

A new fossil kangaroo from the Oligocene-Miocene Etadunna Formation of Ngama Quarry, Lake Palankarinna, South Australia

Benjamin P. Kear^{A,C} and Neville S. Pledge^B

^ADepartment of Genetics, La Trobe University, Melbourne, Victoria 3086, Australia.

^BSouth Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia.

^CCorresponding author. Email: b.kear@latrobe.edu.au

Abstract. Mandibular and postcranial remains attributable to a new fossil kangaroo (Macropodoidea) are described from the Oligocene-Miocene Etadunna Formation deposits of Ngama Quarry at Lake Palankarinna in north-eastern South Australia. The taxon is uniquely differentiated by its straight bunolophodont molar row, elongate P_3 with distinct labial/lingual cingulids and 12–13 fine (shallowly incised) cuspid/transcristids, molars with a rectangular (length at least $0.3 > \text{width}$) occlusal outline, hypolophid formed by a buccally directed crest from the entoconid, absence of a discrete M_1 protostylid, transversely broad trigonid basin on the M_1 , M_4 not markedly smaller than the anterior molars, distal end of humerus with sub-equally sized capitellum and trochlea (the latter also closely abutting the entepicondyle), and ulna with distinctly sinuous ventral edge. Relationships of the Ngama Quarry kangaroo are poorly resolved because of missing data; however, inclusion within the most comprehensive published phylogenetic dataset of Macropodoidea suggests close affinity with the currently extant potorine/macropodid lineage.

Introduction

The Etadunna Formation deposits of Ngama Quarry in the Lake Eyre Basin of central Australia (Pledge 1984; Woodburne *et al.* 1993) have produced some twenty discernable taxa of higher vertebrates, mostly represented by jaw fragments and/or isolated teeth. Only three specimens have been recovered that preserve associated or articulated bones: a crocodilian hind limb referred to *Australosuchus clarkeae*, the lower tibiotarsus and pes of an indeterminate water bird (possibly a flamingo), and the partial postcranium of a small macropodoid (SAM P23821); this specimen is significant because it is the only articulated macropodoid skeleton thus far described from the Oligocene-Miocene deposits of the Lake Eyre Basin.

SAM P23821 was found in July 1981 by a field party from the South Australian Museum, in the saddle section of Ngama Quarry at Mammalon Hill, Lake Palankarinna, north-eastern South Australia (see Pledge 1984, 347, Fig. 1 for locality map). It came from the upper fossiliferous sandy layer of the upper Etadunna Formation (Pledge 1984) and occurred at the same level (and spatially within a few metres) as a calcaneum (SAM P23637, which articulates with the cuboid of SAM P23821), and the jaw of a primitive macropodoid (SAM P23626), here attributed to a new genus and species *Ngamaroo archeri* gen. et sp. nov. These specimens (SAM P23821, P23637, P23626) probably represent a single individual, as evidenced by their close spatial/stratigraphic proximity, comparable size/morphology, and immature ontogenetic stage: epiphyses not fully fused in SAM P23821, P23637, and P_3 not erupted in SAM P23626.

This paper describes remains attributable to *Ngamaroo archeri* gen. et sp. nov. and provides a preliminary assessment of its potential phylogenetic relationships. Postcranial skeletal and myological terminology follows Murray (1995), Bishop (1997) and Kear *et al.* (2007). Dental homology follows Flower (1867)

and Lockett (1993). Institutional abbreviation SAM refers to the South Australian Museum, Adelaide.

Systematics

DIPROTODONTIA Owen, 1866

MACROPODOIDEA Gray, 1821

Genus *Ngamaroo*, gen. nov.

Type and only known species: *Ngamaroo archeri*, sp. nov.

Diagnosis

Fossil macropodoid differentiated from balbarids and hypsiprymnodontids on the basis of an elongate P_3 ($>1.5 M_1/1$) with horizontal occlusal margin, transversely broad trigonid basin on the M_1 , and absence of a discrete M_1 protostylid. Differs from advanced macropodids (e.g. derived bulungamayines, macropodines and sthenurines) by the retention of bunolophodont molars and a lower molar hypolophid formed by a buccally directed crest from the entoconid. Differs from primitive bunolophodont macropodids (i.e. the bulungamayines *Nowidgee* and *Gumardee*) by the P_3 bearing a high number (12–13) of fine (shallowly incised) cuspid/transcristids. Differs from potorines *sensu stricto* in having the P_3 base expanded into distinct labial and lingual cingulids, M_4 not markedly smaller than anterior molars, sub-equally sized capitellum and trochlea on the distal end of the humerus, humeral entepicondyle closely abutting the trochlea, and ulna shaft with sinuous ventral edge. Differs from the *incertae sedis* taxa *Purtia*

in P_3 cuspid/transcristid number (12–13 v. 10), and in the molars having closely aligned longitudinal axes (i.e. molar row straight) and a rectangular (length at least $0.3 > \text{width}$) occlusal outline; *Wakiewakie* in P_3 cuspid/transcristid number (12–13 v. 20) plus the rectangular molar occlusal outline and M_4 being not markedly smaller than the anterior molars; and *Palaeopotorous* by the absence of a discrete M_1 protostylid.

