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)

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ABSTRACT—The Giant Rat Kangaroos (*Ekaltadeta, Propleopus*) were placed in a new subfamily the Propleopinae 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 jamiemulvaneyi* n. sp., from system C local faunas at Riversleigh, is described.

INTRODUCTION

GIANT RAT KANGAROOS (Potoroidae: Propleopinae) may be the plesiomorphic 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 plesiomorphic and *P. chillagoensis* 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 Propleopinae.

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 P_3–M_1 in prominent cul-de-sac; dentary of even depth below molar row; P2 persists in adult dentition; I_1 lanceolate and transversely compressed; diastema between I_1–P_2 small; P3 very large; metaconid and protostylid with anterior cristae on M_1; 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 P_2, P_3, M_{1-2}, M_4, lingual side of M_3, and the alveolus for I_1.

Revised specific diagnosis.—Smallest species of *Ekaltadeta*; entoconid well below hypoconid height on M_1; relative size of P3 particularly large.

Supplement to the original description.—QM F12436, skull, containing LP^3, M^{1-4} and RP^2, P^3, M^{1-4}. 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: P^3 is of very similar size and morphology to P_3 of the holotype; P^2 also very like P_2 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. RP^2: similar to P_2 of holotype. RP^3: less rounded on posterior occlusal margin and less broad basally than P^3 of holotype, otherwise similar. RM^1: wider anteriorly than posteriorly; paracone and metacone reduced relative to protocone and hypocone; edge of posterior cingulum joins cristae emanating from the metacone and hypocone producing a distinct basin. RM^2: less wide posteriorly than RM^1, otherwise similar. RM^3: smaller than RM^2; difference between anterior and posterior widths further exaggerated; metacone smaller than hypocone and reduced relative to preceding molars; RM^4: greatly reduced in size; metacone absent.

QM F12435, complete left dentary, containing I_1, alveolus for I_2, dp_3, P_3, M_{1-4}. From the holotype and previous referred specimens of *E. ima* I_1 and portion of the dentary posterior to M_4 were not known. QM F12435 similar to holotype in that P_2 not evicted as a consequence of eruption of P_3, has a prominent protoconid on M_1 and, a dentary of even depth beneath the molar row. Dentary: dorsal portion of the coronoid process damaged; angular process medially compressed compared to *Hypsiprymnodon* species and raised to height of tooth row; a dorsally oriented flange apparent along lingual margin of angular process; distance from condyle to P_3 relatively shorter than for species of *Hypsiprymnodon*; dentary profile ventrally convex. I_1: medially compressed with root exposed to border of mental foramen; far less robust than *P. oscillans,* less gracile than for species of *Hypsiprymnodon*; no horizontal wear surface as in *P. oscillans.* I_2: only alveolus remains; P_2, P_3, M_{1-3} do not differ significantly from holotype. M_4: smaller than preceding molars; wider anteriorly than posteriorly; entoconid reduced.

