

AUSTRALIAN MARSUPIAL CARNIVORES: RECENT ADVANCES IN PALAEOLOGY

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Over the last two decades, the study of new fossil material has yielded major insights into the evolution of Australia's marsupial carnivores. This material includes the first complete or near-complete crania for Tertiary representatives of Dasyuridae, Thylacinidae and Propleopinae (Hypsiprymnodontidae), as well as the first skulls known for the thylacoleonid genera, *Priscileo* and *Wakaleo*. Also of significance has been the discovery of a new species of marsupial carnivore, *Djarthia murgonensis*, from the Early Eocene Tingmarra local Fauna. Regarding dasyuromorphian evolution, the study of well-preserved material from Oligocene- Miocene deposits of Riversleigh has been particularly illuminating. Many findings have been unanticipated. For example, it is now clear that during the early and middle Miocene, the now ubiquitous dasyurids were rare, while the recently extinct Thylacinidae were unexpectedly diverse. Furthermore, at present there is no hard evidence for the existence of any extant dasyurid genera or subfamily greater than Pliocene in age. The oldest confirmed dasyurid is from early to middle Miocene deposits and forms a sister clade to the three living subfamilies. Moreover, it is argued that dasyurids are highly specialised among dasyuromorphians, particularly with respect to their basicranial morphology and not 'primitive' Australian marsupials as has often been supposed. On the other hand, from results of analysis of late Oligocene-Miocene cranial material, it is now evident that Thylacinidae constitutes a very conservative lineage with the recently extinct *Thylacinus cynocephalus* little more derived than some late Oligocene-Miocene taxa regarding either cranial or dental features. Propleopinae (giant rat-kangaroos), previously known only from dental remains, are now represented by two skulls. Interpretation of this evidence supports the hypothesis that at least some species included significant amounts of meat in their diets, while phylogenetic analysis hints at the possibility of a special relationship with balbarines. With respect to Thylacoleonidae, the study of cranial material leaves the issue of the family's ordinal level affinities uncertain, while the previously accepted tenet that *Wakaleo* could not be ancestral to *Thylacoleo* is also questioned. On the basis of dental evidence to hand, the Early Eocene *Djarthia murgonensis* can not be placed in any marsupial clade with confidence. Thus, biogeographic scenarios excluding the possibility that ameridelphians ever colonised Australia are considered premature. Growing evidence for a diversity of marsupial carnivores in pre-Pleistocene Australia is considered to diminish, if not contradict the argument that the continent's large terrestrial carnivore niches have long been domi-

ated by reptiles. The flip side of this debate is that arguments for reptilian supremacy are commonly based on assumptions regarding the biology and behaviour of fossil varanid, snake and crocodilian taxa that are highly speculative in many cases. A tendency to consider only estimated maximum dimensions for extinct reptilian species may also have generated false impressions with respect to their significance in the ecology of their respective communities.

INTRODUCTION

Historically, a polyphyletic group comprising five Australian marsupial families, or members thereof, have been considered as 'carnivorous marsupials'. Three of these comprise the order Dasyuromorphia: Dasyuridae, Thylacinidae and Myrmecobiidae. The remaining two, Thylacoleonidae and Hysiprymmodontidae, are diprotodontians, members of ?Vombatoidea and Macropodoidea respectively. Since seminal reviews of Australian carnivorous marsupial palaeontology were presented by Archer (1982a, 1982b) and Archer and Dawson (1982), the fossil records for four of the five Australian carnivorous marsupial families have been significantly expanded (Gillespie 1997, Muirhead and Wroe 1998, Wroe 1999a). For taxa of Pliocene age, three new Pliocene species have been added, two dasyurids (Lawson et al. 1999, Wroe and Mackness 2000a) and a propleopine (Ride 1993), while discoveries of pre-Pliocene material have been extraordinary. In 1982, the list of carnivorous marsupial taxa exceeding five million years in age then amounted nine species: a single thylacinid (*Thylacinus potens*), three thylacoleonids (*Wakaleo oldfieldi*, *W. vanderleueri*, *W. alcootaensis*) and four species then considered to be dasyurids (*Ankotarinja tirarensis*, *Keeuna woodburnei*, *Wakamatha tasselli*, *Dasyurinja kokuminola*). To this list can now be added a further 19 formally described species. 10 thylacinids, two thylacoleonids, two dasyurids, three propleopine kangaroos, one species treated as Dasyuromorphia *incertae sedis* by Wroe (1997a) and *Djarthia murgonensis*, an Early Tertiary marsupicarnivore of uncertain ordinal affinity (Godthelp et al. 1999). Moreover, descriptions of at least seven additional taxa of Oligocene-Miocene age are in preparation, these include: three thylacinids, two thylacoleonids and two dasyurids (Wroe 1999a). Most significantly, whereas no pre-Pleistocene marsupial carnivores were represented by significant cranial material in 1982, complete or near-complete skulls of late Oligocene-Miocene age are now known for at least one species of each of the families listed above, excepting Myrmecobiidae. Investigation of this new material has generated quantum leaps in our understanding of the pre-Pliocene diversity, phylogeny and palaeobiology of Australia's marsupial carnivores. New light has also been shed on the origins and relationships of modern taxa. In some instances, previously accepted dictum has been overturned. For example, Dasyuridae, long held to represent a structurally, even actually ancestral position among Australian marsupials, has been shown to constitute a relatively recent and specialised addition to the continent's fauna (Wroe 1999b). On the other hand, Thylacinidae, monotypic in Recent times, is now thought to have been

the more diverse of the three families of Dasyuromorphia during the Miocene (Wroe 1999a).

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. Dental terminology follows Wroe (1999b). Systematic terminology incorporates amendments to Archer's (1982) classification as suggested by Krajewski et al. (1994), Krajewski et al. (2000a) and Wroe (1996a, 1997b) for Dasyuromorphia, Godthelp et al. (1999) for Marsupialia *incertae sedis* and Aplin and Archer (1987) for other taxa. Institutional abbreviations: QM F = Queensland Museum fossil collection; AM F = Australian Museum fossil collection.

AUSTRALIA'S OLDEST MARSUPIAL CARNIVORE AND OTHER MARSUPIALIA INCERTAE SEDIS

On the issue of Australian marsupicarnivore evolution, one of the most significant palaeontological discoveries in recent times is that of the Early Eocene (55 myo) taxon *Djarthia murgonensis* (Godthelp et al. 1999; Fig. 1), from the Tingamarra Local Fauna of south-eastern Queensland. This species is plesiomorphic among marsupials for at least eight of the 18 features considered by Godthelp et al. (1999). Most derived features present in *D. murgonensis* are present in generalised representatives of both ameridelphian and australidelphian clades. Consequently and because the anatomical feature currently given the greatest weight as a potential synapomorphy for Australidelphia, presence of a continuous lower ankle joint, is unknown for this species, Godthelp et al. (1999) considered it prudent to treat *D. murgonensis* as Marsupialia *incertae sedis*. Furthermore, the single derived dental feature common to all extant members of the Australian marsupial radiation, reduction of lower incisor number, is also not preserved. However, *D. murgonensis* does have a potential synapomorphy, presence of a central cusp at the apex of the centrocrista, that could indicate special relationship with two species from the Ngapakaldi Local Fauna of central Australia, *Ankotarinja tirarensis* and *Keeuna woodburnei*. But again, these two taxa, originally described as dasyurids by Archer (1976a), are otherwise plesiomorphic among marsupials for many features. Godthelp et al. (1999) recommend that they too be considered Marsupialia *incertae sedis*. Woodburne and Case (1996) have argued that, excepting microbiotherians, the marsupial faunas of South American and Australia are manifestly distinct. On the basis of the evidence presented by Godthelp et al. (1999) the assertion of Woodburne and Case (1996) is

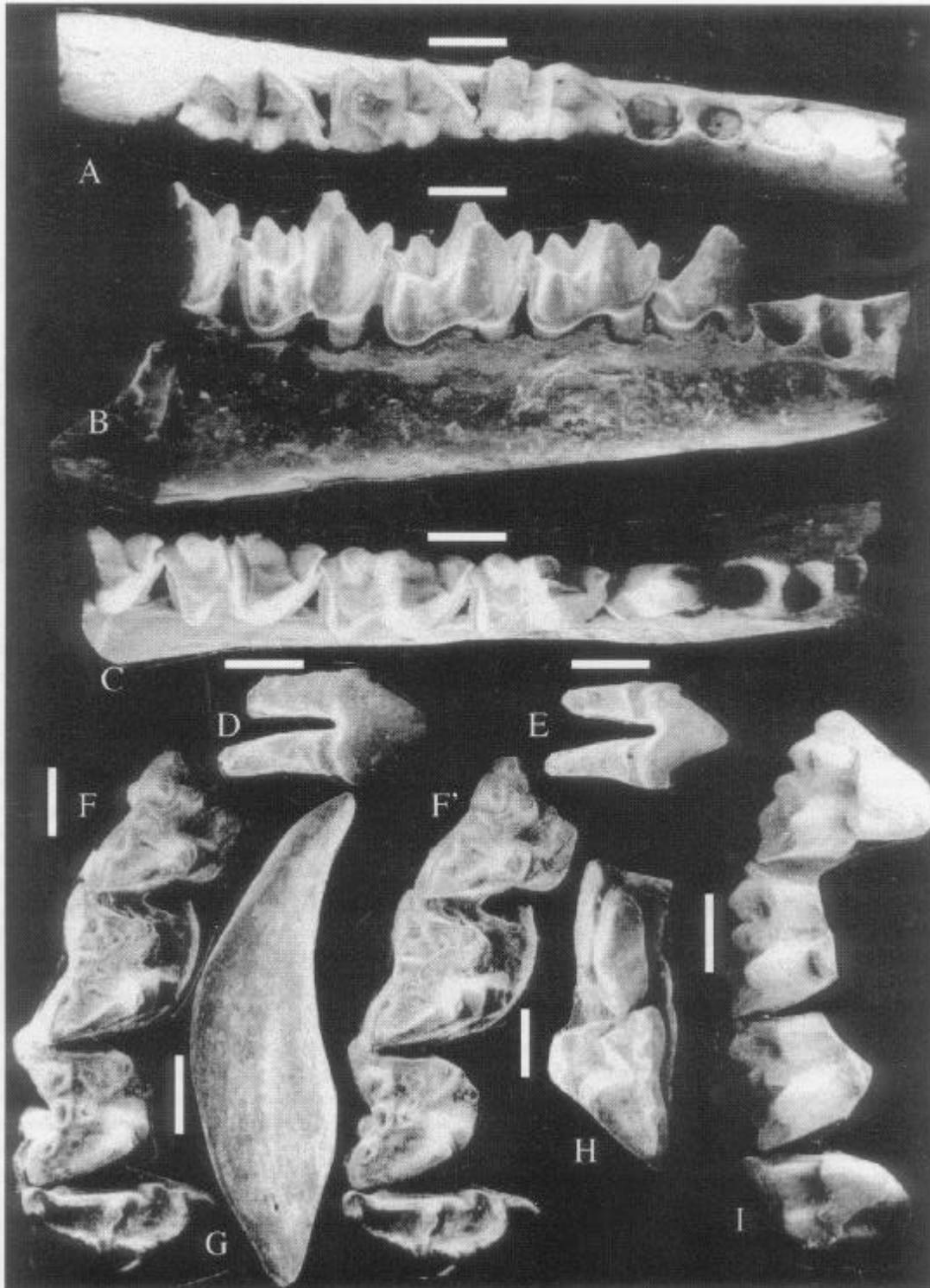


Figure 1 *Djarthia murgonensis*. (A, D–I), QM F31458. (A) M₁₋₃, occlusal view. (B, C), QM F 31460, P₃, M_{1,3} and M₄ trigonid in buccal (B) and occlusal (C) views. (D) right P², buccal view. (E) P¹ or P², buccal view. (F, F') right M¹⁻⁴, stereo occlusal view. (G) partial right C¹, buccal view. (H) left maxillary fragment with P³ and M¹, occlusal view. (I) = right M¹⁻⁴, lingual view. Scale = 1 mm.

