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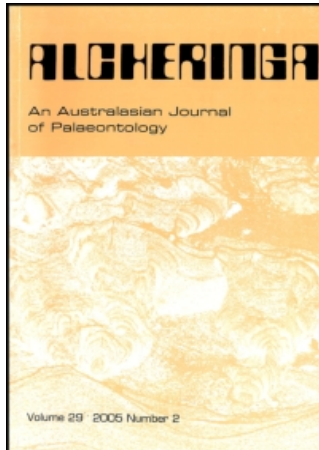
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# Maradidae: a new family of vombatomorphic marsupial from the late Oligocene of Riversleigh, northwestern Queensland

KAREN BLACK

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*Marada arcanum* gen. et sp. nov. is described from the late Oligocene Hiatus Site, Riversleigh World Heritage Property, northwestern Queensland. Although known from only a single dentary, it is assigned to a new family Maradidae, based on a unique combination of both plesiomorphic and apomorphic features. Of the known vombatomorphians, *Marada* is most similar to primitive wynyardiids and diprotodontoids (palorchestids and diprotodontids). Further clarification of the phylogenetic position of Maradidae within Vombatomorpha requires discovery of upper dentitions and crania.

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Key words: Maradidae, *Marada arcanum*, Vombatomorpha, Vombatiformes, Marsupialia, Riversleigh.

SIX FAMILIES are recognized within the infraorder Vombatomorpha: Ilariidae, Wynyardiidae, Thylacoleonidae, Vombatidae, Palorchestidae, and Diprotodontidae. Of these, five families are extinct, two families (Wynyardiidae and Ilariidae) are not known from deposits younger than early Miocene, and all exhibit highly autapomorphic dentitions. Aplin & Archer (1987) noted that known vombatomorphic families represent the remnants of a far more diverse pre-Oligocene radiation. Although monophyly of the infraorder is strongly supported by cranial and postcranial morphology, resolution of phylogenetic relationships based solely on dental morphology has proven difficult. *Marada* gen. nov., described herein, is known from a single right dentary from the late Oligocene Hiatus Site, Riversleigh World Heritage Property, northwestern Queensland. It expresses a

unique combination of primitive and derived features and cannot be assigned to any known vombatomorphic family. Consequently, a new family, Maradidae, has been established.

Material is deposited in the palaeontological collection of the Queensland Museum (QMF). Cusp nomenclature follows Rich *et al.* (1978) and Archer (1984). Molar homology follows Luckett (1993). Premolar homology follows Flower (1867). Mandibular terminology follows Stirton (1967). Higher-level systematic nomenclature follows Aplin & Archer (1987).

## Systematic palaeontology

Superorder MARSUPIALIA Illiger, 1811  
Order DIPROTODONTIA Owen, 1866  
Suborder VOMBATIFORMES Woodburne, 1984  
Infraorder VOMBATOMORPHIA Aplin & Archer, 1987  
Family MARADIDAE new family

*Diagnosis.* Maradidae differs from all other vombatomorphian families in the following combination of features: Dentary gracile, narrow, elongate and mediolaterally compressed; less posteriorly extensive mandibular symphysis; non crest-like or inflated ascending ramus at its point of origin; ascending ramus originates more posteriorly and at a point behind and less lateral to the molar row; less extensive post-alveolar shelf and weak post-alveolar process; lower crowned cheek teeth; short molar row length (50% length of horizontal ramus); a well-developed cristid obliqua; and a well-developed cusate lingual cingulum on  $M_1$ .

**Marada** gen. nov.

*Type and only species.* *Marada arcanum* gen. et sp. nov.

*Generic diagnosis.* The generic diagnosis is that for the family until additional taxa are known.

*Etymology.* *Marada* is the Waanyi (the local Aboriginal language of Riversleigh) word for flat in reference to the narrow, medio-laterally compressed dentary and the shallow fossae for muscle attachment. Gender is masculine.

*Remarks.* Distinctions from all other vombatomorphian taxa are previously listed in the familial diagnosis. Further differences from more specific groups are listed below. (Note that comparisons are made using the primitive members of the respective groups, which are detailed in the proceeding character analysis.)

*Marada* differs from all other vombatiforms (except *Wakaleo* Clemens & Plane, 1974, 50°; and *Warendja wakefieldi* Hope & Wilkinson, 1982, 56-59°) in having a posteriorly inclined ascending ramus where the angle of the anterior border of the ascending ramus (Fig. 1C) is less than 60° (relative to the plane of the horizontal ramus).

*Marada* differs from all other vombatomorphians except diprotodontids and palorchestids in having an elongate diastema and a simple, bicuspid  $P_3$ . *Marada* differs from all other vombatomorphians except wynyardiids, in having a posterolingual pocket between the entoconid, posthypocristid, and posterior cingulum. *Marada* differs from diprotodontids, palorchestids, and wynyardiids in having an  $M_1/M_4$  length less than 1.

*Marada* differs from diprotodontids and palorchestids (i.e. diprotodontoids) in having: smaller teeth; an anteriorly convex rather than concave 'hypolophid' and 'protolophid'; a better-defined paraconid on  $M_1$ ; reduced posterior molars (i.e.  $M_4/M_1$  length < 1); less well-developed preprotoconid crests on  $P_3$ ; a reduced posterior cingulum on the molars; a better-defined paraconid and paracristid on  $M_1$  (except *Raemeotherium* Rich *et al.* 1978); and a well-developed postmetacristid, postentocristid, posthypocristid, preentocristid, and preprotocristid (in  $M_{2-4}$ ).

*Marada* differs from palorchestids in: lacking a well-developed posterior cingulum on  $P_3$ ; and lacking the posterior, buccal, and lingual crests of the protoconid on  $P_3$ . *Marada* differs from diprotodontids in having: less lophodont molars; a longitudinal wear pattern along the buccal cusps on lower molars (rather than a transverse pattern of wear across the lophids); a more lingually positioned protoconid on  $M_1$  (except *Raemeotherium*); a proportionately larger  $P_3$  relative to  $M_1$ ; and a distinct posterior cuspid at the terminus of the postprotocristid on  $P_3$ . *Marada* differs from ilariids and wynyardiids in lacking the neomorph cuspid (Pledge 1987a, Tedford & Woodburne 1987) on  $M_1$ . *Marada* differs from wynyardiids in that the  $P_3$  is not bladed and is considerably shorter than  $M_1$ ; and in having more open, U-shaped transverse valleys on the lower molars. *Marada* differs from ilariids in: lacking a tricuspid, bulbous  $P_3$  and a well-developed anterior cingulum

