

CLADISTIC ANALYSIS OF DASYUROMORPHIAN (MARSUPIALIA) PHYLOGENY USING CRANIAL AND DENTAL CHARACTERS

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Dasyuromorphian relationships were investigated using cladistic analysis for 24 species using 77 cranial and dental features. Among the 7 extinct taxa used were 6 recently described fossil species, each well represented by cranial and dental material (3 ameridelphians, 1 peramelemorphian, and 2 dasyuromorphians). Monophyly for the Dasyuromorphia and several clades widely recognized therein is supported, but in many instances, relationships among extant dasyurids departs greatly from general consensus. Where congruence with previous investigations is evident, few taxa are united by unique synapomorphies within Marsupialia. Many clades are united by combinations of locally derived features only. Bootstrap and Bremer support is weak for most clades. Thus, although supported by cladistic analysis, the status of many synapomorphies identified in the course of this study are tentative. However, for some groups, notably Dasyuridae and a dasyurid clade inclusive of all modern subfamilies, the synapomorphic nature of some derived features appears to be robust, even where they also are present in some outgroup taxa. This argument applies to shared apomorphies of the basicranium in particular. No potential sister taxon to Dasyuromorphia is favored. The case for australidelphian and microbiotheriid affinity of some American and Antarctic fossil taxa was considered to be highly equivocal.

Key words: Ameridelphia, Australidelphia, Dasyuridae, Dasyuromorphia, *Badjcinus*, *Barinya*, fossil, Myrmecobiidae, phylogeny, Thylacinidae

A rapidly expanding body of both paleontological and molecular data has shed new light on Australian marsupicarnivore phylogeny (Cifelli and Muizon 1998; Kirsch et al. 1991, 1997; Krajewski et al. 1996, 1997a, 1997b; Marshall and Muizon 1995; Muirhead 1992, 1997; Muirhead and Wroe 1998; Muizon 1994, 1998; Muizon et al. 1997; Springer et al. 1994, 1997; Wroe 1997b, 1998, 1999a, 1999b). Prior to description of the unallocated Eocene taxon

Djarthia murgonensis (Godthelp et al. 1999), all Australian marsupicarnivores had been placed in a single order, Dasyuromorphia. Following publication of molecular and morphological results in the early 1980s (Lowenstein et al. 1981; Szalay 1982), long-running controversy over the possible borhyaenoid affinity of thylacinids has been laid to rest, with all subsequent authors treating Dasyuromorphia as monophyletic. This position has been reaffirmed by many subsequent investigators (Kra-

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jewski et al. 1997a; Muirhead and Wroe 1998; Thomas et al. 1989; Wroe 1996).

Widely accepted as the most generalized elements of the Australian marsupial radiation, dasyuromorphians, especially dasyurids, have figured prominently in discussions of Australian marsupial origins. Alternatively, Aplin and Archer (1987) and Wroe (1999a) expressed a contradictory view with respect to Dasyuridae. The position of *D. murgonensis* relative to dasyuromorphians is unclear. This new species, less derived for almost all dental features than any other Australian marsupial, may represent a basal element of Dasyuromorphia. However, given that *D. murgonensis* also is plesiomorphic within Marsupialia for most known features, it actually may be didelphimorphian (Godthelp et al. 1999). The relationship of dasyuromorphians to other marsupials also remains controversial. Possible sister taxa to Dasyuromorphia proposed in previous investigations include Didelphidae (Archer 1976b; Bensley 1903), Peramelemorphia (Kirsch 1977), Microbiotheriidae (Szalay 1994), and Microbiotheriidae plus Diprotodontia plus Notoryctidae (Kirsch et al. 1997). Marshall et al. (1990) and Woodburne and Case (1996) suggested a clade inclusive of all non-dasyuromorphian Australian marsupials as the sister clade to Dasyuromorphia. Those same authors proposed that the Paleocene Bolivian species *Andinodelphys cochabambensis* is the sister taxon to all Australian marsupials. The various interpretations of higher level phylogeny for these taxa have been reviewed in several recent papers (Aplin and Archer 1987; Kirsch et al. 1997; Luckett 1994; Marshall et al. 1990; Springer et al. 1997). Microbiotherians are central to the formulation of many hypotheses on Australian marsupial evolution and thus require special attention. In particular, efforts to link fossil microbiotherians and other American taxa with the Australian marsupial radiation demand more detailed consideration. We reviewed the literature bearing on the origins and phylogeny of Dasyuro-

morphia and performed a cladistic analysis using morphological features and new fossil material.

Possible fossil microbiotherians.-Microbiotherians from South America, Antarctica, and Australia have been considered the sister "on to dasyuromorphians (Szalay 1994), diprotodontians (Kirsch et al. 1997), the entire Australian marsupial radiation plus *Andinodelphys cochabambensis* (Marshall et al. 1990; Woodburne and Case 1996), and all other marsupials (Hershkovitz 1992, 1995, 1999). Of particular relevance here are proposals of monophyly for the ?microbiotheriid *Mirandatherium*, the Australian taxon *Ankotarinja tirarensis* (Marshall 1987), and *A. cochabambensis* and all Australian marsupials, a position argued by Marshall et al. (1990) and Woodburne and Case (1996) but rejected by Muizon (1992) and Muizon et al. (1997). Other pertinent issues include the possible microbiotherian affinities of fossil material from the Eocene deposits of Murgon (Archer et al. 1993; Kirsch et al. 1997) and Seymour Island, Antarctica (Goin and Carlini 1995; Marenssi et al. 1994).

