STRATIGRAPHY AND PHYLOGENY OF THE GIANT EXTINCT RAT KANGAROOS (PROPLEOPINAE, HYPSIPRYMNODONTIDAE, MARSUPIALIA)

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The Giant Rat-kangaroos were placed in the Propleopinae by Archer & Flannery (1985) and in the Hypsiprymnodontidae by Ride (1993). Cladistic analysis of *Ekaltadeta* material from Riversleigh, northwestern Queensland (Wroe, 1996) suggested that a middle to late Miocene dichotomy in *Ekaltadeta* may have produced two lineages of Plio-Pleistocene *Propleopus*, indicating polyphyly for *Propleopus* and paraphyly for *Ekaltadeta*. Metrical data for propleopines and stratigraphic information support Wroe's (1996) cladistic analysis of propleopines. ☐ *Propleopinae, Hypsiprymnodontidae, Riversleigh, Ekaltadeta, cladistics.*

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Giant Rat-kangaroos (Hypsiprymnodontidae: Propleopinae) may be the plesiomorphic sister group of potoroids (Flannery, 1987). Archer & Flannery (1985) considered *Ekaltadeta ima*,(Fig. 1) the sister group to *Propleopus* De Vis, 1888 with *P. oscillans* De Vis, 1888 (Fig. 2) the more plesiomorphic and *P. chillagoensis* Archer et al. (1978) (Fig. 2) the more apomorphic within *Propleopus* (Fig. 3). Propleopine species described since 1985 are *Ekaltadeta jamiemulvaneyi* Wroe, 1996, (Fig. 4) and *Jackmahoneya toxoniensis* Ride, 1993. Wroe (1996) suggested another possible phylogeny for the Propleopinae with *E. ima* and *P. chillagoensis* forming the sister group to another clade containing a new species, *E. jamiemulvaneyi*, as the sister taxon to *P. wellingtonensis* and *P. oscillans*.(Fig. 5). As an adjunct to the cladistic analysis (Wroe, 1996), metric and stratigraphic data for propleopines are used to clarify intrasubfamilial relationships.

Dental homology for premolars follows Flower (1867) and Luckett (1993) for molars. Higher level systematics of kangaroos follows Flannery (1987) and Ride (1993). Specimens are housed in the Queensland Museum (QMF). Other prefixes include; UCM (University of California Museum), NMV (Museum of Victoria).

METHODS

Specimens of *Ekaltadeta* from Riversleigh represent 30 individuals from several stratigraphic levels. The relative paucity of specimens and chronological data precludes a strictly stratophenetic approach (*sensu* Gingerich, 1976, 1979; Bown & Rose, 1987) to propleopine phylogeny. However, a more general consideration of stratigraphy in phylogenetic analysis may be appropriate in association with cladistic treatment where specimens are stratigraphically disjunct or sparsely distributed (Gingerich, 1990).

Sites with *Ekaltadeta* are late Oligocene to early late Miocene (Archer et al., 1989, 1994, 1995). A number of characters were analysed to assess the development of time-dependent changes. Specimens were ranked to indicate relative age (Appendix 1). Stratigraphic levels are from Archer et al. (1989, 1995): level 1=late Oligocene early Miocene; level 2=early Miocene; level 3=late early Miocene; level 4=mid Miocene; level 5=late mid Miocene; level 6=early late Miocene; level 7=Pliocene; level 8=Pleistocene.

I included all propleopines possible, although Pliocene and Pleistocene *Jackmahoneya* and *Propleopus* are known from material often limited to portions of upper and/or lower dentitions. Most *Propleopus* are from the Pleistocene, although material has been recorded from early Pliocene local faunas (Archer & Flannery, 1985). *Propleopus chillagoensis* was described as Pleistocene (Archer et al., 1985), but could be older, possibly late Miocene or early Pliocene (Archer pers. comm.). *Jackmahoneya toxoniensis* is Pliocene (Ride, 1993).

Differences in molar gradient were used by Archer & Flannery (1985) and Wroe (1996) to distinguish propleopine species. Molar gradient reflects both the surface area and length of the molar tooth row. In propleopines a high molar gradient correlates with a reduction in both molar surface area and the length of the tooth row.

Reducing the distance between condyle and sectorial tooth maximizes leverage applicable to the tooth (Young et al., 1989). Through shortening the molar row, leverage on the large shearing $P^3/_3$ of propleopines is increased. This effect is achieved at the cost of molar length.

