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Borungaboodie hatcheri gen. et sp. nov., a very large bettong (Marsupialia: Macropodoidea) from the Pleistocene of southwestern Australia

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Abstract – *Borungaboodie hatcheri* gen. et sp. nov., a very large potoroine kangaroo, is described from a dentary collected from a Pleistocene deposit in a cave near Witchcliffe in southwestern Australia. It is clearly distinguished from all other potoroines on the basis of several unique morphological features of the dentary and dentition, as well as its larger size. *Borungaboodie* may represent the least derived member of a lineage containing *Caloprymnus*, *Milliyowi* and *Aepyprymnus*. The dentary of *B. hatcheri* seems to have been capable of generating proportionally larger bite forces than modern bettongs, suggesting a more resistant diet. Its larger body size may also have facilitated a higher degree of opportunistic omnivory than in any modern potoroine. While its ancestral stock may well have inhabited the Miocene wet forest of the southwest, *B. hatcheri* itself was probably adapted to a sclerophyll habitat.

INTRODUCTION

Tight Entrance Cave, near Witchcliffe in southwest Western Australia, was first explored in the early 1970s, but Pleistocene vertebrate remains were not discovered in the cave until late 1991, by Lindsay Hatcher and other members of the Western Australian Speleological Group (WASG). The site was subsequently brought to the attention of the Western Australian Museum and the author. The palaeontology and stratigraphy of the deposit have been described by Gully (1997).

During excavations in August 1996, a partial dentary of a bettong comparable in size to a modern koala was recovered from a fossil-rich sediment layer low in the sedimentary sequence. The bettong is recognized and described here as a new genus and species, *Borungaboodie hatcheri*.

MATERIALS AND METHODS

The holotype of *Borungaboodie hatcheri* gen. et sp. nov. is registered in the vertebrate palaeontological collection of the Western Australian Museum, Perth. The following abbreviations are employed in this paper: ANU = Australian National University, Canberra; FU = Flinders University of South Australia, Bedford Park, South Australia; SAM = South Australian Museum, Adelaide (M: modern mammal collection; P: palaeontological collection); WAM = Western Australian Museum. Dental homology follows Flower (1867) and Luckett (1993). Dental nomenclature follows Tedford and Woodburne (1987) and Ride (1993). All measurements are in millimetres.

The following potoroine specimens were used for comparison with *Borungaboodie hatcheri* gen. et sp. nov., and as the sources of data in the Tables: *Aepyprymnus rufescens* (Gray, 1837): SAM M1724, M12026, M18127; *Bettongia gaimardi* (Desmarest, 1822): SAM M7386, M7387, M7388; *Bettongia lesueur* (Quoy and Gaimard, 1824): SAM M1702, and from Holocene deposits in Corra-Lynn Cave, Yorke Peninsula, South Australia, SAM P32554, P32555; *Bettongia penicillata* Gray, 1837: SAM M6211, M11247, and from Pleistocene deposits in Victoria Fossil Cave, Naracoorte, SAM P28880, P32513, and FU 0154; *Caloprymnus campestris* (Gould, 1843): SAM M3257; *Potorous platyops* (Gould, 1844): from Pleistocene deposits in Victoria Fossil Cave, Naracoorte, South Australia, FU 0176, FU 0999; *Potorous tridactylus* (Kerr, 1792): SAM M9012, M9013 and from Pleistocene deposits in Victoria Fossil Cave, Naracoorte, South Australia, FU 0221, FU 1000, FU 1475.

SYSTEMATIC PALAEONTOLOGY

In this paper I treat the group comprising the bettongs and potoroos as the subfamily Potoroinae, included within the family Macropodidae, on the morphological and molecular grounds outlined by Case (1984), Kirsch (1977), Springer and Kirsch (1991), Kirsch *et al.* (1995, 1997), Springer *et al.* (1997) and Burk *et al.* (1998). This differs from the views of Pearson (1946, 1950), Bartholomai (1978) and Archer (1981) who referred bettongs, potoroos and the Musky Rat-kangaroo, *Hypsiprymnodon moschatus* Ramsay, 1876, to the family Potoroidae, within which Flannery *et al.* (1984) also included the extinct propleopines and bulungamayines. Recent evidence from morphological (Ride 1993; Szalay 1994) and mitochondrial DNA studies (Kirsch *et al.* 1997; Burk *et al.* 1998) suggests that *Hypsiprymnodon* is the sister taxon to all the Macropodidae and should be separated at the family level.

In addition to the genera listed in Materials and Methods above, the following are referred to the Potoroinae and used for comparison with *Borungaboodie hatcheri* gen. et sp. nov.: *Milliyowi* Flannery, Rich, Turnbull and Lundelius, 1992, and *Wakiewakie* Woodburne, 1984. While Case (1984) described the early Miocene *Purtia mosaicus* as a potoroine, Flannery (1989) subsequently highlighted potential bulungamayine affinities that cast sufficient doubt upon its subfamilial assignment to exclude it from comparisons here. I also omit *Gumardee pascuali* Flannery, Archer and Plane, 1983, due to similar doubts over its closest affinities raised by Flannery *et al.* (1984) and Flannery (1989). More recently, Cooke (1997) intimated that *G. pascuali* may be synonymous with the bulungamayine *Wabularoo naughtoni*, the potential of which was foreshadowed by Woodburne (1984).

Name authorities not included in the References may be found in Walton (1988), for modern genera and species, and Aplin and Archer (1987) for higher taxa.

Order Diprotodontia Owen, 1866

Superfamily Macropodoidea Gray, 1821

Family Macropodidae Gray, 1821

Subfamily Potoroinae Gray, 1821

Tribe Bettongini Flannery and Archer, 1987

Genus *Borungaboodie* gen. nov.

Type Species

Borungaboodie hatcheri sp. nov.

Diagnosis

Clearly distinguishable from all other potoroines in possessing a proportionally deeper ramus along its entire length (resulting in a straighter ventral margin than all genera except *Potorous*), larger anterior insertion area for the middle masseter muscle, I_1 more robust and upturned, M_1 protolophid markedly narrower than hypolophid, M_4 hypolophid not as narrow relative to protolophid. It differs from all potoroine genera, except *Wakiewakie* and variably *Bettongia lesueur*, in possessing a posterior mental foramen.

