A new petauroid possum from the Oligo-Miocene of Riversleigh, northwestern Queensland

J. R. Brammall


Djaludjiangi yadjana sp. nov. represents a previously unknown genus of petauroid possum from Riversleigh in northwestern Queensland. Of known phalangerids Djaludjiangi most closely resembles the Petauridae, but lacks synapomorphies previously used to define that family. Although considered likely a plesiomorphic petaurid, D. yadjana is referred here to Petauroidea: incertae sedis, pending comprehensive revision of phalangeriform dental character state distributions. Small possum diversity at Riversleigh indicates a complex and finely partitioned environment such as that found in present-day tropical forests; the discovery at Riversleigh of Australia’s first Tertiary dactylopsiline species also argues for a rainforest palaeohabitat.

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THE PRE-PLEISTOCENE fossil record of the Petauridae has hitherto been remarkably poor, with taxa described only from the early Pliocene Hamilton Local Fauna. The Hamilton Local Fauna contains nine teeth or partial teeth which have been referred to at least two species of Petaurus, one near P. norfolcensis and one near P. australis (Turnbull et al. 1987). Miocene petaurid specimens previously reported from the Tarkarooloo Local Fauna (Rich et al. 1982) were subsequently referred to the Pseudocheiridae (Woodburne 1986).

Archer et al. (1989) note one new petaurid genus and species from the early Miocene Upper Site Local Fauna of Riversleigh, and Archer et al. (1994) report another ?petaurid species from Riversleigh. It is now clear that the Riversleigh local faunas have produced two new petaurid genera containing at least three new species. Two other undescribed small petauroid species are referable to the Acrobatidae. Another new petauroid species is described herein.

Djaludjiangi yadjana is the only species known of its genus, appears to have closest affinities to Petauridae, and may be the most primitive petaurid known. However, it possesses a number of features previously unknown in the Petauridae while lacking others that have, until now, been regarded as diagnostic for the family. Pending revision of family-level synapomorphies within Phalangeriformes, Djaludjiangi is left incertae sedis.

Materials and methods

Dental homology follows Flower (1867) for premolar numbering and Luckett (1993) for the premolar/ molar boundary. Higher level systematic nomenclature follows Aplin & Archer (1987). System nomenclature and assignation of sites to Systems is based on Archer et al. (1989) and Creaser (1997). System A sites are considered to be late Oligocene in age (Myers & Archer 1997). System B sites are regarded to be early Miocene and System C sites are interpreted to be middle Miocene to early late Miocene (Archer et al.
The prefix QMF designates specimens held in the Queensland Museum fossil collection, Brisbane. Measurements in millimetres (mm) were made to the nearest 0.01 mm using a Wild MMS235 Digital Length-Measuring Set attached to a Wild M5A stereomicroscope. Molar lengths and widths, and molar row lengths, were measured as the maximum dimensions of the enamel-covered crown/s with the teeth in occlusal view, with lengths measured along the anteroposterior axis of the tooth and widths measured perpendicular to that axis. For $P_3$ in dorsal view and $P^3$ in ventral view, maximum length was measured along the longitudinal axis of the tooth, and anterior, posterior and maximum widths were measured perpendicular to that axis; buccal and lingual heights were measured from the base of the enamel at the saddle between the roots, to the dorsal (for $P_3$) or ventral ($P^3$) apex.

Material examined. Holotype QMF 30510, a left dentary with $P_2, M_{1,4}$ alveoli for $I$, and $P$, and a mostly complete ascending ramus and angular process. Dentary proportions and low degree of dental wear suggest that this individual was subadult at death. Paratype QMF 30532, a right maxillary fragment with $P^3 M_{1,2}$ and alveoli for $M^3$; broken through lingual and posterior alveoli of $M^4$, broken immediately anterior to $P^3$, dorsal to infraorbital foramen, and palate broken 1-2 mm from, and approximately parallel to, tooth row. Paratype QMF 30523, a left dentary with $P_{1,3} M_{1,4}$ and possible $I$, alveolus; broken posteriorly part way along the ascending ramus and angular process, and anteriorly through the $I$, alveolus, oblique to the longitudinal axis of the dentary. Paratype QMF 30529, a left dentary fragment with $P_2, M_{1,3}$ and alveoli for $P_1, M_2$ and possibly $I_2$; broken posteriorly near the base of the ascending ramus and anterolingually and anteroventrally around the $I$, alveolus.

Systematic palaeontology

Class MAMMALIA Linnaeus, 1758
Supercohort MARSUPIALIA Illiger, 1811
Order DIPROTODONTIA Owen, 1866
Superfamily PETAUROIDEA (Gill, 1872)
Family incertae sedis

Djaludjangi gen. nov.

Type and only species. Djaludjangi yadjana

Diagnosis. As for species by monotypy.

Etymology. Djalu means ‘heavy’ or ‘strong’ and djangi means ‘mouth’ or ‘teeth’ in the Waanyi language, as spoken by the late Ivy George of Riversleigh Station; in reference to the large P3s, relatively high-cusped molars and unreduced posterior molars previously unknown among petaurids, with which Djaludjangi shows closest affinity.

Djaludjangi yadjana sp. nov. (Figs 1-3; Table 1)
Type locality. Dirk's Towers Site, Riversleigh World Heritage property, Lawn Hill National Park, northwestern Queensland.

Distribution and age. System B, Riversleigh World Heritage property, Lawn Hill National Park, northwestern Queensland (early to middle Miocene); Boid Site East Site, Camel Sputum Site, Creaser's Ramparts Site, Dirk's Towers Site, Mike's Menagerie Site, Upper Site and Wayne's Wok Site. System C, Riversleigh Station, northwestern Queensland (middle to early late Miocene): Henk's Hollow Site and Wang Site.

Diagnosis. Small (molar row length 9.0-9.5 mm) non-macropoid phalangeridan with dental formula 1'/2', P3'/4', M1'/2'/3'/4'; I1 elongate, slender, procumbent and slightly curved; P1-3 and M1-4 each two rooted, M2-4 each three rooted; no diastema between P3-J3; P3 colinear with molar row; P3 with large central, conical primary cusp from which a ridge extends anteriorly and posteriorly; P1 apex slightly lower than M1 protocristid; P2 interlocks posteriorly with small notch in anterior face of M1; M1-P3 form shearing unit; bunoselenodont, quadriradicular upper and lower molars; lower molar row straight in occlusal view, slightly bowed at alveolar level in lateral view; slight overall anteroposterior reduction gradient in tooth length, height and relative width along molar row except that M2 shorter posteriorly and narrower than M3; tall M1, protoconid slightly buccal to transverse mid-point of trigonid; non-kinked cristid obliqua terminates on posterior flank of protoconid; two low cuspidate transverse crests on each molar; posterior molars without longitudinal median groove; molar surfaces lightly crenulated; entoconid taller than hypoconid; protostylid absent; maxillary origin of zygomatic arch lateral to anterior end of E2; infraorbital canal exists through single ovoid foramen dorsal to P3; P3 lies at angle (lingual anterior) to P3, molar row and longitudinal axis of skull; upper molar row gently curved (concave lingually) in occlusal view; M1 without protoconule; M2 anterior edge lies almost at right angle to lingual and buccal edges; no marked buccal indentation in crown outline between paracone and metacone; paracone and neomeataconule participate in en echelon fashion to form transverse crests; M2 slightly smaller than M1; deep transverse cleft between metaconid and entoconid, and protocone and metaconule, respectively.

