

KUTERINTJA NGAMA (MARSUPIALA, ILARIIDAE): A REVISED SYSTEMATIC ANALYSIS BASED ON MATERIAL FROM THE LATE OLIGOCENE OF RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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Myers, T.J. & Archer, M. 1997:06:30. *Kuterintja ngama* (Marsupialia, Ilariidae): a revised systematic analysis based on material from the late Oligocene of Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 379-392. Brisbane. ISSN 0079-8835.

The Riversleigh ilariids come from the late Oligocene White Hunter Site and are *Kuterintja ngama* Pledge, 1987. Molar cusp morphologies are compared with those of other ilariids and vombatiforms and several morphoclines identified. The range of variation is similar to that in *Phascolarctos cinereus*. Cladistic analysis suggests several hypotheses about intrafamilial relationships: 1) *Ku. ngama* is an ilariid; 2) *Koobor* is not an ilariid; and 3) ilariids form a monophyletic clade with the wynyardiids, although the relationships of these taxa to other vombatomorphians are not resolved. □ *Ilariidae, Oligocene, Vombatiformes, White Hunter Site, Riversleigh*.

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Ilariids are extinct marsupials discovered in late Oligocene deposits of central Australia. *Ilaria* includes *I. illumidens* and *I. lawsoni* (Tedford & Woodburne, 1987); *Kuterintja* contains *Ku. ngama* (Pledge, 1987). There is also some controversy concerning the placement of *Koobor* within the Phascolarctidae because Pledge (1987) suggested that *Ku. ngama* may have been ancestral to *Ko. jimbarratti*, making the latter a potential ilariid. Tedford & Woodburne (1987) found similarities in upper dentition between *I. illumidens* and *Koobor*, namely: a paraconule on M<sup>1</sup>, no paraconule or neometaconule on M<sup>2</sup> or M<sup>3</sup>, but considered them symplesiomorphic, concluding that *Koobor* shared more synapomorphies with phascolarctids than with ilariids.

We review *Kuterintja ngama* based on material from the White Hunter Local Fauna at Riversleigh, NW Queensland. White Hunter Site on Hal's Hill, on the D-site Plateau (Archer et al., 1994; Creaser, 1997) was questionably assigned to early Miocene System B (Archer et al., 1989, 1994) but the fauna now suggests late Oligocene System A. A tentative correlation is made of White Hunter Local Fauna with the Ngama Local Fauna of the Etadunna Formation at Lake Palankarinna, South Australia.

Pledge (1987) observed that *Kuterintja ngama* differs from *Ilaria* in being smaller, having larger cusps, pre- and posteristae on the styler cusps, postprotocrista and premetaconulecrista separated by a crevice, and an anterior cingulum divided by a stronger preprotocrista. Similarities to *I. illumidens* include a selenodont structure and

well-developed buccal styler cusps. Pledge (1987) described the holotype (SAM P24539) of *Ku. ngama* as a LM<sup>4</sup>. However, material from Riversleigh suggests that the holotype is a LM<sup>3</sup>.

SYSTEMATICS

Material is deposited in the South Australian Museum (SAMP), and the Queensland Museum (QMF). Homology of molars and the dP<sub>3</sub> follows Luckett (1993). Homology of the other premolars follows Flower (1867). Cusp homology follows Archer (1984), Tedford & Woodburne (1987) and Pledge (1987).

Order DIPROTODONTIA Owen, 1866  
Suborder VOMBATIFORMES Woodburne, 1984

Infraorder VOMBATOMORPHIA Aplin & Archer, 1987

Family ILARIIDAE Tedford & Woodburne, 1987

*Kuterintja* Pledge, 1987

TYPE SPECIES. *Kuterintja ngama* Pledge, 1987 from late Oligocene Etadunna Formation at Lake Palankarinna, northern South Australia.

DIAGNOSIS. Relative to *Ilaria*: Small, lacking transverse linking crests on the cheek teeth. I<sub>1</sub> with low, almost horizontal inclination, dorsally flattened, transversely compressed and with anterior portion inflected.

P<sub>3</sub> subrectangular, with 1 large anterior cuspid and two smaller posterior cuspid only slightly

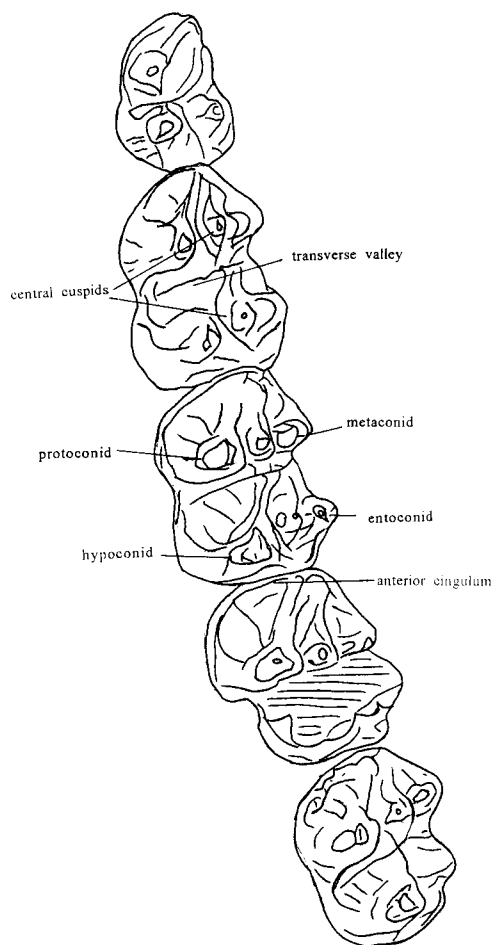


FIG. 1. *Kuterintja ngama*. QMF20810, 23306, left dentary (P<sub>3</sub> - M<sub>4</sub>).

separated, one in a posterolingual position, other in a posteromedial position longitudinally aligned with the anterior cuspid. M<sub>1</sub> subovate, with anterior cingulum medially inflected and less developed, with lingual faces of the buccal cusps near vertical, with less developed preprotocristid and posthypocristid, with preprotocristid and posthypocristid terminating in line with the 'central' cusps, with small lingual basin on the hypolophid; 'central' cuspid on the protolophid in transverse alignment with the lingual and buccal cusps on M<sub>1</sub>-M<sub>3</sub>; metaconid separated slightly from the 'central' cuspid of the protolophid; M<sub>2</sub> with 'central' cuspid on the pro-

tolophid and hypolophid of similar widths and more closely linked, with 'central' cuspid on the hypolophid not linked posteriorly to the entoconid; M<sub>2</sub> and M<sub>3</sub> with preprotocristid and posthypocristid not extending as far lingually; M<sub>3</sub> with lingual basins less developed, with 'central' cuspid on the hypolophid greatly reduced, with posterior cingulum relatively small, with postprotocristid and prehypocristid not blocking transverse valley; M<sub>4</sub> with compressed posterior, with 'central' cuspid not distinguishable on the hypolophid, with the postprotocristid and prehypocristid poorly developed (Fig. 1).

P<sub>3</sub> subovate, much wider both anteriorly and posteriorly compared to the P<sub>3</sub>, with narrow anterior portion, with large cusps, tri-cusped, lacking the posterobuccal cusp, with cusps subequal in height, with twinned central cusps separated by a larger trough, with a larger crevice separating posteromedial and posterolingual cusps, with anterolingual cingulum, with well-developed rib running from the apex of posteromedial cusp to the posterobuccal edge of the posterior cingulum.