Inclusion of *Mirandatherium* within Microbiotheria was formally recognized by Marshall (1987:148), who stated that this taxon is "clearly a member of the subfamily Microbiotheriinae." *Eomicrobiotherium*, *Pachybiotherium*, and a pediomyid clade, which included *Monodelphopsis*, also were treated as microbiotheriids. Marshall et al. (1990) likewise treated pediomyids and *Pachybiotherium* as microbiotherians but reinterpreted *Mirandatherium* as a didelphine after reconsidering the state of 1 character, centrocrista straight or linear (Godthelp et al. 1999). In their cladogram, Marshall et al. (1990:438) portrayed *A. cochabambensis* as monophyletic with the Australian marsupial clade. *Monodelphopsis*, a pediomyine under Marshall's (1987) classification, was rediagnosed as a microbiotheriid by Marshall et al. (1990). Previously, pediomyids had been placed as the sister taxon to Borhyaenoidea (Marshall

1977). Phylogenies presented by Marshall (1987) and Marshall et al. (1990) contained many clades that appeared to be based, at least in part, on presence of shared plesiomorphies or overall similarity (Godthelp et al. 1999; Muizon 1992). For example, presence of a linear centrocrista was used as part of the basis for treating *Ankotarinja tirarensis* as a possible sister taxon to *Mirandatherium* by Marshall (1987), but the same author treated that feature as a marsupial plesiomorphy. Moreover, in our view, the centrocrista of *A. tirarensis* is V-shaped. We consider other proposed synapomorphies to be highly equivocal. Marshall et al. (1990:442) listed 4 possible shared derived features to support their concept of Microbiotheria. None of these features are exclusive to Microbiotheria (sensu Marshall et al. 1990). Some characters are extremely labile and have appeared independently in several marsupial clades (e.g., reduction of the styler shelf; styler cusp B reduced, with D the largest cusp). Of the 13 proposed anatomical synapomorphies uniting Australidelphia (sensu Marshall et al. 1990), 2 are marsupial plesiomorphies (i.e., entoconid and hypoconid large, subequal in size; molars semibrachyodont). Others traits are locally derived dental features, often found in many other marsupicarnivore clades (e.g., subequal styler cusps B and D; talonid wider than trigonid on M2-3; cristid obliqua meets rear of trigonid labial to protocristid notch; entoconid notch weak; upper incisors spatulate shaped).

Godthelp et al. (1999) discussed problems with interpretation of dental data used to support monophyly for the putative australidelphian *Andinodelphys cochabambensis* and Australian marsupials, as suggested by Marshall et al. (1990) and Woodburne and Case (1996), and found those arguments unconvincing, a view shared by Kirsch et al. (1997). Most features used in support of this special relationship are highly mutable among marsupials, some at the intraspecific and even individual level. For example, presence of twinned cusps in the

C position, present in then-known specimens of *A. cochabambensis* and undescribed peramelid material and treated by Marshall et al. (1990) as a possible synapomorphy uniting *A. cochabambensis* and Australian marsupials, was considered a poor basis for the postulation of special relationship (cL Muizon 1992). This skepticism has been vindicated with the discovery of additional specimens of *A. cochabambensis* wherein twinned cusps in the C position are variably present and sometimes present on 1 side of a specimen but not the other (Muizon et al. 1997). Furthermore, from new well-preserved cranial material, it is clear that *A. cochabambensis* is plesiomorphic within Marsupialia for almost all cranial features. The only derived cranial feature identified by Muizon et al. (1997) was considered supportive of a special relationship with 2 other Tiupampan ameridelphians, *Pucadelphys andinus* and *Mayulestes ferox*.

Because Microbiotheriidae (sensu Marshall 1987; Marshall et al. 1990) is not well defined on the basis of dental data, referral of new fossil taxa to this clade should be treated with circumspection. The suggestion that undescribed *Pachybiotherium*-like material from Murgon constitutes evidence for existence of microbiotheriids in Australia (Archer et al. 1993) requires further substantiation. This view is strengthened when it is considered that Microbiotheriidae was defined almost exclusively on the basis of cranial features by Marshall et al. (1990), wherein only 1 dental feature was noted, but *Pachybiotherium*, treated as a microbiotheriid by the same authors, is known only from dental material. Similar problems arise with the classification of other possible fossil microbiotherians. Woodburne and Case (1996:133) regarded *Khasia* from the Paleocene Tiupampa Local Fauna of Bolivia as "completely specialized toward microbiotheres." Proposed synapomorphies supporting the position were "reduction of styler shelf and cusps, styler cusp A reduced versus styler cusps B, C, and D, the

paraconid reduced and positioned anteriorly, the oblique orientation of the protocristid, and the talonid wider than the trigonid." Of those characters, it is unclear as to how 1, i.e., oblique orientation of the protocristid, can be interpreted as suggesting affinity with microbiotheres. This feature is certainly derived within Marsupialia but is not common to *Dromiciops*, *Microbiotherium*, or pediomyids. All of the remaining features are shared with 1 demonstrably nonmicrobiotherian clade, with some features, such as reduction of the styler shelf and styler cusp A relative to other styler cusps, independently derived in many didelphimorphian and dasyuromorphian taxa.

The microbiotherian status of some Early Tertiary Antarctic material also is tenuous. Marenssi et al. (1994) informally and Goin and Carlini (1995) formally referred a partial edentulate dentary from Seymour Island to Microbiotheriidae. That specimen (MLP 88-I-1-1) originally was referred to Didelphimorphia by S. E. Vizcaino et al. (in litt.). Goin and Carlini (1995:205) cited 2 synapomorphies of the dentary, originally presented by Marshall (1982), in support of a microbiotheriid affinity for MLP 88-I-1-1, i.e., "large mental foramen below P, and depth of ramus relatively constant from back to front." A well-developed mental foramen below p2 is present in at least some peramelemorphians (e.g., *Echymipera kalubu*, *Perameles nasuta*), dasyuromorphians (e.g., *Neophascogale lorentzii*, *Dasyurus maculatus*, *Thylacinus cynocephalus*), borhyaenoids (e.g., *Mayulestes ferox*), didelphoids (e.g., *Pucadelphys andinus*), and peradectids (e.g., *Alphadon eatoni*). On the basis of distribution, the phylogenetic value of this feature within Marsupialia is questionable. Given its presence in peradectids, basal representatives of Didelphoidea and Borhyaenoidea, and the undoubted microbiotheriid *Dromiciops gliroides*, it seems likely that this feature 'is plesiomorphic within Marsupialia. The degree of confidence that can be attributed to the 2nd feature is difficult to assess without examining

the specimen. Marshall et al. (1990:438) used neither of these characters to define Australidelphia, Microbiotheria, or Microbiotheriidae in their cladogram.

