



**Muribacinus gadiyuli, (Thylacinidae: Marsupialia), a Very Plesiomorphic Thylacinid from the Miocene of Riversleigh, Northwestern Queensland, and the Problem of Paraphyly for the Dasyuridae (Marsupialia)**

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# *MURIBACINUS GADIYULI*, (THYLACINIDAE: MARSUPIALIA), A VERY PLESIOMORPHIC THYLACINID FROM THE MIOCENE OF RIVERSLEIGH, NORTHWESTERN QUEENSLAND, AND THE PROBLEM OF PARAPHYLY FOR THE DASYURIDAE (MARSUPIALIA)

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**ABSTRACT**—A new genus and species of thylacinid, *Muribacinus gadiyuli*, is described from Miocene deposits of Riversleigh in northwestern Queensland. *Muribacinus gadiyuli* shares six character states associated with carnassialisation common among thylacinids, but is uniformly less derived for each. The closest affinities of this species lie with another plesiomorphic thylacinid from Riversleigh, *Nimbacinus dicksoni*. Two previously recognised thylacinid synapomorphies are reconsidered in the light of new evidence. A growing body of molecular and fossil data indicates that the modern dasyurid radiation is a relatively recent phenomenon. Character analysis suggests that no reliable dental synapomorphies define the Dasyuridae at present. It is proposed that a number of plesiomorphic late Oligocene and Miocene taxa previously considered as dasyurids be regarded as *Dasyuromorphia incertae sedis* pending the identification of shared derived dental characters for the family, or the discovery of more complete material.

## INTRODUCTION

THE DASYUROMORPHIA is a large clade of Australian marsupial insectivore-carnivores. Three families are currently recognised, the Dasyuridae (around fifty extant species), Thylacinidae (extinct) and the monotypic Myrmecobiidae. Prior to Woodburne's (1967) description of *Thylacinus potens*, the fossil record for the Dasyuromorphia was restricted to two specialised taxa, *Glaucodon balleratus* (Stirton, 1957) and *Sarcophilus laniarius* (Owen, 1838), of Pliocene and Pleistocene age respectively. A fourth taxon was added with *Dasyurus dunmalli* (Bartholomai, 1971). The first published descriptions of pre-Pliocene dasyuromorphians, *Ankotarinja tirarensis* and *Keeuna woodburnei*, from the late Oligocene to Miocene Etadunna Formation of South Australia, were forwarded by Archer (1976a). Additional Miocene taxa were described from the Namba Formation of central Australia, *Wakamatha tasselli* (Archer and Rich, 1979) and *Dasyurinja kokuminola* (Archer 1982a), although Archer and Rich (1979) note that the type and only specimen of *W. tasselli* may have been dislodged from the adjacent Pleistocene Eurinilla Formation.

Following the discovery of abundant dasyuromorphian material from late Oligocene and Miocene deposits of Riversleigh in northwestern Queensland, five new taxa have been described (Muirhead and Archer, 1990; Muirhead, 1992; Muirhead, in press; Wroe, in press a), with the description of further taxa in preparation. To date only one pre-Pliocene dasyuromorphian taxon has been unambiguously linked with a modern genus, *Thylacinus macknessi* (Muirhead, 1992). Three other pre-Pliocene taxa have been equivocally associated with elements of the modern dasyurid radiation, *Wakamatha tasselli* (Archer and Rich, 1979), an un-named "Antechinus-like" species from Riversleigh (Van Dyck, 1989), and *Mayigrphus orbus* (Wroe, in press a).

It is now apparent that the dasyuromorphian clade of Oligocene and Miocene Riversleigh deposits was dominated by a diverse thylacinid component (Wroe, 1995; Wroe, in press a). Here a new and very plesiomorphic species of thylacinid is described from middle Miocene deposits of Riversleigh. Description of this new species highlights the need for systematic revision for some fossil dasyuromorphian taxa, with paraphyly suggested for the Dasyuridae as currently recognised.

Ordinal and familial level taxonomic nomenclature follows Marshall et al. (1990), with the Myrmecobiidae considered the sister taxon to a thylacinid-dasyurid clade. Acceptance of this interpretation is based on the albumin data of Lowenstein et al. (1981), and the contention that the strongest proposed synapomorphy uniting myrmecobiids and dasyurids, loss of the foramen ovale and its replacement by a foramen ovale (Archer, 1984), is symplesiomorphous (Case, 1989; Muirhead, 1994). However, it must be noted that given acknowledgment of this phylogenetic scenario the application of foramen ovale loss as a dasyurid synapomorphy by Marshall et al (1990) is inconsistent. Familial level nomenclature deviates from that of Marshall et al. (1990) in that the dasyuromorphian taxa *A. tirarensis*, *K. woodburnei*, *W. tasselli*, *D. kokuminola*, from Oligocene and Miocene deposits of central Australia (Woodburne et al., 1993) are considered *Dasyuromorphia incertae sedis* for reasons considered in the text. Subfamilial systematics of extant dasyurids follows Archer (1982a) with exceptions as indicated below.

Although Archer's (1982a) synthesis of dasyurid relationships has been substantially corroborated by subsequent investigations (Kirsch et al., 1990; Baverstock, et al., 1990), a number of molecular studies have questioned the monophyly of some subfamilies and tribes therein (Baverstock et al., 1990; Krajewski et al., 1992, 1993, 1994; Painter, et al., 1995). In particular the subfamilial-level distinction of the New Guinean Muricinae (*Murexia*), and Phascolosoricinae (*Phascolosorex* and *Neophascogale*) has been queried and all recent investigations have indicated the separation of dasyurids into three clades (Dasyurinae, Phascogalinae and Sminthopsinae). The contention that *Murexia* forms part of the phascogaline radiation has been supported by investigations of immunology (Aplin et al., 1993), cytochrome-b DNA sequences (Krajewski et al., 1992, 1993, 1994), 12 S ribosomal DNA data (Springer et al., 1994), and DNA-DNA hybridisation (Kirsch et al., 1990). A basal position within the Dasyurinae for *Phascolosorex* and *Neophascogale* has been indicated by the results of cytochrome-b analysis (Krajewski et al., 1992, 1993, 1994) and the immunological study of Aplin et al. (1993). Here the results of these molecular analyses are tentatively accepted and the following three families are recognised: Sminthopsinae, Dasyurinae (including *Neophascogale* and *Phascolosorex*), and Phascogalinae

(including *Murexia*). Tribal level designations are not used pending the results more detailed investigation of both morphological and molecular data. Dental nomenclature follows Flower (1867) and Luckett (1993) regarding the molar-premolar boundary, where the adult (unreduced) postcanine cheektooth formula of marsupials is  $P^{1-3}$  and  $M^{1-4}$ . Institutional abbreviations: QM, Queensland Museum;

#### SYSTEMATIC PALEONTOLOGY

Order DASYUROMORPHIA Gill, 1872  
Superfamily DASYUROIDEA Goldfuss, 1820  
Family THYLACINIDAE Bonaparte, 1838  
Genus MURIBACINUS new genus

#### Figure 1

*Type species.* — *Muribacinus gadiyuli* new genus and species.

*Diagnosis.* — *Muribacinus* differs from all dasyurids in the following combination of features:  $P^3$  massive and almost as long (anteroposteriorly) as  $M^1$ , with small but distinct posterior and posterolingual cusps; protocones less anteriorly positioned; centrocrista of  $M^{1-3}$  less invasive of the paracone and metacone basins; preparacrista almost as long as preprotocrista on  $M^1$ ; distinct stylar cusp E on  $M^2$ ;  $M^3$  postmetacrista and preparacrista almost equal in length, with stylar cusp D small; ectoflexus of  $M^3$  a shallow U-shape and very extensive on the long axis;  $P_{1-2}$  separated by diastema, diastema between  $P_{2-3}$ ;  $P_3$  only slightly smaller than  $P_2$ ;  $M_1$  protoconid centrally positioned relative to both long and transverse axes of dentary; paraconid larger than metaconid on  $M_{1-4}$ ; degree of metaconid reduction relatively constant through  $M_{1-4}$ ; combination of derived characters associated with carnassialisation on trigonids of  $M_{1-4}$  without concurrent reduction of talonids, particularly on  $M_4$ . *Muribacinus gadiyuli* can be distinguished from known thylacinids (*Nimbacinus dicksoni* and the species of *Thylacinus*) by: less closely twinned paracones and metacones; larger protocones; less reduced stylar shelf; postmetacrista shorter relative to preparacrista on  $M^{1-3}$ ;  $P_3$  slightly smaller than  $P_2$ ;  $M_{1-4}$  metaconids less reduced; larger talonids; smaller size.