Remarks. Djaludjiangi yadjana differs from all vombatiform diprotodontians (Vombatidae, Phascolarctidae, Ilariidae, Wynnardiidae, Thylacoleonidae, Diprotodontidae, Palorchestidae) in its diminuitive size and from all but thylacoleonids by the possession of P1-2 and P3'. It further differs from thylacoleonids in the lack of a greatly enlarged P3.

It is distinguished from all macropodoids by its smaller size, by the presence of P1 and the absence of a masseteric canal, and from most macropodoids by the possession of P3s with one central primary cusp and without vertical ridlets along its length and extending its full height.

It differs from phalangeroid phalangeridans (Phalangeridae, Miralinidae, Ektopodontidae) in that the M1 cristid obliqua lacks an anterior 'kink' and terminates on the posterior flank of the protoconid, rather than at the protoconid or protostylid. It further differs from phalangerids in lacking a protostylid (present in phalangerids, though developed to varying degrees) in that P3 is not markedly out-turned from the molar row, and from most phalangerids in the possession of two small lower premolars (P1-J3; in phalangerids P1 is usually lost. Distinguished from miralinids and ektopodontids in having molar surfaces less crenulated and molar loph/ids less serrate, and from miralinids in that P3 is not in-turned relative to the molar row.

It differs from burramyids in its larger size; far less pronounced anteroposterior molar row reduction gradient with less simplified molars.
Fig. 1. A-C, Djaludjangi yadjana n. sp. holotype QMF 30510 (Dirk's Towers Site, Riversleigh). Left dentary with P, M_3 in (A) buccal, (B-B') occlusal stereopair and (C) lingual views. Scale = 5 mm.

and much less reduced M4s; the M^1 with protocone more anteriorly-positioned and protoconule absent (in burramyids there is a variably-developed protoconule anterior to the protocone); anterior root of zygomatic arch commencing further back along the molar row; I₁ thicker relative to its length; and M₄ cristid obliqua terminating at a point lingual to the protoconid or lingual postprotoconid, whereas in burramyids it heads towards or merges with the buccal postprotoconid.

It differs from pseudocheirids in having a less lingually-displaced M₃ protoconid; in having the M₄ cristid obliqua terminating on the posterior flank of the protoconid between the protoconid and metaconid, rather than extending to the top of the metaconid; and in having upper and lower molars that are less selenedont and which exhibit a degree of transverse lophodonty.

It differs from pilkipildrids in having I₁ less steeply inclined; anteroposterior molar row reduction gradient far less pronounced; M₄ and M₅ of much less reduced crown height, length and width relative to those of M₃ and M₄; relatively wide M₄ talonid; posterior molars without a longitudinal median groove and with transverse cristids of talonid much less reduced; slightly greater median transverse constriction of the lower molars when seen in occlusal view; and molar row less bowed at alveolar level in lateral view.

It differs from acrobatids in that the upper premolars are not 'secdont'; P^p₂ much shorter relative to P^p₁; metaconule of M₄⁺ less reduced; M₄ and M₅ present; metaconid far less prominent; and entoconid taller than hypoconid.

It differs from species of Dactylopsila, Gymnobelideus and Petaurus in the following features: dentary relatively thicker mediolaterally but relatively shallow dorsoventrally; ascending ramus proportionately thicker,
commencing further back with respect to molars and ascending more steeply; angular process less reduced; there are two subequal mental foramina, one below the saddle between the roots of M1 and another below the posterior root of P3; I1, straighter and more procumbent, curving anterodorsally to a lesser degree; P1 and P2 less simplified and slightly larger relative to molars; P1 slightly smaller than P2; no diastemata between P1-P3 and P3 absolutely and relatively taller, less transversely compressed, more massive, and not oblique to molar row axis; lower and upper molar rows with less anteroposterior reduction; M1 shorter anteroposteriorly and narrower than M2; M2-M4 gradient less steep; M1 not turned lingually towards premolar series and with taller and less lingually-displaced protoconid and better-developed transverse crests between hypoconid and entoconid; M3-M4 with deep transverse cleft between metaconid and entoconid, taller cusps, deeper central and cingular basins and better-developed transverse crests; M2-M4 much less reduced in comparison with M1, and with more anteriorly positioned entoconid; M4 less reduced; maxillary origin of zygomatic arch more posteriorly located, being lateral to the anterior end of M3; infraorbital canal exits through a single foramen dorsal to P3; P1-P3 closely approximated; P3 less transversely compressed, less reduced, and lying at an angle (lingual anterior) to P1, molar row, and longitudinal axis of skull; upper molars less bunodont, more crenulated and more selenodont, with no marked buccal indentation in crown outline between paracone and metacone; curvature of upper cheektooth row less pronounced; anterior edge of M1 approximated at right angles to lingual and buccal edges, both of which are more straight in occlusal outline; M2-M4 with protocone and metacone taller and more widely separated and a deep transverse channel between them, paracone and metacone taller, and paracone and neometacone larger, more clearly defined and participating in en echelon fashion to form low transverse crests; M4 less reduced in comparison with M1, being only slightly smaller than it; M2 with larger posterior cingulum; M3 much less reduced in comparison to M2.

Djaludjangi yadjana further differs from species of Gymnobelideus and Petaurus in having M3 with a less reduced posterolingual corner and M4 with a less reduced metacone.

Description

Dentary. A number of specimens (including QMF 30525) were used in addition to the holotype for description and comparison of the dentary because the holotype appears to have belonged to a young animal and not to have reached adult proportions.

The dentary of D. yadjana appears to be intermediate in size between those of extant Petaurus breviceps and P. norfolcensis. Relative to dentaries of extant petaurids, it is thick mediolaterally, but shallow dorsoventrally. In particular, it is relatively deep below the posterior molars and at the base of the ascending ramus; below P3, at the base of the deep I1 alveolus, it is (relatively) less deep. The dorsal edge is gently concave beneath the molars, so it appears to be slightly less deep below M2-3 than below P3, P4. In buccal view, it is otherwise of approximately uniform depth anterior to the ascending ramus until a point below P3, where it abruptly begins to rise, following the ventral outline of I1. In lingual view, it is of approximately uniform depth between the ascending ramus and M4, anterior to which it becomes deeper until the dorsal inflection beneath P3. The mandibular symphysis is rugous and forms an ovoid plane extending from below P3 to the anterolingual extremity of the dentary. The ascending ramus is thick, rises steeply and commences at a point below the front of the posterior root of M4. The angular process is thicker and more extensive than that of extant petaurids. In dorsal view the medial border is straight and runs parallel to the molar row. Coronoid and condylar processes are not known for D. yadjana. A large inferior dental foramen opens on the lingual side of the dentary, dorsolateral to the junction of the angular process and ramus. There are two mental foramina of approximately the same size: one below the
saddle between the roots of $M_1$, just over half way from the top to the bottom of the dentary, and another higher on the dentary below the posterior root of $P_2$; the single exception to this is specimen QMF 30522 in which the foramina are both shifted slightly further forward.

