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Journal of Paleontology, Vol. 72, No. 4. (Jul., 1998), pp. 738-751.

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THE SKULL OF *EKALTADETA IMA* (MARSUPIALIA, HYPSPRYMNODONTIDAE?): AN ANALYSIS OF SOME MARSUPIAL CRANIAL FEATURES AND A RE-INVESTIGATION OF PROPLEOPINE PHYLOGENY, WITH NOTES ON THE INFERENCE OF CARNIVORY IN MAMMALS

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ABSTRACT—The near-complete skull of the Giant Rat-kangaroo *Ekaltadeta ima* is described from a middle Miocene deposit at Riversleigh, north western Queensland. Surprisingly, the results of phylogenetic analysis indicate no special relationship with the only other hypsiprymnodontids for which substantial cranial material is known (*Hypsiprymnodon moschatus*, *H. bartholomaei*), but within Macropodoidea, a number of derived features present in *E. ima* are found only in another extinct taxon, the Balbarinae. Recent studies have suggested that Balbarinae may not represent a basal macropodid clade as thought by most previous authors and furthermore that the subfamily is perhaps distinct from all other kangaroos. In light of these findings an interesting possibility is noted, i.e., that Propleopinae and Balbarinae may represent a monophyletic clade to the exclusion of all other taxa. Preliminary results of investigation into dietary habitus indicate that Propleopinae represents a radiation of medium- to large-sized omnivorous kangaroos. Within this clade it is reiterated that a tendency toward carnivory might be inferred from the relative importance of high amplitude vertical shearing versus horizontal shearing and/or crushing elements in the dentition.

INTRODUCTION

UNTIL RECENTLY the propleopine (Giant Rat-kangaroo) subfamily has represented an interesting but highly enigmatic element of the macropodoid radiation. The first material attributable to Propleopinae (*Propleopus oscillans*) was described by De Vis (1888) who considered it to be a sister taxon to the extant *Hypsiprymnodon moschatus*. Giant Rat-kangaroo material representing an additional species, *P. chillaensis*, was described by Archer et al. (1978) from the Pleistocene Chillagoe Formation. Archer and Flannery (1985) added a further two new species, *P. wellingtonensis*, from Pleistocene deposits of Wellington Caves in New South Wales and the first pre-Pliocene propleopine, *Ekaltadeta ima*, from middle Miocene deposits of Riversleigh in northwestern Queensland. A new Pliocene genus and species, *Jackmahoneyi toxoniensis*, was described by Ride (1993) from Bow, N. S. W. A second *Ekaltadeta* species, *jamiemulvaneyi*, from early-late Miocene deposits of Riversleigh (Archer et al., 1995; Wroe, 1997a), was described by Wroe (1996a). Ride and Wells (1995) and Ride et al. (1997) introduced the first cranial material for a propleopine, consisting of a maxillo-premaxilla fragment, representing a juvenile *P. oscillans*. The skull of an adult *E. ima*, described below, constitutes the most complete cranial material known for a Giant Rat-kangaroo, offering greatly improved opportunities for elucidation of the clade's phylogeny and paleobiology.

Systematic terminology largely follows Aplin and Archer (1987). Exceptions are noted in the text. Dental nomenclature follows Flower (1867) and Lockett (1993) regarding the molar-premolar boundary, where the adult (unreduced) postcanine cheektooth formula of marsupials is P1–3 and M1–4. Archer's (1976) basicranial terminology is followed excepting that for V3 foramina (see Gaudin et al., 1996; Wroe, 1997b), anterior carotid foramina (see Wible, 1986) and lateral carotid foramina (see Aplin, 1990).

SYSTEMATIC PALEONTOLOGY

Superfamily MACROPODOIDEA Grey, 1821

Family HYPSPRYMNODONTIDAE Ride, 1993

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.—Medium- to large-sized macropodoid; sagittal and nuchal crests well developed; lateral carotid fenestra large, ovate; ectotympanic slightly concave ventrally, partially fused to postglenoid anteriorly and posttympanic processes of squamosal and mastoid part of periotic posteriorly, linear in lateral view; interorbital constriction marked; frontals greatly inflated producing markedly domed profile; dental and masseteric canals separate at anterior ends; masseteric canal terminating below P₃–M₁ in prominent cul-de-sac; dentary of even depth below molar row; P₂ persists in adult dentition; I₁ lanceolate and transversely compressed; diastema between I₁–P₂ small; plagiaulacoid P₃ very large; metaconid and protostylid with anterior cristids on M₁; upper molars basally broad and conical; molar gradient high, particularly in upper dentition.

EKALTADETA IMA Archer and Flannery, 1985

Figures 1–3

Type specimen.—QM F12423, left dentary containing P₂, P₃, M_{1–2}, M₄, lingual side of M₃, and the alveolus for I₁.

Revised specific diagnosis.—Approximately forty percent smaller than *Ekaltadeta jamiemulvaneyi* in overall size; entoconid well below hypoconid height on M₁; P₃ very large relative to M₁.

Supplement to previous descriptions.—QM F12436, skull, containing LP³, M^{1–4}, and RP², P³, M^{1–4}. Dentition of this specimen described by Wroe (1996a). Specimen shows no obvious distortion; near complete, but with following elements broken away: premaxillae, nasals, anterodorsal portions of maxillae,



FIGURE 1—Skull of *Ekaltadeta ima* (Archer and Flannery, 1985), QM F12436. 1, left lateral view. 2, right lateral view. 3, ventral view. Scale bar = 2.0 cm.



FIGURE 2—Skull of *Ekaltadeta ima* (Archer and Flannery, 1985), QM F12436. 1, ventral view of basicranial region. 2, dorsal view. Scale bar = 2.0 cm.

posterior of left jugal and anterior of left squamosal contributions to zygomatic arch. Prominent features include: marked anterodorsal inflation of frontals, producing “domed” profile in lateral view; marked interorbital constriction; hypertrophied sagittal and nuchal crests; no frontal crests or supraorbital processes; zygomatic arches robust.

Nasals taper anteriorly (inferred from anterior sutures of frontals); maxilla shows broad contact with frontal on face (14 mm); infraorbital canal contained within maxilla and extends to about

10 mm above anterior edge of P^3 (broken away beyond this point but probable that external openings of infraorbital canals well anterior to P^3); no masseteric process; well developed orbital wing of maxilla shows broad contact with lachrymal and frontal; ventrally a large maxillary-palatine vacuity extends posteriorly from M^1 – M^2 juncture; frontals very broad and anterodorsally expanded, with posterior sutures poorly defined but probable frontal-squamosal contact (apparent on left side of skull) dorsal to sphenorbital fissure; no supraorbital processes or frontal

