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PHYLOGENETIC RELATIONSHIPS AND A RECONSIDERATION OF HIGHER LEVEL SYSTEMATICS WITHIN THE POTOROIDAE (MARSUPIALIA)

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ABSTRACT—Four synapomorphies are identified suggesting that the potoroids form a monophyletic group. These are: 1) possession of a frontal-squamosal contact; 2) enlargement of the diastatic process leading to the dentary being definitely convex below the middle portion of the molar row; 3) presence of an enlarged massteric canal reaching anteriorly to below P3; and 4) presence of a proximoventral process on the fifth metatarsal. Gumarrdee pascuali and the bulangamayines Wabularoo naughtoni and Bulangamaya delicata are included within the Potoroidea because of their possession of several of these derived states. Similarities between Gumarrdee pascuali and Partia mosaicus Case (1984) suggest that they may be closely related.

INTRODUCTION

The potoroids, colloquially known as rat kangaroos, are a moderately diverse group of omnivorous and herbivorous macropodoids. All living forms are small with an adult body weight of between 500 g and about 3 kg, although some gigantic extinct species are known.

The fossil record of the potoroids was, until recently, meagre. Archer (1979), Archer, Bartholomai and Marshall (1979), Flannery, Archer and Plane (1982), Case (1984) and Woodburne (1984) have now considerably increased knowledge of the early history of the group.

Partly because of the previously poor fossil record, phylogenetic hypotheses involving potoroids have been based almost solely on comparative studies of living species. Two basic alternative interpretations of phylogenetic relationships of potoroids have been developed. Bensley (1903) suggested a diphyletic origin for potoroids and that the potoroids gave rise to the macropodids (the only other family in the Macropodoidea). Others, such as Pearson (1950) and Johnson and Strahan (1982), however, have argued that the potoroids and macropodids represent two distinct monophyletic lineages descended from a common ancestor. This latter view has prevailed among more recent workers. Case (1984) presents a history of phylogenetic studies involving potoroids.

METHODS

The following interpretation of relationships is based on a cladistic analysis (a methodology discussed, for example by Wiley, 1981). Selection of an outgroup is crucial in such a study. Here, the macropodids are used as the immediate outgroup and the phalangerids as the outgroup to the Macropodoidea. Studies supporting the hypothesis that these taxa are closely related include that of Kirsch (1977), based on immunology, and a study of the macropodoids of the Namba Formation (Flannery and Rich, in preparation).

Dental homology follows Archer (1978). Archer noted that true postcanine tooth replacement does not occur in marsupials. He also demonstrated on the basis of ontogeny and morphology that P1–3 belong to one tooth series and M1 (DP3 or DP4 in older terminologies) and M2–5 (M1–4 in older terminologies) to another. The older terminology (e.g., that used by Case, 1984 and Woodburne, 1984) suggests that the deciduous molariform tooth is a premolar (DP3) despite the fact that it is part of the molar series. This distinction may affect interpretation of the polarity of character states in this tooth. Dental terminology follows Archer (1976). QM
SYSTEMATICS

Monophyly of the potoroids.—Previous studies (Pearson, 1950; Johnson and Strahan, 1982) have suggested that the potoroids represent a monophyletic group. This suggestion is supported in this study by the identification of the following synapomorphic character states.

1) In potoroids a frontal-squamosal contact is present on the side of the braincase. In macropodids and phalangerids the parietal and alisphenoid bones contact (Figure 1).

2) Due to enlargement of the digastric process, the dentary is convex below the middle portion of the molar row (Figure 2). This condition is absent in phalangerids and macropodids. It is not universal among potoroids, however, being absent in the species of Potorius and Propleopus and reversion to the primitive condition is presumed to have occurred in these taxa.

3) The masseteric canal is extensive, being confluent with the dental canal and extending to below P₃. The masseteric canal is not found in phalangerids and is always less extensive in macropodids, extending at most only to the anterior part of the molar row.

