**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, \(^2\)-\(^3\) morphology and pre-maxilla 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 of the bettong radiation is an old one.

Sympomorphic 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.


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 *Puritia mosaicus* by Case (1984). Case suggests that it may be ancestral both to the species of *Bettongia* and to *Wakiewahie lawsoni*, a potoroid from the Miocene Kutjumarpu Local Fauna. The relationships of *Puritia 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 I\(_1\) 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 F 13026, a nearly complete skull and associated dentaries, discovered by John Courtenay at the Two Trees site in May, 1984. The skull lacks only the basicranium 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 M4 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

<table>
<thead>
<tr>
<th>Specimen</th>
<th>P, length</th>
<th>P, maximum width</th>
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<tbody>
<tr>
<td>QM F 13007 referred specimen</td>
<td>8.4</td>
<td>3.5</td>
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Referred specimen: QM F 13007 (AR 6666) left dentary fragment containing P3, trigonid of M2, 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 recrystalised calcite underlyng 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 Kutzamarpu Local Fauna of central Australia. These limestones appear to be stratiographically 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 l2; a single large buccal root on M3; 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 l1; 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 lachyrmas 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 l3 and c1. The posterior palatal foramina extend posteriorly from M2. 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 P3. The P3-I, diastema is short.

Of the upper incisors, l1 is elongate and was possibly ever-growing. It extends well ventral to the crowns of l2 and is truncated by a distinct horizontal wear facet. The l2 is smaller than l1 and has a subovate, basined crown. The l3 is subequal in size with l2 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 l3 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) C1-I3 diastema.

The P3 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 montesi, holotype. A, stereophotographs of occlusal view of left P3-M3.
B, stereophotographs of lingual oblique occlusal view of left P3-M3.
Fig. 3. Bettongia moyesi, holotype. A, stereophotographs of left dentary in occlusal view showing alveolus for I₄ (top) and P₂-M₅. B, stereophotographs of same left dentary in oblique buccal occlusal view.
A 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 postero-lingual 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 $M^2$ 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 anterolingually 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 M³ differs from the M² in the following ways. The paraostyle and stylar 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 M⁴ differs from M³ in the following ways. It is smaller. The small cingulum developed anterolingual to the protocone is better developed. The stylar 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 proto- and the posterobuccal root is shifted even further lingually, being positioned purely under the posterior half of the crown.

The M⁵ differs from M⁴ 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 I₁ 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 I₂ positioned just posterior to the I₁ alveolus. Its morphology is similar to that seen in Hypsiprymnodon moschatus.

The P₁ is similar in morphology to that of Bettongia lesueur. It is procumbent and the crown is elongate. There is no dorsal enamel crest.

There is an alveolus for a very small I₂ positioned just posterior to the I₁ alveolus. Its morphology is similar to that seen in Hypsiprymnodon moschatus.

The P₂ is similar in morphology to that of Bettongia lesueur. It is ornamented with eleven buccal and lingual ridgelets. The occlusal crest of P₂ is parallel with the long axis of the molar row. The P₂ crown is broadest anteriorly and narrows gently posteriorly. There is a slight lingual flexion of the occlusal crest at its posterior end.

On M₂, the hypolophid is slightly wider than the protolophid. The lophs are poorly developed, particularly the protolophid which is interrupted in its central portion by a deep fissure. The paracristid joins a weak para- and protocristid, forming a poorly-developed anterior cingulum. A slight cingulum is present anterobuccal to the protoconid. The posterior cingulum is poorly developed.

The M₃ differs from M₂ 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 M₄ differs from M₃ in the following ways. It is smaller and the hypolophid is interrupted by a fissure in its central portion.

The M₅ differs from M₄ 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 13's, and highly elongated pre-maxillae.

The monophyly of Aepyprymnus rufescens and Caloprymnus campestris is suggested by the presence in these taxa of the following synapomorphies. First, the posthypocrista/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 I³ 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 I³ is parallel with that of I². Third, the pre-maxillae of both A. rufescens and C. campestris are both extremely foreshortened relative to all other potoroids, and the I³-P³ diastema is also shorter in these taxa than in any other potoroids except Bettongia lesueur. The presence of a short I³-P³ 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.
antior to the orbit. The species of Bettongia are unique among near relatives in possessing this feature. Second, Bettongia moyesi is phylogenetically 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 P1 morphology (seen only in other Bettongia, Caloprymnus and Aepyprymnus species) precludes any relationship with Hypsiprymnodon or Potorous species, both of which possess less derived P1’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 P3, an P1 which is relatively short and squat, a short and subovate P1, 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 I3, presence of only a single large buccal root under M1-3, a short facial contribution from the lachrymal, and an I2.

There can be little doubt that the configuration of the molar roots, the presence of I4, 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 P1 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.

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 potorine radiation. Because species of Potorous lie outside the clade containing the bettongs, 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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REFERENCES