Although the possibility that some or all of the fossil ?microbiotherian taxa considered above may in fact be microbiotherian can and should not be dismissed, their position remains contentious. Use of these taxa in the construction of phylogenetic and biogeographic scenarios should be qualified.

Previous morphology-based cladistic analyses.—Apart from this study, only 3 investigations have addressed higher level phylogeny of Australian marsupicarnivores using parsimony-based analysis of anatomical data: Kirsch and Archer (1982), Springer et al. (1997), and Rougier et al. (1998). Kirsch and Archer (1982) found that because many anomalous phylogenies were produced, particularly at higher levels, the value of parsimony was called into question. Their study is of particular interest with regard to our own because it represents the only previous anatomy-based investigation that used species as the operational taxonomic unit. Kirsch and Archer (1982) clearly demonstrated that varying the number of taxa included could affect outcomes and inclusion of fossil taxa could significantly impact results. For example, they found that *Thylacinus cynocephalus* formed a monophyletic clade with the South American taxon *Borhyaena tuberata* when no other borhyaenids were included but that support for thylacinid-borhyaenid monophyly disappeared when additional borhyaenids were added. Additionally, they noted that no clades were founded on uniquely derived features; only unique combinations of features and sequences of change served to distinguish taxa in their analyses. Springer et al. (1997) presented both morphology- and molecule-based analyses. Their anatomy-based investigation included diprotodontian, marsupicarnivore, and peramelemorphian taxa, and in further contrast to the work of Kirsch and Archer (1982), they used the family rather than the species as the operational taxo-

onomic unit. Their analysis produced a single most-parsimonious tree with dasyuromorphians plus notoryctids shown as the sister taxon to a clade inclusive of all other living marsupials, a result incongruous with all previous findings. In common with some recent molecular studies, *Dromiciops gliroides* was monophyletic with diprotodontians (Springer et al. 1997). No interordinal relationships were supported by bootstrap values >50%. Most recently, Rougier et al. (1998) presented a cladistic analysis including a wide range of nontherian, eutherian, and metatherian taxa, but only 3 of the 7 orders examined were extant. The results supported monophyly of *D. gliroides* and Dasyuridae. Sister taxa to this clade in decreasing order of relatedness were Didelphidae, *Andinodelphys*, *Pucadelphys*, *Mayulestes*, Borhyaenidae, and a monophyletic clade inclusive of 9 North American and Asian taxa. Elucidation of dasyuromorphian phylogeny was clearly not a prime objective of that analysis (neither thylacinids nor *Myrmecobius* were included), and relationships between dasyurids and non-Australian taxa were not discussed (Rougier et al. 1998). Consequently, we have restricted our comments on those findings. However, their value in determining affinities of Australian marsupicarnivores is limited because only dasyurids were included. As argued by Wroe (1999a, 1999b, in press) and supported by results of the present study, dasyurids, especially the modern subfamilies, constitute a specialized marsupial clade and may have been derived quite recently. Thus, they are unlikely to represent approximations of the "ancestral" Australian marsupial. There are a number of potential synapomorphies, especially in the basicranium, uniting dasyurids and *D. gliroides*. However, to acknowledge these features as synapomorphies uniting these 2 taxa demands that a suite of basicranial plesiomorphies present in thylacinids and myrmecobiids or numerous dental plesiomorphies in *D. gliroides* be consigned to the status of apomorphic reversals to a plesiomorphic condition.

Several possible explanations, including

inappropriate methods of analysis and exclusion of appropriate range of specimens, may account for failure of previous analyses to resolve dasyuromorphian phylogeny. Moreover, the characters themselves may be relatively uninformative, even when analyzed correctly within a cladistic framework. As shown by Kirsch and Archer (1982), inclusion of fossil taxa can significantly affect the outcome of parsimony-based analyses. Aided by access to highly significant new fossil material from Australian and South American deposits, we attempted to give added insight into the question of the evolution of Australian marsupicarnivores.

MATERIALS AND METHODS

Included taxa and scoring of characters.—*Pucadelphys andinus*, the least derived of South American marsupials known from near-complete cranial and dental data (Marshall and Muizon 1995), was treated as the outgroup. Thus, the remaining 6 South American taxa and the peramelemorphians were treated as ingroup taxa to test previous hypotheses of phylogeny. In all, representatives of the following possible sister taxa to Dasyuromorphia were included: Pucadelphyidae, Didelphidae, Mayulestidae, Microbiotheriidae, and Peramelemorphia. Notoryctidae, another potential sister taxon, was not included because extreme specialization of cranial and dental features in this zalambdodont taxon produced a character profile consisting of >70% features that were either unknown or autapomorphic. Novacek et al. (1988) recommended that 30% of the features be scored for robust elucidation of relationships. However, new material representing a possible structurally intermediate notoryctemorphian, recently recovered from Miocene deposits of Riversleigh (M. Gott and M. Archer, in litt.), may be of value in future analyses. Diprotodontians were not included for 2 reasons. This taxon was not suggested as a potential sister to Dasyuromorphia, except as part of a monophyletic clade with *Dromiciops gliroides* (Kirsch et al. 1997), already included in the analysis. Also, the majority of characters, if scored for diprotodontians in the present study, would have constituted autapomorphies. A more detailed character analysis incorporating

extant and new nearly complete fossil diprotodontian taxa is in progress.