4) A proximoventral process is found on the fifth metatarsal of all potoroids (Figure 3). Thus far it is only known to occur elsewhere among the species of Proteusodon, all of which have unusually specialized short feet (Plane, 1967). Its presence in the species of this genus may be due to convergence. This structure is not seen in phalangerids and is thus tentatively accepted here as a synapomorphic condition for potoroids. However, further studies elucidating the construction of the pes in primitive macropodids, such as balbarines, could shed more light on the polarity of this state. It is possible (but not evident) that it is primitive to all macropodoids.

5) In addition to these states, Flannery and Rich (in preparation) indicate that the con-
struction of the trigonid of M2 in potoroids represents a synapomorphic condition for the group.

The following features have been suggested elsewhere to represent synapomorphies for the potoroids but have been brought into question by further studies or are synapomorphies uniting only a particular group of potoroids.

1) With the exception of *Hypsiprymnodon moschatus*, living potoroids possess a large, highly specialized sacciform forestomach whose function is largely unknown (Langer, 1980; Hume, 1982). In macropodids the forestomach is usually small, but a large, specialized tubiform midstomach is present which harbors microbes. Phalangerids and *H. moschatus* possess simple stomachs that lack either of these specializations. As *H. moschatus* is a potoroid (possessing potoroid synapomorphies), it follows that both potoroid and macropodid lineages have independently developed complex, specialized stomachs. Thus possession of a large sacciform forestomach is a synapomorphic condition linking all living potoroids except *H. moschatus*.

2) Enamel of the I1 of the species of *Caloprymnus, Bettongia, Aepyprymnus, Propleopus, Puritia* and *Wakieacakie* is restricted to the ventrolingual portion of the tooth. However, enamel may form a dorsal crest on the unworn tip of the I1 in these forms. The distribution of this feature is misunderstood in Case (1984) where it is reported as being present in all potoroids. In fact, a dorsal enamel crest is present in the species of *Hypsiprymnodon, Potorous* and primitive undescribed bulungamayines from the Kutjumaru local fauna (see below, and Figure 4). This suggests that the condition in which the enamel is restricted to the ventrolingual region of I1 is a synapomorphic state linking only a particular group of potoroids (i.e., all species except *Hypsiprymnodon moschatus* and the species of *Potorous*). It is also likely that restriction of enamel of I1 to the ventrolingual area is due to convergence in bulungamayines and also possibly the species of *Propleopus*.

3) Certain features of the reproductive tract were considered by Pearson (1950) to be highly derived and unique to potoroids. Case (1984) suggests that these states represent synapomorphic conditions for the potoroines (porioroids hence). However, it has been shown that many of these states are also present in *Lagostrophus fasciatus* (Tyndale-Biscoe, 1964). Indeed, Tyndale-Biscoe suggested that the female reproductive systems of potoroids more closely resemble those of phalangerids (the sister group of macropodids) than that of macropodids (Tyndale-Biscoe, 1964, p. 295). Clearly, in light of the apparent similarities of the potoroid female reproductive system to that of the outgroup, and the presence of supposedly derived potoroid states in macropodids, a closer examination of these features is necessary before they can be accepted unequivocally as synapomorphies for the potoroids.

**Relationships of the bulungamayines.**—Flannery, Archer and Plane (1982) proposed the name Bulungamayinae for a small, poorly
represented group of potoroids from middle Miocene sediments in northern Australia. Only two species, *Wabularoo naughtoni* and *Bulungamaya delicata*, have thus far been named. Recently, Case (1984) and Woodburne (1984) have suggested that these taxa represent macropodines (macropodids here) rather than potoroines (potoroids here) but cite no specific evidence for this interpretation. As a result of their having raised this doubt regarding their affinity, the relationships of the group are re-examined. In so doing additional morphological information, based on new material, is presented.

