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Wanburoo hilarus gen. et sp. nov., a lophodont bulungamayine kangaroo (Marsupialia: Macropodoidea: Bulungamayinae) from the Miocene deposits of Riversleigh, northwestern Queensland

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Abstract – *Wanburoo hilarus* gen. et sp. nov. is described on the basis of specimens recovered from a number of Riversleigh sites ranging in estimated age from early Middle Miocene to early Late Miocene. The new species is characterized by low-crowned, lophodont molars in which hypolophid morphology clearly indicates bulungamayine affinity.

The relatively close temporal proximity and lophodont molar morphology of the new species invites comparison with the Late Miocene macropodids, *Dorcopsoides fossilis* and *Hadronomas puckridgi*. While there is a number of phenetic similarities between the species, many of these appear to be symplesiomorphic. However, a number of apomorphies are suggested as indicating a phylogenetic relationship between the new species and early, non-balbarine macropodids represented by *D. fossilis* and *H. puckridgi*. Of these two taxa, the relationship appears stronger with *Hadronomas* than with *Dorcopsoides*. Balbarine-like characters present in *Dorcopsoides* are likely plesiomorphic or the result of convergence. While bulungamayines are herein regarded as more likely than balbarines to be ancestral to macropodids, the possibility of a diphyletic origin for macropodids cannot be dismissed. The suggested relationship between bulungamayines and macropodids casts doubt on the inclusion of Bulungamayinae within Potoroidae.

INTRODUCTION

The Oligo-Miocene freshwater limestone deposits of the Riversleigh World Heritage area of northern Australia have yielded a wealth of kangaroo fossil material. Sixteen new fossil kangaroo species have been described thus far and more await description. Described species include representatives of the Hypsiprymnodontinae: *Hypsiprymnodon bartholomaii* Flannery and Archer, 1987a; Propleopinae: *Ekaltadeta ima* Archer and Flannery, 1985 and *E. jamiemulvaneyi* Wroe, 1996; Potoroinae: *Gumardee pascuali* Flannery, Archer and Plane, 1983 and *Bettongia moyesi* Flannery and Archer, 1987b; Bulungamayinae: *Wabularoo naughtoni* Archer, 1979, *Bulungamaya delicata* Flannery, Archer and Plane, 1983, *Nowidgee matrix* Cooke, 1997b and *Ganguroo bilamina* Cooke, 1997b; and Balbarinae: *Balbaroo gregoriensis* Flannery, Archer and Plane, 1983, *Nambaroo couperi* Cooke, 1997a, *Wururoo dayamayi* Cooke, 1997a and three species of *Ganawamaya* Cooke, 1992. *Galanarla tesselata* Flannery, Archer and Plane, 1983 remains unassigned to a subfamily. No specimens representing unequivocal macropodines or sthenurines have so far been recovered from any pre-Pliocene Riversleigh site.

Possible exceptions to the above are kangaroo cranial remains recovered from Gag Site, a site within the Riversleigh System C of Archer *et al.* (1989), regarded by those authors as middle Miocene in age. Flannery (1989: 32) provided an outline description of these remains, referring to them as belonging to "the Gag Site macropodine". Molar teeth in these remains are low-crowned and bilophodont, but the M_1 trigonid is transversely broad, in contrast to the transversely narrow M_1 trigonid characteristic of balbarines, considered at that time to be the most abundant group of lophodont macropodoids occurring at Riversleigh. If the specimens could be shown to be of an undoubted macropodine they would represent the oldest member of the subfamily so far known and therefore be of considerable phylogenetic significance.

The Gag Site specimens have been re-examined and they, together with material from the more recently discovered Dome and Encore Sites, are described more fully in this paper. A new genus and species is proposed to accommodate this fossil material.

QM F prefixes Queensland Museum, Brisbane, fossil collection catalogue numbers. These supersede the catalogue numbers (prefixed by AR) of the Vertebrate Palaeontology Laboratory of the University of New South Wales, used by Flannery (1989). Numbers in the latter series are indicated in parentheses where appropriate. The abbreviation UCMP = University of California Museum of Paleontology, Berkeley, California, U.S.A. Measurements are in millimetres.

SYSTEMATIC PALAEONTOLOGY

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). Authorities for higher category names are not included in the References but may be found in Aplin and Archer (1987).

Supercohort Marsupialia (Illiger, 1811)

Order Diprotodontia Owen, 1866

Superfamily Macropodoidea (Gray, 1821)

Family *incertae sedis*

Subfamily Bulungamayinae Flannery, Archer and Plane, 1983

Wanburoo gen. nov.

Type Species

Wanburoo hilarus sp. nov.

Diagnosis

Robust, lophodont bulungamayines in which I_1 is deep-bladed in relation to its length, enamel is confined to its buccal surface, and both dorsal and ventral enamel flanges are present. The dorsal flange of I_1 occludes with cutting edges on I^3 and I^2. I^1 is small and caniniform in shape; I^3 is large, unornamented, with a long occlusal edge, crown shortening towards the base. Upper canines present, in close proximity to incisors. Lower molariform teeth with an anterobuccally directed cristid, from the entoconid; hypolophid formed by an elevated, transversely oriented posthypocristid; pre-entocristid, when present, directed anteriorly. In young animals at least, the ventral margin of the dentary is not convex below the cheek teeth and may be straight or slightly concave in this region. Posterior section of inferior dental canal reduced in length to the extent that its anterior opening into the masseteric fossa is overlapped by the mandibular foramen.

Etymology

The name *Wanburoo* is derived from the Gulf of Carpentaria coastal Aboriginal word *wanbu*, which means ghost (Breen 1981), and *roo*, a common Australian vernacular diminutive for kangaroo. Gender is considered to be masculine.

Wanburoo hilarus sp. nov.

Figures 1–5; Table 1

Gag macropodine *incertae sedis*: Flannery 1989: 39

Material Examined

Holotype

QM F20525 (formerly AR4965), the badly crushed remains of the skull of a subadult animal (Figure 1), including parts of the left premaxilla and maxilla preserving I^3, C^1, dP^2, dP^3 (P^3), M^{1-2} and M^3 within its crypt, isolated right premaxillary teeth including I^{1-3}, part of the right maxilla with dP^2 and the badly damaged buccal parts of dP^3 and M^1, together with the crown of the unerupted right P^3. Associated mandibular remains include most of the horizontal ramus and part of the ascending ramus of the left dentary with I_1, dP_2, dP_3 and M_{1-2} *in situ* and the detached crowns of P_3, M_3 and M_4, as well as teeth detached from the right mandible, including the tip of I_1, dP_3, the crown of the unerupted P_3, and M_1.

Paratypes

QM F37021 (formerly AR3651), a left dentary including most of the horizontal ramus and much of the ascending ramus, including the condyle. I_1, dP_2, dP_3 (P_3) and M_1 are present.

QM F19942, the anterior portion of the horizontal ramus of a left dentary containing I_1, dP_2, dP_3 and the damaged remains of M_1 and M_2. The crown of P_3 is present and has been removed from its crypt.

QM F30346, a fragment of a left horizontal ramus from an adult animal, preserving I_1, P_3 and detached M_{1-2}. The fragment is in two pieces, broken just anterior to the M_2 alveolus.

Type Locality and Age

The holotype and QM F37021 are from Gag Site, low in the sequence of Riversleigh System C sites (Archer *et al.* 1989) on Gag Plateau. Those authors considered Riversleigh System C to be Early to Middle Miocene in age. QM F19942 is from Encore Site, and QM F30346 is from Dome Site. A possible mid to late Middle Miocene age has been suggested for Dome Site and a possible early Late Miocene age for Encore Site (Anonymous 1994).

Diagnosis

As for the genus until new species are described.

