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# 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

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**ABSTRACT**—A new species, *Balbaroo fangaroo*, of balbarine kangaroo is described from the freshwater limestone deposits at Riversleigh, northern Australia. The type specimens include two partial skulls which reveal hitherto unknown characters of Balbarinae and provide new evidence relevant to the resolution of the phylogenetic affinities of Balbarinae. A number of the newly-revealed characters, e.g., squamosal-frontal contact on the walls of the neurocranium, are argued as being plesiomorphic for Macropodoidea.

Hypertrophied upper canines which occur in the paratype, have never previously been recorded in kangaroos and represent an example of evolutionary convergence between these herbivorous marsupials and ungulate eutherians.

## INTRODUCTION

THE MACROPODID subfamily Balbarinae was erected by Flannery, Archer, and Plane (1983) to accommodate two new species of fossil, lophodont kangaroos, *Balbaroo camfieldensis* from middle Miocene Bullock Creek Local Fauna of the Camfield Beds in the Northern Territory, and *B. gregoriensis* from late Oligocene-early Miocene deposits in the Riversleigh World Heritage Area of northwestern Queensland. Subsequently Flannery and Rich (1986) described a new balbarine genus, *Nambaroo*, and three new species from late Oligocene deposits at Lake Tarkarooloo in South Australia. They regarded these species as the most plesiomorphic macropodids known at the time. Cooke (1992) described a new genus, *Ganawamaya*, and three new Oligo-Miocene Riversleigh species of balbarines with a slightly more derived dental morphology than that exhibited by *Nambaroo*. Cooke (1997a) described an additional species of *Nambaroo* and a new balbarine genus and species, *Wururoo*, also from Oligo-Miocene deposits at Riversleigh. Premolar morphology in the latter taxon suggests a closer affinity with the species of *Balbaroo* than with *Nambaroo* and *Ganawamaya*. Further balbarine species are reported by Woodburne et al. (1993) from the Oligo-Miocene Namba, Etadunna, and Wipajiri formations of South Australia.

Balbarines have gained considerable phylogenetic significance since Flannery (1989) proposed that they were probably ancestral to both macropodines and sthenurines among macropodids. More recently Cooke (1997b) indicated that lophodonty evolved independently within a second group of Oligo-Miocene kangaroos, the bulungamayines, first described by Flannery, Archer, and Plane (1983) who placed them within Potoroidae. Bulungamayine kangaroos are thus rival candidates for the role of ancestors of modern, lophodont kangaroos. Wroe, Brammal, and Cooke (1998), on the basis of comparisons with undescribed balbarine cranial remains, indicated potential synapomorphies uniting Balbarinae and extinct giant rat kangaroos in the subfamily Propleopinae. Because of the nature of the published Oligo-Miocene fossil material (some balbarine species are known only from isolated molars), until now arguments concerning the relationships of balbarine and bulungamayine kangaroos with recent and modern taxa have relied chiefly on evidence drawn from dental and mandibular morphology.

This paper provides description of dental morphology and the major features of cranial and mandibular remains of a new species of *Balbaroo* from the Riversleigh World Heritage Area.

More detailed descriptions of cranial anatomy catering to specialist interest will be provided in a subsequent paper. The holotype consists of a partial skull and a dentary, both recovered in close proximity to each other from the same block of freshwater limestone, leaving little doubt about their original association. The paratype preserves upper incisors, cheek teeth, and unusually hypertrophied canines. Canines of this type have not previously been reported in kangaroos. Cranial features of the new specimens provide further evidence that can contribute to a resolution of the affinities of Balbarinae.

Suprageneric classification follows Aplin and Archer (1987), molar homology follows Luckett (1993), and premolar homology follows Flower (1867). Cusp homology of upper molars is that of Tedford and Woodburne (1987). Molar descriptive terminology is used as in Cooke (1997a). QMF denotes Queensland Museum fossil collection catalogue numbers. Measurements are in millimeters.

## SYSTEMATIC PALEONTOLOGY

Family MACROPODIDAE Gray, 1821

Subfamily BALBARINAE Flannery, Archer and Plane, 1983

Genus BALBAROO Flannery Archer and Plane, 1983

BALBAROO FANGAROO new species

Figures 1–5; Table 1

**Diagnosis.**—*Balbaroo* having an  $M_1$  with a low, broad-based paraconid positioned close to the anterior margin, anterior and slightly lingual to the protoconid, contacted by a diagonal paracristid.  $M_1$  lacking an anterior cingulid but with a steeply descending precingulid buccal to the paracristid. Anterior lower molars with a well-developed hypocingulid lingually continuous with the postentocristid, lacking a posthypocristid.

Upper molars markedly wider anteriorly than posteriorly, having well-developed anterior cingula crossed by one or more short and poorly-defined enamel ridges. Anterior upper molars with postparacristae and premetacristae sharply lingually inflected in the interloph region and forming the lingual margins of opposed triangular, flat surfaces on the basal, interloph surfaces of buccal cusps. Traces of a neometaconule and associated crista visible on the posterior surface of the metaloph of anterior upper molars.

$I^1$  elongate, slightly recurved, pointed and laterally compressed. Posterior upper incisors low crowned with broad occlusal surfaces.