Remarks

Cooke and Kear (1999) and Kear and Cooke (2001) recently reviewed the taxonomy of Oligocene-Miocene macropodoid genera assigning all to one of four family-level taxa: Balbaridae, an extinct basal clade of lophodont kangaroos previously considered ancestral to macropodids (see Flannery 1989); Hypsiprymnodontidae, containing the Musky rat-kangaroos (*Hypsiprymnodon* spp.) and propleopines (popularly known as 'carnivorous kangaroos'); Potoroidae, incorporating genera ancestral to currently extant potorines only; and Macropodidae, represented by a basal series of paraphyletic

bulungamayine taxa (traditionally allied with potoroids; see Flannery *et al.* 1983) and the ancestors of sthenurines and modern macropodines. All of these groups have representatives in the Oligocene-Miocene deposits of the Lake Eyre Basin in north-eastern South Australia (see Woodburne *et al.* 1993; Callen *et al.* 1995 for detailed stratigraphical/geological summaries). To date, seven valid genera have been reported from the Upper Oligocene to Miocene Etadunna and unconformably overlying Wipajiri formations (Tirari Sub-Basin), plus the laterally equivalent Namba Formation (Callabonna Sub-Basin): the balbarids *Balbaroo* and *Nambaroo* (reported in Flannery and Rich 1986; Woodburne *et al.* 1993); *Palaeopotorous*, an enigmatic taxon possibly related to bulungamayines (Cooke 1997); *Gumardee* based on referred lower teeth (this genus was originally placed in Potoroidae and is otherwise known only from a fragmentary maxilla found at Riversleigh, Queensland; Flannery *et al.* 1983; Flannery and Rich 1986); the derived bulungamayine *Bulungamaya* (see Woodburne *et al.* 1993); and the putative potoroids *Purtia* and *Wakiewakie*. Cooke (1997)

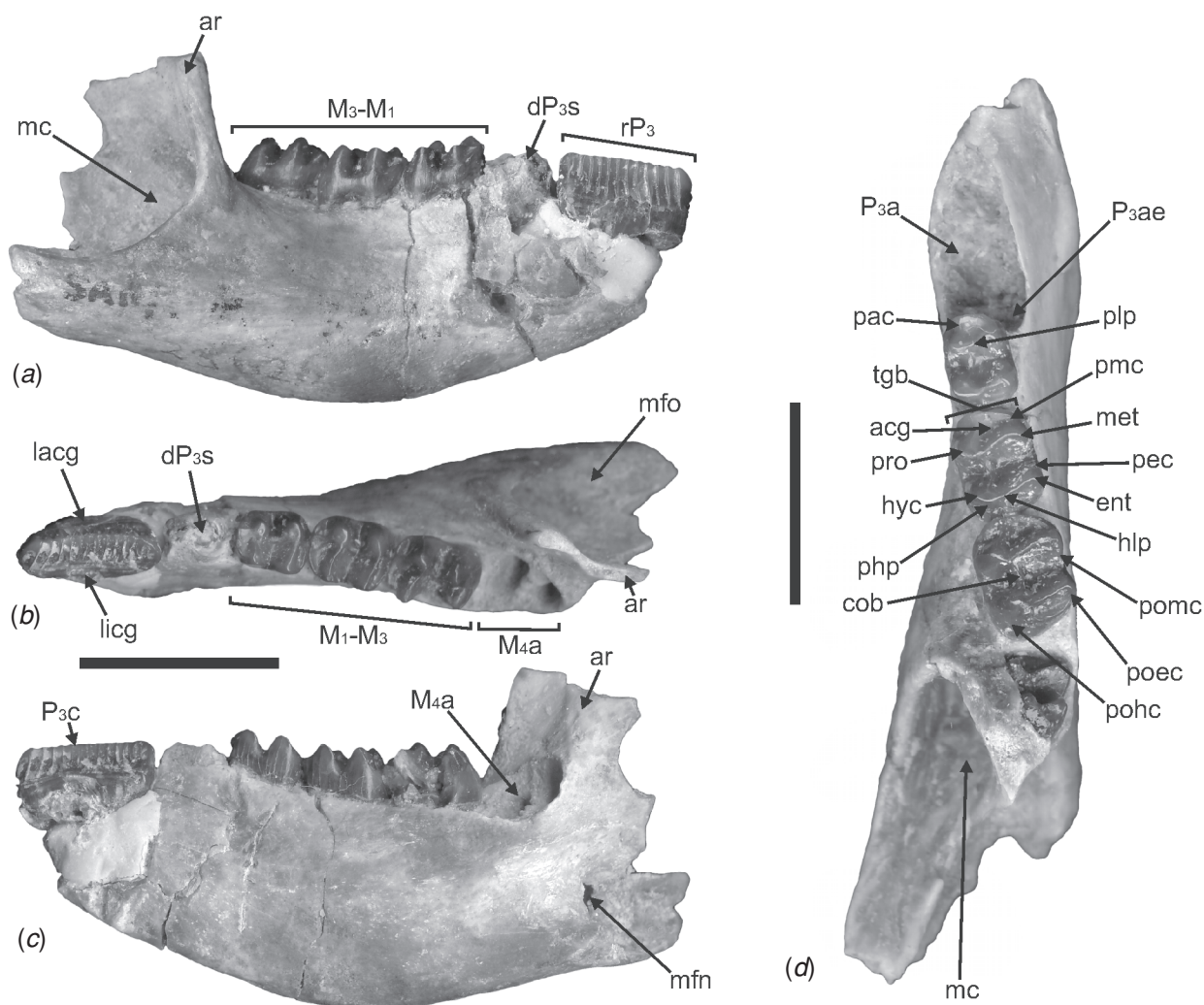


Fig. 1. Mandible and dentition of *Ngamaroo archeri* holotype (SAM P23626) in (a) labial, (b) occlusal, and (c) lingual views (P_3 has been excavated from its crypt and reconstructed anterior to the dP_3 stub). Referred mandible (SAM P27818) in (d) occlusal view showing P_3 alveolus. Anatomical abbreviations are explained in the main text; scale bars equal 20 mm.