M<sub>1</sub>-M<sub>4</sub> with nearly vertical buccal surfaces on cusps. M<sub>1</sub> with stylar cusp C almost as large as the paracone, with stylar cusp D as large as the metacone, with buccal border slanting sharply posterobuccally, with posterior cingulum a round convex structure, with all cusps subequal in height; M<sub>2</sub> with stylar cusp C relatively small, with the cristae forming the borders of the buccal basin on the paracone strongly developed, with the postparacrista separated from stylar cusp C, with stylar cusp E greatly reduced, with preprotocrista strongly developed and dividing the anterior cingulum; M<sub>2</sub> and M<sub>3</sub> with lingual cusps transversely aligned with the buccal cusps; M<sub>2</sub>-M<sub>4</sub> with the anterior portion of the tooth larger than the posterior; M<sub>3</sub> with stylar cusps B and C equivalent in height to the paracone, with the buccal basin on the paracone enclosed at its buccal margin, with stylar cusp D larger, M<sub>3</sub> and M<sub>4</sub> without stylar cusp E; M<sub>4</sub> with the lingual half of the transverse valley inflected less towards the posterolingual corner, with stylar cusp C variable, with metaconule variable in position, and thus the lingual basin variable in size; (Fig. 4).

**COMPARISON:** *Kuterintja ngama* differs from phascolarctids in lacking a paraconule and neometaconule, having longer molars, simpler selenes, separation of buccal selenes, better developed stylar cusps, a strongly developed transverse valley, poorly developed postprotocrista and premetaconulecrista, a protocone that is more

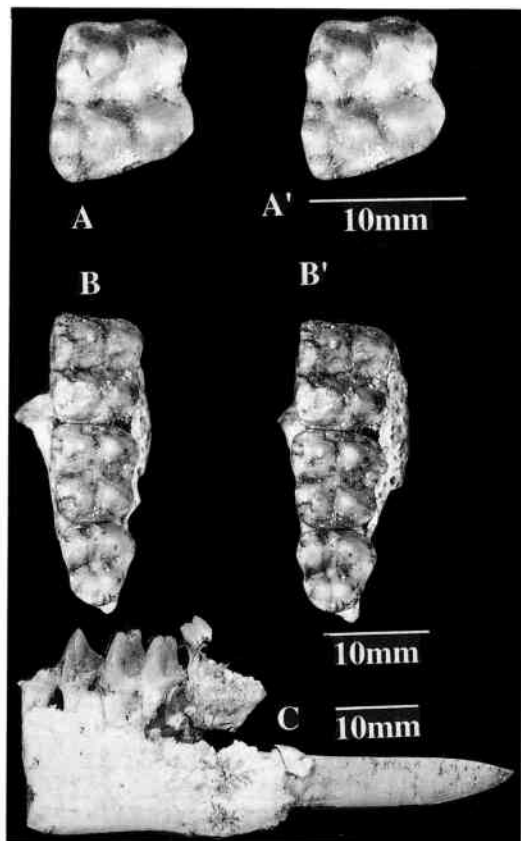


FIG. 2. *Kuterintja ngama*. A, QMF30057, RM<sup>1</sup>, occlusal view, stereo pair. B, QMF31299, RM<sup>2-4</sup>, occlusal view, stereo pair. C, QMF31301, RI<sub>1</sub>-M<sub>2</sub>, buccal view.

compressed relative to the metaconule on M<sup>1</sup>-M<sup>3</sup>, significant separation of stylar cusps C and D, no protostylid, a linguallly convex metaconid, a protoconid that is larger than the metaconid, lingual cusps that are not compressed towards each other, larger crown height, a well-developed posterolingual cusp on P<sup>3</sup>, no posterobuccal cuspid on P<sub>3</sub>, central cuspid, having a posterolingual cuspid on P<sub>3</sub>, a non-bladed P<sub>3</sub> or P<sup>3</sup>, no longitudinal valley, and a bulbous P<sup>3</sup>.

*Ku. ngama* is distinguished from *Koobor* by its larger stylar cusps, higher crown, larger molars, and continuous crest between protocone and metaconule (Pledge, 1987). Other differences include: 1) more conical stylar cusps; 2) lower selene angles on the buccal basins of the upper molars; 3) *Koobor* lacks a lingual basin on the transverse valley; 4) *Koobor* has a poorly developed anterior cingulum; 5) the absence of a pos-

terior depression on the metaconule, as exists on most ilariid molars; 6) *Koobor* has molars which are slightly compressed linguallly; 7) a much wider and longer longitudinal valley exists in *Koobor*; 8) more poorly developed postproto-crista and premetaconulecrista; 9) a protocone that is compressed longitudinally relative to the metaconule on M<sup>1</sup>-M<sup>3</sup>; 10) no paraconule on M<sup>1</sup>; 11) *Koobor* lacks the posterolingual cusp on P<sup>3</sup>; and 12) *Koobor* has an elongated, rather than bulbous, P<sup>3</sup>.

#### *Kuterintja ngama* Pledge, 1987 (Figs 1-5, 7)

**MATERIAL.** Holotype SAMP24539, LM<sup>3</sup>, presumed to be a left M<sup>4</sup> by Pledge (1987) from the saddle between Mammalon Hill and main escarpment, NW corner of Lake Palankarina, 100km N of Marree, South Australia in the late Oligocene (Woodburne et al., 1993) Ngama Local Fauna within the Etadunna Formation. Other material. QMF31302, a right dentary fragment containing P<sub>3</sub>, M<sub>1</sub> and M<sub>2</sub>; QMF23306, QMF20810, a left dentary with all cheek teeth and the alveoli for I<sub>1</sub>; QMF31301, anterior portion of a juvenile right dentary, with I<sub>1</sub>, dP<sub>3</sub>, and M<sub>1</sub>. P<sub>3</sub> is removed from its crypt, and M<sub>2</sub> has only part of the protoconid remaining; QMF17527, RM<sub>3</sub> with roots missing; QMF31300 RM<sub>4</sub> with the anterior portion of the trigonid missing; QMF30057, RM<sup>1</sup>; QMF23203, LM<sup>1</sup> with a broken anterior cingulum; QMF30058, RM<sup>2</sup>; QMF31299, right maxillary fragment containing M<sup>2-4</sup>; and QMF24604, right maxillary fragment with M<sup>3</sup> and M<sup>4</sup>, and alveoli for M<sup>1</sup> and M<sup>2</sup>; QMF30332, partial right maxilla, with partial palate, anterior zygomatic arch, P<sup>3</sup>, M<sup>2</sup> and the alveoli for M<sup>1</sup>. All except type from late Oligocene White Hunter Site, Riversleigh, NW Queensland; previously regarded as possibly System A or early System B (Archer et al., 1989; Archer et al. 1994), late Oligocene or early Miocene. This species suggests comparable age to the South Australian type locality.

**DIAGNOSIS.** As for genus.

**DESCRIPTION.** Dentary. Deepest below the posterior half of M<sub>3</sub>. In lateral aspect alveolus for I<sub>1</sub> inclined slightly on its ventral side, horizontal on dorsal side. Mental foramen at the posterior end of this alveolus in the dorsoventral midline, and just anterior to P<sub>3</sub>, only foramen on the dentary (break dorsoventrally from the junction of M<sub>2</sub> and M<sub>3</sub> may obscure others).