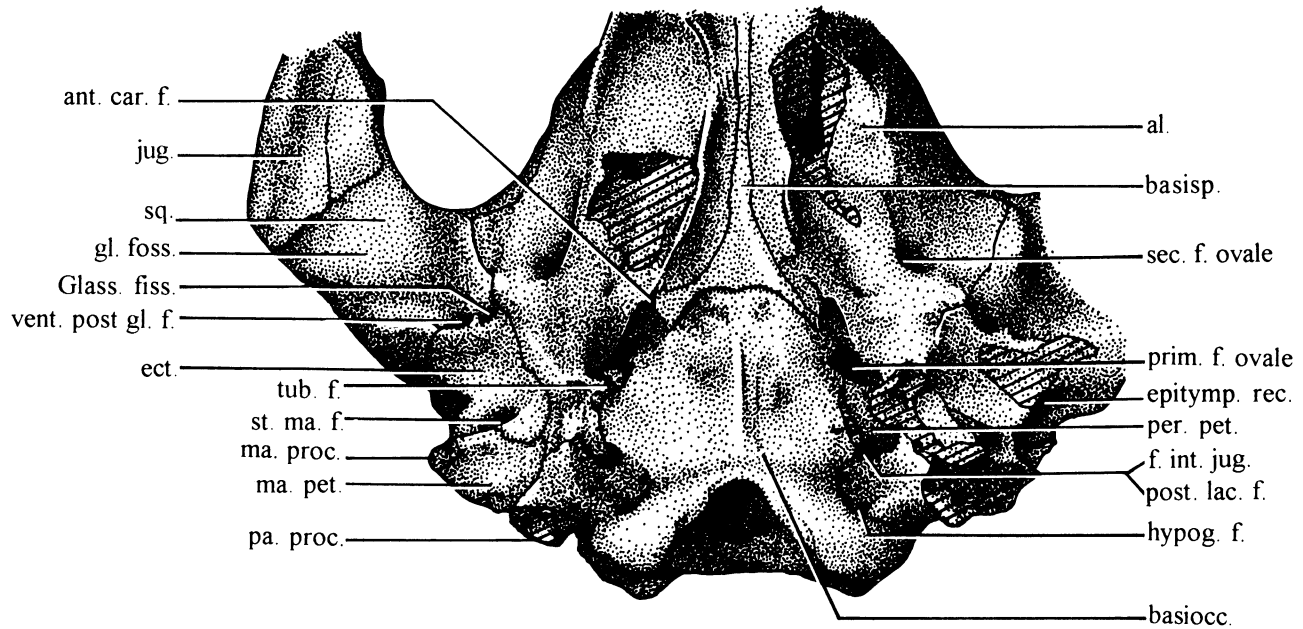


FIGURE 3—Basicranial region of *Ekalta deta ima* (Archer and Flannery, 1985) showing terminology and sutural relations. Abbreviations: al. = alisphenoid, ant. car. f. = anterior carotid foramen, basiocc. = basioccipital, basisp. = basisphenoid, ect. = ectotympanic, epitymp. rec. = epitympanic recess, f. int. jug. = foramen for internal jugular canal, gl. foss. = glenoid fossa, Glass. fiss. = Glaserian fissure, hypog. f. = hypoglossal foramen, jug. = jugal, ma. pet. = mastoid part of petiotic, ma. proc. = mastoid process, pa. proc. = paroccipital process, per. pet. = petrosal part of petiotic, post. lac. f. = posterior lacerate foramen, prim. f. ovale = primary foramen ovale, sec. f. ovale = secondary foramen ovale, st. ma. f. = stylomastoid foramen, sq. = squamosal, tub. f. = tubular foramen, vent. post. gl. f. = ventral postglenoid foramen. Damaged areas denoted by stripes.

crests; ethmoid foramen delimited anteriorly by frontal and posteriorly by orbitosphenoid; parietals bounded anteriorly by frontals and ventrally by squamosals, meet along midline to produce prominent sagittal crest (at least 6 mm high); no interparietal sutures visible; massive posteriorly-oriented nuchal crest produced by interparietals and supraoccipital; lachrymal containing two lachrymal foramina extends anteriorly about 3 mm on to face but orbital component is minor (extends about 8 mm posteriorly); palatine reduced to thin mesial wedge containing small posterolateral palatal foramen in ventral view and sphenopalatine foramen immediately dorsal to maxillae above M^3 , broken away dorsomedially to expose vomer which completes arch of narial passage; presphenoid-basisphenoid juncture broad: anterior extent obscured by matrix, laterally delimited by pterygoids; pterygoids broken away ventrally, remaining portions of lateral and medial pterygoid plates house well developed pterygoid fossae, dorsal element of medial plates extends posteriorly to basisphenoid-basioccipital suture, lateral pterygoid plates moderately developed; posterior pterygoid processes extend to overlay foramina of transverse canal; basisphenoid very long, tapering anteriorly; alisphenoid contacts orbitosphenoid anteriorly to delimit sphenorbital fissure, wholly encloses fenestra rotunda, is separated from sphenorbital fissure by a thin wall; infratemporal extension of alisphenoid delimited by frontal and squamosal; alisphenoid bounded anterodorsally by frontal and squamosal sutures unclear in this region but parietal contact with alisphenoid considered unlikely; ventromesially transverse foramen enclosed about 1 cm anterior to anterior carotid foramen, anterior carotid foramen at junction of alisphenoid-basisphenoid-basioccipital (roofed by alisphenoid), external opening of foramina ovale (lateral to anterior carotid foramina) fully enclosed and floored by alisphenoid forming a canal approximately 1 cm long; small foramen present between secondary foramen ovale and anterior carotid foramen (possibly accessory secondary foramen

ovale carrying branch of V3); posterolateral to primary foramen ovale bony processes are formed by alisphenoid and anterior of ectotympanic, posteriorly a mesial projection of alisphenoid forms a bridge ventral to petrosal part of petiotic contacting lateral processes of basioccipital, Eustachian canal floored by these processes; alisphenoid fused posterolaterally with mesial wing of ectotympanic, thin processes of alisphenoid contact mastoid part of petiotic and paroccipital, alisphenoid tympanic wing very slightly inflated; squamosal robust and laterally extensive, delimited ventrally by parietal and anteroventrally by frontal; squamosal tubercle shallow and perforated by cavernous postzygomatic foramen (clearly visible in posterior view); superior squamosal crest well developed and dorsomesially inclined at approximately 60° ; zygomatic sulcus of squamosal deep and broad on transverse plane; glenoid fossa broad (approximately 18 mm), defined posteriorly by postglenoid processes of squamosals (9 mm on transverse plane) and laterally by glenoid processes of jugals; mesially glenoid fossa delimited by medial glenoid process of squamosal; sulcus on ventromesial margin of glenoid fossa connects with sulcus in anterior of ectotympanic completing postglenoid foramen; medial to last-mentioned foramen is large well developed petrotympanic (Glaserian) fissure also formed by sulci in squamosal and ectotympanic; small subsquamosal foramen dorsal to external auditory meatus; well developed squamosal epitympanic sinus present, open directly into external auditory meatus; basioccipital shows moderately developed keel, posterolaterally contains sulcus for jugular fossa, in which there is a large posterior lacerate foramen dorsally and a small foramen for the combined auricular ramus of the vagus nerve/tympanic nerve laterally; lateral border of jugular fossa provided by sulcus in anterolateral process of paroccipital; no distinct foramen present for internal jugular canal, which is floored by lateral process of basioccipital but is open

dorsally; ectotympanic large with ventral surface slightly concave, linear in lateral view and open dorsally, anklyosed with alisphenoid anteriorly and mesially, exoccipital and mastoid part of petiotic posteriorly and postglenoid process of squamosal laterally; posteriorly sulcus in ectotympanic contributes to well-defined and exposed stylomastoid foramen which is completed posteriorly by sulcus in mastoid part of petiotic; petrosal part of petiotic short along anteroposterior dimension, largely obscured by paroccipital-basioccipital bridge in ventral view, anterior process very poorly developed; mastoid part of petiotic robust, not compressed anteroposteriorly, broad along transverse dimension, shows some pneumatization; tips of both mastoid processes broken away but processes clearly projected laterally, mastoid ascends posterior face of cranium meeting posterodorsal edge of squamosal, paroccipitals slightly pneumatized; tips of both paroccipital processes missing but appear small and posteriorly directed.

Locality and age.—QM F12436 is from Camel Sputum Site, Riversleigh World Heritage Estate, northwestern Queensland. Considered middle Miocene in age by Archer et al. (1995).

PHYLOGENETIC ANALYSIS

Method.—Most previous authors have regarded propleopines and other hypsiprymnodontids as a basal taxon within Macropodoidea (e.g., Archer, 1984; Flannery, 1987, 1989). However, evidence presented by Cooke (1997a, 1997b) indicates that Balbarinae may represent the sister taxon to all other macropodoids. The resolution of relationships within Macropodoidea has been hampered by a lack of consensus regarding immediate sister group identity; this problem is particularly acute regarding the assessment of cranial features.

A majority of workers (e.g., Aplin and Archer, 1987; Flannery, 1987; Flannery et al., 1987; Springer and Woodburne, 1989; Marshall et al., 1990; Ride, 1993) favor the suggestion that macropodoids and phalangeriforms ("possums") are sister groups and form a clade (Phalangerida) to the exclusion of vombatiforms and thylacoleonids. Hence, possums are potential macropodoid outgroup taxa and phalangerids in particular (see below) have been employed as such in previous analyses.

However, some studies are equivocal on the monophyly of Phalangerida, failing to resolve a basal trichotomy between vombatiforms, macropodoids and phalangeriforms (Springer and Kirsch, 1991) or a polychotomy between vombatiforms, macropodoids, tarsipedids and a clade containing all other possums (Luckett, 1994), or even suggesting that some vombatiform taxa arose from an early, burramyid-like stock (Murray et al., 1987). Indeed, in spite of its apparent widespread appeal there is little firm evidence in support of the monophyly of Phalangerida.

Within Phalangerida, in addition to the generally favored macropodoid-phalangeriform sister-group hypothesis there is limited support for a macropodoid-phalangerid relationship, with these taxa together forming the sister group of all other phalangeriforms (see e.g., discussion in Flannery, 1987). However, in recent years Phalangeridae has also been placed in a clade with the extinct Miralinidae, Ektopodontidae and perhaps Pilkipildridae, with Burramyidae as the basal sister taxon to a clade containing all other phalangeriforms (Archer et al., 1987); phalangerids have also been placed outside of a clade containing burramyids, petaurids, pseudocheirids, acrobatids and tarsipedids (Marshall et al., 1990); they have been aligned with burramyids (Springer and Kirsch, 1991); and have even been placed—somewhat spuriously—in a clade with vombatids and phascolarctids (Springer et al., 1994).