and Kear and Cooke (2001) allied *Gumardee*, *Purtia* and *Wakiewakie* with bulungamayines. Indeterminate hypsiprymnodontine (Flannery and Rich 1986), potoroine and macropodine material has also been reported together with an undefined basal potoroid taxon '*Kyeema*', which has never been formally described in publication (see Woodburne *et al.* 1993). The new genus *Ngamaroo* can be distinguished from these sympatric and all other macropodoids by its unique combination of primitive and derived states (see above). It is also differentiated from currently defined higher-level taxonomic groupings and is thus here provisionally assigned to Macropodoidea *incertae sedis*.

Etymology

Ngama, referring to Ngama Quarry, currently the only source of remains; and *-roo* common Australian diminutive for kangaroo.

Ngamaroo archeri, sp. nov.

Material examined

Holotype. SAM P23626 right dentary with fragment of dP₃, unerupted P₃, M₁-M₃, partially erupted M₄.

Other material examined. SAM P23821, incomplete postcranium comprising left and fragmentary right humerus and ulna, right and parts of left femur, left tibia, right fibula, cuboid, calcaneum (SAM P23637), and metatarsal IV, rib fragments. SAM P27817, incomplete left dentary with M₁₋₃; SAM P27818, left dentary with M₁₋₃, M₄ unerupted, P₃ erupted but missing; SAM P31834, right dentary with M₁₋₃, (M₄ damaged in moulding, known from cast); SAM P23031, M₂; SAM P23043, partial P₃; SAM P24255, M₁ fragment; SAM P24256, M₁; SAM P24571, M₄; SAM P24649, M₃₋₄.

Diagnosis

As for genus.

Description

Fossils from the Ngama Quarry are preserved in clay and argillaceous fine sand, which in the moist state of fresh exposure, are infiltrated with a saturated solution of calcium sulfate. On exposure to the air, this rapidly crystallises as flour gypsum and gradually builds up to veins of selenite (CaSO₄·2H₂O), effectively disrupting the sediment and shattering any bones enclosed. This effect was not realised at the time of discovery and resulted in many of the referred postcranial elements (vertebrae, ribs, proximal right forelimb and majority of left hind limb – all incomplete) being reduced to small shards.

The holotype dentary (SAM P23626) preserves ~35 mm from the anterior margin of the P₃ crypt to a point approximately halfway through the masseteric fossa (Fig. 1a–c). The maximum depth of the horizontal ramus is 12 mm below the M₂. The preserved molar tooth-row (M₁-M₃) is 14.4 mm long with the 4 mm

long broken stub of the dP₃ (dP₃s) covering the restored P₃ (rP₃; excavated from its crypt and fixed anterior to the dP₃ stub during early preparation; see Fig. 1a–c). Individual tooth measurements are given in Table 1. The tooth-row is straight in occlusal view (molar longitudinal axes in alignment) and concave in lateral view with the occlusal surface of the M₂ lying below those of the M₁/M₃. The masseteric canal (mc) extends from the buccally expanded masseteric fossa (mfo) anteriorly to at least the midpoint of the M₂ (determined via exploration with a probe). There is no evidence of a partition between the masseteric and inferior dental canals. A small mandibular foramen (mfn) is present on the posterolingual surface of the mandible ventral to the M₄ alveolus (M₄a). Disposition of the posterior mental foramen cannot be determined with the current remains. The broken base of the mandible's ascending ramus (ar) is steeply inclined at around 100°. The ventral margin of the dentary is strongly convex (central digastric prominence weakly defined) and inclined anteriorly as is typical of potoroines (Woodburne 1984). A remnant of the non-ankylosed mandibular symphysis is preserved below the P₃. There is a slight molar gradient: dP₃ < M₁ < M₂ < M₃ > M₄.

The P₃ (Fig. 1a–c; Table 1) is elongate (>1.5 M₁/I₁) with a slightly bulbous base. Its longitudinal crest (P₃c) is horizontal in lateral view (in marked contrast to the sharply convex crest in balbarids and hypsiprymnodontids; Kear *et al.* 2007) and lacks the strongly differentiated, enlarged posterior cuspid reported in some primitive macropodids (e.g. the bulungamayines *Bulungamaya*, *Ganguroo* and *Wanburoo*; Flannery *et al.* 1983; Cooke 1997, 1999) and the putative potoroid/bulungamayine *Purtia* (see Case 1984). Twelve labial and 13 (including a minor posterior cuspid) lingual cuspids (counting the anterior and posterior-most cuspids) and associated unbranched transcrisids (*sensu* Cooke 1997, 1999) are present (branched transcrisids have been reported in the early Pliocene potoroine *Milliyowi*; Flannery *et al.* 1992). The transcrisids are evenly spaced and very fine unlike the deeply incised, coarse transcrisids typical of bulungamayines (Flannery *et al.* 1983; Cooke 1997, 1999) and potoroines (e.g. Flannery and Archer 1987; see also Seebeck and Rose 1989, 730, Fig. 30.7 for comparative diagrams). Both the lingual (licg) and labial (lacg) surfaces of the P₃ are produced into narrow cingulids. The well preserved P₃ alveolus (P₃a) in SAM P27818 (Fig. 1d) shows that the P₃ displaced the P₂ after eruption. A transverse expansion (P₃ae) of the posterior alveolus beyond the lingual edge of the M₁ might also indicate that the P₃ was buccally flexed out of alignment with the molar row (character scored as missing data in this analysis, see Appendix).