QM F24199, juvenile, left dentary containing P_2, unerupted P_3, dp_3, M_{1-4}. QM F24199 is the first juvenile specimen attributed to *E. ima.* Specimen has been referred to *Ekaltadeta ima* as morphology and size of P_2, M_{2-4} 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 M_1 and dorsally from beneath M_2; 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 dp_3 and M_1 exposing the erupting P_3. P_2: 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
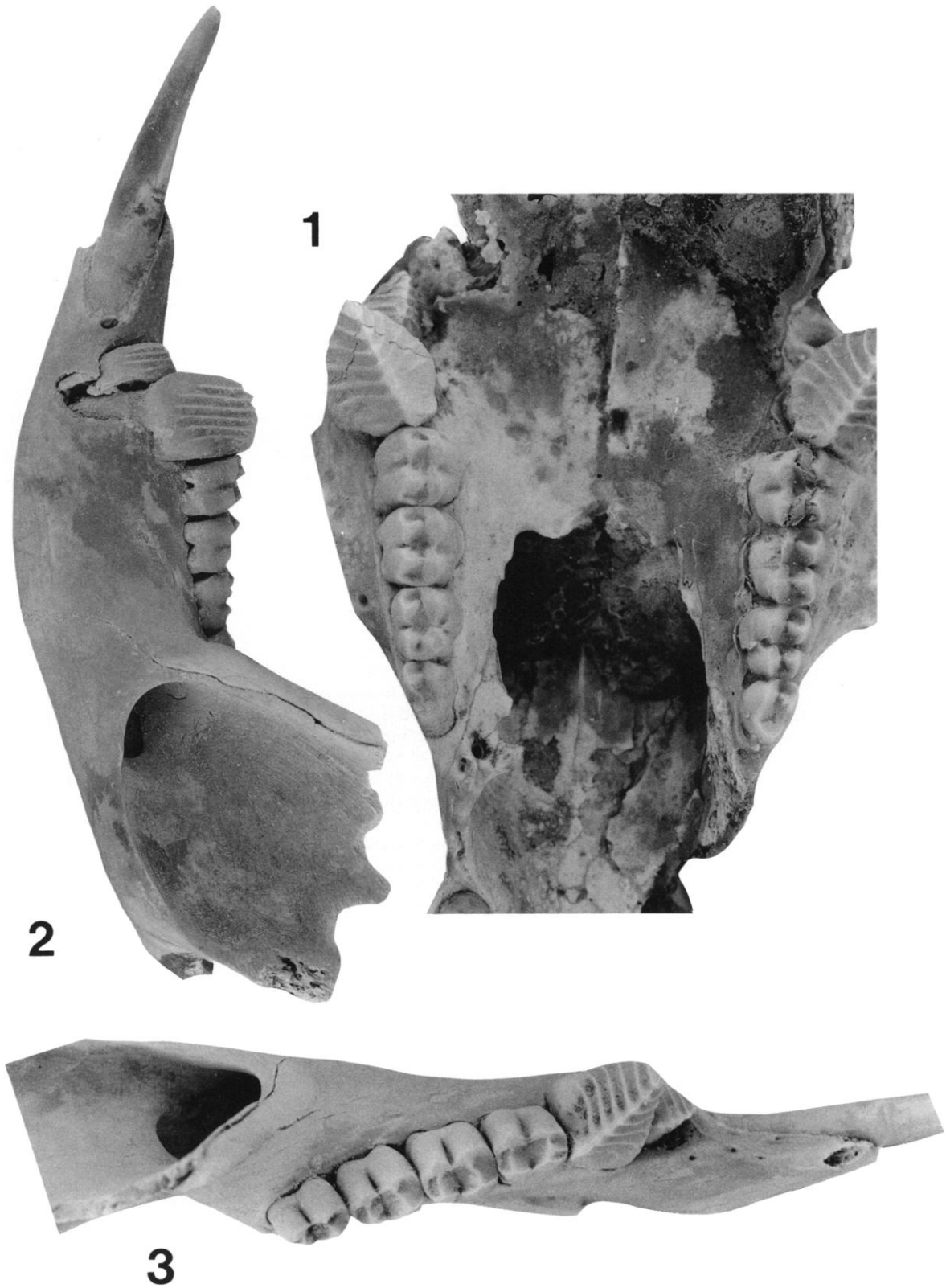
FIGURE *1—Ekaltadeta ima* (Archer and Flannery, 1985), ×2. *1,* occlusal view of QM F12436 (uppers). *2,* buccal view of QM F12435, left dentary containing I_1, alveolus for I_2, P_{2-3}, M_{1-4}. *3,* occlusal view of QM F12435.
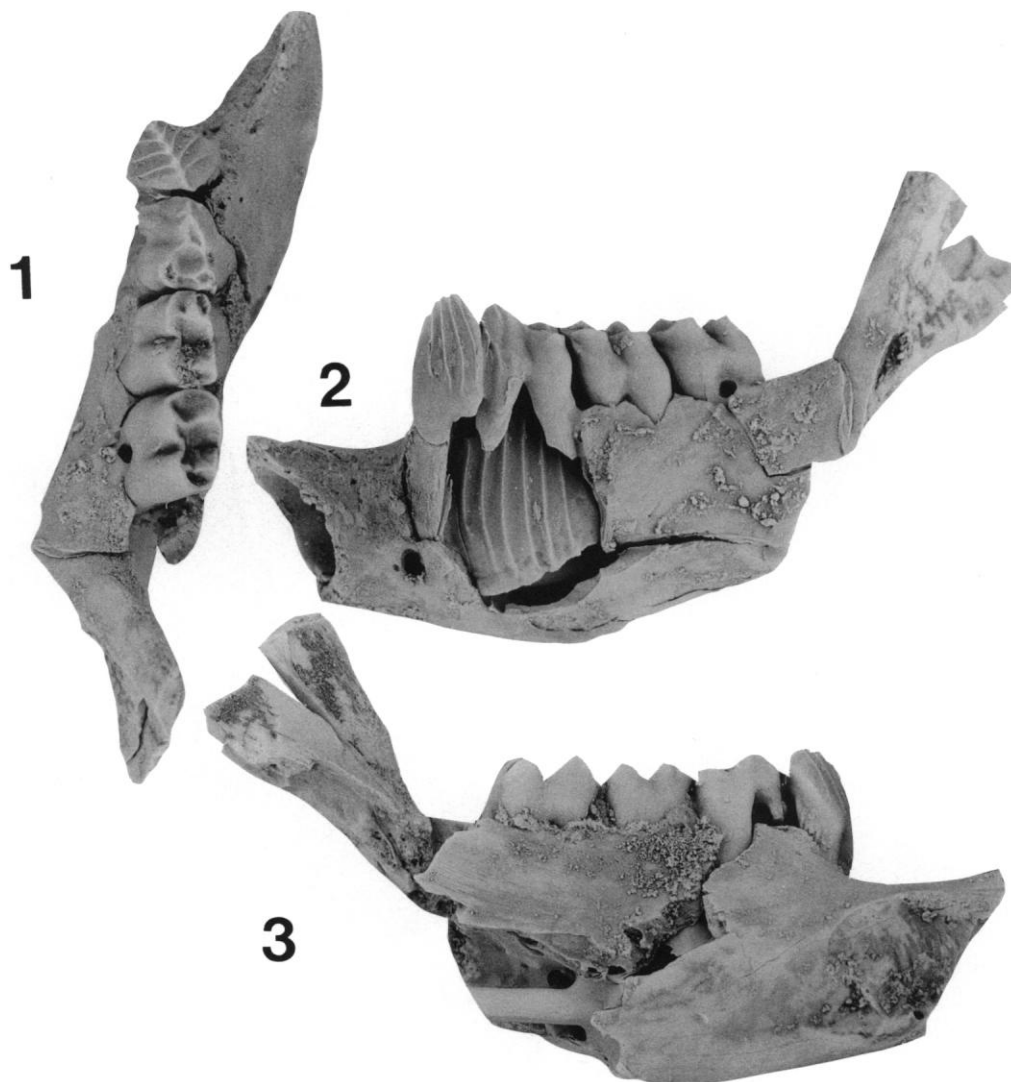
FIGURE 2—*Ekaltadeta ima* (Archer and Flannery, 1985), ×2. *1*, occlusal view of QM F24199, left dentary (juvenile), P_2, unerupted P_3, dp_3, M_{1-4}. *2*, buccal view of QM F24199. *3*, lingual view of QM F24199.