regarded as premature. Uncertainty also surrounds the placement of another central Australian fossil species, *Wakamatha tasselli*. This taxon was originally described as a dasyurid by Archer and Rich (1978) on the basis of a partial lower dentary containing M_{3-4} . Addressing the issue of paraphyly in Dasyuridae as then accepted, Wroe (1996a) observed that this taxon, of uncertain age, possessed a number of potential synapomorphies with the most plesiomorphic peramelemorphian known to date, *Yarala burchfieldi* (Muirhead and Filan 1995, Muirhead 2000). These were: the presence of transverse hypocristids, extreme transverse compression of the M_4 talonid, very well-developed anterobuccal cingulids and very low indistinct hypoconulids. *Wakamatha tasselli* shows an intermediate condition for another peramelemorphian synapomorphy, lingual placement of the hypoconulid. If these prove to be actual synapomorphies, then *W. tasselli* represents the least derived bandicoot species known to date. As expanded on below, there are currently no derived dental features defining Dasyuridae and with the possible exception of upper incisor number, none clearly define Dasyuromorphia. In view of these uncertainties, it is posited here that *W. tasselli* too should be treated as *Marsupialia incertae sedis*.

RECENT DEVELOPMENTS IN DASYUROMORPHIAN PALAEOLOGY

Interordinal and interfamilial relationships

Despite major new palaeontological discoveries and considerable efforts in the field of molecular biology, both the interordinal and interfamilial relationships of Dasyuromorphia remain the subjects of ongoing debate. At the interordinal level many taxa have been advanced as potential sister taxa to dasyuromorphians. These include Didelphidae (Archer 1976b, Bensley 1903), Peramelemorphia (Kirsch et al. 1977), Notoryctidae (Springer et al. 1997) and Microbiotheriidae plus Diprotodontia plus Notoryctidae (Kirsch et al. 1997). Marshall et al. (1990) and Woodburne and Case (1996) posit that all non-dasyuromorphian Australian marsupials represent the sister clade to Dasyuromorphia and that the Palaeocene Bolivian species *Andinodelphys cochabambensis* is the sister taxon to all Australian marsupials. Various interpretations of higher level phylogeny for these taxa offered in the literature have been reviewed in several recent papers (Aplin and Archer 1987, Godthelp et al. 1999, Kirsch et al. 1997, Luckett 1994, Marshall et al. 1990, Springer et al. 1997). Regarding intrafamilial level relationships, *Myrmecobius fasciatus* has been forwarded as the sister taxon to thylacinids and dasyurids in some previous anatomy based studies (Archer 1984, Aplin and Archer 1987), but not in others (Wroe 1997b). Similarly, among molecular investigations, Lowenstein et al. (1981) placed *M. fasciatus* as the sister taxon to Dasyuridae-Thylacinidae, but at least one (Krajewski et al. 1997) placed the Numbat within Dasyuridae (although these authors treated this poorly supported result as anomalous).

Wroe et al. (2000) could not resolve the relative positions of the three dasyuromorphian families, but in the most recent attempts to address this question both Krajewski et al. (2000b) and Wroe and Musser (2001) found dasyurids and thylacinids to be sister taxa. However, support for this relationship in both these latter analyses was weak.

All told, numerical parsimony has been applied on four occasions to anatomical data sets with a view to resolving higher level relationships for dasyuromorphians (Kirsch and Archer 1982, Springer et al. 1997, Wroe et al. 2000, Wroe and Musser 2001). That of Kirsch and Archer (1982), using species as the operational taxonomic unit, produced many anomalous phylogenies. However, their work clearly demonstrated that the inclusion of fossil taxa could significantly impact on results. The morphological investigation presented by Springer et al. (1997), incorporated diprotodontian as well as marsupial carnivore and peramelemorphian taxa, but not Thylacinidae and used the family rather than the species as an operational taxonomic unit. This analysis produced a single most parsimonious tree, with notoryctids the sister to dasyuromorphians and this taxon the sister to a clade inclusive of all other living marsupials, but no interordinal relationships were supported by bootstrap values equal to or greater than 50%. While more recent studies incorporating additional, well represented fossil taxa (Wroe et al. 2000, Wroe and Musser 2001) have far from conclusively solved the major mysteries of dasyuromorphian phylogeny, results constitute a promising basis for further research. The accelerating pace of discovery over the last decade permits the realistic expectation of further significant fossil finds that may well provide deeper insight into questions surrounding the origins, as well as the interfamilial phylogeny of Dasyuromorphia.

Dasyuridae

The most consequential new find in the field of dasyurid palaeontology has been that of near-complete cranial material of early Miocene age from the Neville's Garden Site, Riversleigh, northern Australia. Two skulls, one including both lower jaws, represent the new genus and species, *Barinya wangala* (Figs. 2 and 3). Additional dental material for this taxon has been recovered from the middle Miocene Henk's Hollow Site (AR 6597). Wroe (1999b) identified four dasyurid synapomorphies present in the basicranium of *B. wangala*: development of a tympanic process of the *pars petrosa* to form a distinct periotic hypotympanic sinus, presence of a paroccipital hypotympanic sinus, presence of a deeply invasive sulcus with the posteroventral lip formed by a mesially directed process of the *pars petrosa* for passage of the internal jugular and presence of a distinct tubal foramen for passage of the Eustachian tube. Wroe (1999b) treats *B. wangala* as the sister taxon to modern dasyurids and also forwards an additional four synapomorphies uniting a monophyletic clade, comprising all representatives of the three



Figure 2 *Barinya wangala*, QM F 31408, skull. (A) ventral view, (B) dorsal view, (C) lateral view. Scale = 2 cm.

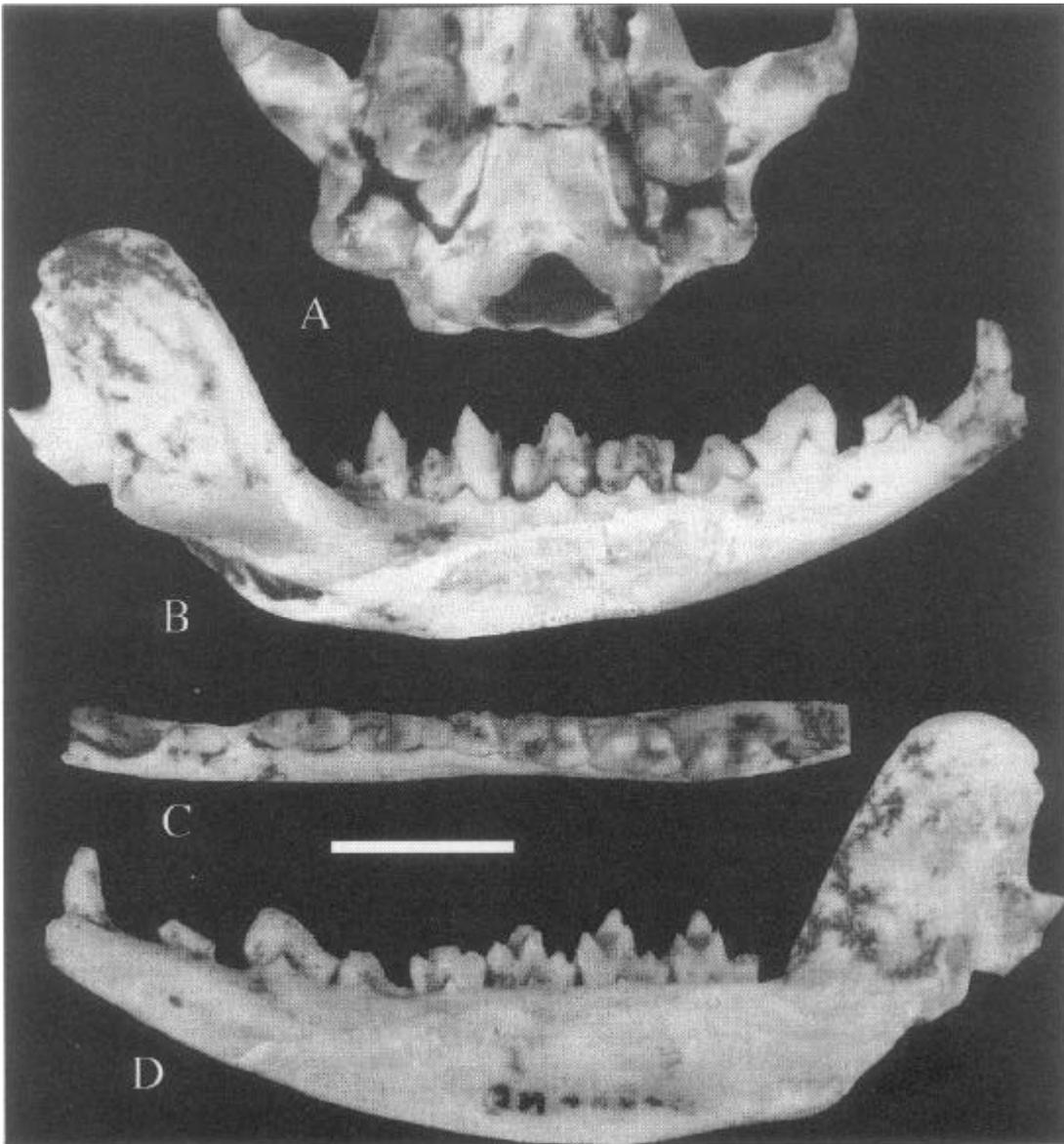


Figure 3 *Barinya wangala*. (A) QMF31409, basicranial region. QMF23889, C₁, P₁₋₃, and M₁₋₄ in (B) lateral view, (C) occlusal view and (D) lingual view. Scale = 2 cm.

extant dasyurid subfamilies. These are: presence of a fully enclosed stylomastoid foramen that includes a periotic component; contact between the pars petrosa and a paroccipital tympanic process that fully encloses the paroccipital hypotympanic sinus ventrally; extensive dorsal enclosure of the internal jugular canal; and contact between the mastoid tympanic process and the pars petrosa. The position of *B. wangala* as sister taxon to all extant subfamilies has been further supported by numerical parsimony analyses (Wroe et al. 2000, Wroe and Musser 2001).

