

Bettongia moyesi, A NEW AND PLESIOMORPHIC KANGAROO (MARSUPIALIA: POTOROIDAE) FROM MIOCENE SEDIMENTS OF NORTHWESTERN QUEENSLAND

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Bettongia moyesi is a plesiomorphic species from Miocene sediments on Riversleigh Station, northwestern Queensland. It shares a number of features (e.g., parietal-alisphenoid contact, large orbital wing of the maxilla, I²⁻³ morphology and premaxilla proportions) with *Bettongia lesueur*. These features are presumed, however, to be plesiomorphic within *Bettongia*. The presence of a species of *Bettongia* in Miocene sediments is suggestive that the bettongin radiation is an old one.

Synapomorphic features suggest that the genus *Bettongia* is a monophyletic group. *Caloprymnus campestris* and *Aepyprymnus rufescens* appear to be close relatives and together represent the sister group of *Bettongia*.

Key Words: *Bettongia moyesi*; Potoroidae; Potoroinae; Miocene; Evolution.

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INTRODUCTION

THE PHYLOGENETIC relationships and fossil record of the species of *Bettongia* have remained little studied. Indeed the few systematic works that have been published have been devoted almost solely to elucidating the taxonomy of the living species. Finlayson (1958) includes a taxonomic revision of the arid zone species of *Bettongia* (*B. lesueur* and *B. penicillata*) and a discussion of the status of the subspecies of these forms. Wakefield (1967) is a further partial taxonomic revision of the genus *Bettongia* which includes the description of a new species, *B. tropica*, known only from eastern Queensland. Wakefield also notes that Finlayson's (1957) *Bettongia penicillata anhydra* belongs within *Bettongia lesueur*. Sharman *et al.* (1980) examined the chromosomes of examples of *B. penicillata* and *B. tropica* and suggest that, because of the great similarity of karyotypes in these forms, the status of *B. tropica* needs re-assessment.

Bensley (1903) includes a brief discussion of the relationships of the species of *Bettongia* to each other. He suggests that, based primarily on premolar morphology, *B. penicillata* is the most plesiomorphic member of the genus and that it lays outside a group containing the other species. Tate (1948), in an even briefer note, suggests that *B. cuniculus* (here *B. gaimardi*) is the most primitive member of the genus because of its small bullae and premolars.

Stirton, Tedford and Woodburne (1968) record the presence of a new species of *Bettongia* (based on a dentary) from the Middle Miocene

Ngapakaldi Local Fauna of northern South Australia. This specimen, however, was named *Purtia mosaicus* by Case (1984). Case suggests that it may be ancestral both to the species of *Bettongia* and to *Wakiewakie lawsoni*, a potoroid from the Miocene Kutjumarpu Local Fauna. The relationships of *Purtia mosaicus* will be discussed elsewhere (Flannery in prep.). It will suffice to say here, however, that it does not appear to be a close relative of the species of *Bettongia*.

Other species of middle Miocene Riversleigh macropodoids have been described by Flannery, Archer and Plane (1983), Flannery, Archer and Plane (1984), Archer and Flannery (1986) and Flannery and Archer (1987).

Dental terminology and homology follows Archer (1976, 1978). QM F is the prefix for Queensland Museum Fossil specimens.

SYSTEMATICS

Macropodoidea (Gray, 1821)

Potoroidae Gray, 1821

Potoroinae (Gray, 1821)

Bettongini new tribe

Diagnosis of Bettongini: Bettongins can be differentiated from other potoroids in possessing the following features. The I₁ lacks a dorsal enamel flange, the digital pads of the pes are fused into a single unit, and only a small portion of the anteroventral end of the periotic can be seen on the basicranium. Taxa included within the Bettongini are the species of *Bettongia*, *Caloprymnus* and *Aepyprymnus*.

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Bettongia Gray, 1837
Bettongia moyesi n. sp.
 (Figs 1-5; Table 1)

Holotype: QM F13026, a nearly complete skull and associated dentaries, discovered by John Courtenay at the Two Trees site in May, 1984. The skull lacks only the basicranial region, the rear face of the cranium and the posterior portion of the right zygomatic arch. The left dentary is lacking its ventral margin. The right dentary is eroded away posterior to M_4 and is also missing its ventral margin. The dentaries were found articulated with the skull.

Table. 1. Dental measurements for *Bettongia moyesi* QM F 13007.

QM F13007	referred specimen	P_3 length = 8.4
		P_3 maximum width 3.5.

Referred specimen: QM F13007 (AR 6666) left dentary fragment containing P_3 , trigonid of M_2 , from Henk's Hollow, Riversleigh.

Type Locality and Age: The Two Trees Site is isolated on the southwestern edge of Ray's Amphitheatre. It is characterised by what appears to be a massive degraded flowstone with a thick layer of recrystallised calcite underlying the detrital carbonate which contains the bones. All of the limestones of this amphitheatre are thought to be approximately middle Miocene in age because they contain some species which are most similar to others known from the middle Miocene Kutjamarpu Local Fauna of central Australia. These limestones appear to be stratigraphically higher than the exposures of the middle Miocene Carl Creek Limestone along the Riversleigh-Lawn Hill Road (Tedford's Locality D) and may not be part of that Formation. The biostratigraphy of this region is presently under study (Archer *et al.* in prep.).