In particular, *Borungaboodie* differs from *Bettongia* in having relatively longer, narrower molars, better developed posthypocristid; from *Caloprymnus* in having a higher concentration of fine vertical ridgelets on P_3, P_3 longer relative to M_1, relatively longer, narrower molars, shorter diastema, no notch between lingual extremity of paracristid and anterior face of metaconid; from *Milliyowi* in having a P_3 with finer vertical ridgelets that lack subsidiary branching, lower molars without a large precingulid anterobuccal to paracristid, no notch between lingual extremity of paracristid and anterior face of metaconid, trigonid shorter anteroposteriorly; from *Aepyprymnus* in having lower-crowned and less lophodont molars, no notch between lingual extremity of paracristid and anterior face of metaconid, trigonid shorter anteroposteriorly; from *Wakiewakie* in having a much more robust I_1, much shorter P_3 relative to molars, relatively longer, narrower molars, strongly developed posthypocristid; and from *Potorous* in having a proportionally shorter and deeper ramus, more robust I_1, longer P_3 relative to molars, P_3 with more and finer vertical ridgelets, relatively wider and less symmetrical molars.

Etymology

Borungaboodie is a combination of the Nyoongar (southwest Western Australian) Aboriginal word *borunga*, which means "large, very big" (Bindon and Chadwick 1992), and Boodie, the vernacular name for the extant Burrowing Bettong, *Bettongia lesueur*, which is derived from a very similar Nyoongar word meaning "ground-rat" (Bindon and Chadwick 1992). The name alludes to the large and robust nature of the dentary of this taxon relative to all other potoroines. Gender is considered to be masculine.

Borungaboodie hatcheri sp. nov.

Figures 1-2; Tables 1-2

Material Examined

Holotype

WAM 97.5.1, right adult dentary with I_1, P_3, M_{1-4}, lacking the ascending ramus and its associated processes (Figures 1-2).

Type Locality and Age

The holotype was collected by the author and G.A. Gully in August 1996 from Tight Entrance Cave (WASG cave reg. no. Wi-101; 34°04'S., 114°01'E.), southwest of Witchcliffe on the Leeuwin-Naturaliste Ridge, southwestern Western Australia. The specimen was recovered from Unit D ("Unit Glory"), approximately 2 m below the surface of the deposit, near the southeastern edge of the main chamber (Gully 1997). Uranium-series dating of flowstone interbedded with Unit D by L.K. Ayliffe, Australian National University, gave an age of

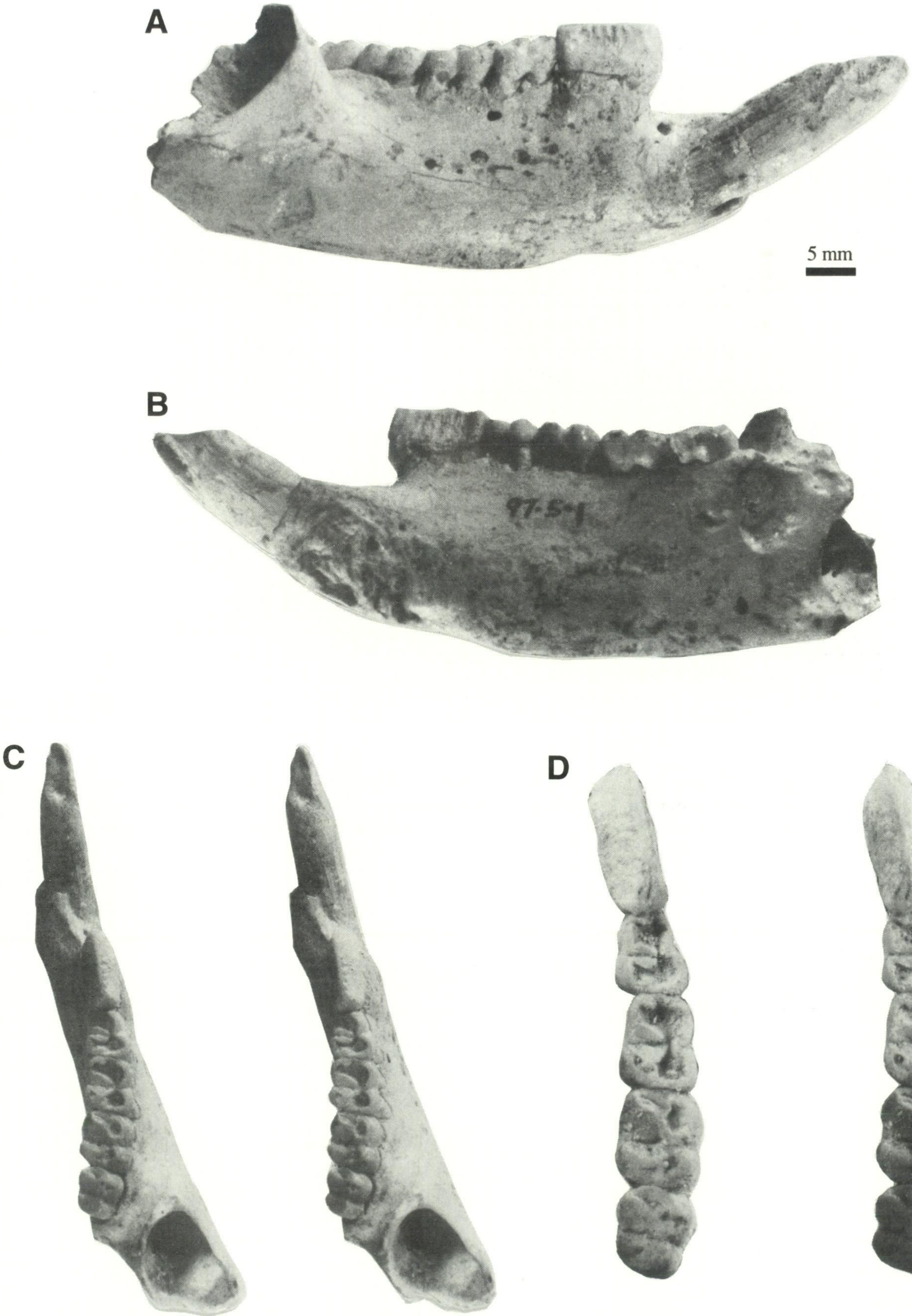

Figure 1 Photographs of *Borungaboodie hatcheri* gen. et sp. nov. holotype right dentary (WAM 97.5.1). A, lateral view; B, mesial view; C, stereopair of dentary in occlusal view; D, stereopair of cheek tooth row in occlusal view.