Polarity decisions regarding the majority of characters used in the present study were based on previous work. Consequently, detailed treatment was unnecessary except where there has not been general consensus. The character analysis is given in Appendix 1. Species were used as the operational taxonomic unit in this analysis for several reasons. First, the investigator introduces assumptions of phylogeny by using higher taxonomic units. Because the phylogenetic position of many marsupicaniivores is extremely contentious (for some species, this uncertainty extends to the ordinal level), such assumptions may confound the generation of accurate results. Second, because elucidation of relationships among new fossil species was a primary goal, they were treated at the specific level. Third, as observed by Simmons (1993), the enduring legacy of parsimony-based phylogenetic analyses is most likely to be the data. Because higher taxonomic units are certain to be redefined, with taxa added or removed in light of new evidence, data based at this level are sure to become redundant. Moreover, particularly where diverse and speciose taxa represent the subject material few investigators can claim to have studied all species referred to higher clades. These difficulties do not arise where data are tabulated at the specific level. An obvious drawback to the methodology applied here is that all available species could not be included. However, this limitation was overridden by the aforementioned advantages.

Seven South American species (3 fossil and 4 extant) and 17 Australian species (2 fossil, 1 recently extinct, and 14 extant) were included. The American taxa were *Pucadelphys andinus* (Pucadelphyidae), *Andinodelphys cochabambensis* (Pucadelphyidae), *Didelphis marsupialis* (Didelphidae), *Metachirus naudicaudatus* (Didelphidae), *Lestodelphys halli* (Didelphidae), *Mayulestes ferox* (Mayulestidae), and *Dromiciops gliroides* (Microbiotheriidae). Australian taxa were 3 peramelemorphians (*Yarala burchfieldi*, *Echymipera kalubu*, and *Perameles nasuta*) and 14 dasyuromorphians, i.e., *Myrmecobius fasciatus* (Myrmecobiidae), 2 thylacinids (*Thylacinus cynocephalus* and *Badjcinus turnbulli*), and 11 dasyurids. Dasyurid taxa comprised representatives from each of the 4 dasyurid subfamilies recognized in the present study: *Barinya wangala* (Barinyainae), *Sminthopsis crassicaudata*, *S. murina*, and *Planigale maculata* (Sminthop-

sinae), *Murexia longicaudata*, *Phascogale tapoatafa*, and *Antechinus flavipes* (Phascogalinae), and 4 dasyurines (*Neophascogale lorentzii*, *Dasyurus hallucatus*, *Dasyurus maculata*, and *Sarcophilus harrisii*). Only fossil taxa known on the basis of complete or nearly complete cranial and dental material were used. Outgroup taxa were the 3 exceptionally well-preserved Paleocene taxa from the Tiupampa Local Fauna of Bolivia (*P. andinus*, *A. cochabambensis*, and *M. ferox*). Australian fossil taxa included were the Miocene bandicoot taxon *Y. burchfieldi* and the only 2 pre-Pleistocene Australian dasyuromorphians represented by significant cranial material (*B. turnbulli* and *B. wangala*).

Phylogenetic analysis.—The data matrix included 24 taxa (6 fossil, 1 recently extinct, and 17 extant) and 77 characters (44 dental and 33 cranial). Analyses were conducted with PAUP 3.1.1 (Swofford 1993) using 50 replicates, ACCTRAN, and TBR branch swapping (random input order) and with characters unordered. Relative stability of clades was assessed using bootstrap (Felsenstein 1985) and Bremer support (Bremer 1988, 1994) analyses. Bootstrapping was based on 1,000 replicates, and pseudoreplicate bias was reduced by using multiple tree-space searches, with 3 trees sampled per iteration (Colgan et al. 1998; Reid 1996). Bremer support indices were determined by studying suboptimal trees. Because different investigators have offered conflicting opinions regarding character states of some important features, only species that were examined directly by us were included in this study. Dental nomenclature follows Flower (1867) and Luckett (1993) regarding the molar-premolar boundary, such that the adult (unreduced) postcanine cheektooth formula of marsupials is P1-3 and M1-4. Systematic terminology was as used by Wroe (1996, 1997b), adapted from that of Marshall et al. (1990) and Krajewski et al. (1994). Institutional abbreviations are QM (Queensland Museum Fossil), AMNH (American Museum of Natural History), NMHN (Laboratoire de Paleontologie, Museum National d'Histoire Naturelle), and YPBF Pal (Paleontology collection of Yacimientos Petroliferos Fiscales de Bolivia in the Centro de Temologia Petrolera). Material examined included that used by Wroe (1997b) and holotype material of *D. murgonensis* (QMF31458), *B. wangala* (QMF31408), *P. andinus* (YPFB Pal 6105), *A. cochabambensis* (NMHN 8264), and *M. ferox* (NMHN 1249).