Etymology

The specific name *hilarus* is Latin for mirthful or

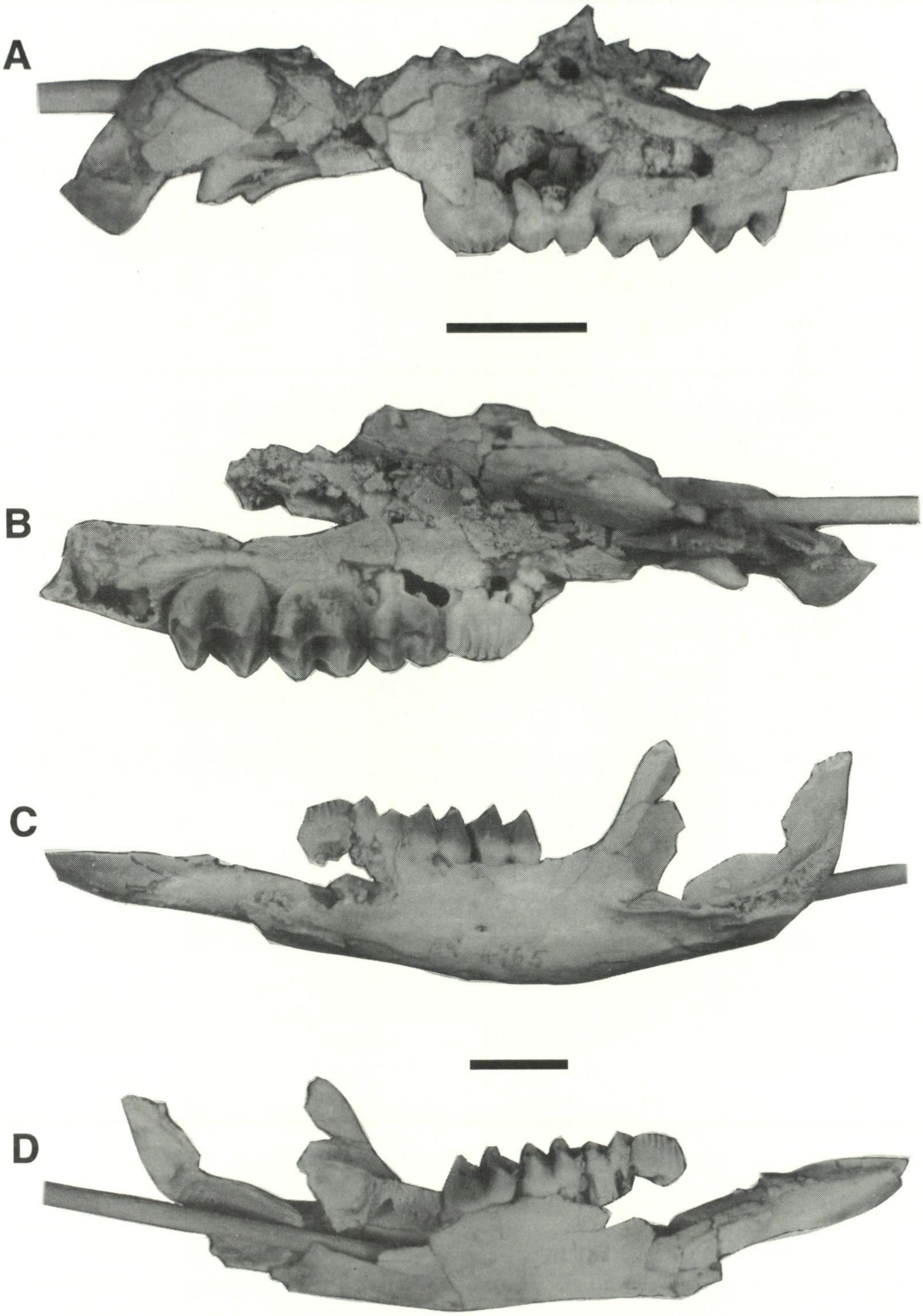

Figure 1 QM F20525, holotype of *Wanburoo hilarus* gen. et sp. nov. A, B. Buccal and lingual views of left premaxilla and maxilla. C, D. Buccal and lingual views of left dentary. Scale bars = 10 mm.

jocund, a reference to Gag Site from which the holotype was recovered.

Description

Premaxilla and Maxilla

The holotype is very badly fragmented and little detail of the premaxillary and maxillary regions can be determined (Figure 1). There are two small foramina in the palatine wing of the maxilla medial to the diastemal region. Part of the zygomatic process of the maxilla is preserved and does not reach the level of the alveolar margin. There appears to be no definite masseteric sulcus between the alveolar process and the zygomatic process of the maxilla. The lower margin of the infraorbital foramen is visible dorsal to dP^3.

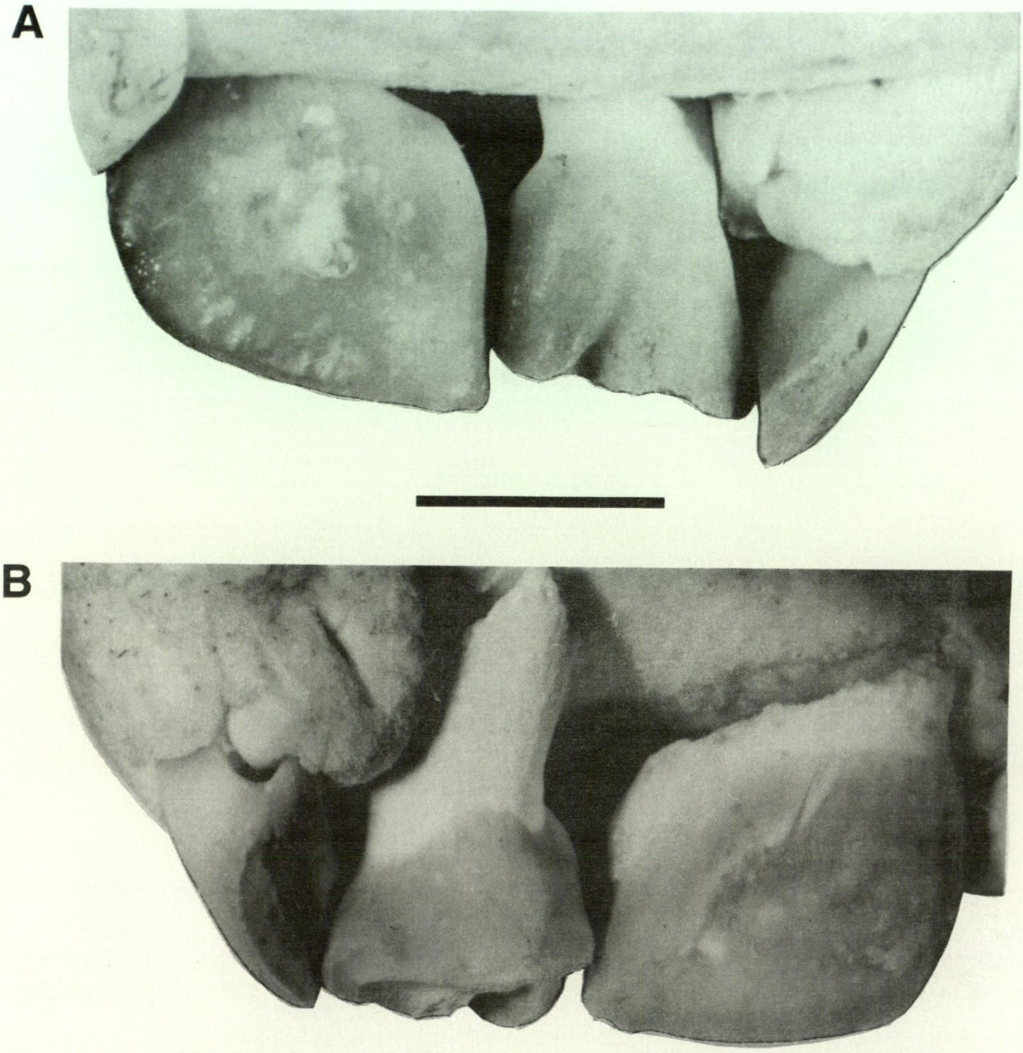

Figure 2 Isolated right I^{1-3} of QM F20525, holotype of *Wanburoo hilarus* gen. et sp. nov. Teeth have been mounted in plasticene to indicate their original arrangement. A. Buccal view. B. Lingual view. Scale bar = 4 mm.