The M₁ (Fig. 1a–d; Table 1) is bunolophodont with brachyodont lophs. It displays a distinctly rectangular occlusal outline

Table 1. Lower tooth measurements (mm) of *Ngamaroo archeri*, gen. et sp. nov.
Holotype and referred mandibles: *measured from cast; °estimate from alveolus; †unerupted tooth

Specimen	l-P ₃	w-P ₃	l-M ₁	w-M ₁	l-M ₂	w-M ₂	l-M ₃	w-M ₃	l-M ₄	w-M ₄
SAMP23626	8.1†	3.8†	4.2	3.4	4.9	3.7	5.1	3.6	–	–
SAMP27817	–	–	3.8	3.15	4.3	3.6	4.7	4.0	–	–
SAMP27818	7.6°	–	3.7	3.25	4.4	3.5	4.9	3.85	4.7†	–
SAMP31834	–	–	4.15	3.6	4.7	3.8	5.5	4.25	4.9*	3.8*

(see Table 1) unlike the square molars reported in primitive bulungamayines such as *Nowidgee* (Cooke 1997), together with *Purtia* (Case 1984) and *Wakiewakie* (Woodburne 1984). The tall lingual cuspids are placed vertically above the lateral margin of the tooth (*sensu* potoroines Case 1984; Cooke 1997); in contrast, the lower labial cuspids are medially situated and have a moderate lateral slope. The metaconid (**met**) and buccally-placed protoconid (**pro**) are of sub-equal size and border the transversely broad trigonid basin (**tg**). There is no evidence of a discrete protostylid otherwise typical of plesiomorphic macropodoids (e.g. balbarids and *Palaeopotorous*; Cooke 1997, 1999). The protolophid (**plp**), formed by a metacristid extending from the metaconid apex to the posterolingual flank of the protoconid, is transversely shorter than the hypolophid (**hlp**). A broad anterior cingulid (**acg**) is present bounded lingually by the premetacristid (**pmc**) and transected buccally by a robust paracristid (**pac**) running anterolingually from the base of the protoconid. A short postmetacristid (**pomc**) and preentocristid (**pec**) constrict the opening of the interloph valley. The low cristid obliqua (**cob**) is aligned with the paracristid and crosses the interloph valley between the anterior flank of the hypoconid and posterior protoconid. The hypolophid is formed by a prominent buccal entocristid (buccal crest *sensu* Cooke 1997) extending from the apex of the entoconid to the hypoconid. A postentocristid (**poec**) extends posteriorly to meet the posthypocristid (**pohe**), the latter enclosing a well defined posthypolophid pocket (**php**, *sensu* Case 1984; Woodburne 1984).

M_{2-4} (Fig. 1*a–d*; Table 1) are similar in form to M_1 except in their more pronounced rectangular outline and protoconid/hypolophid being near equal in transverse length. The M_4 is sub-equal in size to the more anterior molars (see Table 1) but with a tapered posterior margin and transversely narrower hypolophid. The anterior cingulid and interloph valley are longer and broader in M_{2-4} with greater separation of the postmetacristid and preentocristid (except in the M_4 where they remain in close proximity); the posthypolophid pocket is also broader and more strongly defined.

The referred postcranial elements (SAM P23821, P23637) include parts of the left and right forelimb, hindlimb, right tarsus and pes. These represent an immature individual as evidenced by incomplete fusion of long-bone/tarsal epiphyses.

The complete left humerus (Fig. 2*a*) is large (75.2 mm maximum length) relative to the hindlimb elements (as in other primitive macropodoids; Kear *et al.* 2007) and includes both the proximal and distal epiphyses. The humeral shaft is straight and slender (21.3 mm in circumference) with a uniformly low deltoid crest (**dec**) and insignificant lateral deltoid ridge. The supinator crest (**sup**) is damaged and cannot be reconstructed with accuracy. The teres tuberosity is also not readily discernible. The proximal humeral extremity bears a globular glenoid. Conversely, the distal capitulum (**cap**, 7.2 mm in diameter) is sub-equal in size to the trochlea (**trc**, 7.1 mm in diameter). The medial entepicondyle (**ent**) lacks its epiphysis but clearly closely abuts the trochlea. The lateral ectepicondyle (**ect**) is weakly projecting. The entepicondylar foramen (**entf**) is enclosed by a slender entepicondylar buttress. The coronal depression (**crd**) is deeply excavated and reniform in shape.

The better-preserved left ulna (92.8 mm maximum length) lacks only its distal epiphysis and olecranon process (Fig. 2*b*).

The ulnar shaft is slender with a weakly sigmoidal ventral edge (common in derived macropodoids; Wells and Tedford 1995). It expands posteriorly towards the base of the olecranon process (**olcb**), which is broken off but appears to have been dorsoventrally tall (9.5 mm high at base). The semilunar notch (**sln**) of the elbow joint is bounded by the coronoid (**cor**) and anconeal (**anc**) processes, the latter bearing a small anterior projection at its midline for invasion of the olecranon depression on the humerus during flexion of the elbow. The trochlear facet (**trcf**) is shallowly cupped in medial view with a sub-vertical anterior border. The capitular facet (**capf**) has a laterally sloping notch for accommodation of the distal humeral head. The accompanying radial notch is sub-divided by a median ridge (continuous with the coronoid process) that separates the posterior capitular facet from the anterior radial facet (**raf**).