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 postentocristid 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_2, and the possession of basally broad upper molars showing a strong anterioposter 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 JAMIEMULVANEYI 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.
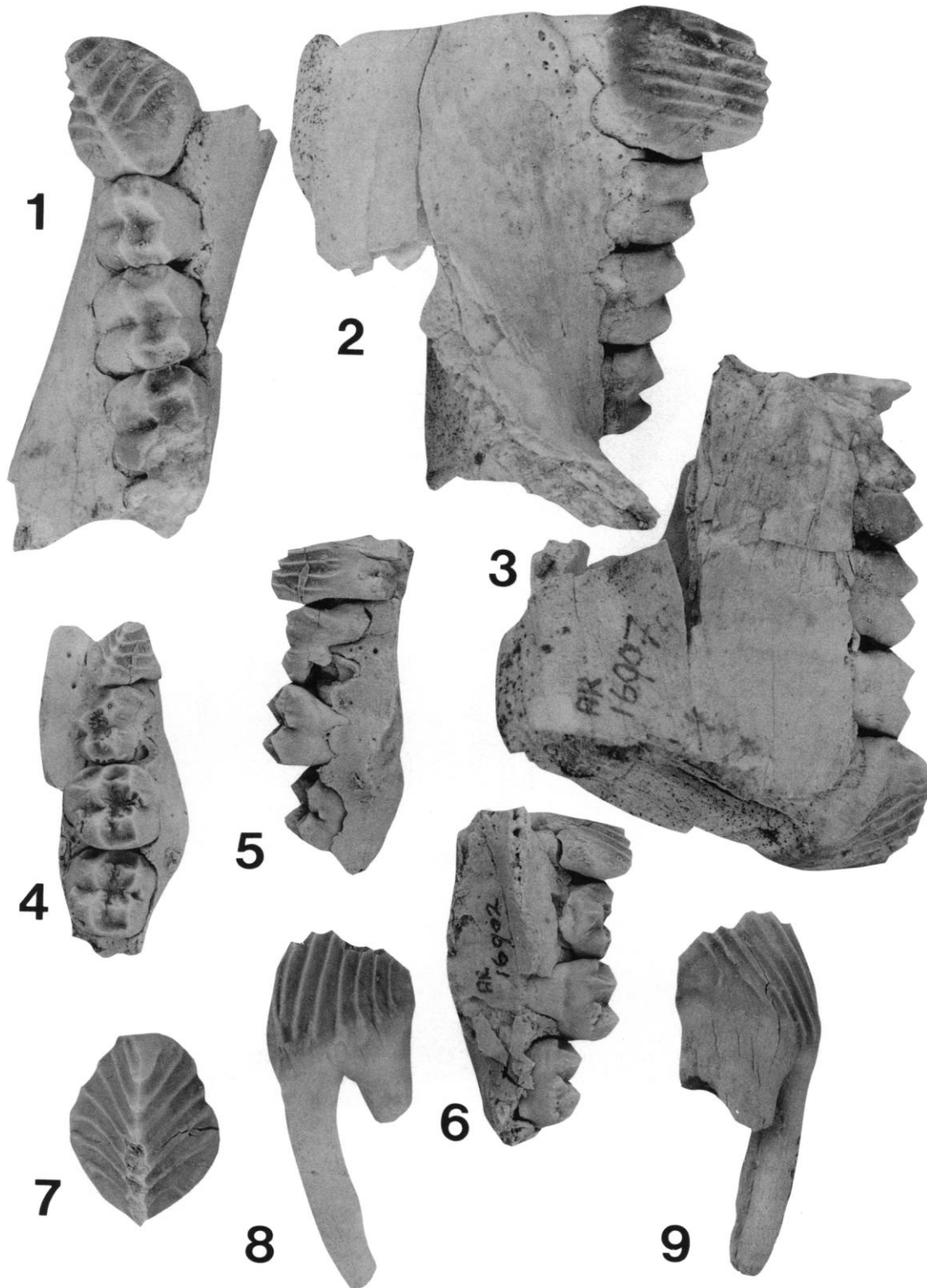
FIGURE 3—*Ekaltadeta jamiemulvaneyi* n. sp. ×2. *1*, occlusal view of QM F24200, left dentary containing P$_3$, M$_{1-3}$, holotype. *2*, buccal view of QM F24200. *3*, lingual view of QM F24200. *4*, occlusal view of QM F24212, left maxillary fragment, containing P^2, dp^3, M$^{1-2}$, referred specimen. *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.