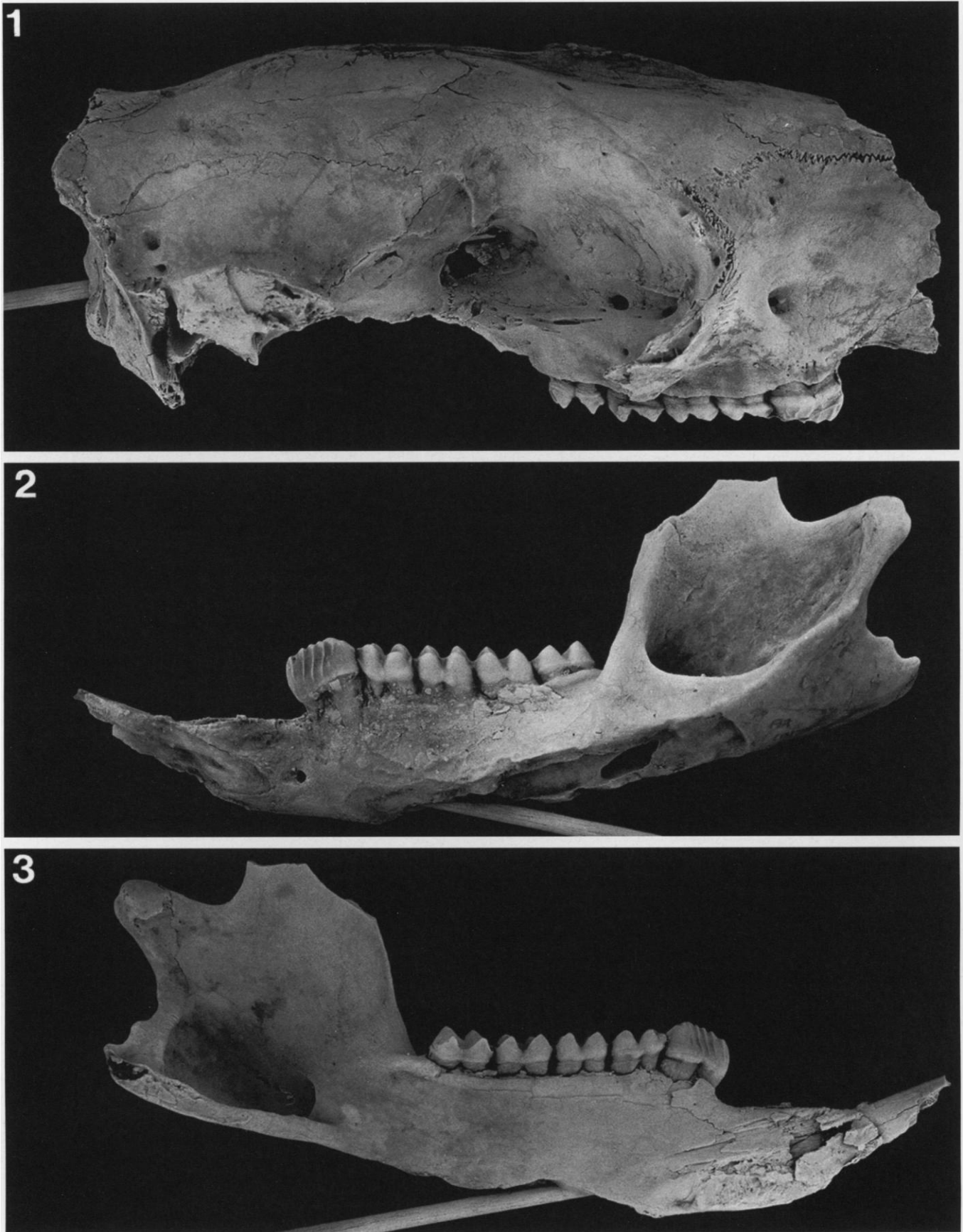


FIGURE 1—QMF36994, holotype of *Balbaroo fangaroo* n. sp. 1, Dorso-lateral view of cranium; 2, buccal view of mandible; 3, lingual view of mandible.