**Lower dentition.** $I_1$ is elongate and procumbent, tapering to a dorsally-upturned point. In dorsal view $I_1$ is gently concave lingually and convex buccally, particularly the anterior part of the tooth, which curves lingually before terminating. Also in dorsal view, a strong longitudinal ridge runs from the lingual side of the posterodorsal margin of the tooth, across the dorsal surface to merge into the tip along its buccal margin. A similar ridge occurs in the centre of the anteroventral surface, running straight back from the tip and terminating approximately half way along the exposed portion of the incisor. Lingually, the tooth is marked by two longitudinal ridges, one about a quarter of the way up from the ventral margin and the other about half way down from the dorsal margin. The surface between the two lingual ridges is slightly concave, as is the surface between the more dorsal of these ridges and the longitudinal dorsal ridge. The surface between the ventral ridge and the lower of the lingual ridges is quite flat and evidently contacted the opposing $I_1$ in life.

$I_2$ is not known for *D. yadjana*, although it occurs in all extant petaurids. However, QMF 30523 appears to have a shallow alveolus anterior to $P_1$, which may have housed a small $I_2$. In a number of other specimens there is some suggestion, albeit equivocal, of an $I_2$ alveolus in the easily-damaged region between $I_1$ and $P_1$.

$P_1$ is a small, double-rooted, cap-like tooth with a variably-positioned weak longitudinal dorsal ridge, sloping away from which are the sub-quadrate lingual and buccal halves of the crown. It is only known from two specimens and is a slightly different shape in each of these; presumably, this reflects intraspecific variation.

$P_2$ is similar in morphology to $P_1$, but is slightly larger; in particular, it is both relatively and absolutely wider. As with $P_1$, shape of the $P_2$ crown outline is variable.
RIVERSLEIGH PETAUROID POSSUM

...ridge reverses gradient at this point, rising to the posterior edge. In these specimens P₃ appears to be less worn. In lateral view the anterior edge of the crown rises dorso-posterio to its apex and is never wider than at its base. Posteriorly, the crown expands as it rises (until it meets the posterior dorsal ridge) and therefore extends beyond the posterior root in lateral view. The posteriormost point of the tooth fits into a small notch in the anterior face of M₁. In dorsal view, the crown extends further on the buccal side of the longitudinal dorsal ridge than on the lingual side, particularly over the posterior root. This forms a pronounced buccal projection in the crown outline, which is otherwise approximately ovoid. Also in dorsal view, two minor ridges, which extend on the lingual and buccal sides of the dorsal apex, respectively, form slightly acute angles antero-lingually and posterobuccally with the primary, longitudinal ridge. The lingual and buccal profiles of the tooth are similar to one another. The main cuspid forms a slightly rounded isosceles triangle rising above the roots, with the base of a further triangular projection or 'heel' adjoining approximately two-thirds of the posterior face of the main triangle and extending posteriorly to an apex which abuts M₁. Between the small apical lingual ridge and the anterior portion of the longitudinal dorsal ridge the crown is slightly concave. There are also slight concavities on the lingual and buccal faces where the main cuspid and the heel intersect.

In dorsal view the lower molar row is straight. The lower molars are slightly longer buccally than lingually, giving the molar row the appearance of being very slightly arced (concave lingually) in some specimens. All lower molars are double-rooted. From M₁ to M₃, they progressively become relatively narrower, but M₄ is relatively (but not absolutely) wider than M₃. Similarly, the slight antero-posterior gradient of each tooth (obtained by dividing anterior width by posterior width) increases from M₁ to M₃ but has the same value for M₄ as for M₃.

The trigonid of M₁ rises high above its anterior root and expands beyond it anteriorly as it...
Table I. Measurements of Djaludjangi yadjana n. sp.

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Table 1. Measurements of Djaludjangi yadjana n. sp. Type = dimensions of type specimens; lower dentition measurements from holotype QMF 30510; upper dentition measurements from paratype QMF 30532. n = number of specimens, OR = observed range, SD = standard deviation, CV = coefficient of variation, L = length, AW = anterior width, PW = posterior width, MW = maximum width, LH = lingual height, BH = buccal height. CV not given where n < 2.

rises. A large protoconid dominates the trigonid and is situated slightly buccal to the transverse midpoint of the trigonid. Extending anteroventrally from the protoconid, a preprotoconid terminates at the anterobasal extreme of the enamel-covered crown, where it meets, and appears colinear with the posterior branch of the longitudinal dorsal ridge of P3. Immediately below this point, a small notch in M1 interlocks with a small protuberance on the back of P3. The lingual postprotoconid runs posterolingually from the protoconid to a small metaconid, from which it swings back more sharply as the postmetacristid and terminates ventrally in a buccal channel that separates the talonid and the trigonid, about three-fifths of the distance from the front edge of the tooth to the back edge. The entoconid is taller and more crescentic than the hypoconid. A transverse crest is produced buccal to the entoconid but is only weakly met by a corresponding crest from the hypoconid. Posterior to this incomplete lophid, a shallow posterior cingulum is bordered by the postentocristid and posthypocristid which swing posteriorly then buccally and lingually, respectively, to define the edge of the crown posteriorly. The cristid obliqua runs anterolingually from the hypoconid and terminates when it meets the steep posterobuccal flank of the postprotoconid-premetacristid. The crown surface is crenulated, mainly in the central basin of the tooth, lingual to the cristid obliqua. In most specimens, the crenulation is more or less obliterated by wear; QMF 30510, which is relatively unworn, and QMF 30524, a pair of subadult dentaries, are the only specimens in which crenulations are visible. In QMF 30510 and QMF 30524 the crenulations radiate from the central basin of the tooth.

M1 is larger than M3. It has a rounded rectangular outline. The metaconid and entoconid are quite crescentic; while the protoconid and hypoconid are crescentic, they are also more rounded. The metaconid and entoconid are close to the lingual side of the tooth and lie slightly anterior to the protoconid and hypoconid; the metaconid is taller than the entoconid and the protoconid is taller than the hypoconid. Weak but distinct lophids, interrupted by crenulations, connect the metaconid and protoconid, and the entoconid and hypoconid respectively. The postmetacristid terminates in a deep lingual cleft which separates it from the pre-entocristid. In some specimens, there is a small metastylid pos-
The transverse crest between the hypoconid and entoconid is weakly developed, although it is quite prominent in specimens exhibiting a mild degree of wear. In some specimens, this posterior transverse crest connects to the posthypocristid and postentocristid rather than directly to the hypoconid and entoconid, thereby reducing the size of the posterior cingulum. The hypoconid is more lingually positioned than in M₂ or M₃, also reducing the size of the posterior cingular basin. The hypoconid and protoconid are of approximately equal height, and the entoconid and metaconid are less disparate in size than those of M₃.

M₄ is similar to M₃ except for being smaller and relatively more narrow, with the posterolingual corner more reduced and the trigonid proportionately slightly larger. Anteroposterior width reduction of M₄ is no greater than that of M₃.

Maxilla. Only fragmentary maxillary remains are known for D. yadjana and no substantial palatal fragments are known. The posterior edge of the maxillary origin of the zygomatic arch is level with the anterior end of M₁ in all specimens except QMF 30466, in which it is further forward, about half way along the length of M₂. However, the little-worn teeth of this specimen suggest that it may belong to an animal that was not fully grown at death. Extant petaurids with fully erupted dentition may nevertheless not have reached full adult skeletal dimensions and in these younger extant animals, the teeth are further back with respect to the zygomatic arch than they are in adults. A large, ovoid infraorbital canal exits the maxilla above P³.