Upper Dentition

The upper cheek tooth row is straight in lateral view but buccally convex in occlusal view. dP^2 is aligned with the molar row.

I^1 is the smallest of the incisors (Figure 2). It is almost caniniform in shape and slightly recurved. Enamel covers most of the crown except for the lingual surface and is thickest close to the crown apex. There is a recess which neatly accommodates the anterior end of I^2, in the enamel of the lingual face of the crown apex. There is a narrow interdental facet on the right I^1, indicating the area of contact with the missing left I^1. There is evidence of slight wear of the enamel of the buccal surface just below the crown apex.

The crown and part of the root of the right I^2 is also preserved. This tooth shows much greater wear than is present on other upper incisors. The crown is triangular in buccal view with an almost vertical posterior margin and a sloping anterior margin. There is a short groove rising nearly vertically up the buccal surface from the occlusal margin close to the posterior end. The occlusal surface is divided by the distal end of this groove into a larger, triangular anterior region and a short, diagonal, posterior blade. The enamel in the anterior occlusal region is breached by wear, as is the enamel of the lingual margin at the level of the posterior groove. The straight lingual margin is elevated to form a ridge which projects posteriorly to form a small prominence lingual to a small notch in the posterior margin which accommodated the anterior end of I^3, helping to lock these teeth in alignment.

I^3 remains *in situ* in the left premaxilla and the crown of the right I^3 has also been preserved. The tooth has a long occlusal edge and is triangular in lateral view but the crown is taller posteriorly than anteriorly. There are no grooves or ridges ornamenting the buccal surface. In its present position the *in situ* tooth is angled anteriorly with the occlusal edge sloping ventrally from anterior to posterior, but it is not certain that this orientation has not resulted from deformation occurring during the depositional process. The blade-like occlusal edge of the tooth is straight, but is flexed lingually out of alignment with the cheek tooth row – possibly also the result of taphonomic deformation.

The alveolus of C^1 lies immediately posterior to that of I^3. The broken root of C^1 is exposed within the maxilla and runs horizontally posteriorly. The crown is short and conical, inclined anteriorly with its apex flexed slightly lingually. The extremely close proximity of incisor and canine is approached only by that in species of *Bettongia* among extant macropodoids, but also occurs in at least one undescribed balbarine species from Riversleigh. The diastema separating C^1 from dP^2 is about equal in length to P^3.

dP^2 is a short, low-crowned, bulbous-based tooth with a short occlusal margin which overhangs the posterior crown base (Figure 3A). In occlusal view the lingual margin is relatively straight while the buccal margin is strongly convex. The lingual surface of the crown inclines steeply to the occlusal margin from its bulbous base while the less steeply inclined buccal surface slopes uniformly from the crown base to the occlusal margin. There are four separate cuspules on the occlusal margin anterior to a less-defined cuspule close to the posterior end. Transcristae associated with the four anterior cuspules are much longer than those associated with the most posterior cuspule. The anterior margin of the occlusal blade is delineated by a crista sloping from the apex of the most anterior cuspule to the crown base.

The crowns of both left and right P^3 have been freed from their crypts. P^3 is very long, more than 1.5 times the length of M^1 (Figure 3B). The crown is low with a serrated occlusal margin and a large, wedge-shaped posterior lingual cuspule. The right P^3, although damaged lingually, has a partially preserved, broad, lingual cingulum extending anteriorly from this cuspule. This portion of the

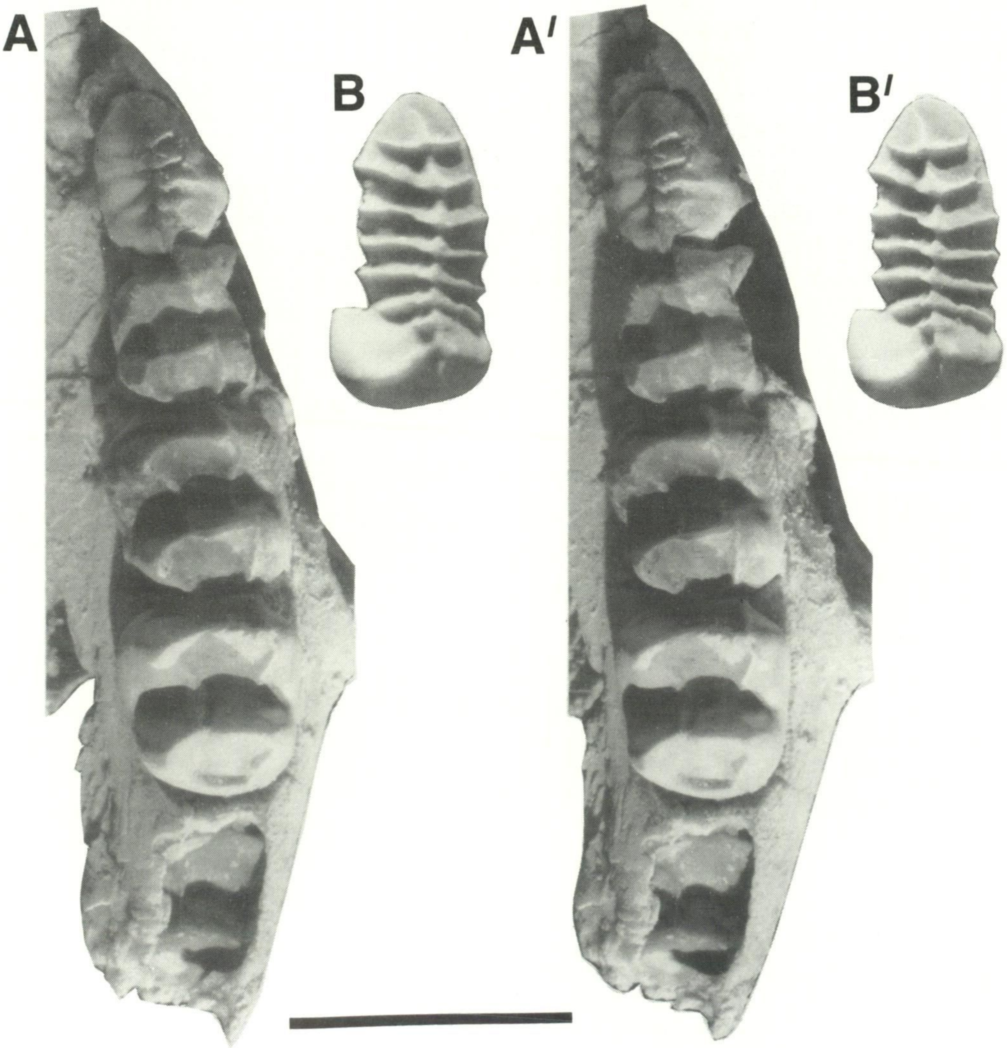

Figure 3 Stereo views of upper dentition of QM F20525, holotype of *Wanburoo hilarus* gen. et sp. nov. A/A′. Left maxilla with dP^{2-3}, M^{1-2}. B/B′. Left P^3. Scale bar = 10 mm.

crown is not preserved in the left P^3. In occlusal view the outline of the crown is elliptical. The eight cuspules present on the occlusal margin are more closely spaced posteriorly than anteriorly. The six most anterior of these cuspules are clearly defined and have long transcristae reaching from their apices to the base of the crown and, on the right P^3, extending onto the lingual cingulum. The seventh cuspule has little development of the buccal component of the transcrista, a shorter lingual component, and is itself imperfectly delineated from a longer posterior 'heel' adjacent to the posterior lingual cuspule. The anterior end of the occlusal blade is defined by a crista sloping anteriorly from the apex of the anterior cuspule to the crown base. A shorter, more vertical crista defines the posterior margin.

dP^3 is much smaller than M^1. It has a straight buccal margin which is longer than the lingual margin. The central region of the anterior margin is concave as it abuts the posterior margin of dP^2 and the posterior margin is convex. The protoloph is narrower than the metaloph. The paracone is narrow and is taller than the metacone. The preparacrista forms a prominent blade-like ridge which projects beyond the anterior margin, meeting the posterobuccal side of the occlusal margin of dP^2. The preparacrista, paracone and very prominent postparacrista form a posterior extension of the occlusal blade of dP^2. The protoloph is convex anteriorly and lowest just lingual of its midpoint. Enamel has been broken from the apex of the protocone. The postprotocrista is buccally inclined on the posterior face of the protocone but turns posteriorly to cross the interloph valley, meeting the anterior face of the metaloph on the lingual side of the midline. The buccal moiety of the interloph valley is narrower (antero-posteriorly) than the lingual moiety. A premetacrista runs anteriorly from the metacone to the interloph valley but does not contact the postparacrista. The metaconule is taller than the metacone and there is a distinct neometaconule forming a short, rounded ridge on the posterior face of the metaloph at about its midpoint. A prominent postmetaconule crista inclines buccally as it runs from the metaconule apex towards the crown base before turning buccally across the crown base to form a posterior cingulum and meeting the equally prominent postmetacrista which inclines lingually towards the crown base from the apex of the metacone.