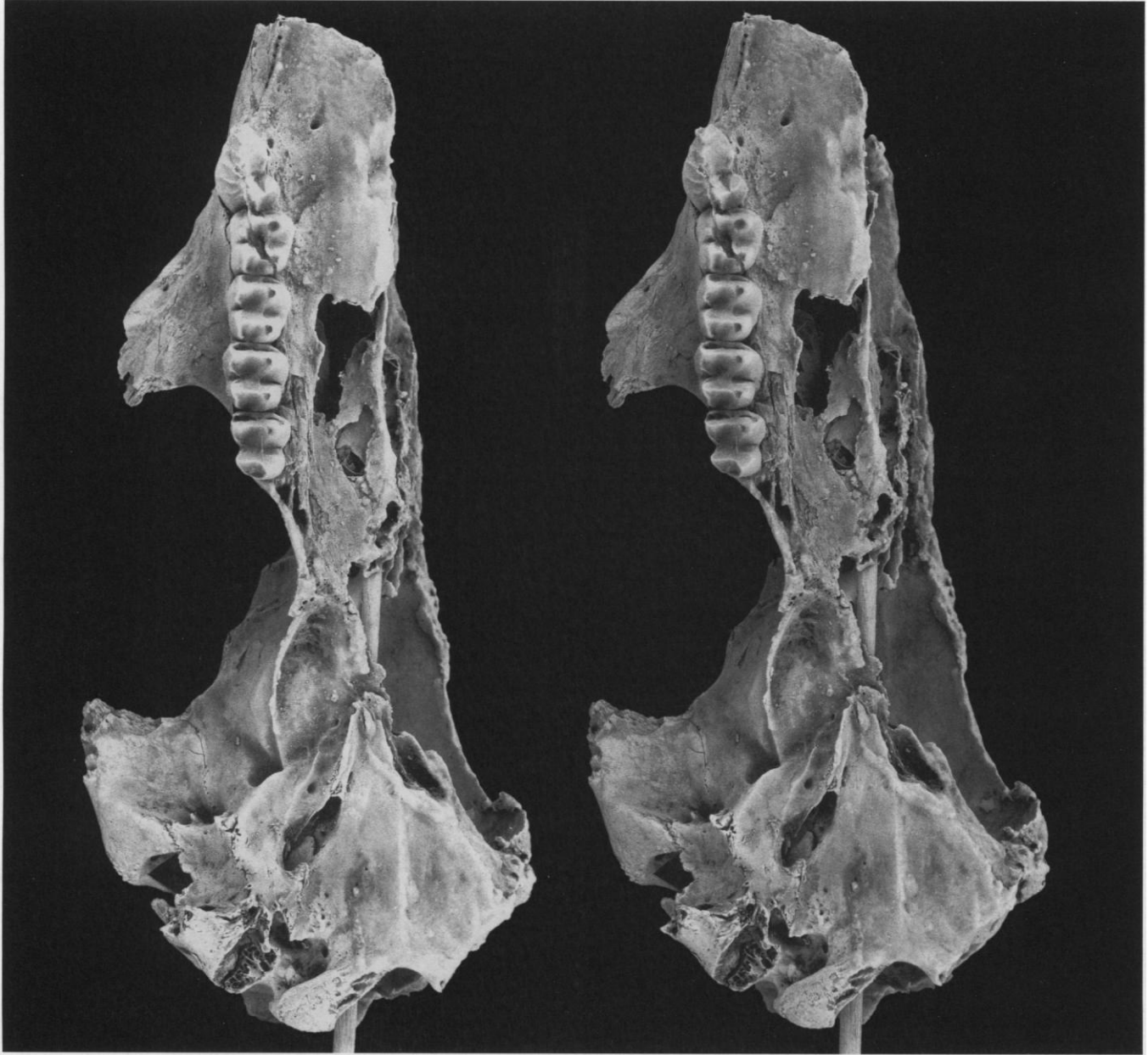


FIGURE 2—QMF36994, holotype of *Balbaroo fangaroo* n. sp., stereo pair of palatal view of cranium.

*Description.*—

QMF36994.—The skull is larger than that of any extant potoroid and approximates that of modern wallabies in size. There is minimal flexion in the basicranial or rostral regions. The skull is shallow dorsoventrally and the neurocranium is relatively narrow transversely but with a broad suprazygomatic sulcus laterally. Strong postorbital constriction accentuates the marked inflation of the frontal sinuses. A shallow median basin is present in the frontal bones anterior to this constriction.

The anterior of the zygomatic arch merges gradually with the facial region, there being no prezygomatic sulcus such as is usual in macropodids. The single infraorbital foramen is dorsal to the posterior margin of P<sup>3</sup>. The masseteric process is short, not reaching the level of the alveolar margin, and is separated from the alveolar process by a shallow sulcus. The shape of the posterior margin of the palatal portion of the maxilla suggests the

presence of a posterior palatal vacuity that extended forward as far as M<sup>2</sup>. The lachrymal bone barely extends onto the facial region but contributes significantly to the mesial wall of the orbit. Two lachrymal foramina, separated by a rugose tuberosity, are present on the anterior orbital margin. There is a deep sub-orbital fossa present within the orbital surface of the jugal.

The dorsal margin of the neurocranium is domed with a strong nuchal crest projecting posteriorly to overhang the supraorbital region. A pair of superior temporal crests converge posteriorly to form a low sagittal crest. A much expanded dorsal wing of the squamosal forms the lower half of the lateral wall of the neurocranium. Its upper half is formed by the parietal. A posterior projection of the frontal makes a 5.5 mm contact with the anterior margin of the squamosal, preventing any contact between the parietal and alisphenoid which forms the anterior part of the wall of the neurocranium.



FIGURE 3—QMF36994, holotype of *Balbaroo fangaroo* n. sp., stereo pair of occlusal view of mandible.

The paroccipital process is broken off at its base. The mastoid process is slightly damaged at its tip, but is still longer than is usual among macropodoids. It is inclined ventrolaterally and extends beyond the ventral margin of the occipital condyle. The base of the mastoid process is broader than the broken base of the adjacent paroccipital process.

The basioccipital is broad, roughly hexagonal in outline and has a low, central longitudinal keel. Its suture with the basisphenoid is indistinguishable, but both bones lie in the same horizontal plane. The ectotympanic is roughly rectangular in ventral view and concave in its central region. It is U-shaped in lateral view, not enclosing the external auditory meatus dorsally. The articular eminence of the glenoid fossa is rectangular and broad transversely.

*Dentary.*—Bone has been lost from the central ventrolateral margin, the anterior lateral margin (exposing the root of  $I_1$ ) and from the anteromedial surface. The mandibular symphysis extends posteriorly to the level of the posterior of  $P_3$ . The mental foramen is located below and slightly anterior to  $P_3$ . The ascending ramus rises at an angle of approximately 80 degrees to the cheek tooth row. A flat, triangular surface is present on the anterior buccal wall of the masseteric fossa, presumably for the attachment of superficial layers of the masseter. The masseteric canal extends anteriorly to the level of  $M_2$ , and is separated from the anterior portion of the inferior dental canal by a bony lamina. The angular process is broad transversely with an undulating posterior margin. The mandibular foramen is vertically elliptical. A short length of inferior dental canal runs anteriorly from here to the masseteric fossa within which it continues anteriorly as a recess in the lingual wall to the level of  $M_4$ . The condyle is broad transversely, rounded on its dorsal and posterior surfaces, with an articular surface which is roughly triangular in outline.

*Upper dentition.*—The cheek tooth row is straight but with  $P^3$  flexed anterobuccally out of alignment. Molar teeth are brachylophodont. Both paracone and metacone shift buccally from  $M^1$ – $M^4$ . The relative height of metaconules increases posteriorly, that of  $M^4$  being about the same height as the protocone. Vertical orientation of buccal cusps changes from being steeply anterodorsally inclined on  $M^1$  to being almost vertical on  $M^4$ . The  $M^4$  metaloph is shorter than those of  $M^1$ – $M^3$ , which are of similar lengths.

$P^3$  does not greatly exceed  $M^1$  in length. Its occlusal crest is slightly concave centrally, the likely result of wear, since a wear facet is present in this region. In occlusal view, the buccal margin and occlusal crest are both convex buccally but the lingual margin is concave. A low, bulbous cusp is present at the posterior lingual corner of the tooth. Presumably originally five cusps occurred on the occlusal crest, since five distinct cristae curve from the crown base to the occlusal crest on the buccal side (corresponding crests on the lingual surface are partly obscured by wear). The most posterior cuspsule is largest and has an abbreviated sixth buccal crest associated with it.

$M^1$  has lost sections of enamel from the interloph valley and from the metaloph. Wear basins occur in the enamel of the posterior faces of the protoloph and metaloph. The protoloph is longer than the metaloph. A poorly-developed anterior cingulum is crossed by a “forelink” or ridge of enamel originating at the anterior base of the protoloph. The interloph is shallow but broad anteroposteriorly. The postprotocrista inclines posterobuccally between the protocone apex and the interloph valley, but then turns posteriorly to meet the metaloph lingual to the midline. Both the postparacrista and premetacrista show a marked lingual flexion as they run from their respective cusp apices to meet in the interloph valley. A much less distinct stylar crest diverges from the point of flexion of the postparacrista, the two crests enclosing a triangular, flat area at the base of the paracone. A similar area occurs at the anterior base of the metacone but there is no corresponding stylar crest.