Diagnosis: *Bettongia moyesi* can be distinguished from all other species of *Bettongia* by possessing the following features; a broad parietal-alisphenoid contact (seen otherwise occasionally in *B. lesueur*); an I_2 ; a single large buccal root on M^{2-3} and a very short lachrymal contribution to the face.

It can be further distinguished from *B. gaimardi* and *B. penicillata* in possessing the following features: a relatively short premaxilla; a small I^3 ; a large orbital wing of the maxilla; and a markedly arcuate nasal-frontal suture.

It further differs from *B. lesueur* in possessing more elongate nasals, and lachrymals that are positioned close to the dorsal surface of the skull.

Etymology: It gives us much pleasure to name this magnificently preserved species in honour of Mr Allan Moyes, Chairman of IBM Australia. When faced in 1984 with the unexpected but welcome crisis of having to transport five more tonnes of Riversleigh limestone south to Sydney than we had expected, IBM very kindly agreed to

meet the extra cost as part of their determination to support things of importance to Australia.

Description: The holotype skull is complete except for the basicranium posterior to the pterygoids, the auditory regions and the rear face of the cranium, which were removed by erosion prior to discovery. The posterior portion of the right zygomatic arch is also missing.

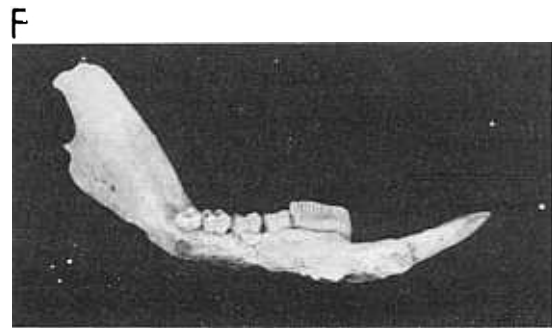
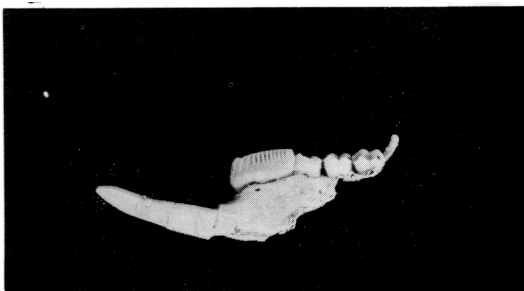
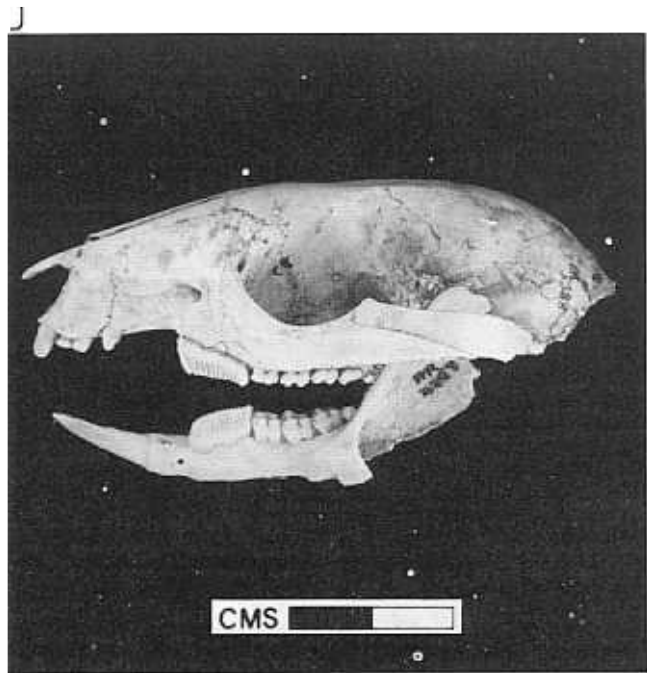
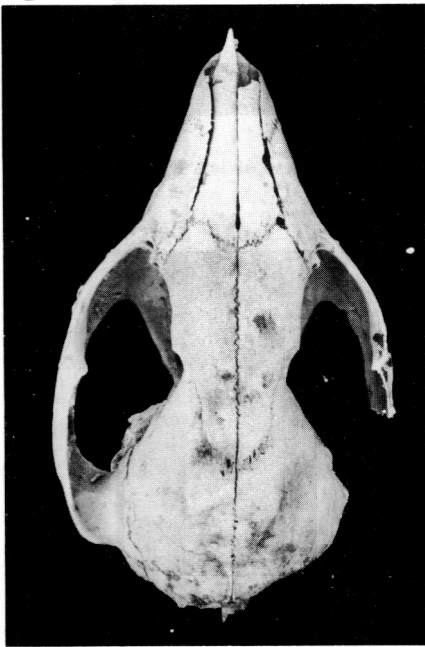
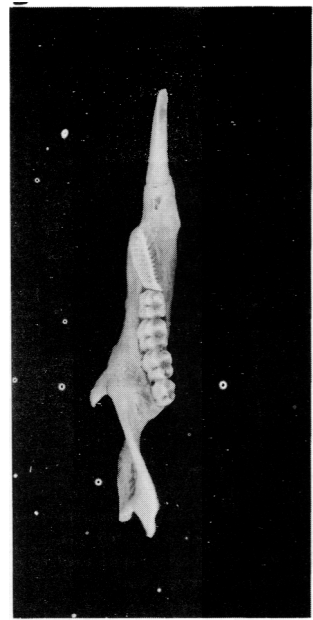
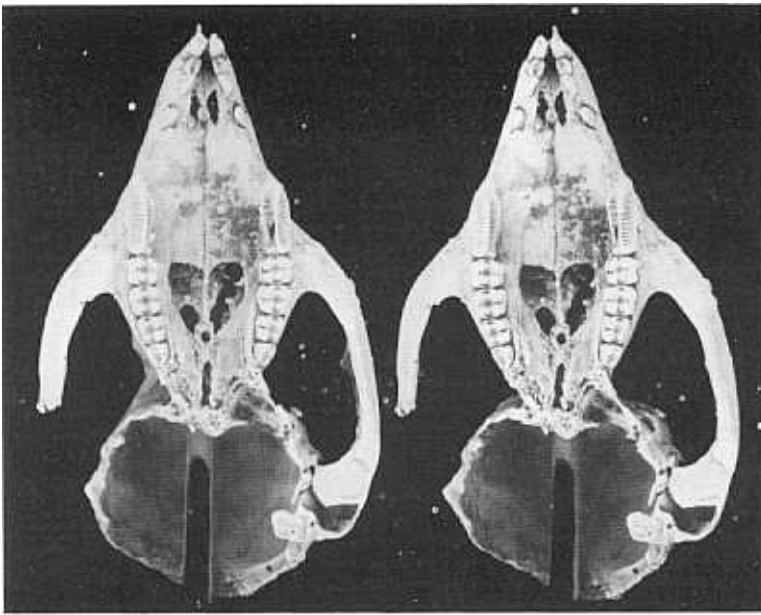
The nasals are elongate and narrow gently towards their tip. The tip extends well beyond (7 mm) the nasal-premaxilla contact. The frontal-nasal contact is arcuate in shape. The premaxilla is short relative to that seen in most other bettong species. The ventral two-thirds of the maxillary/premaxillary suture is near-vertically oriented. The dorsal one-third slopes more gently posteriorly. The jugal extends high onto the face and terminates anterodorsal to the main lachrymal foramen. The lachrymal contributes only a small sliver to the face. The lachrymal tubercle is small when compared to that seen in other bettongins. The anterior palatal foramina are short and broad, being situated between I^3 and C^1 . The posterior palatal foramina extend posteriorly from M^2 . The maxilla has a large orbital wing that extends dorsally to the level of the principal lachrymal foramen. The points of insertion for the temporal muscles are well-defined and lightly pitted. The glenoid cavity is flat and oval in shape. The postglenoid process has been lost through erosion. However, the small ridge remaining suggests that it was probably a substantial structure. There is a distinct parietal alisphenoid contact approximately 4 mm broad.