The right femur lacks only its proximal epiphysis (Fig. 2*c*, 111.8 mm maximum length), and there are fragments of the left femur. The femoral head (**fmh**) is domed and orientated perpendicular to the femoral shaft as is typical for macropodoids (Kear *et al.* 2007). The lesser trochanter (**let**) is incomplete and the greater trochanter is not preserved. The damaged remnant of the trochanteric fossa (**trf**) is longitudinally elongate and aligned with the shaft axis. The femoral shaft is slender (33.2 mm in circumference) but thickens towards its shank. Its posterior surface bears a weakly defined ridge and adjacent groove marking the insertion point for the *m. quadratus femoris* and adductor muscle complex (**qfi**). This differs from the condition in most derived macropodoids in which the *m. quadratus femoris*/adductor insertion area is dominated by a prominent boss (see Hopwood and Butterfield 1976; Wells and Tedford 1995). The distal femoral condyles are separated by a narrow intercondylar fossa (**icf**). The lateral tuberosity (**ltf**) of the distal femur is prominent and posteriorly directed; the medial tuberosity (**mtf**) is weakly developed.

The left tibia (131.9 mm maximum length) lacks only its proximal epiphysis (Fig. 2*d*). The shaft is slightly distorted but was clearly straight in both lateral and posterior views (a feature shared with advanced macropodoids; Murray 1995; Wells and Tedford 1995). The anterior tibial crest (**atc**) is dorsoventrally short, and rises steeply from the shaft. Its lateral surface is inset forming the lateral tibial fossa (**ltf**). The posterolateral tibial crest (**pltc**) borders a shallow concavity that probably accommodated the *m. flexor digitorum longus* in life (see Hopwood and Butterfield 1976). The lateral fibular contact (**ftc**) is elongate (as in advanced macropodoids; Murray 1995) and extends over half the shaft length. The distal epiphysis of the tibia (**det**) is oriented perpendicular to the long axis of the shaft. Its sub-rectangular trochlea (**trt**) bears a low saddle-shaped plateau separating the median and lateral trochlear grooves. The medial malleolus (**mmt**) is produced into a prominent ventromedial tubercle.

The right fibula (Fig. 2*e*) lacks both its proximal and distal epiphyses (120.2 mm long as preserved). The fibular shaft is D-shaped in cross-section (also reported in other primitive macropodoids; Kear *et al.* 2007), becoming rectangular proximally. Its distal half is transversely flattened for contact with the tibia (**tcf**).

The associated right calcaneum (SAM P23637, Fig. 2*f*) is missing its posterior epiphysis (18.9 mm long as preserved).