M^1 is a large tooth, almost square in occlusal outline. Protoloph and metaloph are of about equal width and all cusps are of about equal height. The preparacrista inclines slightly lingually as it runs anteriorly from the paracone apex to the anterior margin where it meets a long, narrow anterior cingulum which crosses the entire width of the anterior margin. The postparacrista and premetacrista are inflected lingually and meet in the interloph to form a continuous centrocrista linking the apices of protocone and metacone across the interloph valley. Stylar cusp C is visible in buccal view as a low prominence on the posterobuccal flank of the protocone, close to the floor of the interloph valley and separated from the postparacrista by a flat, stylar shelf. The postprotocrista is prominent as it crosses the interloph valley and meets the crest of the metaloph at a low point just lingual to the prominent, centrally-positioned neometaconule

Table 1 Dental parameters for type specimens of *W. hilarus* gen. et sp. nov. Abbreviations: h = height; hw = width at hypolophid; l = length; mw = width at metaloph; pw = width at protolophid or protoloph; TCN = no. of transcristids; w = width.

Catalogue No. QM F	AR	I^1	I^2		I^3		C^1	dP^2				P^3				dP^3		
		h	l	h	l	h	h	l	w	h	TCN	l	w	h	TCN	l	pw	mw
20525	4965				5.7	4.8	4.3	6.3	4.7	4.9	5	11.2	6.0	4.3	7	5.8	4.5	5.1
		3.6	4.2	3.5	6.2	4.5						11.2	5.8	4.2	7			

QM F	AR	M^1			M^2		
		l	pw	mw	l	pw	mw
20525	4965	6.2	6.9	6.4	6.9	6.6	6.0

QM F	AR	I_1		dP_2				P_3				dP_3			M_1			M_2		
		l	w	l	w	h	TCN	l	w	h	TCN	l	pw	hw	l	pw	hw	l	pw	hw
19942		15.7	3.8	6.0	4.1	5.1	4	11.8	5.7	5.5	6	5.7	3.4	4.3	6.7	5.4		7.9		
20525	4965	13.5	3.1					10.1	4.1	4.7	5				6.8	4.8	4.9	6.3	5.2	5.1
								10.3	3.6	4.4	5									
37021	3651	15.8	2.8					11.1	3.8	3.6	7				6.3	4.2	4.5			
30346			3.4					9.7	5.0	5.5	7				6.7	4.4	4.6	6.5	4.3	4.6

which forms a rounded ridge on the posterior face of the metaloph. The protoloph has a low point on the lingual side of its midpoint. Postmetaconule crista, posterior cingulum and postmetacrista are as described for dP^3.

M^2 closely resembles M^1 in morphology but has a less prominent neometaconule and stylar cusp C, and the centrocrista is interrupted in the interloph valley.

Dentary

Holotype. The angular process of the holotype has been lost, as has the entire dorsal margin of the diastema (Figures 1 and 4). Parts of the anterior and posterior margins of the ascending ramus are present but the coronoid process and condyle are missing. The lingual surface of the M$_3$ alveolus and the crypt of M$_4$ have been lost. The ventral margin is relatively straight below the cheek tooth row anterior to the M$_3$ alveolus but is inclined dorsally posterior to this. The absence here of marked ventral convexity of the horizontal ramus, common in potoroids and other bulungamayines, may be age related. The poor preservation of the only adult specimen makes assessment of the adult condition speculative. There is a small posterior mental foramen below M$_2$/M$_3$. The masseteric fossa narrows anteriorly and it is unlikely that masseteric insertion reached much farther anteriorly than M$_3$. The ascending ramus rises at an angle of 112° relative to a straight line extending along the molar occlusal surfaces. The mandibular symphysis extends posteriorly to the level of the anterior margin of dP$_2$.

Paratypes. The adult diastema preserved in QM F30346 exceeds the length of P$_3$ and is longer than those of the subadult animals. The masseteric canal in this specimen can be seen to be confluent with the inferior dental canal as far forward as the M$_3$ alveolus.

Most of the dentary is preserved in QM F37021 with the exception of the dorsal margin of the

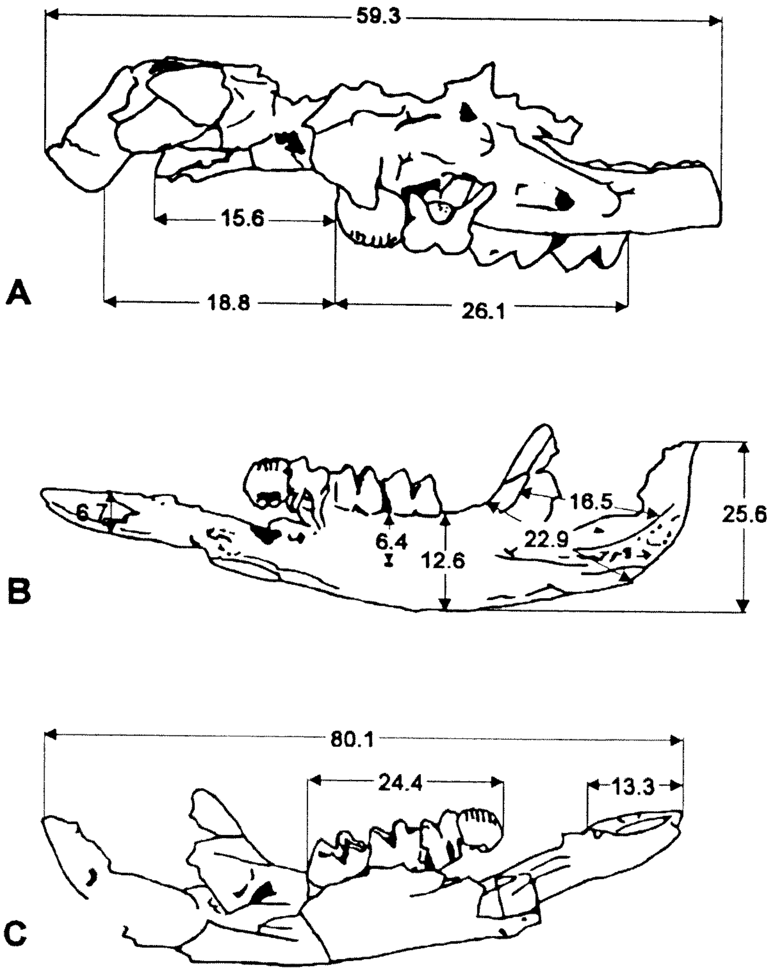

Figure 4 Dimensions of QM F20525, holotype of *W. hilarus* gen. et sp. nov. A. Buccal view of premaxilla and maxilla. B, C. Buccal and lingual views of dentary.