Relative P_3 size and molar gradient for upper and lower dentitions has been quantified. Distinct reduction in tooth size posteriorly occurs in upper and lower dentitions of *E. ima*. In the upper dentition this steep gradient begins with a reduced posterior width (pw) relative to the anterior width (aw) of M^2 which then ramifies through M^{3-4}. In *E. ima* M^4 pw is $<1/2$ M^2 aw. The upper dentition of *P. chillagoensis* is similar to that of *E. ima*. Lower dentition is not known for *P. chillagoensis*. For *P. oscillans* M^{3-4} are missing but M^2 pw is only slightly less than M^2 aw suggesting a less extreme gradient. This supposition is strongly supported by the lower dentition in which molar gradient contrasts strongly with *E. ima*. M_{1-4} tooth widths decrease steadily anteroposteriorly in *E. ima* but are reversed in *P. oscillans* where tooth width increases posteriorly for M_{1-3}, with only a slight decrease in M_4.

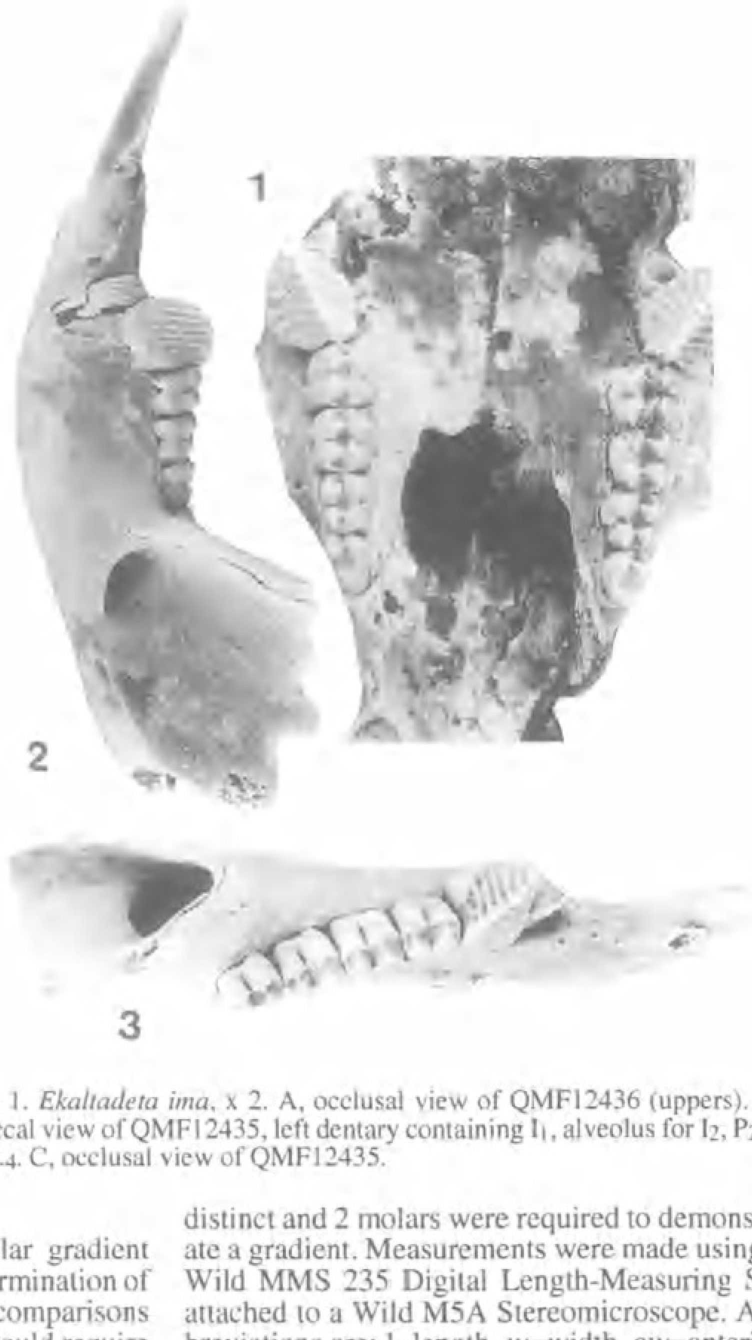

FIG. 1. *Ekaltadeta ima*, x 2. A, occlusal view of QMF12436 (uppers). B, buccal view of QMF12435, left dentary containing I_1, alveolus for I_2, P_{2-3}, M_{1-4}. C, occlusal view of QMF12435.