Flannery, Archer and Plane (1982) listed four states that they considered to be synapomorphic for bulungamayines and other potoroids: 1) The ventral margin of the dentary is convex below the middle portion of the molar row; 2) the masseteric canal is buccally expanded and extensive (although its full anterior extent could not then be ascertained); 3) the premolar is elongate and finely serrate; and 4) the I₁ lacks a dorsal enamel crest. As noted above, the first two of these states are believed to represent synapomorphic conditions for all potoroids. New evidence, however, has been uncovered regarding the masseteric canal in bulungamayines. Flannery, Archer and Plane (1982) noted that the opening of the masseteric canal in bulungamayines is large and buccally expanded. While it was clear from this and remnants of the canal in *B. delicata* that the masseteric canal extended far anteriorly, the limit of its extent could not then be determined. Since that time, additional material of *Wabularoo naughtoni* has been recovered from Riversleigh that shows that the masseteric and dental canals are confluent and that they extend to below P₃ (Figure 5). Thus, this synapomorphic condition, seen in all other potoroids, is present in bulungamayines.

Case (1984) notes the presence of a marked convexity of the ventral margin of the dentary in the species of *Bettongia*, *Caloprymnus*, *Aepyprymnus* and *Wakilewakie* but does not mention its presence in *Hypsiprymnodon moschatus* or bulungamayines. Because of this he does not consider this feature to be synapomorphic for all potoroids, but only for the four genera listed by him. Figure 2 illustrates this state in *Wabularoo naughtoni* and *Aepyprymnus rufescens*.

The presence of an elongate, finely ridged P₃ was considered by Flannery, Archer and Plane (1982) to be a synapomorphic state for all potoroids except *Hypsiprymnodon moschatus* and the species of *Propleopus*, where the primitive condition of having an antero-posteriorly short P₃ occurs. Also, *Caloprymnus canestris* and the species of *Potorous* lack fine ridging on their elongate premolars. Presumably the ridges in these forms have been lost independently of the loss in macropodids. In macropodids, the P₃ may be elon-
gate or short but it is never as finely and evenly ridged as in many potoroids. Despite the claims of Case (1984) and Woodburne (1984) that premolar morphology is plastic and less stable than molar morphology, the synapomorphic nature of this state seems defensible, at least on the basis of outgroup comparison, and it reinforces hypotheses of monophyly based on the other evidently synapomorphic states.

In Flannery, Archer and Plane (1982), the $I_1$ of Bulungamaya delicata was shown to lack a dorsal enamel flange and thus to have the enamel of $I_1$ restricted to the ventrolingual area of the crown. Since that time, additional specimens of primitive bulungamayines from the Kutjumaru local fauna have been found that show that the $I_1$ possesses a dorsal enamel flange. Thus the loss of the flange in B. delicata is probably convergent. Contrary to Case (1984), the dorsal enamel flange is not absent in all potoroids. It is present in the most primitive potoroid, Hypsiprymnodon moschatus, the species of Potorous (Flannery, Archer and Plane, 1982) and in primitive bulungamayines.
In conclusion, it is apparent that three of the four synapomorphies regarded by Flannery, Archer and Plane (1982) to link bulungamayines with other potoroids were correctly interpreted. As noted in Flannery, Archer and Plane (1982), the presence of lophodont molars in bulungamayines is the only possible macropodid synapomorphic state seen in that group. However, the presence of what appears to be a posthypocristid on $M_1$ of *B. delicata* shows that at least in this form all of the molars are not fully lophodont. On the basis of parsimony (three potoroid synapomorphies versus one possible macropodid one) which is the only guide that does not rely heavily on a priori, there are no clear examples in this study that are not reliant on other possibilities within potoroids.

Relationships of Gumardee pascuali.—*Gumardee pascuali* Flannery, Archer and Plane, 1982 is a potoroid known from a single maxilla fragment containing $P_3$ and $M_3$ from the middle Miocene Riversleigh local fauna, Queensland. Both Case (1984) and Woodburne (1984) have suggested that it is a macropodine (macropodid in this study). There is thus a need to re-examine its relationships.