diastema, the dorsal part of the anterior margin of the ascending ramus and the tip of the coronoid process. The mandibular symphysis extends posteriorly to the level of the anterior root of dP_3. The ventral margin of the dentary is undulating, its lowest points occurring beneath dP_2/dP_3 and M_3, the posterior of these points representing the digastric process. Beneath the ascending ramus the ventral margin curves dorsally in an arc to the posterior margin of the angular process. The alveolar margin of the horizontal ramus is concave such that central alveolar margins are lower than those at the ends of the molar row. The mental foramen is close to the dorsal margin of the diastema, just anterior to P_3 and there is a small posterior mental foramen below the anterior edge of the M_2 alveolus. The ascending ramus is inclined at an angle of about 117° relative to a straight line extending along the molar occlusal surfaces. The lateral margin of the masseteric fossa is low on the horizontal ramus and is straight antero-posteriorly. The masseteric canal opens well anteriorly within the masseteric fossa and is confluent with the inferior dental canal. The mandibular foramen opens into an extremely abbreviated length of the posterior part of the inferior dental canal and is overlapped by the masseteric foramen, the anterior opening of this length of canal into the masseteric fossa. The degree of overlap is such that in dorsobuccal view it is possible to see directly from the masseteric fossa to the pterygoid fossa, thus approaching the condition common in Pleistocene and modern macropodoids, in which there is a large opening between the fossae visible in lateral view. The condyle is low, elliptical in outline and has a flat surface. Its long axis is markedly inclined anteromesially-posterolaterally relative to the long axis of the horizontal ramus. In shape and position above the molar row, the condyle more closely resembles those of potoroids than those of macropodids.

Lower dentition

Holotype. The cheek tooth row is straight in occlusal view (Figure 5). Molar teeth are fully bilophodont but crown height is lower than that seen in most extant macropodids. Molar size increases from M_1 to M_2 and then decreases from M_2 to M_4.

I_1 has a short, leaf-shaped crown which is very deep in relation to its length. The anterior tip of the

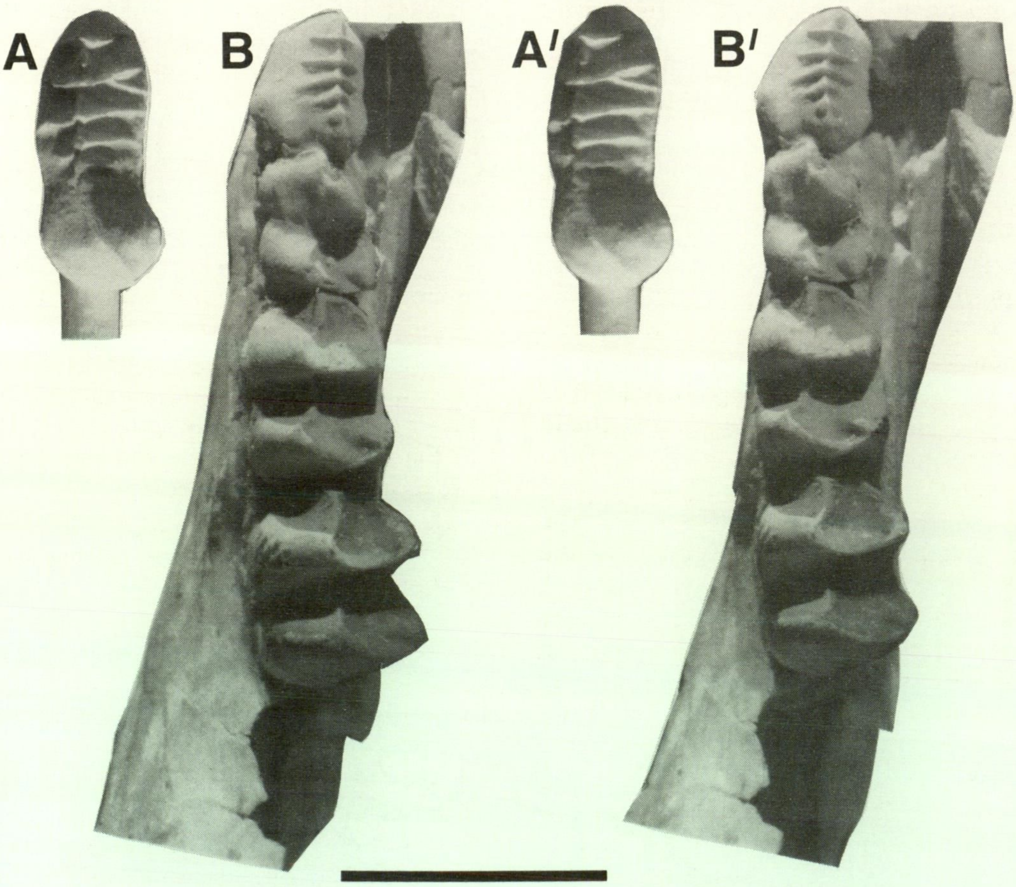

Figure 5 Stereo views of lower dentition of QM F20525, holotype of *Wanburoo hilarus* gen. et sp. nov. A/A′. Left P_3. B/B′. Left dP_{2-3}, M_{1-2}, in left dentary. Scale bar = 10 mm.

crown of the left I_1 has been lost in the holotype but can be seen to be sharply pointed in the remaining portion of the right I_1 and in those of paratypes. Enamel is confined to the buccal surface and there are prominent dorsal and ventral enamel flanges. The root is circular in cross section but the crown is narrowly elliptical in cross section. The dorsal enamel flange forms the occlusal edge of the tooth and the enamelled buccal surface is subvertical. The blade-like dorsal enamel flange on this tooth, the long and narrow occlusal edge on I^3 and the wear patterns on the occlusal surface of I^2 indicate that occlusion of upper and lower incisors induced a cutting action.

dP_2 is a short, blade-like tooth with a convex buccal margin and a concave lingual margin. The lingual face of the occlusal blade is more steeply inclined than the buccal face. The occlusal margin is relatively straight in lateral view and overhangs the posterior base of the crown. There are four clearly delineated cuspids on the occlusal margin anterior to a posterior 'heel' on which two additional cuspids are incompletely differentiated. Distance between cuspids decreases posteriorly. Sharply-defined transcristids are associated with each of the four anterior cuspids. The anterior margin of the occlusal blade is defined by a cristid that slopes anteriorly to the crown base from the apex of the most anterior cuspid. A shorter cristid defines the posterior margin.

dP_3 is narrower anteriorly than posteriorly. The trigonid is dominated by a very tall protoconid from which the short protolophid crest inclines buccally. A cristid, the presumed postmetacristid, descends to the interlophid valley from the posterior end of the lophid, the metaconid being otherwise undifferentiated. A short paracristid descends anteriorly from the protoconid to the prominent paraconid at the anterior margin. A cristid descends almost vertically towards the crown base anterobuccal to the paraconid. The entoconid is taller than the hypoconid. The cristid obliqua runs anterolingually from the apex of the hypoconid, crossing the interlophid valley and ascending the posterobuccal flank of the protoconid. The hypolophid is formed by the elevated and lingually directed posthypocristid. A short cristid from the entoconid descends steeply anterobuccally from the entoconid apex. An anteriorly directed pre-entocristid is also present on the right dP_3, confirming the separate identities of the cristids originating from the entoconid.

P_3 is blade-like, low-crowned and more than half as long again as M_1 (Figure 5A). It has a narrow, crescentic occlusal outline with the buccal margin convex and the lingual margin concave. Both margins are constricted close to the posterior end. Lingual and buccal surfaces are inclined at about the same steep angle. In lateral view the occlusal margin is relatively straight, with the posterior end slightly higher than the anterior end, and in occlusal view can be seen to curve lingually towards its posterior end. The anterior two-thirds of the occlusal margin has five cuspids with which transcristids are associated, spacing between both cuspids and transcristids becoming progressively less from anterior to posterior. Immediately posterior to this region of the occlusal margin there is an imperfectly differentiated cuspid lacking transcristids, but the remaining portion of the occlusal margin is unserrated. Anterior and posterior margins of the occlusal blade are defined by cristids descending to the crown base.