Several methods to quantify molar gradient have been considered. Accurate determination of individual molar surface areas and comparisons between teeth would be useful but would require 2 or more teeth/ specimen, greatly limiting data sets, particularly for upper dentitions. Molar gradient might also be estimated geometrically by determining the angle at which a line drawn buccally or lingually through the faces of the crown intersects the mid-line of the dentary or skull.

In this study the clear initiation of a marked molar gradient at M^2 in the upper dentitions of *E. ima* and *P. chillagoensis* permitted estimation of the gradient from a single molar by comparing aw to pw. In lower dentitions the gradient is less distinct and 2 molars were required to demonstrate a gradient. Measurements were made using a Wild MMS 235 Digital Length-Measuring Set attached to a Wild M5A Stereomicroscope. Abbreviations are: l=length, w=width, aw=anterior width, pw=posterior width, dd=depth of dentary, G-value=ratio of anterior to posterior tooth width.

RESULTS

M^2 aw / M^2 pw VS STRATIGRAPHIC LEVEL. (Fig. 6). For upper dentitions the ratio M^2 aw: M^2 pw (G-value) was used as an arbitrary measure of molar gradient, with M^2 being common to the largest number of specimens.

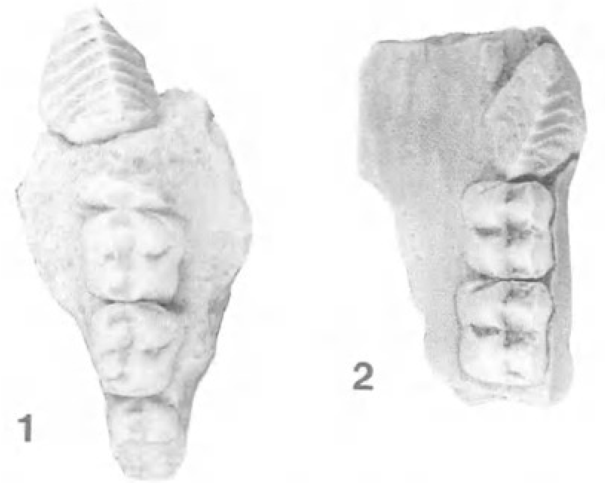

FIG. 2. *Propleopus chillagoensis*, x 2. A, occlusal view of NMV P15917, right maxillary fragment (juvenile), containing unerupted P^3, partial M^1, M^{2-3}, partial M^4 (cast of holotype). B, *Propleopus oscillans*, x 2, occlusal view of QMF6675, left maxillary fragment, containing P^3, M^{1-2}.

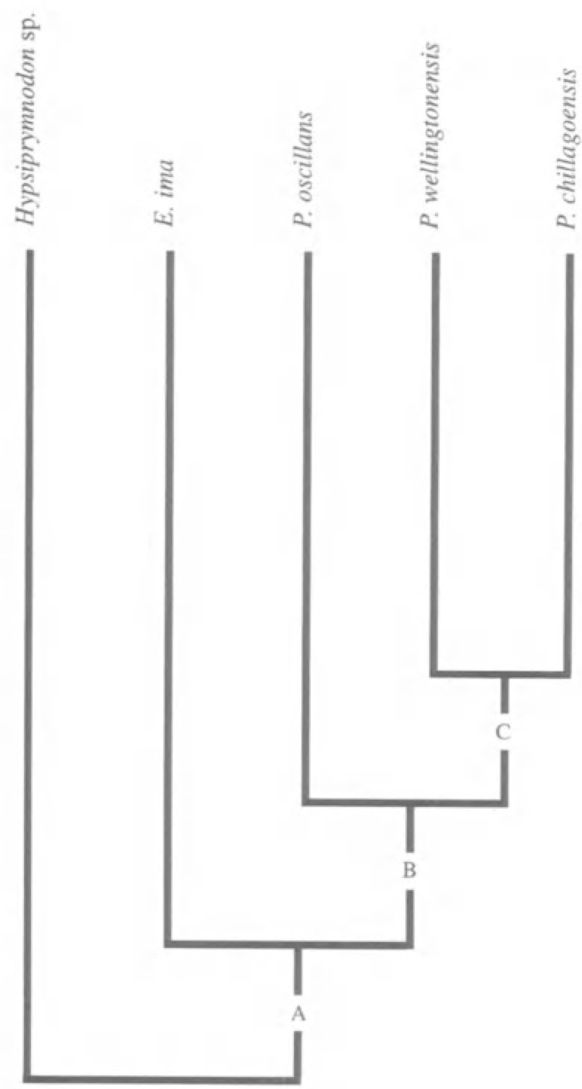

FIG. 3. Cladogram for the propleopines from Archer & Flannery (1985). Character states at nodes: A=gain of an anterior cristid emanating from the metaconid of M_1, gain of derived I_1 morphology; B=incorporation of the protolophid into the anterior lophid of M_1 loss of P_2 with eruption of P3, dentary deeper anteriorly than posteriorly; C=reduction of metacone/entoconid, P3 hypertrophy.