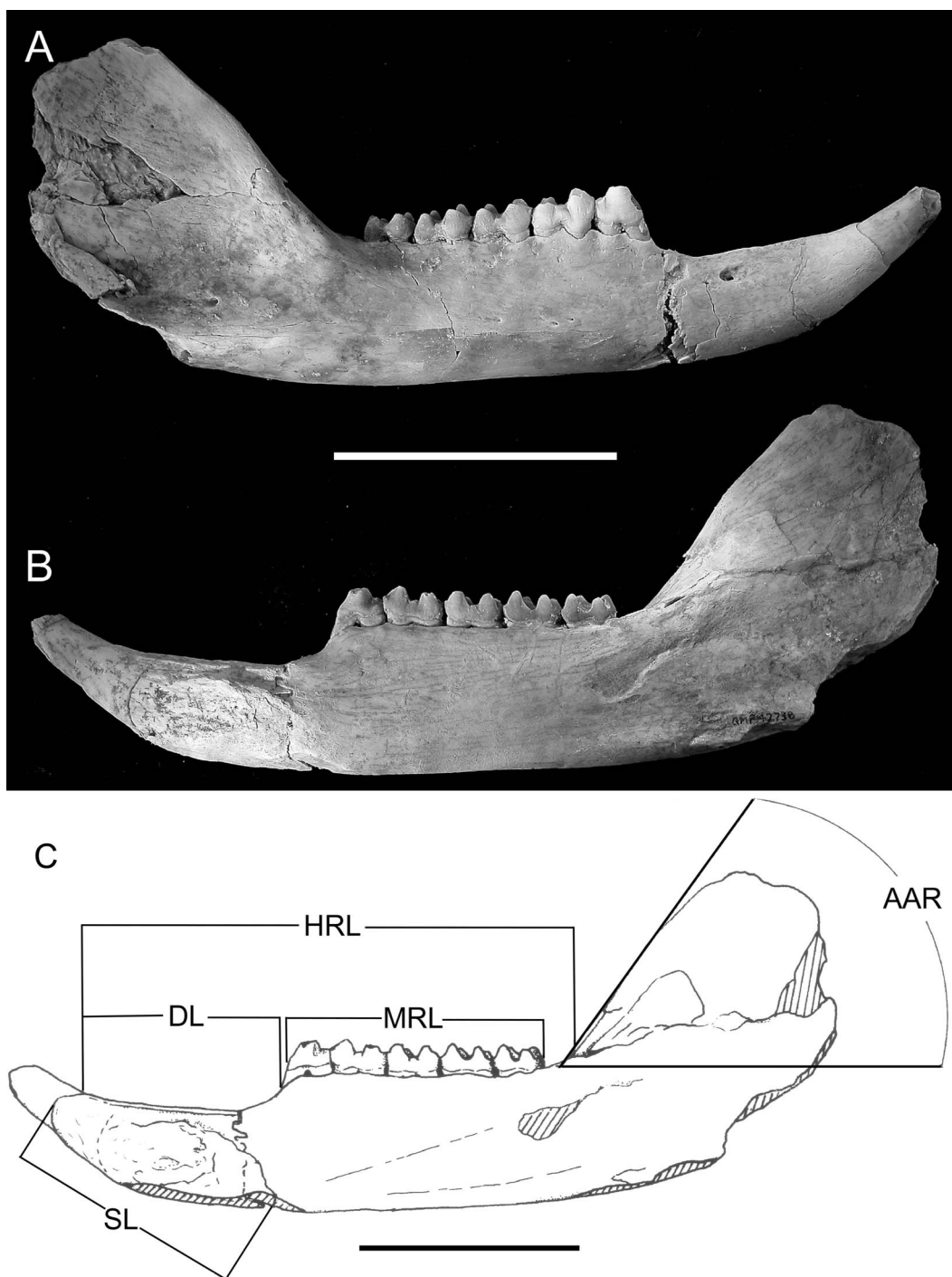


Fig. 1. *Marada arcanum* gen. et sp. nov. Holotype QMF42738. **A**, buccal view of right dentary; **B**, lingual view; **C**, schematic diagram of right dentary of *M. arcanum* showing measurements used in Table 4 and throughout the text. Abbreviations: AAR, angle of anterior border of ascending ramus; DL, diastema length; HRL, horizontal ramus length; MRL, molar row length; SL, symphysis length. Hatching represents broken areas on dentary. Bar = 50 mm.

on the lower molars; and in having less complex molars. *Marada* differs from thylacoleonids in lacking: an elongate, bladed  $P_3$ ; a well-developed, deep masseteric fossa; a deep, rounded symphysis; a highly inclined caniniform  $I_1$ ; and in having a single lower premolar.

***Marada arcanum* sp. nov.** (Figs 1-2, Tables 1-4)



Fig. 2. *Marada arcanum* gen. et sp. nov. occlusal stereopair of QMF42738. Bar = 10 mm.

	$P_3$	$M_1$	$M_2$	$M_3$	$M_4$
L	8.7	11.4	10.9	10.8	10.0
AW		7.4	8.0	8.4	7.2
PW	5.2*	7.3	7.5	7.3	6.3
DR	27.4	27.4	26.3	25.9	26.1

Table 1. Measurements (mm) of dentition of *Marada arcanum*. \*Maximum width of  $P_3$ . DR, depth of horizontal ramus below respective tooth taken between the roots.

**Holotype.** QMF42738, right dentary with  $P_3$ ,  $M_{1-4}$ .  $I_1$  crown broken. Dental formula  $I_1$ ,  $C_0$ ,  $P_3$ ,  $M_{1-4}$ . The posterior area of the dentary is damaged and missing the coronoid process, articular condyle, and angular process.

**Type locality.** Hiatus Site, Riversleigh World Heritage Fossil Property, northwestern Queensland (see Creaser 1997).

**Distribution and age.** Hiatus Site is a System A deposit (Creaser 1997) which, on the basis of stratigraphy and contained faunas, is interpreted to be of late Oligocene age.

**Species diagnosis.** The diagnosis for the species is that for the family until additional taxa are known.

**Specific etymology.** *Arcanum*, meaning mystery in Latin, alludes to the unknown taxonomic position of the species and the strange combination of primitive and derived features exhibited by the single known specimen.

### Description

**Dentary (Fig. 1).** Right dentary with  $P_3$ ,  $M_{1-4}$ .  $I_1$  crown broken. The posterior area of the dentary is poorly preserved and missing the coronoid process, articular condyle, and angular process. The dentary is very gracile and slender with a narrow horizontal ramus. It is unlike the characteristically more robust vombatomorphic dentaries with the exception of the relatively delicate primitive ?diprotodontid *Raemotherium yatkolai* Rich *et al.* 1978. The lingual (medial) surface of the horizontal ramus is flat and straight, as is the ventral border. The maximum depth of the horizontal ramus is 27.9 mm below the anterior base of  $M_1$ . The horizontal ramus thickens opposite  $M_3$  with a maximum width of 14.6 mm. The diastema is relatively long

CHARACTER	PLESIOMORPHIC	APOMORPHIC
1. Inclination angle of $I_1$	High ( $\geq 30^\circ$ )	Low ( $< 30^\circ$ )
2. $P_3$ morphology	Bicuspid	Multi-cusped/bladed
3. Degree of bilophodonty	Absent	Fully bilophodont
4. Development of paraconid and paracristid	Well developed	Weak or absent
5. Development of a protostylid on $M_1$	Present	Absent
6. Presence of a cristid obliqua	Well developed	Weak or absent
7. Posteriorly increasing molar gradient $M_4/M_1$	$< 1$	$\geq 1$
8. Crown height	Low-crowned	High-crowned
9. Angle of anterior border of ascending ramus	Low ( $< 70^\circ$ )	High ( $\geq 70^\circ$ )
10. Posterior extent of symphysis	Short	Elongate, deep
11. Masseteric foramen	Absent	Present
12. Diastema length relative to horizontal ramus	$< 30\%$	$\geq 30\%$

Table 2. Character states used in character analysis of Vombatomorpha.

CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12
<i>Marada</i>	1	0	1	2	1	0	0	1	0	0	1	1
<i>Trichosurus</i>	0	1	1	0	0	0	0	0	0	0	0	0
<i>Madakoala</i>	0	1	0	0	0	0	0	0	1	1	?	?
<i>Wakaleo</i>	0	1	0	?	1	2	0	1	0	0	1	0
<i>Kuterintja</i>	1	1	0	2	1	0	0	2	1	1	?	?
<i>Warendja</i>	1	0*	1	1*	1	1*	0	2	0	1	2	0
<i>Muramura</i>	1	1	1	1	1	1	1	1	0,1	1	1	0
<i>Namilamadeta</i>	1	1	1	1	1	1	1	1	0	1	1	0
<i>Propalorchestes</i>	1	0	2	2	1	1	1	2	1	1	1	1
<i>Raemotherium</i>	1	?	2	2	0	1	1	2	0	1	?	0
<i>Ngapakaldia</i>	1	0	2	2	1	2	1	2	1	1	1	1

Table 3. Character state polarities for select vombatomorphians. Plesiomorphic state = 0; apomorphic state = 1; most apomorphic state = 2; missing data = ?; character polarised using *V. ursinus* = \*.

(38.7 mm) with a distinct dorsal diastemal ridge reminiscent of diprotodontoids. The lingual surface of the diastema drops steeply away to a very rough, short unfused symphysis (50.3 mm long, Fig. 1B). The sublingual fossa is narrow and shallow. The symphysis lies at an angle parallel to the dorsal surface of the diastema, dipping slightly posteriorly. The symphysis terminates posteriorly at a point directly below the anterior root of  $P_3$ .

A relatively large canal-like mental foramen lies 11.6 mm anterior to the base of  $P_3$  and 3 mm ventral to the dorsal surface of the diastema. A smaller nutrient foramen

lies within the entrance to the mental foramen. Three small nutrient foramina are positioned approximately 15.5 mm ventral to the  $M_{1-2}$  alveoli.

The length of the slightly curved cheek tooth row is 51.8 mm. A slightly decreasing posterior molar gradient is evident ( $M_4/M_1$  length = 0.9). A striking feature is the relatively short molar row compared with the overall length of the dentary. Proportionately, this specimen has a relatively shorter molar row (50% relative to the length of the horizontal ramus) than any other Vombatomorphan (Table 4). A longitudinal line of wear is evident along the tooth row mainly

DENTARY CHARACTERS	DL (mm)	MRL (mm)	HRL (mm)	MRL/HRL	DL/HRL	M <sub>4</sub> /M <sub>1</sub> LENGTH
<i>Marada arcanum</i>	38.7	51.8	101.0	0.51	0.38	0.9
<i>Warendja wakefieldi</i>	16.8	32.5	57.8	0.56	0.29	0.8–0.9
<i>Wakaleo oldfieldi</i>	6.0	36.9	52.7	0.70	0.11	0 (no M <sub>4</sub> )
<i>Kuterintja ngama</i>	—	44.2	—	—	—	0.9
<i>Muramura pinpensis</i>	12.0	36.3	51.0	0.71	0.24	1.0
<i>Namilamadeta</i> sp.	14.0	41.8	62.4	0.67	0.22	1.0
<i>Raemotherium yatkolai</i>	13.0	52.7	82.0	0.64	0.16	1.0
<i>Ngapakaldia tedfordi</i>	40.3	64.0	112.2	0.57	0.36	1.1
<i>Propalorchestes novaculacephalus</i>	—	69.5	—	—	—	1.0

Table 4. Measurements and proportions of the dentary used in character analysis. Abbreviations: DL, diastema length (measured from P<sub>3</sub> alveolus to I<sub>1</sub> alveolus on dorsal surface); HRL, horizontal ramus length (measured from incisor alveolus to post-alveolar process); MRL, molar row length (measured from anterior of P<sub>3</sub> to posterior of M<sub>4</sub>, taken at base of crown).

on the buccal cusps with the hypoconid of M<sub>1</sub> and the protoconid of M<sub>2</sub> showing the most wear.

The posterior area of the dentary is incomplete with only the area of the ascending ramus encompassed by the masseteric fossa preserved on the lateral face. Medially, the fragile area of the pterygoid fossa was covered in rice paper for added strength during preparation of the specimen. Consequently, the position of the mandibular foramen cannot be determined. The masseteric fossa is flat and shallow with no distinct anterior border, fading out anteriorly onto the lateral face of the dentary. A small masseteric foramen is present on the ventral border of the masseteric fossa approximately 27.1 mm posterior to and 12.0 mm below the posterior border of M<sub>4</sub>. The masseteric eminence is not preserved, but the flatness of the vertical ramus suggests it would have been weak and low on the dentary.

The ascending ramus is inclined posteriorly, its anterior border positioned at an angle of 55° relative to the horizontal ramus. The ascending ramus originates at a point opposite the posterior border of M<sub>4</sub>, which is further posterior and less lateral than in all other vombatophians. There is no distinct post-alveolar process on the

lingual face of the dentary. In occlusal view, the ascending ramus can be seen to rise gradually along the buccal margin of the post-alveolar shelf. It is such a gradual rise that it is difficult to determine its point of origin. The anterior 'crest' of the ascending ramus is thick and non-carinate.

The pterygoid fossa is very flat and not very laterally expansive. However, this area is obscured slightly by the flaking of the bone. The digastric fossa is a shallow, linear fossa that runs parallel to the ventral border of the horizontal ramus. It is deepest below M<sub>3-4</sub> and extends anteriorly to below the level of the M<sub>1</sub> talonid and fades out posteriorly below the post-alveolar shelf.

*Dentition* (Fig. 2, Table 1). The dental formula is I<sub>1</sub> C<sub>0</sub> P<sub>3</sub> M<sub>1-4</sub> like all other vombatophians (except some thylacoleonids, which retain two lower premolars and may have lost M<sub>4</sub>). Only the distal 16.2 mm of the incisor is preserved, but the elliptical cross-section suggests that it was lanceolate. Enamel is distributed on the ventral and lateral surface. The I<sub>1</sub> projects at an angle of 28° from the horizontal plane of the diastema.

The premolar is simple, small, narrow, bicuspid and two-rooted. A large, very worn (on its anterolingual face), sub-central

protoconid dominates the premolar and is connected to a small posterior cuspid (possibly the metaconid) by a weak, steeply sloping posterior crest. A weak posterolingual cingulum extends anterolingually from the small cuspid, fading into the base of the crown at a point opposite the transverse valley between the large and small cuspids. A buccal cingulum is absent. The anterior, buccal, and lingual faces of the tooth are steeply sloping to the base of the crown. The enamel is slightly wrinkled at the posterior base of the main cuspid.

The molars are low-crowned, bunolophodont, and characterized by very wide, U-shaped transverse valleys. The  $M_1$  is a sub-rectangular, four-cusped tooth consisting of a small lingual metaconid (the least worn of the major cuspids) and large buccal protoconid on the trigonid and a large lingual entoconid and buccal hypoconid in the talonid. It is difficult to determine the relative height of each cuspid due to considerable wear. It appears that the protoconid may have been the tallest cusp in its unworn state, followed by the metaconid, entoconid, and hypoconid. The protoconid and hypoconid exhibit the most wear.