The dentary lacks the entire ventral edge and the extent of the masseteric canal cannot be determined due to abrasion. However, the masseteric foramen is buccally expansive and it appears that the canal would have also been expansive. The coronoid process ascends at a gentle angle, as in *Bettongia gaimardi*, and what remains of the glenoid process is the same shape as in other *Bettongia* species. The dental foramen opens anterior to P_3 . The P_3-I_1 diastema is short.

Of the upper incisors, I^1 is elongate and was possibly ever-growing. It extends well ventral to the crowns of I^{2-3} and is truncated by a distinct horizontal wear facet. The I^2 is smaller than I^1 and has a subovate, basined crown. The I^3 is subequal in size with I^2 and its crown forms a long, posteriorly-sloping crest. A slight buccal groove is present near the anterior edge of the tooth, this groove giving I^3 a macropodine-like appearance.

The upper canine is situated on the maxillary-premaxillary suture. The root is robust but the crown is relatively small. The crown has a typical caniniform structure. There is a small (2 mm) C^1-I^3 diastema.

The P^3 is elongate and extremely similar in shape to that of *Bettongia lesueur*. Eleven buccal and lingual ridgelets are present, as well as a



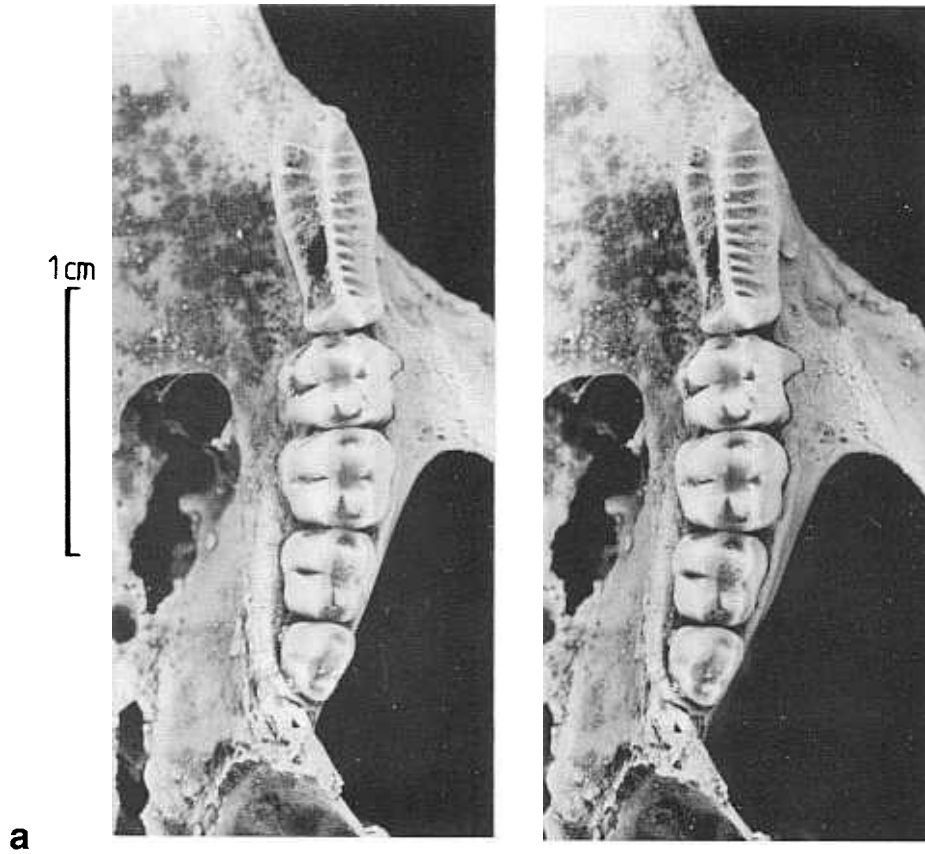
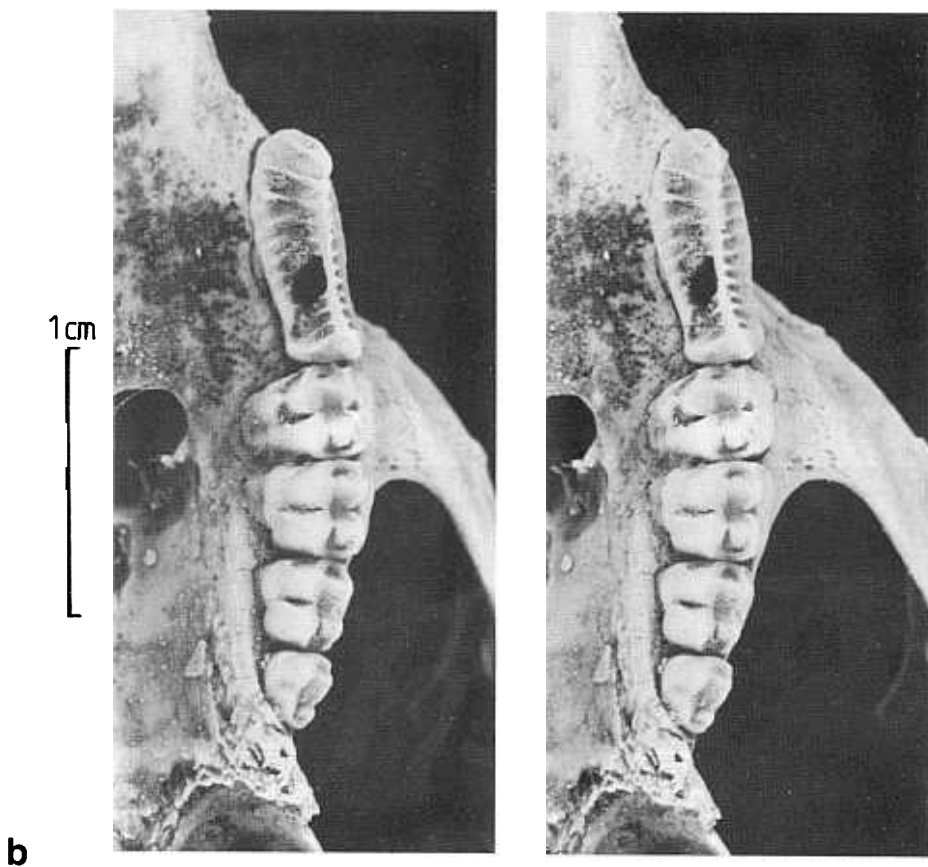
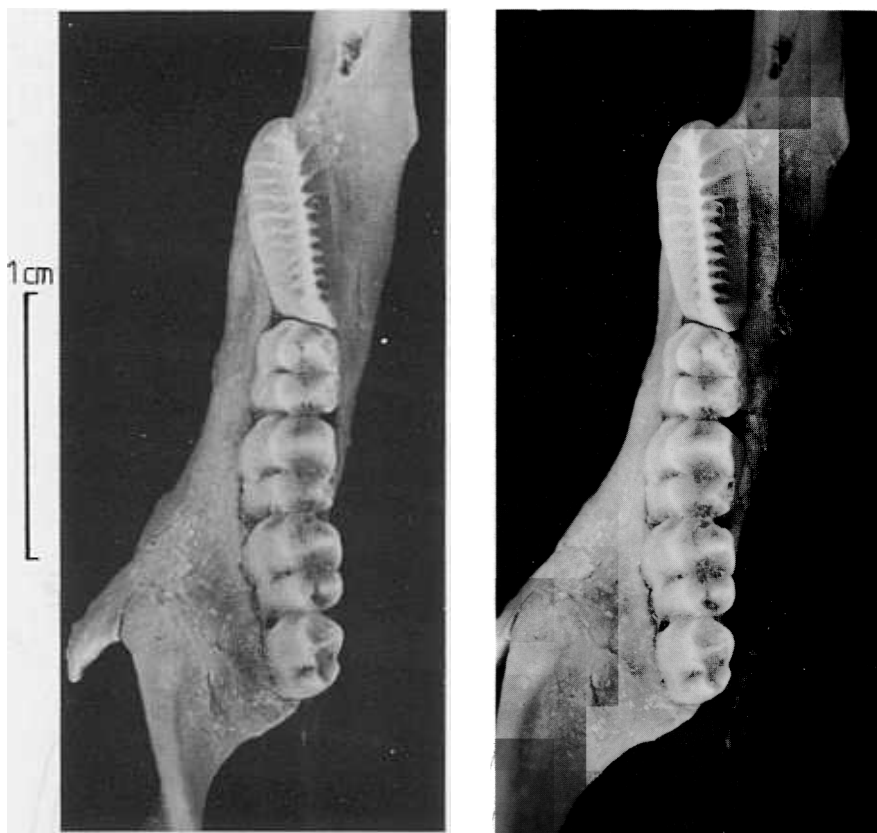