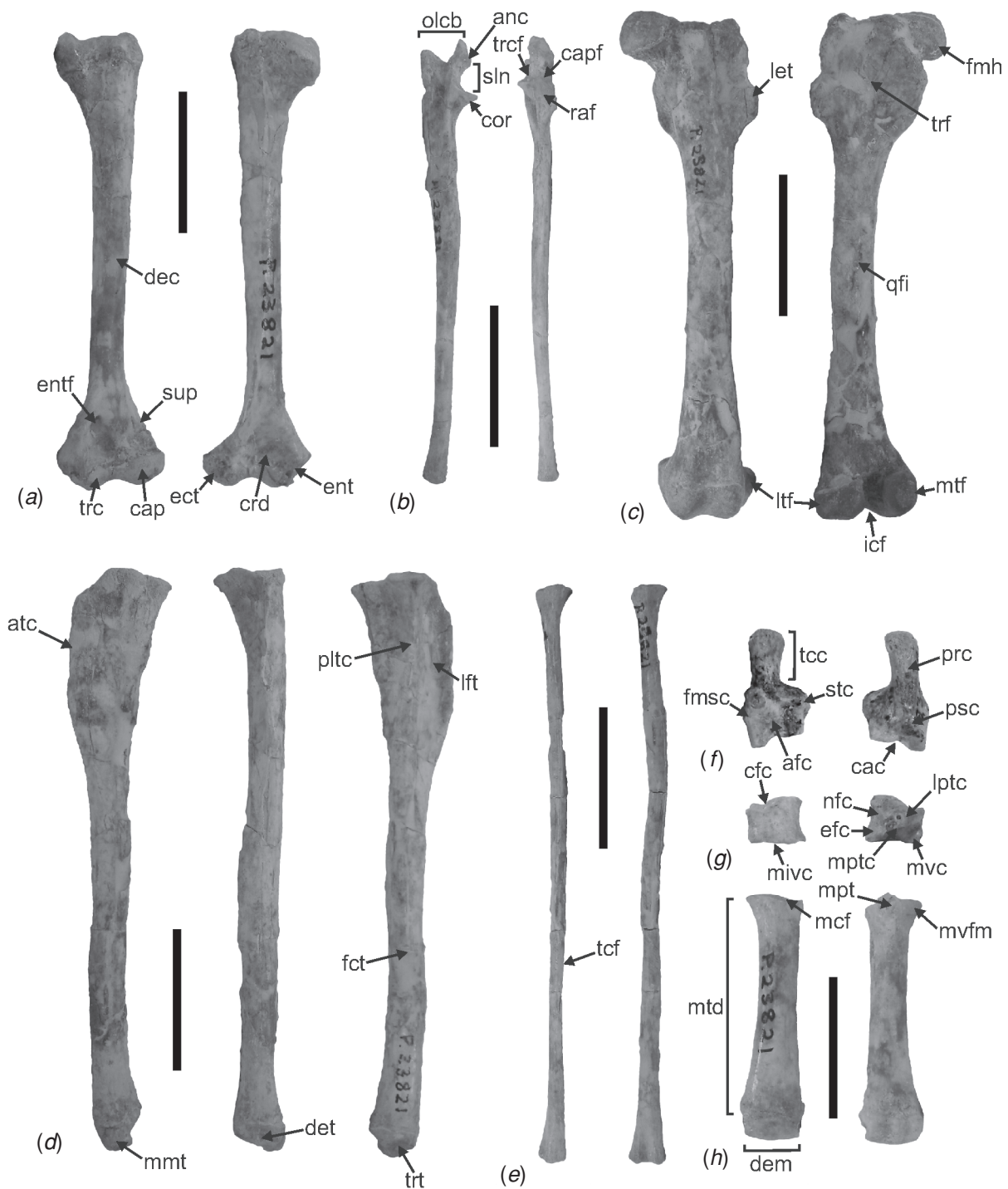


Fig. 2. Postcranial elements (SAM P23821) referred to *Ngamaroo archeri*. Humerus in (a) lateral and medial views. Ulna in (b) lateral and dorsal views. Femur in (c) anterior and posterior views. Tibia in (d) medial, anterior, and lateral views. Fibula in (e) lateral and medial views. Calcaneum (SAM P23637, f), cuboid (g), and metatarsal IV (h) in dorsal (left) and plantar (right) views. Anatomical abbreviations are explained in the main text; scale bars equal 20 mm.

The *tuber calcis* (**tcc**) is dorsoventrally deep and weakly flared posteriorly. The plantar rugosity (**prc**; supporting attachment for the calcaneocuboid ligament) is anteroposteriorly short with a shallow plantar sulcus (**psc**). The *sustentaculum tali* (**stc**) is transversely projected and slightly posteriorly inclined. The astragalar facet of the calcaneum (**afc**) lacks the medial constriction evident in derived macropodids (see Flannery 1989). The facet for the lateral fibular malleolus (**fmsc**) is weakly developed. The deeply stepped cuboid articulation (**cac**; a macropodoid synapomorphy; Flannery 1989) comprises an obliquely projecting dorsolateral facet separated from the median-ventral facet by a shallow groove. The inset dorso-medial facet is separated from the median-ventral facet by an indentation.

The complete right cuboid of SAM P23821 (Fig. 2g) articulates with SAM P23637. The cuboid is weakly proximodistally compressed (comparable to those of plesiomorphic macropodoids; Flannery and Rich 1986; Kear *et al.* 2007) but is still wider (10 mm across proximal facet) than long (8.6 mm maximum anteroposterior dimension). The calcaneal facet (**cfc**) is distinctly stepped with an inset dorsolateral facet and elevated dorsomedial facet. The median-ventral facet is concave and confluent with the ventral borders of both the dorsolateral and dorsomedial facets. The navicular facet (**nfc**) is located on the posterior edge of the medial sulcus. The ectocuneiform facet (**ecf**) is situated opposite the navicular facet. The metatarsal IV-cuboid contact (**mivc**) is shallowly concave. The metatarsal V contact (**mvc**) is restricted to a small lip extending posterolaterally against the cuboid's lateral surface. The lateral plantar tuberosity (**lptc**) is separated from the small knob-like medial plantar tuberosity (**mptc**) by a shallow groove.

The complete right metatarsal IV (with fused epiphysis; Fig. 2h) is slender (40 mm maximum length) and dorsoventrally compressed. The diaphysis (**mtd**) is straight in dorsal profile and slightly concave ventrally. There is no evidence of a plantar crest (characteristic of derived macropodids, Bishop 1997). The distal epiphysis (**dem**; 10.5 mm maximum width) bears a prominent medial articular keel. The proximal plantar tuberosity (**mpt**) is bordered anteromedially by the sesamoid facet, and posteriorly by the ventral lip of the cuboid facet (**mcf**). The intra-articular groove incising the cuboid facet surface is weakly defined. The posteromedial cuneiform facet is concave with a continuous (lacking a median groove) articular face. The metatarsal V facet (**mvfm**) is also continuous and extends ventrolaterally between the proximolateral and plantar tuberosities.

Locality and horizon

All specimens are derived from the Ngama Quarry on Mammalon Hill, Lake Palankarinna (Lake Eyre Basin), north-eastern South Australia. Mammalon Hill has been faunally correlated with the Late Oligocene, Zone D upper Etadunna Formation dated at 24.7–25 Ma (Woodburne *et al.* 1993; Callen *et al.* 1995). Note, there has been contention over precise age ranges for the upper-most Etadunna Formation with early-middle Miocene to Pliocene estimates also suggested for some localities on the basis of palynofloras (see Callen *et al.* 1995 for discussion).

Etymology

Species name *archeri*, in honour of Michael Archer for his extensive contributions to Australian palaeomammalogy.