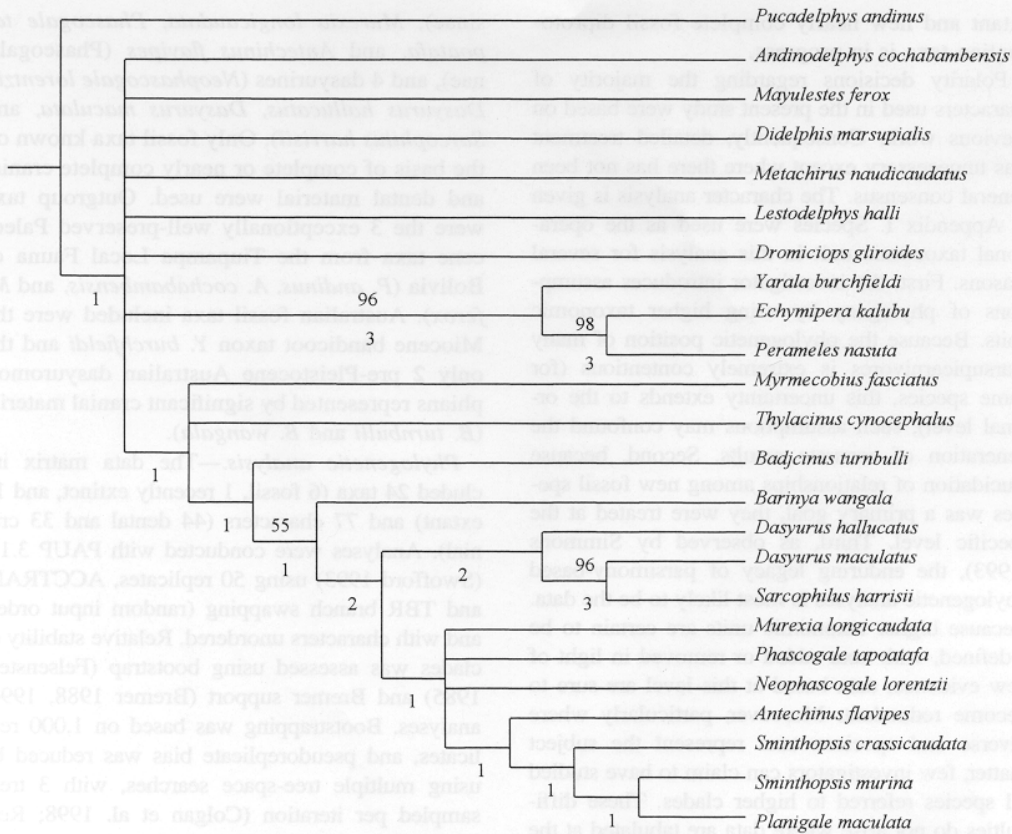


FIG. 1.—Strict consensus of 64 most-parsimonious trees for 24 taxa and 77 dental and cranial characters (length 245, consistency index = 0.4160, homoplasy index = 0.5840, and retention index = 0.6106). Bootstrap values >50% are shown above branches. Bremer support is given below branches.

RESULTS

Sixty-four most-parsimonious trees of 245 steps were produced (excluding uninformative characters, consistency index = 0.4160, homoplasy index = 0.5840, retention index = 0.6106). The strict consensus tree and the bootstrap values and Bremer support indices for resolved nodes are given in Fig. 1. Character state reconstructions for the list of the 64 most-parsimonious trees are given in Appendix II for the nodes shown in Fig. 2. At the ordinal level, only Dasyuromorphia and Peramelmorphia formed natural groups (Fig. 1). No single outgroup taxon emerged as a clear sister to Dasyuromorphia. Within Dasyuromorphia, the positions of *Myrmecobius*

fasciatus and *Thylacinus cynocephalus* were unresolved with respect to a clade comprising the thylacinid *Badjcinus turnbulli* and dasyurids. *Barinya wangala* was the sister taxon to a monophyletic clade inclusive of all extant dasyurids. Among extant subfamilies of dasyurids, only Sminthopsinae was monophyletic. The taxon--character matrix is given in Table 1.

DISCUSSION

Our cladistic treatment of morphological features provided resolution for dasyuromorphian phylogeny that, in at least some important respects, agrees with many previously published phylogenies. However,

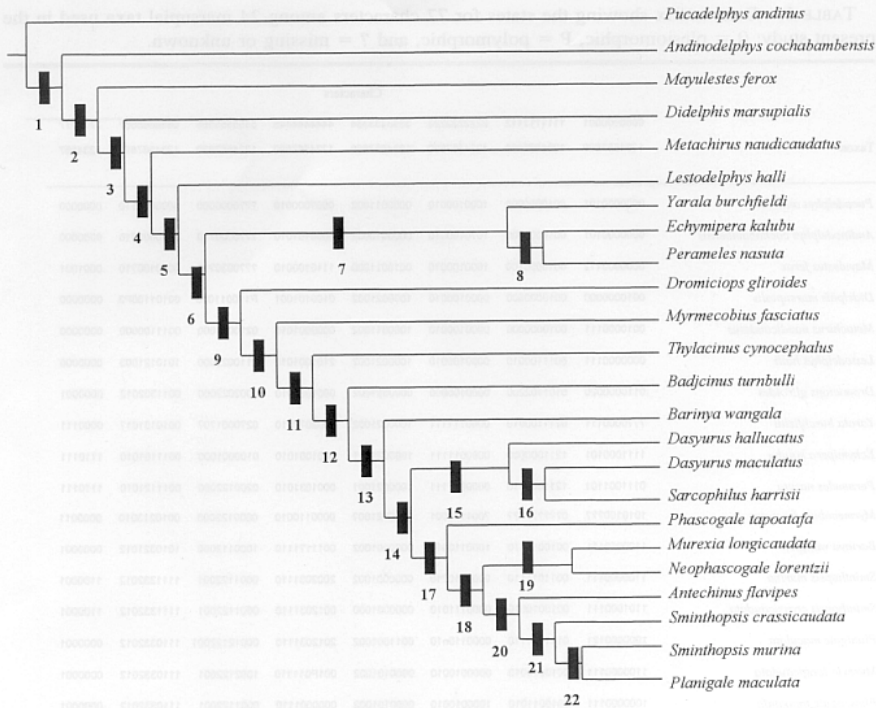


FIG. 2.--One of the 64 most-parsimonious trees of dasyuromorphians (see Appendix II for character state changes).