*Etymology.* — The generic name combines the local Aboriginal (Wanyi) word for father, “muriba” (Green, unpublished data) and “cinus”, from the Greek word kynos (dog), as an allusion to the structurally ancestral position within the Thylacinidae inferred from analysis of the holotype and paratype, here given masculine gender.

#### MURIBACINUS GADIYULI new species

#### Figure 1

*Diagnosis.* — As for genus.

*Etymology.* — “Gadiyuli” is a Wanyi Aboriginal word for little.

*Holotype.* — QMF 30386 (AR 5427), right maxillary fragment and most of jugal, containing  $P^3$ ,  $M^{1-4}$ , all moderately worn and infraorbital foramen.

*Paratype.* — QMF 30385 (AR 7642), right dentary containing  $P_2$  alveolus,  $P_3$ ,  $M_{1-4}$ .

*Type specimen locality and age.* — Gag Site, Riversleigh Station, northwestern Queensland. This site is part of System C assemblage at Riversleigh which has been tentatively dated as medial Miocene (Archer et al., 1989; 1994).

*Description of holotype.* — (QMF 30386). Maxilla: anteriorly maxilla missing beyond anterior root of  $P^3$ ; dorsally maxilla extends to include laterally compressed infraorbital foramen beyond which it is broken away; infraorbital foramen bounded solely by maxilla, with posterior margin about 5 mm anterior

to jugal-maxilla symphysis; jugal largely preserved with only posterior symphysis with squamosal missing.

$P^3$ :  $P^3$  very large relative to molars, almost as long (anteroposteriorly) as  $M^3$ ; in occlusal view  $P^3$  roughly triangular in shape and wider posteriorly than anteriorly, paracone medial; weakly defined crista connects paracone to small posterior cusps; another crista runs from this cusps to tiny posterolingual cusps; small but distinct wear facet exists within region delimited by this crista; in lateral view tooth projects well beyond occlusal plane of molars; crista joining paracone and posterior cusps strongly concave at base; posterior root larger than anterior.

$M^1$ :  $M^1$  tri-rooted with anterior-buccal root smallest and posterior-buccal root largest. In order of decreasing height principle cusps are; metacone, stylar cusp D, stylar cusp B, paracone, stylar cusp B, protoconule, metaconule, protocone; protocone bulbous and basally broad; stylar cusps C and E absent; postmetacrista longest shearing crest, about twice length of preparacrista; postmetacrista longer than postparacrista and postprotocrista longer than preprotocrista; principle shearing crest (postmetacrista) acutely angled to long axis of tooth row; ectoflexus apparent in stylar shelf minimal;  $M^1$  closely associated with  $P^3$  which is secured posteriorly by notch beneath  $M^1$  paracone; weak anterior cingula present.

$M^2$ : larger than  $M^1$ ;  $M^2$  further differs in possession of longer preparacrista and less acutely angled postmetacrista; stylar cusp D sits further above occlusal plane than metacone; both these cusps relatively larger and more widely separated than in  $M^1$ ; stylar cusp B considerably larger than paracone; protocone less basally broad; anterior cingula shorter but well defined on  $M^2$ ;  $M^2$  has tiny stylar cusp E, not present in  $M^1$ ; better developed protoconule and metaconule also present.

$M^3$ :  $M^3$  slightly smaller than  $M^2$  in occlusal view; preparacrista almost as long as postmetacrista, which in conjunction with relatively large paracone contributes to near bilateral symmetry in tooth through transverse axis;  $M^3$  stylar cusp much D smaller than for  $M^{1-2}$  and lower than metacone; stylar cusp E absent; anterior cingula present, better developed than in  $M^2$ ; stylar shelf reduced and deeply concave along buccal margin; protoconule and metaconule slightly larger than in  $M^2$ ; metacone and paracone more closely approximated than for  $M^2$ .

$M^4$ :  $M^4$  differs from  $M^{1-3}$  in further reduction of stylar shelf, protocone more reduced and metacone tiny; no metaconule present and protoconule just visible; preparacrista longest crest, approaching  $M^3$  preparacrista in length; anterior cingula present but smaller than on  $M^{1-3}$ .

Meristic gradients from  $M^{1-4}$ : preparacrista length increases from  $M^{1-3}$ ; about equal on  $M^3$  and  $M^4$ ; postmetacrista length increases from  $M^{1-2}$  then decreases for  $M^3$  (not present on  $M^4$ ), postmetacrista orientation away from transverse axis of tooth row increases  $M^{1-2}$  and equal  $M^{2-3}$ ; paracone height increases from  $M^{1-4}$ ; metacone height increases from  $M^{1-3}$ , greatly reduced on  $M^4$ ; protocone height decreases  $M^{1-4}$ ; talon surface area in occlusal view increases  $M^{1-2}$ , decreases  $M^{3-4}$ ; stylar cusp B height increases from  $M^{1-2}$  then decreases on  $M^3$  (not present on  $M^4$ ); anterior cingula increases in length from  $M^{1-3}$ , decreases on  $M^4$ ; ectoflexus increases  $M^{1-3}$ , not present on  $M^4$ ; angle formed by postparacrista and premetacrista (centrocrista) about ninety degrees in  $M^{1-2}$ , increasingly acute for  $M^3$  and  $M^4$ . Protocone becomes less basally broad from  $M^{1-4}$ .

*Paratype locality and age.* — QMF 30385 is from Henk's Hollow Site System C of the Riversleigh assemblage, estimated to be of medial Miocene age, Archer et al., (1989, 1994).

*Description of paratype.* — Although from a slightly smaller animal than holotype, specimen QMF 30385 is attributed to *M. gadiyuli* as proportions of all major shearing crests in  $M_{1-4}$



match with counterparts in upper dentition (QMF 30386) and both holotype and paratype are from deposits estimated to be of middle Miocene age.

Dentary: dentary QMF 30385 broken away from about 5 mm anterior to  $P_2$  alveolus; ascending ramus of dentary extends for about 15 mm beyond which it is missing; condyle and angular process broken away; dentary tapers anteroposteriorly with depth below centre of  $P_3$  on long axis 7 mm and depth below  $M_4$  protoconid 11 mm; mental foramen beneath  $M_1$  protoconid.

$P_2$ : only alveoli for two roots of  $P_2$  remain; posterior root is larger than the anterior; no roots are apparent for  $P_1$  on 5 mm region extending anterior of  $P_2$  showing the minimal limit of the diastema separating  $P_2$  from  $P_1$ .

$P_3$ : most of crown broken away, size of roots indicate  $P_3$  close to  $P_2$  in length but probably less robust.

$M_1$ :  $M_1$  heavily worn; posterolingual corner including hypoconulid missing; talonid much wider than trigonid; principal cusps in order of decreasing height; protoconid, metaconid, paraconid, hypoconid and entoconid; protoconid largest and most robust cusp; roughly central position on crown in occlusal view; metaconid small, twinned with protoconid and posteriorly placed; distinct anterior cingulid runs from anterior base of paraconid along lingual base of crown terminating above anterior root; hypoconid higher than entoconid with interior angle between cristid obliqua and hypocristid slightly less than 90 degrees; hypocristid angled at about 45 degrees to transverse axis of dentary; posterior cingulid continues anteriorly to circumscribe hypoconid base; paracristid principal vertical shearing crest, running almost parallel to long axis of dentary.

$M_2$ : paraconid and antero-lingual face of metaconid missing;  $M_2$  differs from  $M_1$  in the following ways; trigonid almost as wide as talonid, protoconid larger and less lingually positioned, metaconid larger, less closely approximated to protoconid and less posteriorly positioned, talonid basin more extensive, entoconid larger and higher relative to hypoconid, hypoconulid small and lower than entoconid, protoconid clearly recurved lingually.

$M_3$ :  $M_3$  differs from  $M_2$  as follows; trigonid slightly wider than talonid, protoconid larger, hypoconid smaller with interior angle between cristid obliqua and hypocristid more acute, paracristid more transversely oriented, metacristid more extensive.

$M_4$ :  $M_4$  broken away from postero-buccal base of protoconid diagonally across to posterior tip of hypoconulid.  $M_4$  similar to  $M_3$  except as follows; talonid further reduced where observable, protoconid smaller though equal in height, metaconid smaller and more posteriorly positioned, paracristid more transversely oriented and metacristid less transversely oriented with respect to long axis of dentary.

Meristic gradients from  $M_{1-4}$ : orientation of the paracristid increasingly transverse to long axis of dentary; metacristid not clear on  $M_1$  but increasingly transverse orientation from  $M_{2-4}$ ; in combination these two gradients produce an increasingly acute interior angle between paracristid and metacristid posteriorly; protoconid size increases from  $M_{1-3}$ , then decreases for  $M_4$ , with protoconid about equal in size to  $M_2$ ; metaconid height increases  $M_{1-4}$ ; metaconid size increases from  $M_{1-3}$ , decreasing for  $M_4$ .