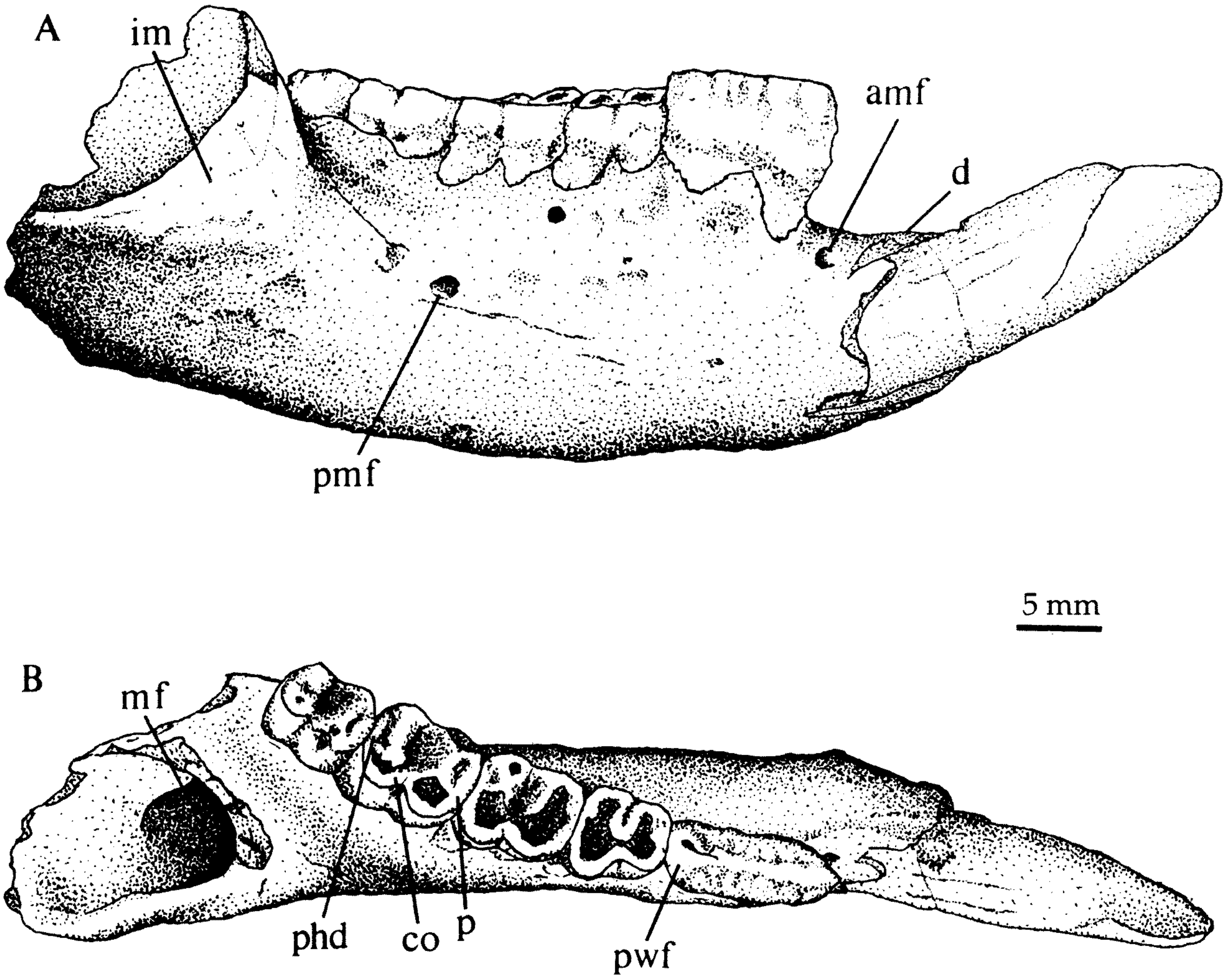

Figure 2 Drawings of *Borungaboodie hatcheri* gen. et sp. nov. holotype right dentary (WAM 97.5.1). A, lateral view; B, occlusal view. Abbreviations: amf = anterior mental foramen, co = cristid obliqua, d = diastema, im = insertion scar for anterior-most layer of middle masseter muscle, mf = masseteric foramen, p = paracristid, phd = posthypocristid, pmf = posterior mental foramen, pwf = posterobuccal wear facet.

137.75 ± 3.83 kyr (ANU ref. no. TE-FS-UG). Ayliffe (pers. comm. 1997) noted that this date should be taken as a maximum age for the flowstone given the high ^{230}Th/^{232}Th activity ratio of 12.0, indicating the presence of detrital contamination.

Diagnosis

As for the genus until further species are described.

Etymology

The species is named in honour of Mr Lindsay M. Hatcher, discoverer of Pleistocene vertebrate fossils in Tight Entrance Cave and major contributor to the preliminary investigation of the site.

Description

Dentary

Very large and robust, with ventral margin of horizontal ramus only slightly convex. Distinct inflection on ventral margin beneath M_1 corresponds to anterior limit of masseteric canal and base of deep I_1 root (Figure 1B). I_1 robust and upturned. Diastema between I_1 and P_3 short. Anterior mental foramen positioned just forward of anterior root of P_3 and just below dorsal margin of diastema. Posterior mental foramen positioned mid-depth on buccal surface of ramus, below M_2 hypolophid (Figures 1A, 2A). Anteroventral border of masseteric fossa quite straight due to large, posteriorly expanded insertion scar of anterior-most layer of middle masseter muscle, which obscures opening of masseteric canal when viewed buccally (Figures 1A, 2A). Postalveolar shelf a rather deep valley. Masseteric foramen wide and deep (Figures 1C, 2B), separated from posterior-most portion of inferior dental canal by thin bony lamina. Inferior mandibular foramen small, oval-shaped (long axis runs dorsoventrally), opening posteriorly (Figure 1B). Posterior region of dentary not preserved, although anterior root of ascending ramus indicates a rather vertical anterior margin originating adjacent to M_4 interlophid valley. Mandibular symphysis non-ankylosed, but posteroventral surface rugose and bordered posteriorly by small genial pit (Figure 1B). Anterior-most portion of ramus surrounding base of I_1 not preserved.

Lower Dentition

I_1 short and thick, with crown considerably worn (Figures 1-2). Remaining enamel largely restricted to triangular portion at anterobuccal extremity, although jagged posterior edge strongly suggests enamel extended posteriorly on ventrobuccal aspect. Enamel continues partially onto ventrolingual surface.

P_3 blade-like, lozenge-shaped in occlusal view (Figures 1C-D, 2B); bears seven fine vertical enamel ridgelets descending from occlusal surface which is positioned above level of molars. Posterior extremity of P_3 crown curves slightly lingually. Wear on P_3 restricted to apex and small, posterobuccal portion of crown (Figures 1D, 2B). Crown height increases anteriorly (anterior height 6.8 mm, posterior height 5.7 mm).