M_1 is larger than dP_3. Protolophid and hypolophid are about equal in width and lingual and buccal cuspids are subequal in height. Lingual surfaces of the crown are more steeply inclined than the buccal. The paracristid runs horizontally directly anteriorly from the base of the protoconid, turns lingually across the anterior margin bordering a short anterior cingulid, before inclining posterolingually to terminate at the base of the metaconid. The cristid obliqua is lingually inclined as it descends the anterior face of the hypoconid but turns anteriorly to cross the broad interlophid valley and ascend a short distance on the posterior face of the protoconid. The hypolophid is formed by the much-elevated posthypocristid which links the apices of hypoconid and entoconid. A short, anterolingually directed, cristid descends steeply from the entoconid apex. There is a slight posterior bulge of the crown base below the hypolophid.

M_2 is larger than M_1 but closely resembles it in crown morphology except that the paracristid originates close to the apex of the protoconid.

M_3 is smaller than M_2 and is similar to it in morphology apart from having a less obvious cristid associated with the entoconid and having a distinct premetacristid whose anterior end is separated from the lingual termination of the paracristid by a narrow cleft. The posterior bulge of the crown base below the hypolophid is more pronounced on this tooth.

M_4 is smaller than M_3 and resembles that tooth in morphology but has a less distinct cristid obliqua and premetacristid.

Paratypes. Except for the variations noted below, the morphology of the lower dentition in the paratypes closely resembles that described for the holotype. More cuspids are differentiated on the occlusal margin of P_3 in the paratypes, there being seven cuspids anterior to the unserrated, posterior 'heel' in QM F37021 and in QM F19942 in which P_3 is also larger, and six or seven in QM F30346. Conversely, dP_2 in the holotype has more differentiated posterior cuspids than those of the paratypes. The M_1 anterior cingulid is shorter in paratypes, apart from QM F30346, in which it is longer. The paracristid links more strongly to the protoconid apex in QM F19942 and QM F30346 than it does in QM F37021 and the holotype.

DISCUSSION

Flannery (1989) considered the lophodont balbarines to be ancestral to both macropodines and sthenurines. However, lophodonty also evolved in Oligo-Miocene bulungamayine kangaroos in parallel with the evolution of this character within balbarines. Cooke (1997b) described a mechanism of hypolophid evolution within Bulungamayinae in which the ancestral hypolophid in bunolophodont lower molars, formed by a strong cristid linking the entoconid apex to the lingual face of the hypoconid, was replaced by a neomorphic hypolophid derived from the posthypocristid which became elevated and transversely oriented. This mechanism is clearly different from that proposed by Flannery and Rich (1986) as leading to hypolophid formation in Balbarinae. The lophodont bulungamayine, *Bulungamaya delicata* retains a remnant of the ancestral bunolophodont hypolophid in the form of an anterobuccally directed cristid, on the anterior face of the entoconid. Such a cristid, distinct from the pre-entocristid, is also retained in the lower molariform teeth of *Wanburoo hilarus*. It is on that basis and its possession of elongate and crescentic lower premolars, that *W. hilarus* is assigned to Bulungamayinae rather than Macropodinae, although it is recognized that monophyly of the Bulungamayinae is not demonstrated.

The otherwise macropodine-like characters noted by Flannery (1989) as occurring in the species now described as *Wanburoo hilarus*, are consistent with the suggestion of Cooke (1997b) that bulungamayines must be considered as potentially ancestral to macropodines. This raises doubts regarding both the monophyly of the subfamily Bulungamayinae and its status within Potoroidae. These considerations, discussed more fully below, are the subject of a phylogenetic analysis (in preparation) of Macropodoidea which incorporates morphological data derived from the new species and other Oligo-Miocene species from Riversleigh and elsewhere. Postcranial remains of balbarine and bulungamayine kangaroos from Riversleigh are currently under study by B. Kear at the University of New South Wales, and the results of that study are likely to impinge significantly on these considerations (Kear pers. comm.). Pending the results of these studies and their potential impact on macropodoid systematics, the systematic position of Bulungamayinae is here regarded as *incertae sedis*.

The morphology of the preserved upper incisors of *Wanburoo hilarus* and patterns of wear on I^2, indicate that the blade-like occlusal crest of I^3 and the smaller, posterior occlusal crest of I^2 produced a cutting action in occlusion with the dorsal enamel flange of I_1. Taken together with the bilophodont molar morphology, this is indicative of a herbivorous diet, but the relatively low condyle and brachyodont molar morphology suggest that plant material consumed was not high in fibre content. *Wanburoo hilarus* was thus most likely a browser.

Sanson (1989) suggested that basal macropodoids were omnivores in which premolar shearing played an important role in initial reduction of relatively large food items before final processing through a crushing and grinding action of the molars. Elongate premolars, a "twisted" molar row and deep insertion of the masseter within the masseteric canal were postulated as occurring in such animals. (Although elongate premolars more likely represent the derived macropodoid condition, see below.) Sanson's next evolutionary level was a "browser grade" of macropodine in which elongate premolars are retained but the molar row is flat and no longer twisted. Dental morphology in *W. hilarus* fits this "browser grade" model in most respects. However, one of the paratypes, QM F37021, differs from the model in that the lower molar row is ventrally concave. This probably represents individual variation since the condition is not obvious on other type specimens, and there is no matching ventral convexity of the upper molar row in the holotype.

Within Bulungamayinae, the lophodont molar morphology of *Wanburoo hilarus* ranks it with the derived, lophodont species such as *Bulungamaya delicata* and *Ganguroo bilamina*. However, it differs from these species in being much larger, having a relatively shorter and much more broad-bladed I_1, and a dentary whose ventral margin is not strongly convex, at least in subadult individuals. Molar morphology in *W. hilarus* is more similar to that of *B. delicata* in that both species retain traces of their bunolophodont ancestry in having an anterobuccal ridge from the entoconid, a remnant of the ridge linking entoconid and hypoconid and forming the hypolophid crest in bunolophodont lower molariform teeth.

The macropodid-like characters observed in the derived, lophodont bulungamayine *Wanburoo hilarus* prompt its comparison with more recently evolved bilophodont macropodids. Apart from the balbarine *Balbaroo camfieldensis* Flannery, Archer and Plane, 1983, the next oldest such species are *Dorcopsoides fossilis* Woodburne, 1967 and *Hadronomas puckridgi* Woodburne, 1967, both from the late Miocene Alcoota Fauna. Although *D. fossilis* was originally included in the Potoroinae within

Macropodidae by Woodburne (1967), Bartholomai (1978) moved it to the Macropodinae. *Hadronomas puckridgi* was described *incertae sedis* by Woodburne (1967), but Murray (1991) placed it in the Sthenurinae within Macropodidae. These two species are here considered collectively as early macropodids rather than as representives of particular macropodid subfamilies. While there is considerable phenetic similarity between *W. hilarus* and both these species, the polarity of the common character states is problematic.

Both *Wanburoo hilarus* and *Dorcopsoides fossilis* have a deeply penetrating masseteric canal anteriorly confluent with the inferior dental canal. The unique significance of masseteric insertion within the body of the dentary in macropodoids was first noted by Abbie (1939). He postulated a sequence of development of this insertion in which deep insertion of the masseter and coalescence of the masseteric and inferior dental canals to form a common canal (the condition seen in potoroids) represented the most derived condition. Since that time, the latter condition has been widely accepted as a potoroid synapomorphy (e.g., Woodburne 1984; Case 1984; Flannery *et al.* 1984). Abbie's sequence of development of this condition was based on comparisons of extant species, but the fossil record of macropodoids, as presently known, is not in agreement with this sequence. Deep penetration of the masseter and the development of a common canal within the horizontal ramus of the mandible can be argued to represent the plesiomorphic condition within Macropodoidea: it is apparently universal in the oldest known fossil kangaroos, including the Oligocene/Miocene species of Balbarinae, Bulungamayinae, Hypsiprymnodontinae, Propleopinae and Potoroinae. Conversely, a more shallow penetration of the masseter and, probably more importantly, separation of the masseteric and inferior dental canals by a bony lamina is the condition seen in macropodines and sthenurines which appear later in the fossil record. Observation of deep masseteric penetration within the mandible prompted Woodburne (1967) to include the late Miocene *Dorcopsoides fossilis* and the extant species of *Dorcopsis* and *Dorcopsulus* within his Potoroinae.