An additional genus and species of Miocene-aged dasyurid, *Ganbulanyi djadjinguli* (see Fig. 4), has been referred to Dasyuridae by Wroe (1998). Dasyurid apomorphies present in this taxon were considered to potentially unite *G. djadjinguli* with either *Sarcophilus* or *Barinya*. Possible synapomorphies with *Sarcophilus* included approximation of the metacone and paracone, antero-posterior orientation of the postmetacrista, and approximation of stylar cusp B and the paracone on M², as well as hyper-robusticity of P². However, the homology of the then known teeth of *G. djadjinguli* was uncertain and Wroe (1998) also flagged the

possibility that the then only upper premolar known for the species might be a P³, in which case this taxon might be more parsimoniously allied with *Barinya*. The subsequent discovery of a specimen from the Rick's Rusty Rocks Local Fauna supported the latter of these scenarios (Arena et al. 1999).

New dasyurid taxa, as well as additional material of previously known species of Pliocene age, have also been described. '*Dasyercus*' *worboysi* (Lawson et al. 1999; see Fig.4) and *Archerium chinchillaensis* (Wroe and Mackness 2000a; see Fig. 4) from the Big Sink and Chinchilla Local Faunas respectively, represent two new dasyurines of uncertain affinity within the subfamily. Both are known from partial dentitia only and while the presence of derived features shared with most dasyurines permits allocation within Dasyurinae with reasonable confidence, the position of either taxon within the subfamily can not be determined with any precision at present. New material from the Chinchilla Local Fauna has been referred to *Dasyurus dummalli* (Wroe and Mackness 1998, Wroe and Mackness 2000b). Cladistic analysis incorporating data from these specimens placed *D. dummalli* within a clade inclusive of *D. albopunctatus*, *D. spartacus*, *D. maculatus* and *Sarcophilus harrisii* (Wroe and Mackness 2000b).

The study of this new material has impacted on preconceptions of dasyurid evolution and phylogeny. While dasyurids have generally been held to represent structural approximations of the archetypal Australian marsupial, it is now clear that the extant subfamilies, in particular, are in fact highly specialised, at least with regard to basicranial features. That said, it is accepted that many dasyurids possess generalised dentitia that do not differ greatly from those of basal ameridelphians. Wroe (1997b) dismisses the only widely accepted dental synapomorphy previously advanced for the family, i.e., a tendency to reduce P₃ (Archer 1982a, Marshall et al. 1990), as an underlying synapomorphy (*sensu* Saether 1986), a practice criticised by a number of authors (Farris 1986, Kitching 1993). Consequently, it is presently impossible to refer specimens of unspecialised fossil marsupials to Dasyuridae on any basis other than overall similarity, unless they are represented by cranial material. A further inference based on palaeontological evidence is that dasyurids represent a relatively recent addition to the Australian fauna. This is particularly so of the monophyletic clade comprising the three extant subfamilies, none of which are represented by diagnosable specimens pre-dating the early Pliocene (Wroe 1999b). Recent molecular evidence indicates an origin for the modern subfamilies of around 24 million years ago (Krajewski et al. 2000a). If this is correct, then the lack of modern dasyurid material in otherwise fossil rich deposits, especially those of Riversleigh in northern Australia, suggests that the modern subfamilies existed in low species abundance during the early Miocene, with the major radiations occurring in the mid Miocene or later. Again this view is not incompatible with recent molecular evidence (Krajewski et al. 2000a).

Thylacinidae

The fossil record of Thylacinidae has increased more dramatically than that of any other Australian marsupial carnivore family. Ten new species have been formally described over the last decade: six from late Oligocene-Miocene sites of Riversleigh (*Thylacinus macknessi*, *Wabulacinus rides*, *Ngamalacinus timmulvaneyi*, *Nimbacinus dicksoni*, *Badjcinus turnbulli*, *Muribacinus gadiyuli*), two from the Bullock Creek Local Fauna of the Northern Territory (*Mutpuracinus archiboldi*, *Nimbacinus richi*), one from the late Miocene Alcoota Local Fauna, *Tjarrpecinus rothi*, and another from the late Miocene Ongeva Local Fauna of central Australia, *Thylacinus megiriani* (Tables 1, 2, 3, Figs 5, 6). Two of these fossil taxa (*Badjcinus turnbulli* and *Nimbacinus dicksoni*) are represented by significant cranial material (Muirhead and Wroe 1998, Wroe and Musser 2001). The rest are known almost entirely from dentitia and jaw fragments. The study of this new material has further corroborated findings based on tarsal morphology (Szalay 1994) and molecular evidence (Lowenstein et al. 1981, Krajewski et al. 1997) that firmly place Thylacinidae within the dasyuromorphian radiation (Muirhead and Wroe 1998, Wroe et al. 2000, Wroe and Musser 2001). But, as noted above, where resolution of the interfamilial relationships of thylacinids has been reported in recent studies, it is only weakly supported (Krajewski et al. 2000, Wroe and Musser 2001).

Two analyses using numerical parsimony have addressed the intrafamilial relationships of thylacinids (Muirhead and Wroe 1998, Murray and Megirian 2000). The analysis by Muirhead and Wroe (1998) incorporated five fossil species, as well as *Thylacinus cynocephalus*, *Thylacinus potens* and five outgroup taxa. In this study six synapomorphies were identified for the family: loss of the mastoid epitympanic sinus; loss of contact between the alisphenoid and petrosal tympanic processes; lateral broadening of the ectotympanic; reduction in size of styler cusp B; reduction in size of the entoconid; and elongation of P3 in the upper and lower dentitia. However, the validity of some of these synapomorphies seems questionable, the first two of the three middle ear features in particular. This is because, once acquired, it generally accepted that such adaptations are rarely lost (MacPhee 1981). More recently, Murray and Megirian (2000) performed two analyses using Hennig86 (Farris 1988) on data from all 12 described thylacinid taxa. The first of these was performed on a data matrix modified after Muirhead and Wroe (1998) using one cranial and 22 dental characters and the second was based on a set of eight dental features. Murray and Megirian (2000) favoured the results of their second analysis over the first. The basis for this preference appears to be anchored in their assessment of the contentious area of character weighting. Murray and Megirian (2000) dismissed the use of ordered, multistate characters by Muirhead and Wroe (1998) opting for another form of character weighting, i.e. character exclusion. The

Table 1 Australian fossil carnivorous marsupial fossil species not represented in modern faunas. Abbreviations for local fauna's are: A = Alcoota; ALL = Allingham; AL = AL 90; B = Bow; BA = Bite's Anttenary; BC = Bullock Creek; C = Chinchilla; CC = Chillagoe Caves; BD = Bluff Downs; BS = Big Sink,, CA = Cleft of Ages; CS = Camel Sputum; DT = Dirk's Tower; E = Encore, F = Floraville; FC = Fisherman's Cliff, G = Gag; H = Hiatus; HH = Henk's Hollow., I = Inabeyance; jj = jim's jaw; K = Kutjamarpu; N = Ngapakaldi; O = Ongeva; RRR = Rick's Rusty Rocks; S = Smeaton; T = Tingamarra; TC = Town Cave; US = Upper Site; WC = Wellington Caves; ;y = Yanda; ' = from Riversleigh, northwestern Queensland * = to numerous to list; ? = local fauna unknown; i. s. = *incertae sedis*.

Species	Family	Deposit/s	Age	Author/s
<i>Ganbulanyi djadjinguli</i>	Dasyuridae	'E, 'RRR	middle to early-late Miocene	Wroe 1998
<i>Barinya wangala</i>	Dasyuridae	'NG, 'US, 'JJ, 'HH 'BA	early to middle Miocene	Wroe 1999b
<i>Sminthopsis floravillensis</i>	Dasyuridae	F	Pliocene	Archer 1982a
<i>Dasyuroides achilpatna</i>	Dasyuridae	FC	Pliocene	Archer 1982a
' <i>Dasyercus</i> ' <i>worboysi</i>	Dasyuridae	BS	Pliocene	Lawson et al. 1999
<i>Archerium chinchillaensis</i>	Dasyuridae	C	Pliocene	Wroe & Mackness 2000a
<i>Dasyurus dunmalli</i>	Dasyuridae	B, BD, C,	Pliocene	Bartholomai 1971
<i>Glaucodon ballaratensis</i>	Dasyuridae	S	Pliocene	Stirton 1957
<i>Sarcophilus moornaensis</i>	Dasyuridae	FC	Pliocene	Crabb 1982
<i>Muribacinus gadiyuli</i>	Thylacinidae	'G, 'HH	middle Miocene	Wroe 1996a
<i>Badjcinus turnbulli</i>	Thylacinidae	'WH	late Oligocene	Muirhead & Wroe 1998
<i>Wabulacinus ridei</i>	Thylacinidae	'CS, 'H	late Oligocene to early Miocene	Muirhead 1997
<i>Thylacinus macknessi</i>	Thylacinidae	'NG, 'G, 'H, 'E, 'DT	late Oligocene to early-late Miocene	Muirhead 1992
<i>Thylacinus megiriani</i>	Thylacinidae	O	late Miocene	Murray 1998
<i>Thylacinus potens</i>	Thylacinidae	A	late Miocene	Woodburne 1967
<i>Ngamalacinus timmulvaneyi</i>	Thylacinidae	'I, 'NG, 'CS	early Miocene	Muirhead 1997
<i>Nimbacinus dicksoni</i>	Thylacinidae	'HH, 'A, 'VVH, 'BC, 'CA	late Oligocene to early-late Miocene	Muirhead & Archer 1990
<i>Nimbacinus richi</i>	Thylacinidae	BC	middle Miocene	Murray & Megirian 2000
<i>Mutpuracinus archiboldi</i>	Thylacinidae	BC	middle Miocene	Murray & Megirian 2000
<i>Tjarrpecinus rothi</i>	Thylacinidae	A	late Miocene	Murray & Megirian 2000
<i>Mayigrampus orbus</i>	Dasyurornorpha i. s.	'E	early-late Miocene	Wroe 1997a
<i>Djarthia murgonensis</i>	Marsupialia i. s.	T	early Eocene	Godthelp, Wroe & Archer 1999
<i>Ankotarinja tirarensis</i>	Marsupialia i. s.	N	late Oligocene	Archer 1976a
<i>Keeuna woodburnei</i>	Marsupialia i. s.	N	late Oligocene	Archer 1976a
<i>Wakamatha tasselli</i>	Marsupialia i. s.			Archer & Rich 1979
<i>Dasyurinja kokuminola</i>	Marsupialia i. s.	Y	late Oligocene	Archer 1982a
<i>Priscileo roskellyae</i>	Thylacoleonidae	'U	early Miocene	Gillespie 1997
<i>Priscileo pitikantensis</i>	Thylacoleonidae	N	late Oligocene	Rauscher 1987
<i>Wakaleo oldfieldi</i>	Thylacoleonidae	K, 'CA	early Miocene to early-late Miocene	Clemens & Plane 1974
<i>Wakaleo vanderleueri</i>	Thylacoleonidae	'BC, 'E	middle Miocene to early-late Miocene	Clemens & Plane 1974
<i>Wakaleo alcootaensis</i>	Thylacoleonidae	A	late Miocene	Archer & Rich 1982
<i>Thylacoleo hilli</i>	Thylacoleonidae	B, TC	Pliocene	Pledge 1977 Bartholomai
<i>Thylacoleo crassidentatus</i>	Thylacoleonidae	ALL, C, B, BD	Pliocene	1962
<i>Thylacoleo carnifex</i>	Thylacoleonidae	*	Pleistocene	Owen 1859
<i>Ekaltadeta ima</i>	Hypsiprymnodontidae	r.*	late Oligocene to middle Miocene	Archer & Flannery 1985
<i>Ekaltadeta jamiemulvaneyi</i>	Hypsiprymnodontidae	'EE, 'CA	early-late Miocene	Wroe 1996b
<i>Jackmahoneyi toxoniensis</i>	Hypsiprymnodontidae	B	Pliocene	Ride 1993
<i>Propleopus oscillans</i>	Hypsiprymnodontidae	*	Pleistocene	De Vis 1888
<i>Propleopus wellingtonensis</i>	Hypsiprymnodontidae	WC	Pleistocene	Archer & Flannery 1985
<i>Propleopus chillagoensis</i>	Hypsiprymnodontidae	C	Pleistocene	Archer et al. 1978

Table 2. Character state changes for nodes 1-8 in the first of 24 shortest trees (see Fig. 7).