Several authors (e.g., Flannery, 1987, 1989; Cooke, 1997a) have used members of Phalangeridae as outgroup taxa when

determining the polarity of macropodoid dental characters. However, the lack of consensus as to the sister-group relations of both Macropodoidea and Phalangeridae, together with the fact that phalangerids are apomorphic for many basicranial characters within Phalangerida (Aplin and Archer, 1987; Springer and Woodburne, 1989; Marshall et al., 1990), renders this choice of outgroup problematic.

An alternative phalangeriform taxon for use in determining character state polarities in Macropodoidea is the Burramyidae. Burramyids have long been involved in discussions on the evolution of character states in macropodoids (e.g., Broom, 1896, 1898; Tate, 1948; Ride, 1956) and possess features that are uniquely plesiomorphic amongst phalangeriforms and perhaps in some cases Phalangerida (Aplin and Archer, 1987). Nevertheless, the position of Burramyidae within Phalangerida is also controversial. Broom (1896) originally regarded *Burramys* as a form intermediate between macropodoids and possums, an idea finally put to rest by Ride (1956). It is worth noting, however, that basicranial material was unknown for the taxon at that time and a thorough study of basicranial anatomy of *Burramys* has not been conducted since its discovery as a living animal in 1966. More recently, Archer et al. (1987) treated burramyids as the plesiomorphic sister taxon to a clade containing all other possums. Marshall et al. (1990) unite burramyids in a clade with petaurids, pseudocheirids, acrobatids and tarsipedids—an interpretation also preferred by Springer and Woodburne (1989)—whereas Springer and Kirsch (1991) suggest a burramyid-phalangerid relationship. Edwards and Westerman (1995) concur with Aplin and Archer (1987) in relegating Burramyidae to a third phalangeriform unit, separate from the Phalangeroidea and Petauroidea and with its affinities to those superfamilies regarded as unresolved; this position is also adopted by the present authors.

Outgroup sampling has included representatives of all genera and most species of possum. Moreover, because of discordance between phylogenetic interpretations within Diprotodontia at both familial and suprafamilial levels, a wide range of outgroup taxa have been considered with a view to identifying morphoclines and establishing the polarity of cranial features within Macropodoidea. Character states shown by taxa considered to be the least derived members of their respective clades known from cranial material are of particular importance. These include: *Pucadelphys andinus* (Didelphidae), *Badjcinus turnbulli* (Thylacinae), *Murexia longicaudata* (Dasyuridae), species of *Echymipera* and *Peroryctes* (Peramelidae), *Yalkaparidon coheni* (Yalkaparidontidae), *Wakaleo vanderleueri* (Thylacoleonidae), and *Wynyardia bassiana* (Wynyardiidae).

Regarding ingroup comparison for Macropodoidea, a basal position for *Hypsiprymnodon* (Hypsiprymnodontidae) has been suggested by Archer (1984) and Flannery (1987, 1989). As noted above, although most previous authors have considered balbarines to be the sister taxa to other macropodids (Archer, 1984; Flannery 1987, 1989), Cooke (1997a, 1997b) contends that balbarines may represent a basal macropodoid clade. A specimen representing an unnamed species of balbarine (referred to herein as balbarine sp.) has been used in the present study. Within Potoroidae Flannery (1989) considers the species of *Potorous* to be the least specialized. Recent authors have concurred on a basal position for the species of *Dorcopsulus* within Macropodidae (Flannery 1989; Kirsch et al., 1995).

Character analysis.—Morphology of the squamosal epitympanic sinuses: Squamosal epitympanic sinuses are absent in most Didelphidae (Marshall and Muizon, 1995; Archer, 1976), *Yalkaparidon coheni* (Archer et al. 1988), and a single dasyuromorphian taxon, *Badjcinus turnbulli* (Muirhead and Wroe, in press). Posterior squamosal epitympanic sinuses are absent in

basal peramelemorphians (e.g., *Echymipera kalubu*, *P. longicauda*), but present in derived taxa (e.g., *Perameles* spp.). Within Diprotodontia squamosal epitympanic recesses may be present dorsal and posterior to the meatal process of the ectotympanic. These may be open or fully enclosed. Squamosal epitympanic sinuses are open and poorly developed in *Wynyardia bassiana*, *Wakaleo vanderleueri* and *Vombatus ursinus*, but are well developed and fully enclosed in all possum taxa (less so in *T. rostratus* and *C. lepidus* than in other phalangeriforms—Aplin, 1990) except *Burramys parvus*. In *B. parvus*, uniquely amongst possums, there is a large epitympanic fenestra that brings the well developed zygomatic, dorsal and posterior squamosal epitympanic sinuses into direct communication with the exterior of the mascerated skull (contra Springer and Woodburne, 1989 and Marshall et al., 1990). Species of *Cercartetus* lack an epitympanic fenestra but do possess a slight recess in the squamosal, immediately dorsal to the external auditory meatus, that is not seen in other possums. Amongst macropodoids both *Ekaltadeta ima* and balbarine sp. show very large dorsal and posterior epitympanic recesses of the squamosal which are not enclosed by ectotympanic or squamosal processes. These recesses are clearly visible in external view. For remaining macropodoid taxa squamosal epitympanic sinuses are present but smaller, with morphology ranging from open (e.g., *Hypsiprymnodon*, *Potorous*) to partially enclosed (e.g., *Macropus giganteus*).

As noted by various authors (Aplin, 1987; Aplin and Archer, 1987; Springer and Woodburne, 1989) no macropodoid shows complete lateral and ventral enclosure of squamosal epitympanic sinuses. The open squamosal epitympanic sinuses of *Ekaltadeta ima* and balbarine sp. are plesiomorphic for Phalangerida and Macropodoidea. However, the large size of these recesses may constitute a synapomorphy uniting *E. ima* and balbarine sp. The presence of open squamosal epitympanic sinuses in *Burramys parvus* contradicts the suggestion of Springer and Woodburne (1989) that enclosure of these sinuses represents a synapomorphy possessed by all possum taxa.

Morphology of the ectotympanics.—Three aspects of ectotympanic morphology are considered here: morphology of the anterior and posterior limbs, the degree of mesial-lateral expansion, and the grade of dorsal completeness. Ectotympanics are unknown for *Pucadelphys andinus*. Reig et al. (1987) note that “U-shaped” ectotympanics are plesiomorphic among ameridelphians. Within Dasyuromorphia and Peramelemorphia all taxa show ectotympanics that are “U-shaped” in lateral view (i.e., do not form complete tubular bony ear canals). Some taxa show distinct mesial-lateral expansion [particularly well developed in *Badjcinus turnbulli*, *Thylacinus cynocephalus* (Thylacinidae) and *Sarcophilus harrisi* (Dasyuridae)] but in no species does the ectotympanic contact the postglenoid process of the squamosals anteriorly or the mastoid part of the periotic, or posttympanic process of the squamosal, posteriorly. Ectotympanics are unknown for *Yalkaparidon coheni* or *Wynyardia bassiana*. In *Wakaleo vanderleueri* and *Vombatus ursinus* the ectotympanics are “U-shaped” and complete respectively. Both taxa show very loosely articulated ectotympanic contact with the mastoid part of the periotic and posttympanic process of the squamosal posteriorly, and no contact with the postglenoid process anteriorly. In possums the mediolaterally extensive ectotympanic is firmly fused to the mastoid posteriorly, to the postglenoid portion of the squamosal anteriorly, and to the tympanic bulla medially. The single exception is *Burramys parvus*, in which the ectotympanic is firmly affixed to the mastoid posteriorly but shows less intimate association with the alisphenoid tympanic wing or the postglenoid process of the squamosal; in some adult specimens of *B. parvus* the ectotympanic-mastoid unit moves freely with respect to those elements (contra Springer and Woodburne,

1989; Marshall et al., 1990). In all phalangeriforms there is a groove lateral to the stylomastoid foramen (more pronounced in phalangerids and pseudocheirids than in petaurids, burramyids or acrobatids), however this groove is not strictly homologous with that seen between the ectotympanic and posttympanic squamosal process in macropodoids (see below), being entirely within the mastoid in some possum taxa though overlying the mastoid-ectotympanic suture in others. In all possums there is a complete bony external auditory meatus, but in no phalangeriform examined do the anterior and posterior limbs of the ectotympanic appear to meet to form a complete ring; the “ring” of the external auditory meatus is completed dorsally by the squamosal. Within Macropodoidea both *Ekaltadeta ima* and balbarine sp. have an ectotympanic that is linear in lateral view (the ectotympanic plays no role in enclosing squamosal epitympanic recesses) and greatly expanded both laterally and anteroposteriorly to unite closely with the postglenoid process, the mastoid part of the periotic and the posttympanic process of the squamosal. All other Macropodoidea show “U-shaped” or complete tubular bony ear canals. In less specialized taxa (e.g., *Hypsiprymnodon*, *Potorous*) there is no intimate contact with the postglenoid process anteriorly, but a more intimate fusion of these elements is present in derived macropodids (e.g., *Macropus* spp.). In all macropodoids other than *Ekaltadeta ima* and balbarine sp. a distinct groove separates the ectotympanic from the posttympanic squamosal process.