FIGURE 4—*Propleopus chillagoensis* (Archer, Bartholomai, and Marshall, 1978), ×2. *1*, occlusal view of NMV P15917 (cast), holotype right maxilla (juvenile), containing P^3 (partially erupted), partial M^1, M^{2-3}, partial M^4. *2*, *Propleopus oscillans* (de Vis, 1888), ×2. Occlusal view of QM F6675, left maxillary fragment, containing P^3, M^{1-2} (cast).
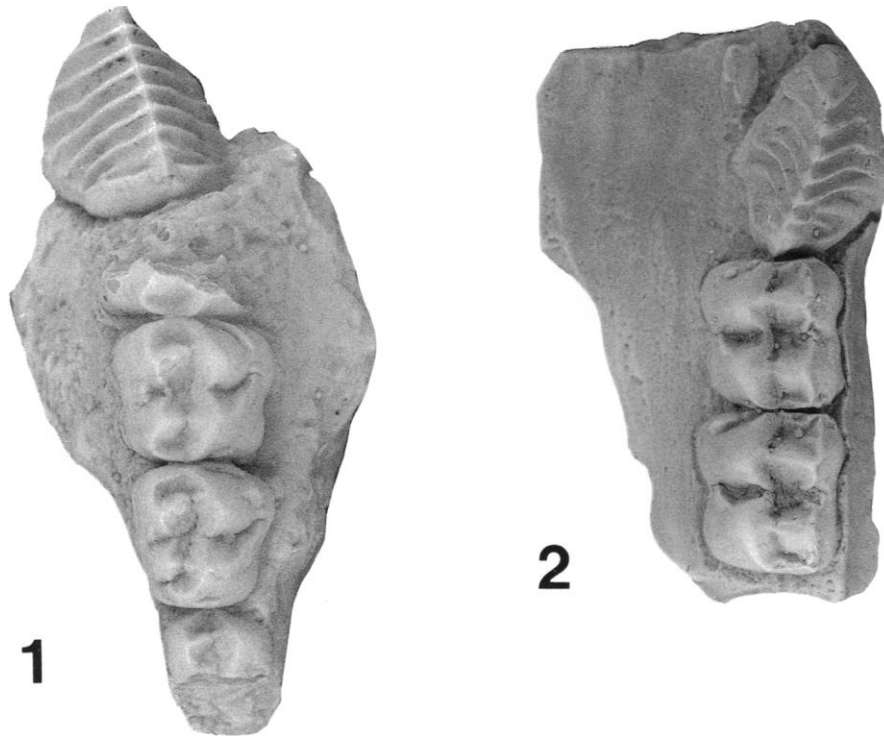
Diagnosis.—Very large species; P_3 raised high above occlusal plane of molars; hypoconid and entoconid of M_1 near equal in height; molar gradient of upper molars moderate.

Description.—QM F24200, holotype. Dentary: missing beyond anterior end of P_3 alveolus; dorsally coronoid process, angle and articular condyle missing; ventrally dentary broken away from approximately 12 mm below anterior end of M_2 alveolus; depth of the dentary measured from M_1 alveolus 28.8 mm; apart from size, where observable, the dentary closely resembles that of *E. ima*. P_3: larger in absolute terms than in *E. ima* and raised further above occlusal plane of molars, but relatively smaller; wear on anterior root of P_3 suggests that like *E. ima*, *E. jamiemulvaneyi* retained P_2 into adulthood. M_1: moderately worn; hypoconid and entoconid of equal height; lophid development more prominent than in *E. ima*. M_2: slightly wider posteriorly than anteriorly; entoconid lower than hypoconid; lophs well developed between principal cusps. M_3: entoconid broken away; anterior width of M_3 almost equals anterior width of M_4.