Molars bunodont and worn, with roots directed slightly posteriorly (Figures 1-2). M_1 extremely worn, retaining only enamel rim of crown and lingual portion of interlophid valley (protolophid height 3.5 mm, hypolophid height 3.5 mm). Protolophid markedly narrower than hypolophid (Figures 1D, 2B). M_2 similarly worn, although slightly more enamel remains on posterolingual corner of crown (protolophid height 3.5 mm, hypolophid height 3.5 mm). Protolophid and hypolophid of M_{2-3} subequal in width. M_3 with enamel of protoconid and hypoconid breached, and enamel chipped from lingual side of metaconid (protolophid height 3.4 mm, hypolophid height 3.4 mm). Paracristid very limited in anterior extent and either curves to meet metaconid apex or becomes confluent with short premetacristid, producing antero-posteriorly short trigonid (Figures 1D, 2B). Posthypocristid apparently well-developed, curving across posterior extremity of molar to meet short postentocristid at posterolingual extremity of tooth. Remnant of strong cristid obliqua present near buccal edge of interlophid valley (Figures 1D, 2B). M_4 worn, with enamel breached at very tip of protoconid, and tiny enamel chip broken from buccal side of protoconid (protolophid height 3.7 mm, hypolophid height 3.3 mm). M_4 hypolophid narrower than protolophid. Paracristid crescent-shaped, linking protoconid and metaconid. No precingulid visible anterobuccal to paracristid. All four cuspids large and close together. Buccally placed cristid obliqua and postmetacristid strongly developed. Posthypocristid shorter and thicker than on M_{2-3}, but apparently well-developed and extending from hypoconid apex to posterolingual extremity of crown, immediately posterior to entoconid (Figures 1D, 2B).

Remarks

Although *Borungaboodie hatcheri* gen. et sp. nov. is known only from the holotype dentary, a specimen with considerably worn molars, it is considered to lie outside of the range of morphological variation that might be expected within any of the four monotypic bettong genera (e.g. *Aepyprymnus*), or that is seen between the species of *Bettongia*. Its dentary and teeth are approximately 30% larger than the next largest species, the Rufous Bettong, *Aepyprymnus rufescens*. Below I highlight the distinctive morphological features of *B. hatcheri* through comparison with the relevant potoroine taxa.

Comparison With Other Potoroines

Mandibular Ramus. Aside from its much larger size, one of the most distinctive features of the holotype of *Borungaboodie hatcheri* is the shape of the horizontal ramus. With the exception of *Potorous*, which has a uniquely slender and elongate dentary, potoroines possess a notably convex ventral margin to the dentary (Flannery 1989). In *B. hatcheri*, the ventral margin is much straighter, being only slightly convex ventrally. This is due to a relative increase in ramus depth posteriorly and, especially, anteriorly, providing the dentary with a more robust appearance relative to all other potoroines. This is probably an autapomorphy for *Borungaboodie*.

Posterior Mental Foramen. Apart from *Borungaboodie hatcheri*, a posterior mental foramen is only seen among potoroines in *Wakiewakie lawsoni* and variably in *Bettongia lesueur*. The feature is present in a range of macropodoids, including bulungamayines, balbarines, sthenurines and *Hypsiprymnodon*, and is probably a macropodoid symplesiomorphy.

Middle Masseter Muscle Insertion and Ascending Ramus. The attachment scar for that component of the middle masseter muscle layer which inserts anterior to the anteroventral border of the masseteric fossa, is more pronounced in *Borungaboodie hatcheri* than in any other potoroine. It is less pronounced in *Potorous* and *Bettongia lesueur*, and barely detectable in *Caloprymnus*, *Aepyprymnus* and the other *Bettongia* species. However, the manner in which the opening to the masseteric canal is obscured in *B. hatcheri* by the posterior extension of this area, when viewed

Table 1 Dental measurements of *Borungaboodie hatcheri* gen. et sp. nov., *Aepyprymnus rufescens, Caloprymnus campestris, Bettongia penicillata, Be. lesueur, Be. gaimardi, Wakiewakie lawsoni* (from Woodburne 1984) and *Milliyowi bunganditj* (from Flannery *et al.* 1992). Mean, standard deviation (parentheses), range (brackets).

Tooth	Species	Length	Anterior Width	Posterior Width	Sample Size
P_3	*Borungaboodie hatcheri*	11.3	4.4	4.3	1
	Aepyprymnus rufescens	8.0 (0.50)	2.7 (0.17)	2.8 (0.17)	3
		[7.3-8.3]	[2.5-2.9]	[2.6-3.0]	
	Caloprymnus campestris	4.7	1.7	1.9	1
	Bettongia penicillata	6.1 (0.31)	2.7 (0.00)	2.2 (0.12)	3
		[5.7-6.4]	[2.7]	[2.1-2.4]	
	Bettongia lesueur	6.8 (0.42)	2.2 (0.14)	2.2 (0.19)	3
		[6.4-7.4]	[2.1-2.4]	[2.1-2.5]	
	Bettongia gaimardi	6.9 (0.24)	2.8 (0.09)	2.8 (0.12)	3
		[6.6-7.2]	[2.7-2.9]	[2.6-2.9]	
	Wakiewakie lawsoni	11.0	2.9	2.6	1
M_1	*Borungaboodie hatcheri*	6.8	4.6	5.8	1
	Aepyprymnus rufescens	5.2 (0.28)	3.6 (0.16)	4.0 (0.05)	3
		[4.8-5.4]	[3.3-3.7]	[3.9-4.0]	
	Caloprymnus campestris	3.6	3.1	3.5	1
	Bettongia penicillata	3.9 (0.05)	3.3 (0.17)	3.7 (0.22)	3
		[3.8-3.9]	[3.1-3.5]	[3.4-3.9]	
	Bettongia lesueur	3.8 (0.09)	3.0 (0.21)	3.6 (0.22)	3
		[3.7-3.9]	[2.8-3.3]	[3.4-3.9]	
	Bettongia gaimardi	4.2 (0.00)	3.6 (0.09)	3.9 (0.12)	3
		[4.2]	[3.5-3.7]	[3.7-4.0]	
	Wakiewakie lawsoni	3.8	3.1	3.4	1
M_2	*Borungaboodie hatcheri*	7.4	5.9	6.2	1
	Aepyprymnus rufescens	5.8 (0.21)	4.2 (0.12)	4.4 (0.14)	3
		[5.6-6.1]	[4.1-4.4]	[4.2-4.5]	
	Caloprymnus campestris	4.0	4.0	3.8	1
	Bettongia penicillata	4.0 (0.17)	3.9 (0.29)	3.7 (0.24)	3
		[3.8-4.2]	[3.6-4.3]	[3.4-4.0]	
	Bettongia lesueur	4.1 (0.09)	3.7 (0.33)	3.8 (0.26	3
		[4.0-4.2]	[3.3-4.1])	[3.6-4.2]	
	Bettongia gaimardi	4.6 (0.05)	4.4 (0.08)	4.2 (0.12)	3
		[4.5-4.6]	[4.3-4.5]	[4.0-4.3]	
	Wakiewakie lawsoni	4.0	3.5	3.6	1
M_3	*Borungaboodie hatcheri*	7.4	6.5	6.3	1
	Aepyprymnus rufescens	6.0 (0.08)	4.7 (0.14)	4.5 (0.12)	3
		[5.9-6.1]	[4.6-4.9]	[4.3-4.6]	
	Caloprymnus campestris	3.7	3.7	3.3	1
	Bettongia penicillata	3.8 (0.25)	3.7 (0.17)	3.2 (0.37)	3
		[3.5-4.1]	[3.5-3.9]	[2.7-3.6]	
	Bettongia lesueur	4.0 (0.22)	3.8 (0.36)	3.7 (0.22)	3
		[3.8-4.3]	[3.5-4.3]	[3.5-4.0]	
	Bettongia gaimardi	4.7 (0.08)	4.4 (0.09)	3.8 (0.09)	3
		[4.6-4.8]	[4.3-4.5]	[3.7-3.9]	
	Wakiewakie lawsoni	4.4	3.7	3.6	1
	Milliyowi bunganditj	6.7	4.9	5.0	1
M_4	*Borungaboodie hatcheri*	6.5	5.5	4.8	1
	Aepyprymnus rufescens	5.8 (0.15)	4.7 (0.25)	3.6 (0.35)	2
		[5.6-5.9]	[4.4-4.9]	[3.2-3.9]	
	Caloprymnus campestris	3.1	3.1	2.0	1
	Bettongia penicillata	2.9 (0.24)	2.9 (0.33)	2.2 (0.34)	3
		[2.6-3.1]	[2.5-3.3]	[1.9-2.7]	
	Bettongia lesueur	3.2 (0.21)	2.9 (0.34)	2.3 (0.34)	3
		[2.9-3.4]	[2.6-3.4]	[2.0-2.8]	
	Bettongia gaimardi	4.0 (0.00)	3.8 (0.12)	3.0 (0.09)	3
		[4.0]	[3.6-3.9]	[2.9-3.1]	