#### PHYLOGENETIC ANALYSIS

*Method.*—A character analysis is provided below. Although the basic principles of "phylogenetic systematics" (sensu Wiley,

1981) are subscribed to here, the results of the character analysis are not subjected to computer-generated parsimony analysis. That parsimony analysis using computer algorithms has proven a valuable tool in phylogenetic studies is not questioned. However, the capacity of this method to resolve phylogenies is questionable where homoplasy is common (Felsenstein, 1983; Felsenstein and Sober, 1986; Harvey and Pagel, 1991; Stewart 1993). Most adherents to the cladistic method argue that the demonstration of homoplasy must be the result of parsimony analysis and that it is circular to incorporate data assuming an *a priori* interpretation of relationships in phylogenetic studies (Sundberg and Svenson, 1994). Webb (1994) dismisses dogmatic adherence to this principle, concluding that non-biotic data (e.g. evidence of stratigraphic or geographic separation, and ecological congruence) must be considered *a priori* in order to avoid erroneous phylogenetic inference in some instances. Computer-generated parsimony analysis based on morphological data has only been applied once to the question of interfamilial relationships of dasyuromorphians. Results of this investigation (Kirsch and Archer, 1982), with a high number of shortest possible, but very improbable cladograms produced, led the authors to conclude that parsimony was inappropriate for the task at hand, identifying very high levels of homoplasy as the principle confounding factor. Convergence and parallelism have long been recognised as particularly problematic regarding the elucidation of dasyuromorphian phylogeny (Ride, 1964; Kirsch and Archer, 1982; Szalay, 1994). Similarly, in an analysis of carnivoran phylogeny, Martin (1989) notes that the incidence of homoplasy may out number synapomorphy for many features by a factor as high as five. Martin (1985) suggests that this phenomenon may be attributed to a restricted number of viable form-function solutions to selective regimes for carnivoran taxa, and questions the utility of numerical procedures in the evaluation of phylogeny for the clade. A like explanation for homoplasy among marsupial carnivores may well apply. Certainly, some of the most extraordinary known instances of homoplasy among mammals are to be found between carnivorous marsupial taxa (e.g. *Thylacinus* and *Borhyaena*).

The potential value of parsimony analysis in this study, which is based largely on fossil taxa, is further compromised by the problem of missing data, an area of concern to most paleontologists (Cracraft, 1981; Novacek et al., 1988; Simmons, 1993; Luckett, 1994). All fossil taxa considered here are represented by incomplete material, with several known from a few teeth only. Missing data in this study (>50 percent) greatly exceeds the minimum level (30 percent) suggested by Novacek et al. (1988) as a benchmark for the reliable reflection of phylogeny.

The clear demonstration of high levels of homoplasy for the Dasyuromorphia by previous investigators and the restricted data set available, are considered reasonable grounds to dismiss the option of parsimony analysis here. However, with around twenty dasyuromorphian taxa yet to be described (including complete cranial material), from sites ranging from Eocene to Pleistocene in age, it is anticipated that parsimony-based investigation will eventually become practicable.

*Character analysis.*—1. Infraorbital foramen: For plesiomorphic ameridelphians the infraorbital foramen is positioned well anterior to the symphysis of the maxilla and jugal. A like condition is typical of most dasyurids. However, for the most derived carnivorous dasyurid, *S. harrisi*, this foramen is situated posteriorly, very close to the maxilla/jugal symphysis. This

FIGURE 1—*Muribacinus gadiyuli* new genus and species. Holotype QM F30386, right maxillary and jugal fragments containing  $P^3$ ,  $M^{1-4}$ . 1, buccal view; 2, lingual view; 3, stereo pair in occlusal view. Paratype QM F30385, right dentary fragment containing partial  $P_3$ ,  $M_{1-4}$ . 4, stereo pair in occlusal view. Scale bars = 1 cm.

feature is not known for *A. tirarensis*, *K. woodburnei*, or *D. kokuminola*. In *M. gadiyuli* the infraorbital foramen is situated well anterior to the symphysis of the maxilla and jugal, above the anterior root of  $M^2$ . For the derived thylacinid, *T. cynocephalus* the infraorbital canal lies on the maxilla/jugal symphysis and dorsal to the junction of  $M^3/M^4$ . Muirhead and Archer (1990) considered posterior placement of the infraorbital canal as a thylacinid synapomorphy. However, the precise position of the infraorbital foramen relative to the jugal-maxilla is difficult to determine in the species of thylacinid, *N. dicksoni*, described by Muirhead and Archer (1990), because the jugal is missing. Certainly in *N. dicksoni* the foramen lies above the anterior root of  $M^2$ , as for *M. gadiyuli* and most dasyurids.

2. Styler cusp B morphology: Styler cusp B is moderately developed in stem marsupials. Marshall et al., (1990) consider this to represent the likely ancestral state for Australidelphians. For *A. tirarensis* styler cusp B is small on  $M^{2-3}$ , the only uppers known for this taxon. Styler cusp B on  $M^{2-3}$  is also small on *K. woodburnei*, although slightly larger than for *A. tirarensis*. *Dasyurinja kokuminola* is known from a single  $M^3$ , on which styler cusp B is larger than in *K. woodburnei* and *A. tirarensis*. Styler cusp B is clearly present on all upper molars of most dasyurids, but reduced or lost on  $M^1$  of derived carnivorous taxa (e.g., *Dasyuroides*, *Sarcophilus*, *Dasyurus*). *Nimbacinus dicksoni* shows marked reduction of styler cusp B on all upper molars compared to less specialised dasyurids, but not more marked than for derived dasyurid taxa (i.e. styler cusp B is not lost on  $M^1$  in *N. dicksoni*). *Muribacinus gadiyuli* is similar, to *N. dicksoni* in styler cusp B morphology. Styler cusp B of *T. macknessi* is tiny on  $M^1$ , the only known upper molar for the taxon. Poor preservation of the styler shelf region in *T. potens* precludes accurate assessment for this taxon. For *T. cynocephalus* styler cusp B is present but minute on all upper molars.

3. Styler cusp D morphology: In plesiomorphic ameridelphians styler cusp D is small on all upper molars. For two fossil dasyuromorphian taxa, *A. tirarensis* and *K. woodburnei* styler cusp D is also relatively small on all upper molars available for comparison ( $M^{2-3}$  for both *K. woodburnei* and *A. tirarensis*). *D. kokuminola* is known from a single upper molar ( $M^3$ ). Styler cusp D is moderately well developed on this tooth and larger than for *K. woodburnei* and *A. tirarensis*. For most dasyurids styler cusp D is large on all upper molars, although for all taxa this cusp is smaller on  $M^3$  than for the preceding molars. The apomorphic *S. harrisii* shows reduction of all styler cusps, with styler cusp D lost on  $M^3$ . In *M. gadiyuli* styler cusp D is only moderately reduced in size relative to that of most dasyurids for  $M^{1-2}$ , but styler cusp D is tiny on  $M^3$ . In thylacinids styler cusp D is small or lost on all upper molars. Styler cusp D is small on  $M^{1-2}$  of *N. dicksoni* and vestigial on  $M^3$ . For *T. potens*  $M^3$  is damaged on the only known specimen, but a small styler cusp in the "D" position suggests a like condition to that shown in *N. dicksoni*. *Thylacinus cynocephalus* has been considered to have lost styler cusp D on all upper molars (Archer, 1982b). However, Muirhead and Archer (1990), consider it likely that the cusp identified as "E" for *T. cynocephalus* by previous authors is in fact "D". This cusp is tiny but discernible on  $M^{1-3}$  for *T. cynocephalus*. The interpretation of Muirhead and Archer (1990) is accepted here, as for all other known dasyuromorphians styler cusp E is always the smallest cusp (when present at all), and it seems improbable that styler cusp D would be lost and styler cusp E retained in the highly apomorphic *T. cynocephalus*.

If the small styler cusp D on  $M^3$  for *A. tirarensis* and *K. woodburnei* is considered plesiomorphic for the order, then three interpretations are possible regarding the polarity decision for the tiny  $M^3$  styler cusp D of *M. gadiyuli* and *N. dicksoni*. Firstly

the small  $M^3$  styler cusp D might represent a symplesiomorphy for *M. gadiyuli* and *N. dicksoni*, with dasyurids then united by the shared derived acquisition of an enlarged  $M^3$  styler cusp D. Alternatively, enlargement of  $M^3$  styler cusp D might represent a synapomorphy uniting thylacinids and dasyurids, with the subsequent reduction of this cusp representing an apomorphic reversal in *M. gadiyuli* and *N. dicksoni*, or, enlargement of styler cusp D evolved independently in both ancestral thylacinids and dasyurids, with apomorphic reversal convergently acquired in specialised thylacinids and dasyurids. The contention that  $M^3$  styler cusp D reduction represents a retained plesiomorphy in *M. gadiyuli* and *N. dicksoni* is rejected as styler cusp D is relatively large on  $M^{1-2}$  for both taxa compared to *A. tirarensis* and *K. woodburnei*, and styler cusp D reduction correlates with carnassialisation for marsupial carnivores generally. Consequently, the second or third hypotheses above are supported here, with a small  $M^3$  styler cusp D considered plesiomorphic in *A. tirarensis* and *K. woodburnei*, and an apomorphic reversal in derived dasyurids and all thylacinids.