(QM F24212), left maxillary fragment (juvenile) containing P^2, unerupted P^3 (partial), dp^3, M^{1-2}. Maxilla: missing dorsally from a point 9 mm above alveolus of M^1; does not extend beyond the anterior end of P^2 or beyond posterior of M^2. P^2: similar in size and shape to P^2 of *E. ima*. P^3: has not erupted. dp^3: unworn, with anterior transversely compressed to form part of a sectorial blade complex with P^2; a crista runs anteriorly from paracone to intersect with mid line of the P^2; paracone higher than, and anterior to protocone; hypocone and metacone of equal height. M^1: wider anteriorly than posteriorly; paracone and metacone lower than hypocone and protocone; preprotocrista runs anterio-buccally to a well defined anterior cingulum;

crest emanating from paracone runs anteriorly to the same cingulum producing a basin; clearly defined cingulum exists lingually around protocone; cristae emanate from hypocone and metacone extending to posterior cingulum, forming a basin; lophid development between principal cusps weak. M^2: anterior width greater than posterior width of M^1; differs from M^1 in being almost as wide posteriorly as anteriorly, producing a more rectilinear tooth; metacone and paracone further reduced; protocone and hypocone relatively better developed than in *E. ima*.

QM F20842. Isolated left P^3. As in the holotype from the same site (Encore) the P^3 is larger than in *E. ima* specimens measured but otherwise very similar.

Remarks.—*Ekaltadeta jamiemulvaneyi* differs from *Ekaltadeta ima* in size, dentary being around 50 percent larger, approaching that of *Propleopus oscillans* (Figure 4), P3 smaller relative to molars, molar gradient less steep than *Ekaltadeta ima*, hypoconid and entoconid of M_1 near equal height in *Ekaltadeta jamiemulvaneyi*, entoconid well below hypoconid in *E. ima*, M^2 wider posteriorly than anteriorly in *E. jamiemulvaneyi*, reversed state in *E. ima*, M^{1-2} exhibit lingual cingula absent in *E. ima*, M^2 of *E. jamiemulvaneyi* wider posteriorly, paracone and metacone of M^{1-2} further reduced on the condition in *E. ima*. *Ekaltadeta jamiemulvaneyi* is similar to *E. ima* in possessing a prominent protoconid on M_2 and a dentary of even depth beneath the molar row. Wear on anterior root of P_3 suggests that like *E. ima*, *E. jamiemulvaneyi* retained P_2 into adulthood.

Etymology.—The species name is derived directly from J. Mulvaney in recognition of his contribution to the Riversleigh Society.
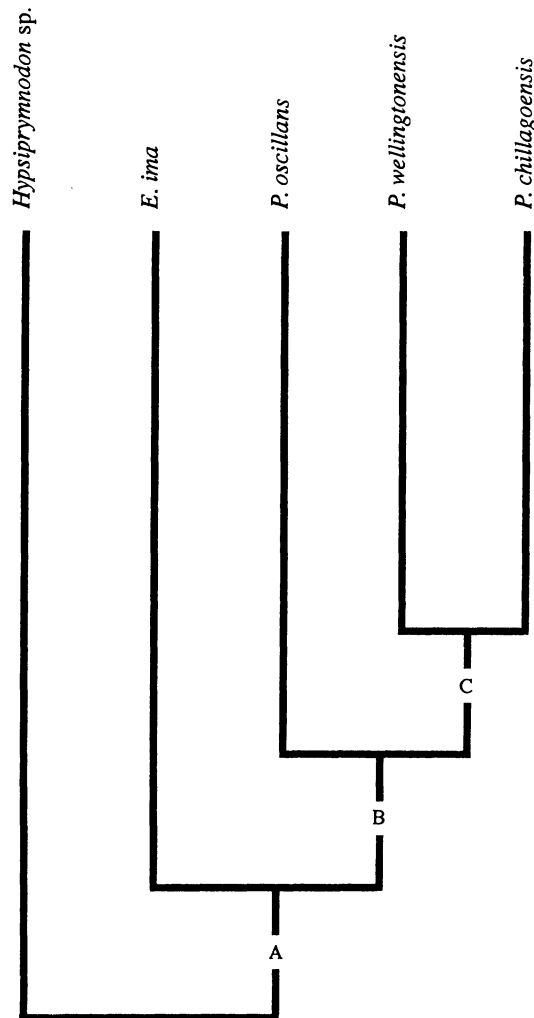
Material.—QM F24212, QM F20842.