The $P_3$ of *Gumardee pascuali* is the elongate, finely ridged $P_3$ which is seen only in a particular unnamed group of potoroids (see above). Woodburne’s (1984) suggestion that the ridgelets of $P_3$ of *G. pascuali* are coarser than those of the species of *Propleopus*, *Betongia* and *Aepyprymnus* cannot be substantiated. The enamel ridgelets of the $P_3$ of *G. pascuali* are clearly defined, fine and evenly spaced, and are more abundant than in several of the taxa mentioned by Woodburne; *Propleopus oscillans* has approximately 6 ridgelets per cm, *Aepyprymnus rufescens* has about 10 per cm and *G. pascuali* has approximately 11 per cm (Figure 6). This contrasts sharply with the condition in *Dorcopsoides fossilis* (Woodburne, 1967), where five or six rounded, poorly defined enamel ridgelets are present, with the anteriormost being far more sharply defined than the others. It is worth noting here that although Case (1984) dismisses ridging (“serrations”) of the pre-molars as “... better fitted for generic or species level distinctions...” (Case, 1984, p. 1084), he cites the finely and evenly serrate $P_3$ of *Purina mosaicus* in his diagnosis as supporting referral of this taxon to the Potoroinae.

Woodburne (1984) notes that the $P_3$ of *G. pascuali* resembles that of *Dorcopsoides fossilis* in basal outline. Although these taxa are similar in this respect, they also resemble a great many other kinds of kangaroos, e.g., the species of *Protemnodon* and *Dorcopsis* and this similarity is probably convergent.

The molars: Woodburne (1984) interprets the molars of *G. pascuali* to be “sublophodont” in form but does not define the term. Flannery, Archer and Plane (1982) interpret them to be bunodont. It is of some impor-
stance here to define the terms "lophodont" and "bunolophodont" (= bunodont) in the context of the morphology of kangaroo molars. Definition of the term "sublophodont" is not clear from its usage in Woodburne (1984) but presumably, from its context, means lophodont.

The upper molars of macropodids are usually described as being lophodont and those of most potoroids (e.g., the species of Bettongia) as bunolophodont. The difference between these molar morphologies is largely a matter of proportion. In lophodont forms, the transverse lophs (protophil and hypoloph) are better developed than the longitudinal "links" (preparacrista, midlink and posthypocrista), the posterior portion of the midlink is greatly reduced and the forelink is sometimes lost. An extra structure present in lophodont upper molars of macropodids is a lingual extension of the anterior cingulum. This structure is also seen in G. pascuali and the species of Propileopus. The latter have never been referred to as having lophodont molars and clearly the presence of this structure alone does not make a molar "lophodont." In bunolophodont upper molars, the longitudinal links are well developed while the transverse structures, the lophs, are less well developed, often not reaching the apex of the paracone and metacone on their buccal margins (Figure 7).

In lower molars similar proportional differences between lophodont and bunolophodont types occur. The protolophid and hypolophid are better developed than the longitudinal links (paracristid and cristid obliqua) in lophodont forms but, in addition, two longitudinal structures, the postmetacristid and the posthypocristid, are usually lost. The remaining longitudinal structures are also usually shifted lingually but this can also occur in molars described as bunolophodont (e.g., those of Caloprymnus camppestris, Figure 8).

Because of the trivial structural differences, it is not difficult to imagine the transformation of the bunolophodont molar pattern into the lophodont one. In the past, some confusion has existed regarding which forms have "lophodont" and which "bunolophodont" molars. Indeed, some molars from the middle Miocene Namba Formation, South Australia, show an intermediate morphology (Flannery and Rich, in preparation). These two molar types may work in quite different ways, emphasizing as they do transverse (lophodont) and longitudinal (bunolophodont) cutting crests. Despite the small differences between these molar types, both Case
(1984) and Woodburne (1984) emphasize the importance of molar morphology relative to premolar morphology: "... molar morphology of the Potoroinae is grossly more stable than that of the premolars, at least at the generic level..." Woodburne (1984, p. 1070).