A trend is apparent in this scatter graph of G-value against stratigraphic level. *P. chillagoensis* and *P. oscillans* represent 2 extremes with G-values of 1.23 and 1.06 respectively, with the lower number indicating a lesser molar gradient. *Ekaltadeta ima* from levels 3 and 4 has a limited range of G-values (1.09-1.15).

The 2 *Ekaltadeta* from level 6 both fell outside the range of *E. ima* from older strata. *E. jamiemulvaneyi* (QMF24212; Cleft of Ages 4 Site) had a low G-value of 1.05, slightly less than that of *P. oscillans*. *E. ima* (QMF24211; Henk's Hollow Site) had a relatively high G-value of 1.19 approaching that of *P. chillagoensis*. These results indicate a divergence in the *Ekaltadeta* lineage with one population leading to *P. oscillans* and another leading to *P. chillagoensis*.

M_1 pw / M_2 pw VS STRATIGRAPHIC LEVEL. (Fig. 7). The molar gradient of the dentary was estimated by dividing M_1 pw by M_2 pw (G-value). *P. oscillans* had the lowest G-value at 0.93. The G-values for *P. wellingtonensis* and *J. toxoniensis* were slightly higher at 0.96. At levels 3 and 4 the G-values for *Ekaltadeta* were 1.01-1.08. The G-value for *E. jamiemulvaneyi*, from level 6 (QMF24200, Encore Site) was 0.97. This placed *E. jamiemulvaneyi* about halfway between the lowest G-value from levels 3 and 4 and *P. oscillans*. Again the highest degree of divergence among *Ekaltadeta* was for the *E. jamiemulvaneyi* from level 6, possibly indicating a trend toward the species with low molar gradients (*J. toxoniensis*, *P. oscillans* and *P. wellingtonensis*).

P_3 w/M_1pw VS STRATIGRAPHIC LEVEL. (Fig. 8). In *P. oscillans* P_3 width was small compared to M_1 posterior width (1.09). For *J. toxoniensis* relative P_3 width was greater (1.27). *E. ima* from levels 3 and 4 had ratios of P_3 w / M_1 pw of 1.35-1.52. *E. jamiemulvaneyi* from Encore site (QMF24200) again positioned between *E. ima* from lower strata and *J. toxoniensis* / *P. oscillans*, with a ratio of 1.28.

DEPTH OF DENTARY AGAINST STRATIGRAPHIC LEVEL. Depth of dentary against stratigraphic level (Fig. 9). Dentary depth was measured from the alveolar margin of M_1 to the ventral margin of the dentary perpendicular to the molar row. Variation in the depth of dentaries was small for *E. ima* from levels 3 and 4 (19.3-21.1mm). *E. jamiemulvaneyi* (QMF24200) was much larger with a dentary depth of 28.8mm approaching *P. oscillans* (32.6mm). *J. toxoniensis* between *E. ima* and *E. jamiemulvaneyi*/*P. oscillans* with a dentary depth of 23.3mm.

STATISTICAL ANALYSIS. (Table 1). Because all *Ekaltadeta* material has come from a relatively small area (Riversleigh), a regional population of potoroids was considered an appropriate control. Sixteen specimens from the Australian museum of *Potorous tridactylus* collected around Hobart were used, this being the largest potoroid specimen sample available. Variation in the G-values of *Ekaltadeta* from levels 3 and 4 approached that of *P. tridactylus*. When G-values from the 2 *Ekaltadeta* from level 6 were included the variation fell well outside that of the local *P. tridactylus* population.