Node	Character state changes
1	C2 0=> 1; C3 0 => 1; C7 0 => 1; C9 0 => 1; C 11 0 => 1; C12 0=> 1; C16 0 => 1; C19 0 => 1; C21 0 => 1
2	C3 1 => 2; C5 0=> 1 C6 0 => 1; C8 0 => 1; C10 0 => 1; C15 0=> 1; C17 0 => 1
3	C1 0 => 1; C12 1 => 0; C19 1 => 2; C21 1 => 2, C22 0 => 1
4	C10 0 => 1; C11 1 => 2; C16 1 => 2; C18 0 => 1; C23 0 => 1
5	C3 2 => 3; C4 0 => 1; C6 1 => 2; C7 1 => 2; C9 1 => 2; C11 2 => 3; C12 2 => 3; C16 2 => 3; C17 1 => 0
6	C3 3 => 4; C5 1 => 2; C11 3 => 4; C16 3 => 4; C19 2 => 3; C21 2 => 3
7	C2 1 => 2; C16 4 => 5
8	C2 2 =>3; C4 1 => 2; C5 2=>3

product was an input data matrix in which four pairs of taxa, including one ingroup and one outgroup taxon, had identical coding for all characters. A deficiency of this procedure is that neither of two resultant shortest trees distinguishes Thylacinidae on the basis of synapomorphy. Moreover, while it is conceded that the use of multistate characters has its problems (Wiley 1981, Lipscombe 1992), results based on the methodology of Muirhead and Wroe (1998) are preferred here primarily because they are far less subject to *apriorism* than those favoured by Murray and Megirian (2000). That said, with most thylacinids currently known primarily from incomplete dental material, it may be imprudent to place too much faith in any hypotheses of intrafamilial relationships at present. Because tables of character state transformations were not provided by either Muirhead and Wroe (1998) or Murray and Megirian (2000) the data presented by these latter authors has been reanalysed and results are given below (Figs. 7-9 and Tables 2-3).

As well as a near-complete skull and skeleton of *Nimbacinus dicksoni* (Wroe and Musser 2001), other thylacinid material discovered from Riversleigh since the description of *B. turnbulli* includes a M_2 (QM F23358, Hiatus Site, late Oligocene) referred here to *Wabulacinus* sp. and a M_4 (QM F12972, Wayne's Wok Site, late Oligocene) referred here to *Thylacinus* sp. This latter find confirms the prediction by Murray and Megirian (2000) that *Thylacinus* had originated by late Oligocene times. Further extending the temporal range of *Thylacinus* at

Riversleigh has been the discovery of a M_2 (QM F 30862) from the early-late Miocene Encore Site. Additional material (AR 10427) representing *Nimbacinus* has also been retrieved from the late Oligocene White Hunter Site. The presence of considerable thylacinid diversity, including specialised *Thylacinus* and *Wabulacinus*, in late Oligocene deposits, indicates that the origin of the thylacinid clade predates estimates forwarded on the basis of molecular data, i.e. 7 to 25 million years (Lowenstein et al. 1981, Sarich et al. 1982).

Dasyuromorphia incertae sedis

One new taxon has been assigned to Dasyuromorphia *incertae sedis*. *Mayigriphus orbus* (Wroe 1997a, see Fig. 4) shares a number of features, derived among dasyuromorphians, that might be construed as indicative of a special relationship with either sminthopsine dasyurids or thylacinids. Specifically, *M. orbus* shares two potential synapomorphies with *Planigale*, a greatly reduced M_1 paraconid concurrent with a moderately reduced M_1 metaconid and reduction of M_{2-4} metaconids. However, at least three derived features are also shared with thylacinids and/or some specialised dasyurines: lack of a clear differential between reduction of M_1 and M_{2-4} metaconids; an obtuse angle formed between the paracristid and metacristid; and reduction of the talonid with the cristid obliqua terminating in a lingual position.

Table 3 Character state changes for nodes 1-8 in the first of 2 shortest trees (see Fig. 9).

	Character state changes
1	0 length branch
2	C1 0 => 1
3	C1 1 => 2
4	C2 0 => 1
5	C1 2 => 3; C3 0 => 1; C8 0 => 1
6	C1 3 => 4; C5 0 => 1
7	C7 0 => 1
8	C4 0 => 1; C6 0 => 1

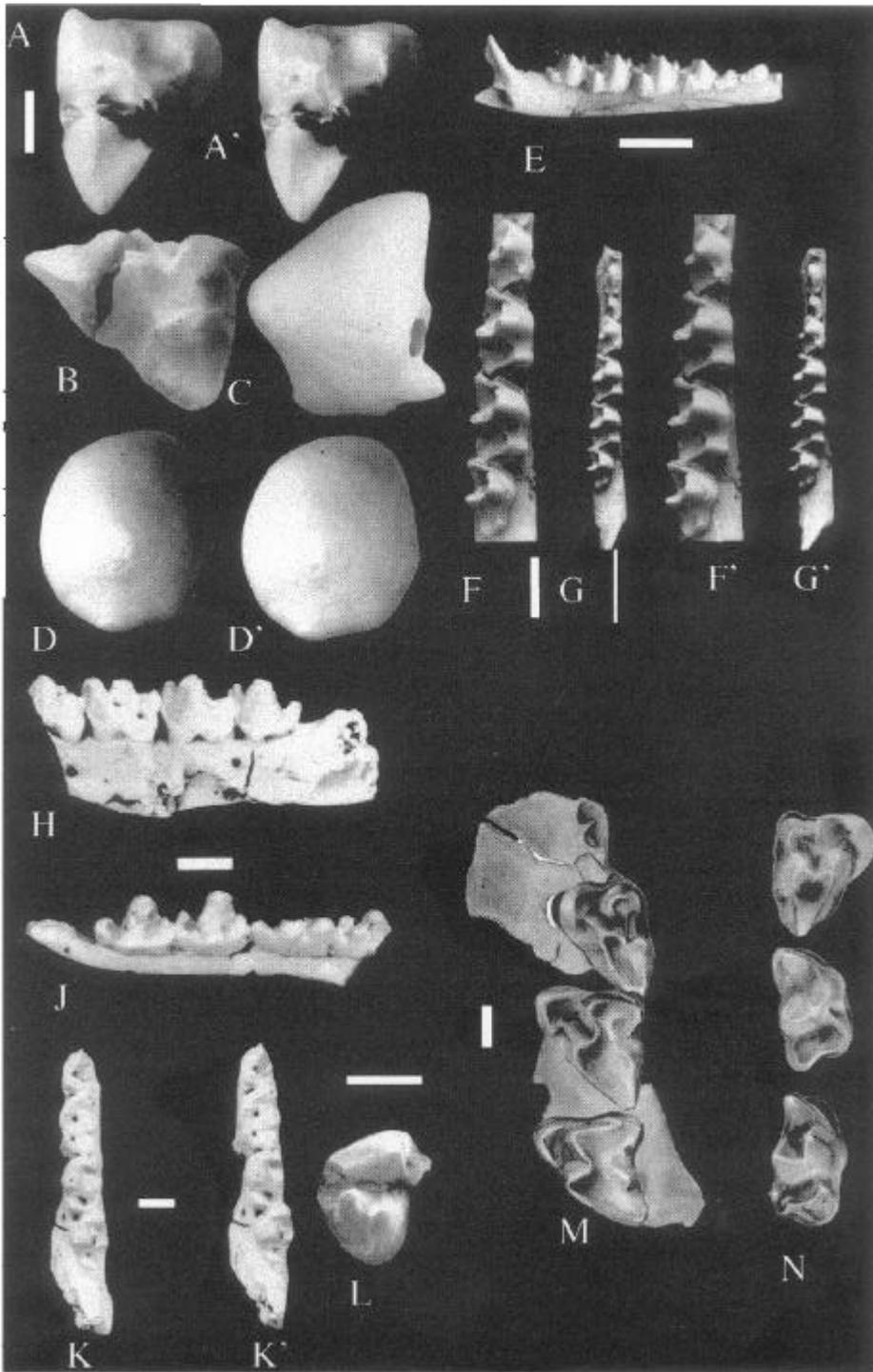


Figure 4. *Ganbulanyi djadjinguli*. QMF24537, right M¹ or M². (AA') stereo occlusal and (B) lingual view. QMF24537, P³. (C) lateral view, (D,D') = stereo occlusal view. Scale = 2 mm. *Mayigriphus orbis*. QM F23780, P₂₋₃, M₁₋₄. (E) buccal view, (F' and G'') stereo occlusal views. Scale = 2 mm. *'Dasycercus' worboysi*. AM F69805, M¹⁻⁴. (H) buccal view, (I) lingual view, (KK') stereo occlusal view. AM F69805, right M¹ fragment. (L) = occlusal view. Scale = 2 mm. *Archerium chinchillaensis*. QM F39847, P¹, M¹⁻³. (M) occlusal view. (N) from top to bottom occlusal views of. QM F39848, right M¹; QM F39849, right M², QM F39850, right M². Scale = 1 mm.