Are the molars of *Gumardee pascuali* best described as lophodont or bunolophodont? In the least worn molar (the M3), the protoloph is poorly developed relative to the greatly enlarged paracone and ill-defined but large pre- and postparacrista (Flannery, Archer and Plane, 1982). The protoloph is thin and low and the paracone forms a high prominence. The hypoloph is nonexistent, the posterior part of the molar forming a low "heel" (Figure 9). This morphology is more consistent with the bunolophodont pattern where the longitudinal rather than the transverse structures are emphasized. Unfortunately, M2-4 are too heavily worn to determine their original pattern. The wear pattern noted by Woodburne (1984) as being similar to *Dorcopsoides fossili* is also similar to that seen in potoroids (Figure 9). As a result, these molars are described here as bunolophodont.

As noted above, an unusual feature of the molars of *G. pascuali* is the extension of the anterior cingulum towards the lingual margin of the tooth. This condition is seen elsewhere in the species of *Proleopus* and in macropodids. While it could be a macropodid synapomorphic state, the fact that it is seen in undoubted potoroids (species of *Proleopus*) indicates that it is subject to convergence. In macropodids and the species of *Proleopus*, upper molars with a lingual extension of the anterior cingulum are invariably associated with lower molars with a pronounced buccal extension of the anterior cingulum (a "pocket" buccal to the paracristid). This condition is clearly derived as it is not seen in the outgroup (phalangerids) or the most primitive potoroids (e.g., *Hypsiprymnodon moschatus*). While the presence of a pronounced buccal extension of the anterior cingulum is uncommon among potoroids, such a condition is seen in *Purtia mosaicus* Case, 1984. Because *P. mosaicus* is known only from lower and *G. pascuali* only from upper teeth, these taxa cannot be directly compared. However, both have elongate premolars with buccal and lingual cingula and a large number of fine ridgelets, and molars with extensions of the anterior cingulum. These are uncommon and derived states among potoroids. Case (1984) neglected to compare these taxa, but nonetheless their complementary morphology suggests that they may be closely related. They are not, however, conspecific. *Purtia mosaicus* has a P3 that projects buccally from the straight molar row, while *G. pascuali* has a buccally convex molar row and an anteroposteriorly aligned P3. Such differences, how-
ever, are encompassed within a single extant genus (*Bettongia*) of potoroids.

Other aspects of the molar morphology of *Gumardee pascuali* are of some interest. These include the steep molar gradient and the root pattern. The steep molar gradient (the posterior molars becoming increasingly smaller) is a plesiomorphic state seen in phalangerids and primitive potoroids. However, it is unknown in macropodids. The molar roots of *G. pascuali* form an unusual pattern in that there is only a single large lingual root that extends far posteriorly. This condition is seen in phalangerids and other primitive macropodoids such as *Dorcopsoides fossilis*. This is therefore presumed to be a plesiomorphic condition.

In summary, the elongate, finely ridged premolar of *G. pascuali* is a synapomorphic state for a group of advanced potoroids. The extended anterior cingulum on the molars and premolar basal outline are convergent features seen in several other unrelated forms. Further, similarities between *G. pascuali* and *P. mosaicus* suggest that they may be closely related and perhaps even congeneric.

A taxonomy for potoroids.—Many alternative ways of constructing classifications are available (see Wiley, 1981). Here the Linnean system is used, but the sequencing convention of Nelson (1974) is also applied. This modification is adopted to prevent the unnecessary proliferation of higher taxonomic ranks that would occur in a fully ranked Linnean classification.