FIGURE 5—Cladogram for the propleopines from Archer and Flannery (1985). Character states at nodes: A; gain of an anterior cristid emanating from the metaconid of M_1, gain of derived I_1 morphology. B; incorporation of the protolophid into the anterior lophid of M_1, loss of P2 with eruption of P3, dentary deeper anteriorly than posteriorly. C; reduction of metacone/entoconid, P3 hypertrophy.

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 Propleopinae has been scarce in the extreme with all material referable to a single Pleistocene species first described by De Vis as *Triclis oscillans* (1888). This species was redescribed as *Propleopus oscillans* by Longman (1924). Following a ninety year hiatus, Archer, Bartholomai and, Marshall (1978) described a new propleopine, *Propleopus chillagoensis* 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, *Ekaltadeta ima* from Oligo–Miocene local faunas of Riversleigh.
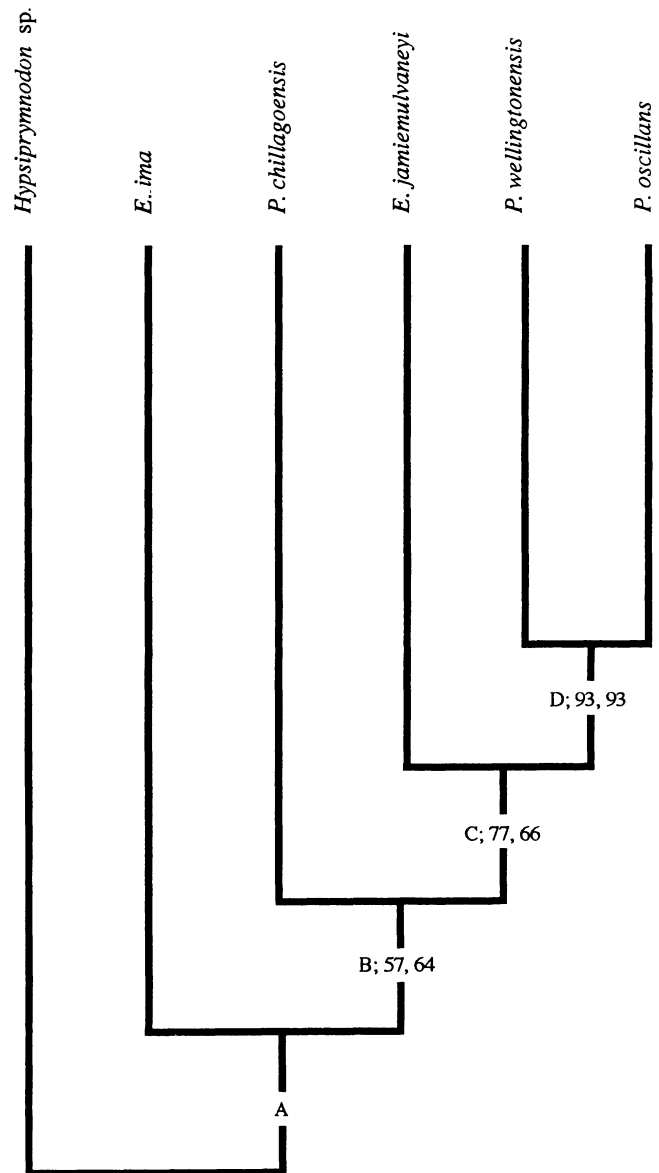
FIGURE 6—Minimal tree produced by Wagner analysis and fifty percent majority rule consensus trees generated by bootstrap analyses for the Propleopinae were each of identical topology. Character states at nodes: A; gain of an anterior cristid emanating from the metaconid of M_1; basally broad conical upper molars. B; presence of lingual cingula on the upper molars. C; reduced molar gradient, reduced P3. D; incorporation of the protolophid into the anterior lophid of M_1, a dentary deeper posteriorly than anteriorly. Values from bootstrap analyses are given at nodes B–D. The second value (right) is from the analysis in which character five (relative width of P3) was treated as part of a single character complex.

The inclusion of *Ekaltadeta jamiemulvaneyi* 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 *Hypsiprymnodon* and the identification of propleopines and hypsiprymnodontines as sister groups has been accepted by all subsequent authors (Tate, 1948; Woods, 1960; Archer and Flannery, 1985).

TABLE *1*—Distribution of character states used in Wagner and bootstrap analysis: 0 = plesiomorphic; 1 = apomorphic; ? = missing.

Species	1	2	3	4	5	6	7	8	9	10	11
Hypsiprymnodon sp.	0	0	0	0	0	0	0	0	0	0	0
E. ima	1	0	0	0	0	0	0	0	0	0	0
E. jamiemulvaneyi	1	0	0	1	1	0	?	?	?	1	1
P. chillagoensis	?	?	?	0	0	0	?	?	?	1	1
P. wellingtonensis	1	?	1	1	1	1	?	1	?	?	?
P. oscillans	1	1	1	1	1	1	1	1	1	1	0

TABLE *2*—M^2 aw divided by M^2 pw (G-value) for propleopines and a *Hypsiprymnodon* sp. from Riversleigh local faunas. Measurements in mm.

