An Investigation of Phylogeny in the Giant Extinct Rat Kangaroo Ekaltadeta (Propleopinae, Potoroidae, Marsupialia)

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AN INVESTIGATION OF PHYLOGENY IN THE GIANT 
EXTINCT RAT KANGAROO EKALTADETA 
(PROPLEOPINAE, POTOROIDAE, MARSUPIALIA) 

STEPHEN WROE 

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ABSTRACT—The Giant Rat Kangaroos (Ekaltadeta, Propleopus) were placed in a new subfamily the Propleopinaceae by Archer and Flannery (1985). The discovery of new Ekaltadeta material from Riversleigh, northwestern Queensland has stimulated a review of propleopine phylogeny. Cladistic analysis of five propleopine taxa suggests possible paraphyly for Ekaltadeta and polyphyly for Propleopus. A new species of Miocene propleopine, Ekaltadeta jamiemulvanyei n. sp., from system C local faunas at Riversleigh, is described.

INTRODUCTION

GIANT RAT KANGAROOS (Potoroidae: Propleopinaceae) may be the pliosiomorphic sister group of all other potoroids (Flannery, 1987). Archer and Flannery (1985) considered Ekaltadeta ima to be the sister group to Propleopus, with P. oscillans the more pliosiomorphic and P. chilagoensis the more apomorphic within the genus.

An investigation of recently discovered Ekaltadeta material from Riversleigh has provided more complete data and questions the polarity proposed for three character states in the phylogeny of Archer and Flannery (1985), facilitating a reassessment of relationships within the Propleopinaceae.

Dental homology follows Luckett's (1993) definitions regarding the molar premolar boundary. Higher level systematics of kangaroos follows Flannery (1987). Most specimens are registered in the fossil vertebrate collection of the Queensland Museum and denoted by the abbreviation QM. Other prefixes include: UCMP (University of California Museum of Paleontology), NMV (Museum of Victoria) and AR (provisional catalogue numbers of the University of New South Wales database). All specimens referred to are presented in Tables 2–4.

SYSTEMATIC PALEONTOLOGY

Superfamily MACROPODOIDEA Grey, 1821 
Family POTOROIDAE Grey, 1821 
Subfamily PROPLEOPINAE Archer and Flannery, 1985 
Genus EKALTADETA Archer and Flannery, 1985

Type species.—Ekaltadeta ima Archer and Flannery, 1985 p. 1331–1349.

Revised generic diagnosis.—Dental and masseteric canal separate at anterior ends; masseteric canal terminating below P2 – M1, in prominent cul-de-sac; dentary of even depth below molar row; P2 persists in adult dentition; I1 lanceolate and transversely compressed; diastema between I1 – P2 small; P3 very large; metaconid and protostylistid with anterior crista on M1; upper molars basally broad and conical; molar gradient high, particularly in upper dentition.

EKALTADETA ima Archer and Flannery, 1985

Figures 1, 2, 5, 6

Type specimen.—QM F12423, left dentary containing P2, P3, M1, M2, M3, lingual side of M1, and the alveolus for I1.

Revised specific diagnosis.—Smallest species of Ekaltadeta; entoconid well below hypoconid height on M1; relative size of P3 particularly large.

Supplement to the original description.—QM F12436, skull, containing LP1, m1, m2 and RP1, P1, M1. A full description of the skull is in progress, the dentition only is described here. This specimen has been attributed to E. ima for the following reasons: P1 is of very similar size and morphology to P1 of the holotype; P2 also very like P2 of holotype and similarly retained in adulthood; lower dentitions attributable to E. ima have been found in the same site, indicating that only a single Ekaltadeta taxon present. RP1: similar to P2 of holotype. RP2: less rounded on posterior occlusal margin and less broad basally than P1 of holotype, otherwise similar. RM1: wider anteriorly than posteriorly; paracone andmetacone reduced relative to protocone and hypocone; edge of posterior cingulum joins cistae emanating from the metacone and hypocone producing a distinct basin. RM2: less wide posteriorly than RM1, otherwise similar. RM3: smaller than RM2; difference between anterior and posterior widths further exaggerated; metacone smaller than hypocone and reduced relative to preceding molars; RM4: greatly reduced in size; metacone absent.