despite this correspondence, synapomorphies that actually support these clades often do not concur with those determined by subjective means used in most earlier anatomy-based works. Examples include cases where supporting synapomorphies, not previously suggested, appear in addition to those proposed in earlier works, e.g., only 4 of the 7 synapomorphies defining Dasyuridae (node 13, Fig. 2), changes in characters 61, 65, 66, and 70, were considered by Wroe (1999a). Examples also exist where previously proposed synapomorphies are not supported. These include development of a laterally extensive tubular ectotympanic (character 58), present in *Thylacinus cynocephalus* and *Badjcinus turnbulli*, as a synapomorphy for Thylacinidae

(Muirhead and Wroe 1998). However, the ectotympanic of an undescribed thylacinid from the Miocene of Riversleigh material (QMF36357) shows the same morphology as in *T. cynocephalus* and *B. turnbulli*, increasing the likelihood that this feature represents an actual thylacinid synapomorphy. Similar to Kirsch and Archer (1982), few groups are defined by unique synapomorphies, and many characters have undergone multiple reversals. Synapomorphies uniting some clades include large numbers of reversed characters. Of the 9 putative synapomorphies defining the *B. turnbulli*-dasyurid clade, 8 are reversals to a plesiomorphic state in dental features (see Appendix II). Overall, reversals to plesiomorphic states are more common in dental than cra-

TABLE 1.—Data matrix showing the states for 77 characters among 24 marsupial taxa used in the present study; 0 = plesiomorphic, P = polymorphic, and ? = missing or unknown.

Taxon	Characters							
	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567
<i>Pucadelphys andinus</i>	000000101	001000000	1000100010	0000011002	0007000010	??70000000	0000000110	0000000
<i>Andinodelphys cochabambensis</i>	000000101	001000000	1070100010	0000010002	0000101010	??70000710	0010000710	0000000
<i>Mayulestes ferox</i>	000000112	0010000100	1000100010	0010011000	1110100010	??70030710	0000100710	0001001
<i>Didelphis marsupialis</i>	0010000000	0010000000	0000100010	1000021002	0100101001	P110011000	00101100P3	0000000
<i>Metachirus naudicaudatus</i>	0010000111	0010000000	0000100010	1000011002	0000001010	0210021000	0011100000	0000000
<i>Lestodelphys halli</i>	0000000111	0011100010	0000100010	1000021002	2101001010	0110022000	1010121003	0000000
<i>Dromiciops gliroides</i>	0110000020	01011022u0	0000100000	0000021002	0001031010	0002022000	00011302012	0000001
<i>Yarala burchfieldi</i>	??770000111	0211100010	0000111111	1000021002	0002077010	0270000170?	0010101017	0000111
<i>Echymipera kalubu</i>	1111000101	1211000000	0000011111	1000021001	0001001010	0100001000	00011101010	1110111
<i>Perameles nasuta</i>	0111001101	1211000010	0000011111	1000021001	0001031010	0200122000	0011121010	1110111
<i>Myrmecobius fasciatus</i>	10101007??	07?????????	7001110001	001072100?	0000110010	0000122000	0010213010	0000011
<i>Barinya wangala</i>	1100010111	0010010010	1000110010	0000101002	0011171110	1000112000	1010321012	0000001
<i>Sminthopsis murina</i>	1100000111	0011011110	0000110710	0000001002	2002031110	0001122001	1111332012	1100001
<i>Sminthopsis crassicaudata</i>	1101000111	0010010010	0000111010	0000001000	0012031110	0001122001	1111332012	1100001
<i>Planigale maculata</i>	1000000121	0111111110	0000110n10	0011001002	2012031110	00012122001	1110332012	0000001
<i>Murexia longicaudata</i>	1100000111	0010010010	0000010010	0000101002	001P011110	1002122001	1110332012	0000001
<i>Phascogale tapoatafa</i>	1000000111	0010011010	1000010010	0000101002	0000001110	0001122001	1110332012	0000001
<i>Antechinus flavipes</i>	1000000111	0010010010	1000010010	0000101002	0012021110	0001122001	1110332012	1100001
<i>Neophascogale lorentzii</i>	1110100101	0210000010	0000011010	0000101002	001001P10	0002122001	1117332012	1000001
<i>Dasyurus hallucatus</i>	1000200111	0310011010	0000010010	0101111002	0021101110	00P1122001	1110332012	0000001
<i>Dasyurus maculatus</i>	1010200122	0310010011	0000110010	0111121102	0022111110	P102122101	1110332012	0000001
<i>Sarcophilus harrisi</i>	1010210123	0311010011	0000110011	0112121102	1022121110	1101122201	1110332012	0000001
<i>Badjcinus turnbulli</i>	1770777112	0710011110	0007010010	0000000000	0011117770	01000012100	0011100000	0000001
<i>Thylacinus cynocephalus</i>	1010000113	011112200	0001110010	002011112?	1102121111	2100112100	0011100000	0000001

nial features (19 versus 7). No reversals to plesiomorphic states occur in middle ear features at any branches in the strict consensus tree, a result consistent with the idea that complex adaptations of the middle ear are unlikely to be lost (MacPhee 1981).

Ambiguity of these results regarding the origin of Australian marsupicarnivores necessitates qualification in the erection of phylogenetic and biogeographic scenarios.

For *Andinodelphys*, no special relationship with any Australian taxon was supported. This finding is in keeping with the interpretation of Muizon et al. (1997), who on the basis of more complete material argued that this Tiupampan taxon was not australidelphian but didelphoid.

Our finding of monophyly for dasyuromorphians is consistent with results of all studies since those of Lowenstein et al.

