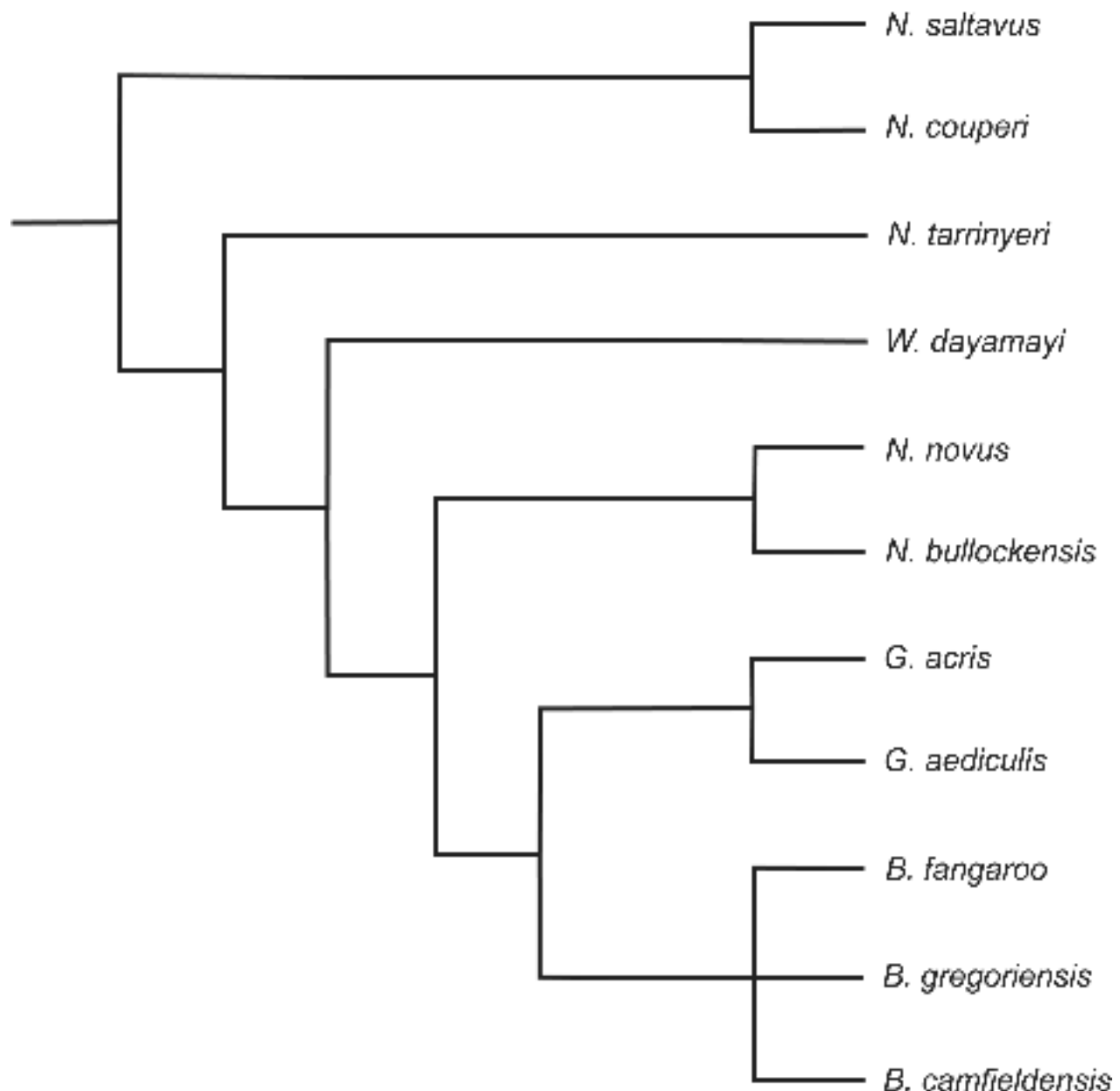


FIGURE 4. Most parsimonious cladogram produced from the phylogenetic analysis. Tree length = 11, CI = 0.82, RI = 0.90. *N* = *Nambaroo*, *B* = *Balbaroo*, *G* = *Ganawamaya*, *W* = *Wururoo*.

Nambaroo bullockensis groups more closely with *N. novus* than with all other species of *Nambaroo*, with *Wururoo dayamayi* interposed between the *N. novus* + *N. bullockensis* clade and the more plesiomorphic *Nambaroo* species. The *N. novus* + *N. bullockensis* clade is shown to be the plesiomorphic sister group to the *Ganawamaya* + *Balbaroo* clade. Therefore, Cooke's (1997) grouping of *Wururoo* and *Ganawamaya* with *Nambaroo* to the exclusion of *Balbaroo* is unsupported, as is the *Nambarinae* sensu Kear and Cooke (2001).