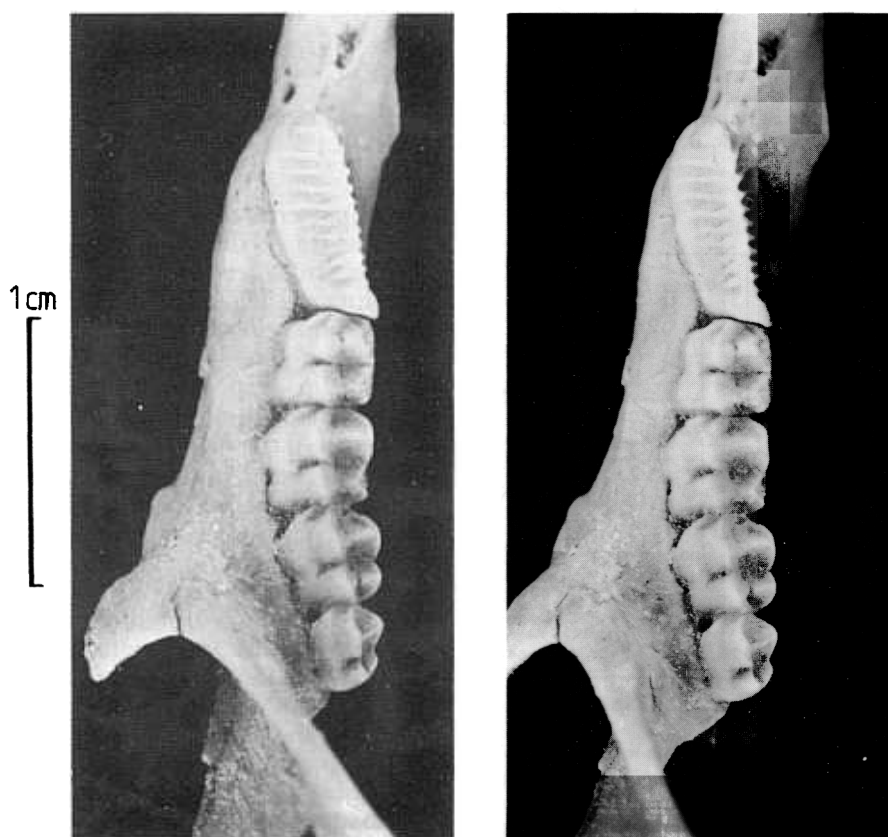
Fig. 2. *Bettongia moyesi*, holotype. A, stereophotographs of occlusal view of left P³-M⁵. B, stereophotographs of lingual oblique occlusal view of left P³-M⁵.





a

Fig. 3. Bettongia moyesi, holotype. A, stereophotographs of left dentary in occlusal view showing alveolus for I_2 (top) and P_3 - M_5 . B, stereophotographs of same left dentary in oblique buccal occlusal view.