(1981) and Szalay (1982). However, both bootstrap values and Bremer support was low. Monophyly for the clade is based on acquisition of 9 synapomorphies (Appendix 11), but only 1 of these, reduction of upper incisor number, has been proposed previously (Aplin and Archer 1987; Marshall et al. 1990). None of these 9 synapomorphies represent uniquely derived features within Marsupialia. Thus, at present our ability to define Dasyuromorphia is limited to a handful of equivocal features. Moreover, perhaps the most important of these characters, incisor number, is unknown in significant but poorly represented fossil taxa not included in this analysis (e.g., *Djarthia murgonensis*).

Furthermore, our results lend no support to interpretations of dasyuromorphian relationships at the family level. In some previous anatomy-based studies (Aplin and Archer 1987; Archer 1984), but not in others (Wroe 1997b), *Myrmecobius fasciatus* has been suggested as the sister taxon to thylacinids and dasyurids. Among studies based on molecular evidence that have included *M. fasciatus*, Lowenstein et al. (1981) and Krajewski et al. (in press) supported the contention of plesiomorphic sister taxon status for Myrmecobiidae. Krajewski et al. (1997a) placed the numbat within Dasyuridae. However, this position was supported by very low bootstrap values. The finding that the 2 thylacinids included were not monophyletic is inconsistent with the results obtained by Muirhead and Wroe (1998). The position of *Barinya wangala* as a sister species to extant dasyurid subfamilies supports the conclusion of Wroe (1999a).

At lower taxonomic levels within Dasyuridae, relationships between some taxa were consistent with those of previous studies. Examples include monophyly for both *Dasyurus* and *Sarcophilus harrisii* (Archer 1982; Krajewski et al. 1994, 1997b) and Sminthopsinae (Archer 1982a; Krajewski et al. 1994), but other relationships were highly incongruent (e.g., paraphyly for Dasyu-

rinae and Phascogalinae). Our results were perhaps not surprising given the long history of conflict over the intrafamilial relationships of dasyurids (see Krajewski et al. 1997b, in press; Wroe 1997b).

Monophyly was supported for a number of accepted natural groups that have previously proven resistant to resolution using cladistic analysis of anatomical data. These groups include Peramelemorphia, Dasyuromorphia, and Dasyuridae (including the fossil taxon *Barinya wangala*) and a clade inclusive of all extant dasyurids. In some instances, the actual status of many features identified as synapomorphies for these respective clades seems questionable, particularly regarding labile dental features. However, the standing of others, particularly basicranial apomorphies, is more concrete. Our results also support the argument of Wroe (1999a) that the common perception of extant dasyurids as Australian marsupial paradigms is no longer tenable.

Additional work remains to be done in the area of anatomy-based cladistic treatment of the origins of Dasyuromorphia, relationships among its constituent families, and intrafamilial affinities. Although monophyly for Dasyuromorphia and certain widely recognized clades was achieved in the present study, it is clear that most characters employed were inherently uninformative because there were very few non-homoplastic synapomorphies at each node. Ongoing character analyses, inclusion of additional taxa, and new fossil discoveries will be of value in further analyses.

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Appendix I

Character analysis

1. *Upper incisor number*.-5 (0); 4 (1). See Archer(1976b), Marshall et al. (1990), and Wroe (1999a).
2. *Shape of upper incisors*.-Peg shaped (0); spatulate (1). Szalay (1994) proposed the presence of spatulate incisors as an australidelphian synapomorphy. In their character state matrix dealing with American taxa, Reig et al. (1987) score only microbiotheriids as showing spatulate upper incisor morphology. However, Archer (1976b) noted that both spatulate and peg- shaped upper incisors are found in representatives of Australidelphia and Ameridelphia. Thus, apomorphic reversal to a plesiomorphic state must have occurred within both clades regardless of the polarity accepted. Nevertheless, each of these authors and Wroe (1999a) agree that

peglike morphology is plesiomorphic for marsupials.

3. *Height of I1*.-Not hypsodont (0); hypsodont (1). See Archer (1976b), Reig et al. (1987), and Wroe (1999a).

4. *Morphology of Cl*.--Caniform (0); pre-molariform (1). See Archer (1976b).

5. *Height of P3*.-Higher crowned than P2 (0); lower crowned than P2 (1); absent (2). See Archer (1976b), Reig et al. (1987) and Wroe (1997b, 1999a).

6. *Shape of P3*.-Laterally compressed in occlusal view (0); bulbous and ovate in occlusal view (1). See Wroe (1998).

7. *Posterolingual cuspule present or absent on P3*.-Absent (0); present (1). See Wroe (1996).

8. *Relative size of paracone and metacone M1-3*.-Paracone and metacone equal or almost equal in size to metacone (0); metacone much larger than paracone (1). See Cifelli (1993), Godthelp et al. (1999), and Szalay and Trofimov (1996).

9. *Metacone on M4*.-Present and distinct from metastylar corner of tooth (0); present but not distinct from metastylar corner of tooth (1); absent (2). See Wroe (1999a).

10. *Shape and orientation of the centrocrista*.-Centrocrista straight, with apex of postparacrista and premetacrista oriented dorsoventrally and terminating dorsally at or almost level with the talon basin (0); apex of centrocrista oriented buccally and well above talon basin, with an acute angle evident between the postparacrista and premetacrista and a distinct V shape in occlusal view (1); apex of centrocrista oriented buccally and well above protocone basin, with an oblique angle apparent between the postparacrista and premetacrista (2); apex of centrocrista positioned well above protocone basin with linear centrocrista (3).