Upper dentition. P¹ is not known for D. yadjana. In extant petaurids it is a transversely compressed, double-rooted tooth with a single central cusp and is larger than P². There is a small gap between P¹ and P² in extant petaurids. In QMF 30530 there is a large alveolus directly in front of the P² alveoli and perhaps the remains of a further, possibly smaller alveolus, in front of that. Specimen QMF 30531 shows a similar
configuration. These alveolar fragments suggest a fairly large, double-rooted P\textsuperscript{1} which is nevertheless probably smaller than P\textsuperscript{3}.

P\textsuperscript{2} is known from two specimens: QMF 30531 and QMF 30532. It lies parallel to the buccal edge of the maxilla, which turns medially anterior to P\textsuperscript{3}. Thus P\textsuperscript{2} turns in anterolingually relative to P\textsuperscript{3} and the anteroposterior axis of P\textsuperscript{3} forms an angle lingually with that of P\textsuperscript{3} and the molar row. P\textsuperscript{2} is small, with two subequal roots, and although similar to P\textsuperscript{2}, it is longer and narrower and lacks the large posterolingual extension of some P\textsuperscript{3}s. In ventral view the crown outline approximates a diamond shape with rounded corners. The crown is produced into a small apical cusp ventral to the posterior root; from this cusp, a ridge extends posterobuccally to the back of the tooth. A weak ridge also runs anteriorly from the cusp to the anterior edge of the tooth and a short, weak ridge extends posterobuccally from the cusp about half way down the buccal face of the crown. The anterior and posterior ridges are not colinear; an angle is subtended between them buccally at the apical cusp. In lateral view, the crown extends beyond the posterior root, terminating at the end of the posterior ventral ridge and at that point, abutting P\textsuperscript{3} at the anterior terminus of its ventral ridge. The area of contact between P\textsuperscript{2} and P\textsuperscript{3} is much less than that between P\textsuperscript{3} and P\textsuperscript{4}; P\textsuperscript{2} does not appear to buttress P\textsuperscript{3} as in the lower premolars. The portion of the crown anterior to the ventral apex is longer than the posterior portion and the anterior tip of the crown is more dorsally positioned, i.e. closer to alveolar level, than the posterior tip, which extends further ventrally. Thus the posterior ventral ridge slopes towards the maxilla more steeply than does the anterior ventral ridge.

P\textsuperscript{3} is of similar morphology to P\textsuperscript{3}, with a single dominant cusp from which ridges extend to the anterior and posterior ends of the tooth and minor ridges extend lingually and buccally; but it differs in a number of ways. It is shorter dorsoventrally and the central cusp is more posteriorly positioned, being ventral to the saddle between the roots in P\textsuperscript{3} but slightly anterior to the saddle in some P\textsuperscript{3}s. In lateral view the anterior profile of the crown, between the apex and the dorsal terminus of the anterior ventral ridge, is slightly concave in P\textsuperscript{3} whereas it is convex in P\textsuperscript{2}. The base of the crown is inflated lingually above the saddle between the roots and buccally, to a lesser extent, above the posterior root, so that the ventral outline approximates a rounded diamond with the lingual apex of the diamond skewed more anteriorly than the buccal apex. In QMF 30531 and QMF 30530 the lingual projection is quite long and pointed and extends further in an anterolingual direction than it does in the paratype QMF 30532, in which is more rounded and less extensive; this is assumed to represent intraspecific variation. In ventral view, the anterior and posterior ridges are not colinear; as with P\textsuperscript{2}, an angle is formed between them buccally. This angle is not formed right at the apex but posterior to it, at a point about half way along the posterior ridge, where the ridge changes gradient abruptly before ascending at a much reduced gradient to the posterior margin of the crown. Posteriorly the crown abuts the anterobuccal corner of M\textsuperscript{1}; the posterior ridge of P\textsuperscript{3} terminates slightly buccal to the anterior terminus of the M\textsuperscript{1} preparacrista.

In occlusal view the molar row is gently curved, concave lingually. Each of the upper molars has three roots, with two alveoli on the buccal side of the tooth and a larger lingual alveolus. Molar widths decrease from the front of the molar row to the back, but the gradient is steeper posteriorly. Posterior widths of each molar decrease progressively with respect to anterior molar widths. Molar length decreases at a steady rate from front to back except that M\textsuperscript{1} is proportionately much shorter than M\textsuperscript{4}. Moving back along the molar row, molar length decreases with respect to anterior molar width, but increases with respect to posterior molar width.

M\textsuperscript{1} is quadritubular and bunoselenodont, with an approximately square outline reduced at the rounded posterolingual corner. The paracone is the largest cusp and the protocone is the smallest. The metacone and metaconule are subequal in height. The metacone is slightly
more buccally positioned than the paracone. The protocone is more anteriorly positioned than the paracone and the metaconule is even further anterior to the metacone. The posterolingual corner of the tooth is consequently reduced. Each of the four primary cusps is weakly selenedodont. The pre- and post- paracristae and metacristae form an approximately straight row of blades parallel to the buccal side of the tooth. A lingual preprotocrista extends anterolingually from the protocone to the anterolingual corner of the base of the crown. The buccal preprotocrista and postprotocrista together form a crescent-shaped blade, concave buccally, which merges with the anterior cingulum. Posteriorly, it terminates at a lingual, transversely-oriented channel that separates the crests of the protocone and metaconule. The premetaconulecrista and postmetaconule-crista similarly form a crescent-shaped blade which merges with the posterior cingulum and the lingual transverse channel. The postmetaacrcta curves buccally when it reaches the postobuccal corner of the stylar shelf, and partially encloses a small basin which merges into the flank of the metacone on its buccal side. A similar, but smaller indentation is enclosed by the lingually-curving anterior portion of the preparacrista at the anterobuccal corner of the tooth. In the centre of the buccal margin, stylar cusps C and D are visible on the buccal edge of a pocket which is bound anteriorly, posteriorly and lingually by the swollen flanks of the paracone and metacone. Crenulations radiate from the centre of the central and posterior cingular basins of M'. Crenulations interrupt a slightly oblique metaloph, which connects the metacone and metacune and incorporates a small neometacune lingual to the metacone. Anterolingual to the paracone and interrupting the small anterior cingulum is a paraconule, which is slightly larger than the neometacune and occupies a considerable portion of the poorly-defined paraloph. The paraloph, like the metaloph, is interrupted by crenulations. A crest runs from the metacone down its flank anterolingually to connect with the neometacune; a weak crest also runs from the paracone to the paraconule. The posterior cingular basin is floored by a groove which is obliquely oriented (anterior lingually) due to the anterior displacement of the metaconule. Similarly, the central basin is dominated by an oblique groove which is parallel to that of the posterior basin and runs from the junction of the postparacrista and premetaconule towards the base of the protocone. As the tooth wears down the crenulations are obliterated and the paraconule, neometacune and lophs are gradually reduced towards the level of the basins.