Macropodoids had already achieved a high level of diversity by the Late Oligocene to Early Miocene and their origins are likely to lie much earlier in the Oligocene (or perhaps even in the Eocene, as suggested by Flannery 1989). It is conceivable that the development of masseteric insertion within the body of the mandible evolved within the ancestral kangaroos in a manner similar to that described by Abbie (1939), achieving the 'potoroid' condition by late Oligocene times, with subsequent reversion to a more plesiomorphic state occurring by about the Late Miocene. Unfortunately, no kangaroo remains older than Late Oligocene are known and the polarity of deep masseteric insertion and confluence of masseteric and inferior dental canals can only be argued on the basis of the evidence that is available. That evidence favours the view that this condition is plesiomorphic. It may well have evolved quite rapidly among ancestral kangaroos as the developing masseteric fossa breached the inferior dental canal, thereby immediately allowing an anterior insertion of part of the masseter within the newly common canal.

In Riversleigh balbarines and most species of bulungamayines, the masseteric foramen opening into the inferior dental canal is distinctly separated from the mandibular foramen by a short posterior length of that canal. In both macropodines and sthenurines, this posterior section of the inferior dental canal is reduced to the extent that there is a single foramen connecting the masseteric and pterygoid fossae of the dentary. The condition in *W. hilarus*, in which there is overlap between the mandibular and masseteric foramina, is intermediate between these two states. In view of the age difference between Riversleigh balbarines and bulungamayines, and macropodines and sthenurines, separation of the two foramina is the likely plesiomorphic condition, seen also in *Dorcopsoides fossilis* (Woodburne 1967).

In both *Wanburoo hilarus* and in the figured holotype, UCMP 70563, of *Hadronomas puckridgi* (Woodburne 1967: 87), the mental foramen is positioned close to the dorsal margin of the diastema, just anterior to P_3, the position in which it occurs consistently in bulungamayines. In balbarines the foramen is consistently lower on the lateral wall of the diastemal region and more anterior to P_3, similar to the position in which it occurs in the figured paratype, UCMP 65912, of *Dorcopsoides fossilis* (Woodburne 1967: 59). The position of the mental foramen in phalangerids is variable, making assessment of the polarity of this character state impossible on the basis of outgroup comparison.

Elongate premolars, postulated as plesiomorphic for macropodoids by Sanson (1989), occur in *Wanburoo hilarus*, *Dorcopsoides fossilis* and *Hadronomas puckridgi*. Similar premolars occur in macropodines such as *Dorcopsis*, *Dorcopsulus* and *Dendrolagus*, and are universal in both potoroines and bulungamayines. Their widespread occurrence in this diversity of macropodoid taxa is in agreement with Sanson's view. However, taller and shorter premolars occur in balbarines, hypsiprymnodontines and propleopines, resembling in shape, if not always in relative size, those seen in phalangerids or even burramyids. While balbarines are truly lophodont, their molar morphology is in many ways more plesiomorphic than that of other macropodoid taxa: a narrow M_1

trigonid is universal, a protostylid and a hypoconulid on M_1 are retained in some species, as are stylar cusps C and D on upper molars. Outgroup comparison and the simultaneous occurrence of short premolars and plesiomorphic molar characters both suggest that elongate premolars represent a more derived condition within Macropodoidea. Flannery (1989), on the basis of outgroup comparison with phalangerids, also regarded the hypsiprymnodontine/propleopine premolar type as plesiomorphic. Since lophodont bulungamayines and early macropodids both have the derived premolar condition, this character suggests that such macropodids have a closer phylogenetic relationship with bulungamayines than with balbarines.

P^3 in both *Dorcopsoides fossilis* and *Wanburoo hilarus* has a wedge-shaped posterolingual cuspule. Similar cuspules occur in this position in other bulungamayines and also in balbarines from Riversleigh. They also presumably represent retained plesiomorphic characters. *Hadronomas puckridgi* is more derived in this respect since the cuspule is there reduced to a strong posterolingual ridge. P^3 in *W. hilarus* has a slight lingual cingulum, a character not present in more plesiomorphic bulungamayines, while P^3 of *H. puckridgi* has both lingual and buccal cingula. P^3 in *D. fossilis* has abrupt lateral flarings at the base of the crown, although Woodburne (1967) hesitated to consider these cingula. Well-developed lingual cingula occur on upper premolars of early macropodines and sthenurines, and the structures on the upper premolars of *W. hilarus, D. fossilis* and *H. puckridgi* may represent stages in the evolution of such cingula.

Upper molars in both *Dorcopsoides fossilis* and *Wanburoo hilarus* retain stylar cusp C (the mesostyle of Woodburne 1967). This cuspule, commonly present in bulungamayines, is considered here to be stylar cusp C since it is associated with the posterobuccal base of the paracone. In balbarines a second cuspule, stylar cusp D, associated with the anterobuccal base of the metacone, is also commonly present. Woodburne (1967) described triangular postparaconal and premetaconal "facettes" in *D. fossilis* and *Hadronomas puckridgi.* Similar structures also occur in Riversleigh bulungamayines and balbarines, in which their development is associated with stylar crests linked to stylar cusps C and D. Molar "facettes" are thus also probably retained plesiomorphies.

Lower molar morphology in *Wanburoo hilarus* is more closely similar to that of *Hadronomas puckridgi* than that of *Dorcopsoides fossilis.* In both *W. hilarus* and *H. puckridgi* there is an anterior cingular shelf, bordered anteriorly by a lingual extension of the paracristid which turns posteriorly to terminate at the base of the metaconid, from which it is clearly separated by a notch or "emargination", in the term of Woodburne (1967). There is very little development of a precingulid in either species. In *W. hilarus* and *H. puckridgi* M_1 protolophid and hypolophid are of similar widths and molar size is least at the ends of the molar row. Lower molars of both *W. hilarus* and *H. puckridgi* have posterior bulging of the crown base below the hypolophid, although this is more developed in *H. puckridgi.* In *Dorcopsoides* the M_1 protolophid is narrower than the hypolophid, there is a precingulid buccal to the more centrally positioned paracristid on this tooth, and molar size increases posteriorly.

Dorcopsoides fossilis differs from both *Wanburoo* and *Hadronomas* in having a posterior cingulid on lower molars, being, in this character at least, more similar to derived balbarines such as *Balbaroo* than to bulungamayines. This structure may be neomorphic in *D. fossilis,* and its incipient development may be represented by the slight posterior bulge of the molar crown base in *W. hilarus* and its stronger development in *H. puckridgi.* Similar posterior cingulids have arisen apparently independently within other macropodid lineages including *Protemnodon* (e.g. *P. anak* Owen, 1874) and *Troposodon* (e.g. *T. bowensis* Flannery and Archer, 1983, *T. gurar* Flannery and Archer, 1983). There is therefore no conclusive evidence indicating that the posterior cingulid of *Dorcopsoides* is homologous with the posterior cingulid of balbarines, argued by Cooke (1997a) to be a hypocingulid.

Increased width of the protolophid relative to the hypolophid, and lingual extension of the paracristid across the anterior margin to terminate at the metaconid base, may well represent synapomorphies uniting *Wanburoo* and *Hadronomas,* since a narrow trigonid region has been regarded as plesiomorphic (Flannery *et al.* 1983, who termed it "a greatly compressed trigonid"). Derivation of the lower molar morphology of *H. puckridgi* from that of *W. hilarus* would require only minor morphological changes: loss of the remnant of the entoconid crest and expansion of the posterior base of the hypolophid. Derivation of a *Hadronomas*-like morphology from a derived balbarine, such as a species of *Balbaroo,* would also involve increase in the width of the M_1 protolophid to approximate that of the hypolophid, together with loss of the postentocristid and the associated hypocingulid.