The postmetacrista forms the buccal margin of a relatively broad metacingulum whose lingual and posterior margins are formed by the postmetaconule crista. A poorly-defined swelling on the posterior face of the metaloph represents the position of a worn neometaconule (or perhaps a poorly-developed postlink without a corresponding cusp on the metaloph).

$M^2$  has depressions resulting from wear in the enamel of the posterior, lingual surfaces of protocone and metaconule. A better-defined and transversely longer anterior cingulum is present, narrowing gradually from the buccal to lingual end. The shallow trough between the protoloph base and the anterior margin of the cingulum is crossed by a very small “forelink” at about the

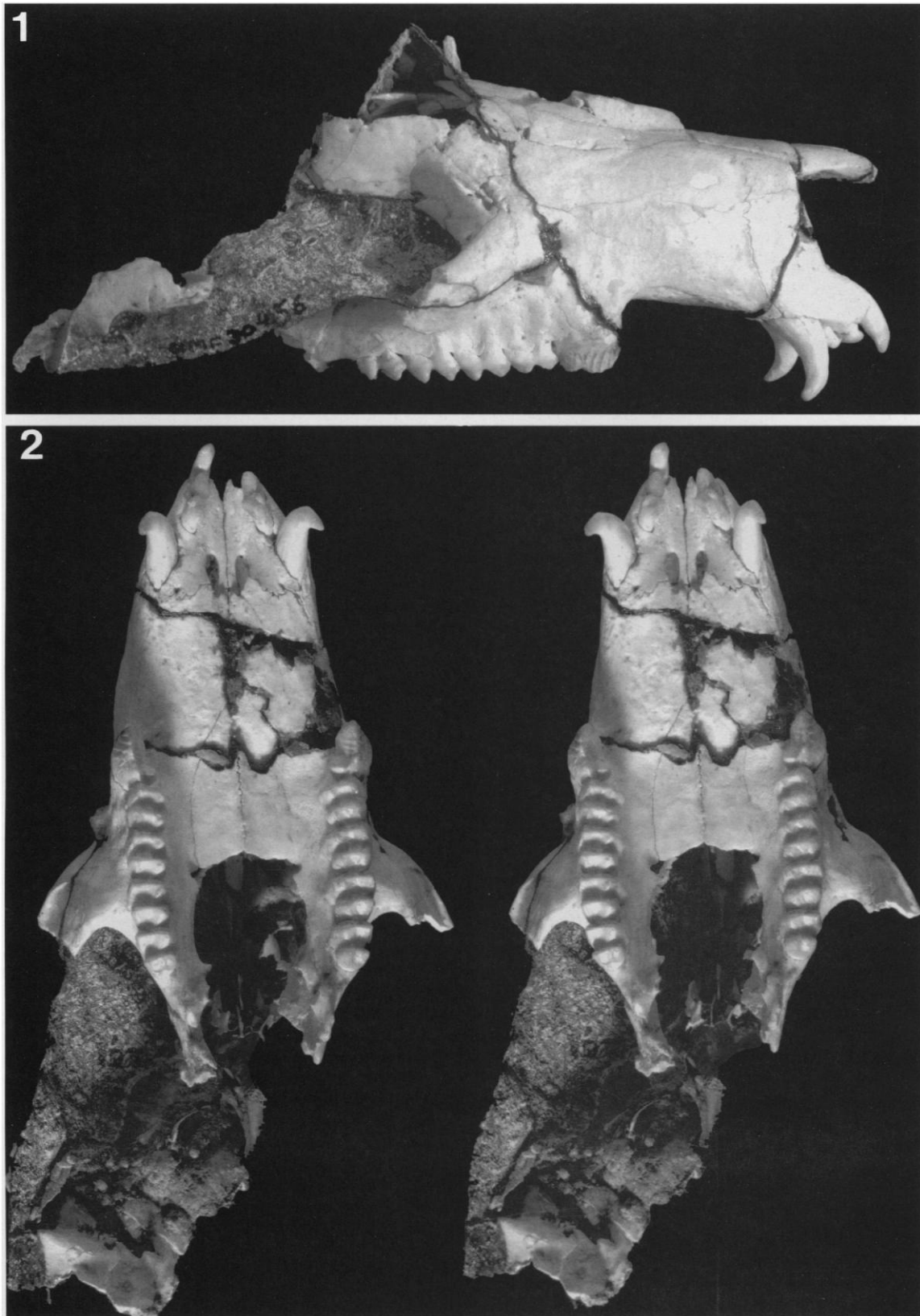


FIGURE 4—QMF30456, paratype of *Balbaroo fangaroo* n. sp. 1, Right lateral view; 2, stereo pair of palatal view.