QM F12435, complete left dentary, containing I1, alveolus for I2, dp1, P3, M1. From the holotype and previous referred specimens of E. ima I1 and portion of the dentary posterior to M4 were not known. QM F12435 similar to holotype in that P2 not evicted as a consequence of eruption of P3, has a prominent protoconid on M1 and, a dentary of even depth beneath the molar row. Dentary: dorsal portion of the coronoid process damaged; angular process medially compressed compared to Hysiprymnodon species and raised to height of tooth row; a dorsally oriented flange apparent along lingual margin of angular process; distance from condyle to P1 relatively shorter than for species of Hysiprymnodon; dentary profile ventrally convex. I1: medially compressed with root exposed to border of mental foramen; far less robust than P. oscillans, less gracile than for species of Hysiprymnodon; no horizontal wear surface as in P. oscillans. I2: only alveolus remains; P3, P3, M3 do not differ significantly from holotype. M4: smaller than preceding molars; wider anteriorly than posteriorly; entoconid reduced.

QM F24199, juvenile, left dentary containing P2, unerupted P3, dp1, M1. QM F24199 is the first juvenile specimen attributed to E. ima. Specimen has been referred to Ekaltadeta ima as morphology and size of P2, M1 does not appreciably differ from holotype or other referred specimens. Dentary: the dentary is broken away from 3 mm anterior to mental foramen; posteriorly ventral portion of dentary missing from beneath M1, and dorsally from beneath M2; a small part of the ascending ramus extends for 15 mm; buccally an area of about 11 mm2 is broken away from beneath the crowns of dp1 and M1, exposing the erupting P3. P2: crown similar to holotype but sits higher (about 12 mm) above anterior dorsal surface of dentary; anterior root extends approximately 9 mm from base of crown to mental.
Figure 1—*Ekaliadeta ima* (Archer and Flannery, 1985), ×2. 1. occlusal view of QM F12436 (uppers). 2, buccal view of QM F12435, left dentary containing I₁, alveolus for I₁, P₂, M₁,₂. 3, occlusal view of QM F12435.
foramen; posterior lingual root extensive; buccal root missing; occlusal edge of \( P_2 \) oriented obliquely to dentary. \( P_3 \); similar to holotype where visible; \( dp_3 \); trigonid shows extreme transverse compression to produce an occlusal edge; principal cusps not defined; two weakly delimited ridgelets apparent buccally and lingually; talonid below horizontal plane of trigonid; well developed crista connects entoconid obliquely to occlusal edge of trigonid; tips of entoconid and hypoconid broken away; weak loph connects these two cusps; posthypocristid and postento-cristid form posterior cingulum; cristid obliqua well developed. \( M_{1-4} \); similar to those of holotype.

Remarks. — From examination of the above new *E. ima* specimens it is clear that some of the predictions made by Archer and Flannery (1985) based on fragmentary material were erroneous, particularly concerning the morphology of \( I_1 \) and the anterior portion of the dentary. Archer and Flannery (1985) suggested that the \( I_1 \) of *E. ima* was probably similar to that of *P. oscillans* (spatulate) rather than lanceolate as is now evident.

This, in addition to other new information, including the lack of a well developed diatema between \( I_1 \) and \( P_3 \), and the possession of basally broad upper molars showing a strong anterio-poster gradient in *E. ima* clearly impact on interpretations of phylogeny and biology for the species (see below).

Material. — QM F12436, QM F12435, and QM F24199.

Occurrence. — All specimens are from Riversleigh Local Faunas of northwestern Queensland and have been tentatively dated at early to middle Miocene in age (Archer et al., 1989): QM F12423 (holotype) and QM F24199 from Gag Site, QM F12436 from Camel Sputum Site, and QM F12435 from Upper Site.