The protoconid of  $M_1$  is positioned lingually such that the apex appears to have been just buccal to the horizontal midline of the tooth. There is no protostylid. In the unworn state, the apices of the protoconid and metaconid may have been joined by a short transverse ridge (which is tentatively referred to as a protolophid, though less developed than in wynyardiids and diprotodontoids). The base of the protoconid is large and rounded. A well-developed but considerably worn preprotocristid (or paracristid) extends anterolingually from the protoconid apex and terminates in a slight swelling at the anterior tooth margin, posterolingual to the posterior cuspid of  $P_3$ . This swelling may represent a weak

paraconid. A similarly weak, short, anterior cingulum runs buccally from the paraconid. The buccal face of the paraconid slopes steeply to the base of the crown.

The apex of the metaconid lies 2.0 mm lingual to the protoconid apex. The anterolingual and posterolingual faces of the metaconid slope steeply to the base of the crown. A weak postmetacristid extends posterolingually to meet the lingual cingulum at the lingual border of the transverse valley.

The transverse valley of  $M_1$  is wide, shallow, and U-shaped, and separates the anterior trigonid and posterior talonid. It is closed off lingually by a well-developed cusped lingual cingulum. The homology of this lingual cusp with the metastylid of phascolarctids is doubtful because it does not originate as a swelling of the postmetacristid (as it does in koalas). A similar cusp is variably expressed in diprotodontids, and a thickening of the enamel on the preentocristid is evident in some *Namilamadeta* Rich & Archer, 1979, specimens (Dirk's Towers Local Fauna, System B, Riversleigh) although not to the extent seen in *Marada*. The lingual cingulum connects anteriorly to the postmetacristid and posteriorly to the weak preentocristid.

A well-developed, worn cristid obliqua connects the apices of the protoconid and hypoconid, effectively sealing off the transverse valley buccally. In its unworn state, the cristid obliqua may have been cusped.

A weak swelling at the buccal base of the entoconid meets a similar swelling at the lingual base of the hypoconid, resulting in a weak lophid (tentatively referred to as the hypolophid) that traverses the longitudinal valley between these cusps. In its unworn state, the hypolophid is unlikely to be a continuous crest linking the apices of the entoconid and hypoconid. The lingual base of the entoconid slopes steeply to the base of the crown. The hypolophid is longer than the protolophid.



A buccal cingulum is absent; however, there is a slight swelling or bulge in the enamel at this point. A weak postentocristid and posthypocristid are continuous with a weak posterior cingulum that runs the length of the posterior border of the tooth. A resultant postero-lingual pocket is formed between the posterior base of the entoconid, the posthypocristid and the posterior cingulum. This feature is also found in the lower molars of wynyardiids such as *Namilamadena*.

The  $M_2$  is similar to  $M_1$  except for the arrangement of the cusps on the trigonid. The protoconid is positioned more buccally than in  $M_1$ , but the bases of the metaconid and protoconid are connected so that transverse wear across the tooth gives the impression of a weak protolophid. The metaconid is larger than in  $M_1$ , and its apex more worn. The lingual cuspid is reduced, and the lingual cingulum is a short crescentic ridge connecting the weak postmetacristid and weak preentocristid, effectively sealing off the transverse valley lingually. The cristid obliqua is well developed although less so than in  $M_1$ , and it is non-cusperate. The buccal cingulum is more ridge-like than in  $M_1$  where it constitutes a swelling of the enamel. A small crenulated pocket is formed between the buccal base of the cristid obliqua and the lingual border of the buccal cingulum. The connection between the entoconid and hypoconid occurs further down their bases and is not lophid-like as in  $M_1$ . The 'protolophid' and 'hypolophid' are similar in length.

The less worn  $M_3$  is similar to  $M_2$  except for the following: the lingual cingulum is reduced, and the talonid is noticeably narrower than the trigonid; the protolophid and hypolophid are better developed, with the protolophid being longer than the hypolophid; the protoconid is the most worn of the cuspids followed by the hypoconid; the metaconid is only slightly worn, and the entoconid is unworn. In

lingual view, the apices of the metaconid and entoconid are relatively tall and well rounded (i.e. no sharp peaks).

The  $M_4$  is similar to  $M_3$  except for the following:  $M_4$  smaller with a rounded, less linear posterior tooth margin; the cristid obliqua is more prominent as a result of less wear, and of the major cuspids, only the protoconid and hypoconid are worn; the hypolophid is shorter than the protolophid; the posterolingual pocket between the entoconid, posterior cingulum, and posthypocristid is deeper; the protoconid and hypoconid are positioned slightly more posteriorly than the metaconid and entoconid, respectively. Consequently, the protolophid and hypolophid curve posteriorly in the buccal half of the molar. This feature is more reminiscent of other semi-lopodont taxa such as ilariids and phascolarctids wherein the lingual cuspid is positioned more anteriorly than its transversely opposing buccal cuspid (i.e. the metaconid is more anterior than the protoconid, and the entoconid is more anterior than the hypoconid).

## Character analysis

Recent classifications (e.g. Aplin & Archer 1987, Marshall *et al.* 1989) acknowledged that phascolarctids are the sister group of Vombatomorpha. Hence, character polarities were determined using the plesiomorphic phascolarctid *Madakoala devisi* Woodburne *et al.* 1987c, as an outgroup. *Trichosurus vulpecula* (Kerr, 1792) (Diprotodontia, Phalangeridae) was used as a more distant outgroup of the Suborder Vombatiformes.

The following taxa, which have comparable dentary material, are considered plesiomorphic for their respective families: *Kuterintja ngama* Pledge, 1987b (Ilariidae); *Warendja wakefieldi* (Vombatidae); *Propalorchestes* Murray, 1986 (Palorchestidae); and *Wakaleo oldfieldi* Clemens & Plane, 1974 (Thylacoleonidae). Species of *Muramura*

Pledge, 1987a and *Namilamadeta* (Wynyardiidae) are both considered because their phylogenetic relationships have yet to be determined by a cladistic analysis. *Raemeotherium yatkolai* is tentatively assigned to Diprotodontidae and is possibly the most primitive member of the group, but *Ngapakaldia tedfordi* Stirton, 1967 (an unquestionable diprotodontid: see Murray 1990, Black 1997) is also considered. Species of *Koobor* Archer & Wade, 1976, are excluded from the analysis, as lower dentitions are unknown for this taxon. Three of the characters of the dentition cannot be polarized for *Warendja wakefieldi* due to extreme wear on the molars. Consequently, unworn, juvenile *Vombatus ursinus* (Shaw 1800) specimens have been used to polarize characters 2, 4, and 6 in Table 3. Only characters of the dentary and lower dentition are used in the analysis, as the cranium, upper dentition, and postcranium are unknown for *Marada*. Consequently, a computer-generated parsimony analysis was not performed due to the high level of missing data: many cranial and postcranial characters used in previous analyses to delineate vombatomorphian phylogeny cannot be employed here, resulting in a significantly biased analysis. Character states and character state polarities are listed in Tables 2 and 3, respectively.

1. *Inclination angle of I<sub>1</sub>*. A synapomorphy used by Marshall *et al.* (1989) for a wynyardiid/ vombatid/diprotodontoid clade to the exclusion of ilariids and thylacoleonids. A high inclination angle ( $\geq 30^\circ$ ) is considered primitive and is found in *Trichosurus*, *Madakoala*, and *Wakaleo*. A low inclination angle of I<sub>1</sub> ( $< 30^\circ$ ) is present in *Marada*, *Kuterintja*, *Ngapakaldia*, *Propalorchestes*, *Namilamadeta*, *Raemeotherium*, *Muramura*, and *Warendja*.