Partial fusion of the ectotympanic with postglenoid squamosal elements in *Ekaltadeta ima* is a derived feature also present in specialized macropodoid and possum clades. Separation of the posterolateral limb of the ectotympanic from the posttympanic wing of the squamosal is plesiomorphic for marsupials. This plesiomorphic state is retained in all macropodoids except *E. ima* and balbarine sp. A “U-shaped” ectotympanic is plesiomorphic for Marsupialia and Macropodoidea. Lateral expansion of the ectotympanic has occurred independently in several marsupial clades. However, for all taxa considered here except *E. ima* and balbarine sp., this expansion is always concomitant with maintenance of a “U-shaped” lateral profile, or further development of this morphology to produce a complete external auditory meatus. In *E. ima* and balbarine sp. the considerable lateral expansion of the ectotympanic on the transverse plane alone, producing a linear profile in lateral view, may be a derived feature unique to these two taxa.

Morphology of the postglenoid process.—A well developed postglenoid process is present in the vast majority of marsupial taxa. Exceptions include *Yalkaparidon coheni*, *Vombatus ursinus*, and only *Tarsipes*, *Hypsiprymnodon moschatus* and species of *Potorous* among Phalangerida [in *H. moschatus* and *Potorous* hypertrophy of the anterior limb of the ectotympanic appears to provide a functional replacement for the postglenoid process (Flannery, 1989)].

Presence of a postglenoid process, as in *E. ima* and balbarine sp., is clearly plesiomorphic for Australidelphia. However, loss of this feature is apparent within a number of clades including Yalkaparidontia, Vombatidae, Hypsiprymnodontidae and Potoroidae. Flannery (1987) and Flannery and Archer (1987) consider reduction or loss of the postglenoid process to represent an independently-derived character state for *Hypsiprymnodon moschatus* and *Potorous*. In contrast Flannery (1989) treats absence of this feature as a macropodoid plesiomorphy but comments on the high level of uncertainty regarding this polarity decision. Because the vast majority of outgroup taxa to Macropodoidea possess a postglenoid process and the few taxa in which this feature is lost show a high degree of masticatory specialization, we consider the presence of a postglenoid process to be a likely plesiomorphy for macropodoids.

Morphology of the ventral postglenoid foramen.—This foramen is positioned posterior to a well developed postglenoid process and not enclosed ("sheathed") by ectotympanic and/or squamosal elements in Didelphidae, Microbiotheriidae, Dasyuromorphia, Peramelemorphia, *Wynyardia bassiana*, and *Wakaleo vanderleuerei*. Anteromesial placement of the ventral postglenoid foramen is apparent in many taxa which show marked lateral development and close association of the ectotympanic with the postglenoid process of the squamosal, e.g. many Macropodoidea and all possums. Springer and Woodburne (1989, p. 216) consider that "... sheathing of the ventral postglenoid foramen by the postglenoid process and the medial wall of the mandibular fossa" represents a synapomorphy uniting all possum taxa which is absent in all macropodoids. However, it appears to us that the degree of sheathing of the ventral postglenoid foramen, and the relative contributions of ectotympanic and squamosal components, is variable both within Macropodoidea and Phalangeriformes, although all possums show a greater degree of sheathing than most (but not all) macropodoids. Within Phalangeriformes, complete sheathing by the squamosal occurs within Burramyidae, Phalangeridae and Petauridae, but some burramyids and petaurids also have ectotympanic involvement in this foramen, indicating homoplasy at both intra- and inter-familial levels. Within Macropodoidea, *Ekaltadeta ima*, balbarine sp., and some derived macropodids show a well developed foramen delimited by both ectotympanic and squamosal elements, whilst *Hypsiprymnodon moschatus*, *Potorous* spp. and other macropodoids show laterally-incomplete foramina in this position. The shared character states evident in *E. ima* and balbarine sp. represent a possible synapomorphy uniting the two taxa, though this implies independent derivation of this feature in some derived macropodids as well as in possums.

Presence of alisphenoid-parietal or frontal-squamosal contact.—Alisphenoid-parietal contact is present for all didelphids (Archer, 1976), most Dasyuromorphia, fossil peramelemorphians (Muirhead 1994), *Wakaleo vanderleuerei*, most possums, all Macropodidae, and *Hypsiprymnodon bartholomaii* (Flannery, 1989). Squamosal-frontal contact is present in *Thylacinus cynocephalus*, some Dasyuridae (e.g., some *Sminthopsis*), extant Peramelemorphia, vombatids, *Yalkaparidon coheni*, *Wynyardia bassiana*, *Thylacoleo carnifex* (Murray et al., 1987), only *Petaurus* and *Gymnobelideus* among possums, and *Ekaltadeta ima*, *Hypsiprymnodon moschatus* and all Potoroidae among macropodoids.

Alisphenoid-parietal contact is almost certainly plesiomorphic for Australidelphia and squamosal-frontal contact has arisen independently in a number of Australian and South American marsupial clades. Because all possums except for nondactylopsiline petaurids show parietal-alisphenoid contact, most previous authors have maintained that this character state is plesiomorphic for Macropodoidea (Pearson, 1950; Flannery et al., 1984) and that squamosal-frontal contact is a derived feature uniting *Hypsiprymnodon moschatus* with Potoroidae. However, the presence of squamosal-frontal contact in otherwise unspecialized outgroup taxa (e.g., *Yalkaparidon*, *Wynyardia*) detracts from any certainty in the polarity decision regarding Macropodoidea. The presence of alisphenoid-parietal contact in the basal macropodoid *Hypsiprymnodon bartholomaii* further complicates the use of squamosal-frontal contact as a hypsiprymnodontid-potoroid synapomorphy (Flannery and Archer, 1987). Given the above character-state distributions we consider that squamosal-frontal contact shown by *Ekaltadeta ima* may represent a synapomorphy for Hypsiprymnodontidae or a plesiomorphy for macropodoids. There is currently little to recommend either hypothesis over the other.

Position of the external opening of the infraorbital canal.—

The external opening of the infraorbital canal is above P³ in some Didelphidae (e.g., *Pucadelphys andinus*), some Thylacinidae [e.g., *Muribacinus gadiyuli* (Wroe, 1996b)], most possums and some macropodoids (e.g., *Potorous* sp., *Aepyprymnus rufescens* and *Dendrolagus* sp.). A more posterior position for this foramen is evident in some Didelphidae (e.g., *Didelphis marsupialis*), Microbiotheriidae, some Thylacinidae (e.g., *Thylacinus cynocephalus*), all Dasyuridae and Peramelemorphia examined, a single possum taxon (*Acrobates pygmaeus*), and some Macropodoidea (e.g., *Macropus giganteus*). An infraorbital foramen anterodorsal to P³ is common to *Wakaleo vanderleuerei*, some possums, *Hypsiprymnodon moschatus* and *Ekaltadeta ima* among macropodoids. This feature is unknown for *H. bartholomaii*, *Yalkaparidon*, and *Wynyardia bassiana*, and can not be assessed for *Tarsipes rostratus* because of difficulties with the elucidation of tooth homology in this highly derived taxon.

Flannery (1989) considers placement of the infraorbital canal anterodorsal to P³ to be plesiomorphic for Potoroidae (sensu Flannery, 1989, i.e., includes *Hypsiprymnodon* and propleopines). We treat this polarity decision as equivocal in light of the considerable variation shown among outgroup taxa.

Morphology of the lachrymal.—The lachrymal has a well developed facial wing in didelphid, microbiotheriid, thylacinid, dasyurid and peramelemorph, vombatimorphian, and most possum and macropodoid taxa for which this feature is known, including *Ekaltadeta ima*. Flannery and Archer (1987) treat the restricted anterior extension of the lachrymal onto the face as a possible synapomorphy uniting the species of *Hypsiprymnodon*. We support this proposition. *Ekaltadeta ima* retains the plesiomorphic condition for Macropodoidea, having a relatively unrestricted lachrymal.