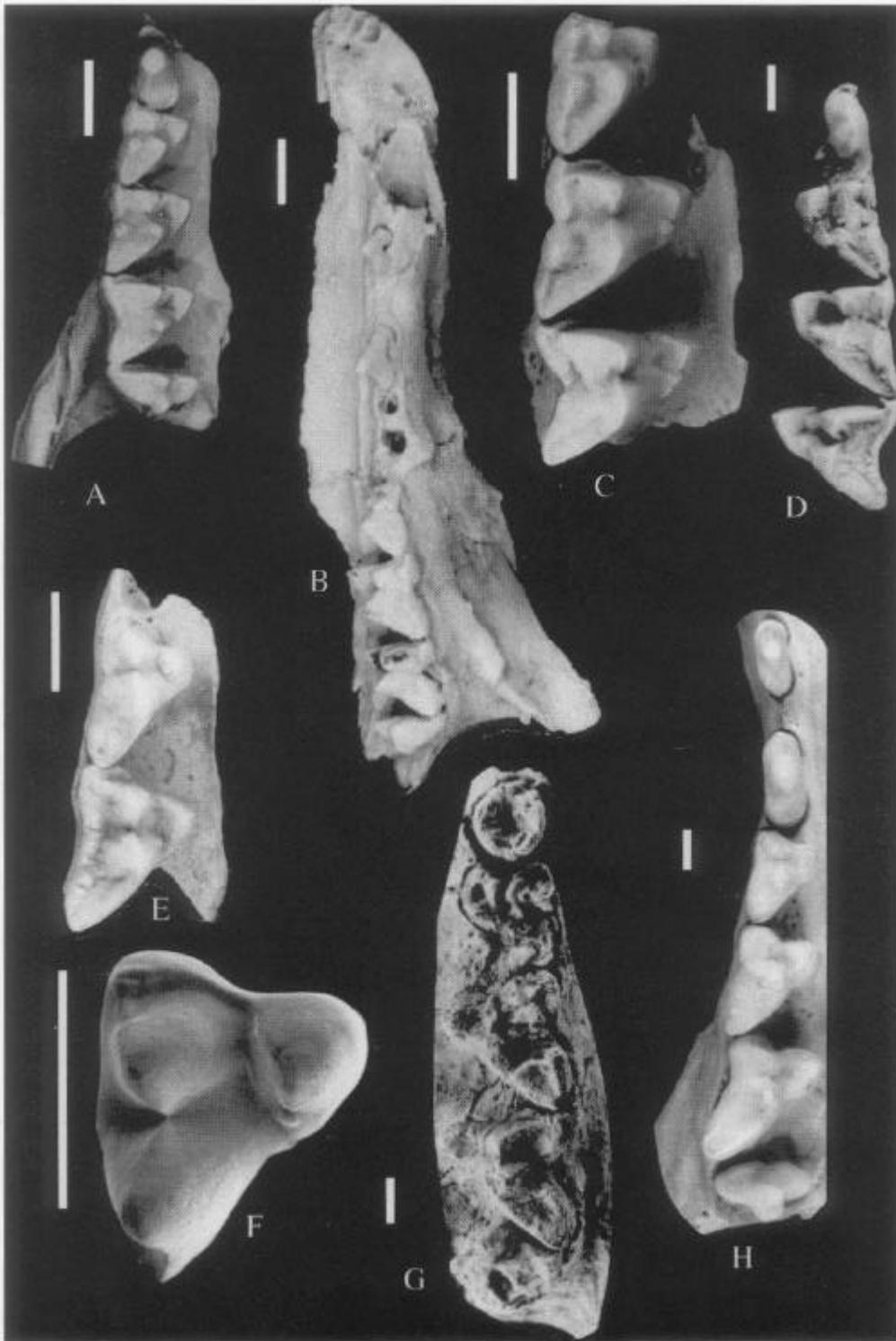


Figure 5 Maxillary fragments. All in occlusal view. (A) *Muribacinus gadyuli*. QM F 30386, P², M¹⁻⁴. (B) *Badjcinus turnbulli*. QMF 30488, P¹⁻², M¹⁻⁴. (C) *Nimbacinus dicksoni*. QMF 16803, M¹⁻³. (D) *Ngamalacinus timmulvaneyi*. QMF 30300, P³, M¹⁻³. (E) *Wabulacinus ridei*. QMF 16851, M³. (F) *Thylacinus mocknessi*. QMF 16850, M1. (G) *Thylacinus potens*. CPC 6746, P¹, M¹⁻⁴. (H) *Thylacinus cynocephalus*. AM 217, P²⁻³, M¹⁻⁴. Scale = 5 mm.

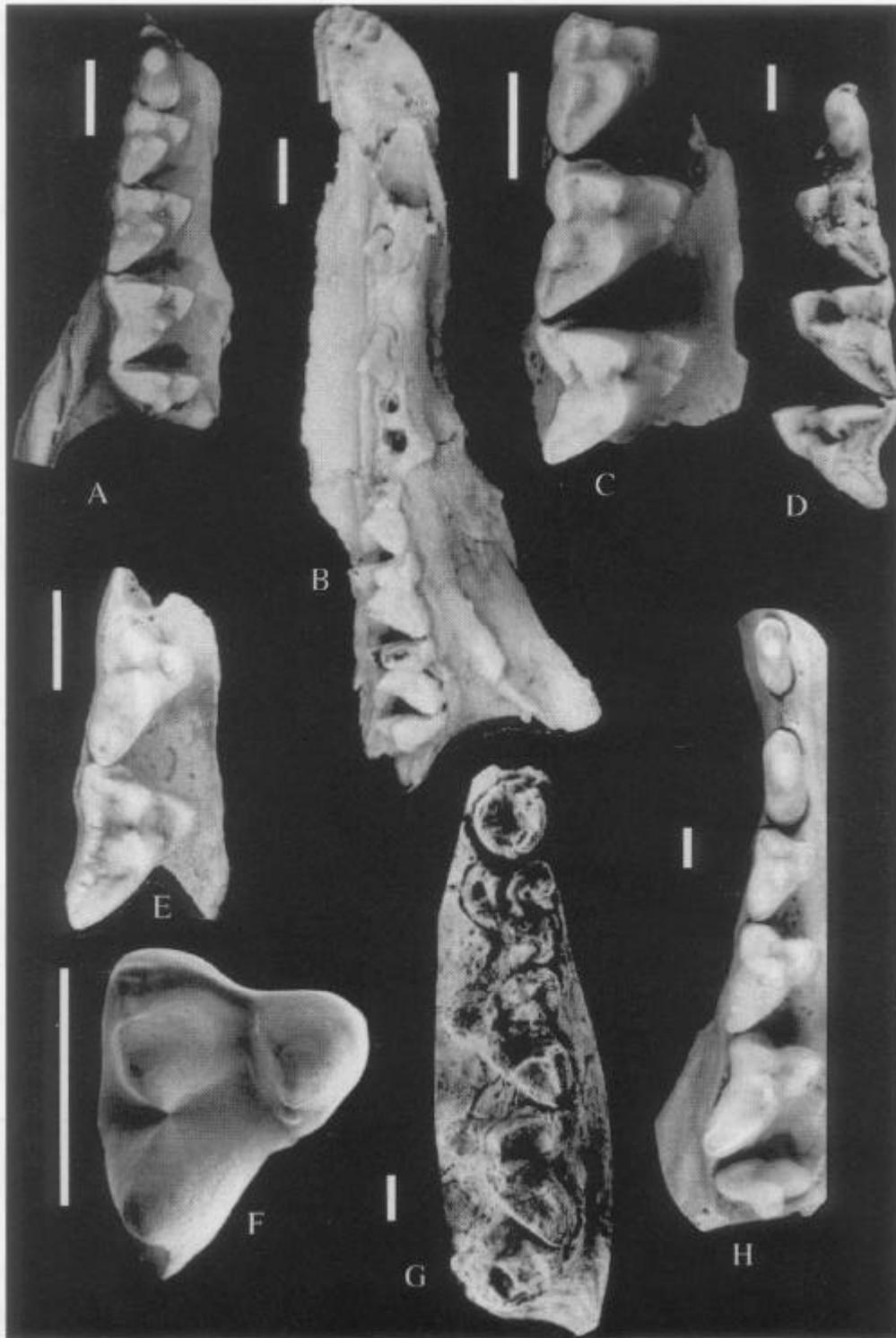


Figure 5 Maxillary fragments. All in occlusal view. (A) *Muribacinus gadiyuli*. QMF 30386, P³, M¹⁻⁴. (B) *Badjcinus turnbulli*. QMF 30488, P¹⁻², M¹⁻⁴. (C) *Nimbacinus dicksoni*. QMF 16803, M¹⁻³. (D) *Ngamalacinus timmulvaneyi*. QMF 30300, P³, M¹⁻³. (E) *Wabulocinus ridei*. QMF 16851, M³. (F) *Thylacinus mocknessi*. QMF 16850, M¹. (G) *Thylacinus potens*. CPC 6746, P¹, M¹⁻⁴. (H) *Thylacinus cynocephalus*. AM 217, P²⁻³, M¹⁻⁴. Scale = 5 mm.

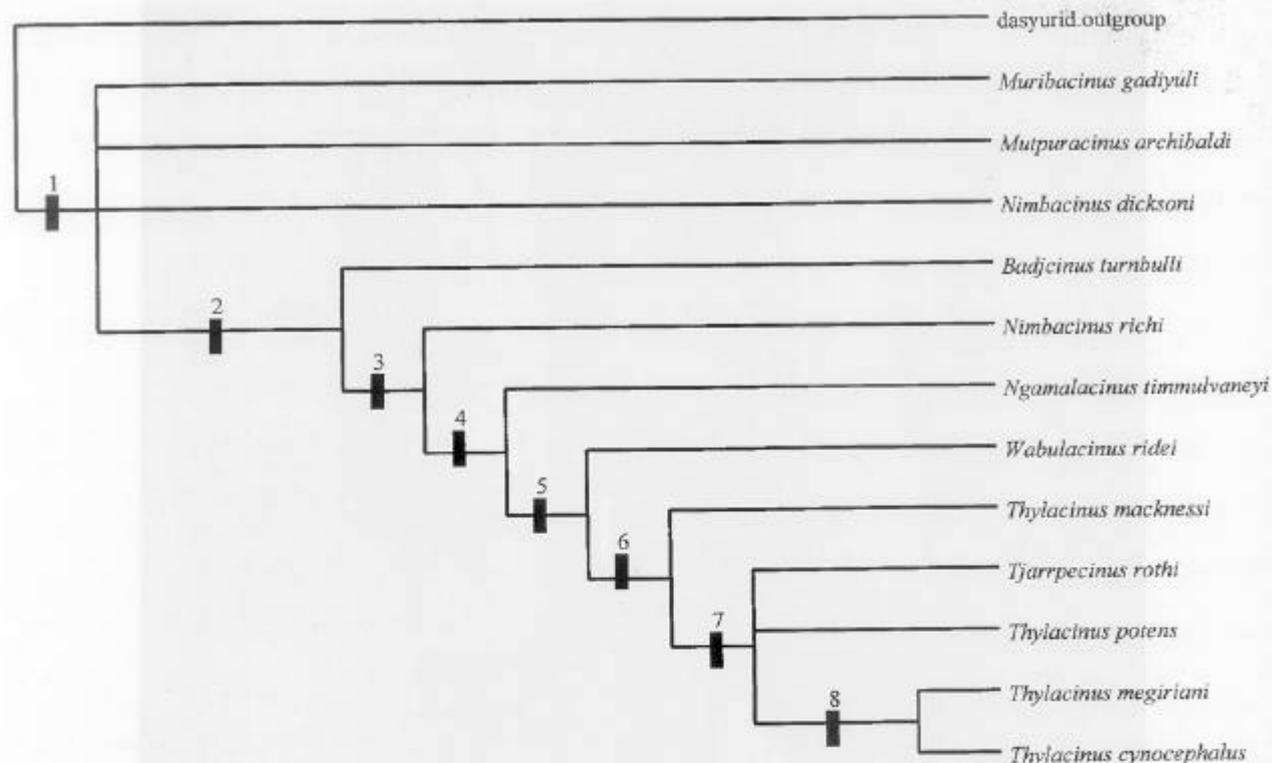


Figure 7 Intrafamilial relationships of Thylacinidae. First of 24 shortest trees of 67 steps based on the treatment of 23 characters modified after Muirhead and Wroe (1998) by Murray and Megirian (2000). See Table 2 for character state changes at nodes.