Phylogenetic analysis

To test the relationships of *Ngamaroo archeri*, a cladistic analysis was conducted using a revised version of the most comprehensive published phylogenetic dataset of Tertiary Macropodoidea – Kear *et al.* (2007). This character matrix (see NEXUS format in Appendix) has been recoded to correct various minor errors and three new taxa added (*Bettongia penicillata*, *Purtia mosaicus*, *Wanburoo hilarus*) to help resolve placement among basal potoroids/macropodids. Three modified and four novel characters have also been added; these are listed and described below.

23. P^3_3 – (0) short ($<1.5 M^{1/1}$); (1) elongate ($>1.5 M^{1/1}$). Original description included nature of the transcrists; now distinguished as separate characters.
27. P_3 – (0) cingulids absent; (1) with distinct labial and/or lingual cingulids. Modified to accommodate additional presence of a labial cingulid.
33. Hypolophid formation – (0) hypolophid and buccal crest from entoconid absent; (1) formed by buccal crest from entoconid with posthypocristid low and posteriorly positioned; (2) formed by elevated posthypocristid, buccal crest from entoconid reduced or lost. Original character included information on other crests that needed to be more clearly conceptualised. Ordered 0–1–2.
105. Ventral margin of mandible – (0) convex (anterior mandible steeply inclined); (1) straight (anterior mandible shallowly inclined).
106. P_3 transcrists – (0) absent; (1) coarse, deeply incised; (2) fine, shallowly incised. Character ordered 0–1–2 because state 1 is expressed in basal Macropodoidea.
107. P_3 transcristid number – (0) transcristae absent; (1); 5 or less; (2) between 5 and 10; (3) 10 or more. Character is unordered because polarity of derived states is unclear.
108. Lower molar occlusal outline – (0) rectangular (length at least $0.3 > \text{width}$); (1) square (sub-equal length/width).

Phylogenetic analyses (incorporating a total of 108 characters and 29 taxa) returned identical trees whether all multistate characters were left unordered or were ordered where possible into morphoclines. Maximum parsimony trees, bootstrap frequencies (1000 replicates) and Bremer support were calculated using heuristic searches in PAUP* ver. 4.0b10 (Swofford 2002) with 200 random-addition replicates. Analyses with characters ordered yielded 160 most parsimonious trees (Length = 282; Consistency Index = 0.461, Retention Index = 0.716); relationships between major macropodoid clades are resolved *sensu* Kear *et al.* (2007) but show low bootstrap/Bremer support ($<50/1$ influenced by large amounts of missing data) at nodes other than Balbaridae (60/1), Potoroidae+Macropodidae (90/3), Macropodidae (50/1, including bulungamayines), Macropodinae+Sthenurinae (100/3), and Sthenurinae *sensu stricto* (100/4). A 50% majority rule consensus tree is shown in Fig. 3; strict consensus trees failed to resolve the basal bulungamayine polytomy within Macropodoidea.

Relationships of *Ngamaroo archeri*

The present phylogeny nests *Ngamaroo* in a polytomy with potoroine taxa and a discrete macropodid clade (Fig. 3). Affinity with these lineages (and differentiation from balbarids/hypsiprymnodontids) is supported by several strong synapomorphies (subscript numbering refers to characters listed above and those in the matrix of Kear *et al.* 2007): elongate P_3 [$>1.5 M^{1/1}$] with horizontal occlusal margin₂₃, M_1 with transversely broad trigonid basin₃₀, absence of a discrete M_1 protostylid₃₁. *Ngamaroo* lacks the derived states characterising advanced bulungamayines and macropodines/sthenurines (lophodont molars₂₄, hypolophid formed by elevated posthypocristid, buccal crest from entoconid reduced or lost₃₃). However, it does share key synapomorphies (P_3 with fine and shallowly incised transcrisids₁₀₆, P_3 transcrisid number >10 ₁₀₇) with the controversial genera *Purtia* and *Wakiewakie*, which have been variously allied with either basal bulungamayine macropodids (e.g. *Nowidgee*; Flannery 1989; Cooke 1997; Kear and Cooke 2001), or more traditionally, potoroines (Case 1984; Woodburne 1984). The principal character states common to these taxa (bunolophodont molars₂₄, hypolophid formed by a buccal crest from the entoconid₃₃) are symplesiomorphic; however, *Purtia*,

Wakiewakie and *Nowidgee* do display a derived square (sub-equal length/width) lower molar occlusal outline₁₀₈, which may be homologous (see Cooke 1997). *Ngamaroo* manifests rectangular molars (length at least $0.3 >$ width) – the primitive condition among macropodoids. Nevertheless, the presence of an M_4 that is not markedly smaller than the anterior molars₂₅ (an unexpected apomorphy considered unique to advanced macropodines and sthenurines; Kear *et al.* 2007), together with a P_3 that bears distinct labial and lingual cingulids₂₇ constitute robust dental synapomorphies that might support a potential macropodid relationship.

The postcranial skeleton of *Ngamaroo* is rather generalised but includes some novel derived traits also suggestive of macropodid affinity: humerus with entepicondyle closely abutting the trochlea₉₆ – this feature occurs elsewhere in *Hypsiprymnodon* and the macropodine *Dorcopsis* but differs from potoroines and most other macropodids, in which the entepicondyle and trochlea are typically separated by a broad groove (Kear *et al.* 2001, 2007); humerus with capitellum and trochlea of sub-equal size₉₈; and ulna shaft with distinctly sinuous ventral edge₉₉. The latter two characters are typical of advanced macropodids (Kear *et al.* 2001, 2007).