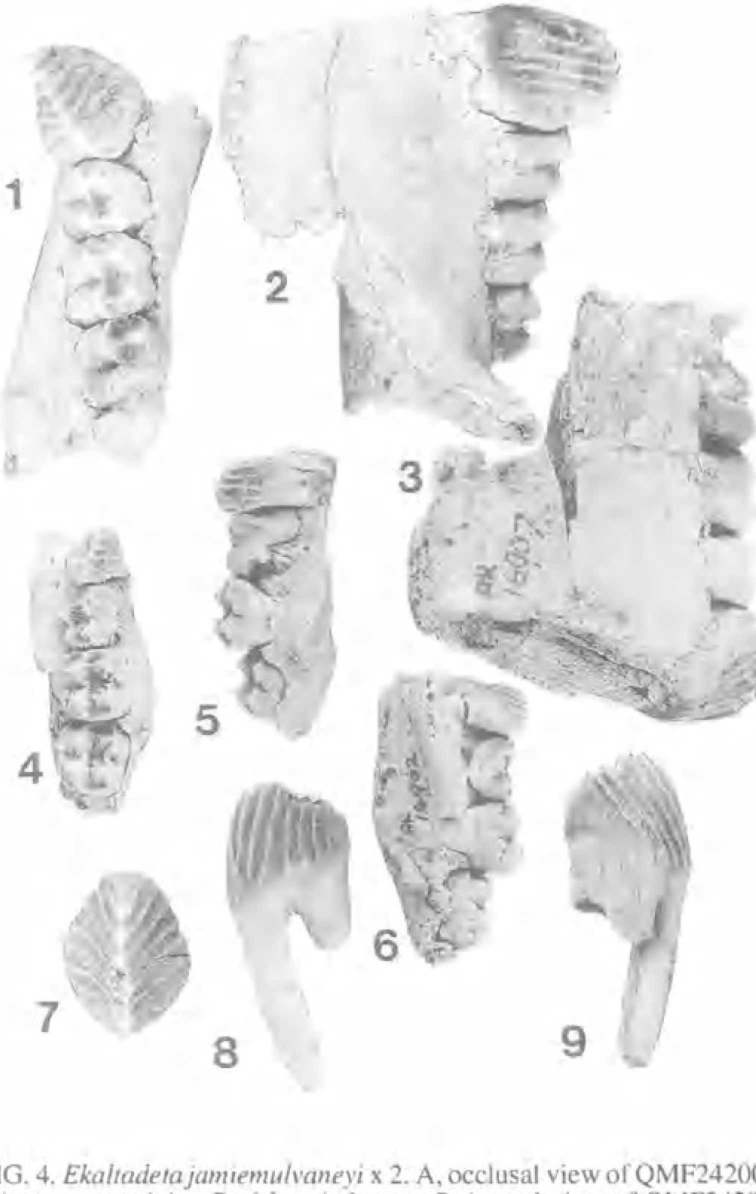

FIG. 4. *Ekaltadeta jamiemulvaneyi* x 2. A, occlusal view of QMF24200, left dentary containing P_3, M_{1-3}, holotype. B, buccal view of QMF24200. C, lingual view of QMF24200. D, occlusal view of QMF24212, left maxillary fragment, containing P^2, dP^3, M^{1-2}, referred specimen. E, buccal view of QMF24212. F, lingual view of QMF24212. G, occlusal view of QMF20842, left P^3, referred specimen. H, buccal view of QMF20842. I, lingual view of QMF20849.

DISCUSSION

Increases in premolar and molar shear within the Propleopinae appear to be mutually exclusive and their relative importance probably reflects dietary preference. A requirement for high premolar shear might be associated with carnivory (Abbie, 1939), while a more extensive molar array may indicate a more herbivorous diet (Wells et al., 1982).

Species with a large molar surface area and low molar gradient (*P. oscillans*, *P. wellingtonensis*, *J. toxoniensis*) have relatively small premolars. Species with high molar gradients and reduced molar shear (*E. ima*, *P. chillagoensis*) are characterised by P3 hypertrophy. The extraordinary change in function for P2 shown by individ-