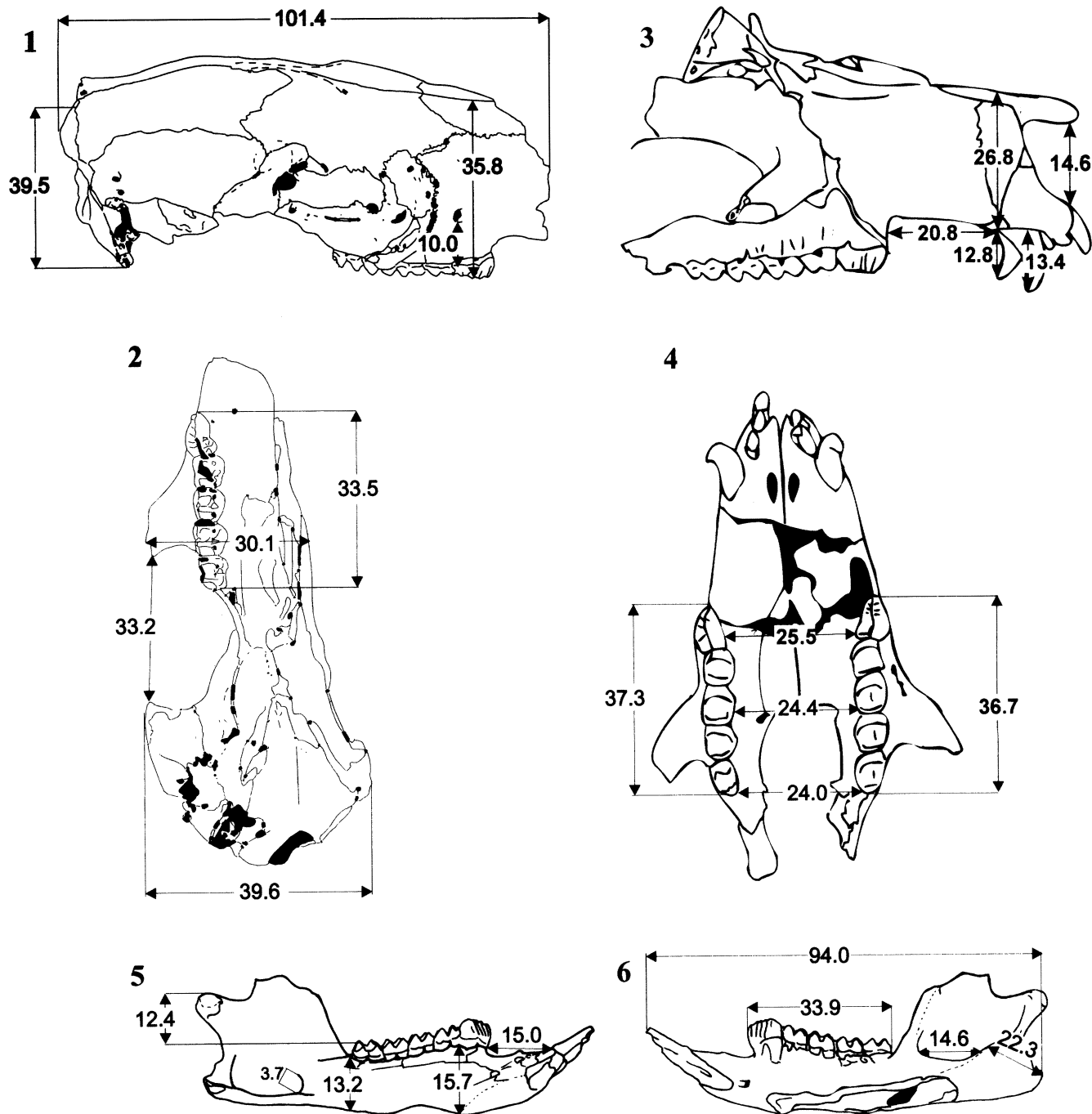


FIGURE 5—Dimensions of type specimens of *Balbaroo fangaroo* n. sp. 1, 2, QMF36994, holotype, cranial dimensions; 3, 4, QMF30456, paratype, cranial dimensions; 5, 6, QMF36994, holotype, mandibular dimensions.

midline. The postprotocrista is worn. Similar triangular flat surfaces to those described on  $M^1$  occur on the interloph surfaces of paracone and metacone, but no styler crests are present. The metacingulum is transversely shorter than that of  $M^1$  and the putative neometaconule is marked only by a slight swelling on the posterior face of the metaloph.

$M^3$  is similar in size to anterior molars. Small wear basins occur in the enamel on the posterolingual face of the protoloph and the lingual side of the metaloph crest. The anterior cingulum narrows less than that of  $M^1$  and is crossed by two worn enamel

ridges from the base of the protoloph. The postprotocrista is more worn than that of anterior molars. The metacingulum is more basally situated.

$M^4$  is shorter than  $M^3$  and its protoloph is considerably longer than the metaloph. A small wear basin is present on the posterior, lingual surface of the protoloph. The anterior face of the metaloph has been thegosed such that there is a sharp drepanon between metaconule and metacone. This is the only molar to display such well-defined thegotic function, perhaps because of its later eruption. Two enamel ridges cross the anterior cingulum.

TABLE 1—Dental measurements for type specimens of *Balbaroo fangaroo* n. sp. Abbreviations: al = length at alveolar margin; aw = width at alveolar margin; ah = height measured from alveolar margin; ch = maximum crown height; hw = width at hypolophid; l = maximum length; mw = width at metaloph; pw = width at protoloph or protolophid; w = maximum width.

Catalog no.		I <sup>1</sup>			I <sup>2</sup>			I <sup>3</sup>			C <sup>1</sup>					
		l	w	ch	l	w	ch	l	w	ch	al	aw	ah			
QMF30456	L	3.7	2.8	3.3	4.1	2.9	1.1	3.5	3.6	1.3	8.1	4.6	11.6			
	R				3.8	2.7	1.1	3.8	3.5	2.1	8.4	4.5	12.7			
		P <sup>3</sup>			M <sup>1</sup>			M <sup>2</sup>			M <sup>3</sup>			M <sup>4</sup>		
		l	w	ch	l	pw	mw	l	pw	mw	l	pw	mw	l	pw	mw
QMF30456	L	9.9	6.5	6.0	7.1	6.7	6.4	7.0	7.0	5.9	7.4	6.8	5.6	7.1	5.9	4.6
	R	8.6	6.4	6.2	6.6	6.7	6.1	7.4	7.0	5.8	7.3	7.0	5.6	7.1	6.2	4.7
AR10175	R	8.9	5.7	5.1	6.2	6.2	5.6	6.4	6.2	5.5	6.7	6.1	5.2	6.7	5.7	4.6
		P <sub>3</sub>			M <sub>1</sub>			M <sub>2</sub>			M <sub>3</sub>			M <sub>4</sub>		
		l	w	ch	l	pw	hw	l	pw	hw	l	pw	mw	l	pw	hw
AR10175	L	8.4	4.6	5.5	6.3	3.9	4.9	6.2	4.7	5.0	6.5	5.1	4.8	6.7	4.9	4.4

The “midlink” (postprotocrista) is largely obliterated by wear. The flat surfaces on the interloph faces of paracone and metacone are not evident on this tooth. The metacingulum is transversely shorter than that of M<sup>3</sup>, but on this tooth there is no direct connection between the posterior margin of the cingulum and the postmetacrista.