I<sub>1</sub>. Lower first incisor projecting horizontally from the dentary, curving linguallly at its anterior (distal) extremity, subcylindrical, transversely compressed, with dorsal surface transversely flat-

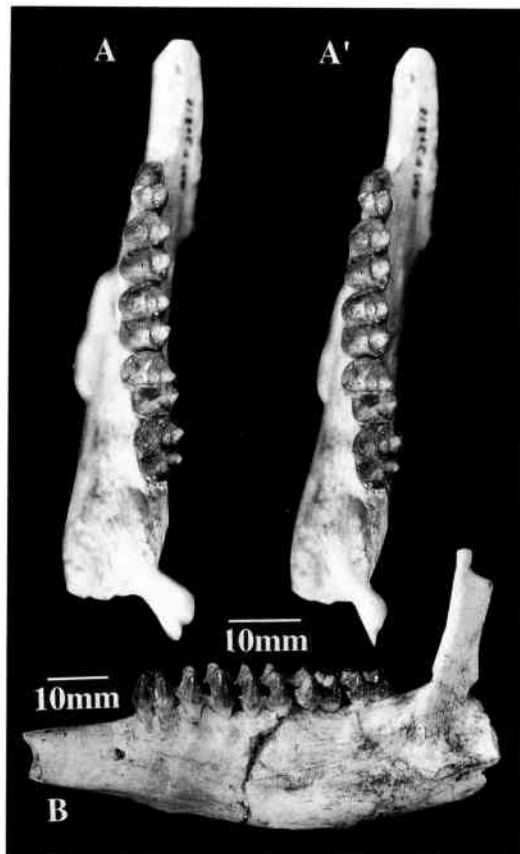


FIG. 3. *Kuterintjangama*. A, QMF20810, left dentary, occlusal view, stereo pair. B, QMF23306, buccal view.

tened, with enamel from the buccal to ventral surfaces.

dP<sub>3</sub>. Same as P<sub>3</sub> except in size, tricuspid, subtriangular.

Anterior cuspid tallest, with widest base. Smaller cuspid posterolingually from anterior cuspid. Third cuspid posterobuccally from anterior cuspid and equivalent in size to the posterolingual cuspid. All cuspids closely linked, conical, with wide bases.

P<sub>3</sub> (Fig. 1). Transversely compressed, tricuspid. Large, subovate, conical cuspid anteriorly larger, taller and more broadly based than the twin cuspids posteriorly. More buccal of these anteroposteriorly aligned with the large, anterior

cuspid. Posterolingual cuspid taller than its worn buccal counterpart.

Thin, low cristid running from the anterolingual corner of the apex of the anterior cuspid, anterolingually to the base of the cuspid, then turning posterolingually and running further down towards the root, then turning posterobuccally up the cuspid and terminating about half way up the height of the cuspid, in line with the posterior side of the apex of the large cuspid. Anterior cuspid located over the posterior portion of the anterior root; posterior cuspids located directly over the posterior root.

A minor crevice on the anterolingual corner of

TABLE 1. Measurements (mm) of dentition of *Kuterintjangama*. Le=length; Mw=maximum width; Ha=height of anterior cuspid; Aw=anterior width; Pw= posterior width; Hp=height of paracone; Hpr=height of protocone; Hm=height of metacone; Hml=height of metaconule; Hprd= height of protoconid; Hmd=height of metaconid; He=height of entoconid; Hh=height of hypoconid. Italicised numbers indicate dimension may have been lessened by wear.

QM No/ID	Le	Mw	Ha	Aw	Pw	Hp	Hpr	Hm	Hml
30332 RP <sup>3</sup>	8.9	7.5	4.2	-	-	-	-	-	-
30057 RM <sup>1</sup>	9.7	-	-	8.7	7.7	5.4	4.6	5.2	4.7
31299 RM <sup>2</sup>	10	-	-	8.6	8.0	4.8	5.4	4.9	5.1
30058 RM <sup>2</sup>	9.4	-	-	8.9	8.8	4.7	5.4	5.1	5.1
30332 RM <sup>2</sup>	10	-	-	9.5	9.5	?	?	3.3	3.1
31299 RM <sup>3</sup>	8.4	-	-	7.6	6.5	4.4	5.3	4.1	5.1
24604 RM <sup>3</sup>	8.5	-	-	8.1	7.0	4.5	5.6	4.4	4.8
31299 RM <sup>4</sup>	7.2	-	-	6.7	4.9	3.8	4.4	3.3	3.3
24604 RM <sup>4</sup>	7.6	-	-	6.8	5.5	4.0	5.1	3.4	3.5
23203 LM <sup>1</sup>	10	-	-	8.3	8.0	4.2	4.8	4.2	4.2
31301 dP <sub>3</sub>	3.9	3.6	2.8	-	-	-	-	-	-
31301 RP <sub>3</sub>	6.7	4.9	5.7	-	-	-	-	-	-
31302 RP <sub>3</sub>	6.6	5.0	4.8	-	-	-	-	-	-
31301 RM <sub>1</sub>	10	-	-	6.8	7.4	5.6	5.0	5.7	6.4
31302 RM <sub>1</sub>	9.5	-	-	6.5	7.3	3.7	3.7	4.2	4.0
31301 RM <sub>2</sub>	9.8	-	-	?	?	6.5	?	?	?
31302 RM <sub>2</sub>	9.9	-	-	6.9	7.2	3.8	3.6	4.0	3.7
31301 RM <sub>3</sub>	10	-	-	6.3	5.8	6.0	4.4	4.3	6.1
17527 RM <sub>3</sub>	9.7	-	-	6.4	6.0	6.3	4.4	4.4	6.2
31300 RM <sub>4</sub>	9.1	-	-	?	5.6	3.8	3.5	3.2	3.7
23306 LP <sub>3</sub>	6.8	5.4	5.9	-	-	-	-	-	-
23306 LM <sub>1</sub>	9.9	-	-	6.4	6.9	4.9	4.5	4.7	5.4
23306 LM <sub>2</sub>	9.7	-	-	7.4	7.5	4.9	4.4	4.5	5.1
23306 LM <sub>3</sub>	9.4	-	-	7.2	?	4.4	4.9	4.1	5.0
23306 LM <sub>4</sub>	9.2	-	-	6.8	5.7	4.1	4.2	3.7	3.7

the tooth. A deeper crevice dividing the tooth into sub-equal halves, with the large anterior cuspid on the anterior side and the twinned posterior cusps on the posterior side, blocked half way along by a crest linking the anterior cuspid to the posterobuccal cuspid. A shallower crevice between the posterior cusps blocked by a minor crest running from the apices of these cusps.

Small cristid running posteroventrally from the posterobuccal corner of the apex of the posterobuccal cuspid, turning posterolingually, joining a wider posterior cingulum. Posterior cingulum curving anterolingually before joining the base of the posterolingual cuspid.

**Lower Molars.** Subrectangular. M<sub>1-3</sub> subequal; M<sub>4</sub> smaller. Crown heights decreasing from M<sub>1-4</sub>. Tooth row curving posterolingually (Fig. 1).