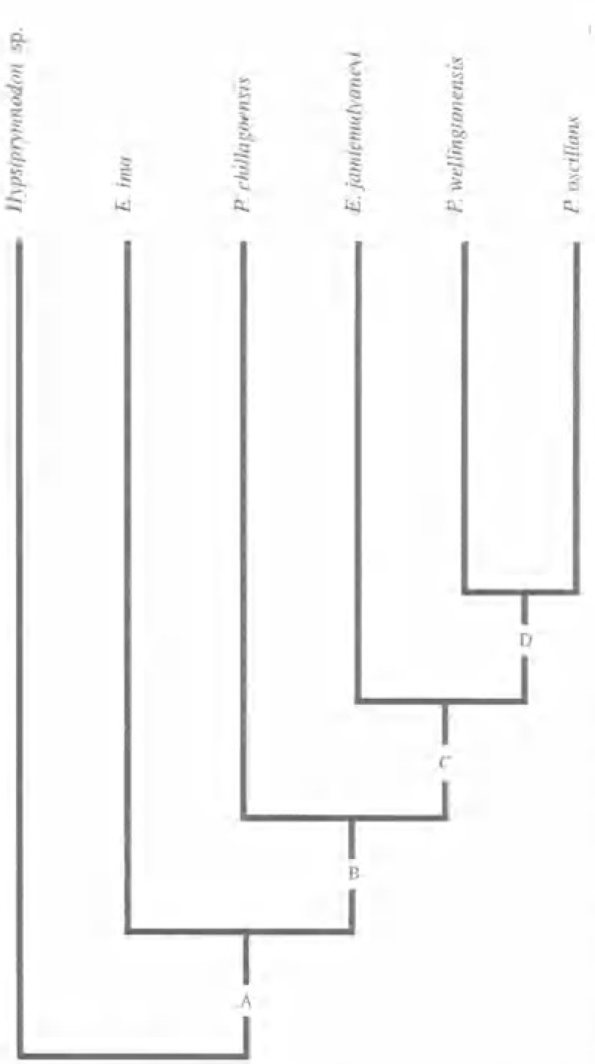

FIG. 5. Minimal tree produced by Wagner analysis for the Propleopinae (from Wroe, 1996). Character states at nodes: A = gain of an anterior cristid emanating from the metaconid of M_1; basally broad conical upper molars; B = presence of lingual cingula on the upper molars; C = reduced molar gradient, reduced P3; D = incorporation of the protolophid into the anterior lophid of M_1, a dentary deeper posteriorly than anteriorly.

ual *E. ima* (Wroe & Archer, 1995) probably constitutes a response to the increased loading placed on P3. Regarding molar gradient and relative size of the P_3, *E. jamiemulvaneyi* is intermediate, falling between *E. ima* specimens from lower levels and *P. oscillans/P. wellingtonensis/J. toxoniensis*. Using the same criteria *J. toxoniensis* lies between *E. jamiemulvaneyi* and *P. oscillans/P. wellingtonensis*. In terms of variation in P3 size and molar gradient *P. chillagoensis* and *P. oscillans* represent opposite extremes in propleopine evolution and it is suggested that *P. oscillans*

TABLE 1. Statistical summaries for M^2 aw / M^2 pw (G-value) for propleopines and a local *P. tridactylus* population.

	N	SD	CV	SE
Propleopines to level 8	13	0.05	4.53	0.01
Ekaltadeta to level 6	11	0.38	3.35	0.01
Ekaltadeta to level 4	9	0.02	2.07	7.71 E-3
P. tridactylus	16	0.02	1.70	4.61 E-3

was largely if not wholly herbivorous. Other derived features interpreted as adaptations to herbivory for *P. oscillans* include a large diastema between P_3 and I_1, and large spatulate lower incisors (Wroe, 1996). Regarding dentary depth *E. ima* is the smallest propleopine with a general increase in depth for taxa at higher stratigraphic levels probably reflecting a general increase in body size.

Stratigraphic and metric analysis support the proposal of a late Miocene dichotomy in *Ekaltadeta* producing 2 lineages of *Propleopus*, and a reversal of previous assumptions on relative apomorphy within *Propleopus*, with *P. oscillans* considered the most derived and *P. chillagoensis* the most plesiomorphic (Wroe, 1996). However, broad trends suggested in this study are not interpreted here chronoclines in the stratophenetic sense (*sensu* Bown & Rose, 1987). The scarcity of material and uncertain chronology of both the Oligo-Miocene Riversleigh deposits and the Plio-Pleistocene local faunas from which most propleopine specimens are known necessitates caution in the interpretation of results. A considerable temporal gap exists between estimated ages of the most recent *Ekaltadeta* specimens and all other propleopines. As noted by Ride (1993), the period separating the latest known incidence of *Ekaltadeta* from Plio-Pleistocene *Propleopus* and *Jackmahoneya* may be sufficient to have permitted a secondary reversal of character states within *Propleopus* to produce *P. chillagoensis*.

Many questions remain concerning the age, stratigraphy and method of deposition of Riversleigh's Oligocene-Miocene limestone deposits (Archer, 1994, 1995; Megirian, 1992, 1994). If the phylogeny for propleopines suggested by Wroe (1996) reflects evolutionary events, then it provides tacit support for Archer et al.'s (1989) proposed stratigraphy, with an agreement of hypothesised superpositional and phylogenetic patterns.