Morphology of the primary foramen ovale.—This foramen carries the mandibular branch of the trigeminal nerve (V3). Exocranially this foramen may be intimately associated with the alisphenoid tympanic wing. As noted by Gaudin et al. (1996) and Wroe (1997b) terminology regarding V3 foramina has been complicated following the observation by Muizon (1994) that an alisphenoid tympanic wing may be a derived feature within Marsupialia. The distribution of this feature is considered in detail for polyprotodont marsupials by Wroe (1997b) who concludes that a primary foramen ovale delimited by the alisphenoid and periotic is plesiomorphic for Marsupialia, Dasyuromorphia, and Peramelemorphia. An alisphenoid-periotic endocranial exit for V3 is present in all diprotodontians examined in the present study.

This character-state distribution supports the contention of plesiomorphy for an alisphenoid-periotic enclosed primary foramen ovale for Marsupialia, Australidelphia and probably Diprotodontia. Consequently, we consider that the alisphenoid-periotic enclosed primary foramen ovale common to *Ekaltadeta ima* and other macropodoids is likely a retained plesiomorphy.

Morphology of secondary foramina ovale.—Wroe (1997b) treats presence of secondary foramina ovale as apomorphic for Australidelphia, being independently derived within some didelphid, dasyuromorphian, and peramelemorphian clades. Complete secondary foramina ovale are present in *Wakaleo vanderleuerei*, most possums and most macropodoids including both *E. ima* and balbarine sp. This feature is absent in the majority of acrobatids, petaurids, *C. caudatus* and *C. nanus* examined, and some potoroids (e.g., *Potorous tridactylus*) among macropodoids.

There is considerable variation among possums in the development of secondary foramina ovale. In specimens of many taxa a complete or incomplete secondary foramen ovale is formed by

anteromediodorsally directed wings, struts or spicules of the alisphenoid tympanic wing, or posterolateroventrally oriented projections from the ascending lamina of the alisphenoid, or a composite of both. Some pseudocheirids (e.g., some individuals of *P. cupreus* and *P. peregrinus*) may have two or three secondary foramina ovale. In most *Petaurus australis* and one individual of *Acrobates pygmaeus* examined a complete strut isolated a secondary foramen ovale on both left and right sides of the cranium. The range of morphologies present among phalangeridan outgroups to Macropodoidea prohibits reliable polarization of this feature for macropodoids.

Morphology of the lateral carotid fenestra (median lacerate foramen)—Aplin (1990, p. 184) observes that the lateral carotid fenestra is a "... constant feature of the macropodoid basicranium" which carries "... a major portion of the internal carotid nerves." In many marsupial taxa the lateral carotid, sensu Aplin (1990), forms a common aperture with the primary foramen ovale dorsally. Topographically the position of the lateral carotid fenestra among extant macropodoids (i.e., bounded by the petrosal part of the periotic, alisphenoid and basisphenoid) is equivalent to or closely approximates that of the medial lacerate foramen (sensu MacIntyre, 1967; Marshall and Muizon, 1995), the pyriform fenestra of Murray (1991), the foramen pseudovale of Archer (1976, 1982) or the primary foramen ovale as used in the present study and that of Wroe (1997b).

Romer and Parsons (1977) report that the medial lacerate foramen carries the internal carotid artery into the braincase in mammals. Marshall (1979) notes that the medial branch of the internal carotid enters the cranium via an entocarotid canal in marsupials, thereby differing from placentals (wherein the medial branch enters the medial lacerate foramen). However, Marshall (1979) does not allude to which, if any, vessels or nerves pass through the medial lacerate foramen among Marsupialia. Because the "medial lacerate foramen" of placental and marsupial mammals evidently does not carry the same vessels it is likely that they are nonhomologous structures. The validity of the hypothetical morphotype for the course of the internal carotid artery as used by Marshall (1979), with separate lateral and medial internal carotid arteries recognized, has been questioned by subsequent authors (Presley, 1979; Wible, 1986; Novacek, 1993). These authors contend that all adult amniotes possess only one internal carotid artery. To further complicate the issue, the pyriform fenestra, sensu Wible (1986), primitively carries a branch of the stapedia artery in eutherians. Several recent authors (Wible, 1986; Meng and Fox, 1995) have suggested that the stapedia artery is not present for adult marsupials. The foramen pseudovale (sensu Archer, 1976, 1982) carries V3 in many marsupial taxa and may carry small arterial or venous anastomoses and a small branch of the internal carotid. Aplin (1990) observes that this foramen carries branches of a number of different nerves and arteries among different possum taxa, but restriction of this foramen to carriage of nerves of the internal carotid artery appears to be confined to extant Macropodoidea among phalangeridans. The development of an independent foramen for nerves of the internal carotid has been reported in a number of placental taxa (Packer and Sarmiento, 1984).

For many marsupial taxa a single foramen evidently carries V3 and whatever vessels and/or nerves are associated with the lateral carotid fenestra (in taxa that possess separate foramina). The decision as to whether this common foramen should be termed a primary foramen ovale or a lateral carotid fenestra is perhaps a semantic one. But, because the carriage of V3 by this foramen is not disputed, whilst the identity of elements passing through the lateral carotid fenestra are variable between taxa, or unknown, we have elected to use the term primary foramen ovale for the single foramen state.

Marshall and Muizon (1995) note the presence of a distinct primary foramen ovale and a small lateral carotid foramen (their medial lacerate foramen) which are not endocranially confluent in *Pucadelphys andinus*. In *Dromiciops australis*, unspecialized fossil Peramelemorphia, most Dasyuromorphia, and *Yalkaparidon coheni* a single foramen is evident in this position (i.e., no independent foramina separate V3 from other vessels and/or nerves). However, many taxa show an independent lateral carotid foramen associated with processes of the alisphenoid. Division of the primary foramen ovale (endocranial exit for V3) into two separate foramina by a strut of the alisphenoid is evident in some Didelphidae (e.g., *Didelphis marsupialis*) and Dasyuromorphia (e.g., *Thylacinus cynocephalus*, *Dasyurus spartacus*). In these taxa the lateral opening probably carries V3. Topographically, the medial of these two foramina might be considered a lateral carotid fenestra/medial lacerate foramen. Distinct lateral carotid fenestra and secondary foramina ovale which are dorsally confluent with the primary foramen ovale are present in many taxa which have complete or incomplete secondary foramina ovale including some Dasyuromorphia (e.g., *Badjcinus turnbulli*, *Sarcophilus harrisii*), extant Peramelemorphia (e.g., *Peroryctes raffrayana*, *Echymipera kalubu*), *Wakaleo vanderleueri*, all possum taxa examined which possess secondary foramina ovale, and all Macropodoidea. In many possum taxa, including *B. parvus*, the lateral carotid fenestra is large and rounded, but in some pseudocheirid species (e.g., *P. archeri*) the primary foramen ovale is almost completely closed off by a projection of the petrosal, leaving a slitlike lateral carotid fenestra. For all extant macropodoids a large secondary foramen ovale and a tiny slitlike lateral carotid fenestra (almost completely closed over in some forms, e.g., *Potorous*) is confluent with the primary foramen ovale. This is also true of the fossil taxon *Hypsiprymnodon bartholomaii*. *Ekaltaleta ima* and balbarine sp. are unique within Macropodoidea and similar to some phalangeriforms (including *B. parvus* and many phalangerid species) in possessing a very large ovate lateral carotid fenestra confluent with the primary foramen ovale.

Most taxa considered to be structurally unspecialized within the Australian marsupial radiation (i.e., unspecialized dasyurids, peramelemorphs, *Yalkaparidon*) show no distinct lateral carotid fenestra separate from the primary foramen ovale. In these taxa it is presumed that the nerves/vessels which pass through the lateral carotid fenestra of other species share a common opening with the mandibular branch of the trigeminal nerve, i.e., the primary foramen ovale. In most australidelphian taxa examined a distinct lateral carotid fenestra was only present in conjunction with a secondary foramen ovale. In these taxa the lateral carotid fenestra and secondary foramina ovale converge dorsally with the primary foramen ovale. Confluence of the secondary foramen ovale and "medial lacerate foramina" has been reported in a number of phylogenetically disparate taxa (Woodburne, 1967; Murray, 1991; Aplin, 1990). In our view a lateral carotid fenestra (i.e., the middle lacerate foramen or pyriform fenestra of some other authors), as used in descriptions of Australian taxa, is commonly produced by the development of secondary foramina ovale (treated as a derived feature within Australidelphia here). Consequently we consider the development of a lateral carotid fenestra to be an apomorphic feature within Australidelphia which has probably been independently derived in a number of clades. We consider it unlikely that the lateral carotid fenestra of some Australian taxa is homologous with the medial lacerate of Marshall and Muizon (1995) in *Pucadelphys andinus*. It is also possible that the medial lacerate foramen of *P. andinus* is not homologous with that of some other authors (e.g., Romer

and Parsons, 1977). Detailed examination of soft tissue structures for a wide variety of taxa is required to fully resolve homologies of features in this region.