Derivation of the M_1 morphology of *Dorcopsoides* from a *Wanburoo*-like form would require a greater number of changes. In addition to those listed above for *Hadronomas,* lingual extension of the paracristid, expansion of the precingulid and acquisition of a neomorphic posterior cingulid would also be required. Such a cingulid is present on lower molars of *Balbaroo* species in which trigonid morphology is also more similar to that of *Dorcopsoides*, the latter resemblance being likely symplesiomorphic. However, evolution of *Dorcopsoides* from a *Balbaroo*-like ancestor would also require acquisition of elongate premolars, regarded here as being the derived condition.

Besides elongate premolars, lophodont molars and P^3 lingual cingula (incipient only in *Dorcopsoides*), there are but few potential dental synapomorphies uniting *Wanburoo*, *Dorcopsoides* and *Hadronomas*. However, lateral expansion of the M_1 trigonid represents a further synapomorphy suggesting a closer relationship of *Wanburoo* with *Hadronomas* than with *Dorcopsoides*.

A character potentially of great importance in defining relationships among these taxa is alisphenoid-parietal contact on the lateral wall of the neurocranium. This occurs in *Hadronomas puckridgi* and also among all Riversleigh bulungamayines in which this region of the skull is preserved (including remains referable to *Bulungamaya*, *Ganguroo* and probably *Wabularoo*). Unfortunately, this region of the skull is not known in either *Wanburoo* or *Dorcopsoides*. All known Riversleigh balbarine skulls preserving this region (including remains referable to *Nambaroo* and *Balbaroo*) have squamosal-frontal contact. Hitherto, squamosal-frontal contact has been known to occur only in potoroids, and previous workers, including Pearson (1950), Woodburne (1984) and Case (1984), have regarded the condition as representing the derived state among Macropodoidea, a view supported by outgroup comparison with phalangerids. Discovery of the occurrence of alisphenoid-parietal contact in skulls of *Hypsiprymnodon bartholomaii* and *Bettongia moyesi* prompted Flannery and Archer (1987b) to conclude that squamosal-frontal contact could "clearly no longer be recognised as a synapomorphy for potoroids." However, it is significant that squamosal-frontal contact has not been observed within what are currently regarded as macropodid taxa other than balbarines.

It may be argued on the basis of parsimony that squamosal-frontal contact is the plesiomorphic condition within Macropodoidea and that alisphenoid-parietal contact is derived. If so, then alisphenoid-parietal contact must have evolved independently within Bulungamayinae, *Hypsiprymnodon*, the potoroine lineages indicated above, and, if Balbarinae is considered ancestral to Macropodinae and Sthenurinae, at least once within Macropodidae, possibly in a post-balbarine ancestor common to both those taxa. However, if Bulungamayinae is the common ancestor to Macropodinae and Sthenurinae, then the requirement for independent evolution of the condition within Macropodidae is removed. If, on the other hand, it is assumed that alisphenoid-parietal contact is plesiomorphic, then squamosal-frontal contact must have arisen independently within Balbarinae, Propleopinae, Hypsiprymnodontinae, *Bettongia* and, according to Flannery and Archer (1987b), the species of *Potorous* and the *Aepyprymnus*/*Caloprymnus* clade.

As indicated above, *Hadronomas* and *Dorcopsoides* have been used for comparison with *Wanburoo hilarus* on the basis of their status as early, non-balbarine, macropodids, closest in age to that of the new taxon. Suggested synapomorphies indicating a phylogenetic relationship between bulungamayines, as represented by *Wanburoo*, and early macropodids, represented by *Hadronomas* and *Dorcopsoides*, include lophodont molars, elongate premolars with at least incipient development of lingual cingula on upper premolars, lateral expansion of the M_1 trigonid (although *Dorcopsoides* is closer to the plesiomorphic state for this character), and possibly alisphenoid-parietal contact on the side wall of the braincase.

In arguing the case for inclusion of Bulungamayinae within Potoroidae, Flannery *et al.* (1984) identified three skeletal character states that they considered to be synapomorphic for Potoroidae: a convex ventral margin of the dentary, deepest below the central portion of the molar row (although noting that this is not universal in Potoroidae, being absent from *Potorous* and *Propleopus*), deep insertion of the masseter within the dentary, and an elongate and finely serrate permanent premolar. Elongate premolars are here considered to be apomorphic within Macropodoidea, not merely Potoroidae, and deep insertion of the masseter is considered to be plesiomorphic for Macropodoidea. While other bulungamayines, e.g. *Bulungamaya delicata*, have a convex ventral margin of the dentary, this is not the case in *Wanburoo hilarus*, at least in subadult animals, although its molar and premolar morphology is closely similar to that of *B. delicata*. *Dorcopsoides fossilis*, now an accepted macropodid, shows ventral convexity of the dentary (Woodburne 1967), although maximum convexity is somewhat more posteriorly located in that species. Earlier bulungamayines, such as *B. delicata*, share the derived condition of convexity of the ventral margin of the dentary with potoroids, suggesting a potoroid origin for bulungamayines, but reversion to the plesiomorphic condition may have occurred in later species such as *W. hilarus*. If bulungamayines, in turn, are phylogenetically ancestral to macropodids, the condition in *Dorcopsoides* may represent a retention of what would then be the plesiomorphic condition for a bulungamayine-macropodid clade.

Bulungamayines exhibit variation in other characters, notably in molar morphology, with basal members of the group, e.g. *Nowidgee matrix*, exhibiting bunolophodont morphology, and more derived species such as *W. hilarus*, *Bulungamaya delicata* and *Ganguroo bilamina* exhibiting undoubted lophodonty. Bulungamayines thus exhibit a spectrum of characters ranging (phenetically-speaking) from potoroid-like to macropodid-like, and it is not surprising that they have been the subject of debate regarding their status as potoroids (Flannery *et al.* 1984) or macropodids (Woodburne 1984; Case 1984). The range of variation exhibited by the group does cast doubt on its monophyly, although crescentic lower premolars represent a possible bulungamayine synapomorphy. Evolution of lophodonty within Bulungamayinae is an example of phyletic gradualism which makes it difficult to establish boundaries for the taxon. The same process appears to continue beyond Bulungamayinae into basal members of the Macropodidae in which molar teeth display no trace of bunolophodont ancestry and become increasingly hypsodont, and premolars are elongate (though no longer crescentic) and have developed elevated lingual cingula. In view of this, and the absence of other synapomorphies within Bulungamayinae, it is most likely that Bulungamayinae is a paraphyletic, stem group basal to Macropodidae, occupying the phylogenetic position formerly assigned to Balbarinae by Flannery (1989). As a corollary to this hypothesis, the systematic status of Balbarinae within Macropodidae is rendered uncertain.

The fossil record at Riversleigh and elsewhere provides some circumstantial evidence supporting a likely bulungamayine origin for macropodids. Only a single, and as yet undescribed balbarine species has so far been identified from the younger system C deposits at Riversleigh (Cooke 1997c). The Riversleigh record discovered to date suggests that balbarines were in decline by the middle Miocene, while the number of lophodont bulungamayine species was increasing. However, balbarines were present, then and possibly later, as indicated by *Balbaroo camfieldensis*, known from the Camfield beds at Bullock Creek, estimated by Murray and Megirian (1992) to be middle Miocene in age. Several balbarine-like characters, at least some of which (such as the posterior cingulid on lower molars) are apparently apomorphic, are present in the late Miocene *Dorcopsoides*. If the homology of these characters can be demonstrated, then the uncomfortable possibility of a diphyletic origin for the early macropodids represented by *Dorcopsoides* and *Hadronomas* must be considered.

Considerable numbers of cranial and postcranial remains of both balbarines and bulungamayines have now been recovered from Riversleigh. These preserve new morphological data which can provide the basis for a more comprehensive phylogenetic analysis of Macropodoidea than has hitherto been possible. It is to be hoped that the results of such an analysis will clarify the phylogenetic relationships of both Bulungamayinae and Balbarinae.

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