**Ekaltadeta jamiemulyaneyi** n. sp.

Figures 3, 6

*Type specimen.* — QM F24200, left dentary fragment containing \( P_3 \), \( M_{1-2} \), trigonid and hypoconid of \( M_3 \), symphysial region and ascending ramus missing, ventral margin of dentary beneath \( M_{2-3} \) broken away.
Figure 3—Ecalitadeta jamieulvanayi n. sp. × 2. 1, occlusal view of QM F24200, left dentary containing P3, M1–2, holotype. 2, buccal view of QM F24200. 3, lingual view of QM F24200. 4, occlusal view of QM F24212, left maxillary fragment, containing P3, dp3, M1–2, referred specimen. 5, buccal view of QM F24212. 6, lingual view of QM F24212. 7, occlusal view of QM F20842, left P3, referred specimen. 8, buccal view of QM F20842. 9, lingual view of QM F20842.
**Description.**—Very large species; P₃ raised high above occlusal plane of molars; hypoconid and entoconid of M₁ near equal in height; molar gradient of upper molars moderate.

**Diagnosis.**—Very large species; P₃ raised high above occlusal plane of molars; hypoconid and entoconid of M₁ near equal in height; molar gradient of upper molars moderate.

**Remarks.**—E. jamiemulvaneyi differs from E. ima in size, dentary being around 50 percent larger, approaching that of Proleopus oscillans (Figure 4), P₃ smaller relative to molars, molar gradient less steep than E. ima, hypoconid and entoconid of M₁ near equal height in E. jamiemulvaneyi, entoconid well below hypoconid in E. ima, M₂ wider posteriorly than anteriorly in E. jamiemulvaneyi, reversed state in E. ima, M₂ wider than anteriorly in E. jamiemulvaneyi, wider posteriorly, paracoon and metacone of M₁–M₂ further reduced on the condition in E. ima. E. jamiemulvaneyi is similar to E. ima in possessing a prominent protoconid on M₁, and a dentary of even depth beneath the molar row. Wear on anterior root of P₃ suggests that like E. ima, E. jamiemulvaneyi retained P₃ into adulthood.

**Etymology.**—The species name is derived directly from J. Mulvaney in recognition of his contribution to the Riversleigh Society.

**Material.**—QM F24212, QM F20842.
Occurrence. — All specimens are from Riversleigh Local Faunas of northwestern Queensland. QM F24200 (holotype) and QM F20842 from Encore Site, and QM F24212 from Cleft of Ages Site. These sites have been tentatively dated at late middle or early late Miocene in age (Archer et al., 1989).

PHYLOGENETIC ANALYSIS

Previous phylogenetic interpretations. — Until recently the fossil record of the Propleopinaceae has been scarce in the extreme with all material referable to a single Pleistocene species first described by De Vis as *Triclis oscilans* (1888). This species was redescribed as *Propleopus oscilans* by Longman (1924). Following a ninety year hiatus, Archer, Bartholomai and, Marshall (1978) described a new propleopine, *Propleopus chillagensis* from the Pleistocene Chillagoe formation of northeastern Queensland. Archer and Flannery (1985) described a further two species, *Propleopus wellingtonensis* from the Wellington Caves in New South Wales and the first Tertiary propleopine, *Ekaiaedeta imia* from Oligo–Miocene local faunas of Riversleigh.

The inclusion of *Ekaiaedeta jamieulvaneyi* brings the total to five species with another propleopine from the Pliocene Bow local fauna of southwestern Queensland currently being described by W.D.L. Ride.

De Vis (1888) allied *Propleopus* with *Hysiprymnodon* and the identification of propleopines and hysiprymnodontines as sister groups has been accepted by all subsequent authors (Tate, 1948; Woods, 1960; Archer and Flannery, 1985).
Archer and Flannery (1985) proposed a phylogeny for the *Propleopinae* in which *E. ima* was considered to be the sister group to *Propleopus*. Within *Propleopus* they considered *P. oscilans* the more plesiomorphic and *P. chilagoensis* the more apomorphic (Figure 5). The discovery of more complete *E. ima* material and a new species of *Ekalitadeta* have encouraged a revision of this phylogeny based on a reevaluation of character polarities.