*Lower dentition.*—I<sub>1</sub> is badly damaged: its distal end and buccal surface have been lost. Its proximal portion suggests an elliptical cross-section at the base. The tooth rises at an angle of approximately 10 degrees to the dorsal margin of the diastema.

There is a small, anteriorly-directed alveolus located immediately posterior to I<sub>1</sub>, indicating the presence of a small tooth, either a procumbent I<sub>2</sub>, or a small canine tooth.

P<sub>3</sub> is taller than the molars and flexed anterobuccally out of alignment with the molar row. In occlusal view the lingual margin of the tooth is relatively straight while the buccal margin is convex. Maximum width is attained at about the mid point of the long axis of the tooth. The anterior and posterior margins of the tooth are delineated by vertical ridges of which the anterior is more prominent. On the buccal side of the tooth there are five (or possibly six, wear having obliterated detail from the posterior flanks of the crown) transcrisids which arise from the basal part of the crown and curve posteriorly as they ascend to terminate in five (or possibly six) small cusps on the crest of the tooth. The posterior cuspid (or cuspids if there are six) accounts for about one-third of the length of the tooth. On the lingual side, four of five similar transcrisids are visible and intact, but only the occlusal end of the fifth is evident, the rest having been obscured by wear. A small depression has been worn in the occlusal tip of the posterior cuspid.

The M<sub>1</sub> trigonid ramps upwards to rest against the posterior face of P<sub>3</sub>. M<sub>1</sub> approximates M<sub>2</sub> in size but has a much narrower protolophid. The protoconid is positioned buccal to the midline of the tooth, but well lingual of the buccal margin. The protoconid height is considerably greater than the hypoconid height, this feature being unique to this molar in the tooth row. The paracristid is anterolingually inclined from the protoconid apex. Before reaching the anterior margin, there is a low eminence on the paracristid crest and an expansion of its lingual surface, these features marking the position of the paraconid. At its anterior end, the paracristid meets the lingual end of an anteroposteriorly narrow precingulid which descends towards the crown base on the buccal side, becoming progressively less distinguishable as it does so. There is no comparable anterior cingulid on the anterolingual corner of the crown. The anterobuccal corner of the metaconid is swollen such that it approximates the expanded

lingual base of the paraconid, thereby defining an elevated trigonid basin with an opening on the lingual side via a shallow, furrow which represents a gap between the metaconid and the paraconid. The interlophid valley is moderately long and is open both lingually and buccally. It is crossed by a cristid obliqua passing from the anterolingual area of the hypoconid to terminate on the lingual side of the base of the protoconid. A postentocristid meets the lingual end of a hypocingulid which terminates abruptly before it reaches the buccal base of the hypolophid and is separated from the base of the hypolophid by a distinct groove. Small depressions caused by wear are visible in the enamel at the apex of the protoconid, the posterior of the metaconid, the lingual surface of the hypoconid, and the posterior, lingual surface of the entoconid.

The hypolophid of M<sub>2</sub> is slightly wider than the protolophid. The trigonid basin is broader and much better-developed than it is in M<sub>1</sub>, is bordered lingually by a premetacristid and has a horizontal anterior floor. There is a short, steep precingulid buccal to the paracristid. The interlophid valley and the cristid obliqua are as described for M<sub>1</sub> except that the cristid obliqua intersects the protolophid well lingual to the protoconid. The hypocingulid is similar to that described for M<sub>1</sub>, but is shorter, terminating at a point posterior to the approximate mid-point of the hypolophid. Small, worn depressions in the enamel occur on the anterior, lingual surface of the protoconid, the posterior surface of the metaconid, the anterior, lingual surface of the hypoconid and the posterior surface of the entoconid.

The lophids of M<sub>3</sub> are equal in length. The trigonid basin resembles that of the M<sub>2</sub> but is bounded on the lingual side by a more prominent premetacristid. The interlophid valley and cristid obliqua are as described for M<sub>2</sub>. The hypocingulid is longer and more centrally positioned at the base of the hypolophid than that of the M<sub>2</sub>. Small, worn depressions occur in the enamel on the anterior, lingual surface of the protoconid, the lingual surface of the hypoconid and, to a lesser extent, on the posterior face of the entoconid.

The hypolophid of M<sub>4</sub> is narrower than the protolophid. The trigonid basin is about the same transverse length and width as that on the M<sub>3</sub>. There is no precingulid. The cristid obliqua is less well-defined than those on the anterior molars, but the interlophid valley is generally similar to that seen in the other molars. The hypocingulid is very much reduced, consisting of a short, horizontal shelf forming the basal portion of a shallow depression in the medial region of the posterior face of the hypolophid. There is a thickened band of enamel running transversely across the posterior, basal portion of the crown below the remnant of the hypocingulid.



Meristic gradients along the lower molar row are as follows: the proportional width of the trigonid increases posteriorly with the anterior cingulid increasing proportionately in length as that of the precingulid decreases; the hypocingulid, except for that of  $M_2$ , decreases in length from  $M_1$  to  $M_4$ ; crown height is relatively constant from  $M_{1-3}$ , and then reduces in  $M_4$ ; the entoconid becomes anteroposteriorly shorter from  $M_1$  to  $M_4$  as does the metaconid from  $M_2$  to  $M_4$ ; the protolophid becomes longer from  $M_1$  to  $M_4$ ; the lingual profile of the midvalley changes from V-shaped in  $M_1$  to U-shaped in  $M_4$ ; the molar row is torted such that the lophids of  $M_1$  are subhorizontal while those of  $M_4$  are inclined ventrolingually; all lophids and cusps exhibit diffuse wear facets except the hypolophids of  $M_3$  and  $M_4$  which display distinct thegotic facets on their posterodorsal edge.

QMF30456.—The lateral walls of the rostrum are slightly inflated dorsal to the diastema. Lateral margins of the nasals converge acutely anterior to the canines, are roughly parallel dorsal to the diastemal region, but are divergent more posteriorly. Damage to the specimen prevents determination of the position of the posterior margins of the nasals.