4. Relationship of styler cusp D to the metacone: For plesiomorphic metatherians the metacone is well separated from styler cusp D on all upper molars, with this distance greatest for  $M^3$ . This relationship between the two cusps is maintained in *A. tirarensis*, *K. woodburnei*, and *D. kokuminola*. Upper molars are unknown for *W. tasselli*. For unspecialised dasyurids the plesiomorphic condition is also retained. However, derived carnivorous dasyurids (*Dasyurus*, *Sarcophilus*) show marked approximation of styler cusp D and metacone for  $M^{1-3}$ . For *M. gadiyuli* and *N. dicksoni*, although styler cusp D is more reduced on  $M^3$  than for all derived dasyurids excepting *S. harrisii*, this cusp remains widely separated from the metacone. The morphology of this region is not known for *T. macknessi*. The relationship of the reduced styler cusp D and the metacone on  $M^3$  of *T. potens* also follows that of unspecialised marsupials. For *T. cynocephalus* styler cusp D is lost on  $M^3$ . However, the greatly diminished styler cusp D of  $M^2$  is widely separated from the metacone. Muirhead and Archer (1990) note this fundamental difference in the styler region of *T. cynocephalus* and carnivorous dasyurids.

5. Morphology of anterior cingula on upper molars: Plesiomorphic marsupials show a well developed notch in the anterior cingula of upper molars for the reception of the metastylar corner of the preceding tooth. This feature is common to *A. tirarensis*, *K. woodburnei*, *D. kokuminola* and plesiomorphic dasyurids, but incomplete in derived dasyurids (e.g. *D. maculatus*, *Dasyuroides byrnei*, *S. harrisii*). A poorly developed notch is present in the anterior cingula of *M. gadiyuli*. This reduction is further pronounced in *N. dicksoni*. For *T. macknessi* a well developed cingula is present on  $M^1$ , but no notch is present. Anterior cingula are absent in all upper molars of *T. cynocephalus*. Again, poor preservation prevents determination of this feature in *T. potens*.

6. Approximation of paracone and metacone: For plesiomorphic marsupials the paracone and metacone are not closely appressed. A like condition is common to *A. tirarensis* and *K. woodburnei*. Moderate appression of paracone and metacone is shown on  $M^3$  of *D. kokuminola*. For most dasyurids these two cusps are well spaced. However, in derived carnivorous dasyurid taxa appression of the paracone and metacone ranges from moderate to advanced. *Muribacinus gadiyuli* shows moderate appression of the paracone and metacone. Approximation of these cusps relative to *M. gadiyuli* is further developed in increasing order of specialisation for thylacinids as follows: *N. dicksoni*, *T. macknessi*, *T. potens* and *T. cynocephalus*.

7. Preparacrista and postmetacrista length: For plesiomorphic marsupials the preparacristae is only slightly longer than the



TABLE 1—*M. gadiyuli*, QM F30386, Type; QM F30386, Referred specimen. Dental measurements (mm). For upper dentition: l = maximum anteroposterior length; w = maximum transverse width; ul = anteroposterior length, from antero-buccal tip to metastylar corner; uwl = protocone (lingual face) to metastylar corner; uw2 = antero-buccal tip to protocone (lingual face). For lower dentition: ll = anteroposterior length, from antero-lingual tip to hypoconulid tip; lw1 = maximum transverse dimension of trigonid; lw2 = maximum transverse dimension of talonid. “\*” = damaged.

| Ref. #    | p <sup>3</sup> |     |     | M <sup>1</sup> |     |     | M <sup>2</sup> |     |     | M <sup>3</sup> |     |     | M <sup>4</sup> |     |
|-----------|----------------|-----|-----|----------------|-----|-----|----------------|-----|-----|----------------|-----|-----|----------------|-----|
|           | 1              | w   | ul  | uw1            | uw2 | l   | uw1            | uw2 | ul  | uw1            | uw2 | l   | uw1            | uw2 |
| QMF 30386 | 5.4            | 3.3 | 5.9 | 5.9            | 4.3 | 5.8 | 7.3            | 5.4 | 5.6 | 6.9            | 6.1 | 4.7 | 3.4            | 6.0 |
| Ref. #    | P <sub>3</sub> |     |     | M <sub>1</sub> |     |     | M <sub>2</sub> |     |     | M <sub>3</sub> |     |     | M <sub>4</sub> |     |
|           | 1              | w   | ll  | lw1            | lw2 | ll  | lw1            | lw2 | ll  | lw1            | lw2 | ll  | lw1            | lw2 |
| QMF 30385 | —              | —   | 4.5 | 2.3            | 2.8 | *   | 2.9            | 3.1 | 5.6 | 3.3            | 3.0 | *   | 3.2            | *   |

postmetacrista on M<sup>2-3</sup>. This feature is also common to *K. woodburnei*. On M<sup>3</sup> of *A. tirarensis* the preparacrista is about two thirds the length of the postmetacrista (M<sup>2</sup> is not known). The M<sup>3</sup> of *D. kokuminola* shows a preparacrista less than half the length of the postmetacrista. For most dasyurids the preparacrista length is about half that of the postmetacrista on M<sup>2</sup> and about two thirds the length of the preparacrista on M<sup>3</sup>. Apomorphic carnivorous dasyurid taxa depart from this generality, showing greatly reduced preparacristae and hypertrophied postmetacristae. *Muribacinus gadiyuli* is comparable in this feature to unspecialised dasyurids, as is *N. dicksoni*. The species of *Thylacinus* each show considerable elongation of the postmetacristae relative to the preparacristae on M<sup>2-3</sup>.

8. Postmetacrista orientation: Plesiomorphic marsupials show postmetacristae oriented close to the transverse axis of the maxilla. Similar morphology for this feature is apparent in *A. tirarensis* and *K. woodburnei*. For *D. kokuminola* postmetacrista orientation of the M<sup>3</sup> is derived on this condition, being aligned more anteroposteriorly. Unspecialised dasyurids show a similar condition to those of plesiomorphic marsupials. Apomorphic carnivorous dasyurids are variously derived regarding postmetacristae orientation, with *S. harrisii* showing postmetacristae orientation approaching the long axis of the maxilla. *Muribacinus gadiyuli* and *N. dicksoni* show the plesiomorphic state for this feature. All species of *Thylacinus* are apomorphic for postmetacristae orientation, with *T. cynocephalus* showing postmetacristae only slightly less anteroposteriorly directed than for *S. harrisii*.

9. Protocone size: The protocone on all upper molars is large for plesiomorphic metatherians. Where comparable, this is also true of *A. tirarensis* and *K. woodburnei*. *Dasyurinus kokuminola* shows very moderate protocone reduction. For dasyurids the protocone is unreduced in nearly all taxa. *Dasyurus maculatus* and *S. harrisii* are clear exceptions here, showing considerable reduction of this feature. *Muribacinus gadiyuli* shows protocone hypertrophy which exceeds that of all dasyurids excepting *Dasyurus maculatus* and *S. harrisii* (comparable to that of *D. maculatus*). Protocone hypertrophy is slightly more advanced in *N. dicksoni* than *M. gadiyuli* and further pronounced in all species of *Thylacinus*.

10. P<sub>3</sub> morphology: P<sub>3</sub> is large in unspecialised metatherians. The morphology of this tooth is unknown for *A. tirarensis*, *K. woodburnei* or *D. kokuminola*. Archer (1976a) considers a large P<sub>3</sub> plesiomorphic for dasyurids, and in derived carnivorous dasyurids P<sub>3</sub> is lost. For *M. gadiyuli* and *N. dicksoni* P<sub>3</sub> is large. This is also the case for *T. potens* and *T. cynocephalus*. P<sub>3</sub> is unknown for *T. macknessi*. Although the large size of P<sub>3</sub> is almost certainly a plesiomorphy for *M. gadiyuli*, the presence of posterior and posterolingual cusps on this tooth may represent a synapomorphy with *N. dicksoni*.