The problem of whether the potoroids should constitute a family or subfamily is relatively trivial. What is more important is that the classification should accurately reflect the phylogenetic hypothesis. The concept of Potoroidae used here is broader than in Case (1984) and Woodburne (1984), including as it does the Bulungamayinae and *Gumardee pascuali*. If one considers that some kind of "equivalence of diversity" is necessary between equivalent ranks, then the Potoroidae as constituted here is at least as diverse as many other marsupial families (e.g., Peramelidae or Phalangeridae).

Regarding previous usage, the concept of Potoroidae has received wide usage (e.g., Pearson, 1950; Archer and Bartholomai, 1978; Flannery, Archer and Plane, 1982). Even among workers of the last 100 years who did not use Potoroidae, the majority have recognized two closely related subfamilies of rat kangaroos, the Hypsiprymnodontinae Collett, 1877 and the Potoroinae Gray, 1821. The classification supported by Case (1984) and Woodburne (1984), i.e., the placement of all potoroids in a single subfamily divided into several tribes, follows Marshall (1981). Marshall's paper is largely a checklist of the families and genera of marsupials and the classification of the Potoroinae presented there is not rationalized or even discussed. Thus far it has been utilized only by Woodburne and Case. The placement of potoroids in a family therefore, seems at least as defensible. Case (1984) lists other interpretations of potoroid taxonomy.

**DISCUSSION**

Arguments in defense of the monophyly of high-level taxonomic groups are sometimes based on very few synapomorphic features. This is certainly true for some groups of kangaroos and, to exacerbate the problem, the few apparently useful characters often display convergence. The case of the Bulungamayinae is one in point. Three synapomorphic features indicate that they are potoroids most closely related to the Potoroinae. However, presuming that they are potoroids, a further state (lophodont molars), long regarded as a hallmark of the Macropodidae, must have arisen independently in the Bulungamayinae. As noted above, the transition from a lophodont to a bunodont molar pattern involves only minor structural changes. It is not unlikely that such a transition occurred twice in kangaroo evolution.

Case (1984) presents a definition of the Potoroinae (=Potoroidae here) that excludes bulungamayines. Of the seven character states listed in the definition, the condition of four is unknown in the bulungamayines. Of the remaining three, Case acknowledges that one (the presence of bunodont molars) is plesiomorphic and thus useless in phylogenetic analysis. A further state (enamel of I1 restricted to the ventrolingual area of the crown) is shown here not to be synapomorphic for all potoroids, but only for a particular group. The remaining state (masseteric canal extending to below P3) is now definitely known in bulungamayines and is a synapomorphy for all potoroids. Thus, even within Case's
The relationship of *Gumardee pascuali* to other potoroids is based on a single derived state—the presence of an elongate, finely ridged P\(_3\). Arguments in Woodburne (1984) regarding the original molar pattern and premolar morphology of *G. pascuali* cannot be supported. There is no good evidence for a relationship between this species and macroPodids. While the data are poor, referral of *G. pascuali* to the Potoroidae is the most defensible hypothesis. Figure 10 is a cladogram for the taxa discussed in this paper.

**CONCLUSIONS**

The potoroids are a monophyletic group. Character states that support this hypothesis are: 1) presence of a frontal-squamosal contact; 2) extension of the masseteric canal to below M\(_2\); 3) enlargement of the digastic process producing a pronounced convexity of the dentary below the middle of the molar row; and 4) presence of a proximovenral process on the fifth metatarsal. Because bulungamayines possess two of these states as well as a further state (elongate, finely grooved premolar) that is synapomorphic for potoroids excluding *Hypsiprymnodon moschatus* and the species of *Propleopus*, they are included in the Potoroidae. *Gumardee pascuali* is also included within the Potoroidae because it possesses an elongate, finely grooved premolar.

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**REFERENCES**


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ANNOUNCEMENT

SECOND INTERNATIONAL CONFERENCE ON PALEOCEANOGRAPHY

The Second International Conference on Paleoceanography will be held at Woods Hole, Massachusetts, from 7–12 September, 1986. For further information please contact W. A. Berggren, Department of Geology and Geophysics, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543 USA.