b

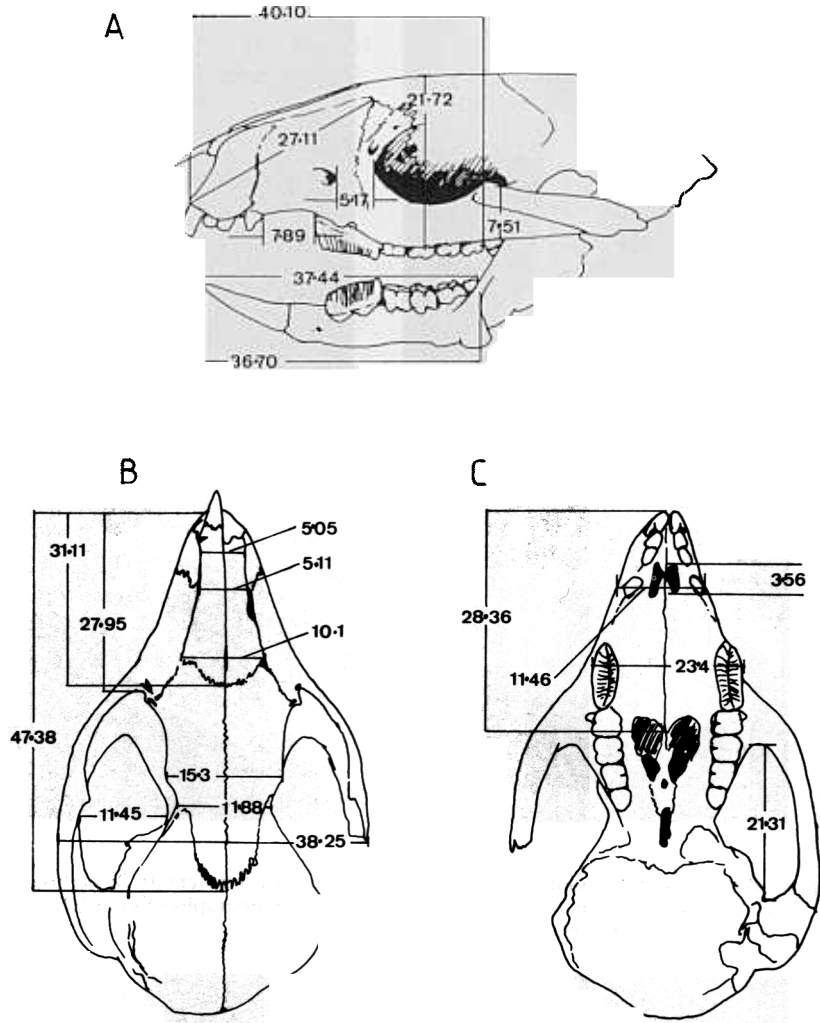


Fig. 4. Measurements (in mm) of skull and left dentary of holotype of *Bettongia moyesi*. A, lateral view. B, dorsal view. C, occlusal view.

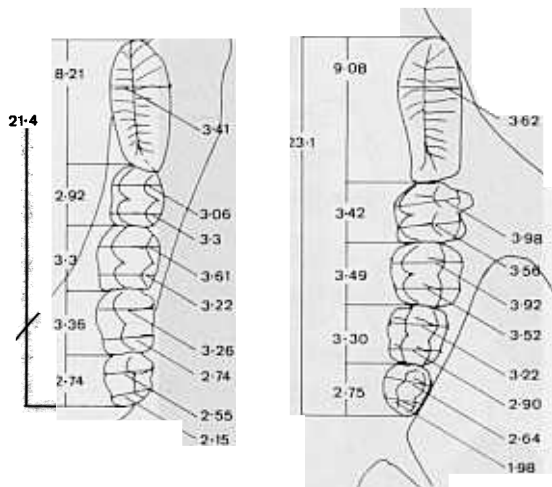


Fig. 5. Measurements (in mm) of LP₃-M₅ (on left) and LP₃-M₅ (on right) of the holotype of *Bettongia moyesi*. Tooth lengths are maximum anteroposterior crown lengths; tooth widths are maximum anterior and posterior transverse crown widths.

small posterobuccal cusp. This cusp is only half the height of the main crest and is fused to it for its entire length. Although there is a slight swelling of the base of the crown at the posterolingual margin of the tooth, there is no lingual cingulum. The occlusal crest is very slightly arcuate in shape, being concave buccally. The occlusal crest is approximately parallel with the long axis of the molar row.

The crown of M² is squat and bulbous, both the lingual and buccal tooth surfaces sloping gently from the narrow crown apex to the broader crown base. A slight cingulum is present anterolingual to the protocone. The lophs are poorly developed, the hypoloph being interrupted by a broad, shallow cleft. A very slight parastyle is present which is connected to a broad, well-developed preprotocrista. A single stylar cusp is present just buccal to the buccal end of the interloph valley. A slight swelling of the hypoloph suggests the presence of a metaconule. The posterior cingulum is broad and well developed. There is a single broad lingual and two buccal roots.

The M^3 differs from the M^2 in the following ways. The parastyle and styler cusp are reduced. The bulge in the hypoloph is also less obvious. The lingual root is restricted to the anterior portion of the crown while the posterobuccal root has shifted lingually and is just visible under the posterolingual portion of the crown.