In lateral view the posterior, lateral margins of the premaxilla are shallowly anteriorly concave as they ascend the walls of the rostrum before turning abruptly posteriorly close to the dorsal surface and terminating at a point dorsal to the anterior third of the diastema. Left and right premaxillae are not strongly fused in the midline of the palatal surface and their medial margins diverge in the region of P-I. Incisive foramina are elongate, tear-drop shaped and broader anteriorly. Their posterior margins extend to the premaxillae-maxillary boundaries. Smaller foramina occur on these boundaries just medial to the canines.

The lateral margins of palatal foramina are visible at the lateral edges of the anterior margin of the apparently single, large palatal vacuity. Other skull elements are similar to those described in the holotype.

**Dentition.**—Molar rows are laterally convex in occlusal view and slightly convergent posteriorly. Molar size decreases posteriorly. Anterior molar occlusal surfaces are inclined lingually, those of more posterior molars are inclined buccally. P3 is flexed buccally out of alignment with the molar row. Occlusal surfaces of P<sup>2</sup> and P<sup>3</sup> lie in about the same horizontal plane as molar occlusal surfaces, but the distal end of P<sup>1</sup> projects below this plane. P<sup>1</sup> is a large, elongate, laterally compressed and ventrally tapering tooth, slightly recurved in lateral view. Its crown height is about twice that of the more posterior incisors. Enamel is confined to the anterior and labial surface of the crown. In anterior view the tooth is slightly mesially inclined.

Both P<sup>2</sup> and P<sup>3</sup> show signs of considerable wear on their occlusal surfaces, indicating that crown height has been reduced in both these incisors. Occlusal surfaces of both are inclined towards the midline of the palate, buccal crown walls being taller than lingual walls. Presumably occluding surfaces of P<sup>1</sup> were oppositely inclined. P<sup>2</sup>: enamel on the oval-shaped occlusal surface is confined to the margins. In lateral view the crown is longest at the occlusal margin, anterior and posterior walls converging towards the crown base.

P<sup>3</sup> abuts the posterior margin of P<sup>2</sup>. The crown is heart-shaped in occlusal view, tapering posteriorly. There is a short, vertical furrow in the enamel of the mid-buccal surface.

Upper canines are closely posterior to the posterior incisors (the alveolus of LC<sup>1</sup> communicates with that of LI<sup>3</sup>), and are lateral to the incisor row. The canines are more than twice as tall as P<sup>1</sup>, strongly recurved and inclined slightly ventrolaterally. The size and orientation of these teeth are such that they may have been visible externally, even when the mouth was closed. Morphology of upper premolars and molars closely resembles

that described in the holotype, although the teeth are less worn and the M<sup>1</sup> preprotocrista is more obvious in this specimen.

**Etymology.**—Because of the pronounced “fangs” present in the paratype specimen, Michael Archer bestowed upon it the laboratory name, “fangaroo.” The new species has since had popular media recognition under this name and it has therefore been preserved as the specific epithet.

**Types.**—Holotype, QMF36994, right half of a cranium and an associated left dentary; paratype, QMF30456, anterior portion of a skull preserving most of the rostrum and the anterior portions of the orbits.

The holotype is from Outasite, a fossil locality from the mid to lower levels of the System B deposits (Archer et al., 1989; Creaser, 1997) on Godthelp’s Hill at Riversleigh. The paratype is from Margan’s Immense Might, a locality low on the northern flank of the plateau on which occurs D Site of Tedford, 1967 (D-Site Plateau). Archer et al. (1989) include D site in their Riversleigh System A which includes Riversleigh’s oldest (Late Oligocene) sites.

**Occurrence.**—Myers and Archer, (1997) correlate the fauna of the Riversleigh White Hunter Site (included in Riversleigh System A by Creaser, 1997) with the Late Oligocene Ngama Local Fauna of the Etadunna Formation of South Australia, dated at 24.7–25.0 Ma (Woodburne et al., 1993). The age of the holotype is therefore younger than this, possibly later Oligocene or early Miocene. Age of the paratype remains uncertain, but its site locality suggests it is likely to be older, rather than younger than the holotype.

**Discussion.**—*Balbaroo fangaroo* exhibits a number of cranial features normally associated with potoroids rather than macropodids. Notable among these is the presence of squamosal-frontal contact on the side of the braincase. Similar contact occurs in other undescribed balbarine cranial remains recovered from Riversleigh and the condition is here regarded as symplesiomorphic for the subfamily. Alisphenoid-parietal contact has been assumed to be the plesiomorphic condition for Macropodoidea, since it occurs in phalangerids. Case (1984) and Woodburne (1984) both considered the presumed derived squamosal-frontal contact to be a diagnostic feature of potoroids among macropodoids. Similar views were expressed by Pearson (1950). Unilateral or bilateral alisphenoid contact sometimes occurs in the potoroid *Bettongia leseur* (Johnson and Strahan, 1982), while squamosal-frontal contact in *Hypsiprymnodon moschatus* is very short (Pearson, 1950). Flannery and Archer (1987a, 1987b) demonstrated that alisphenoid-parietal contact also occurs in Oligo-Miocene potoroids (*Bettongia moyesi*) and hypsiprymnodontines (*Hypsiprymnodon bartholomai*) and concluded that squamosal-frontal contact could no longer be recognised as a potoroid synapomorphy. They suggested that this feature evolved independently at least four times within Potoroidae. Its occurrence among balbarines may represent the fifth such independent evolution within Macropodoidea and its first recorded instance among macropodids. If, as Flannery (1989) has suggested, balbarines were ancestral to both sthenurines and macropodines, reversion to the assumed plesiomorphic condition would have to have occurred in each of the descendant taxa. It is more parsimonious to regard squamosal-parietal contact as plesiomorphic within Macropodoidea, since this would require the derived condition (alisphenoid parietal contact) to evolve independently a maximum of four times—within Hypsiprymnodontidae, Potoroinae Macropodinae and Sthenurinae, but possibly only three if the reversion occurred in the common ancestor of macropodids. Significantly, since bulungamayines have been suggested as candidates for that role (Cooke, 1997b), all Riversleigh bulungamayine skulls so far recovered and in which the condition is evident, have alisphenoid-parietal contact.