buccally, and the relative straightness of its posterior edge (the anteroventral border of the masseteric fossa) is quite similar to the condition in *Potorous*.

Unfortunately, extremely little of the ascending ramus is preserved in the *B. hatcheri* holotype, but the rather vertical anterior root is suggestive of a more vertical ascending ramus than in any other potoroine, except *Wakiewakie*. A more vertical ascending ramus may be part of a functional complex which includes anterior expansion of the middle masseter, a muscle layer with a near-vertical orientation.

Mandibular Symphysis. Given the greater overall robustness of the dentary of *Borungaboodie hatcheri*, there is surprisingly little difference in the overall morphology and extent of the symphysis relative to *Aepyprymnus*. The symphysis seems to have been just as kinetic in *B. hatcheri* as in the remaining potoroines. Certainly, the symphysis is relatively deeper in *B. hatcheri*, but this is a direct correlate of its ramus proportions and diastema length.

Diastema Length. The diastema of *Borungaboodie hatcheri* is proportionally shorter than those of most potoroine taxa, except *Aepyprymnus* and *Bettongia lesueur*, which are very similar. While the diastema of *Wakiewakie* is unknown, the orientation of the I_1 alveolus points to a similarly short diastema in this taxon.

Lower Incisor. The I_1 preserved in the holotype of *Borungaboodie hatcheri* is a robust and deep-rooted tooth, which is most similar in proportion and morphology to that of *Aepyprymnus* at the same wear stage. However, it is distinguishable from *Aepyprymnus* and all other potoroines by its more upturned (less procumbent) nature. This results in the occlusal surface being oriented at a much less acute angle relative to the longitudinal axis of the I_1 crown than in the other potoroines. I consider the form of the I_1 a significant autapomorphy for *Borungaboodie*.

Lower Permanent Premolar. Although the P_3 of *Borungaboodie hatcheri* is substantially larger in absolute size than either *Aepyprymnus* or *Bettongia* (Table 1), they are all very similar in overall morphology (including number of vertical ridgelets) and length relative to the molars. As in most potoroine taxa, P_3 is not flexed buccally relative to the molar row (cf. *Be. penicillata*). The limited wear sustained by the premolar, relative to the molars, in the holotype of *B. hatcheri* is more akin to *Bettongia* than to *Aepyprymnus*, which shows more similarity in the degree of wear sustained by the P_3 and the molars.

Lower Molar Crown Height. Although worn, the molars of *Borungaboodie hatcheri* are proportionally lower-crowned and less lophodont than those of *Aepyprymnus*, as judged primarily from the least worn teeth, M_{3-4}. In this regard they approach the more typically bunodont molars of *Bettongia*.

Relative Width of M_1 Protolophid. In *Borungaboodie hatcheri* the protolophid of M_1 is markedly narrower than the hypolophid, being only about 80% of the hypolophid width (0.79; Table 2) compared with *Aepyprymnus* (0.90), *Caloprymnus* (0.88) and *Wakiewakie* (0.91). While *Bettongia lesueur* (0.83) approaches the lophid width disparity of *B. hatcheri*, this is probably convergence, considering that the proportional protolophid width of other *Bettongia* species, including the plesiomorphic *Be. moyesi*, ranges between 0.88 and 0.93. This may represent a possible autapomorphy for *Borungaboodie*.

Molar Proportion. The molars of *Borungaboodie hatcheri* are longer relative to their width than those of any other bettong besides *Aepyprymnus* (Table 2) and *Milliyowi* (Flannery *et al*. 1992). This similarity between these taxa is more likely to represent convergence than a synapomorphy, because the trigonids of *Aepyprymnus* and *Milliyowi* are antero-posteriorly elongated. In *B. hatcheri* the trigonid is quite short, similar to that of *Bettongia* and *Wakiewakie*. This molar form is a possible autapomorphy for *Borungaboodie*.

Table 2 Some proportional dental measurements of *Borungaboodie hatcheri* gen. et sp. nov., *Aepyprymnus rufescens*, *Caloprymnus campestris*, *Bettongia penicillata*, *Be. lesueur*, *Be. gaimardi* and *Wakiewakie lawsoni* (from Woodburne 1984). AW = protolophid width; L = length; MW = mean of protolophid and hypolophid widths; PW = hypolophid width.