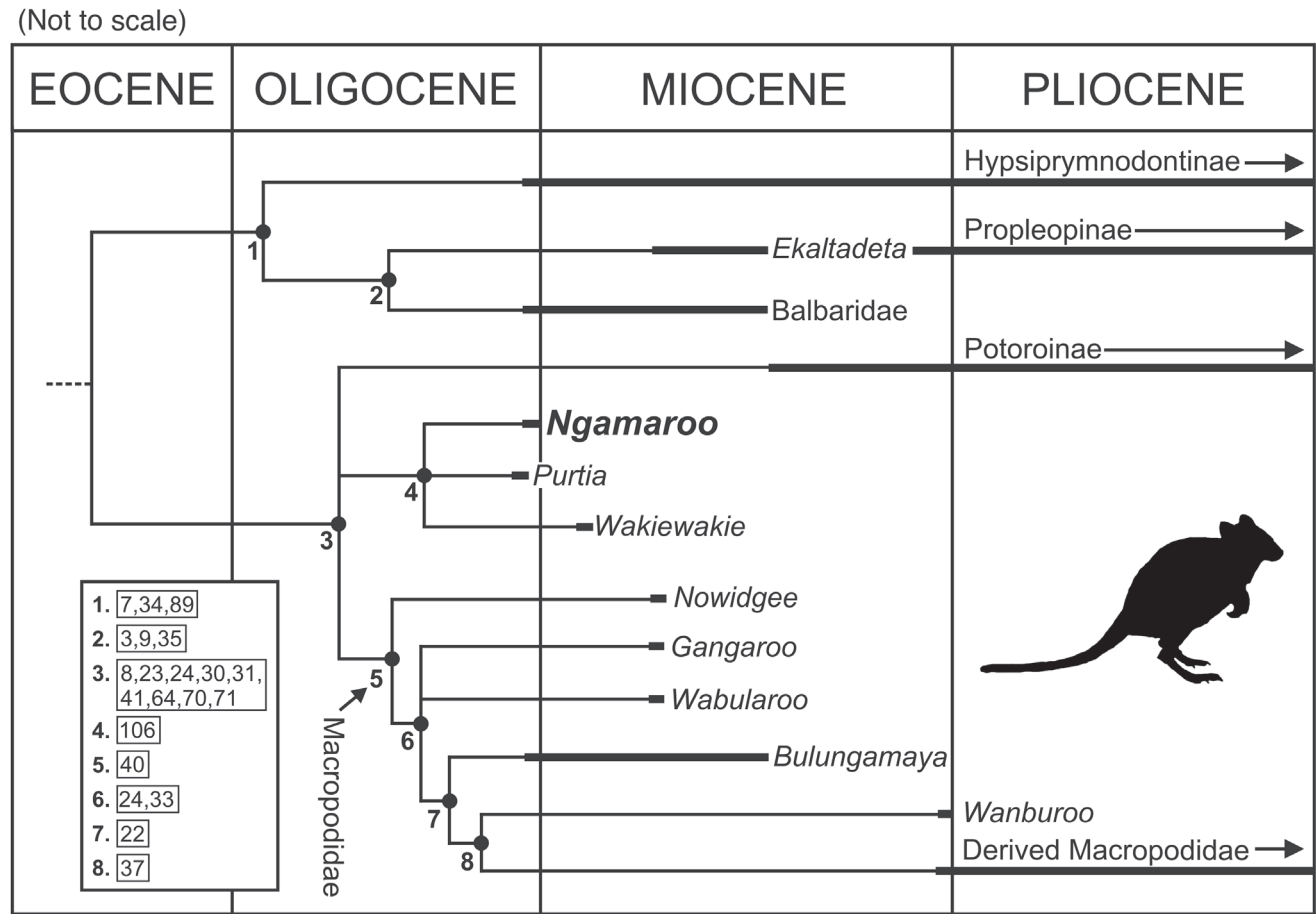


Fig. 3. Phylogeny and stratigraphic record of macropodoids including *Ngamaroo* (see Appendix). Boxed numbers represent unambiguous apomorphic character states supporting selected nodes (•). Topology presented is a 50% majority rules consensus tree of all most parsimonious trees; bootstrap/Bremer support values for major clades are provided in the text.

Both potoroids (comprising potoroidines only *sensu* Cooke and Kear 1999; Kear and Cooke 2001) and basal macropodids (*vis-à-vis* bulungamayines) are morphologically conservative and their monophyly/inter-relationships are poorly resolved in most recent analyses (see Cooke 1997, 1999; Burk and Springer 2000; Cardillo *et al.* 2004; Kear *et al.* 2007). Accordingly, bootstrap frequencies in the present phylogeny are relatively weak (influenced by >50% missing data for most fossil taxa in these groups) and examination of the 160 best trees shows that *Ngamaroo*, and the dentally comparable *Purtia* and *Wakiewakie*, form alternate clades with either potoroids (54 trees) or macropodids (24 trees) respectively. Given these results, definitive placement of *Ngamaroo* (together with *Purtia* and *Wakiewakie*) is deferred with a recommendation that Potoroidae and Bulungamayinae be treated as *incertae sedis* within Macropodoidea (see also Burk and Springer 2000; Cooke and Kear 1999; Kear and Cooke 2001; Kear *et al.* 2007), pending discovery of more complete material and/or the re-evaluation of existing taxa using expanded morphological/molecular datasets.

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