2. *P<sub>3</sub> morphology*. Diprotodontids and palorchestids possess a simple bicuspid P<sub>3</sub>

with a large central protoconid and a small posterior cuspid (metaconid), the apices of which are joined by a postprotocristid. This premolar morphology has changed little from the plesiomorphic P<sub>3</sub> of peramelamorphians and dasyuromorphians. *Muramura*, like the diprotodontoids, has a simple P<sub>3</sub>, but three cusps lie along the longitudinal midline: an anterior protoconid, medial metaconid, and posterior hypoconid. These cusps are linked by a longitudinal crest resulting in a bladed appearance to the P<sub>3</sub>. *Kuterintja* has a tricuspid P<sub>3</sub> with a large protoconid, a well-developed posterior cuspid (metaconid), and a well-developed posterolingual cuspid. A P<sub>3</sub> is unknown for *Raemeotherium*. Due to the extremely worn nature of the *Warendja* P<sub>3</sub>, this feature has been polarized with *V. ursinus*, which shows the plesiomorphic bicuspid condition. The premolars of both outgroups are highly specialized. *Trichosurus vulpecula* has a multi-cusped, bladed P<sub>3</sub>. *Madakoala devisi* has a 6-cusped premolar: 4 cusps are situated along a longitudinal crest in addition to a posterobuccal cusp and a much weaker lingual cusp. *Wakaleo oldfieldi* has a bladed P<sub>3</sub>, the blade extending posterobuccally from an apex positioned above the anterior root, then curving lingually along the posterior third of the blade. The bicuspid P<sub>3</sub> of *Marada arcanum* is considered the primitive condition.

3. *Degree of bilophodonty*. Bilophodonty has developed independently in several diprotodontian lineages including Macropodidae, Phalangerioidea (to a lesser extent), Wynyardiidae, Palorchestidae, Diprotodontidae, and Vombatidae (in unworn molars). Absence of bilophodonty is considered plesiomorphic for Vombatomorpha. *Madakoala devisi*, *K. ngama*, and *W. oldfieldi* do not possess bilophodont molars. *Trichosurus vulpecula*, *Muramura*, *Namilamadeta*, and *Warendja* exhibit semi-bilophodont molars. *Marada arcanum* possesses semi-bilophodont molars

with weak transverse crests linking the apices of the metaconid and protoconid, and the entoconid and hypoconid respectively, forming a weak protolophid and hypolophid. *Raemeotherium*, *Ngapakaldia*, and *Propalorchestes* possess fully bilophodont molars. Selenodonty/bunodonty = 0; semilophodonty = 1; bilophodonty = 2.

4. *Development of the paraconid and paracristid (= preprotocristid) on M<sub>1</sub>*. The paraconid and paracristid are well developed in most marsupial taxa including dasyuromorphians and peramelemorphians; hence their presence is considered plesiomorphic. *Madakoala* and *Trichosurus* possess the primitive state. *Muramura* and *Namilamadeta* possess a distinct paracristid culminating in a weak paraconid. *Marada*, *Kuterintja*, *Raemeotherium*, *Propalorchestes*, and *Ngapakaldia* possess weak or absent paracristids and paraconids. This character cannot be polarized for *Warendja*; *V. ursinus* shows the apomorphic condition. The M<sub>1</sub> of *Wakaleo oldfieldi* has a simple anterior apical cusp on the trigonid (the metaconid of Woods 1956). From this cusp extends an anterior ridge that occupies a similar position to a paracristid; however, the homology of this ridge is uncertain, as is the case for the main cuspid on the trigonid. Hence, this character is designated 'unknown' for this taxon. Character coding is: presence of a triangular trigonid (i.e. paraconid present and paracristid well developed) = 0; paracristid present but low = 1; absent paraconid and weak or absent paracristid = 2.

5. *Development of a protostylid on M<sub>1</sub>*. A protostylid on M<sub>1</sub> is present in plesiomorphic macropodoids (Cooke 1997), pseudocheirids (Woodburne *et al.* 1987b), pilkipildrids, petaurids, miralinids (Woodburne *et al.* 1987a), phascolarctids and possibly ilariids (Tedford & Woodburne

1987). Archer (1978) and Marshall *et al.* (1989) interpreted the presence of a protostylid on M<sub>1</sub> as plesiomorphic for Diprotodontia. Cooke (1997) suggested that the formation of a protostylid is plesiomorphic in macropodoids but is reduced or absent in more derived members of the group. Alternatively, in phascolarctids, the protostylid ranges from weak in the plesiomorphic genus *Madakoala* to very large in more derived forms such as species of *Nimiokoala* Black & Archer, 1997, *Litokoala* Stirton *et al.* 1967, and *Phascolarctos* (Black & Archer 1997). In *T. vulpecula*, the protostylid is reduced to a ridge (Cooke 1997), but a small protostylid is present in the plesiomorphic phalangerids *Strigocuscus reidi* and *Trichosurus dicksoni* (Flannery & Archer 1987). The absence of a protostylid in *Marada*, vombatids, wynyardiids, thylacoleonids, and diprotodontoids (except possibly *Raemeotherium* [Rich *et al.* 1978]) is interpreted as derived. *Kuterintja ngama* is interpreted as lacking a protostylid following Myers & Archer (1997).

6. *Presence of a cristid obliqua*. A cristid obliqua is well developed within most diprotodontian groups. In *Madakoala*, *T. vulpecula*, *Kuterintja*, and *Marada*, it extends anterolingually from the hypoconid apex to meet the postprotocristid, effectively sealing off the transverse valley buccally. In *Muramura* and *Propalorchestes*, the cristid obliqua is more anteriorly directed, originating from a more lingual position on the hypolophid and meets the protolophid just buccal to or on the longitudinal midline of the M<sub>1</sub>, hence the derivation of the term 'midlink'. A moderate anterolingually directed cristid obliqua is present in *Raemeotherium* but terminates at the base of the protoconid. A cristid obliqua is absent in *Ngapakaldia* and *Wakaleo*. This character cannot be polarized for *Warendja*; *V. ursinus* has a moderately developed cristid

obliqua. Character states are coded: well-developed anterolingual cristid obliqua connected to postprotocristid = 0; anteriorly directed midlink = 1; Weak or absent cristid obliqua = 2.

7. *Posteriorly increasing molar gradient.* A posteriorly increasing molar gradient is found in several derived vombatomorphic taxa, in particular the diprotodontoids. It is possibly associated with an increase in the abrasiveness of the diet. An increase in the size of the posterior molars increases the masticatory force posteriorly towards the temporomandibular joint, effectively reducing some of the stress placed on the mandibular symphysis (Beecher 1977).  $M_4/M_1L$  ratios are listed in Table 4. *Trichosurus*, *Madakoala*, *Kuterintja*, *Warendja*, and *Marada* exhibit the plesiomorphic condition with an  $M_4/M_1L$  ratio less than one. *Namilamadeta*, *Muramura*, *Raemeotherium*, *Ngapakaldia*, and *Propalorchestes* have an  $M_4/M_1L$  ratio greater than or equal to one. An  $M_4$  is completely lost in *Wakaleo oldfieldi*; hence this character is coded as primitive.