11. Metaconid morphology: Two features of metaconid mor-

phology are considered here: firstly overall metaconid reduction and, secondly, a differential between M<sub>1</sub> metaconid reduction and M<sub>2-4</sub> metaconid reduction. The M<sub>1-4</sub> metaconids are unreduced in plesiomorphic marsupials, *A. tirarensis*, *K. woodburnei* and *W. tasselli*. The lower dentition is unknown for *D. kokuminola*. Unreduced metaconids are common to most dasyurids. In some carnivorous dasyurids, notably *D. maculatus* and *S. harrisii*, marked diminution of the metaconids is apparent on all lower molars. For *M. gadiyuli* metaconid reduction exceeds that of all the above mentioned taxa excepting *S. harrisii*. Diminution of the metaconids is further developed in *N. dicksoni*, and the metaconids are lost on all lower molars of the three species of *Thylacinus*.

For the taxa showing metaconid reduction, a disparity is apparent in the relative degree to which this cusp is reduced on M<sub>1</sub> as opposed to M<sub>2-4</sub>. For *M. gadiyuli* and *N. dicksoni*, diminution of the metaconid is relatively uniform on all lower molars, whilst carnivorous dasyurids always show M<sub>1</sub> metaconid reduction greatly advanced over that of M<sub>2-4</sub>.

12. M<sub>1</sub> paraconid morphology: The M<sub>1</sub> paraconid is a well developed cusp on plesiomorphic marsupials. This is also true of *A. tirarensis*, and *K. woodburnei*. This cusp is not known for *D. kokuminola* or *W. tasselli*. A relatively large M<sub>1</sub> paraconid is shown by most dasyurids, excepting derived carnivorous taxa, in which this cusp is greatly reduced, or lost. For *M. gadiyuli* and *N. dicksoni* the M<sub>1</sub> paraconid is unreduced. The species of *Thylacinus* each show some reduction of this cusp. However, in no thylacinid is the M<sub>1</sub> paraconid as reduced as in the species of *Dasyurus* or *S. harrisii*.

13. M<sub>4</sub> length: M<sub>4</sub> is shorter on the anteroposterior axis than M<sub>3</sub> in plesiomorphic metatherians. A like condition is common to *A. tirarensis*, and *W. tasselli*. M<sub>4</sub> is not known for *D. kokuminola* or *K. woodburnei*. For *M. gadiyuli* and *N. dicksoni*, and *T. macknessi* M<sub>4</sub> is also shorter on the long axis of the dentary than M<sub>3</sub>. *Thylacinus cynocephalus* and *T. potens* are clearly apomorphic within the Dasyuromorphia in showing an M<sub>4</sub> greater on the anteroposterior dimension than M<sub>3</sub>.

14. P<sub>3</sub> morphology: An unreduced P<sub>3</sub> has been considered plesiomorphic for marsupials (Archer 1976a). Cifelli (1993) is noncommittal regarding polarity for this character. Qualification is required here. If the unspecialised peradectid condition is taken to be plesiomorphic, then this suggests a P<sub>3</sub> slightly larger than P<sub>2</sub> on both the ventro-dorsal (height) and anteroposterior (length) dimensions. For *A. tirarensis* P<sub>3</sub> is slightly smaller than P<sub>2</sub> for both height and length. By inference from the alveolus the P<sub>3</sub> of *W. tasselli* was enormous, relatively larger than for any other known dasyuromorphian. P<sub>3</sub> morphology is unknown for *D. kokuminola* or *K. woodburnei*. For dasyurids a tendency to reduce P<sub>3</sub> has been considered a possible synapomorphy (Tate, 1947; Archer, 1982b; Marshall et al., 1990). Although reduction and sometimes loss of P<sub>3</sub> is common to many dasyurid lineages,

a number of plesiomorphic dasyurid taxa show an unreduced  $P_3$  morphology (e.g. *Murexia* and *Sminthopsis* species), and the suggestion of Archer 1982b and Marshall et al. (1990) is not followed here (see below for further discussion).  $P_3$  is missing from the paratype of *M. gadiyuli*, but judging from the alveoli, the tooth was slightly shorter than  $P_2$ . Regarding *N. dicksoni*, Muirhead and Archer (1990) suggest that  $P_3$  was slightly larger than  $P_2$ , based on alveoli length.  $P_3$  is much larger than  $P_2$  for the species of *Thylacinus*.

15. Entoconid morphology: Possession of a distinct entoconid on all lower molars represents the plesiomorphic condition for metatherians. Well developed entoconids are present on the lower molars of *A. tirarensis*, *K. woodburnei*, and *W. tasselli*. Most dasyurids also possess entoconids on at least  $M_{1-3}$ . However, complete loss of the entoconids on all lower molars has been noted for a number of dasyurid taxa, including species of *Sminthopsis*, *Planigale* and *Pseudantechinus*, and the entoconid is lost from  $M_4$  for all but a few plesiomorphic dasyurids (e.g. *Neophascogale*). Entoconids are present and relatively large on all lower molars of *M. gadiyuli*. *Nimbacinus dicksoni* shows a tiny entoconid on  $M_1$ , wear in this region of remaining molars precludes further assessment for this feature. For *T. macknessi* small but distinct entoconids are present on  $M_{1-3}$ , with the entoconid lost on  $M_4$ .  $M_1$  is not known for *T. potens* and the single  $M_2$  is heavily worn. A small entoconid is present on  $M_3$ , but this cusp is lost on  $M_4$ . For *T. cynocephalus* there is no entoconid on  $M_1$  or  $M_4$ . However, small entoconids are present on  $M_{2-3}$ , with that of  $M_3$  the largest.

16. Talonid compression on the anteroposterior axis: Talonids of the lower molars are not compressed on the anteroposterior axis in plesiomorphic marsupials. This is likewise the case for *A. tirarensis* and *K. woodburnei*. The  $M_{3-4}$  talonids of *Wakamatha tasselli* are moderately compressed (these are the only teeth known for this taxon). Dasyurid clades show variable morphology regarding compression of the talonid. Plesiomorphic taxa (e.g. *Neophascogale*, *Murexia* and *Antechinus*), show no compression. Reduction of the talonid on the long axis is, however, common to species of *Sminthopsis*, *Planigale* and derived species of *Dasyurus* and *S. harrisi*. Talonid compression is not a feature of *M. gadiyuli*, *N. dicksoni*, or the species of *Thylacinus*.

17.  $M_4$  talonid morphology: An unreduced  $M_4$  talonid with the entoconid, hypoconid and hypoconulid distinct, is considered the unspecialised marsupial condition by Archer (1976a), Marshall et al. (1990) and Cifelli (1993). *Ankotarinja tirarensis* shows the plesiomorphic condition for this feature. The  $M_4$  talonid of *W. tasselli* is greatly reduced, with only the hypoconid remaining.  $M_4$  talonid morphology is not known for *D. kokuminola* or *K. woodburnei*. However, judging from the large size of the  $M^4$  alveoli for *K. woodburnei*, it is reasonable to conclude that both  $M^4$  protocone, and its occlusal counterpart in the lower dentition (the  $M_4$  talonid) were unreduced. Some plesiomorphic dasyurids retain the unspecialised condition regarding the  $M_4$  talonid (e.g. *Neophascogale*, *Murexia*, *Myoictis*), but most dasyurid taxa show some diminution in both size and cusp number. In carnivorous dasyurids the  $M_4$  talonid is greatly reduced on both the long and transverse axes, and in *S. harrisi* only a single cusp is present. For *Muribacinus gadiyuli* the region of  $M_4$  containing the hypoconulid is broken away, but a small entoconid and hypoconulid are clearly discernible on the remaining lingual portion of the tooth.  $M_4$  talonid morphology is unknown for *N. dicksoni*. For *T. macknessi* the  $M_4$  talonid is reduced on the condition of plesiomorphic metatherians, but still retains a hypoconid and hypoconulid. Both *T. potens* and *T. cynocephalus* show a single cusp only on  $M_4$ , the hypoconid. Although the  $M_4$  talonid of both taxa is considerably reduced neither shows

transverse compression to the degree apparent in many specialised dasyurid taxa. Unique to the species of *Thylacinus* among dasyuromorphians, and possibly marsupial carnivores generally, is the morphology of the posterior shearing crest on the lower molars including  $M_4$ , with the protoconid and hypoconid connected by union of the postprotocristid and cristid obliqua (Ride, 1964a).