**Methodology.**—Analyses were performed using the PAUP (version 3.0) computer program by D. L. Swafford (1989).

Wagner analysis was performed using the “exhaustive” algorithm. DELTRAN character optimisation was used to identify the most parsimonious array of transformations. The DELTRAN option delays the evolutionary transformation of characters, pushing them up the tree and effectively favouring parallelisms over reversals where there is an equally parsimonious choice (Wiley et al., 1991). Use of this option was considered judicious given that twenty percent of the data matrix was missing, though this figure is well within the minimum suggested by Novacek et al. (1988) for expectation of reflecting true relationships (i.e., thirty percent). Missing data in a sister taxa allows the possibility that a transformation might have evolved at a lower point on the tree. DELTRAN optimisation includes these transformations at the minimal level (Simmons 1993).

The bootstrap method of parsimony analysis was also applied.

The bootstrap technique produces majority-rule consensus trees and places confidence estimates on groups contained in the most parsimonious trees (Felsenstein, 1983). The bootstrap provides an alternative for the problem of small data sets (Potvin and Roff, 1993). In this study the method was applied with a branch and bound search and one hundred replications.

**Character analysis.**—Eleven characters were identified as useful indicators of propleopine phylogeny. Ten of these were used by Archer and Flannery (1985) to produce the cladogram shown in Figure 5. The polarity of some characters has been revised in the light of new fossil material using a new species of *Hypospyrmnodon* (Müller and Archer, in press), also from the Oligo-Miocene deposits of Riversleigh, as the out group (Table 1).

1. Presence or absence of anterior cristae emanating from the metaconid of *M*₂. Presence of an anterior cristae emanating from the metaconid of *M*₂ was identified as a synapomorphy uniting the *Propleopinae* by Archer and Flannery (1985). Their evaluation was supported in this study by the presence of cristae extending anteriorly from the metaconid of *M*₂ in *E. jamiemulvaneyi*. Lack of anterior cristae in *Hypospyrmnodon* sp. was considered plesiomorphic.

2. *I*₁ morphology. Archer and Flannery (1985) concluded that *E. ima* possessed a large spatulate *I*₁, similar to *P. oscilans* based on examination of the *I*₁ alveolus in the *E. ima* holotype. New material shows that the *I*₁ of *E. ima* was lanceolate, more closely resembling that of *Hypospyrmnodon* sp. Consequently the spatulate *I*₁ of *P. oscilans* was treated as derived within the *Propleopinae* in this study.

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#### Table 2—M₂ aw divided by M₂ pw (G-value) for propleopines and a *Hypospyrmnodon* sp. from Riversleigh local faunas. Measurements in mm.

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<th>M₂ pw</th>
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* = Skull; (R) = right tooth row; (L) = left tooth row; + = damaged.

3. Partial or complete incorporation of the protoconid into the anterior lophid of *M*₁. In *E. ima*, *E. jamiemulvaneyi* and *Hypospyrmnodon* sp. the protoconid of *M*₁ was distinct. The *M*₁ protoconid was incorporated into the anterior protolophid in *P. oscilans* and *P. wellingtonensis*. This character state in *Propleopus* was treated as apomorphic.

4. Molar gradient. Differences in molar gradient were used by Archer and Flannery (1985) to distinguish *P. chilagoensis* from *P. oscilans* and *P. wellingtonensis*. Molar gradient reflects both the surface area and length of the molar tooth row. In this study an attempt to quantify molar gradient was made for both upper and lower dentitions. From observation a distinct reduction in tooth size posteriorly was apparent in both the upper and lower dentitions of *Ekalitadeta ima*. In the upper dentition this steep gradient clearly began with a reduced posterior width (pw) relative to the anterior width (aw) of *M*₂ which then ramped through *M*₃ to *M*₄. In *E. ima* *M*₄ pw was less than half *M*₂ aw. For *P. oscilans* *M*₄ was missing, however, in this specimen the *M*₂ pw was only slightly less than *M*₂ aw suggesting a less extreme gradient. This supposition was strongly supported by the condition apparent in the lower dentition, in which molar gradient again contrasted strongly with *E. ima*. *M*₄, *M*₅, *M*₆ tooth width decreased at a steady rate antero-posteriorly in *E. ima* but was reversed in *P. oscilans* where tooth width increased posteriorly for *M*₃, with only a slight decrease in size for *M*₄.