**M<sub>1</sub>:** 'Central' cusps on the protolophid and hypolophid are neomorphs (Tedford & Woodburne, 1987). 6-cuspid; anterior portion narrower than posterior. Trigonid triangular; anterolingual border inclined posterolingually; anterobuccal border of trigonid inclined posterobuccally; both these inflections originating from an anteromedial position of the anterior cingulum, at termination of preprotocristid. Talonid wider than trigonid. Protoconid over the posterior portion of the anterior root; posterior cusps aligned over the central portion of the posterior root. Preprotocristid (or paracristid) relatively wide, generally low, with pocket between the buccal margin, the anterior cingulum and the anterior face of the protoconid, with smaller and less well defined pocket between the anterior cingulum, the lingual margin of the preprotocristid and the anterior surfaces of the 'central' cuspid and metaconid. 'Central' cuspid of protolophid with apex slightly anterior to the protoconid and metaconid. Anterior positioning of 'central' cuspid or neomorph more exaggerated on the hypolophid. Both 'central' cusps of similar height, lower than main cusps. 'Central' cuspid on protolophid forming a lingual basin with the metaconid, not totally enclosed, with small openings anteriorly and posteriorly. Similar, small basin formed between the 'central' cuspid of the hypolophid and the entoconid, with comparable openings to its counterpart on the protolophid, with anterior opening much smaller.

A deep crevice dividing 'central' cusps from the main buccal cusps, continuous anteroposteriorly, shallower in the central part of the tooth. Transverse valley interrupting this lon-

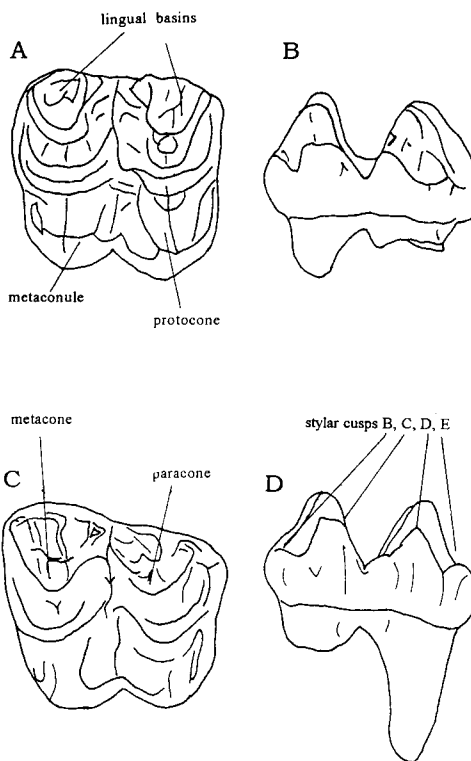


FIG. 4. *Kuterintja ngama*. A-B, QMF30058, RM<sup>2</sup>. A, occlusal view; B, buccal view. C-D, QMF30057, RM<sup>1</sup>. C, occlusal view; D, buccal view.

gitudinal crevice wide, blocked at its buccal extremity by a small, posterobuccally slanting cingulum linking the base of the protoconid to the base of the hypoconid. Thin crevice in the transverse valley preventing symmetrical postprotocristid and prehypocristid (cristid obliqua) and postmetacristid and preentocristid from linking. Metaconid and entoconid with apices steeply inclined, rather than conical, with lingual surface of each much taller than the buccal. Entoconid higher than metaconid higher than 'central' cusps, with slight gradient descending from lingual to buccal. A thin posterior cingulum and a small pocket in the posterolingual corner of the tooth; pocket bordered by the lingual end of the posterior cingulum, with 2 crests from the posterolingual and posterobuccal sides of the apex of the entoconid, respectively.

In QMF31301 protoconid and hypoconid with lingual surfaces slightly more vertically orien-

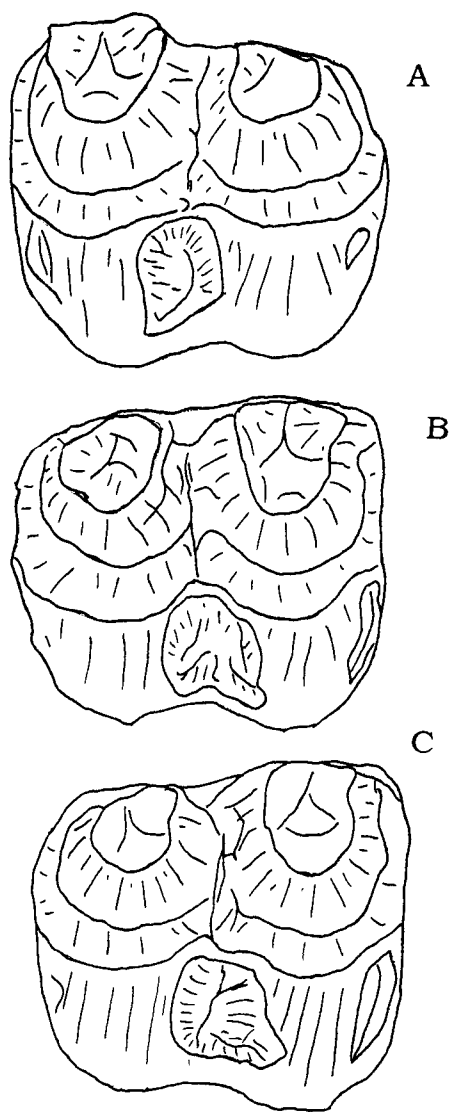


FIG. 5. *Kuterintja ngama*. A, SAMP24539, holotype, LM<sup>3</sup>. B, QMF24604, RM<sup>3</sup>. C, QMF31299, RM<sup>3</sup>.

tated, possibly due to less wear than observed in QMF23306.

M<sub>2</sub>. Like M<sub>1</sub> except: anterior end resting upon the posterior cingulum of M<sub>1</sub>; trigonid subrectangular rather than triangular, due to the anterior cingulum being more transversely linear, anterior

pockets formed with the anterior cingulum smaller; trigonid and talonid equal in transverse width. 'Central' cuspid on the protolophid in direct transverse alignment with the protoconid and metaconid; 'central' cuspid on the hypolophid more to anterior; hypoconid slightly more posterior. Crevice between the linked lingual cusps and the buccal cuspid shallower (possibly due to wear on protoconid and hypoconid). Cuspid height gradient from lingual to buccal much steeper (possibly due to wear). Pocket at the buccal end of the transverse valley larger. Cristid obliqua (or prehypocristid) and hypocristid (posthypocristid) more developed. Lingual pocket on the protolophid less well defined, with the openings between the metaconid and 'central' cuspid larger. Small posterolingual pocket bordered by postentocristid, hypocristid and a small posterior cingulum, with most of the latter hidden by M<sub>3</sub>.

M<sub>3</sub>. Same as M<sub>2</sub> except: anterior cingulum rounded. Crown height reduced; with height gradient. Metaconid and 'central' cuspid not closely linked, separate entities with a crevice between the two cusps. Crevice of variable depth. 'Central' cuspid on the protolophid larger, highlighting an increase in size from M<sub>1</sub> to M<sub>3</sub>. Crevice between 'central' and buccal cusps shallower, decreasing in depth down the tooth row. Despite damage to the talonid, 'central' cuspid on the hypolophid much reduced. Entoconid sub-equal in height to the 'central' cuspid on the hypolophid, transversely compressed. Posterior cingulum and posterobuccal basin much shorter.

Juvenile M<sub>3</sub> with an anterolingual basin bigger than in M<sub>1</sub> or M<sub>2</sub>, paracristid terminating in longitudinal alignment with the buccal side of the metaconid.

M<sub>4</sub>. Shortest and narrowest molar, with lowest crown, rounded subrectangular, with a very rounded anterior cingulum. Same as M<sub>3</sub> except: protolophid and hypolophid slanting more anterolingually, due to the buccal cusps being posterior to the lingual cusps.