The current paraphyly of *Nambaroo* can be explained by the use of the protostylid as a distinguishing characteristic of *Nambaroo* species. This is problematic, as possession of a protostylid is a symplesiomorphy for macropodoids (Flannery and Rich, 1986).

Although phylogenetically distinct, *Balbaroo camfieldensis*, the only other macropodoid known from Bullock Creek, and *Nambaroo bullockensis* have similarly sized molars and are similar (also to *B. fangaroo*) in having m4 as the longest tooth in the series (Table 1). *Balbaroo camfieldensis* and *N. bullockensis* differ in only two characters, namely the presence in *N. bullockensis* of a protostylid and a protostylid crest. As already outlined above, these characters appear to have been lost independently of each other within *Balbarinae*. The derivation of *B. camfieldensis* is therefore partly by loss of primitive structures, and it is conceivable that these structures could be variably expressed in some *balbarine* populations as vestigial characters. The current concept of *Nambaroo* relies on the assumption that the presence or absence of the protostylid is not subject to this kind of variation, and therefore, despite its morphometric similarity to *B. camfieldensis*, *bullockensis* belongs in *Nambaroo*, with size similarities ascribed to convergence.

Paraphyly in *Nambaroo* is not an artifact of taxonomy. Assigning *N. bullockensis* to *Balbaroo* would simply mean that both *Nambaroo* and *Balbaroo* are paraphyletic. *Balbaroo* emerges from this analysis as an unresolved trichotomy. Resolution within the genus is reliant upon the addition of characters other than those on m1. Like *Balbaroo*, *Ganawamaya* is also monophyletic. Kear and Cooke (2001) suggested that two other character states unite *Nambaroo*, which they claim is monophyletic. Neither of these characters is assessable on four out of the five *Nambaroo* species currently known, due to limited material for all species except *N. couperi*.

The difficulties in attempting to resolve *balbarine* phylogeny with sparse material are manifest. The analysis presented here is limited to characters of m1. For many *balbarine* species, especially the first three species of *Nambaroo* described, the m1 is the holotype, and often the only material known. Only one species, *Ganawamaya ornata*, is not represented by an m1.

CONCLUSION

Nambaroo bullockensis is assigned to the genus *Nambaroo* based on its possession of a protostylid. While this character is a symplesiomorphy for macropodoids, other synapomorphies suggest a close relationship of *N. bullockensis* to *N. novus*. These species are closer to other *balbarine* genera than they are to the other species of *Nambaroo*. *Nambaroo bullockensis* is both the largest *Nambaroo* species known, and the youngest, extending the range of this genus into the middle Miocene. In the absence of any molar synapomorphies to unite the genus, and given the analysis of the *Balbarinae* performed here, *Nambaroo* is considered a paraphyletic group, in agreement with Flannery and Rich (1986). The creation of *Nambarinae* as suggested by Kear and Cooke (2001) is rejected on the basis of the paraphyly of the proposed subfamily and the likely close relationship between *Ganawamaya* and *Balbaroo*.

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LITERATURE CITED

- Archer, M. 1978. The nature of the molar-premolar boundary in marsupials and a reinterpretation of the homology of marsupial cheek teeth. *Memoirs of the Queensland Museum* 18:157-64.
- Archer, M., and T. F. Flannery. 1985. Revision of the extinct gigantic rat-kangaroos (Potoroidae: Marsupialia), with description of a new Miocene genus and species and a new Pleistocene species of *Proleopus*. *Journal of Paleontology* 59:1331-1349.
- Case, J. A. 1984. A new genus of Potoroinae (Marsupialia: Macropodidae) from the Miocene Ngapakaldi Fauna, South Australia, and a definition of the Potoroinae. *Journal of Paleontology* 58:1074-1086.
- Cooke, B. N. 1992. Primitive macropodids from Riversleigh, northwestern Queensland. *Alcheringa* 16:201-217.
- Cooke, B. N. 1997. Two new *balbarine* kangaroos and lower molar evolution within the subfamily. *Memoirs of the Queensland Museum* 41:269-302.
- Cooke, B. N. 1999. *Wanburoo hilarus* gen. et. sp. nov., a lophodont bulungamayine kangaroo (Marsupialia: Macropodoidea: Bulungamayinae) from the Miocene deposits of Riversleigh, northwestern Queensland. *Records of the Western Australian Museum, Supplement* 57:239-253.
- Cooke, B. N. 2000. Cranial remains of a new species of *balbarine* kangaroo (Marsupialia: Macropodoidea) from the Oligo-Miocene freshwater limestone deposits of Riversleigh World Heritage Area, northern Australia. *Journal of Paleontology* 74:317-326.
- Cooke, B. N., and B. Kear. 1999. Evolution and diversity of kangaroos (Macropodoidea, Marsupialia). *Australian Mammalogy* 21:27-29.
- Flannery, T. F. 1989. Phylogeny of the Macropodoidea; a study in convergence; pp. 1-46 in G. Grigg, P. Jarman, and I. Hume (eds.), *Kangaroos, Wallabies and Rat-Kangaroos*. Surrey Beatty and Sons, Sydney.
- Flannery, T. F., and T. H. Rich. 1986. Macropodoids from the Middle Miocene Namba Formation, South Australia, and the homology of some dental structures in kangaroos. *Journal of Paleontology* 60:418-447.
- Flannery, T. F., M. Archer, and M. Plane. 1983. Middle Miocene kangaroos (Macropodoidea: Marsupialia) from three localities in northern Australia, with a description of two subfamilies. *Bureau of Mineral Resources, Journal of Australian Geology and Geophysics* 7:287-302.
- Gray, J. E. 1821. On the natural arrangement of vertebrate animals. *London Medical Repository* 15:296-310.
- Hand, S. J., P. Murray, D. Megirian, M. Archer, and H. Godthelp. 1998. Mystacinid bats (Microchiroptera) from the Australian Tertiary. *Journal of Paleontology* 72:538-545.
- Kear, B. P., and B. N. Cooke. 2001. A review of macropodoid (Marsupialia) systematics with the inclusion of a new family. *Riversleigh Symposium 1998, Association of Australian Paleontologists, Memoir* 25:83-101.
- Luckett, W. P. 1993. An ontogenetic assessment of dental homologies in therian mammals; pp. 182-204 in F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians and Marsupials*. Springer-Verlag, New York.
- Maddison, D. R., and W. P. Maddison. 2001. *MacClade 4: Analysis of Phylogeny and Character Evolution*. Sinauer Associates, Sunderland, Massachusetts.
- Megirian, D. 1994. Approaches to marsupial biochronology in Australia and New Guinea. *Alcheringa* 18:259-274.
- Megirian, D., and P. Murray. 1999. Chelid turtles (Pleurodira, Chelidae)