A number of methods were considered for their potential to indicate molar gradient. Accurate determination of individual molar surface areas and comparisons between teeth would have been useful but would have required two or more teeth per specimen, greatly limiting the data sets, particularly for the upper dentitions. However, for the purposes of this study the clear initiation of a marked molar gradient at *M*₂ observed in the dentitions of *E. ima* and *P. chilagoensis* permitted the estimation of this gradient from a single molar by comparing aw to pw (Table 2). In the lower dentitions this gradient was less distinct and two molars (*M*₁ and *M*₂) were required to demonstrate a gradient by comparing *M*₁ pw with *M*₂ pw (Table 3). The values of *M*² aw divided by *M*² pw and *M*₁ pw divided by...
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<td><em>E. jamiemulaneyi</em></td>
<td>QM F24200</td>
<td>8.200</td>
<td>8.000</td>
<td>0.965</td>
</tr>
<tr>
<td><em>P. wellingtonensis</em></td>
<td>UCM P45171</td>
<td>9.200</td>
<td>9.600</td>
<td>0.958</td>
</tr>
<tr>
<td><em>P. oscillans</em></td>
<td>QM F3302 (cast)</td>
<td>9.700</td>
<td>10.400</td>
<td>0.933</td>
</tr>
<tr>
<td><em>Hypsiprymnon donsp.</em></td>
<td>QM F24148</td>
<td>2.300</td>
<td>2.200</td>
<td>1.045</td>
</tr>
<tr>
<td><em>Hypsiprymnon donsp.</em></td>
<td>QM F13426</td>
<td>2.400</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td><em>Hypsiprymnon donsp.</em></td>
<td>QM F24166</td>
<td>2.400</td>
<td>2.300</td>
<td>1.043</td>
</tr>
<tr>
<td><em>Hypsiprymnon donsp.</em></td>
<td>QM F24169</td>
<td>2.300</td>
<td>2.300</td>
<td>1.000</td>
</tr>
<tr>
<td><em>Hypsiprymnon donsp.</em></td>
<td>QM F24171</td>
<td>2.300</td>
<td>2.300</td>
<td>1.000</td>
</tr>
</tbody>
</table>

M₂, pw are presented as G-values. For the upper dentitions two extremes of molar gradient were shown by *P. oscillans* and *P. chillagoensis* with G-values of 1.057 and 1.231, respectively, with the lower number indicating a lesser molar gradient. The estimated gradient for *E. jamiemulaneyi* (1.045) approached that of *P. oscillans* whilst the *E. ima* specimens showed relatively high estimated gradients (ranging from 1.091 to 1.191), as did specimens of a species of *Hypsiprymnon donsp.* from Riversleigh which ranged from 1.120 to 1.602. For the lower dentitions *P. oscillans*, *P. wellingtonensis* and *E. jamiemulaneyi* showed an apparent reversal in molar gradient in comparison to *E. ima* and *Hypsiprymnon donsp.* *Proleopous oscillans* had a G-value of 0.933 whilst *P. wellingtonensis* and *E. jamiemulaneyi* showed G-values of 0.958 and 0.965 respectively. In *Ekaladeta ima* and *Hypsiprymnon donsp.* the tendency for the molars to markedly decrease in size posteriorly was demonstrated by gradient estimates ranging from 1.014 to 1.084 for *E. ima* and 1.000 to 1.045 for *Hypsiprymnon donsp.* As a high molar gradient in the upper molars and a tendency for the molars to decrease in size anterior-posteriorly in the lower dentition was a feature of *Hypsiprymnon donsp.* they were treated as the plesiomorphic character state. Molar gradient in the upper and lower dentitions appeared to vary in concert, subsequently it was considered appropriate to treat both as a character complex (i.e., as a single character state (Klug and Farris, 1969)).