Species	Catalogue no.	M^2 aw	M^2 pw	G-value
E. ima	QM F24203	6.800	6.100	1.115
E. ima	QM F24204	6.800	6.200	1.097
*E. ima**	QM F12436	6.400	5.800	1.103
*E. ima**	QM F12436	+	5.900	
E. ima	QM F24205	6.500	5.900	1.102
E. ima	QM F24206	6.800	5.900	1.150
E. ima	QM F24207	7.200	6.600	1.091
E. ima	QM F24208	6.700	5.900	1.136
E. ima	QM F24209	6.200	5.400	1.148
E. ima	QM F24210	7.400	6.600	1.121
E. ima	QM F24211	6.900	5.800	1.19
E. jamiemulvaneyi	QM F24212	6.900	6.600	1.045
P. oscillans	QM F6675 (cast)	9.200	8.700	1.057
P. chillagoensis	NMV P15917 (cast)	10.70	8.700	1.231
Hypsiprymnodon sp.	QM F29840	2.700	2.400	1.125
Hypsiprymnodon sp.	QM F24156	2.700	2.400	1.129
Hypsiprymnodon sp.	QM F24159	2.900	2.500	1.160
Hypsiprymnodon sp.	QM F24153	2.800	2.500	1.120
Hypsiprymnodon sp.	QM F24155	2.900	2.500	1.160
Hypsiprymnodon sp.	QM F24161	2.800	2.400	1.145
Hypsiprymnodon sp.	QM F24152	2.700	2.400	1.125
Hypsiprymnodon sp.	QM F24157	2.900	2.600	1.115

* = Skull; (R) = right tooth row; (L) = left tooth row; + = damaged.

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. oscillans* the more plesiomorphic and *P. chillagoensis* the more apomorphic (Figure 5). The discovery of more complete *E. ima* material and a new species of *Ekaltadeta* 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 (Felsenstien, 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 *Hypsiprymnodon* (Muller 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_1. Presence of an anterior cristae emanating from the metaconid of M_1 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_1 in *E. jamiemulvaneyi*. Lack of anterior cristae in *Hypsiprymnodon* 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. oscillans* 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 *Hypsiprymnodon* sp. Consequently the spatulate I_1 of *P. oscillans* was treated as derived within the Propleopinae in this study.

3. Partial or complete incorporation of the protoconid into the anterior lophid of M_1. In *E. ima*, *E. jamiemulvaneyi* and *Hypsiprymnodon* sp. the protoconid of M_1 was distinct. The M_1 protoconid was incorporated into the anterior protolophid in *P. oscillans* 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. chillagoensis* from *P. oscillans* 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 *Ekaltadeta 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 ramified through M^{3-4}. In *E. ima* M^4 pw was less than half M^2 aw. For *P. oscillans* M^{3-4} were 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_{1-4} tooth width decreased at a steady rate anterio-posteriorly in *E. ima* but was reversed in *P. oscillans* where tooth width increased posteriorly for M_{1-3}, 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. chillagoensis* 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

TABLE 3—M_1 pw divided by M_2 pw (G-value) for propleopines and a *Hypsiprymnodon* sp. from Riversleigh local faunas. Measurements in mm.

Species	Catalogue no.	M_1 pw	M_2 pw	G-value
E. ima	QM F24195	6.700	6.300	1.063
E. ima	QM F24196	6.300	5.900	1.068
E. ima	QM F24197	6.500	6.000	1.083
E. ima	QM F24198	5.700	5.500	1.036
E. ima	QM F12435	6.500	6.200	1.048
E. ima	QM F24199	6.500	6.100	1.066
E. ima	QM F12423	7.000	6.900	1.014
E. jamiemulvaneyi	QM F24200	8.200	8.500	0.965
P. wellingtonensis	UCM P45171 (cast)	9.200	9.600	0.958
P. oscillans	QM F3302 (cast)	9.700	10.400	0.933
Hypsiprymnodon sp.	QM F24148	2.300	2.200	1.045
Hypsiprymnodon sp.	QM F13426	2.400	+	
Hypsiprymnodon sp.	QM F24166	2.400	2.300	1.043
Hypsiprymnodon sp.	QM F24169	2.300	2.300	1.000
Hypsiprymnodon sp.	QM F24171	2.300	2.300	1.000

+ = damaged.

TABLE 4—P_3 w divided by M_1 pw (G-value) for propleopines and a *Hypsiprymnodon* sp. from Riversleigh local faunas. Measurements in mm.