Immediate outgroup data regarding the presence/absence of the lateral carotid foramen for Macropodoidea is equivocal. In most phalangeridan material studied here a distinct lateral carotid fenestra is present. Intraspecific variation is great, but individuals of some possum species (see above) lack a distinct lateral carotid foramen. Additionally, the contribution of various tympanic and nontympanic elements to this foramen is variable within potential phalangeridan outgroups to Macropodoidea. Whether the large ovate lateral carotid fenestra of *Ekaltadeta ima* and balbarine sp. is plesiomorphic or apomorphic within Phalangerida is unclear. The slitlike lateral carotid foramen that conducts a nerve of the internal carotid artery (Aplin, 1990) in living macropodoids and *Hypsiprymnodon bartholomaii* may represent a synapomorphy uniting all Macropodoidea excepting *Ekaltadeta ima* and balbarines. Alternatively, the large, ovate lateral carotid foramen of *E. ima* and balbarine sp. could constitute a synapomorphy for a clade containing these taxa to the exclusion of other macropodoids.

Morphology of the alisphenoid tympanic wing.—The distribution of this feature among marsupicarnivores is covered by Wroe (1997b). This feature is absent in basal ameridelphians (e.g., *Pucadelphys andinus*, *Mayulestes ferox*) and only acrobatids among australidelphians. A weakly-developed alisphenoid tympanic wing which does not contact other tympanic elements (other than the ectotympanic) is present in most Didelphidae, some Peramelemorphia, *Yalkaparidon coheni*, Thylacinidae and *Wakaleo vanderleueri*.

Contact between the alisphenoid tympanic wing and tympanic processes of other basicranial elements is common to many marsupial taxa, but the homology of these elements is variable. Alisphenoid and periotic (petrosal part) tympanic wings contact and floor the middle ear in some derived Ameridelphia [e.g., *Caluromys philander*, *Caluromysiops irrupta* (Reig et al., 1987)], *Dromiciops australis*, some Peramelemorphia, all Dasypodidae, and *Tarsipes* among possums (Aplin, 1990).

The alisphenoid tympanic wing contacts the mastoid part of the periotic in *Myrmecobius fasciatus*, and all Phalangerida except Acrobatidae and *Tarsipes* (no alisphenoid tympanic wing develops in acrobatids). Springer and Woodburne (1989) report that in phalangerids, acrobatids, petaurids and pseudocheirids the alisphenoid tympanic wing extends posteriorly to the posterior lacerate foramen and/or paroccipital process. However, Springer and Woodburne's (1989) "posterior lacerate foramen" (their Fig. 1) is in fact a fossa into which at least three foramina may open. In all phalangeridans, the posterior lacerate foramen and foramen for the combined auricular ramus of the vagus nerve/tympanic nerve open ventrally into a cavity referred to by Aplin (1990) as the jugular fossa. The interior jugular canal (=inferior petrosal sinus—see Marshall et al., 1995) also opens posteriorly into this fossa: in some phalangeriforms this canal is enclosed and terminates posteriorly in a foramen for the internal jugular canal, whereas in others it is not enclosed and does not form a complete foramen.

Contact between the alisphenoid tympanic wing and paroccipital process is apparent in most possums and many macropodoids, but these processes do not contact in burramyids (except *Cercartetus concinnus*), *Gymnobelideus leadbeateri* and *Pseudochirops corinnae*, and some macropodoids including *Hypsiprymnodon*, *Ekaltadeta ima*, and balbarine sp.

Posterior development of the alisphenoid tympanic process is clearly a derived feature within Diprotodontia. A posteriorly extensive alisphenoid tympanic wing may represent an independently derived feature uniting Macropodoidea or a synapomorphy uniting macropodoids in a higher phalangeridan taxon. The

acquisition of a distinct jugular fossa may represent a synapomorphy for Phalangerida.

Masseteric process morphology.—A masseteric process is absent in all marsupicarnivoran taxa examined, and barely developed, if at all, among some Vombatimorphia (e.g., *Wakaleo vanderleueri*), many small possums (e.g., Burramyidae, Acrobatidae, *Dactylopsila tatei*, *D. palpator*) and some Macropodoidea, including *Ekaltadeta ima* and *Hypsiprymnodon*. A well developed masseteric process is present in many vombatimorphians (e.g., *Vombatus*, *Phascogale*), many possums (e.g., *T. vulpecula*, *S. rufoniger*, *S. maculatus*), and derived macropodoids (e.g., *Macropus giganteus*).

Development of a masseteric process is apomorphic for marsupials and has undoubtedly evolved independently in several diprotodontian lineages. *Ekaltadeta ima* shows the plesiomorphic state for Marsupialia and Macropodoidea.

Frontal sinus morphology.—In both *Ekaltadeta ima* and two undescribed balbarine taxa (B. Cooke, unpublished data) the frontal sinuses are markedly inflated. Many marsupial taxa show inflation of the frontal sinuses, particularly carnivorous species (e.g., *Thylacinus*, *Wakaleo*). However, the characteristic domed frontal morphology of *Ekaltadeta ima* is not evident in any non-phalangeridan taxa examined. Within Phalangerida we have observed similar morphology only in the phalangerids *Spilogale maculatus* and *S. rufoniger*; Flannery et al. (1987) consider this a derived feature within Phalangeridae.

Frontal sinus inflation, as evident in *E. ima* and balbarines, is certainly apomorphic within Macropodoidea and represents a possible synapomorphy uniting proleopines and balbarines. The "domed" morphology of this region in *E. ima* represents an autapomorphy within Macropodoidea.

Phylogenetic conclusions.—Results of this analysis exemplify the difficulty of assessing character state polarity for Macropodoidea. For at least five of the polarity assignments attempted we regard our conclusions as equivocal, but for many cranial features *Ekaltadeta ima* is almost certainly plesiomorphic within Macropodoidea (i.e., completely open zygomatic, dorsal and posterior squamosal epitympanic sinuses; presence of a postglenoid process; extent of facial wing of lachrymal; presence of an alisphenoid-periotic delimited primary foramen ovale; extent of posterior development of alisphenoid tympanic wing; lack of masseteric processes). However, two surprising findings have emerged. Firstly, we have been unable to identify any apomorphic cranial features which clearly unite *Ekaltadeta ima* with any extant macropodoid taxon, including *Hypsiprymnodon moschatus*. Secondly, five possible macropodoid apomorphies present in *Ekaltadeta ima* are shared only with balbarines among kangaroos (i.e., very large squamosal epitympanic sinuses, ectotympanic roughly linear in lateral view; ectotympanic intimately associated with the glenoid process of the squamosal anteriorly and the squamosal posttympanic process and mastoid part of periotic posteriorly; presence of large, ovate lateral carotid fenestra; greatly expanded frontal sinuses). On the other hand, the narrow slitlike lateral carotid foramen shared by all macropodoids except *Ekaltadeta ima* and balbarines may represent a synapomorphy uniting those macropodoids to the exclusion of proleopines and balbarines.