- from the Miocene Camfield Beds, Northern Territory of Australia, with a description of a new genus and species. *The Beagle: Records of the Northern Territory Museum of Arts and Sciences* 15:75–130.
- Murray, P., and D. Megirian. 1992. Continuity and contrast in middle and late Miocene vertebrate communities from the Northern Territory. *The Beagle: Records of the Northern Territory Museum of Arts and Sciences* 9:195–218.
- Murray, P., and D. Megirian. 2000. Two new genera and three new species of Thylacinidae (Marsupialia) from the Miocene of the Northern Territory, Australia. *The Beagle: Records of the Northern Territory Museum of Arts and Sciences* 16:145–162.
- Murray, P., D. Megirian, T. H. Rich, M. Plane, and P. Vickers-Rich. 2000. *Neohelos stirtoni*. A new species of Zygomaturine (Diprotodontia: Marsupialia) from the mid-Tertiary of the Northern Territory, Australia. *Records of the Queen Victoria Museum* 105:1–47.
- Plane, M., and C. Gatehouse. 1968. A new vertebrate fauna from the Tertiary of northern Australia. *Australian Journal of Science* 30: 272–273.
- Randal, M. A., and M. C. Brown. 1967. The geology of the northern part of the Wiso Basin. Bureau of Mineral Resources, Geology and Geophysics Bulletin 110:1–55.
- Rich, T. H. 1991. Monotremes, placentals and marsupials: their record in Australia and its biases; pp. 893–1004 in P. Vickers-Rich, J. M. Monaghan, R. F. Baird, and T. H. Rich (eds.), *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio and Monash Publications Committee, Melbourne.
- Ride, W. D. L. 1993. *Jackmahoneya* gen. nov. and the genesis of the macropodiform molar. *Memoirs of the Association of Australian Paleontologists* 15:441–459.
- Szalay, F. S. 1994. *Evolutionary History of the Marsupials and an Analysis of Osteological Characters*. Cambridge University Press, New York, 455 pp.
- Tyler, M. J. 1994. Hylid frogs from the Mid-Miocene Camfield beds of northern Australia. *The Beagle: Records of the Northern Territory Museum of Arts and Sciences* 11:141–144.
- Woodburne, M. O. 1984. *Wakiewakie lawsoni*, a new genus and species of Potoroinae (Marsupialia: Macropodidae) of medial Miocene age, South Australia. *Journal of Paleontology* 58:1062–1073.
- Woodburne, M. O., R. H. Tedford, M. Archer, W. D. Turnbull, M. D. Plane, and E. L. Lundelius. 1985. Biochronology of the continental mammal record of Australia and New Guinea. Special Publication of the South Australian Department of Mines and Energy 5: 347–363.
- Wroe, S., J. Brammall, and B. Cooke. 1998. The skull of *Ekaltadeta ima* (Marsupialia, Hypsiprymnodontidae?): an analysis of some marsupial cranial features and a re-investigation of proleopine phylogeny, with notes on the inference of carnivory in mammals. *Journal of Paleontology* 72:738–751.

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