RECENT DEVELOPMENTS IN PROPLEOPINE PALAEOLOGY

Until 1985, Propleopinae was represented by only two species, *Propleopus oscillans* (De Vis 1888) and *P. chillagoensis*, both of Pleistocene age. The pace of discovery began to escalate in 1985 with the description of the first Miocene species, *Ekaltadeta ima* and an additional Pleistocene taxon, *P. wellingtonensis* (Archer and Flannery 1985). Subsequently, a further two species have been described, the early-late Miocene *E. jamiemulvaneyi* (Wroe 1996b) and the Pliocene *Jackmahoneyi toxoniensis* (Ride 1993). Of particular value interest are the first descriptions of cranial material referred to the subfamily: the partial skull of a juvenile *P. oscillans* (Ride et al. 1997) and the near-complete skull of *E. ima* (Wroe et al. 1998, see Fig. 10).

Historically, propleopines have been allied with potoroids in general and the species of *Hypsiprymnodon* in particular (De Vis 1888, Archer and Flannery 1985). Ride (1993) concurred with the conclusion of sister taxon status for Propleopinae and *Hypsiprymnodon*, but considered that both formed a clade of sufficient distinction as to merit higher taxonomic status, hence the erection of a new family, Hypsiprymnodontidae. Monophyly of this clade was based on shared presence of plagiaulacoid upper and lower

premolars, specialised trigonids on dP_3 and M_1 with the main crest formed by the parametacristid, retention and withdrawal from the plane of occlusion of P_2 (see Wroe and Archer 1995), a deeply invasive masseteric canal and the characteristic hypsiprymnodontid mandible. Alternatively, Wroe et al. (1998) regard each of these features as possible macropodoid symplesiomorphies and thus no basis for the postulation of a special relationship. Wroe et al. (1998) further contend that reasonable grounds exist for the consideration of monophyly for propleopines and another extinct macropodoid subfamily, Balbarinae. Features flagged as possible propleopine-balbarine synapomorphies were: very large squamosal epitympanic sinus; ectotympanic roughly linear in lateral view, ectotympanic intimately associated with the glenoid process of the squamosal anteriorly and the squamosal posttympanic and mastoid part of petrosal posteriorly; presence of large ovate lateral carotid fenestra and a greatly expanded frontal sinus. Regarding intrasubfamilial relationships, no studies have included all known taxa and only one has applied numerical parsimony (Wroe 1996b). Balbarines were not included in this latter investigation and it was based on a dental data set only. Work is in progress using additional taxa and a cranial-dental data set (B. Cooke and B. Kear, unpublished data).

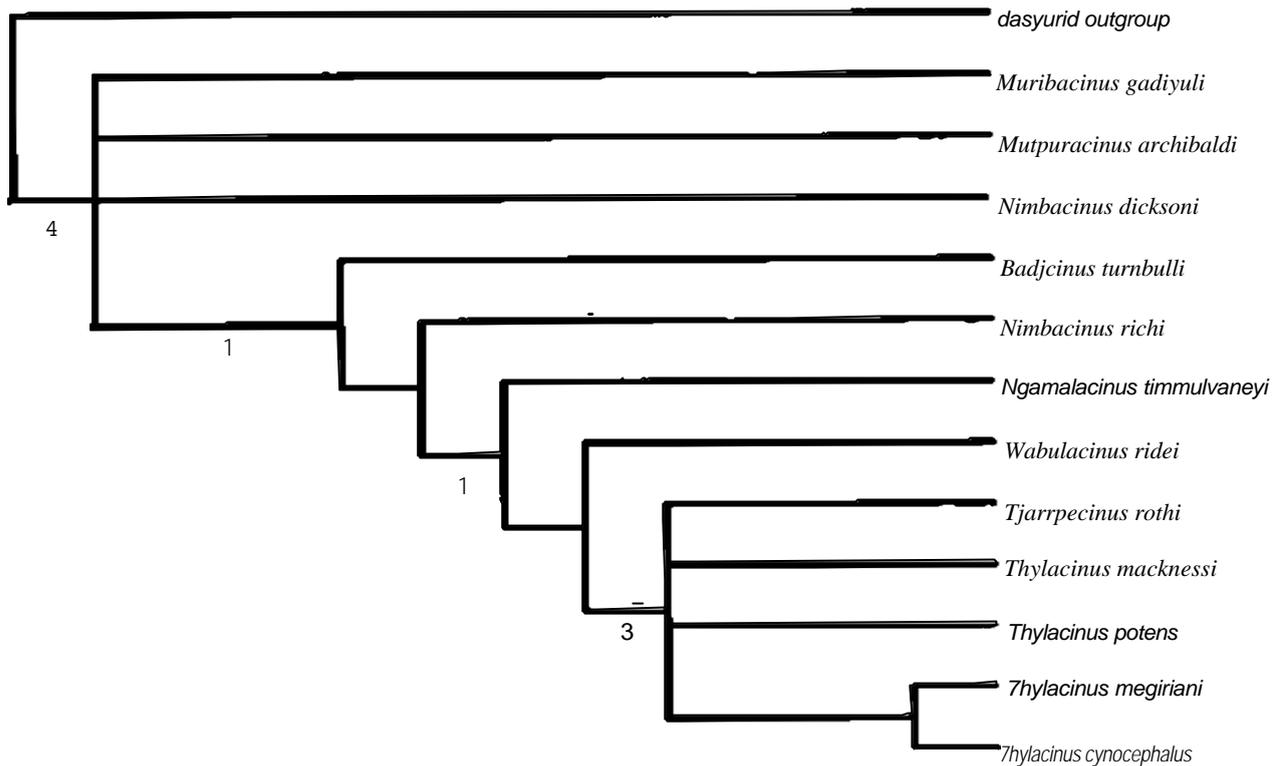


Figure 8 Intrafamilial relationships of Thylacinae. Strict consensus of 24 shortest trees with Bremer support (Bremer 1994) given below branches. Analysis conducted using PAUP 3. 1.1 (Swofford 1993) with multistate characters ordered, ACCTPAN character optimisation and a branch and bound search (CI excluding uninformative characters = 0.73, HI excluding uninformative characters = 0.262, RI = 0.85, PC = 0.64). Polarised character states as abridged by Murray and Megirian (2000) after Muirhead and Wroe (1998): **1**, infraorbital foramen: bound by jugal (0), not bound by jugal (1). **2**, size of paracone: unreduced (0), slight reduction (1), significant reduction (2), extreme reduction (3). **3**, styler cusp B: well developed (0), slight reduction (1), significant reduction (2), distinct reduction (3), extreme reduction or loss (4). **4**, anterior cingulum: complete (0), incomplete (1). **5**, protocone and conules: well developed (0), slightly reduction (1), significant reduction (2), loss of conules (3). **6**, length of postmetacrista: not elongate (0), significant elongation (1), pronounced elongation (2). **7**, angle of centrocrista: acute (0), obtuse (1), colinear (2). **8**, direction of preparacrista: perpendicular (0), slightly oblique (1), parallel to long axis (2), directly anterior to paracone (3). **9**, angles formed by paracristae and metacristae: narrow (0), significantly wider (1), wide (2). **10**, size of M_1 metaconid relative to those of M_{2-4} : uniform reduction (0), differentially reduced on M_1 relative to M_{2-4} (1). **11**, metaconid reduction on M_{2-4} : unreduced (0), slight reduction (1), further reduction (2), greatly reduced (3), lost (4). **12**, size of entoconid: unreduced (0), slight reduction (1), further reduction (2), greatly reduced (3), lost (4). **13**, shape of entoconid: uncompressed (0), compressed (1). **14**, diastema between P_1 and P_2 : present (0), absent (1). **15**, diastema between P_2 and P_3 : present (0), absent (1). **16**, hypoconulid notch: unreduced (0), slight reduction (1), further reduction (2), significantly reduced (3), greatly reduced (4), lost (5). **17**, posterior cingulid and hypocristid: separated (0), joined (1). **18**, carnassial notch of cristid obliqua: absent (0), present (1). **19**, hypocristid: parallel to transverse axis of dentary (0), slight angle (1), moderate angle (2), pronounced angle (3). **20**, carnassial notch in hypocristid: absent (0), present (1). **21**, anterior termination of cristid obliqua: ventral and buccal to carnassial notch of protocristid (0), slightly shifted buccally and dorsally (1), moderately shifted buccally and dorsally (2), markedly shifted buccally and dorsally (3). **22**, height of P_3 : higher than P_2 (0), lower than P_2 (1). **23**, length of M_4 : shorter than M_2 (0), longer than M_2 (1).

RECENT DEVELOPMENTS IN THYLACOLEONID PALAEOLOGY

Since 1982 two new species of thylacoleonid have been placed in a third thylacoleonid genus, *Priscileo*. *Priscileo pitikantensis* (Rauscher 1987), from the late Oligocene Ngapakaldi Local Fauna of central Australia and *P. roskellyae* (Gillespie 1997), from the early Miocene Upper Site Local fauna of Riversleigh. Both have been described on the basis of partial upper dentitia.

Near-complete crania have been discovered for both *P. roskellyae* (Gillespie 1999) and *Wakaleo vanderleueri* (Murray et al. 1987). Thus, skulls are now known for representatives of each thylacoleonid genus.

The origin of the thylacoleonid radiation is a contentious issue. Broom (1898) alluded to a special relationship between marsupial 'lions' and burramyids on the basis of P_3 morphology. While Bensley (1903) considered the thylacoleonid dentition to