5. Relative size of P₃. A measure of relative P₃ size was determined by dividing P₃ width (w) by M₂ posterior width (pw) (Table 4). In *P. oscillans* the P₃ was small compared to the M₂, pw (1.093). The *Ekaladeta ima* specimens had high values ranging from 1.354 to 1.515. *Ekaladeta jamiemulaneyi* positioned between *E. ima* and *P. oscillans*, with a value of 1.280. In *Proleopous wellingtonensis* only the alveolus was observed. Although P₃ alveolus size in *P. wellingtonensis* suggested that this tooth may have been larger than the P₃ of *P. oscillans*, it was relatively small compared to the alveolus for P₃ in *E. ima* or *Hypsiprymnon donsp.* No P₃ exists for *Proleopous chillagoensis*, however P₃ was huge, at least fifty percent larger than the P₃ in *P. oscillans*. For the out-group *Hypsiprymnon donsp.*, the range (1.390 to 1.462) was similar to *E. ima*, and a relatively large P₃ was treated as plesiomorphic. From observation it was apparent that increases in molar gradient and reduction in P₃ w may have been proportionally related and thus might constitute a character complex. As the independence of relative P₃ size was in doubt analysis was also run excluding this character.

6. Reduced or unreduced metacone and encondon in posterior molars. A reduction of metaconid and encondon size posteriorly was considered a synapomorphy uniting *P. chillagoensis* and *P. wellingtonensis* by Archer and Flannery (1985). The presence of a reduced metacone in *Ekaladeta jamiemulaneyi*, *E. ima* and *Hypsiprymnon donsp.* contradicted this proposal and confirmed this character state as plesiomorphic for proleopines.

7. Retention or loss of P₂ with the eruption of P₃. The loss of P₂ with the eruption of P₃ was treated as a synapomorphy of *Proleopous* by Archer and Flannery (1985). In *Ekaladeta jamiemulaneyi* the dentary was missing anteriorly of the P₁, and retention or loss of P₂ with eruption of P₃ could not be confirmed for *Proleopous chillagoensis*. The brief persistence of P₂ after the eruption of P₃ in *Hypsiprymnon donsp.* supported the treatment of this character state as a plesiomorph.

8. Dentary morphology. The dentaries of *Proleopous oscillans* and *P. wellingtonensis* were markedly deeper anteriorly than posteriorly. In *Hypsiprymnon donsp.*, *Ekaladeta ima* and *E. jamiemulaneyi* depth along the jaw did not vary noticeably and this was considered the plesiomorphic state.

9. Diastema. A large diastema was present in *Proleopous oscillans* anterior to the P₁. The absence of a marked diastema as shown by *Hypsiprymnon donsp.* and *E. ima* suggested plesiomorph for this character, with a large diastema treated as apomorphic. Unfortunately no material exists to identify the presence or absence of this character in *P. wellingtonensis*, *P. chillagoensis*, or *E. jamiemulaneyi*.

10. Cingula on upper molars. *Ekaladeta jamiemulaneyi* had cingula on M₁-₄ around the anterior base of the protocone and partial cingula extending from the hypocone toward the posterior base of protocone. This character was also present in *P. oscillans* but most highly developed in *P. chillagoensis* where a cingula ran continuously from the hypocone to the anterior base of the protocone in the first two upper molars. Cingula were not apparent in the upper molars of *Hypsiprymnon donsp.* and *E. ima* and their absence was considered a plesiomorph.