8. *Crown height.* Low-crowned bunodont/selenodont molars are common among diprotodontians and are consequently coded plesiomorphic within Vombatomorpha. Both *Trichosurus* and *Madakoala* possess low-crowned molars (coded 0). *Marada* and wynyardiids are moderately crowned (coded 1) and diprotodontoids, vombatoids and ilariids are high-crowned (coded 2). In *W. oldfieldi*, the functional teeth ( $P_3$  and  $M_1$ ) are moderately crowned (coded 1), whereas  $M_{2-3}$  are lower crowned as a consequence of their vestigial nature.

9. *Angle of the anterior border of the ascending ramus* (Fig. 1C). Hope & Wilkinson (1982, p. 116) listed the angle of inclination of the ascending ramus for

various marsupial taxa. Dasyurids, perame-lids, and most diprotodontians have angles less than  $70^\circ$ . Consequently, a posteriorly inclined ( $<70^\circ$ ) ascending ramus is considered plesiomorphic, and a more upright ascending ramus ( $\geq 70^\circ$ ) is derived. The angle is low in *Wakaleo oldfieldi* ( $50^\circ$ ), *T. vulpecula* ( $65^\circ$ ), *Raemeotherium* ( $62^\circ$ ), *Warendja* ( $56-59^\circ$ ), *Namilamadeta* ( $65^\circ$ ), and *Marada* ( $55^\circ$ ). It is upright in *Kuterintja* ( $70^\circ$ ), *Ngapakaldia* ( $70^\circ$ ), phascolarctids ( $70-80^\circ$ ), and *Propalorchestes* ( $70^\circ$ ). Both character states are displayed by species of *Muramura* ( $65-70^\circ$ ).

10. *Posterior extent (elongation) of symphysis.* The mandibular symphysis in *Marada* extends posteriorly to the anterior border of  $P_3$  (Fig. 1C). The symphysis is proportionately shorter in *Trichosurus* and *Wakaleo*, but extends further posteriorly to below the posterior root of  $P_3$ . The symphysis becomes more posteriorly elongate in *Ngapakaldia*, *Kuterintja*, *Namilamadeta*, *Muramura*, *Raemeotherium*, *Warendja*, and *Madakoala*, extending to below the anterior root of  $M_1$ . The most posteriorly extensive symphysis is evident in *Propalorchestes*, extending to below the posterior root of  $M_1$ . A long symphysis is deemed apomorphic for Vombatomorpha.

11. *Masseteric foramen.* A masseteric foramen is absent in *Trichosurus*. It is small in *Marada*, *Wakaleo*, *Namilamadeta*, *Muramura*, *Propalorchestes*, and *Ngapakaldia*, and large in *Warendja*. It is unknown for *Raemeotherium*, *Kuterintja*, and *Madakoala*. Absence of a masseteric foramen is determined to be plesiomorphic for Vombatomorpha = 0; small or moderate masseteric foramen = 1; large masseteric foramen = 2.

12. *Diastema length proportionately  $> 30\%$  of horizontal ramus length.* Dasyuromorphians,

peramelemorphians and most diprotodontians lack a diastema between  $I_1$  and  $P_3$  due to the presence of  $C_1$  and  $P_{1-2}$ . Hence, the absence of a functional diastema is regarded to be plesiomorphic, and therefore elongation of the diastema with respect to the length of the horizontal ramus is deemed derived. Measurements of diastema and horizontal ramus length for taxa in the current study are listed in Table 4. The diastema length is greater than 30% of the horizontal ramus length in *Marada*, *Propalorchestes*, and *Ngapakaldia*. The diastema is less than 30% of the horizontal ramus length in *Warendja*, *Wakaleo*, *Raemeotherium*, *Namilamadeta*, and *Muramura*. This character cannot be polarized for *Madakoala* and *Kuterintja*. A diastema is absent in *Trichosurus* due to the presence of vestigial  $I_2$  and  $P_{1-2}$ , and deemed absent for *Wakaleo* (only 6 mm in length) due to the presence of  $P_2$ .

## Discussion

*Marada arcanum* gen. et sp. nov. is known from a single dentary recovered in 2001 from the late Oligocene Hiatus Site, Riversleigh. It is the first occurrence of the new vomatomorphian family Maradidae despite the tonnes of fossiliferous material processed from the Riversleigh deposits over the past 30 years. With the addition of Maradidae, there are now seven families within the infraorder Vombatomorpha.

The monophyly of Vombatomorpha is strongly supported by both cranial and postcranial morphology. In particular, most recent phylogenetic studies recognize the squamosal contribution to the tympanic cavity as a synapomorphy uniting vomatomorphians to the exclusion of phascolarctomorphians (e.g. Murray 1986, Aplin & Archer 1987, Tedford & Woodburne 1987, Marshall *et al.* 1989, Springer & Woodburne 1989). However, as Aplin & Archer (1987) noted, the highly autapomorphic

dentitions of vomatomorphian families provide limited use in phylogenetic analyses. Many taxa cannot be assigned at the familial level based on dentitions alone. For example, the placement of both *Namilamadeta* and *Muramura* within Wynyardiidae is tentative, based on a presumed association of dentitions with limb material wherein the limbs were similar to those known for the type species *Wynyardia bassiana* (Tedford *et al.* 1977). Aplin (1987) concluded *Wynyardia* to be the plesiomorphic sister group to all other vomatomorphians on the basis of its basicranial morphology. Aplin & Archer (1987) recognized greater affinities between *Namilamadeta* and *Muramura* with the diprotodontoids, and Murray (1990) suggested affinities specifically with palorchestids. The enigmatic genus *Koobor* has been assigned to both the Phascolarctomorpha and Vombatomorpha. Similarly, *Raemeotherium* could be either a plesiomorphic diprotodontid or a primitive macropodoid. The affinities of thylacoleonids with Vombatomorpha have also been questioned. Murray *et al.* (1987) regarded thylacoleonids to be closer to phalangerids than vomatomorphians. However, Aplin & Archer (1987) included the marsupial lions within Vombatomorpha but recognized that they are highly plesiomorphic and occupy a distant position with respect to the rest of the group.

Placement of *Marada* within Vombatomorpha has proven difficult due to the absence of cranial and postcranial data. Of all previous analyses of vomatomorphian phylogeny (e.g. Archer 1984, Aplin & Archer 1987, Tedford & Woodburne 1987, Marshall *et al.* 1989, Munson 1992, Murray 1998), only one (Tedford & Woodburne 1987), recognized synapomorphies of the dentary. These include: 1, widely flaring submasseteric crest; 2, long pterygoid flange of the horizontal ramus; 3, unconstricted mandibular foramen; and 4,

narrow, transversely elongate and dorsally curved mandibular condyles. Unfortunately, none of these features are preserved on the *Marada* dentary.

*Marada arcanum* is, however, tentatively placed within the Vombatomorpha (rather than Phascolarctomorpha) based on: its large size; the presence of more lophodont molars; the absence of a well-developed premetacristid, postmetacristid, and metastylid in the lower molars; a reduced cristid obliqua; and the absence of a protostylid on  $M_1$ .