Species	M_1 L/MW	M_2 L/MW	M_1 AW/PW	M_4 PW/AW	L P_3/M_1	Sample Size
Borungaboodie hatcheri	1.31	1.22	0.79	0.87	1.66	1
Aepyprymnus rufescens	1.37	1.35	0.90	0.78	1.54	3
Caloprymnus campestris	1.10	1.03	0.88	0.65	1.31	1
Bettongia penicillata	1.11	1.05	0.89	0.76	1.56	3
Bettongia lesueur	1.15	1.10	0.83	0.79	1.79	3
Bettongia gaimardi	1.12	1.07	0.93	0.79	1.64	3
Wakiewakie lawsoni	1.17	1.12	0.91	-	2.89	1

Trigonid Morphology. The trigonid of *Borungaboodie hatcheri* is antero-posteriorly short, which is most reminiscent of *Bettongia* and *Wakiewakie*. The manner in which the paracristid curves from the protoconid apex across the front of the tooth and becomes smoothly confluent with the premetacristid is very similar in each of these three taxa. Unlike *Aepyprymnus*, *Caloprymnus* and *Milliyowi*, there is no notch between the anterolingual extremity of the paracristid and the smaller premetacristid. Similarly, no distinct precingulid appears have been present anterobuccal to the paracristid in *B. hatcheri*. Both conditions are most reminiscent of *Wakiewakie* and *Bettongia*, although I have observed a very slight precingulid in *Be. penicillata* (e.g. SAM M11247).

M_4 Hypolophid Width. In all potoroines, the hypolophid of M_4 tends to be markedly narrower than the protolophid. *Borungaboodie hatcheri* expresses this to a lesser degree (Table 2) than all other potoroine taxa, presumably autapomorphically.

Posthypocristid Morphology. Although the molars of the *Borungaboodie hatcheri* holotype have sustained significant wear, it is quite clear that the posthypocristid was well-developed, meeting a short postentocristid at the posterolingual corner of the tooth, as it does in *Aepyprymnus* and *Caloprymnus*, and on the dP_3 of *Milliyowi*.

DISCUSSION

Potoroine Systematics

Potoroines survive today as one of only two well-represented macropodoid lineages, but their known pre-Quaternary record is surprisingly meagre. This makes an assessment of interrelations extremely difficult because the genera almost certainly diverged well before the medial Miocene (Flannery and Archer 1987; Woodburne *et al.* 1994; Springer *et al.* 1997). Moreover, the three extinct genera (*Borungaboodie, Wakiewakie, Milliyowi*) are monotypic and known only from extremely limited material. Among the modern genera, only *Bettongia* is known from the late Tertiary (Flannery and Archer 1987; Cooke 1997). For these reasons, a comprehensive phylogenetic analysis of the potoroines may be best left until new potoroines from the Late Oligocene of the Lake Eyre Basin (Woodburne *et al.* 1994) are described, and B.N. Cooke's analysis of basal macropodoid relationships is completed.

Fortunately, relationships between the modern genera appear relatively clear, and give some idea at least, of the broad framework of potoroine phylogeny. There is little doubt that *Potorous* lies outside of the clade containing *Bettongia* and *Aepyprymnus*, based as much on molecular evidence (Kirsch 1977; Kirsch *et al.* 1997; Burk *et al.* 1998) as craniodental and pedal morphology. While inferences drawn from the female urogenital system tend to support this relationship (Pearson 1946), the polarities and phylogenetic utility of these reproductive features remain poorly understood. Differences in craniodental and pedal morphology between *Potorous* and the other modern potoroine genera have most recently been flagged by Flannery and Archer (1987) and Flannery (1989), resulting in the erection of the tribes Bettongini for *Bettongia*, *Aepyprymnus* and *Caloprymnus*, and Potoroini for the species of *Potorous*. Although the phylogenetic position of *Caloprymnus* has proven slightly more contentious, the weight of morphological evidence supports a greater affinity to *Bettongia* and *Aepyprymnus* (Flannery and Archer 1987; Flannery 1989) than to *Potorous* (cf. Bensley 1903). Unfortunately, its recent extinction has so far precluded *Caloprymnus* from molecular studies (Kirsch *et al.* 1997).

Borungaboodie is here aligned with the tribe Bettongini on the basis of four character states which separate the members of this group from *Potorous*: the dentary is stout and its ventral margin is convex; the I_1 lacks a well-developed ventral enamel flange; P_3 possesses many fine vertical ridgelets; and the buccal crests of the lower molars (paracristid, cristid obliqua, posthypocristid, protocristid, metacristid) are much less developed than their lingual counterparts. Other members of the tribe Bettongini whose morphologies are more completely documented, are also distinguished from *Potorous* by the possession of a postglenoid process, a discrete periotic ectotympanic process, a short I^3 crown, upper molars with better-developed buccal crests, and pedal digital pads fused into a single unit. Although these character states are useful for distinguishing bettongins from potoroins, character state polarities will remain conjectural until the sister group to the Potoroinae is revealed. For this reason, I define the Bettongini (Figure 3) only by those character states considered most likely to represent bettongin synapomorphies, as judged by their absence in other macropodoid groups. Indeed, the Bettongini appear to be characterized more by the retention of numerous plesiomorphic character states than by a suite of derived features.

Within the Bettongini, the relationships of the three modern genera appear relatively clear. Only one strong synapomorphy (jugal extending to at least the level of the large lachrymal foramen) appears to unite the species of *Bettongia*, which suggests that the genus diverged close to the base of the bettongin radiation (Flannery and Archer 1987; Flannery 1989; Figure 3). The inflated hypotympanic sinus has been suggested as another synapomorphy (Flannery and Archer 1987; Flannery 1989), on the assumption that the feature