On the basis of cranial material alone there are reasonable grounds to hypothesize monophyly for Proleopinae and Balbarinae to the exclusion of all other Macropodoidea. Consequently, the evidence for a monophyletic Hypsiprymnodontidae (sensu Ride, 1993) which includes proleopines warrants reconsideration. In support of the inclusion of Proleopinae within Hypsiprymnodontidae Ride (1993, p. 453) states that proleopines and *Hypsiprymnodon* "... share the plagiaulacoid upper

and lower premolars, specialized trigonids in the first lower molariform tooth (dP_3 and M^1) with the principal crest formed from the parametacristid, the manner in which P2 is retained and withdrawn from occlusion when P3 erupts (Wroe, 1992), the extent of the masseteric canal, and the characteristic hypsiprymnodontid mandible." We are not convinced that any of these features represent grounds for postulating a special relationship between propleopines and *Hypsiprymnodon* for the following reasons: A plagiaulacoid P3 is found in all balbarines (Cooke, 1997a, 1997b) and the least derived (in the authors' opinion) known possum taxon (*Burramys parvus*). Abbie (1939) suggests independent acquisition of a large plagiaulacoid P3 in *Burramys* and *Hypsiprymnodon*, but the possibility that this feature was present in a common ancestor of both taxa cannot be excluded (see discussion in Archer et al., 1987; Flannery, 1987). As noted by Ride (1993, p. 454) "... the structure of the dP_3 trigonid is correlated with sectorial specialization. As well as in *Ekaltadeta* and *Hypsiprymnodon*, it occurs in the Potoroinae (*Bettongia*, *Aepyprymnus*, and *Caloprymnus*)" and "... Specialized trigonids of dP_3 , by themselves, provide no evidence of unity." Retention of P2 in *Hypsiprymnodon* has commonly been regarded as a macropodoid plesiomorphy (Archer, 1984; Flannery, 1989; Wroe and Archer, 1995). Regarding *Ekaltadeta*, Wroe and Archer (1995) were unable to ascertain whether retention of P2 represented a retained plesiomorphy, or secondary reversal to a plesiomorphic state. The withdrawal of P2 from the occlusal plane in *Hypsiprymnodon* and *Ekaltadeta ima* may simply represent an intermediate stage between presence of P2 in the adult dentition (macropodoid plesiomorphy) and complete ejection of P2 (macropodoid apomorphy). The extent of masseteric invasion of the dental canal in *Ekaltadeta ima* (i.e., broad separation of masseteric and dental canals at their anterior ends) was considered a macropodoid plesiomorphy by Archer and Flannery (1985) not present in any other kangaroo taxon, including *Hypsiprymnodon moschatus* and *Propleopus*. Interestingly, the masseteric and dental canals are also widely separate in species of balbarine (Cooke, 1997a). Ride (1993, p. 453) considers the hypsiprymnodontid mandible to be "characteristic," but does not define any features of the dentary that might be synapomorphic for the clade. We are unaware of any a priori basis for concluding that the dentary of propleopines and hypsiprymnodontines is not plesiomorphic within Macropodoidea.

Evidence from dental and mandibular material does not strongly confirm or refute the monophyly of Hypsiprymnodontinae and Propleopinae to the exclusion of other taxa. All features used by Ride (1993) in the erection of Hypsiprymnodontidae are, in our view, possible plesiomorphies. Alternatively, most of these dental and mandibular character states, if considered apomorphic within Macropodoidea, could represent shared derived states uniting Balbarinae with Hypsiprymnodontinae and Propleopinae. On the basis of cranial features Propleopinae and Balbarinae may represent a monophyletic taxon. The inclusion/exclusion of Hypsiprymnodontinae as the sister taxon to this propleopine-balbarine clade depends on whether a derived macropodoid feature (narrow slit-like lateral carotid fenestra), present in *Hypsiprymnodon* and all other macropodoid taxa except Propleopinae-Balbarinae, is considered synapomorphic or homoplasious.

Flannery (1989) concluded that convergence is pervasive within Macropodoidea. Findings of the present study raise interesting questions and possibilities regarding the extent of convergence within Macropodoidea in addition to those already fielded by Cooke (1997a), wherein similarities in dental morphology shown between balbarines and Macropodidae are considered to be homoplasious (contra Archer, 1984; Flannery, 1989). Cooke (1997a) has suggested that Balbarinae may be the

sister taxon to all other macropodoids. Cooke's conclusions were drawn without the benefit of the comparative propleopine basicranial material available in the present study. The new evidence presented herein lends support to the hypothesis of a basal position within Macropodoidea for Balbarinae, but with the inclusion of Propleopinae as an immediate sister taxon. The possible monophyly of Propleopinae-Balbarinae will be the subject of a detailed analysis by B. Cooke following the description of more complete balbarine cranial material. If the argument for monophyly of these two taxa is found to be persuasive, then there can be little doubt that the clade recognized should attract family level distinction, in light of the broad range of dental adaptation shown by balbarines and propleopines.

PALEOBIOLOGY

Speculation on the dietary habitus of propleopines has continued since the description of *Propleopus oscillans* (De Vis, 1888), with many subsequent contributions to the understanding of paleobiology for the subfamily (Pledge, 1981; Archer, 1984; Archer and Flannery, 1985; Sanson, 1991; Vickers-Rich and Rich, 1993; Wroe, 1996a; Ride et al., 1997). Most authors have hypothesized an omnivorous to carnivorous niche for members of the clade. Specializations unique to individual taxa clearly suggest a range of dietary preference within Propleopinae (Archer and Flannery, 1985; Wroe, 1996a).

As noted above, the discovery of a near-complete propleopine skull provides a rich source for further investigation of diet and habit in *Ekaltadeta* and possibly other propleopines. Detailed examination of cranio-dental form and function is beyond the scope of the present study and is the subject of a paper in preparation. However, as a prelude to a comprehensive treatment of paleobiology for the Giant Rat-kangaroo radiation the following observations are offered for consideration. Prior to making any predictions regarding diet in propleopines, it is perhaps wise to bear in mind the cautions of Lauder (1995) regarding the inference of function from structure in extinct taxa. Lauder (1995) emphasizes that success in this field is greatest where general predictions are required and is highly sceptical of functional inference in extinct taxa for which homologous morphology is not known and understood in extant members of the same clade.

Because controversy over paleobiological inference has largely centred on the degree to which respective members of Propleopinae were carnivorous, it is necessary to review the findings of previous authors on the evolution and distinguishing features of terrestrial carnivorous mammals. Carnivorous mammals have long been identified on the basis of their carnassial dentition (Flower and Lydekker, 1891). In a seminal work Savage (1977, p. 238, 264) considers that a carnassial dentition is the "... hallmark of a truly carnivorous land mammal" and that the length of the carnassial blade is proportional to "... the degree to which the diet is carnivorous." Savage further comments (p. 262) that the main "... trends which can be distinguished in the evolution of carnivore molars are the simplification of tooth pattern, the loss of crushing function in the truly carnivorous types, the loss of post-carnassial teeth and the increasing efficiency in carnassialization." Van Valen (1969, p. 96) states that mammalian carnivores are defined by the presence of teeth "... specialized for the vertical shearing of food." The importance of vertical shear as an adaptation to carnivory among mammalian carnivores has been consistently reiterated in the literature (MacIntyre, 1966; Jernvall, 1995). The relative significance of vertical shear versus crushing or horizontal shear in the dentition has been shown to reliably predict the relative proportions of vertebrate, as opposed to vegetable matter eaten by carnivores (Van Valkenburgh, 1989). Consequently, indices of vertical versus horizontal shear have been used to infer the proportion of

vertebrate prey included in the diets of a number of extinct placental taxa (Van Valkenburgh, 1991, 1994; Viranta and Andrews, 1995; Viranta, 1996).

The degree to which indices of carnassialisation derived from placental carnivores might be transferable to marsupial counterparts requires consideration. In Carnivora, vertical and horizontal shearing is compartmentalized, with vertical shear largely restricted to the carnassial and horizontal shear to the post-carnassial dentition. Among dasyuromorphian and ameridelphian carnivorous taxa each molar retains both vertical and horizontal shearing capacity. Werdelin (1987, 1988) argues that this lack of regional specialization in the marsupial molar row is explained by constraints linked to differences in tooth replacement between marsupials and placentals. Among Marsupicarnivora (sensu Ride, 1964), the importance of vertebrate prey in the diet is strongly reflected in the relative hypertrophy/hypotrophy of vertical and horizontal shearing elements in each molar. In carnivorous-insectivorous taxa (e.g., *Dasyurus hallacatus*) the principle vertical shearing complex (postmetacrista-paracristid) is not greatly enlarged relative to that of the horizontal (protoconetalonid). Obligate carnivorous Dasyuromorphia and Ameridelphia (e.g., *Sarcophilus*, *Thylacinus*, *Borhyaena*) are characterized by the extreme hypertrophy of high amplitude vertical shearing elements whilst horizontal shearing capacity is vestigial. We believe that the basic principles for interpretation of vertical and horizontal shear apply equally to Marsupicarnivora and Carnivora, but indices that have been used for Carnivora are not necessarily appropriate for Marsupicarnivora. For example, relative carnassial blade length versus postcarnassial molar row length, considered an indicator of dietary preference in Carnivora by Van Valkenburgh (1991, 1994), is not applicable to marsupicarnivores. However, other indices, such as the area available for horizontal shear or crushing versus aggregate vertical shearing blade length, might be applied to both placental and marsupial taxa. Werdelin (1988) suggests that thylacoleonids have circumvented factors constraining molar specialization in Marsupicarnivora by adopting the only postcanine tooth which is replaced (dP3/P3) as the principal, or only, high amplitude vertical shearing blade, thus permitting greater specialization in the postcarnassial molars. In this respect analogy can be drawn between thylacoleonids and propleopines. Consequently, most indices of carnassialisation applied to Carnivora might also be used as dietary predictors within and between Thylacoleonidae and Propleopinae, although not necessarily in comparisons between these taxa and Marsupicarnivora.