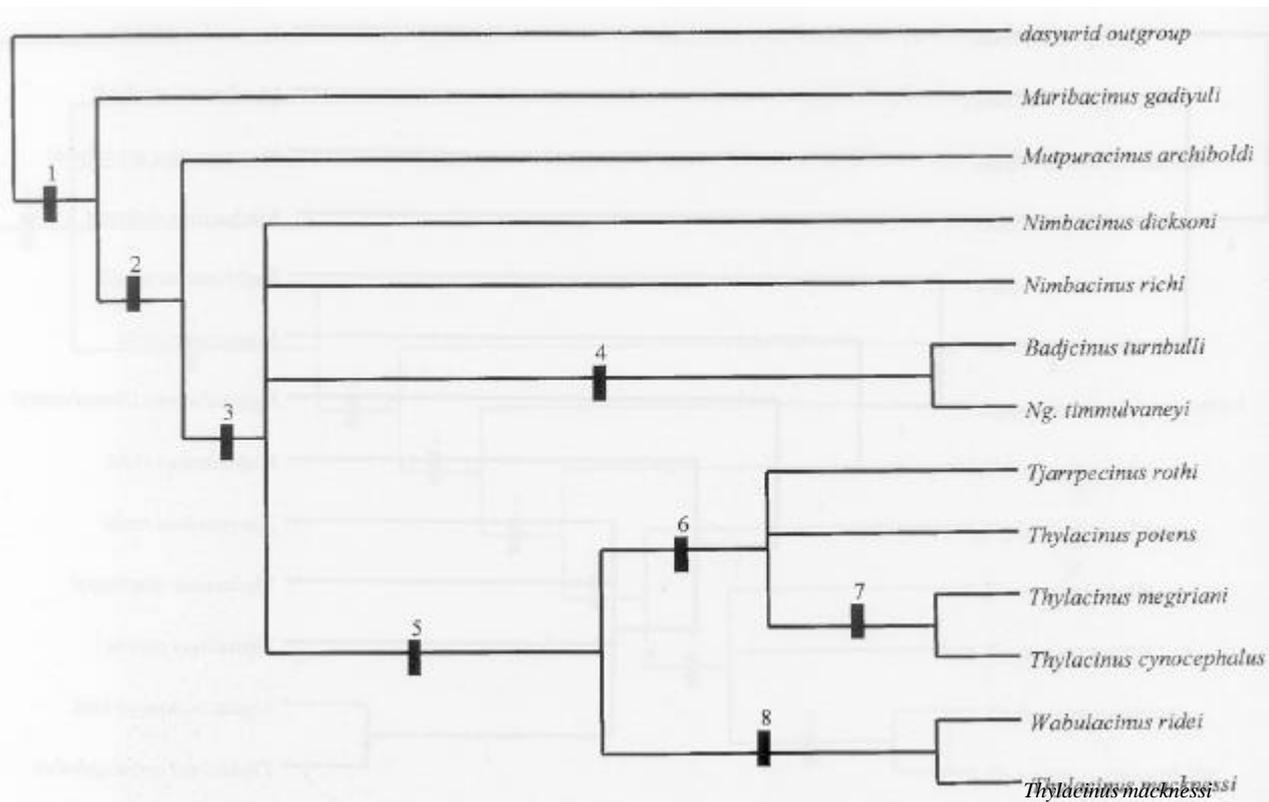


Figure 9. Intrafamilial relationships of Thylacinidae. Least well resolved of two shortest trees of 11 steps from data set provided by Murray and Megirian (2000). Analysis conducted using PAUP 3. 1.1 (Swofford 1993) with multistate character (1) ordered, ACCTRAN character optimisation and a branch and bound search (CI excluding uninformative characters = 1.0, HI excluding uninformative characters = 0.0, RI = 1.0, RC = 1.0). Bremer support (Bremer 1994) given below branches. See Table 3 for character state changes at nodes. Character and character states from Murray and Megirian (2000): 1, pattern of metaconid expression: (0) slight, uniform, (1) slight M_4 , (2) differential, marked on M_1 , slight M_4 , (3) near obsolescence on all molars, (4) entirely lost on all molars. 2, carnassial notch in hypocristid: (0) absent, (1) present. 3, elongation of postvallum, shearing surfaces: (0) slight, (1) significant. 4, stylocone B: (0) present, (1) extremely reduced or lost. 5, paracone reduction/hypertrophy of metacone: (0) slight-moderate, (1) conspicuous. 6, ectoflexus: (0) strong expression, (1) weak expression. 7, precingulum: (0) present, strong (1) reduced-absent. 8, entoconid: (0) distinct, (1) reduced-absent.

be a modification of the phalangerid type. Phalangeroid affinities for the family seem to have gone unquestioned until 1983, when Aplin and Archer argued for a special relationship with vombatiforms, a position reiterated by Aplin and Archer (1987) and accepted by at least some others (Marshall et al. 1990, Gillespie 1999, Wroe et al. 1998). The presence of a marsupial apomorphy, i.e. bulla enclosed fully by the squamosal shared by *Thylacoleo carnifex* and other vombatiforms, is the primary synapomorphy underlying this interpretation. Study of the cranium of *W. vanderleueri* by Murray et al. (1987) led these authors to dispute the phylogeny proposed by Aplin and Archer (1983) and re-advocate phalangeroid affinities with burramyids as their immediate sister taxon. Murray et al.'s (1987) interpretation stands on the acceptance of the bilaminar bulla in *W. vanderleueri*, i.e. with alisphenoid and squamosal contributions, as a diprotodontian plesiomorphy. These

authors also treat the absence of a hypocone in thylacoleonids as a retained plesiomorphy. Alternatively, Rauscher (1987) considers the absence of this feature to be an apomorphic reversal to a plesiomorphic state. In Murray et al.'s (1987) scenario, the complete enclosure of the middle ear by the squamosal in *Thylacoleo* and vombatiforms is treated as homoplasious. The interpretation of thylacoleonid intrafamilial relationships is also in a state of flux. While all authors seem to concur on plesiomorphic sister taxon status for *Priscileo* within Thylacoleonidae, the relationship of *Wakaleo* to *Thylacoleo* is less certain. The presence of a thylacoleonid apomorphy in then known specimens of *Wakaleo* that was absent in *Thylacoleo*, i.e. loss of P1 or P2, was thought to have precluded the possibility of an ancestor-descendent relationship for the two genera (Clemens and Plane 1974, Rauscher 1987, Archer 1984, Murray et al. 1987). However, because a new species of *Wakaleo* retains a full complement

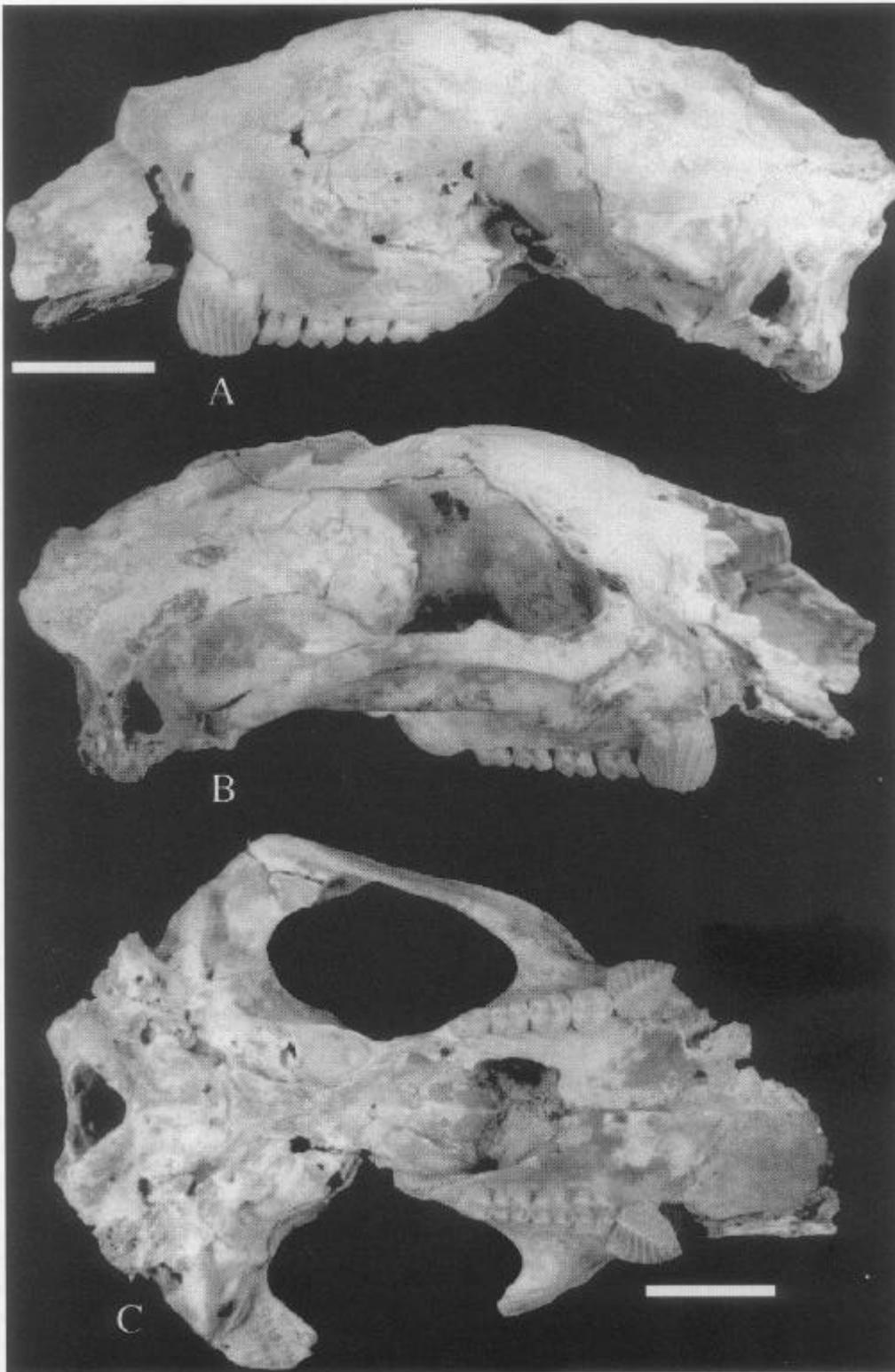


Figure 10 *Ekaltodeta ima*. QM F12426, partial skull. (A) left lateral view. (B) right lateral view. (C) ventral view. Scale = 20 mm.

of three premolars this rationale no longer stands (Gillespie 1999). Cladistic analysis currently under way by A. Gillespie may ultimately resolve these issues.

PALAEOBIOLOGY

While in recent years progress has been made into the biology and ecology of extant Australian marsupial carnivores (Jones 1996, 1997) and the recently extinct *Thylacinus cynocephalus* (Case 1985, Jones and Stoddart 1998), relatively few detailed analyses have centred on the same for fossil taxa. Exceptions include some species of propleopine (Archer and Flannery 1985, Ride et al. 1997, Sanson 1991, Wroe et al. 1998) and *Thylacoleo carnifex* (Case 1985, Finch and Freedman 1986, Finch and Freedman 1988, Wells et al. 1982, Wroe et al. 1999). The dietary habitus of both giant rat-kangaroos and the Pleistocene marsupial 'lion' have been the subject of much speculation (Wroe et al. 1998, Wroe et al. 1999, Wroe et al. in press). In particular their proclivity for vertebrate flesh has been questioned (Flower 1868, Sanson 1991).

Regarding the question of diet in propleopines, most recent contributors have agreed that vertebrates constituted a significant proportion thereof (Ride et al. 1997, Wroe et al. 1998). However, cranial and dental morphology differs considerably between giant rat-kangaroo species and a polarised debate has emerged over which taxa were more or less 'carnivorous'. Ride et al. (1997) treat *Propleopus oscillans* as primarily predacious, drawing analogy between *P. oscillans* and *Thylacinus*. The same authors consider *Ekaltadeta ima* to be less well adapted to a carnivorous lifestyle, alluding to the fact that in *E. ima* the condyle sits above the molar row, a feature not typical of carnivorous mammals. Archer and Flannery (1985), Wroe (1997c) and Wroe et al. (1998) take a contrary view. Based on the relative proportions of vertical to horizontal shear in their respective dentitions, these authors contend that the teeth of *E. ima* and *Propleopus chillagoensis* were better adapted than *P. oscillans* to slicing through hide, flesh and sinew. Hence they deduce that *P. oscillans* was, in fact, the more omnivorous among propleopines.

With respect to carnivory versus herbivory, controversy over the diet of *T. carnifex* effectively ended following convincing arguments for a meat-eating habit levelled by Wells et al. (1982). However, another contentious issue has arisen, that of body size. As observed by Wroe et al. (1999), weight estimates for *T. carnifex* have been in decline. Owen (1859, 1883) believed that the Pleistocene marsupial 'lion' was comparable in size to *Panthera leo*, but in recent years estimates have dropped from 75-100 kg (Murray 1984) down to 40-60 kg Flannery (1997). More recently still, Webb (1998) gave a weight estimate of 20 kg. Wroe et al. (1999) dispute these figures and in the first quantitative assessment of body weight in *T. carnifex*, posit an average of between 101 and 130 kg for the species. Ramifications of this finding impact directly on the interpretation of lifestyle. Moreover, based on

endocranial volume, Wroe et al. (in press) predict an average body mass of 97 kg. Thus, given its robusticity and weight, it appears unlikely that *T. carnifex* was capable of sustaining high speed for any extended period. It also seems improbable that such a large animal was semi-arboreal but increasingly likely that *T. carnifex* regularly preyed on megafauna, as suggested by Owen (1887).