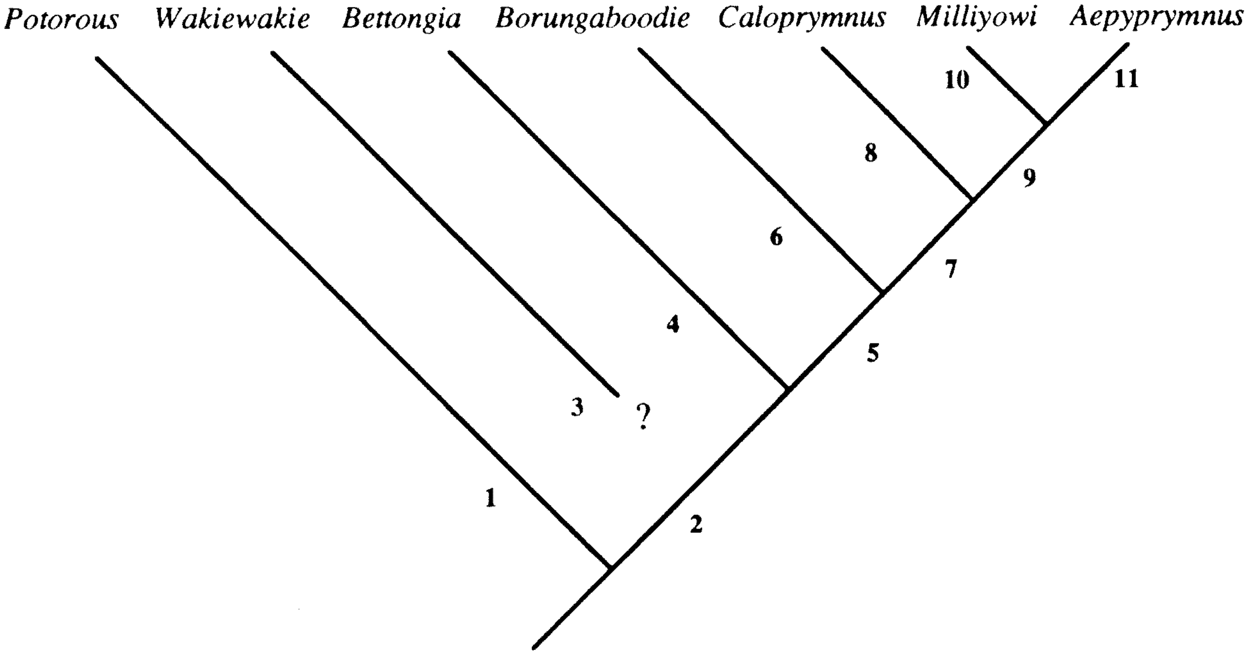

Figure 3 Dendrogram showing proposed relationships in subfamily Potoroinae. **1**, I^3 bears single elongate occlusal crest; dentary slender and elongate; permanent premolars with few coarse vertical ridgelets and unworn profile dominated by large anterior and posterior cusps; molars markedly symmetrical in occlusal profile, with crests on buccal side similarly developed to crests on lingual side. **2**, ectotympanic process of periotic discrete; ventral enamel flange of I_1 absent; pedal digital pads fused into single unit (characters not assessable in extinct genera except I_1 in *Borungaboodie*). **3**, ascending ramus near vertical; central region of ramus extremely deep; I_1 very steeply oriented; permanent premolars extremely elongate; buccal side of lower molars markedly sloped. **4**, jugal extends at least to level of large lachrymal foramen. **5**, premaxilla extremely foreshortened (character not assessable in *Borungaboodie, Milliyowi*); posthypocristid and postmetaconule crista well-developed and extended across entire posterior face of loph(id); P^3-C^1 diastema shortened (character not assessable in *Borungaboodie, Milliyowi*). **6**, ramus deep along entire length (straighter ventral margin); anterior insertion area for middle masseter layer marked; I_1 robust and upturned; molars elongate relative to length, but trigonid antero-posteriorly short; M_1 protolophid markedly narrower than hypolophid; M_4 hypolophid not greatly narrowed relative to protolophid. **7**, trigonid with notch between lingual extremity of paracristid and anterior face of metaconid; lower molars with well-developed precingulid; **8**, rostrum and nasals very broad; frontals with incipient supraorbital crest; masseteric process well-developed; periotic exposed on basicranium; C^1 very reduced; permanent premolars arcuate with few coarse vertical ridgelets. **9**, molars elongate relative to length and trigonid antero-posteriorly elongated; molars relatively high-crowned and sublophodont. **10**, P_3 elongate with coarse vertical ridgelets bearing subsidiary branching, lingual side of anterior upper molars and buccal side of anterior lower molars with markedly sloping edges; posthypocristid reduced in extent in M_3; precingulid hypertrophied. **11**, palate lacks vacuities (character not assessable in *Milliyowi*); I^3 very stout and markedly rotated anteromesially; molar precingulid reduced.

arose independently in *Caloprymnus*. It is important to note though that this feature is also present in *Potorous platyops*.

Flannery (1989) cited four synapomorphies in support of the monophyly of *Caloprymnus* and *Aepyprymnus*: the I^3 occlusal crest is rotated anteromesially; the posthypocristid and postmetaconule crista are well-developed and extend across the entire posterior face of the hypolophid and metaloph, respectively; the premaxilla is extremely foreshortened; the P^3-C^1 diastema is shortened. I concur with all but the first character state, which is also expressed in *Be. lesueur* and *Be. penicillata*, albeit not nearly to the same degree as it is in *Aepyprymnus* (Figure 3).

Similarly, *Borungaboodie* also appears to represent a more derived bettongin than *Bettongia*. While the lower molars of the holotype are worn, the posthypocristid clearly dominates the posterior aspect of the lower molar, a possible synapomorphy shared with *Caloprymnus, Aepyprymnus* and *Milliyowi* (Figure 3). Elongation of the molars is also shared between *Borungaboodie, Milliyowi* and *Aepyprymnus*, but this probably represents convergence, due to the absence of this feature from *Caloprymnus* and because molar elongation is primarily due to trigonid elongation in *Milliyowi* and *Aepyprymnus*. *Caloprymnus, Milliyowi* and *Aepyprymnus* are united to the exclusion of *Borungaboodie*, by the presence of a precingulid and a notch between the paracristid and metaconid, both characters considered less likely to be susceptible to convergence than relative molar elongation (Figure 3).

Potential autapomorphies for *Borungaboodie* are a deep ramus along its entire length, a marked anterior insertion area for the middle masseter layer, I_1 robust and upturned, an M_1 protolophid that is markedly narrower than the hypolophid and an M_4 hypolophid that is not as narrow relative to the protolophid as it is in the remaining bettongins (Figure 3). The large size of *Borungaboodie* also distinguishes it from other known bettongins.

Only with the discovery of a greater diversity of early potoroines and more complete material of known species is a relatively comprehensive understanding of potoroine phylogeny likely to emerge. Until that time, the balance of evidence suggests that *Borungaboodie* split from the main potoroine line after *Bettongia*, but before *Caloprymnus*, *Milliyowi* and *Aepyprymnus* (Figure 3).

Functional Morphology of *Borungaboodie hatcheri* gen. et sp. nov.

Deductions on the adaptations of any extinct animal are based on numerous assumptions, including a heavy reliance on uniformitarian principles. Even more limited is that which can be inferred about the natural history of a taxon represented by one fragmentary dentary bearing worn teeth. Fortunately, the phylogenetic affinities of *Borungaboodie hatcheri* appear to lie close to the two living genera of bettongs and, although around 30% larger, the dentition is not markedly different from them. Its bunodont molars are most similar to those of species of *Bettongia* and appear to have been primarily capable of crushing and to a lesser degree grinding. Their morphology suggests a diet that is neither abrasive nor in need of poly-shearing (Sanson 1989). By comparison, the Rufous Bettong, *Aepyprymnus rufescens*, has notably higher-crowned molars with better-developed lophs, and is known to consume a significant proportion of herbs, grass shoots, succulent roots and tubers (Dennis and Johnson 1995), as well as the typical potoroine dietary staple of truffles when abundant. However, there is no shortage of anecdotal evidence attesting to its omnivorous habits (e.g. oophagy, Archer 1984; bone chewing, Dennis and Johnson 1995).