M2 is similar to M' except as noted below. It is slightly narrower and is shorter. The metaconule is not as far ahead of the metacone and the posterolingual corner of the tooth is less reduced. The protocone is larger than that of M' and is subequal to the metaconule. The paracone and metacone are each smaller than their counterparts on M'; the metaconule is about the same size. The paracone-metaconule crista originates on the preparacrista, anterior to the paracone. The paraconule is slightly smaller than that of M' and is more clearly distinguished from both the paracune and the anterior cingulum, into which it does not impinge; the anterior cingulum is therefore more complete. The small anterobuccal pocket is seen to be virtually continuous with the anterior cingulum, being separated from it only by the preparacrista before it turns buccally to define the pocket. The postobuccal pocket is smaller than in M' and stylar cusps C and D are less clearly defined. The primary crests associated with the paracone and metacone are more crescentic than are those of M', with the crests concave lingually. The anterior half of the tooth is slightly wider than the posterior part, whereas M' is slightly wider posteriorly than anteriorly.

A damaged M' is known only from QMF 30531. It is smaller and more reduced posteriorly than M', but otherwise appears to be similar. A crest from the paracone connects with the paracone, as in M', rather than joining the preparacrista, as in M'.

M' is only known from an isolated molar QMF 20773. It is referred to D. yadjana on the basis of its size and its morphological congru-
ency with M\textsuperscript{3}. Compared with M\textsuperscript{2} it is much reduced, especially posteriorly and posterolingually. The metaconule is much reduced and the metacone is much smaller than the paracone or protocone. The crown outline is trapezoidal, with the posterior end narrower than the anterior end. The metacone and metaconule are both close to the posterior edge of the tooth and to the buccal and lingual edges, respectively. The anterior cingulum is clearly defined, but the posterior cingulum is very small. There is no large posterior cingular basin. Presumably M\textsuperscript{4} was crenulated, as are M\textsuperscript{3} in unworn specimens, but QMF 20773 is worn and no crenulations remain. A transverse crest extends from the paracone lingually to about half way across the central basin, and a short blade connects the metacone and metaconule, just in front of the posterior cingulum. The central basin occupies most of the crown surface. The simplicity of the crown (lacking crenulations, lacking paraconule and neometacone, with transverse blades only weakly defined) is similar to that seen in worn specimens of M\textsuperscript{3}. M\textsuperscript{4} is more reduced and much shorter than M\textsuperscript{3}.

Phenetic similarities aside, the phylogenetic position of *Djaludjangi* is difficult to ascertain. It possesses a unique array of dental character states which, taken in isolation, give conflicting indications of family-level affinity. Either *Djaludjangi* represents a new family of non-macropodoid phalangeridans, or current family definitions require revision to accomodate this new genus. Other small possum taxa from Oligocene and Miocene deposits at Riversleigh also challenge current understanding of character state distributions and polarities within Phalangerida. A comprehensive review of phalangeridan dental character states is beyond the scope of this paper. The following discussion of character state distributions in possum families is directed specifically towards clarifying the affinities of *D. yadjana*.

Aplin & Archer (1987) refer possums to four superfamilies: Burramyoidea, containing the family Burramyidae only; Phalangeroidea, comprised of Phalangeridae together with the extinct families Ektopodontidae and Miralinidae; Petauroidea, containing Petauridae and Pseudocheiridae; and Tarsipedoidea, containing Acrobatidae and Tarsipedidae. The extinct family Pilkipildridae is left incertae sedis.

Woodburne, Pledge & Archer (1987) place pilkipildrids within the Phalangeroidea as the sister-group of an ektopodontid-miralinid clade, but Archer et al. (1987) favour a petauroid affinity for pilkipildrids. Albumin immunology (Baverstock et al. 1990) and DNA-DNA hybridisation (Edwards & Westerman 1995) studies consistently indicate that acrobatids, tarsipedids, petaurids and pseudocheirids form a monophyletic group, but interfamilial relationships within this clade remain unresolved. Marshall et al. (1990) place the Burramyidae within their Petauroidea, but this is not supported by any other morphological or molecular studies. In this paper, three higher level possum taxa are recognised: Burramyoida and Phalangeroidea (*sensu* Aplin & Archer 1987) and Petauroidea, which is taken to include the families Petauridae, Pseudocheiridae, Acrobatidae and Tarsipedidae as well as the Pilkipildridae. This classification

**Discussion**

*Djaludjangi yadjana* is clearly a non-macropodoid phalangeridan, but its affinities within the possum radiation are more difficult to determine. Of all diprotodontian families, *D. yadjana* is morphologically most similar to extant petaurid species, sharing similar dentary morphology, a long, slender, procumbent and slightly curved I\textsubscript{1}, bunoselenodont molars and dental formula of I\textsubscript{1}/1-2, C\textsubscript{1}/0, P\textsubscript{1}/3/1-3, M\textsubscript{1}/1-4/1-4. Dentary size and molar row length also indicate that it falls within the size range of extant petaurids. It is smaller than all known phalangerids, ektopodontids, miralinids and extant pseudocheirids (but only slightly smaller than the Miocene pseudocheirids *Pildra antiquus*, *P. tertius* and *Pajlara tirarentae*, and perhaps slightly larger than *Marlu praecursor*), and larger than any known burramyid, acrobatid or tarsipedid.

Phenetic similarities aside, the phylogenetic position of *Djaludjangi* is difficult to ascertain. It possesses a unique array of dental character states which, taken in isolation, give conflicting indications of family-level affinity. Either *Djaludjangi* represents a new family of non-macropodoid phalangeridans, or current family definitions require revision to accommodate this new genus. Other small possum taxa from Oligocene and Miocene deposits at Riversleigh also challenge current understanding of character state distributions and polarities within Phalangerida. A comprehensive review of phalangeridan dental character states is beyond the scope of this paper. The following discussion of character state distributions in possum families is directed specifically towards clarifying the affinities of *D. yadjana*.
is congruent with the taxonomic conclusions of Edwards & Westerman (1995).

**Phalangeroidia:** *Djaludjangi yadjana* differs from all phalangeroids in lacking an anterolingually-kinked M\textsubscript{1} cristid obliqua, a feature cited by several authors (e.g. Archer et al. 1987; Marshall et al. 1990) as a phalangeroid synapomorphy. It does not possess an anterobuccal notch in the anterior cingulum of the lower molars. Within possums this feature has been observed only in phalangeroids, but since it does not occur in all phalangeroids (Archer et al. 1987) its absence in *D. yadjana* is of limited phylogenetic interest. *Djaludjangi yadjana* also lacks an M\textsubscript{1} protostylid, the presence of which is cited by Woodburne et al. (1987) as a phalangeroid synapomorphy, but which in some phalangerid taxa is indicated by little more than a groove posterobuccal to the protoconid (Flannery & Archer 1987). In phalangeroids the cristid obliqua of M\textsubscript{1} terminates either at the protostylid or protoconid, whereas in *D. yadjana* it terminates on the posterior flank of the protoconid, posterobuccal to the centre of the premetacristid-buccal postprotocristid.