'Central' cuspid on the protolophid not linked to the metaconid; crevice between these 2 cusps deeper. 'Central' cuspid on the hypolophid greatly reduced, more so than in M<sub>3</sub>, further to posterior. Posterior cingulum short, extending to the medial line of the tooth. Posterolingual basin greatly reduced. Transverse valley closed lingually and buccally. Lingual end of the transverse

valley curving posterolingually; buccal end curving posterobuccally. Cristid obliqua and hypocristid relatively short. All cuspids subequal in height, with the metaconid slightly larger than the entoconid = protoconid and hypoconid.

P<sup>3</sup>. Subovate, tricusped, transversely wide. Anterior portion narrower than posterior. Cusps 3, large, subequal in height. Anterior and posteromedial cusps longitudinally aligned, separated by a shallow trough. A large crevice separating the posteromedial and posterolingual cusps. With very small anterolingual cingulum and larger posterior cingulum. A thin rib running from the apex of the posteromedial cusp to the posterobuccal edge of the posterior cingulum.

Upper molars. Styler cusps well-developed; general selenodont cusp pattern; high crowned, with a general gradient towards the lingual side, with 4 major cusps (paracone, protocone, metacone and metaconule), with a styler shelf consisting of styler cusps B,C,D and E.

M<sup>1</sup> (Fig. 4). Buccal cusps of RM<sup>1</sup> positioned more posteriorly than in other molars, with posterobuccal slant, wider posteriorly than anteriorly, giving an anterolingual slant to the buccal border. Styler cusp B smaller and further anterior than in other molars. Styler cusp C as large as that on M<sup>2</sup>, anterior to the postparacrista; crista not forming part of the posterior face of the styler cusp. Styler cusp D largest cusp, subequal in height to the metacone, larger than in any other molar. Styler cusp E more developed than in other molars, larger than styler cusp B. A minor cusplule on the anterior of styler cusp D, buccal to the termination of the postmetacrista, larger than styler cusp B, but slightly smaller than styler cusp E. All styler cusps subconical to triangular, except posterobuccally-aligned ridge, styler cusp C. Buccal margin wider than lingual; blocking crests in the transverse valley absent (some minor partial blockages buccally); anterior cingulum curving posterobuccally at its buccal extremity; preparacrista orientated less transversely than in other upper molars; minor depression on the posterior face of the metaconule less developed than in M<sup>2</sup>; buccal basins on the paracone and metacone poorly developed compared to other molars; posterior cingulum thinner than in other molars.

M<sup>2</sup> (Fig. 4). Square. Cusp sizes: paracone >metacone> protocone = metaconule. Styler

cusp height: C>D>B>E. Styler cusp B connected to the paracone by a preparacrista, and styler cusp C via a postparacrista. Styler cusp D connecting to the metacone by a premetacrista, and styler cusp E connected to the metacone by a postmetacrista. Buccal basin deep, formed between styler cusps B and C and the paracone. The homologous basin on the metacone less distinct, enclosed less tightly, slanting steeply posterobuccally towards the reduced styler cusp E. Basin on the metacone deepest anterolingual to styler cusp E. Large transverse valley dividing this tooth in half, containing the paracone (and associated styler cusps) and protocone anteriorly, and the metacone and metaconule posteriorly, partially blocked buccally by an incomplete crest linking premetacrista and postprotocrista, blocked centrally by a small crest linking postprotocrista and premetaconule crista, stopped at its lingual extremity by a very low crest linking the lingual sides of protocone and metaconule (lingual cingulum). Buccal faces of protocone and metaconule steeply inclined, almost to the point of being vertical; anterior cingulum well-developed, running buccally from the protocrista to the anterior side of styler cusp B, and lingually from the anterolingual corner of the base of the protocone to the protocrista; posterior cingulum smaller than anterior cingulum, with the former extending from styler cusp E to join the postmetaconulecrista; small depression on the lingual side of the postmetaconulecrista and medial posterior base of the metaconule (perhaps remnant of the lingual portion of the posterior cingulum); all cusps over the mid-line of the roots; styler cusps triangular, rather than round or conical; buccal cusps with very round apices.

M<sup>3</sup> (Fig. 5). Same as M<sup>2</sup> except: crown lower; 4 major and styler cusps retaining same relative heights; styler cusp E further reduced, virtually non-existent; posterior cingulum less defined; small pocket on the posterior side of the metaconule on M<sup>2</sup> absent; lingual cusps closer to the anterior side of their respective roots. Styler cusp C more to posterior than in M<sup>2</sup>, with postparacrista forming part of this styler cusp; buccal basin on the paracone of M<sup>3</sup> larger than in M<sup>2</sup>, triangular, with wider buccal edge. Transverse valley partially blocked buccally by a crest linking styler cusps C and D, but not by a crest linking the premetaconulecrista and postparacrista, with central and lingual blocking crests. Crest linking styler cusp D and the metacone larger and more uniform; styler cusp E more

TABLE 2. Characters and character states used in the ilariid intrafamilial phylogenetic analysis.

Characters		States
1	Stylar cusp development	0=poor; 1=well
2	Transverse valley on lower molars	0=absent; 1=moderate; 2=well-developed
3	Transverse linkages between cuspids	0=none; 1=poor; 2=moderate; 3=well-developed
4	Post protocrista and pre metaconulecrista	0=strongly developed; 1=poorly developed
5	Protocone compressed longitudinally relative to metaconule (on M-M <sup>1</sup> )	0=absent; 1=present
6	Separation of stylar cusps C and D	0=no significant separation; 1=significant separation by large trough
7	Paraconule on M <sup>1</sup>	0=well developed; 1=poorly developed; 2=absent
8	Paraconid on M <sub>1</sub>	0=absent; 1=weak; 2=strongly developed
9	Protostylid	0=present; 1=absent
10	Metaconid	0=conical; 1=lingually convex crest
11	Relative heights of the anterior cuspids	0=subequal; 1=protoconid larger than metaconid
12	Overall tooth size	0=small; 1=large
13	Lingual cusps	0=compressed together; 1=not compressed
14	Crown height	0=low; 1=moderate; 2=high
15	Posterolingual cusp on P <sup>3</sup>	0=absent; 1=slight cusp; 2=moderate; 3=well-developed
16	I <sub>1</sub> (unorderd)	0=dorsoventrally flattened; 1=caniniform and conical; 2=dorsally flattened and distally inflected
17	Posterobuccal cuspid on P <sub>3</sub>	0=absent; 1=present
18	'Central' cuspid	0=absent; 1=present
19	Posterolingual cuspid on P <sub>3</sub>	0=absent; 1=present
20	lingual closure of transverse valley by a cingulum (on upper molars)	0=cingulum absent; 1=incipient cingulum (in form of cuspules); 2=cingulum present
21	Bladed P <sub>3</sub>	0=present; 1=absent
22	Bladed P <sup>3</sup>	0=strongly bladed; 1=weakly bladed; 2=absent
23	Posterobuccal cusp on P <sup>3</sup>	0=absent; 1=present
24	Longitudinal valley (i.e. distance between lingual & buccal cusps / ids)	0=well-developed; 1=moderately developed; 2=absent
25	P <sup>3</sup>	0=bulbous; 1=elongate

anteriorly positioned; buccal basin on the metacone narrower, slanting more anterobuccally.

M<sup>4</sup>. Sub-triangular, posteriorly compressed. Same as M<sup>3</sup> except: crown height very small, with the protocone>paracone=metacone>metaconule. Stylar cusp B>D; stylar cusp C non-existent; stylar cusp E extremely reduced or missing. Crevice between the paracone and protocone transversely wider. Buccal surface of the metaconule and protocone far less vertically inclined. Anterobuccal basin larger; buccal basin on the metacone absent; buccal basin on the paracone very shallow, slanting posterobuccally. Transverse valley not blocked buccally, curving posterobuccally rather than being transverse, with lingual end enclosed slightly, by a low crest (i.e. the crest does not continue to the base of the protocone). Anterior cingulum very small. Posterior root slants posteriorly rather than vertically.