Species	Catalogue no.	P_3 w	M_1 pw	G-value
E. ima	QM F24201	10.300	6.800	1.515
E. ima	QM F12435	8.700	6.500	1.338
E. ima	QM F12424	8.800	6.500	1.354
E. ima	QM F12423	9.600	7.000	1.371
E. jamiemulvaneyi	QM F24200	10.500	8.200	1.280
P. oscillans	QM F3302 (cast)	10.600	9.700	1.093
Hypsiprymnodon sp.	QM F24148	3.200	2.300	1.390
Hypsiprymnodon sp.	QM F24168	3.500	2.400	1.460
Hypsiprymnodon sp.	QM F24166	3.400	2.400	1.420
Hypsiprymnodon sp.	QM F24169	3.400	2.300	1.480
Hypsiprymnodon sp.	QM F24168	3.300	2.300	1.430

M_2 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. jamiemulvaneyi* (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 *Hypsiprymnodon* sp. from Riversleigh which ranged from 1.120 to 1.602. For the lower dentitions *P. oscillans*, *P. wellingtonensis* and *E. jamiemulvaneyi* showed an apparent reversal in molar gradient in comparison to *E. ima* and *Hypsiprymnodon*. sp. *Propleopus oscillans* had a G-value of 0.933 whilst *P. wellingtonensis* and *E. jamiemulvaneyi* showed G-values of 0.958 and 0.965 respectively. In *Ekaltadeta ima* and *Hypsiprymnodon* sp. 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 *Hypsiprymnodon* sp.

As a high molar gradient in the upper molars and a tendency for the molars to decrease in size anterio-posteriorly in the lower dentition was a feature of *Hypsiprymnodon* sp. 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 (Kluge and Farris, 1969)). 5. Relative size of P3. A measure of relative P3 size was determined by dividing P_3 width (w) by M_1 posterior width (pw) (Table 4). In *P. oscillans* the P_3 w was small compared to the M_1 pw (1.093). The *Ekaltadeta ima* specimens had high values ranging from 1.354 to 1.515. *Ekaltadeta jamiemulvaneyi* positioned between *E. ima* and *P. oscillans*, with a value of 1.280. In *Propleopus wellingtonensis* only the alveolus for P_3 remained. Although P_3 alveolus size in *P. wellingtonensis* suggested that this tooth may have been larger than the P_3 of *P. oscillans*, it was relatively small compared to the alveoli for P_3 in *E. ima* or *Hypsiprymnodon* sp. No P_3 exists for *Propleopus chillagoensis*, however P^3 was huge, at least fifty percent larger than the P^3 in *P. oscillans*. For the out-group *Hypsiprymnodon* sp., 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 entoconid in posterior molars. A reduction of metaconid or entoconid size posteriorly was considered a synapomorphy uniting *P. chillagoensis* and *P. wellingtonensis* by Archer and Flannery (1985). The presence of a reduced metacone in *Ekaltadeta jamiemulvaneyi*, *E. ima* and *Hypsiprymnodon* sp. contradicted this proposal and confirmed this character state as plesiomorphic for propleopines. 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 *Propleopus* by Archer and Flannery (1985). In *Ekaltadeta jamiemulvaneyi* the dentary was missing anteriorly of the P_3, and retention or loss of P2 with eruption of P3 could not be confirmed for *Propleopus chillagoensis*. The brief persistence of P2 after the eruption of P3 in *Hypsiprymnodon* sp. supported the treatment of this character state as a plesiomorphy. 8. Dentary morphology. The dentaries of *Propleopus oscillans* and *P. wellingtonensis* were markedly deeper anteriorly than posteriorly. In *Hypsiprymnodon* sp., *Ekaltadeta ima* and *E. jamiemulvaneyi* depth along the jaw did not vary noticeably and this was considered the plesiomorphic state. 9. Diastema. A large diastema was present in *Propleopus oscillans* anterior to the P_3. The absence of a marked diastema as shown by *Hypsiprymnodon* sp. and *E. ima* suggested plesiomorphy 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. jamiemulvaneyi*. 10. Cingula on upper molars. *Ekaltadeta jamiemulvaneyi* had cingula on M^{1-2} 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 *Hypsiprymnodon* sp. and *E. ima* and their absence was considered a plesiomorphy. 11. Shape of upper molars. In *Propleopus oscillans* the upper molars were dorsoventrally regular in width. *Hypsiprymnodon* sp., *Ekaltadeta ima*, *E. jamiemulvaneyi*, 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 *Ekaltadeta*, 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. *Ekaltadeta 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 a *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 cristid emanating from the metaconid of M_2, 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 M_1 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 carnivorans (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_1 with a horizontal wear facet. The relationships of *Ekaltadeta jamiemulvaneyi* and *P. chillagoensis* as presented in this study are provocative. Monophyly for a *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 proposition must remain tentative as it is founded on monophyly implied by two synapomorphies which may constitute a single character complex. Bootstrapping forwarded 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* as was 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. jamiemulvaneyi* and/or *P. chillagoensis* to resolve the problems of paraphyly and polyphyly that would exist under the current scheme.

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