Within Vombatomorpha, *Marada* is morphologically most similar to primitive members of the Wynyardiidae, Palorchestidae, and Diprotodontidae, sharing five derived states with each (Table 3). The low-crowned semi-lophodont molars, the position of the major cuspids with respect to each other, the posterolingual pocket in the lower molars, the development of the postmetacristid and preentocristid, and in particular, the construction of the  $M_1$ , are strikingly similar to *Namilamadeta* material from Riversleigh. The main differences in the dentitions of these taxa are the lack of a well-developed anterior cingulum, the more open, U-shaped transverse valleys on the lower molars, the absence of a 'neomorph' cuspid, and the bicuspid premolar of *Marada*. The last feature is most similar to the simple plesiomorphic bicuspid  $P_3$  of diprotodontids and palorchestids. Derived features shared with wynyardiids, diprotodontids, and palorchestids include a low angle of inclination of  $I_1$  and a tendency towards lophodont molars. Features shared exclusively with the diprotodontids and palorchestids include its large size, a weak paraconid, and paracristid on  $M_1$ , an elongate diastema with a prominent diastemal ridge, and a large mental foramen.

*Marada* is precluded from being a primitive member of Diprotodontoidea due to the presence of a postmetacristid, posthypocristid, postentocristid, and pre-

entocristid on the lower molars and the primitive construction of the weak lophids on the lower molars. The lophids are more reminiscent of ilariids and wynyardiids wherein the protoconid lies posterior to the metaconid, and the hypoconid lies posterior to the entoconid, resulting in a posteriorly curved or oriented lophid in the lower molars. In diprotodontids and palorchestids, the crescentic lophs curve forward and may represent one of the few synapomorphies of the superfamily Diprotodontoidea.

*Marada arcanum* possesses several unique primitive features, including: a gracile, narrow dentary; a less posteriorly extensive symphysis; a non-crested or inflated ascending ramus at its point of origin; and a more posterior origin of the ascending ramus. *Marada* differs from all other vombatomorphians except *Wakaleo*, in having a trigonid that is wider than the talonid and a small angle of inclination of the ascending ramus.

In addition, *Marada* exhibits a longitudinally oriented pattern of wear most pronounced on the buccal cuspids of the molars, in particular, the protoconids of  $M_{2,3}$  and the hypoconids of  $M_{1,2}$ . This wear is reminiscent of that found in ilariids, wynyardiids, and phascolarctids as opposed to the even wear across the transverse lophs seen in the fully lophodont diprotodontoids.

A striking feature of the dentary in *Marada* and one that is unique among vombatomorphians is the short molar row length, which occupies only 50% of the length of the horizontal ramus. It would appear that the *Marada* dentary evolved along a similar path to the diprotodontoids in becoming larger, but this was achieved by lengthening the diastema with little or no increase in molar row length.

Another unique feature is the flattened linear dentary and absence of pronounced areas for muscle attachment (i.e. the shallow masseteric, pterygoid, and digastric fossae). The degree to which these features are

attributable to sexual dimorphism is not known. The *Marada* dentary may represent a gracile female of the species. Unfortunately, the coronoid process and articular condyle are not preserved in *Marada*, so it is difficult to assess the relative strengths of the temporalis and masseter/pterygoid muscle complexes. The large mental foramen (which suggests increased innervation to the anterior lower jaw) may be suggestive of a large mobile lip. In any case, the longitudinal pattern of tooth wear, the shortened cheek tooth row, the lack of pronounced areas for muscle attachment, and the construction of the mandibular symphysis suggest a unique masticatory action and ecological niche for *Marada arcanum* that will remain a mystery until more complete specimens are known.

On the basis of the dentary and lower dentition, *Marada* does not fit into any known vombatomorphic family, as they are currently defined. Most features used in the generic diagnosis to define *Marada* are plesiomorphic with respect to Vombatomorpha. However, the combination of these primitive features with the possession of two unique features for *Marada* (the short length of the cheek tooth row with respect to horizontal ramus length; and the presence of a distinct cuspid on the lingual cingulum of the lower molars) makes this dentary strikingly different to any other vombatomorphic presently known and, consequently, warrants the establishment of a new family Maradidae.

Hiatus Site is interpreted to be from Riversleigh's stratigraphically oldest sediments and is late Oligocene in age (Creaser 1997). Each of the seven vombatomorphic families was distinct by the late Oligocene. However, the lack of an Australian fossil mammal record between 55 and 26 million years makes any refined assessment of the time of familial differentiation difficult. Aplin & Archer (1987) suggested a Paleogene origin for Vombatomorpha and con-

cluded that known families represent the remnants of a diverse pre-Oligocene radiation. The presence and only known occurrence of *Marada* in one of the oldest deposits at Riversleigh certainly supports a higher diversity of Vombatomorpha. Like the wynyardiids, which do not have a fossil record younger than the middle Miocene, *Marada* may represent an early experiment in vombatomorphic evolution that failed to survive beyond the Miocene, possibly as a result of competition with diprotodontoids and macropodoids.