#### DISCUSSION

*Paraphyly and the Dasyuridae*.—Before a treatment of the relationship of *M. gadiyuli* to other dasyuromorphians is presented, some issues of fundamental concern regarding dasyuromorphian phylogeny must be considered. The unravelling of ordinal and familial level relationships for dasyuromorphians, especially regarding the distinction of synapomorphies based on cranial and dental features, has proven problematic for all students of the field (Ride, 1964a; Aplin and Archer, 1987; Marshall et al., 1990; Szalay, 1994). Of particular interest here, are questions centering on the relationships of dasyurids and thylacinids. At the crux of this issue has been the difficulty in defining the Dasyuridae on morphological grounds. Regarding dental evidence (the only evidence relevant for *M. gadiyuli*), only one putative dasyurid synapomorphy has been consistently advanced for dasyurids, a “tendency” to reduce  $P_3$  (Tate, 1947; Archer, 1982a,b; 1984; Marshall et al., 1990). The phylogenetic value of this feature is eminently debatable. A number of dasyurid taxa do not show  $P_3$  reduction (some species of *Sminthopsis*, *Murexia*, and *Ningau*). Application of the term synapomorphic implies that diminution of  $P_3$  was a character shown by the common ancestor of all dasyurids. Strong contradictory evidence confronts this proposal. Firstly, it requires the consideration of  $P_3$  reduction as an underlying synapomorphy (sensu Saether, 1983; 1986), i.e., “. . . close parallelism as a result of inherited factors within a monophyletic group causing incomplete synapomorphy” (Saether, 1983 p. 343). The use of underlying synapomorphy in phylogenetic analysis is strongly criticised by a number of authors (Farris, 1986; Foley et al., 1994). If  $P_3$  reduction is not used in this sense then it can only be regarded as synapomorphic for the Dasyuridae if  $P_3$  reductions in the above taxa are considered as reversals to a plesiomorphic state. As a mounting body of morphological and molecular evidence now places the Sminthopsinae as the plesiomorphic sister clade to all other extant dasyurids (Kirsch et al., 1990; Krajewski et al., 1993; Krajewski et al., 1994), this position is difficult to defend. Secondly, reduction or loss of  $P_3$  has evidently occurred independently within several marsupial carnivore lineages including some didelphids (Goin, 1993), borhyaenoids (Marshall, 1977), and at least three dasyurid genera (*Ningau*, *Planigale*, and *Antechinus*) (Archer, 1976a; Ride, 1964b). Functionally this trend is most easily explained as a facilitator of brachycephalisation, permitting retraction of the canines closer to the point of maximum bite force in the tooth row, and increasing torsion resistance in the skull (Covey and Greaves, 1994). Alternatively, Russel et al. (1995) show that premolar loss need not correlate with shortening of the face, and demonstrate that loss of  $P_2$  in *Lynx* may be a phenomenon associated with changing proportions within the deciduous tooth row. Whether or not this latter suggestion might apply to marsupial clades requires further investigation. Ultimately, the widespread distribution of premolar reduction and loss among unrelated taxa further diminishes its phylogenetic value.

The plesiomorphic nature of dental and cranial features for the Dasyuridae has led many investigators to consider the taxon as basal to the thylacinid and myrmecobiid clades (Szalay, 1994). However, the monophyly of extant dasyurids has not been seriously questioned in recent times, and all molecular studies



have concurred on this issue (Baverstock et al., 1982, 1990; Harding, 1982; Young et al., 1982; Kirsch, et al., 1990; Krajewski et al., 1992, 1993, 1994; Westerman and Woolley, 1990, 1993). In addition all molecular studies for the Dasyuromorphia which have included *T. cynocephalus* have placed the taxon outside of the Dasyuridae (Lowenstein et al., 1981; Sarich et al., 1982; Thomas et al., 1989; Krajewski et al., 1992). In a multidisciplinary analysis of suprafamilial relationships for marsupials, Luckett (1994) notes that *T. cynocephalus* was plesiomorphous relative to known dasyurids for most molecular based characters used in his study. This evidence implies a relatively recent origin for the modern dasyurid radiation. An argument first proposed by Archer (1982a). This position is passively supported by the fossil record, with all pre-Pliocene "dasyurid" taxa identified largely on the basis of shared plesiomorphies, and none showing unequivocal evidence of relationship with modern taxa. Archer (1982a) very tentatively suggests a possible relationship between the early Miocene *W. tasselli* from central Australia and the species of *Sminthopsis*, and Van Dyck (1989) postulates that a relationship between an un-named Miocene taxon from Riversleigh and the species of *Antechinus* is likely. Wroe (in press, a) considers the possibility that a very small early-late Miocene taxon may share affinity with the species of *Planigale*.

A clear consequence here is the implication of paraphyly for the Dasyuridae as previously recognised. For the palaeontologist the situation is daunting. Without the advantage of molecular data plesiomorphic fossil dasyurids cannot be identified as such, on dental evidence alone, as no reliable dental synapomorphies currently define the family. It is proposed here (pending the identification of reliable dental synapomorphies for the Dasyuridae), that fossil dasyuromorphian taxa represented solely by dental material should not be included within the Dasyuridae unless they show unambiguous synapomorphies linking them with known dasyurid clades. Where fossil dasyuromorphian taxa can not be clearly assigned to the modern dasyurid radiation the following options are available. Fossil dasyuromorphian taxa may be considered as Dasyuromorphia *incertae sedis*, placed within one of the remaining dasyuromorphian taxa (Thylacinidae, Myrmecobiidae) where justified by the demonstration of unifying derived characters, or, if evidence is sufficient, they might be placed within a South American clade. Alternatively, fossil taxa may be placed in a new dasyuromorphian taxon where derived characters are present that bar allocation to recognised taxa, and these apomorphies are of a degree warranting the erection of a new family. In accordance with this line of reasoning it is proposed that the following fossil taxa be considered Dasyuromorphia *incertae sedis*; *A. tirarensis*, *K. woodburnei*, *D. kokuminola*, and *W. tasselli*. None of these taxa possess synapomorphies that unambiguously unite them with any known dasyurid clade, or dasyuromorphian family. However, each show at least some of the dental synapomorphies considered by Marshall et al. (1990) to ally basal australidelphians (small twinned stylar cusps in the "C" position, a V-shaped centrocrista, and development of stylar cusp D), and dasyuromorphians (elongation of M<sup>4</sup> preparacrista, and reduction of talonids relative to trigonids). *Dasylyrinja kokuminola*, and *W. tasselli* are moderately derived dasyuromorphians compared to *A. tirarensis* and *K. woodburnei*. *Dasylyrinja kokuminola* shows features associated with carnassialisation in both derived dasyurids and thylacinids (e.g. postmetacrista hypertrophy, protocone reduction), but on these characters alone could be included within either clade, and assignment to either family on the basis of a single tooth is not supportable. For *W. tasselli* the degree of M<sub>4</sub> talonid reduction is otherwise found only in some modern dasyurid taxa among dasyuromorphians. Archer (1982a) suggests that *W. tasselli* may form part of the *Sminthopsis* radiation, sharing

hypocristid-entoconid contact with *Sminthopsis crassicaudata* in particular, and retention of a large P<sub>3</sub>, and transverse hypocristids/metacristids with members of this subfamily in general. However, these last two characters are possible plesiomorphies, and hypocristid entoconid contact is found in at least one bandicoot species (Muirhead personal communication). In light of new material from Miocene Riversleigh another phylogenetic possibility now warrants consideration. *Wakamatha tasselli* shares the following features with the most plesiomorphic peramelemorphian described to date, *Yarala burchfieldi* (Muirhead and Filan, 1995); transverse hypocristids, extreme transverse compression of M<sub>4</sub> talonid, very well developed antero-buccal cingulids, and very low, indistinct hypoconulids. Polarity decisions regarding the first three of these characters are equivocal, particularly given the extreme divergence of opinion regarding peramelemorphian origins (Hall, 1987; Retrieff et al. 1995; Springer et al., 1994). However, the very low-crowned hypoconulid morphology in *W. tasselli*, is considered synapomorphic for bandicoots (Muirhead and Filan, 1995). Additionally, *W. tasselli* shows a condition intermediate between dasyuromorphians and bandicoots for another peramelemorphian synapomorphy, lingual placement of the hypoconulid. On the very limited evidence available at present, *W. tasselli* can only be placed within the Dasyuridae on the basis of shared plesiomorphies, and from a cladistic perspective it might be argued that a basal peramelemorphian position is more supportable. At present, evidence for either argument is relatively weak.

The question of dasyurid paraphyly has been addressed by two previous authors regarding the most plesiomorphic Australian taxon described to date, *A. tirarensis*. Although accepted as a dasyurid by most investigators (Archer, 1976b; Marshall et al., 1990), *A. tirarensis* has been formally classified as a peradectid by Reig et al. (1987; p. 18, 76, 81), and is considered to show distinctly microbiotheroid features by Marshall (1987, p. 143). Characters thought to demonstrate peradectid affinity for *A. tirarensis* by Reig et al. (1987; p. 18) are "... similar-sized paracones and metacones, a little developed metastylar spur, presence of well-developed conules, unreduced protocones, and uncompressed trigonids with unreduced metaconids." Marshall (1987) does not formally postulate a relationship between *A. tirarensis* and any South American taxa, but does consider similarities between *A. tirarensis* and plesiomorphic microbiotheriids. The taxon Marshall (1987; p. 143) compares with *A. tirarensis*, specifically *Mirandatherium*, is characterised for the lower dentition, by "... trigonids moderately elevated above talonids, M<sub>2-4</sub> (M<sub>1-3</sub> here) talonids distinctly basined and wider than trigonids, and M<sub>5</sub> (M<sub>4</sub> here) reduced relative to M<sub>4</sub> (M<sub>3</sub>)." For the upper dentition features of interest are "... stylar shelf moderately developed, centrocrista nearly rectilinear, stylar cusps B and D moderately developed and subequal in size, cusp C present but smaller than stylar cusps B and D, ectoflexus on M<sup>4</sup> moderately developed."