In common with phalangeroid taxa, *D. yadjana* has conules arranged into transverse ridges or loph/ids on the upper and lower molars. However, molar conules and crenulations are less elaborated, and transverse ridges considerably less developed, in *D. yadjana* than in any phalangeroid species examined with the possible exception of the Miocene phalangerid *Trichosurus dicboni*. In addition, unworn molars of some extant petaurids in the genus *Petaurus* possess transverse ridges that are similar, though poorly-developed in comparison, to those seen in *D. yadjana*. Other phalangeroid dental synapomorphies reported in the literature include reduction of selenodonty (Woodburne et al. 1987) and the possession of bunodont semi-selenodont molars (Archer et al. 1987). The molars of *D. yadjana* are certainly less selenodont than those of pseudocheirids and could be described as both bunodont and semi-selenodont. However, reduced selenodonty is characteristic of acrobatids, burramyids and petaurids as well as phalangeroids, and the molars of extant petaurids are also bunodont (though more so than in phalangeroids) and semi-selenodont (though less so than in phalangeroids).

**Djaludjangi yadjana** also differs from phalangeroids in its much smaller size and in that P\textsubscript{3} and P\textsubscript{4} are not markedly out-turned in relation to the molar row, and from miralinids in that P\textsubscript{1} is not intumed. The molar loph/ids of *D. yadjana* are less serrate and molar surfaces less crenulated than those of miralinids or ektopodontids and *D. yadjana* does not show the modified M\textsubscript{1} cristid obliqua characteristic of those families (Woodburne et al. 1987).

Thus, the strongest evidence for *D. yadjana* having its closest affinities within the Phalangeroidea is the possession of conules in the upper and lower molars that are arranged in an *en echelon* fashion between the primary cusps to form transverse loph/ids. Against this is the fact that the molars of extant petaurids - universally agreed not to be phalangeroids - show a similar configuration to those of *D. yadjana* in this respect. Although considerably reduced in comparison to those of *D. yadjana*, the intermediate conules and transverse ridges of extant petaurids could easily have been derived from a condition such as that seen in *Djaludjangi*. The absence in *D. yadjana* of typical phalangeroid modifications of the cristid obliqua further indicates that it does not belong within the Phalangeroidea.

**Burramyoidia:** Few dental synapomorphies have previously been identified for the Burramyidae or Burramyoidea. Nevertheless, *D. yadjana* differs from all known species of *Burramys* and *Cercartetus* on a number of features including its considerably greater size.

The molars are more simplified, M4s much more reduced and molar row reduction gradient much steeper in burramyids than in *D. yadjana*. All burramyids lack the distinct conules and the loph/ids present in *D. yadjana*. Burramyids have a protoconule anterior to the M\textsubscript{1} protocone.
(though in some species of Cercartetus the protoconule is only very weakly developed). There is no protoconule in D. yadjana and the M₁ protocone is closer to the anterior edge of the tooth than in any burramyid. The anterior root of the zygomatic arch commences further back along the cheektooth row in D. yadjana than in burramyids. In all burramyids the M₃ cristid obliqua heads towards or merges with the posterior end of the buccal postprotocristid, whereas in D. yadjana it terminates lingual to the protoconid or postprotocristid, with a sloping vertical channel clearly separating the lingual postprotocristid and the cristid obliqua. It is stouter in D. yadjana than in burramyids. Reduction of P1-2 has been cited as a diagnostic feature of burramyids (e.g. Archer 1984; Turner & McKay 1989; Marshall et al. 1990). The P1-2 of D. yadjana are slightly less reduced than in some burramyids. Djaludjiangi yadjana also differs from species of Burramys in that it lacks a plagiaulacoid third premolar, has P₂ present and has much less simplified molars; and from Cercartetus species in that the latter have more triangular upper molars, mainly by virtue of reduction of the posterolingual corner of each tooth. There is little reason to suggest a burramyoid affinity for D. yadjana.

Petauroidea: It is difficult to establish or refute membership of the Petauroidea on the basis of dental synapomorphies, since none have been reported except by Marshall et al. (1990) for their Petauroidea, which includes Burramyidae. Each of the petauroid families will be dealt with in turn.

Acrobatidae: Djaludjiangi yadjana differs from the extant acrobatids Acrobates pygmaeus and Distoechurus pennatus in many respects, including its greater size. Work is in progress on fossil material from Riversleigh that apparently represents two extinct Miocene acrobatid species, both of which may challenge some currently recognised synapomorphies for the Acrobatidae. Pending completion of analysis of these Miocene acrobatids, the following observations apply to A. pygmaeus and D. pennatus only.

In extant acrobatids both P¹ and P² are tall, 'secodont' teeth (Aplin & Archer 1987), and P₁ is taller than P². In D. yadjana P₁-² do not approach this secodont condition, and P₁ is distinctly taller than P². In acrobatids the metaconule is much reduced, but this is not the case in D. yadjana. Extant acrobatids have lost M₄, but M₄s of D. yadjana are unreduced. In acrobatids the entoconid is by far the shortest cusp on the lower molars, being distinctly lower than both the metaconid and hypoconid. In D. yadjana the entoconid is higher than the hypoconid and is only a little shorter than the metaconid. The M₁ metaconid of D. yadjana is far less prominent than that of acrobatids. D. yadjana clearly is not an acrobatid.

Tarsipedidae: The dentition of Tarsipes rostratus is characterised by extreme reduction; the dentary is splint-like and the teeth vestigial, with premolars and molars undifferentiated. D. yadjana shows no resemblance to and shares no apparent dental apomorphies with T. rostratus.

Pseudocheiridae: Djaludjiangi yadjana lacks the following pseudocheirid synapomorphies (from Archer et al. 1987; and Woodburne et al. 1987): M₃ protoconid displaced to the lingual side of the trigonid (in D. yadjana it is midway or slightly buccal to midway across the transverse axis of the trigonid); M₃ cristid obliqua extending to the top of the metaconid rather than to the protoconid or protostylid (in D. yadjana it terminates on the posterior flank of the protoconid at a point between the apices of the protoconid and metaconid); and hypoconids and posterior protoconids extend across each lower molar to the lingual side of the crown (in D. yadjana the valleys separating the hypoconid from the entoconid and the protoconid from the metaconid respectively are approximately medial on the posterior molars, and slightly buccal to the transverse midpoint of the anterior molars). Pseudocheirids show no trace of the transverse lophids seen in D. yadjana and in various phalangeroids. Rather, there are uninter-
rupted deep valleys between the hypoconid and entoconid, and the protoconid and metaconid, respectively.

Other features diagnostic for pseudocheirids are cited by McKay (1989). Some of these would exclude *D. yadjana* from the Pseudocheiridae but are equally inapplicable to Miocene pseudocheirid taxa. The molars of *D. yadjana* are considerably less selenodont than those of most pseudocheirids and slightly less so than those of *Pildra antiquis*. *D. yadjana* does have three upper premolars (as do pseudocheirids and extant petaurids, acrobatids and *Cercartetus* spp.), but P3 has only one primary cusp. However, P's of Miocene pseudocheirids such as *Pildra antiquus* and *Marlu kutjumarpensis* are also single-cusped. In buccal view the Pp, of extant pseudocheirids is about the same length and height as M1, but, in all Miocene pseudocheirids for which P is known it is, in buccal view, considerably shorter anteroposteriorly than M1. The condition in *D. yadjana* is unlike that in extant pseudocheirids and similar to that in known Miocene pseudocheirids. In both *D. yadjana* and those species of *Pildra*, *Paljara* and *Marlu* for which P is known, it is a large tooth with one primary cusp (P is, however, larger relative to the size of the lower molars in *D. yadjana* than in any Miocene pseudocheirid). Lower molars of *D. yadjana* are all approximately equal in size similar to the condition found in extant pseudocheirids. However, in the small Miocene pseudocheirids *P. antiquus* and *M. kutjumarpensis*, but not *P. tirarensae*, M1 is more reduced relative to M1,2,3.