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## References

- APLIN, K., 1987. Basicranial anatomy of the early Miocene diprotodontian *Wynyardia bassiana* (Marsupialia: Wynyardiidae) and its implications for wynyardiid phylogeny and classification. In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed., Surrey Beatty & Sons Pty Ltd and the Royal Zoological Society of New South Wales, Sydney, 369-391.
- APLIN, K. & ARCHER, M., 1987. Recent advances in marsupial systematics with a new syncretic classification. In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed., Surrey Beatty & Sons Pty Ltd and the Royal Zoological Society of New South Wales, Sydney, xv-lxxii.
- ARCHER, M., 1978. Koalas (phascolarctids) and their significance in marsupial evolution. In *The Koala*, T.J. BERGIN, ed., Zoological Parks Board of New South Wales, Sydney, 20-28.
- ARCHER, M., 1984. The Australian marsupial radiation. In *Vertebrate Zoogeography and Evolution in Australasia*, M. ARCHER & G. CLAYTON, eds, Hesperian Press, Perth, 633-808.
- ARCHER, M. & WADE, M., 1976. Results of the Ray E. Lemley expeditions Part 1: Allingham Formation and a new Pliocene vertebrate fauna from northern Queensland, Australia. *Memoirs of the Queensland Museum* 17, 379-398.
- BEECHER, R.M., 1977. Function and fusion at the mandibular symphysis. *American Journal of Physical Anthropology* 47, 326-335.
- BLACK, K., 1997. A new species of Palorchestidae (Marsupialia) from the late middle to early late Miocene Encore Local Fauna, Riversleigh, north-western Queensland. *Memoirs of the Queensland Museum* 41, 181-185.
- BLACK, K. & ARCHER, M., 1997. *Nimiokoala* gen. nov. (Marsupialia, Phascolarctidae) from Riversleigh, northwestern Queensland, with a revision of *Litokoala*. *Memoirs of the Queensland Museum* 41, 209-228.
- CLEMENS, W.A. & PLANE, M., 1974. Mid-Tertiary Thylacoleonidae (Marsupialia, Mammalia). *Journal of Paleontology* 48, 652-660.
- COOKE, B.N., 1997. Two new balbarine kangaroos and lower molar evolution within the subfamily. *Memoirs of the Queensland Museum* 41, 269-280.
- CREASER, P., 1997. Oligocene-Miocene sediments of Riversleigh: the potential significance of topography. *Memoirs of the Queensland Museum* 41, 303-314.
- FLANNERY, T.F. & ARCHER, M., 1987. *Strigocuscus reidi* and *Trichosurus dicksoni*, two new fossil phalangerids (Marsupialia: Phalangeridae) from the Miocene of northwestern Queensland. In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed., Surrey Beatty & Sons Pty Ltd and the Royal Zoological Society of New South Wales, Sydney, 527-536.
- FLOWER, W.H., 1867. On the development and succession of teeth in the Marsupialia. *Philosophical Transactions of the Royal Society of London* 157, 631-641.
- HOPE, J.H. & WILKINSON, H.E., 1982. *Warendja wakefieldi*, a new genus of wombat (Marsupialia, Vombatidae) from Pleistocene sediments in McEacherns Cave, western Victoria. *Memoirs of the National Museum of Victoria* 43, 109-120.
- ILLIGER, C., 1811. *Prodromus Systematis Mammalium et Avium Additus Terminus Zoographicis Utriudque Classis*, C. Salfeld, Berlin, 301 pp.
- KERR, R., 1792. *The Animal Kingdom*, or zoological system, of the celebrated Sir Charles Linnaeus; Class 1. Mammalia, containing a complete systematic description, arrangement, and nomenclature, of all the known species and varieties of the Mammalia, or animals which give suck to their young; being a translation of that part of the Systema Naturae, as lately published, with great improvements, by Professor Gmelin of Goettingen. Together with numerous additions from more recent zoological writers, and illustrated with copper plates. J. Murray & R. Faulder, London, 1 Pt 1 xl 400 pp. 9 pls.
- LUCKETT, W.P., 1993. An ontogenetic assessment of dental homologies in therian mammals. In *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians and Marsupials*, F.S. SZALAY, M.J. NOVACEK & M.C. MCKENNA, eds, Springer, New York, 182-204.
- MARSHALL, L.G., CASE, J.A. & WOODBURNE, M.O., 1989. Phylogenetic relationships of the families of marsupials. *Current Mammology* 2, 433-502.
- MUNSON, C.J., 1992. Postcranial descriptions of *Ilaria* and *Ngapakaldia* (Vombatiformes, Marsupialia) and the phylogeny of the vombatiforms based on postcranial morphology. *University of California Publications in Zoology*, P.B. MOYLE, J.L. PATTON, D.C. POTTS & D.S. WOODRUFF, eds, University of California, Berkeley, 1-99.
- MURRAY, P., 1986. *Propalorchestes novaculacephalus* gen. et sp. nov., a new palorchestid (Diprotodontidae: Marsupialia) from the middle Miocene Camfield Beds, Northern Territory, Australia. *The Beagle, Occasional Papers of the Northern Territory Museum of Arts and Sciences* 3, 195-211.
- MURRAY, P., 1990. Primitive marsupial tapirs (*Propalorchestes novaculacephalus* Murray and *P. ponticulus* (Marsupialia: Palorchestidae sp. nov.) from the mid-Miocene of north Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 7, 39-51.
- MURRAY, P.F., 1998. Palaeontology and palaeobiology of wombats. In *Wombats*, R.T. WELLS & P.A. PRIDMORE, eds, Surrey Beatty & Sons, Chipping Norton, Australia, 1-33.



- MURRAY, P.F., WELLS, R. & PLANE, M., 1987. The cranium of the Miocene thylacoleonid *Wakaleo vanderleuri*: Click go the shears- A fresh bite at thylacoleonid systematics. In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed., Surrey Beatty & Sons Pty Ltd and the Royal Zoological Society of New South Wales, Sydney, 433-466.
- MYERS, T.J. & ARCHER, M., 1997. *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, 379-392.
- OWEN, R., 1866. *On the Anatomy of Vertebrates*, Vol. II. Longmans, Green, London.
- PLEDGE, N.S., 1987a. *Muramura williamsi*, a new genus and species of ?wynyardiid (Marsupialia: Vombatoidae) from the middle Miocene Etadunna Formation of South Australia. In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed., Surrey Beatty & Sons Pty Ltd and the Royal Zoological Society of New South Wales, Sydney, 393-400.
- PLEDGE, N.S., 1987b. A new genus and species of primitive vombatoid marsupial from the medial Miocene Ngama Local Fauna of South Australia. In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed., Surrey Beatty & Sons Pty Ltd and the Royal Zoological Society of New South Wales, Sydney, 419-422.
- RICH, T.H.V. & ARCHER, M., 1979. *Namilamadeta snideri*, a new diprotodontan (Marsupialia, Vombatoidae) from the medial Miocene of South Australia. *Alcheringa* 3, 197-208.
- RICH, T.H., ARCHER, M. & TEDFORD, R.H., 1978. *Raemeotherium yatkolai* gen. et sp. nov., a primitive diprotodontid from the medial Miocene of South Australia. *Memoirs of the National Museum of Victoria* 39, 85-91.
- SHAW, G., 1800. General Zoology or systematic natural history. Quadrupeds, G. Kearsley, London, 249-552.
- SPRINGER, M.S. & WOODBURN, M.O., 1989. The distribution of some basicranial characters within the Marsupialia and a phylogeny of the Phalangeriformes. *Journal of Vertebrate Paleontology* 9, 210-221.
- STIRTON, R.A., 1967. The Diprotodontidae from the Ngapakaldia Fauna, South Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia* 85, 1-44.
- STIRTON, R.A., TEDFORD, R.H. & WOODBURN, M.O., 1967. A new Tertiary formation and fauna from the Tirari Desert, South Australia. *Records of the South Australian Museum* 15, 427-462.
- TEDFORD, R.H., ARCHER, M., BARTHOLOMAI, A., PLANE, M., PLEDGE, N.S., RICH, T., RICH, P. & WELLS, R.T., 1977. The discovery of Miocene vertebrates, Lake Frome area, South Australia. *BMR Journal of Australian Geology and Geophysics* 2, 53-57.
- TEDFORD, R.H. & WOODBURN, M.O., 1987. The Ilariidae, a new family of vombatiform marsupials from Miocene strata of South Australia and an evaluation of the homology of molar cusps in the Diprotodontidae. In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed., Surrey Beatty & Sons Pty Ltd and the Royal Zoological Society of New South Wales, Sydney, 401-418.
- WOODBURN, M.O., 1984. Families of marsupials: relationships, evolution and biogeography. In *Mammals: Notes for a short course*, T.W. BROADHEAD, ed., University of Tennessee Department of Geological Science, Studies in Geology 8, 48-71.
- WOODBURN, M.O., PLEDGE, N.S. & ARCHER, M., 1987a. The Miralinidae, a new family and two new species of phalangeroid marsupials from Miocene strata of South Australia. In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed., Surrey Beatty & Sons Pty Ltd and the Royal Zoological Society of New South Wales, Sydney, 581-602.
- WOODBURN, M.O., TEDFORD, R.H. & ARCHER, M., 1987b. New Miocene ringtail possums (Marsupialia: Pseudocheiridae) from South Australia. In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed., Surrey Beatty & Sons Pty Ltd and the Royal Zoological Society of New South Wales, Sydney, 639-679.
- WOODBURN, M.O., TEDFORD, R.H., ARCHER, M. & PLEDGE, N.S., 1987c. *Madakoala*, a new genus and two species of Miocene koalas (Marsupialia: Phascolarctidae) from South Australia, and a new species of *Perikoala*. In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed., Surrey Beatty & Sons Pty Ltd and the Royal Zoological Society of New South Wales, Sydney, 293-317.
- WOODS, J.T., 1956. The skull of *Thylacoleo carnifex*. *Memoirs of the Queensland Museum* 13, 125-140.