The capacity of stratigraphic occurrence to explicitly mirror phylogenies is questionable (Engelmann & Wiley, 1977). Although strong

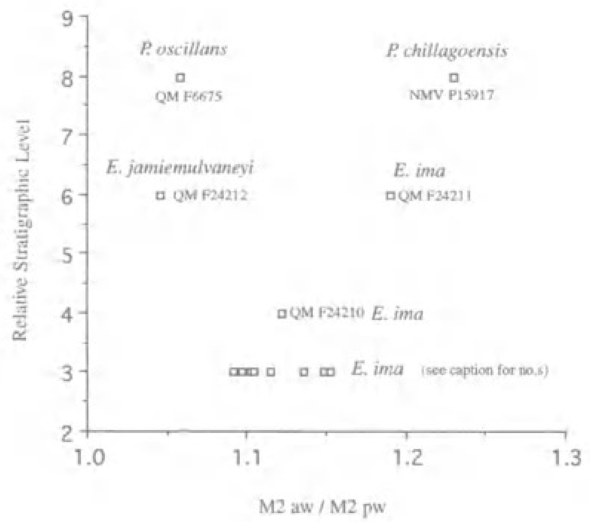

FIG. 6. M^2 aw / M^2 pw vs relative stratigraphic level for propleopines. *Ekaltadeta ima* from level 3, left to right, QMF24207, 24204, 24205, 12436, 24203, 24208, 24209, and 24206.

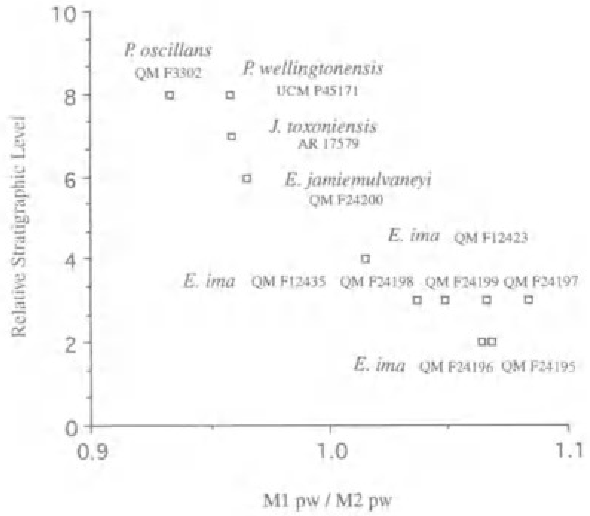

FIG. 7. M_1 pw / M_2 pw vs relative stratigraphic level for propleopines.

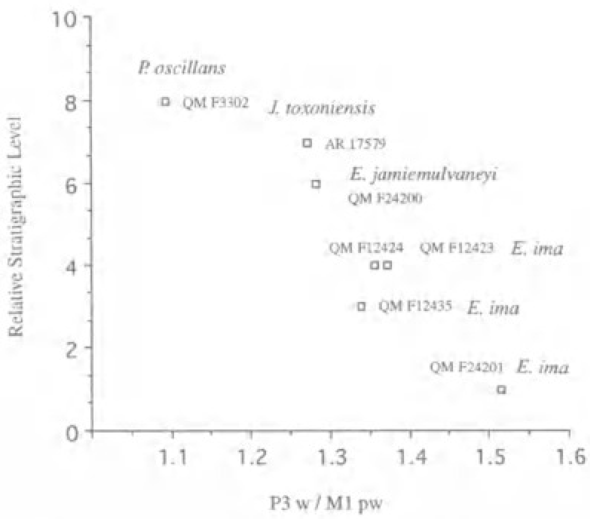

FIG. 8. P_3 w / M_1 pw vs relative stratigraphic level for propleopines.

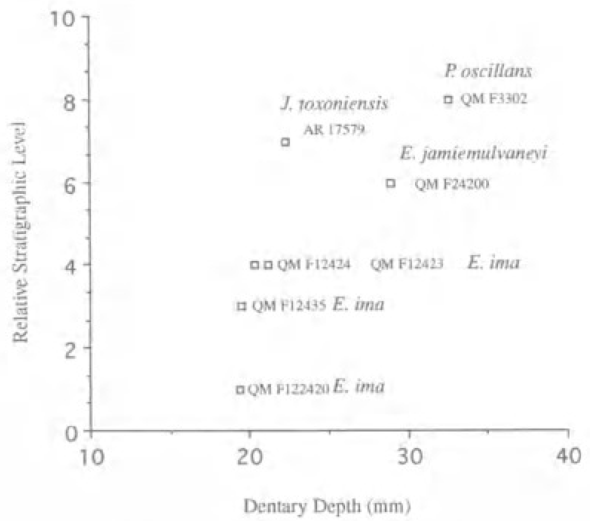

FIG. 9. Depth of dentary vs relative stratigraphic level for propleopines.