Thus there are numerous character states shared by pseudocheirids but not *D. yadjana*. Some relatively plesiomorphic Miocene pseudocheirids (especially species of *Paljara* and *Pildra*) resemble *D. yadjana* in some respects, including P3 morphology, degree of selenodonty and overall size - features which may turn out to be symplesiomorphic for these taxa. *Paljara* and *Pildra* species share with other pseudocheirids a number of features that are absent or less developed in *D. yadjana*, such as lingual displacement of the M1 protoconid; M1 cristid obliqua extending to the top of the metaconid; hypoconids and entoconids that occupy comparatively more of the lingual side of the molar crowns; and a complete absence of transverse lophiids. *D. yadjana* is not a pseudocheirid.

**Pilkipildridae**: In both pilkipildrid species for which sufficient material is known (*D. gillespieae* and *P. handae*; Archer et al. 1987; Archer 1989), in lateral view the lower molar row is considerably bowed (higher at the anterior and posterior ends than in the middle) at alveolar level, whereas in *D. yadjana* bowing of the molar row is very slight. Although I1 of *D. yadjana* is quite robust, it is less steeply inclined than that of pilkipildrids (known only by the I1 alveolus of *D. gillespieae*). *Djilgaringa gillespieae* has a more massive P3 than does *D. yadjana*, and unlike the P3 of *D. yadjana*, that of *D. gillespieae* has a bladed dorsal edge with three cusps, from each of which is produced a buccal and a lingual vertical ridge. However, P3 of *Pilkipildra handae* appears to have been more slender, shorter and less sectorially specialised than that of *D. gillespieae*, and was possibly no larger than the P3 of *D. yadjana*. The upper molars of *D. yadjana* have comers less rounded than those of *D. gillespieae*, but since upper molars have not yet been reported for any other pilkipildrid species, it is difficult to say whether upper molars with rounded corners are a pilkipildrid synapomorphy. In *D. gillespieae* there is a marked anteroposterior lower molar row reduction gradient and M4 is markedly reduced and low-crowned, with a very narrow talonid. The lower molar alveoli of *P. handae* suggest that its M3 was proportionately wider than that of *D. gillespieae*, but nevertheless smaller than the more anterior molars. The molars of *D. yadjana* show only a slight decline posteriorly, with M only slightly smaller than the other molars and having a relatively unreduced talonid. Similarly, transverse cristids on the talonids of the posterior lower molars are less reduced in *D. yadjana* than in pilkipildrids; in particular, the hypolophid of M3 is as well-formed as those of M1,2,3, whereas M3,4 of *D.
gillespieae have virtually no ectolophid. In D. gillespieae there is a longitudinal median groove on the posterior lower molars, but in D. yadjana the presence of such a groove is precluded by the retention of the ectolophid.

Pilkipildrids share several features with D. yadjana. Both have large P3's and quadrutubcular, bunoselenodont molars showing some degree of crenulation, with low transverse loph/ids formed by an en echelon arrangement of cusps and cuspules (although the lophids of D. yadjana are better-formed than those of D. gillespieae). Like D. yadjana, pilkipildrids have reduced selenodonty in comparison with pseudocheirids. Selenodonty is slightly more reduced in D. gillespieae than in D. yadjana. In spite of these similarities, the features discussed above are sufficient to exclude D. yadjana from the Pilkipildridae.

Petauridae: Djalu'udjangi shows none of the apomorphies that characterise the petaurid subfamily Dactylopsilineae. The only feature it shares with dactylopsilines to the exclusion of petaurines is the plesiomorphic retention of a relatively unreduced molar row. As noted above, D. yadjana shares with all extant petaurids small size, similar dentary morphology, long, slender, procumbent and slightly curved I1 and quadrutubcular, bunoselenodont molars. Nevertheless, many synapomorphies that have been proposed for the Petauridae are absent from D. yadjana, including (most from Archer et al. 1987) marked reduction of P3, loss of distinction of conules of the upper molars, reduction of en echelon crest relationships, reduced selenodonty, very low-crowned posterior molars, M4 reduced with very reduced talonid width, transverse cristids on talonids of posterior molars reduced, and presence of a longitudinal median groove on the posterior lower molars.

However, it seems possible that this combination of molar and premolar characteristics, together with the curved I1 of extant petaurids (developed to greatest degree in species of Dactylopsila, in which it is strongly curved and greatly enlarged), represent a suite of relatively derived features linked to the increasing specialisation by petaurids on soft foods such as plant and insect exudates and on wood-gouging as a means of procuring exudates (Cartmill 1974; Kay & Cartmill 1976). More plesiomorphic petaurids may be expected not to display all of these apomorphic character states. A hypothetical ancestral petaurid might be predicted to have less reduced P3's, a less steep anteroposterior molar reduction gradient and therefore less reduced M4's, and less simplified molar crown morphology. Djalu'udjangi yadjana possesses exactly this combination of features, whilst lacking key synapomorphies for each of the other possum families. Although D. yadjana lacks character states regarded as synapomorphic for the Petauridae, the differences between it and extant petaurids are a matter of degree rather than of kind. Supposed petaurid dental synapomorphies have generally been described (e.g. Archer et al. 1987) as states of reduction from presumed plesiomorphic states which could quite conceivably be those seen in Djalu'udjangi. Indeed, no plesiomorphic petaurid could satisfy current definitions of the Petauridae, which are based on highly-derived, modern taxa.

In summary, Djalu'udjangi shares a number of derived features with pilkipildrids and some with pseudocheirids (see above). It shows no close ties with burramyids and lacks phalangeroid synapomorphies such as a kinked cristid obliqua. Its affinities certainly appear to lie within the Petauroidea, rather than within or close to the Phalangeroidea or Burramyoidae. Djalu'udjangi either represents a new family of non-phalangeroid, non-burramyoid possums, or is a plesiomorphic petaurid. Although it possesses character states consistent with those predicted for a plesiomorphic petaurid, it cannot confidently be placed in Petauridae until a thorough review of petaurid dental synapomorphies is completed and the redefined family found to encompass the new genus. Incorrect placement of Djalu'udjangi within Petauridae would render that family paraphyletic, so for the present it is preferable to assign Djalu'udjangi to Petauroidea.
gillespieae have virtually no ectolophid. In D. gillespieae there is a longitudinal median groove on the posterior lower molars, but in D. yadjana the presence of such a groove is precluded by the retention of the ectolophid.