Whilst we consider dental features to be the most reliable indicator of dietary preference in extinct taxa, a complex of cranial character states has also been identified as characteristic of mammalian carnivores (Maynard Smith and Savage, 1959; Turnbull, 1970; Janis, 1995). These include: dominance of the temporalis over the masseter muscles; well developed sagittal and nuchal crests; a mandibular condyle level with the tooth row; presence of a well developed postglenoid process; and a relatively short face which lacks a diastema. However, it is important to note that presence or absence of any one of the above features can not be treated as conclusive evidence in the inference of diet, and many taxa show contradictory character state constellations. For example, well developed sagittal crests are present in a number of herbivorous and wood gnawing species (e.g., *Gorilla*, *Dactylopsila palpator*); postglenoid processes are poorly developed in carnivorous dasyuromorphians compared to those of most placental counterparts; and many omnivorous, gnawing or herbivorous taxa (e.g., *Trichosurus*, *Dactylopsila*, *Ursus*) show a mandibular condyle level with the tooth row as in "typical" carnivores. Morphometric analyses performed by Radinsky (1981a, 1981b) generated evidence for the correlation

of functionally significant cranial measurements with dietary habit among more specialized faunivorous Carnivora, but also showed that correlation between these factors greatly diminished among omnivorous members of the taxon. The case of *Thylacoleo carnifex*, the "Marsupial Lion," represents a particularly good example of the dangers inherent in excessive reliance upon the carnivore cranial morphotype in dietary inference. Despite the presence of extraordinary carnassial hypertrophy and molar reduction in this extinct species many early investigators concluded that *T. carnifex* was a herbivore (Gill, 1954; Savage, 1977) because it lacked cranial features typical of known carnivorous mammals (e.g., in *T. carnifex* the masseteric musculature was large relative to that of the temporalis). However, detailed investigation of form and function with the benefit of additional postcranial material has convinced all recent authors that this animal was a committed carnivore (Wells et al., 1982; Archer, 1984; Case, 1985).

Following the accepted importance of vertical as opposed to horizontal shear in the dentitions of carnivorous mammals Archer and Flannery (1985) postulated that *Propleopus chillagoensis* (characterized by a very large P3 and reduction of the posterior molars) represented the carnivorous extreme of propleopine adaptation, whilst *Propleopus oscillans* (P3 relatively small and molar surface area large) was more omnivorous. Wroe (1996a) quantified dental data for propleopines and concurred with the above suggestions of Archer and Flannery (1985). It is important to note that although a carnassial function has been inferred for the plagiaulacoid P3 of all propleopines, there are no propleopine taxa that show the extreme postcarnassial tooth reduction that typifies obligate carnivores (e.g., *Thylacoleo*, Felidae). In *P. chillagoensis*, considered the most carnivorous of propleopines by Archer and Flannery (1985) and Wroe (1996a), the bunodont postcarnassial dentition is anteroposteriorly extensive relative to that of even omnivorous carnivoran taxa (e.g., *Vulpes*). Consequently, we consider it unlikely that any known propleopine was an obligate carnivore. There can be little doubt that all known propleopines possessed a capacity to effectively ingest nonvertebrate foods.

The skull of *Ekaltadeta ima* shows a number of features that are common to carnivorous mammals. These include well developed sagittal and nuchal crests, and robust, broad zygomatic arches. However, many features typically associated with carnassialization are absent (e.g., the mandibular condyles are not level with the tooth row, the masseteric musculature does not appear to be reduced compared to that of the temporalis and the postglenoid process is relatively small). For reasons noted above the absence of such features does not provide a strong basis for the dismissal of a predominantly carnivorous habitus for *E. ima*. But, when considered in conjunction with the retention of a substantial bunodont molar battery in *Ekaltadeta* (relative to known carnivores) and pending results of a more detailed analysis, we currently consider it likely that the species was omnivorous.

Recently, Ride et al. (1997, p. 320) concluded that *P. oscillans* was "... primarily carnivorous" with many dental and cranial features interpreted as adaptations to carnivory. We are sceptical of this finding. *Propleopus oscillans* is closest to *H. moschatus* among extant taxa in terms of dental morphology (Sanson, 1991). Whilst the analysis of molar occlusal relations by Ride et al. (1997) represents a very useful contribution to the understanding of masticatory function in propleopines, it is our opinion that much of the subsequent inference regarding *P. oscillans* could be applied equally to *H. moschatus*. *Hypsiprymnodon moschatus* has been described as an omnivore by Johnson and Strahan (1982) and a cursorial frugivore by Dennis (1995). Although the much larger size of *P. oscillans* may have enabled this taxon to consume far larger prey than does *H. moschatus*,

conclusive evidence for a greater proportion of animal tissue in the diet of propleopines is, in our view, lacking. Ride et al. (1997, p. 285) demonstrate that shearing and puncture-crushing were distributed along the molar row in *P. oscillans*. However, the same could be said for a wide variety of extant bunodont-omnivorous or frugivorous taxa and we believe that the use of analogy with the highly "carnassialized" molars of *Thylacinus* is misleading (p. 290 and 320). Functionally, the most obvious difference between the molar shearing blades of *P. oscillans* and those of specialized mammalian carnivores is the massive disparity in shearing amplitude (sensu Sanson, 1989, p. 156). For example, in *Thylacinus* the relief, or height, of principal vertical shearing blades vastly exceeds that present in molars of *P. oscillans*. The only post-canine tooth in *P. oscillans* (and other propleopines) comparable with the vertical shearing blades of derived Dasyuromorphia and Carnivora in terms of shearing amplitude is the plagiaulacoid third premolar. P3 of *P. oscillans* is small relative to those other propleopines and is positioned well anterior to the point at which maximum bite force could be applied (Wroe, 1996a, 1997a), whilst the bunodont molar battery is relatively extensive. If the P3 of propleopines is treated as a carnassial analogue then the relatively insignificant contribution of this tooth to the dentition of *P. oscillans* indicates that this taxon was the least committed carnivore within the subfamily. We also consider that appropriate indices quantifying the relative importance of high amplitude vertical shear may apply to a comparison between Propleopinae and known carnivorous mammalian taxa. The latter proposition requires metrical substantiation which is the focus of work in progress.

CONCLUSIONS

We tentatively suggest that Propleopinae may represent the sister taxon to Balbarinae. Together these taxa may be basal to all other Macropodoidea, including Hypsiprymnodontinae. The strength of this proposal will be tested following the analysis of more complete balbarine material recently recovered from Miocene deposits of Riversleigh. If Propleopinae and Balbarinae are monophyletic, they clearly represent an ancient and structurally/ecologically diverse taxon. The results of preliminary investigation suggest that propleopines were omnivorous. All Giant Rat-kangaroos show a variably well developed capacity for high amplitude vertical shear, a distinguishing feature of all known terrestrial mammalian carnivores. However, the extent to which this capacity was actually applied in the processing of vertebrate prey remains contentious. If it is shown that propleopines did habitually dispatch vertebrates, or scavenge on vertebrate carcasses, we reiterate the suggestion of Archer and Flannery (1985) and Wroe (1996a), that differences in the proportion of high amplitude vertical shear (P3 size) versus molar row surface area/length are likely indicators of the relative importance of meat in the diet of individual taxa.

ACKNOWLEDGMENTS

M. Archer, H. Godthelp, K. Black, W. D. L. Ride, R. E. Wells and P. A. Pridmore provided thought-provoking criticism and comment. Vital support for this research has been given by the Australian Research Council (to M. Archer); the National Estate Grants Scheme (Queensland) (grants to M. Archer and A. Bartholomai); the Department of Environment, Sports and Territories; the Queensland National Parks and Wildlife Service; the Commonwealth World Heritage Unit (Canberra); the University of New South Wales; ICI Australia Pty Ltd; the Australian Geographic Society; the Queensland Museum; the Australian Museum; Century Zinc Pty Ltd; Mt Isa Mines Pty Ltd; Surrey Beatty & Sons Pty Ltd; the Riversleigh Society Inc.; the Royal Zoological Society of New South Wales; the Linnean Society of

New South Wales; and many private supporters. Skilled preparation of most of the Riversleigh material has been carried out by A. Gillespie.

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ACCEPTED 23 NOVEMBER 1997