REMARKS. Comparing LM<sup>1</sup> QMF23203 to RM<sup>1</sup> QMF30057: buccal half of the anterior cingulum transversely shorter; stylar cusps B and E less developed; cusplule on the anterior face of stylar cusp D absent. M<sup>3</sup> of QMF24604 exhibits variation compared to the M<sup>3</sup> of QMF31299 as follows: 1) stylar cusp D is larger; 2) the distance between stylar cusps D and E is greater and therefore a bigger buccal basin is found on the metacone; and 3) the medial lingual basin is divided into two sub-basins at its lingual margin by a very small transverse crest.

QMF24604 highlights the variability in M<sup>4</sup>, as follows: posterior half not as compressed as in M<sup>4</sup> of QMF31299, and therefore has a longer and wider posterior cingulum. Stylar cusp E is much reduced. Therefore the buccal basin on the metacone is also present and it is as deep as the basin on the paracone. Stylar cusp D is also more defined and larger than in M<sup>4</sup> of QMF31299. The medial lingual basin is smaller. The anterior cingulum extends further lingually to the base of the protocone. The transverse valley is blocked in two places rather than one. It is blocked buccally by a crest linking stylar cusps C and D, and is partially blocked by a small crest linking postparacrista and premetaconulecrista. The crest partially blocking the lingual extremity in QMF31299 is not present. Large stylar cusp C is not present in QMF31299. A well developed and enclosed buccal basin on the paracone is absent in QMF31299.



TABLE 3. Ilariid intrafamilial data matrix as used by PAUP. ? = fossil material missing or status uncertain; a = 1 &amp; 2; b = 0 &amp; 1; c = 0 &amp; 2

Taxa	CHARACTERS AND STATES																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>Madakoala</i> spp.	0	0	1	0	0	0	0	2	0	0	0	0	0	0	1	?	1	0	0	c	0	0	0	0	0
<i>P. cinereus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	0	1	1	0	0
<i>Koobor notabilis</i>	0	?	?	0	0	0	0	?	?	?	?	0	0	0	0	?	?	?	?	1	?	1	0	1	0
<i>Ilaria illumidens</i>	1	2	2	1	1	1	1	2	0	0	0	1	1	2	2	1	1	1	1	2	0	1	0	2	0
<i>Ilaria lawsoni</i>	?	2	2	?	?	?	?	1	1	1	1	1	?	2	?	1	1	1	1	?	1	2	1	2	1
<i>Kuterintja ngama</i>	1	2	1	1	1	1	2	0	1	1	1	0	1	2	3	2	0	1	1	2	1	?	?	2	?
wynyardiids	1	1	3	0	0	1	2	0	1	0	1	0	1	1	a	2	0	0	0	0	1	2	0	2	1

### PHYLOGENETIC SYSTEMATICS

Twentyfive dental characters with up to 4 states each (Table 2) were used to develop the data matrix following character argumentation and polarisation (Table 3) for the intrafamilial analysis of ilariids. Three outgroups used to determine polarities are: 1) the modern Koala, *Phascolarctos cinereus*; 2) *Madakoala*; and 3) wynyardiids. The former is the most derived member of a primitive outgroup because the Phascolarctidae is the stem taxon from which the vombatomorphian radiation diverged (Marshall et al., 1990; Aplin & Archer, 1987). *Madakoala devisi* and *Madakoala wellsi* are employed because of the primitive position of *Madakoala* within the phascolarctid radiation (Woodburne et al., 1987). Primitive and derived phascolarctids were used to determine the relationships of species of *Koobor*. Wynyardiids include *Namilamadeta snideri* and *Muramura sp.* and are a closer sister group of the ilariids than the phascolarctids, therefore providing a basis for polarising character states within the Vombatomorpha.

Character optimisation is performed after the character analysis has been completed and the most parsimonious trees found. The two optimisation algorithms used by PAUP are ACCTRAN and DELTRAN. ACCTRAN accelerates the evolutionary transformation of characters so that changes occur at the earliest possible stage on the optimal tree. As far as homoplasy is concerned, this algorithm has the effect of favouring reversal of character states over convergences. DELTRAN delays transformation of characters so that changes occur as far up the optimal tree as possible. This has the effect of favouring convergences over character reversals (Wiley et al., 1991). DELTRAN analyses are favoured here because of the large amount of missing character data in the matrices.

RESULTS. the optimal tree (Fig. 6) has 50 steps; a consistency index (CI) of 0.800; a homoplasy index (HI) of 0.260; a retention index (RI) of 0.778; and a rescaled consistency index (RC) of 0.622. Notably the ingroup (*Koobor notabilis*, *I. lawsoni*, *I. illumidens* and *Kuterintja ngama*) did not form a monophyletic clade. *Ko. notabilis* is sister taxon to the Wynyardiidae, *Ku. ngama*, *I. illumidens* and *I. lawsoni* clade. *Madakoala* and *Phascolarctos cinereus* formed a basal monophyletic clade.

Bootstrap analysis for the most parsimonious tree had the clade excluding phascolarctids and *Koobor* supported 99% of the time. The ilariid clades, excluding and including *Ku. ngama*, occurred 78% and 95% of the time respectively.

Removal of the wynyardiids as an outgroup had no effect on the topology in the optimal tree. A bootstrap analysis on data excluding the wynyardiids found the clade containing *I. illumidens* and *I. lawsoni* to be supported 62% of the time, slightly lower than in the previous analysis. While the clade including all 3 ilariid species was supported on all occasions.

Another method of testing support for the optimal tree is to examine the frequency and topology of the 'next best' trees (Simmons, 1993). PAUP evaluated 945 trees and found one optimal tree of 50 steps. Two trees of length 51 were observed as well as one tree of 52 steps. Neither of the trees of 51 steps in length are considered here as the phyletic relationships presented by each do not represent the phascolarctids as a monophyletic clade. In both cases *Koobor* is intermediate between *Madakoala* spp. and *Phascolarctos cinereus*.

### DISCUSSION

Classification of *Ku. ngama* as an ilariid was tentative (Pledge, 1987) and controversy surrounded placement of *Koobor*. Comparison of the

Riversleigh ilariid with species of *Ilaria* and *Kuterintja ngama*, confirms that the Riversleigh animal is indistinguishable from the latter. Dental variation in *Phascolarctos cinereus*, one of *Ku. ngama*'s closest living relatives, suggests that: 1) variation in Riversleigh fossil material is in the range for vombatiform species, and represents only one taxon; and 2) the Riversleigh species is *Ku. ngama*.