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In summary, Djaludjangi shares a number of derived features with pilkipildrids and some with pseudocheirids (see above). It shows no close ties with burramyids and lacks phalangeroid synapomorphies such as a kinked cristid obliqua. Its affinities certainly appear to lie within the Petauroidea, rather than within or close to the Phalangeroidea or Burramyoidae. Djaludjangi either represents a new family of non-phalangeroid, non-burramyid possums, or is a plesiomorphic petaurid. Although it possesses character states consistent with those predicted for a plesiomorphic petaurid, it cannot confidently be placed in Petauridae until a thorough review of petaurid dental synapomorphies is completed and the redefined family found to encompass the new genus. Incorrect placement of Djaludjangi within Petauridae would render that family paraphyletic, so for the present it is preferable to assign Djaludjangi to Petauroidea.
Djaludjangi shares with pilkipildrids, phalangerids, miralinids and sometimes ektopododontids, but not with extant petaurids, features such as a tendency to form cuspidate transverse crests by elaboration of the paraconule and neometaconule; an M1-P3 shearing unit incorporating a large P3, and the development of trigonid basins on M3, with associated metalophids. That pilkipildrids share these features with phalangeroids but not extant petaurids (or other petauroids) has previously (Woodburne et al. 1987) been interpreted as support for a pilkipildrid-phalangeroid clade; their presence in the petauroid Djaludjangi refutes this argument, since these features now appear either to be symplesiomorphic, or to have been independently derived in both the Phalangeroidea and Petauroidea. The form of the transverse crests in the upper molars of D. yadjana may provide further evidence (see Archer et al. 1987) that the poorly-formed transverse crests of extant petaurid molars developed from transverse rows of cones and conules, such as are possessed by pilkipildrids. Archer (1976) suggests the operation of a similar mechanism in the evolution of transverse lophodonty in marsupials.

P3 morphology of D. yadjana also lends support to a previously-developed hypothesis (Archer et al. 1987) regarding the evolution of the M1-P3 shearing unit. An M1-P3 shearing unit occurs in members of the Macropodoidea, Miralinidae, Pilkipildridae, Phalangeridae, Burramyidae, Thylacoleonidae and now Petauroidea (possibly Petauridae). Its occurrence in a primitive member of yet another diprotodontian family increases the possibility of this being a symplesiomorphic feature of diprotodontians, rather than having evolved independently in each of these groups.

Distribution and palaeoecology

Djaludjangi yadjana is so far known only from seven assemblages in the System B sequence and two (Henk’s Hollow Site and Wang Site) in the System C sequence at Riversleigh. Within System B, specimens of D. yadjana are known from sites thought to be low in the sequence (Creaser’s Ramparts, Wayne’s Wok) to those high in System B (Upper Site, Boid Site East), as well as the mid-B sites Mike’s Menagerie, Camel Spurtum and Dirk’s Towers. Henk’s Hollow and Wang Sites are both high in the System C sequence. At Henk’s Hollow, D. yadjana is represented only by isolated molars, and small metrical features place the single Wang Site dentary at the edge of size distributions for D. yadjana. The Wang and Henk’s Hollow specimens are referred to D. yadjana here but small differences between them and other specimens of D. yadjana may, with the recovery of further material, prove sufficient to warrant taxonomic distinction or at least the identification of a morphcline. Djaludjangi yadjana appears, therefore, to extend through Systems B and C, but may turn out to be restricted to System B.

The small burramyid species Burramys bruyyi (Brammall & Archer 1997) also persists through a long sequence of assemblages at Riversleigh, from System A to high in System C. Two undescribed acrobatid species span System B and extend up to lower System C local faunas but have not yet been recorded from any sites higher in the sequence than mid-System C.

The I1 of D. yadjana is similar in shape and size to that of G. leadbeateri which, like species of Petaurus, uses its lower incisors to scar trees to obtain exudates. Despite having larger P3s (combining with M1 to form a functional sectorial shearing unit) and more selenodont molars than extant petaurids, D. yadjana, like extant petaurids, probably fed on plant and insect exudates to satisfy the bulk of its energetic needs as well as insects and perhaps pollen to meet its protein requirements. Energetic considerations imply that D. yadjana was too small to have relied solely upon plant foliage for its nutritional requirements (Kay & Hylander 1978; Smith & Lee 1984). Similar arguments could be forwarded for small Miocene pseudocheirids (Pildra, Paljara and some Marlu spp.). The extant Pygmy Ringtail Pseudochirulus mayeri,
with a body weight of around 150 g (Flannery 1994), has teeth and dentary slightly larger than the small Miocene pseudocheirids. It has been suggested (e.g. Flannery 1994) that P. mayeri may be too small to be exclusively folivorous. Nevertheless, there is evidence from stomach contents that P. mayeri may practise significant folivory (I.D. Hume, pers. comm. cited in Cork 1995). Although leaf-eating is extremely rare below 700 g body mass, there are a number of exceptions including some microtine and criketid rodents, primates and marsupials - though none of these are exclusively folivorous at such small body masses (Cork 1995; Hume 1995). The selenodont molars of pseudocheirids shear leaves finely to break them into tiny pieces, which speeds the digestion of this high-fibre diet (Kay & Hylander 1978) and contributes to their ability to practise significant folivory at smaller body masses than may otherwise have been predicted. Small selenodont or bunoselenodont petaurid taxa such as Djaludjangi, Pildra, Paljara and Marlu may have included significant quantities of foliage in their diets.

Up to twelve living petaurid species are recognised (Flannery 1994). New Guinea and Australia each have six petaurid species, but only P. breviceps and D. trivirgata inhabit both areas. Presently there are three undescribed petaurid species recognised from Riversleigh in addition to D. yadjana (possibly a primitive petaurid). Within a given assemblage, species diversity appears to be similar to that in extant communities. Up to three petaurid species have been identified in a number of Riversleigh local faunas and today, up to three species of petaurid may be sympatric within a given area. Petaurus breviceps, P. norfolcensis and P. australis are sympatric over a significant portion of their range in Queensland, New South Wales and Victoria (Ziegler 1981) and up to three petaurid species may be sympatric in some regions of New Guinea (Flannery 1994). Petaurid species diversity at Riversleigh is probably underestimated because the scarcity of material (relative to that available for living taxa) necessitates conservative interpretation of variation between specimens; it is therefore possible that petaurid diversity within communities at Riversleigh exceeded that known in any area today.

Total possum diversity at Riversleigh certainly exceeds present-day maxima. Up to six small possum species (2-3 petaurid, 1-2 acrobatid and 1-2 burramyid) are found together in some assemblages at Riversleigh together with larger possum taxa including phalangeroids and, at some sites, up to nine pseudocheirid species of varying sizes (Archer et al. 1994). Over fifteen possum species appear to have occurred sympatrically in some Riversleigh assemblages. Today, up to thirteen possum species occur sympatrically in parts of New Guinea and up to nine species in the montane rainforests of northeastern Queensland (Flannery 1994). The high diversity of possum species in several sites at Riversleigh (e.g. Upper Site, Gag Site) suggests a complex resource base, finely partitioned by such mechanisms as distinct activity times, selection of different portions of the habitat, and diet differentiation (see e.g. Leite et al. 1996 on resource partitioning within present-day tropical forests). Djaludjangi yadjana is similar in tooth size and morphology to some relatively plesiomorphic pseudocheirid species (e.g. Pildra spp.). In Miocene times at Riversleigh, petaurids and pseudocheirids had not achieved the almost complete eco-morphological separation seen between extant representatives of these families.

It has been hypothesised (Archer 1984; Archer et al. 1994) that the scarcity of petaurids in the pre-Pliocene fossil record may reflect the fact that open forests, the present habitat of these small, and today mostly gliding, possums, were not widespread until the end of the Tertiary. The Riversleigh local faunas show that petaurids were indeed present and were a morphologically diverse group in the Miocene, although at least some Tertiary petaurid and petaurid-like species were quite different to extant gliding forms.

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