congruence between cladistic and stratigraphic arrangements has been demonstrated for many vertebrate taxa by Norell & Novacek (1992a,b), the same authors advised that correlation between the 2 diminishes rapidly where cladistic or stratigraphic data is poorly resolved. Debate over conformity of age and cladistic information commonly centres around the value of superpositional data as an adjunct to phylogenetic reconstruction. Where cladistic analysis is sound it may be useful as a test of stratigraphic interpretations.

The propleopine phylogeny of Wroe (1996) is based on analysis of an incomplete data matrix, with important characters unknown for several species. Consequently the cladistic data presented cannot be viewed as a robust basis for testing superpositional pattern. However, the productivity of the Oligocene-Miocene deposits of

Riversleigh engenders reasonable expectation for the reliable resolution of phylogenies.

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APPENDIX TO FIGURES 6-9

Data for Fig. 6. M^2 aw divided by M^2 pw (G-value) vs. relative stratigraphic level for propleopines. Measurements in mm. * = skull, (R) = right tooth row, (L) =

Species	Cat. no.	M^2 aw	M^2 pw	G-value	Level
E. ima	QMF24203	6.80	6.10	1.12	3
E. ima	QMF24204	6.80	6.20	1.10	3
E. ima *	(R)QMF12436	6.40	5.80	1.10	3
E. ima *	(L)QMF12436	+	5.90		3
E. ima	QMF24205	6.50	5.90	1.10	3
E. ima	QMF24206	6.80	5.90	1.15	3
E. ima	QMF24207	7.20	6.60	1.09	3
E. ima	QMF24208	6.70	5.90	1.14	3
E. ima	QMF24209	6.20	5.40	1.15	3
E. ima	QMF24210	7.40	6.60	1.12	4
E. ima	QMF24211	6.90	5.80	1.19	6
E. jamiemulvaneyi	QMF24212	6.90	6.60	1.05	6
P. oscillans	QMF6675	9.20	8.70	1.06	8
P. chillagoensis	NMVP15917	10.7	8.70	1.23	8

Data for Fig. 7. M_1 pw divided by M_2 pw (G-value) vs. stratigraphic level. Measurements in mm.

Species	Cat. no.	M_1 pw	M_2 pw	G-value	Level
E. ima	QMF24195	6.70	6.30	1.06	2
E. ima	QMF24196	6.30	5.90	1.07	2
E. ima	QMF24197	6.50	6.00	1.08	3
E. ima	QMF24198	5.70	5.50	1.04	3
E. ima	QMF12435	6.50	6.20	1.05	3
E. ima	QMF24199	6.50	6.10	1.07	3
E. ima	QMF12423	7.00	6.90	1.01	4
E. jamie mulvaneyi	QMF24200	8.20	8.50	0.97	6
P. wellington ensis	UCMP45171	9.20	9.60	0.96	8
P. oscillans	QMF3302	9.70	10.4	0.93	8
J. toxoniensis	AR17579	7.00	7.40	0.96	7

Data for Fig. 8. P_3 w divided by M_1 pw (G-value) vs. stratigraphic level for propleopines. Measurements in mm.

Species	Cat. no.	P_3 w	M_1 pw	G-value	Level
E. ima	QMF24201	10.3	6.80	1.56	1
E. ima	QMF12435	8.70	6.50	1.34	3
E. ima	QMF12424	8.80	6.50	1.35	4
E. ima	QMF12423	9.60	7.00	1.37	4
E. jamie mulvaneyi	QMF24200	10.5	8.20	1.28	6
P. oscillans	QMF3302	10.6	9.70	1.09	8
J. toxoniensis	AR17579	8.9	7.00	1.27	7

Data for Fig. 9. Depth of dentary vs. stratigraphic level for propleopines. Measurements in mm.

Species	Cat. no.	Dentary depth	Level
E. ima	QMF24201	19.3	1
E. ima	QMF12435	19.4	3
E. ima	QMF12424	21.1	4
E. ima	QMF12423	20.3	4
E. jamie mulvaneyi	QMF24200	28.9	6
P. oscillans	QMF3302	32.6	8
J. toxoniensis	AR17579	23.3	7