**DISCUSSION OF THE PHYLOGENETIC ANALYSIS.** *Kuterintja ngama* as the sister taxon of a clade containing *Ilaria illumidens* and *Ilaria lawsoni* (Fig. 6), and not united with wynyardiids or *Koobor*, reinforces classification of this animal as an ilariid. Synapomorphies used by DELTRAN to unite ilariids include: 1) a well-developed transverse valley; 2) poorly-developed postparacrista and premetaconulecrista; 3) protocone longitudinally compressed relative to the metaconule on  $M^1$ - $M^3$ ; 4) large crown height; 5) moderately well-developed posterolingual cusp on  $P^3$ ; 6) closure of the transverse valley on upper molars by a lingual cingulum; 7) a non-bladed and bulbous  $P^3$ ; 8) a non-bladed  $P_3$  and 9) a 'central' cuspid on the protolophid and hypolophid of lower molars. These synapomorphies only apply to the Ilariidae relative to the other taxa used in this analysis, and may prove to be symplesiomorphies when all other vombatomorphian taxa are included. Some of these synapomorphies refer to the upper dentition, which is unknown for *Ilaria lawsoni*. However, the close similarities between the lower dentition of both *Ilaria* species suggests that these synapomorphies will be generically significant when upper dentition for *I. lawsoni* is found. Synapomorphies used by the same algorithm to unite species of *Ilaria* include: 1) moderately well-developed transverse linkages between cuspids; 2) weak paraconid; 3) large tooth size; and 4) transversely compressed, caniniform lower first incisors.

In constructing the most parsimonious tree, 9 characters were found to exhibit some degree of homoplasy. According to DELTRAN moderately well-developed transverse linkages between cuspids is due to convergence between primitive wynyardiids and species of *Ilaria*, with *Kuterintja ngama* with plesiomorphic poorly developed linkages. Conversely, ACCTAN suggests that moderately well-developed transverse linkages were already a feature of the common wynyardiid/ilariid ancestor, possibly before *Koobor* diverged from the vombatomorphian lin-

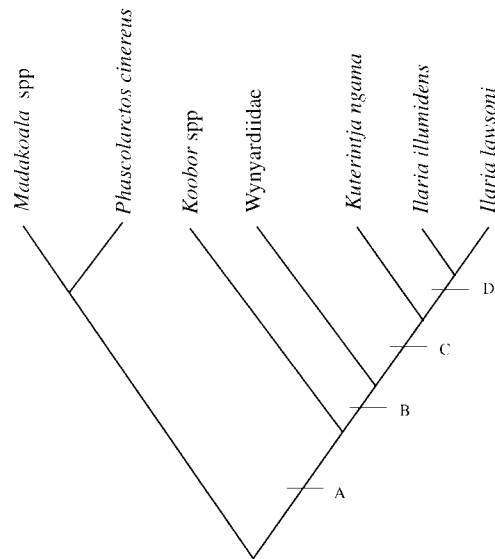


FIG. 6. Relationships of the Ilariidae and *Koobor*. DELTRAN Synapomorphies: A-weak longitudinal valley; B-well-developed styler cuspids; moderately developed transverse valley; separation of styler cuspids C and D; weak paraconule on  $M^1$ ; no protostylid; protoconid > metaconid; no compression of lingual portion of tooth; moderate crown height; dorsally flattened and distally inflected  $I_1$ ; no longitudinal valley; C- well-developed transverse valley; poorly developed postprotocrista and premetaconulecrista; protocone longitudinally compressed relative to metaconule on  $M^1$ - $M^3$ ; large crown; moderately developed posterolingual cusp on  $P^3$ ; 'central' cuspid; posterolingual cuspid on  $P_3$ ; lingual closure of transverse valley on uppers by a cingulum; non-bladed  $P_3$  and  $P^3$ ; D-moderately well developed transverse linkages; weak paraconid on  $M_1$ ; large teeth; caniniform and conical  $I_1$ . ACCTAN Synapomorphies: A-moderately developed transverse valley; moderately developed transverse linkages; no protostylid; protoconid metaconid; dorsally flattened and inflected  $I_1$ ; no posterobuccal cuspid on  $P_3$ ; moderately developed longitudinal valley; B-well-developed styler cuspids; separation of styler cuspids C and D; no paraconule; uncompressed lingual portion of tooth; moderate crown height; moderately developed posterolingual cusp on  $P^3$ ; no longitudinal valley; C- well-developed transverse valley; poorly developed postprotocrista and premetaconulecrista; protocone longitudinally compressed relative to metaconule on  $M^1$ - $M^3$ ; metaconid a lingually convex crest; high crowns; 'central' cuspid; posterolingual cuspid on  $P_3$ ; transverse valley closed lingually by cingulum; non-bladed  $P_3$  and  $P^3$ ; bulbous  $P^3$ ; D-poorly developed paraconule; weak paraconid on  $M_1$ ; large teeth; caniniform, conical  $I_1$ ; posterobuccal cuspid on  $P_3$ ; and  $P^3$ .

age. Poorly-developed transverse linkages in *Ku. ngama* would therefore be the result of a reversal to the phascolarctid state. The ACCTTRAN model appears preferable, although discovery of a lower dentition for *Koobor* would help resolve its classification.

The poorly-developed paraconule on  $M^1$  of *Ilaria illumidens* (Tedford & Woodburne, 1987), is either a plesiomorphy dating from some time after divergence of *Koobor* (DELTRAN), or the result of a reversal (ACCTTRAN). The former hypothesis implies that loss of the paraconule is convergent between wynyardiids and *Ku. ngama*, while the latter, and possibly more parsimonious, hypothesis suggests that the paraconule was already lost from the vombatiform lineage before the wynyardiids and ilariids diverged.

The paraconid on  $M_1$  is another homoplastic character. For both algorithms character transformation suggests that a well-developed paraconid is convergent between *I. illumidens* and *Madakoala*. A poorly developed paraconid is deemed to be convergent between species of *Ilaria* and primitive *Madakoala*, with absence of a paraconid being the plesiomorphic phascolarctid character state. However, a more likely solution is: 1) that a well-developed paraconid is the plesiomorphic condition; 2) that absence of a well-developed paraconid in *P. cinereus* is a derived condition; 3) that the paraconid was gradually reduced or lost before or after *Koobor* diverged; 4) that the paraconid in species of *Ilaria* represents a reversal to the plesiomorphic state; and 5) that loss of a paraconid is convergent between *P. cinereus*, wynyardiids and possibly *Koobor*. Knowing whether there was or was not a paraconid in *Koobor* would help clarify this situation.

Both algorithms suggest that a protostylid on  $M_1$  of *Ilaria illumidens* represents a reversal to the plesiomorphic phascolarctid condition. The only discrepancy between the two character transformation pathways is the point at which the protostylid was lost. DELTRAN delays loss of the protostylid until after the divergence of *Koobor*, while ACCTTRAN maintains that loss occurred before the divergence. An identical character transformation occurs for 'relative heights of the anterior cuspids' (character 11), such that cuspids which are subequal in height represent a reversal to the plesiomorphic condition for *I. illumidens*. Possessing a protoconid larger than the metaconid is therefore a synapomorphy uniting wynyardiids, *I. lawsoni*, *Kuterintja ngama* and possibly *Koobor*. A

posterobuccal cuspid on  $P_3$  of species of *Ilaria* is deemed to be a reversal to the plesiomorphic phascolarctid condition by ACCTTRAN, while DELTRAN suggests that absence of this structure is convergent between wynyardiids and *Kuterintja ngama*. Again, ACCTTRAN seems to be the most parsimonious, implying that the posterobuccal cuspid was lost before wynyardiids and ilariids, and possibly *Koobor*, diverged.