11. Shape of upper molars. In *Proleopous oscillans* the upper molars were dorsoventrally regular in width. *Hypsiprymnon donsp.*, *Ekaladeta ima*, *E. jamiemulaneyi*, and particularly *P. chillagoensis* had basally broad conical upper molars which were interpreted as plesiomorphic in this study. Archer and Flannery (1985), lacking specimens of upper dentitions for *Ekaladeta*, considered this character to be an apomorphy of *P. chillagoensis*.

**Results of phylogenetic analysis**—Wagner parsimony analysis produced a single most parsimonious tree (Figure 6) requiring twelve steps. *Ekaladeta ima* was the sister taxon to all other
propleopines. Among these _P. chillagoensis_ was the plesiomorphic sister species to the remaining taxa and _E. jamiemulvaneyi_ was the sister species of _P. oscillans_ and _P. wellingtonensis_ clade. This tree produced a high consistency index (CI) of 0.917, and high rescaled consistency index (RC) of 0.875. Examination of character plots identified characters 1 and 11 (gain of an anterior crista emanating from the metaconid of M₃, and basally broad conical upper molars) as synapomorphies of the Propleopinae. The lack of basally broad upper molars in _P. oscillans_ was treated as a reversal to a primitive state. The _P. chillagoensis, E. jamiemulvaneyi, P. oscillans_ and _P. wellingtonensis_ clade was united by character 10 (presence of lingual cingula on the upper molars). Characters 4 and 5 (reduced molar gradient and reduced P3) defined _E. jamiemulvaneyi, P. oscillans_ and _P. wellingtonensis_ as a monophyletic group. Monophyly for _P. oscillans_ and _P. wellingtonensis_ was inferred by shared derived characters 3 and 8 (incorporation of the protolophid into the anterior lophid of M₃, and a dentary deeper posteriorly).

The fifty percent majority-rule consensus tree produced by bootstrapping formulated a tree of identical topography to that produced by Wagner parsimony analysis (Figure 6). Monophyly for a _Ekaltadeta ima, P. chillagoensis, E. jamiemulvaneyi, P. wellingtonensis_, and _P. oscillans_ clade was supported in fifty seven percent of replications. _Ekaltadeta jamiemulvaneyi, P. oscillans_ and _P. wellingtonensis_ were united by synapomorphies in seventy seven percent of replications, and the monophyly of a _P. wellingtonensis_ and _P. oscillans_ clade was supported in ninety three percent of replications. No other groupings received more than twenty percent support. Although bootstrapping analysis found the tree produced in Wagner analysis to be the most probable, only the monophyly of _Propleopus wellingtonensis_ and _P. oscillans_ was strongly supported given the small data set used.

As mentioned in the character analysis above, P3 width may not have constituted an independent character, and may have varied proportionately with increased molar gradient. Support for this proposal was not purely circumstantial and a hypothetical model based on variation in dietary preference can be constructed to explain the relationship. A high molar gradient translates into both a reduced capacity for horizontal shear and a reduced distance from the condyle to the P3. The P3 of propleopines was potentially analogous to the carnassial of carnivores (Abbie, 1939). In an animal adapted to carnivory a decreased reliance on horizontal shear would be expected (Wells, Horton and Rogers, 1982) as would a reduction in the distance between the principal sectorial tooth and condyle (Young, Yupp and Krugger, 1989). Increased vertical shear, reflected by a larger P3 would accompany the above adaptations. Conversely, adaptation to herbivory might logically be associated with an increased requirement for horizontal shear and decreased vertical shear.

With the status of P3 width as an independent character unclear, both Wagner and bootstrapping analyses were re-run, treating high molar gradient and high relative P3 width as a single plesiomorphic character state. Tree topology was not effected in the Wagner analysis, though lesser values for CI and RC were obtained (0.909 and 0.779 respectively). Bootstrapping the alternative data matrix, with fifty percent confidence limits again produced identical tree topology (Figure 6). A _Propleopus chillagoensis, E. jamiemulvaneyi, P. wellingtonensis_, and _P. oscillans_ clade was supported in sixty six percent of replications. An _E. jamiemulvaneyi, P. wellingtonensis_, and _P. oscillans_ clade received sixty four percent support, and a _P. oscillans, P. wellingtonensis_ grouping was produced in ninety three percent of replications. Again only monophyly for a _P. oscillans, P. wellingtonensis_ clade was strongly supported.