ON REPTILIAN DOMINATION OF AUSTRALIA'S LARGE TERRESTRIAL CARNIVORE NICHES

The palaeoecological implications of this 'up-sizing' of *T. carnifex* contradict the current consensus view, at least in part and this is considered in detail by Wroe (2002). Over recent decades, many investigators have observed that Australia has been characterised by a paucity of large carnivorous mammal species during Pleistocene and Recent times (Hecht 1975, Archer and Bartholomai 1978, Rich and Hall 1984, Flannery 1991, 1994). Hecht (1975) speculated that the gigantic varanid, *Megania prisca*, was the dominant, or only predator of Australian megafaunal taxa during the Pleistocene. He suggested (p. 247) that the largest carnivorous marsupial present during this epoch, *Thylacoleo carnifex*, '...could not have filled the big felid niche', although supporting evidence for this hypothesis was not supplied. More recently, Flannery (1991, 1994) expanded on Hecht's argument, positing that a scarcity of large mammalian carnivores, in particular, was symptomatic of long-standing soil nutrient deficiency, further contending that this regime may have extended back until at least early Miocene times. A simple rationale underpinned this hypothesis: poor soils and fluctuating climatic conditions constrained plant biomass; this in turn restricted mammalian herbivore size and species richness; together these limitations culminated in an impoverished large mammalian carnivore fauna in Australia and New Guinea (Meganesia). Flannery (1991, 1994) also suggested that in Meganesia, reptiles, advantaged by lower metabolic requirements, successfully filled large terrestrial carnivore niches taken by mammals elsewhere.

If the estimates forwarded by Wroe et al. (1999) and Wroe et al. (in press) are close approximations of actual body-weight in *T. carnifex*, then the hypothesis of reptilian domination of large carnivore niches is somewhat diminished with respect to Pleistocene Meganesia. Being homeothermic it seems reasonable to conclude that a 100 kg *T. carnifex* would require more food than even the largest *M. prisca* (see below). Wroe et al. (1999) draw attention to additional pertinent facts. For example, *M. prisca* constitutes a relatively rare find in Pleistocene deposits (Rich and Hall 1984) and that, of the two, only *T. carnifex* has been strongly implicated in the butchery of (Horton and Wright 1981, Runnegar 1933) and actual predation on megaherbivores (Scott and Lord 1924).

In addition to the trend towards downsizing *T. carnifex*, another factor that has probably contributed to misconceptions with respect to the roles of reptilian and mammalian carnivores in Pleistocene Australia is a tendency to provide only maximum estimated dimensions for large reptiles. Reliance on maximum dimensions, especially for taxa of indeterminate growth, may lead to heavily skewed interpretations of ecology. Hecht (1975) estimated that *M. prisca* might have reached 7 m and 620 kg, but gave no estimates of minimum, mean or average sizes. He did, however, give the data necessary to determine these values in the form of estimated head-body lengths. Using this data and Hecht's (1975) methodology, the length of the smallest mature specimen can be calculated at less than 2.2 m and the average at around 3.45 m. Ciofi (1999) alludes to a robust male Komodo dragon (*Varanus komodoensis*) of about 2.5 m long weighing 45 kg. With respect to the average weight of *M. prisca*, Auffenburgh (1972) determined that a 33 m *V. komodoensis* would weigh around 79 kg. On this basis it is reasonable to postulate that the average Pleistocene *Megalania* would have weighed around 90 kg, assuming no significant difference in shape between 3.3 and 3.45 m long individuals. Using other methods give maximum averages of less than 160 kg (Wroe 2002). Reliance on maximum dimensions also appears to extend to the two remaining large Pleistocene reptiles commonly invoked in support of hypotheses of reptilian domination, the madtsoiid snake *Wonambi naracoortensis* and the mekosuchine crocodile *Quinkana fortirostrum*. Indeed this is commonly the case for many extant reptilian taxa because the data required to determine average body weights is not generally available (Ernst and Zug 1996).

Another factor to be considered in this debate is that doubts persist over fundamental placement of these three Pleistocene reptiles with respect to niche. In fact, it has not yet been clearly established that any were terrestrial. Molnar (1990) raises the possibility that *M. prisca* was semi-aquatic and Molnar (1981) draws attention to the fact that, in the absence of postcranial material, there is no direct evidence to support the interpretation of *Q. fortirostrum* as a terrestrial crocodile. Most fossils of this species are associated with aquatic taxa and the few found in cave or fissure fill deposits are all within 10 miles of major water courses, an overland distance known to be well within the range of living crocodiles (Cott 1961). These same arguments apply to all Australian crocodylians for which a terrestrial habitus has been suggested, all of which are known from either little or no postcranial material and have been found only in association with aquatic species. Wills (1997a) notes that a high degree of regional endemism among Australian crocodiles of the late Oligocene-Miocene for which a terrestrial lifestyle had been hypothesised may count against the abilities of such species to traverse terrestrial environments. As with both *M. prisca* and *Q. fortirostrum*, the ecology of *W. naracoortensis* also remains enigmatic. Barrie (1990, p. 148) argues that '... large prey capable of struggling vigorously are unlikely to have been taken, since

Wonambi's jaws were rather weak' and that '...reduction in lateral flexion would limit its ability to constrict animals, thus implying that it subsisted mainly on small prey'. Indeed, at present there is no firm evidence that *W. naracoortensis* (or, for that matter, any madtsoiid) was in fact a constrictor by habit. The presence of a large number of relatively small weak teeth in this species lead Barrie (1990) to further posit that 'It is possible that *Wonambi* had feeding habits similar to those of *Acrochordus* [aquatic file snakes], fish being available in the lagoons of its habitat.' While *W. naracoortensis* had a wide distribution throughout southern and eastern Australia, it was apparently uncommon throughout this range (Scanlon 1992).

Notwithstanding uncertainty over the size and habits of the largest reptiles, there can be little doubt that there were relatively few large marsupial carnivore species in Pleistocene Australia by way of general comparison with other continents. However, all other continents are much larger and directly contrasting Australian mammalian carnivore diversity with arbitrarily delimited sub-areas of other continents is inappropriate. Basic principles of island biogeography predict that an isolated landmass will harbour fewer species than an area of the same dimensions within a larger continent because of differing balances between rates of immigration and extinction (MacArthur and Wilson 1967, Flessa 1975). Many other factors and conditions unique to the Australian continent may also have contributed to relatively low diversity during the Pleistocene. These include aridity and a lack of geographical barriers such as mountain ranges and large rivers, as well as soil nutrient levels and climatic variables such as temperature. But the relationship between such factors and species richness is unlikely to be simple. For example, the influence of productivity on diversity is not straightforward (Kondoh 2001) and there is strong evidence to suggest that soil nutrient levels do not necessarily effect either productivity or diversity (Jordan and Herrera 1981). In addition to being less diverse, in general, Australia's Pleistocene marsupial carnivores may not have been as large as the largest of presumably analogous taxa elsewhere. This phenomenon may also be explained through the application of biogeographical theory, as mammalian body size clearly correlates with continental area (Marquet and Taper 1998). Also of significance is the possible primacy of phylogeny over vegetation and habitat as a constraint on the distribution of mammalian body size (Seimann and Brown 1999). Finally, and perhaps even more importantly, using differences in species richness as a measure of the relative ecological significance of higher taxa could be inappropriate. Abundances and ranges of individual species may be the real measure of impact. These factors are difficult to quantify with respect to fossil species (Behrensmeyer 1991).

Prima facie evidence for reptilian carnivore supremacy over terrestrial mammalian counterparts during the middle-late Tertiary is perhaps even less convincing than for the Pleistocene. For example, although five crocodile species are known to have existed in the fossil rich Oligocene--Miocene deposits of

Riversleigh (Willis 1993, 1997a, 1997b), whether any were terrestrial is debatable. Four of these five, including *Baru wickeni*, the largest at around 4 m, are known only from late Oligocene deposits. Remaining species are all under 2 m in length and two were less than 1 m long (P.M. Willis pers. comm.). The largest snake, '*Montypythonoides riversleighensis*', was approximately 4 m, large, but not gigantic (J. D. Scanlon pers. comm.). At 2.5 m in length, the madtsoiid *Wonambi barriei* was the next largest snake from these deposits (Scanlon and Lee 2000). Two other madtsoiids were less than 1.5 m (Scanlon 1997 and pers. comm.). As with *W. naracoortensis* the habits of these Riversleigh madtsoiids are not well understood. None have been found in cave or fissure fill deposits. With regard to the estimation of size, data on Riversleigh's marsupial carnivores is also lacking. However, most of the 15 marsupial carnivore species known from these Riversleigh local faunas appear to fall within the size range of *Dasyurus maculatus* or larger, the only exceptions being the tiny *Sminthopsis*-sized *Mayigriphus orbus* and *Dasyurus hallucatus*-sized *Barinya wangala*. The biggest are a thylacoleonid at least as large as *Wakaleo vanderleueri* (A. Gillespie pers. comm.), an animal that weighed in at around 44-56 kg (Wroe et al. 1999). At least 10 of these larger species are known from Miocene deposits. On the other hand, in some pre-Pleistocene local faunas marsupial carnivores are rare. Scanlon and Mackness (in press) observe that only two terrestrial marsupial carnivores have been recorded from the early Pliocene Bluff Downs Local Fauna, *Thylacoleo crassidentatus* and *Dasyurus dunmalli*, while three large reptiles are known for which a terrestrial lifestyle has been proposed. An additional, potentially confounding factor effecting the understanding of palaeoecology in Riversleigh and other Tertiary faunas, is the possibility that giant dromornithid birds may have encroached on large terrestrial carnivore-omnivore niches (Wroe 1999c). Similarly, being omnivorous, casuariid birds may have competed with generalist marsupial carnivores such as giant rat-kangaroos.

FUTURE DIRECTIONS

While the wealth of new fossil material has already provided considerable insight into the evolution and palaeobiology of Australia's carnivorous marsupial lineages, studies completed to date constitute only a preliminary phase. Mile numerical parsimony analyses incorporating some of these new specimens have been conducted (Muirhead and Wroe 1998, Wroe et al. 2000), a number of studies are either incomplete, or in early stages (Wroe unpublished data, Cooke and Kear unpublished data, Gillespie unpublished data). Other areas that require more rigorous, quantitative analysis are those of palaeobiology and palaeoecology. In addition to requirements for more data on marsupial carnivore palaeontology is a like need for more data on the ecology of possible competitors among Reptilia and Aves. Ultimately, information gleaned from investigating both the phylogeny and trophic diversity of Australian marsupial carni-

vore clades and guilds may enable the identification of long term trends. Correlation with changes in climate and habitat will help to identify factors that have influenced the evolution of communities and their structures.

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