The smooth transition of the zygomatic arch onto the cheek region and the absence of an antorbital sulcus in *Balbaroo fangaroo* are also conditions more usual in potoroids than in macropodids in which there is an abrupt transition to the cheek region and an antorbital sulcus anterior to the zygoma. The deep infraorbital sulcus noted in this species is also common in potoroids. Where such a fossa occurs in macropodids it is much more shallow. *B. fangaroo* also lacks the prominent development of the masseteric process which extends to the alveolar margin in all but the most plesiomorphic macropodids, e.g., the species of *Dorcopsis*. Similarly small masseteric processes occur in other undescribed balbarines and this is the condition also seen in potoroids.

Similar minimal flexion of the skull in either the basicranial or rostral regions, as seen in *Balbaroo fangaroo*, occurs in other undescribed balbarines. The balbarine condition more closely resembles the condition in potoroids than the usual condition seen in macropodids. Among potoroids the basisphenoid ascends anterodorsally at a shallow angle relative to the basioccipital and the palate lies in more or less the same plane as the basioccipital. In macropodines (except *Dorcopsis* and *Dorcopsulus*) the basisphenoid ascends anterodorsally at a steeper angle and the palate is flexed downwards relative to the basioccipital. In sthenurines the basioccipital plane is above the palatal plane, more markedly so in the brachycephalic species (Tedford, 1966). Murray (1989) indicates that the basicranial axis and palatal plane are considerably less deflected in *Hadronomas* than in *Macropus* and is thus closer to the condition seen in *B. fangaroo* and in potoroids.

Flexion in the basicranial region of the skull is a derived condition among macropodoids and may be associated with the development of bipedalism and an increasingly upright stance. Lack of such flexion in *Balbaroo fangaroo* together with the development of strong nuchal crests and enlarged mastoid processes indicating powerful neck musculature, are suggestive of quadrupedal gait and posture in this species. This hypothesis can be tested by discovery of appropriate post-cranial remains.

Downward flexion of the rostrum in modern and recent macropodoids correlates with anteriorly directed lower incisors whose dorsal margins are capable of being used as cutting surfaces, a feature useful in animals with a grazing or coarse browsing habit. The lowered position of these surfaces require downward flexion of the rostrum in order to maintain occlusion of upper and lower incisors. Absence of such rostral flexion in *Balbaroo fangaroo*, together with its more forcipulate lower incisors and low-crowned but distinctly lophodont molars, suggests a selective browsing habit. Modern grazing kangaroos are hypsilophodont and have anterior progression of sequentially erupted molars to cope with increased wear associated with their more abrasive diet. No such molar progression is evident in *B. fangaroo*.

Occurring as they do in a wide variety of plesiomorphic macropodoids, cranial features such as lack of flexion of the skull, short or absent masseteric processes of the zygoma, deep infraorbital fossae and squamosal-frontal contact most likely represent plesiomorphic conditions for macropodoids. The more derived conditions of these cranial features observed within sthenurines and macropodines represent synapomorphies for a clade containing these groups and excluding balbarines.

Lower molar morphology in *Balbaroo fangaroo* and other species of *Balbaroo*, is more derived than that of the species of *Nambaroo*, *Ganawamaya* and *Wururoo*, plesiomorphic structures such as the protostylid or protostylid crest, hypoconulid and posthypocristid having been lost. However, the robust, plagiolacoid premolars of *B. fangaroo* more closely resemble those seen in the species of *Wururoo* and other species of *Balbaroo*, than they do those of the smaller, more gracile premolars

of the species of *Nambaroo* or *Ganawamaya*. Robust premolars with convex occlusal surfaces are inferred to be plesiomorphic within Balbarinae since they more closely resemble in shape, and in size relative to that of molars, those of phalangerids or burramyids. Phalangerids have been suggested as the sister group of macropodoids by a number of authors (e.g., Kirsch, 1977; Flannery, Archer and Plane, 1983; Flannery and Rich, 1986; Flannery, 1989; Baverstock et al., 1990). Within Macropodoidea, such premolars more closely resemble those of the hypsiprymnodontines and propleopines than they do those of other potoroids or even plesiomorphic macropodids.

Within *Balbaroo*,  $M_1$  trigonid morphology of *B. fangaroo* is more plesiomorphic than that of any other known species of the genus. The central position of the paraconid, absence of any development of an anterior cingulid lingual to the paracristid, the steeply-sloping precingulid and the prominent, straight paracristid indicate a primarily shearing functional interaction between the precingulid, paracristid and the posterior part of the  $P^3$  occlusal crest. While there is a prominent posterolingual cusp on  $P^3$ , any crushing function of this cusp would have been limited by the absence of an adequately developed receiving basin on  $M_1$ , and relied largely on interaction with the expanded lingual base of the paraconid. This expansion in *B. fangaroo* may represent an evolutionary trend towards development of a crushing role for the  $P^3$  posterolingual cusp, a suggestion which assumes the need for such a function. Incorporation of harder or more fibrous material in the diet could provoke such a need.

The presence of extremely large upper canines in an herbivorous kangaroo is a unexpected example of evolutionary convergence with Tertiary and even extant ungulates. Enlarged canines are common in a number of extinct ungulate taxa of comparable or earlier age: artiodactyls (traguloids, pecorans); dinoceratans (uintatheriids); pantodonts; notoungulates (homalodotheriids); astrapotherians (Scott, 1937). Large canines are present among a variety of extant taxa of some of these lineages, e.g., *Tragulus*, *Moschus*, *Hydropotes*, *Cervulus*, *Elaphodus* (Scott, 1937), in which canine size is sexually dimorphic. As can be seen from Figures 2 and 4 and Table 1, cranial and molar dimensions are larger in the paratype, although molar development indicates that both specimens are from mature animals. The larger size of the paratype may be an indication that sexual dimorphism also occurred in this species, a hypothesis which may be tested if more such specimens are recovered from Riversleigh. The adaptive significance of enlarged canines in herbivores is the subject of another paper (Molnar and Cooke, in press).

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