Whilst the plesiomorphic nature of *A. tirarensis* is beyond question, it is considered here that formal, or informal inclusion of this taxon within any plesiomorphic South American clade is currently untenable. Five of the eight features forwarded by both authors are based on upper molars for *A. tirarensis*, of uncertain homology. Archer (1976b), in the original description, considered these teeth as "probably" M<sup>2-3</sup>, but indicated that they could represent M<sup>1-2</sup>. A number of the features used above to demonstrate a relationship between *A. tirarensis* and plesiomorphic South American taxa are no less derived in *A. tirarensis* than in some plesiomorphic extant dasyurids, such as *Murexia* and *Neophascogale* (e.g., well developed conules, uncompressed trigonids, and unreduced metaconids). Aplin and Archer (1987), concerning the question of *Ankotarinja-Miran-*

*datherium* affinity, suggest that common features might well be symplesiomorphies and therefore of no phylogenetic value. Furthermore as noted by Marshall (1987; p. 143), *A. tirarensis* shows apomorphies not present in plesiomorphic microbiotheriids including increased paracrista size and "... para- and metcones more subequal in size." A final factor signalling the need for caution here is the considerable geographic and temporal distance separating the late Oligocene *A. tirarensis* from the South American taxa considered by Reig et al. (1987) or Marshall (1987).

In short, *A. tirarensis* can not be confidently placed within any South American clade, nor can it be assigned to the Dasyuridae on the basis of known material, as it is plesiomorphic for all known characters, no synapomorphies define the family, and it can not be placed within any more derived dasyurid clade. *A. tirarensis* does show two synapomorphies determined by Marshall et al. (1990) to unite taxa within the Australidelphia (small twinned stylar cusps in the "C" position, and a V-shaped centrocrista) and at least one synapomorphy for the Dasyuromorphia (reduction of talonids compared to trigonids). On the basis of these synapomorphies, and geographic and temporal position, it is proposed here that *A. tirarensis* be considered *Dasyuromorphia incertae sedis*. A like argument applies to the following pre-Pliocene fossil dasyuromorphian taxa: *Keeuna woodburnei*, *Wakamatha tasselli*, and *Dasyurinja kokumina*.

**The phylogenetic position of *M. gadiyuli*.**—*Muribacinus gadiyuli* shares six apomorphies with thylacinids (reduction of stylar cusp B, stylar cup D, anterior cingula on upper molars, protocones and metaconids, and approximation of paracones and metacones). Each of these characters are associated with carnassialisation. For each of these characters *M. gadiyuli* is less derived than all thylacinids. Concerning all remaining characters *M. gadiyuli* is either plesiomorphic compared to all other thylacinids, or, symplesiomorphic with *N. dicksoni* (relative length of paracristae and postmetacristae, and postmetacristae orientation).

Features shared by *M. gadiyuli* and thylacinids are also found in some specialised dasyurids (e.g. *Dasyercus*, *Dasykulata Dasyuroides*, *Dasyurus*, *Sarcophilus*), excepting the nature of M<sup>3</sup> stylar cusp D reduction. However, the hypothesis that *M. gadiyuli* is structurally ancestral to, or included within a specialised dasyurid clade is rejected for the following reasons. M<sup>3</sup> stylar cusp D morphology in *M. gadiyuli* is more derived than for any dasyurid taxa excepting *S. harrisii*, in being further reduced. Additionally, two features which correlate with M<sup>3</sup> stylar cusp D reduction in all known carnivorous dasyurid taxa are not apparent in *M. gadiyuli*, appression of stylar cusp D with the metacone, and anterior placement of the cusp. Neither of these features in *M. gadiyuli* preclude affinity with thylacinids, which are characterised by stylar cusp D reduction without increased proximity to the metacone, or posterior placement of the cusp. The differential between stylar cusp D reduction and other characters associated with carnassialisation (e.g. protocone and metaconid reduction, anteroposterior alignment of principle shearing crests) distinguishes thylacinids from carnivorous dasyurid clades, with the rate of diminution for this cusp greatly advanced over that of other characters in *M. gadiyuli*. Regarding diminution of both the M<sup>1-4</sup> protocones and M<sub>2-4</sub> metaconids, and the appression of the paracones and metacones, *M. gadiyuli* is apomorphic on the condition shown by all carnivorous dasyurids (or any other dasyurid clade) excepting *D. maculatus* and *S. harrisii*.

Monophyly for the species of *Dasyurus* is widely accepted (Archer, 1982a; Van Dyck, 1987), with the possible exception of the Pliocene fossil taxon *D. dunmalli* (Archer, 1982a; Wroe, in press b), and a well demonstrated structural morphocline links

the carnivorous dasyurids *D. maculatus* and *S. harrisii* through the Late Tertiary species of *Glaucodon balleratus* and *Sarcophilus moornaensis* (Ride, 1964; Crabb, 1982; Archer, 1982b). Monophyly for *D. maculatus* and *S. harrisii* has been suggested by both morphological and molecular evidence (Archer, 1982b; Kirsch et al., 1990 and Krajewski et al., 1992; 1993 and 1994).

Alliance of *M. gadiyuli* with the *Dasyurus-Sarcophilus* clade, or any other carnivorous dasyurid taxon would require acceptance of multiple reversals to a plesiomorphic state for either *M. gadiyuli* or the dasyurid clade with which a relationship is postulated; i.e., either, the six characters for which *M. gadiyuli* is more derived than *Dasyuroides*, *Dasyercus* and the less specialised species of *Dasyurus* have been reversed in these dasyurid lineages, with five (characters 2,5,6,9, and 11) subsequently reacquired in *D. maculatus* and *S. harrisii* or, the eleven characters (1, 4, 7, 8, 10, 12, 13, 14, 15, 16, and 17) for which *M. gadiyuli* is less derived than all carnivorous dasyurids represent reversals to a plesiomorphic state in *M. gadiyuli*.

Three other phylogenetic alternatives must be considered here. That *Muribacinus gadiyuli* may be independently derived on stem dasyurine stock, or, on some other unknown plesiomorphic dasyurid taxon can not be excluded. A third possibility is that *M. gadiyuli* represents part of a hereto unknown dasyuromorphian clade. In the light of firmly established antiquity for the Thylacinidae (well in excess of 25 ma, (Muirhead, 1992)), and mounting evidence for a recent origin for extant dasyurid clades (Aplin et al., 1994; Archer, 1982b; Baverstock et al., 1990; Westerman et al., 1990; Krajewski, et al., 1992,1993,1994; Kirsch and Springer, 1993) the first two hypotheses are considered unlikely. The third scenario, that *M. gadiyuli* formed part of a previously unknown discrete dasyuromorphian radiation is rejected here, as no aspect of the taxon's known morphology indicates family level distinction. Of course, this possibility can not be completely dismissed, without the discovery of more complete material.

Within the Thylacinidae *M. gadiyuli* is the most plesiomorphic thylacinid described to date, being less derived for all characters than any other thylacinid taxon. In terms of overall similarity *M. gadiyuli* is closest to *N. dicksoni*, but as no unequivocal synapomorphies unite the two taxa to the exclusion of other thylacinids a special relationship can not be secured in a cladistic scheme (Allmon, 1992).

With the description of *M. gadiyuli* some revision is required for the diagnosis of the Thylacinidae. In particular the standing of two thylacinid synapomorphies recognised by previous authors is questioned; the posterior position of the infraorbital foramen (Muirhead and Archer, 1990) and possession of a P<sub>3</sub> larger than P<sub>2</sub> (Bensley, 1903; Stirton, 1961 and Muirhead and Archer, 1990).

As noted above, only in *T. cynocephalus* can the presence of this foramen on the jugal-maxilla symphysis be confirmed, although it seems likely that this is also the case for the other species of *Thylacinus*. For *N. dicksoni*, however, the placement of the infraorbital foramen relative to the jugal-maxilla is less certain, with part of the external component broken away from the type specimen. Relative to the tooth row this foramen is above the juncture of M<sup>2</sup> and M<sup>3</sup> in *N. dicksoni*, where it is also commonly found in dasyurids. Interestingly, the most derived carnivorous dasyurid, *S. harrisii*, also shows a posteriorly placed infraorbital canal. Convergence for *S. harrisii* and the species of *Thylacinus* in this character may be related to size and/or advanced carnassialisation.