The M^4 differs from M^3 in the following ways. It is smaller. The small cingulum developed anterolingual to the protocone is better developed. The styler cusp is absent. The fissure in the hypoloph is more prominent and a slight pit is developed buccal to the hypocone. The hypoloph is also much narrower than the protoloph and the posterobuccal root is shifted even further lingually, being positioned purely under the posterior half of the crown.

The M^5 differs from M^4 in the following ways. It is much smaller and the anterolingual cingulum on the protocone is absent. The hypoloph is extremely reduced and does not contact the apex of the metacone. The roots are not visible.

The I_1 is similar in morphology to that of other species of *Bettongia*. It is procumbent and the crown is elongate. There is no dorsal enamel crest.

There is an alveolus for a very small I_2 positioned just posterior to the I_1 alveolus. Its morphology is similar to that seen in *Hypsiprymnodon moschatus*.

The P_3 is similar in morphology to that of *Bettongia lesueur*. It is ornamented with eleven buccal and lingual ridgelets. The occlusal crest of P_3 is parallel with the long axis of the molar row. The P_3 crown is broadest anteriorly and narrows gently posteriorly. There is a slight lingual flexion of the occlusal crest at its posterior end.

On M_2 , the hypolophid is slightly wider than the protolophid. The lophids are poorly developed, particularly the protolophid which is interrupted in its central portion by a deep fissure. The paracristid joins a weak premetacristid, forming a poorly-developed anterior cingulum. A slight cingulum is present anterobuccal to the protoconid. The posterior cingulum is poorly developed.

The M_3 differs from M_2 in the following ways. The protolophid is broader than the hypolophid. The protolophid is much better developed and is not interrupted by a fissure. The cingulum positioned anterobuccal to the protoconid is better developed.

The M_4 differs from M_3 in the following ways. It is smaller and the hypolophid is interrupted by a fissure in its central portion.

The M_5 differs from M_4 in being smaller and in lacking a distinct hypolophid (even though the talonid is well developed).

DISCUSSION

The relationships of the three genera of bettongins (*Bettongia*, *Aepyprymnus* and *Caloprymnus*) have not previously been investigated in detail. As a result of this study it has become clear that two monophyletic groups exist, one containing the species of *Bettongia* and the other the species of *Aepyprymnus* and *Caloprymnus*. Surprisingly, evidence in support of the monophyly of the genus *Bettongia* is not as strong as that supporting the monophyly of *Aepyprymnus* and *Caloprymnus* species.

Evidence for the monophyly of the genus *Bettongia* comes from analysis of cranial features. The most striking evidence is the form of the jugal. In all of the species of *Bettongia* the jugal reaches high onto the face, and terminates at a level equal to or dorsal to the large lachrymal foramen. In the species of *Hypsiprymnodon*, *Aepyprymnus*, *Caloprymnus* and *Potorous* the jugal terminates ventral to the facial exposure of the lachrymal, as it does in plesiomorphic macropodids such as the species of *Dorcopsis*.

A second synapomorphy may be that all *Bettongia* species exhibit inflated hypotympanic sinuses. However, this feature is also present in *Caloprymnus campestris*, where it may have been independently derived.

Within *Bettongia*, there is a clearly monophyletic clade containing *B. penicillata*, *B. tropica* and *B. gaimardi*. Apparent synapomorphies for this clade include the presence of a crest on the tail, elongated I^3 's, and highly elongated premaxillae.

The monophyly of *Aepyprymnus rufescens* and *Caloprymnus campestris* is suggested by the presence in these taxa of the following synapomorphies. First, the posthypocristae/ids are very well developed and diagonally cross the rear face of the hypolophs/ids. This feature is better developed on the posterior molars of *C. campestris* than the anterior ones. Second, the occlusal crest of I^3 in both *A. rufescens* and *C. campestris* is rotated medially, more so in the former than the latter. In all other potoroids the occlusal crest of I^3 is parallel with that of I^2 . Third, the premaxillae of both *A. rufescens* and *C. campestris* are both extremely foreshortened relative to all other potoroids, and the I^3 - P^3 diastema is also shorter in these taxa than in any other potoroids except *Bettongia lesueur*. The presence of a short I^3 - P^3 diastema in *B. lesueur* is probably a convergent development.

Bettongia moyesi is here placed within the genus *Bettongia* for the following reasons. First, it possesses a jugal that extends high onto the face

anterior to the orbit. The species of *Bettongia* are unique among near relatives in possessing this feature. Second, *Bettongia moyesi* is phenetically extremely similar to the living species of *Bettongia*, particularly *B. lesueur*. It possesses no synapomorphies shared with other potoroids (e.g., *Potorous* spp. or *A. rufescens*) and thus there is no suggestion that it could belong to any other group. Further, its derived I_1 morphology (seen only in other *Bettongia*, *Caloprymnus* and *Aepyprymnus* species) precludes any relationship with *Hypsiprymnodon* or *Potorous* species, both of which possess less derived I_1 's.