Given the marked similarity in form, the premolar of *B. hatcheri* almost certainly functioned in a very similar manner to that of modern bettongs. However, deepening of the crown anteriorly may correlate to a more resistant diet. This feature is also seen in the robust-jawed *Wakiewakie lawsoni* and the Brush-tailed Bettong, *Be. penicillata*. In a series of behavioural comparisons (Prideaux 1990), I observed that the latter species used its premolars to break open hard nuts (walnuts, brazil nuts, hazelnuts) much more frequently than the Eastern Bettong, *Be. gaimardi*, or *A. rufescens*, which generally avoided biting resistant food items with their premolars.

More convincing evidence that *B. hatcheri* consumed a quite different diet to the modern bettongs may be provided by the upturned and robust nature of the lower incisor. Despite the amount of wear sustained, the occlusal surface is clearly short and oriented at a much less acute angle relative to the longitudinal axis of the tooth compared with other potoroines. This could indicate a relatively shorter upper incisor arcade, possibly implying that a large surface area for apprehension of food items was not important. Theoretically, a reduced contact area between the upper and lower incisors should permit a greater transmission of bite force to the food being grasped.

Not only is the ramus around 30% larger in *B. hatcheri* than the modern bettongs, it is also considerably more robust and consistently deep along its entire length. The fragment that remains of the anterior root of the ascending ramus suggests that this was quite vertical. Anteroventral to the masseteric fossa, the large and rugose insertion area for the vertically-oriented middle masseter muscle layer indicates that this must have been well-developed. The wide masseteric foramen and deep masseteric canal that extends to beneath P_3, immediately posterior to the incisor root, point to a similarly well-developed deep masseter. This muscle layer is important for moderating the precise occlusion of the premolar blade in opposition to the pterygoid muscles (Sanson 1989). Relative to its size, these characteristics reflect an ability to generate greater masticatory power than any other potoroine, with the possible exception of *Wakiewakie lawsoni*.

Because *Borungaboodie hatcheri* is known only from southwestern Australia, it was initially tempting to consider it a possible ecological vicar of the gigantic Quaternary rat-kangaroos (species of *Propleopus* Longman, 1924), which are unknown to the west of the mid-north of South Australia (Williams 1980). The likely diet of these macropodoids has been the matter of strong debate for some time, the most recent propositions in complete opposition to one another. Ride *et al.* (1997) suggested that *Propleopus oscillans* (De Vis, 1888) may have been a pursuit carnivore, while Wroe (1997: 453) considered the same species to have been "... largely if not wholly herbivorous". In any case, *Propleopus* and *Borungaboodie* have little in common besides the fact that they are larger than most bunolophodont macropodoids. *Propleopus oscillans* is around twice the size of *B. hatcheri*, has a comparatively more slender dentary, very procumbent lower incisor, massive plagiaulacoid premolar and molars that would have provided a considerably greater shearing capacity. Whatever *Propleopus* ate, the numerous differences in craniodental morphology suggest that its diet was quite different from that of *Borungaboodie*.

While *B. hatcheri* is estimated to have weighed up to 10 kg, very little of its known morphology suggests that it was adapted to a carnivorous diet. Like many modern bettongs, *B. hatcheri* was probably opportunistic, scavenging meat or killing small vertebrates when the opportunity presented, but it seems better adapted to a quite resistant herbivorous diet. Perhaps nuts or stony fruits formed a significant portion of the diet. Once the husk or toughest part of the fruit had been cracked open the soft inner contents could have been easily crushed by the bunodont molars.

Biogeographic Implications for Southwestern Australia

From an evolutionary biogeographic perspective, the discovery of *Borungaboodie hatcheri* is both fascinating and important. While southwestern Australia is noted for its extraordinarily high floral endemism and diversity (Hopper 1979), its vertebrates do not follow suit. Besides the Honey Possum, *Tarsipes rostratus* Gervais and Verreaux, 1842, and Quokka, *Setonix brachyurus* (Quoy and Gaimard, 1830), no extant southwestern mammals are endemic above the species level. *Borungaboodie* is the first extinct endemic genus to be described, although *'Zaglossus' hacketti* Glauert, 1914 is so distinct in morphology and size from other large echidnas, that it probably represents an unnamed genus (Murray 1984). The numerous species endemic to the southwest Quaternary are most likely to reflect biogeographic patterns developed during the last few million years (Archer 1996). Unfortunately, there is no direct evidence of southwest faunal history because not one pre-Quaternary vertebrate assemblage is known from the area.

Like much of the continent, vegetative responses to increased climatic aridity were well underway in the southwest of Australia by the Pliocene. A pollen assemblage from Lake Tay, in central southern Western Australia, described from sediments considered to be early Pliocene in age by Bint (1981), but late Miocene by Macphail (1997), is generally suggestive of sclerophyll forest or woodland with a lake edge or marsh component. Very rare *Nothofagus* and podocarpaceous pollen are most likely to have blown in from wet forest refugia in ranges adjacent to the Lake Tay region, or been reworked from an older, underlying sedimentary layer. Hopper's (1992) model of Pleistocene Rainfall Zones provided the basis for Archer's (1996) hypothesis which suggested that the extreme paucity of pre-Quaternary relictual taxa in the southwest may have been a direct result of climatic oscillations during the Pleistocene. The superimposition of glacial maxima upon the general trend toward increasing aridity would have induced the complete loss of the High Rainfall Zone and its associated vegetation from southwestern Australia during these times. Any taxa not able to survive in small wet forest refugia would have either adapted to the lower rainfall Transitional Rainfall Zone or become extinct. When wetter forest returned in the Holocene the remainder of the Tertiary forest dwellers were gone and the forest was colonized by inhabitants of the Transitional Rainfall Zone (Archer 1996). Colonization of the area by invading mammals from eastern Australia is likely to have been moderated by the toxicity of many potential food plants in Western Australia, the consumption of which can require specialized metabolic adaptations (e.g., King *et al.* 1978).

Initially, I had considered it a possibility that *Borungaboodie hatcheri* may represent a relict of wet Tertiary forest in the southwest, given its generally plesiomorphic nature and the likely origin of the bettong genera prior to the medial Miocene. However, the apparent adaptation of *B. hatcheri* to the consumption of more resistant food items suggests that it too had originated in or become adapted to a sclerophyll-dominated region. Unlike the macropodine *Setonix brachyurus*, which is unlikely to have arisen prior to the late Miocene (Flannery 1989), there is a distinct possibility that the ancestral stock which gave rise to *B. hatcheri* inhabited the putative wet southwest forests of the medial Miocene. Among the remaining southwest endemic mammals, only *Tarsipes rostratus* and *'Zaglossus' hacketti* seem likely to have had a similar heritage.

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