**DISCUSSION**

The tree topology generated in this analysis contrasts strongly with that forwarded by Archer and Flannery (1985), suggesting possible polyphyly for _Propleopus_ and paraphyly for _Ekaltadeta_. _Propleopus oscillans_ was considered plesiomorphic, and _P. chillagoensis_ apomorphic by Archer and Flannery (1985). A reversed polarity is suggested by results of this analysis, in which _P. chillagoensis_ was determined to be plesiomorphic and _P. oscillans_ apomorphic. This reversal is the result of a reassessment of character state polarities regarding molar gradient and relative size of the P3, in conjunction with the identification of apomorphies in _P. oscillans_. Within _Propleopus_ plesiomorphy for _P. chillagoensis_ is suggested by its high molar gradient, premolar hypertrophy, and basally broad conical upper molars. Apomorphy for _P. oscillans_ is proposed for the following reasons: hypotrophy of P3, reduced molar gradient, extension of the diastema and, development of a short broad I, with a horizontal wear facet. The relationships of _Ekaltadeta jamiemulvaneyi_ and _P. chillagoensis_ as presented in this study are provocative. Monophyly for _E. jamiemulvaneyi, P. oscillans_ and _P. wellingtonensis_ clade is proposed on the basis of reduced molar gradient and P3 hypotrophy, suggesting possible polyphyly for _Propleopus_ and paraphyly for _Ekaltadeta_. This proposal must remain tentative as it is founded on monophyly implied by two synapomorphies which may constitute a single character complex. Bootstrapping forward an identical tree to that produced by Wagner analysis, however, only a _P. oscillans_ and _P. wellingtonensis_ clade is strongly supported. Caution is also required as the analysis is based on relatively few characters, with some significant data unavailable. Use of a small data matrix is not necessarily inappropriate, with some authors citing the use of a few well analysed characters as preferable to large numbers of poorly analysed characters (Gaffney et al., 1991). Missing data is of greater concern. The discovery of new material completing the missing data set could firmly support or deny the phylogeny forwarded in this study. Evidence determining whether the P2 was retained in adulthood by _P. chillagoensis_ and _E. jamiemulvaneyi_ was as the case for _E. ima_ (Wroe, 1992; Wroe and Archer, 1995), or lost, as in _P. oscillans_ and _P. wellingtonensis_, would be of particular interest.

_Propleopus oscillans_ and _P. chillagoensis_ may represent two extremes of propleopine adaptation. _Propleopus oscillans_, with premolar hypotrophy and an extended molar battery possibly included more plant material in its diet, whilst _P. chillagoensis_ with a reduced molar array and premolar hypertrophy appears better adapted for a carnivorous niche. The results of this study raise the possibility that a middle to late Miocene dichotomy in _Ekaltadeta_ may have given rise to two lineages of _Propleopus_, one characterised by a reversed molar gradient and premolar hypotrophy, and another characterised by a high molar gradient and premolar hypertrophy. However, given the incompleteness of the data set used, and the considerable temporal gap between _Ekaltadeta_ and _Propleopus_, it remains plausible that a single propleopine lineage survived the late Miocene “bottle-neck” caused by encroaching aridity (Hope, 1982), to produce a secondary radiation within _Propleopus_. The plesiomorphies of high molar gradient, relatively large premolars, and basally broad conical upper molars present in _P. chillagoensis_ may prove to be reversals of character states accompanying a secondary propleopine adaptation to carnivory.

The alternative phylogeny for propleopines forwarded here remains tentative and is offered only for consideration in the
advent of further discoveries. Substantiation of propleopine relationships as indicated by this study would clearly necessitate renaming of E. jamiesonvanei and/or P. chillagoensis to resolve the problems of paraphyly and polyphyly that would exist under the current scheme.

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REFERENCES


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