Bettongia moyesi shares a large number of features with *B. lesueur* that are not seen in other species of *Bettongia*. These include presence of a parietal-alisphenoid contact (variable in *B. lesueur*), a large orbital wing of the maxilla, an infraorbital foramen that opens above the anterior part of P^3 , an I^3 which is relatively short and squat, a short and subovate I^2 , and a relatively short premaxilla. However, *B. moyesi* differs from *B. lesueur* (but is similar to other species of *Bettongia*) in possessing frontals that are domed and that reach high above the level of the lachrymal tubercles. In *B. lesueur*, this portion of the cranium is flattened. In addition, *Bettongia moyesi* possesses several features that are unique within the genus. These include the presence of a buccal groove on I^3 , presence of only a single large buccal root under M^{2-3} , a short facial contribution from the lachrymal, and an I_2 .

There can be little doubt that the configuration of the molar roots, the presence of I_2 and the short facial contribution of the lachrymal seen in *B. moyesi* are all plesiomorphic features because they are seen in all plesiomorphic potoroids (hypsiprymnodontines and propleopines where known) as well as plesiomorphic macropodids. The presence of a buccal groove on I^3 in *B. moyesi* may well be autapomorphic because it is otherwise unknown in the family. Many of the features shared between *B. moyesi* and *B. lesueur* are more difficult to interpret. If these features are shared derived states, they suggest that *B. moyesi* and *B. lesueur* are close relatives. If, however, they are merely retained primitive similarities, they would only indicate that *B. lesueur* alone among living species retains a number of primitive features.

There can be little doubt that the retention of a parietal-alisphenoid contact in both *B. moyesi* and *B. lesueur* (where it is variable) is a plesiomorphic feature. A parietal-alisphenoid contact is seen in all macropodoids as well as *Hypsiprymnodon bartholomaii*, a plesiomorphic hypsiprymnodontine (Flannery and Archer 1987). The retention of this feature in species of *Bettongia* merely indicates that frontal-squamosal contacts have been independently derived in the species of *Potorous*, the *Aepyprymnus/Caloprymnus* clade

and some *Bettongia* species. This feature can clearly no longer be recognised as a synapomorphy for potoroids.

The large orbital wing of the maxilla seen in *B. moyesi* and *B. lesueur* is more difficult to interpret. Although *Hypsiprymnodon moschatus* has a large orbital wing of the maxilla, the species of *Potorous* do not. *Aepyprymnus rufescens* lacks an orbital wing, while *Caloprymnus campestris* does not. Thus it is not possible at present to make a confident statement about polarity in this character.

The incisor morphology of the species of *Bettongia* is also difficult to evaluate. Although the differences are subtle, the I^2 and I^3 of *B. moyesi* and *B. lesueur* are more similar to those of *Hypsiprymnodon moschatus* than are the I^{2-3} of other *Bettongia* species. They are also similar in morphology to those of plesiomorphic phalangerids. Thus it is possible that similarities in I^{2-3} morphology between *B. moyesi* and *B. lesueur* are retained symplesiomorphies.

The short premaxilla seen in *B. moyesi* and *B. lesueur* is also difficult to interpret. Elongate premaxillae are seen in *Potorous* species and, to a lesser extent, *Hypsiprymnodon moschatus*, *Caloprymnus campestris* and *Aepyprymnus rufescens*, however, possess very short premaxillae. It is possible that this is a derived similarity uniting these forms with *B. moyesi* and *B. lesueur*. We regard it as more likely, however, that elongation of the premaxillae has occurred independently in some *Bettongia* species and in the species of *Potorous*.

Thus, for all of the features shared between *B. moyesi* and *B. lesueur* where it is possible to make a confident interpretation about polarity, the features appear to be plesiomorphic. For this reason, we favour here the hypothesis that *B. lesueur* is a plesiomorphic species of *Bettongia* which, although sharing a large number of features with *B. moyesi*, is not closely related to it.

The occurrence of a species of *Bettongia* in Miocene sediments is of interest in interpreting the timing of the potoroine radiation. Because species of *Potorous* lie outside the clade containing the *Bettongia* species, they must also have differentiated by Miocene times. Because the species of *Aepyprymnus* and *Caloprymnus* also lie outside *Bettongia*, their ancestors as well must have differentiated by then.

CONCLUSIONS

Bettongia moyesi is the most plesiomorphic known member of the genus. *Bettongia lesueur* shares many plesiomorphic similarities with *B. moyesi* and both of these species appear to lie outside a clade containing the other living species of *Bettongia*.

The presence of a species of *Bettongia* in Miocene sediments suggests that differentiation of the *Potorous* and *Aepyprymnus/Caloprymnus* lineages must also have taken place by that time.

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We are also extremely grateful to the various funding bodies that have made this research possible. Archer's work at Riversleigh was supported by the Australian Research Grants Scheme (Grant No. E7915864 and PGE85/16519). Additional aid was provided by the Queensland Museum and anonymous donors.

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The Burketown Shire Council then provided essential support in transporting the rocks from Riversleigh Station to Mount Isa following both the 1984 and 1985 expeditions. To both the Shire and the RAAF, our backs extend sincerest

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