For lingual closure of the transverse valley on upper molars (character 20) the pathway for character transformation is unclear due primarily to the variable nature of this structure in *Madakoala*. However, the suggested transformation sequence is: 1) a partial cingulum, in the form of 2 cuspules on the anterolingual and posterolingual bases of the metaconule and protocone respectively, was present in the ancestral koala; 2) the two cuspules eventually joined, convergently forming the derived lingual cingulum in *P. cinereus*, some specimens of *Madakoala* and ilariids; and 3) other *Madakoala* and wynyardiids developed in the opposite direction, convergently losing the cuspules altogether. The two cuspules occur in *Koobor notabalis* but not in *Koobor jimbaratti* (Archer, 1977), perhaps suggesting that the latter is more derived than the former. Alternatively, a lingual cingulum may be a plesiomorphic phascolarctid condition, implying that the cuspules in *Ko. notabalis* are an apomorphic vestige. In this case, absence of a lingual cingulum would be a more derived condition, convergent between some specimens of *Madakoala*, *Ko. jimbaratti* and wynyardiids.

The final character transformation found to contain some degree of homoplasy involved a cusp on the posterobuccal margin of  $P^3$  (character 23). The sequence of change suggested by the algorithms is that absence of such a cusp is the plesiomorphic condition, and that species of *Madakoala*, *Ilaria illumidens* and possibly *I. lawsoni* convergently share a derived posterobuccal cusp. This transformation sequence seems unlikely because *Madakoala* are overall more plesiomorphic phascolarctids (Woodburne et al., 1987) and a posterobuccal cusp on  $P^3$  is more likely to be the plesiomorphic condition. If so, loss of this structure is a synapomorphy for *Koobor*, wynyardiids and *Ku. ngama*, and is convergent on the condition in *Phascolarctos cinereus*. Absence of the cusp in this context is yet another potential character state separating *Koobor* from phascolarctids.

According to Simmons (1993) the expected

value for the consistency index of a tree with 7 taxa is:

$$CI = 0.90 - 0.022 (7) + 0.000213 (7)^2 = 0.736 \text{ (3 s.f.)}$$

The observed CI for the optimal intrafamilial tree is 0.800, 0.064 from the expected value. The observed CI value implies slightly less homoplasy for the intrafamilial analysis than would be expected for seven taxa. Similarly the retention index (RI) and the rescaled consistency index (RC) are reasonably large, emphasising the low degree of homoplasy and potential for homoplasy respectively.

The optimal tree which includes all outgroup taxa is reasonably well-supported by bootstrap analysis and by the lack of significantly different trees, of plausible topology, within a few steps of the most parsimonious. The low bootstrap result for the *Ilaria* clade is almost totally due to the amount of missing data for *I. lawsoni*. This study supports the notion that *Ku. ngama* is an ilariid and forms a monophyletic clade with *Ilaria*.

#### CLASSIFICATION OF *KOOBOR*

Pledge (1987) discussed the possibility that *Kuterintja ngama* is more closely related to *Koobor* than *Ilaria*. The lower dentition and upper molars in addition to M<sup>3</sup> demonstrates that *Ku. ngama* is an ilariid. One of the few similarities between *Koobor* and *Kungama* is the smooth rounding of the lingual faces of the lingual cusps, a character state previously thought to unite the taxa phylogenetically (Pledge, 1987). However, smooth and rounded lingual faces on lingual cusps are also a feature of wynyardiids, and to a lesser extent *Madakoala*, suggesting that it is plesiomorphic. The ambiguity of this character state also increases the possibility of homoplasy. Pledge (1987) hypothesised that *Ku. ngama* may be ancestral to *Koobor*. Our study does not support this view.

*Koobor notabalis* appears to be the primitive sister-group of wynyardiids plus ilariids. We have no clear support, however, for *Koobor* being in the Phascolarctidae. This may be indirect support for the suggestion that *Koobor* represents a distinct family of vombatiform marsupials. DELTRAN found only one synapomorphy potentially uniting *Koobor* with the wynyardiids and ilariids: the less well-developed longitudinal valley on the molars. ACCTRAN found 7 synapomorphies for a *Koobor*, wynyardiid and ilariid clade. This should not be taken at face value, however, as 6 of these character states refer to the lower dentition which is unknown for *Koobor*. 10

synapomorphies were found by DELTRAN to unite wynyardiids and ilariids to the exclusion of *Koobor* (Fig. 6).

#### BIOCORRELATION OF RIVERSLEIGH AND THE ETADUNNA FORMATION

*Ku. ngama* occurs in the White Hunter Local Fauna at Riversleigh and in the Ngama Local Fauna in the upper Etadunna Formation. *Ilaria lawsoni* occurs in the Ditjimanka Local Fauna in the lower Etadunna Formation. *Ilaria illumidens* occurs in the Pinpa Local Fauna of the Namba Formation, at Lake Pinpa.

Woodburne et al. (1993) suggested at least 6 magnetic reversals within the Etadunna sequences, correlated them with a biostratigraphic zonation and the MPTS (Fig. 7) and suggested 24-28 Ma for the base of the Etadunna Formation.

Woodburne et al. (1993) correlated Zone D with the Ngama and Tarkarooloo Local Faunas. Correlation of magnetic polarity and biostratigraphic zones places zone D in lower magnetozone R3, which in turn correlates with Chron 7n.1r of the MPTS, or 24.7 - 25.0 Ma. *Ku. ngama* therefore, correlates White Hunter Site with the Ngama Local Fauna at 24.7 - 25.0 Ma providing: 1) that ilariid material in White Hunter Site has not been reworked from older deposits (which, given the lack of evidence for weathering or transport, does not appear likely); and 2) that the apparently short temporal range of *Ku. ngama* in the Etadunna Formation is the full range of this species.

#### ACKNOWLEDGEMENTS

Vital support for research at Riversleigh has come from the Australian Research Grant Scheme, the National Estate Grants Scheme (Queensland), the University of New South Wales, the Commonwealth Department of Environment, Sports and Territories, the Queensland National Parks and Wildlife Service, the Commonwealth World Heritage Unit, ICI Australia, the Australian Geographic Society, the Queensland Museum, the Australian Museum, the Royal Zoological Society of New South Wales, the Linnean Society of New South Wales, Century Zinc, Mount Isa Mines, Surrey Beatty & Sons, the Riversleigh Society, and private supporters including Elaine Clark, Margaret Beavis, Martin Dickson, Sue & Jim Lavarack and Sue & Don Scott-Orr. Vital assistance in the field has come

MPTS	MAGNETOZONE		Etadunna Mammal Zone	Etadunna Formation Assemblage	Namba Formation Assemblage	Riversleigh Assemblage
24.2 Ma	_____ ? _____					
	6 Cr                      R4		E	"Treasure/ Lungfish"		
24.7 Ma	7n.1n                      N3		?			
	7n.1r                      R3		D	Ngamia	Tarkarooloo	White Hunter Site
25.0 Ma	7n.2n                      N2		?			
	7r                              R2		C+B	Ngapakaldi Ditjimanka	Ericmas	
25.5 Ma	7an                              N1		A			
	7ar                              R1		?	"Wynyardiid"	Pinpa	
25.7 Ma	_____ ? _____					

FIG. 7. Geochronology and biocorrelation of the Etadunna and Namba Formations, Lake Palankarinna and Lake Pinpa, S.A. and lower Riversleigh faunas, northwestern Queensland. (Modified from Woodburne et al., 1993, figs 2 and 15). N = Normal magnetic polarity; R = Reversed magnetic polarity; MPTS = magnetic polarity time scale.

from many hundreds of volunteers as well as staff and postgraduate students of the University of New South Wales. Skilled preparation of most of the Riversleigh material has been carried out by Anna Gillespie. TJM acknowledges the assistance of Prof. Alberto Albani, Karen Black, Jenni Brammall, Henk Godthelp, Steve Salisbury, Anne Musser, Mary Knowles and his family.

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