From the P<sub>3</sub> alveolus it is probable that P<sub>3</sub> was slightly smaller than P<sub>2</sub> in *M. gadiyuli*. It is considered here that a P<sub>3</sub> slightly smaller than P<sub>2</sub> on the anteroposterior and dorsoventral axes is plesiomorphic for thylacinids and dasyurids. Consequently, the

extremely large P<sub>3</sub> shown by the species of *Thylacinus* is interpreted as synapomorphic for *Thylacinus*, but not the Thylacinidae. P<sub>3</sub> hypertrophy is considered a synapomorphy of derived borhyaenids by Marshall et al. (1990), although the functional value is unclear. The extraordinary degree of convergence in borhyaenids and the species of *Thylacinus* for many characters associated with a carnivorous habit (Archer, 1976a,b; 1982b; Marshall, 1977), indicates that P<sub>3</sub> enlargement for both lineages may also correlate with similar adaptive regimes.

#### PALEOBIOLOGY

*Muribacinus gadiyuli* is the smallest thylacinid described to date (Table 1), comparable in size to *D. maculatus* among extant dasyuromorphians. *Dasyurus maculatus* is the largest of *Dasyurus* species (1.6–4.0 kg (Jones, 1993)) and a powerful carnivore, with medium-sized mammals constituting the bulk of prey animals taken by adults (Fleay, 1948; Belcher, 1993). The dentition of *M. gadiyuli* lacks the very robust protoconids and relatively advanced brachycephalisation that aid *D. maculatus* in dispatching prey sometimes as large or larger than itself. It is likely that *M. gadiyuli* was more restricted in the upper size range of prey taken. At the lower end of the scale, *M. gadiyuli* does not appear well adapted to an insectivorous habitus, with reduction of features common to dasyurid insectivores and less derived *Dasyurus* species (e.g. well developed stylar cusps, protocones/talonid basins, and metaconids). This evidence suggests that *M. gadiyuli* concentrated on small vertebrates as prey items. A rainforest environment has been suggested for the early to middle Miocene of Riversleigh (Archer et al., 1994) and an arboreal niche for *M. gadiyuli* is certainly possible, although purely hypothetical pending the identification of post-cranial material.

With the description of *M. gadiyuli* the tally of thylacinid species now stands at five. Three of these species are known from the Miocene of Riversleigh, with the description of at least two more thylacinids from Riversleigh deposits imminent (Muirhead, in press). This diversity contrasts strongly with that of dasyurid taxa from the same deposits. No taxa from the late Oligocene or Miocene deposits of Riversleigh have been unambiguously assigned to the Dasyuridae, although Archer (1982a) describes a probable phascogaline upper molar from D Site, Van Dyck (1989) notes similarities between a single "dasyurid" dentary from Panoramia Site and species of *Antechinus*, and Wroe (in press, b) suggests possible affinity between a tiny middle to late Miocene species from Encore Site and *Planigale*. However, as shown by Van Valkenburgh (1988; 1994) in studies of North American predatory mammals, major phylogenetic variation over time does not necessarily produce wide variation in morphological diversity. Whilst the Miocene radiation of dasyurids into large carnivorous niches may have been constrained by a pervasive thylacinid presence, small bandicoots occupied insectivorous positions (Muirhead, 1994). Although dasyurids appear to have been minor players in the ecology of Riversleigh's Miocene habitats, the five known thylacinid species may have competed with several other carnivorous taxa, including medium to large sized marsupial lions (Archer et al., 1994), two species of giant carnivorous rat-kangaroo (Archer and Flannery, 1985; Wroe and Archer, 1995; Wroe, 1996), madtsoiid snakes (Scanlon, 1992), and terrestrial crocodiles (Willis, 1995). The finding of a large number of medium to large carnivorous mammalian taxa present in Miocene Riversleigh deposits contradicts Flannery's (1991, 1993) proposal that restricting abiotic factors, such as inherently nutrient deficient soil, have limited the diversification of marsupial carnivores in Australasia over the last twenty million years.

Disparate diversity during the Miocene for thylacinids and dasyurids has clearly been reversed in Pliocene to present times. The radiation of dasyurid lineages into niches for small to medium sized carnivores may have been facilitated passively by the widespread extinction of thylacinids following late Miocene climatic change (Martin and McMin, 1994), or actively through competitive exclusion.

It is possible that the acquisition of specialisations in the auditory region of dasyurids (discussed below) ultimately gave the clade an adaptive edge over thylacinids. As noted by Heard and Hauser (1995), such "key innovation" hypotheses can only be supported through evidence of ecological mechanism and comparative analysis. The independent expansion and evolution of a floor to the middle ear in numerous mammalian lineages, including small insectivorous clades, demonstrates an almost universal adaptive advantage for this character (Novacek, 1977). Among dasyuromorphians differences in the auditory region of *T. cynocephalus* and extant dasyurids are considerable (Archer, 1976c). The test of any hypothesis for advantage imparted by the advent of evolutionary novelty will require the investigation of thylacinid and dasyurid basicranial material from pre-Pliocene sites.

The presence of apomorphies in the auditory region in all dasyurids, may also provide support for the contention that known carnivorous dasyurids are relatively recent descendants of a small insectivorous taxon. For small nocturnal animals a large middle ear cavity maybe of great importance for predator avoidance (Webster and Webster, 1975, 1980). Because an absolute theoretical minimum volume exists for the middle ear to enable efficient low frequency hearing, small taxa are likely to possess relatively large, fully enclosed auditory bulla (Webster, 1966). Archer (1976c, p. 314) notes that differences between thylacinids and dasyurids are "marked" regarding periotic morphology. A feature common to all dasyurids is development of the periotic hypotympanic sinus, an important contributor to the floor of the middle ear. This sinus is not present in *T. cynocephalus*. A lack of specialisation in this region for thylacinids may reflect less rigorous selective pressure, with large carnivores being both less susceptible to predation, and unaffected by the lower limit on inner ear volume. The periotic hypotympanic sinus may constitute a dasyurid synapomorphy. This suggestion is complicated by the possession of a very poorly developed periotic hypotympanic sinus in *M. fasciatus*. However, *M. fasciatus* clearly differs from all dasyurids in the degree of posterior extension of the alisphenoid and contribution of the mastoid part of the petrosal to the floor of the middle ear (Archer, 1976c). Archer and Kirsch (1978) and Archer (1982) observe that the petrosal part of the periotic does not form a tympanic wing in numbats as it does in all dasyurids. Perhaps the most convincing feature previously used to unite the dasyurid and myrmecobiid clades, development of a foramen pseudovale and loss of the foramen ovale (Archer, 1984), has recently been considered symplesiomorphous by Case (1989) and Muirhead (1994). Furthermore, the only molecular study including representatives of all three dasyuromorphian families placed *M. fasciatus* outside of thylacinids and dasyurids, based on albumin data (Lowenstein et al., 1981). In the light of this evidence independent derivation of a periotic hypotympanic sinus in dasyurids and myrmecobiids is a distinct possibility.

#### CONCLUSIONS

*Muribacinus gadiyuli* is a plesiomorphic thylacinid possessing the following synapomorphies for the family: some reduction of all stylar cusps, and extreme reduction of M<sup>3</sup> stylar cusp D without concomitant anterior placement or appression with the metacone, relatively uniform diminution of the metaconids on

$M_{1-4}$ , reduction of anterior cingula on the upper molars, reduction of protocones, and approximation of the paracones and metacones.

Extant dasyurids represent a monophyletic clade on the basis of cranial and molecular data. However, character analysis shows that the Dasyuridae are not united by any reliable dental synapomorphies advanced to date, and that dental characters of plesiomorphic extant dasyurids (e.g. *Murexia*, *Neophascogale*) were probably present in the common ancestor of both extant dasyurids and thylacinids (and possibly myrmecobiids). The phylogenetic position of some fossil dasyuromorphians known from dental material only is uncertain within this context, and two late Oligocene "dasyurids", *A. tirarensis* and *K. woodburnei* are structurally ancestral to all other known dasyuromorphian clades (with the possible exception of *M. fasciatus*), possibly forming metasppecies (sensu Archibald, 1993). Clearly paraphyly is indicated for the Dasyuridae as recognised by most previous authors. Whilst paraphyletic classification is accepted by many phylogenetic systematists (Bryant, 1994), Schwenck (1994) shows that such classifications may lead to false generalisations and incorrect phylogenetic inference. It is suggested here that *A. tirarensis*, *K. woodburnei*, *W. tasselli*, and *D. kokuminola* be considered Dasyuromorphia *incertae sedis* until less equivocal dental synapomorphies are identified for the Dasyuridae, or basicranial material for these taxa is discovered providing unambiguous evidence of relationships.

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