The character states centrocrista straight or linear versus V-shaped and predilambdodont versus dilambdodont have been used synonymously by some authors (Marshall et al. 1990; Reig et al. 1987), although there is a distinction (Cifelli 1993; Johanson 1996). In practical terms, this is an academic point with regard to the investigations concerned because in the taxa under consideration a V-shaped centrocrista is intrinsic to dilambdodonty sensu Crochet (1980; i.e., preparacrista + centrocrista + postmetacrista form a W in occlusal view). Johanson (1996) provided a very useful and more thorough de-

scription of dilambdodonty - predilambdodonty, aspects of which are incorporated here. But for the range of taxa included in the present study, further refinement is required because a mosaic of features evident in some carnivorous marsupials precludes their consideration as either strictly dilambdodont or predilambdodont (sensu Johanson 1996). In potential outgroup taxa to Marsupialia (e.g., *Deltatheridium*), some generalized marsupials of uncertain affinity (e.g., *Aenigmadelphys archeri*), and most peradectids, a linear centrocrista is always concurrent with both the presence of an apex of the centrocrista, which is directed dorsally, and either very slight or no clear distinction in height between the trigon and talon basins. This combination of features was included under the category predilambdodonty by Johanson (1996). However, in peradectids and generalized australidelphian and ameridelphian marsupicarnivore taxa, a V-shaped centrocrista is always accompanied by other features incorporated under the category dilambdodonty by Johanson, i.e., presence of a buccally oriented apex and a clear distinction in height between the trigon and talon basins. In derived carnivorous marsupials (e.g., *Thylacinus*, *Sarcophilus*, *Borhyaena*), the centrocrista is linear in occlusal view but the trigon and talon basins are not of nearly equal height, in contrast to the condition in generalized taxa with linear centrocrista (e.g., peradectids). In thylacinids, a distinct morphocline is evident supporting the notion that the linear centrocrista in *Thylacinus* was secondarily derived from a dilambdodont condition as is present in basal thylacinid taxa (e.g., *Muribacinus*). The centrocrista in *Muribacinus* forms a distinct V shape; however, the inner angle of the V is obtuse in contrast to that of generalized ameridelphians and australidelphians. The size of this angle increases among other thylacinid taxa, culminating in the linear centrocrista of *Thylacinus*.

11. *Proximity of apex of centrocrista to ectoloph in dilambdodont taxa*.-Does not approach or breach ectoloph (0); approaches or breaches ectoloph (1). See Muirhead and Filan (1995).

12. *Orientation of preparacrista on M1*.-M1 preparacrista forms a nearly perpendicular angle with respect to the long axis of the tooth (0); M1 preparacrista oriented anterobuccally relative to long axis of the tooth (1); M1 preparacrista runs posterobuccally relative to long axis

of the tooth (2); M 1 preparacrista absent (3). See Muirhead and Wroe (1998).

13. *Relative lengths of M3 and M4 preparacristae*.-M4 preparacrista shorter than or equal to that of M3 (0); M4 preparacrista longer than that of M3 (1). See Godthelp et al. (1999).

14. *Protoconule present or absent*.-Present (0); absent (1). See Archer (1976b), Godthelp et al. (1999), Reig et al. (1987), and Wroe (1999a).

15. *Metaconule present or absent*.-Present (0); absent (1). See Archer (1976b), Godthelp et al. (1999), and Reig et al. (1987).

16. *Stylar cusp A distinct or indistinct from parastylar corner of tooth*.-Distinct (0); indistinct (1). See Archer (1976b).

17. *Size of stylar cusp B on M3*.-Large (0); small (1); absent (2). See Wroe (1996).

18. *Size of stylar cusp D on M3*.-Large (0); small (1); absent (2). See Wroe (1996) and Wroe (1997b).

19. *Relative size of stylar cusp B and stylar cusp D on M2*.-Stylar cusp B > stylar cusp D (0); stylar cusp D > stylar cusp B > (1). See Wroe (1996).

20. *Relationship of stylar cusp D to metacone*.-Not oppressed (0); oppressed (1). See Ride (1964) and Wroe (1996).

21. *Presence or absence of stylar cusp C*.-Stylar cusp C absent (0); stylar cusp C present (1). See Godthelp et al. (1999), Marshall et al. (1990), and Wroe (1999a).

22. *'Central cusp'*.-Absent (0); present (1). See Godthelp et al. (1999).

23. *Twinned cusps in the C position*.-Absent (0); present (1). See Godthelp et al. (1999).

24. *Presence or absence of anterior cingulum on M1*.-Present (0); absent (1). See Muirhead and Wroe (1998).

25. *Presence or absence of posterior cingulum on M1*.-Present (0); absent (1). See Muirhead and Wroe (1998).

26. *Lower incisor number*.-4 (0); 3 (1). See Archer (1976b), Marshall and Muizon (1995), and Wroe (1999a).

27. *i3 bilobed or not bilobed*.-Not bilobed (0); bilobed (1). See Archer (1976b) and Muirhead and Filan (1995).

28. *Position of hypoconulid*.-positioned posterolingual to entoconid (0); positioned posterior to entoconid (1). See Muirhead and Filan (1995).

29. *i3 staggered or not staggered*.-Not stag-

gered (0); staggered (1). See Hershkovitz (1995).

30. *Presence or absence of hypoconulid notch*.-Present (0); absent (1). See Wroe (1997a, 1997b).

31. *Presence or absence of well-developed sulcus formed by anterior cingulid*.-Absent (0); present (1). See Wroe (1996).

32. *Size of metaconid on m1 relative to that of m2-4*.-Metaconid in m1 not reduced relative to m2-4 (0); metaconid reduced relative to m2-4 (1). See Wroe (1996).

33. *Size of metaconid in m2-4*.-Large (0); reduced (1); absent (2). See Wroe (1996).

34. *Size of paraconid in m1*.-Large (0); reduced (1); absent (2). See Archer (1976b) and Wroe (1999a).

35. *Orientation of postprotocristid with respect to long axis of dentary*.-Transverse (0); oblique (1). See Archer (1976b), Wroe (1999a).

36. *Size of posterior cingulid in m1-3*.-Posterior cingulid present and well developed (0); posterior cingulid reduced (1); posterior cingulid absent (2). See Muirhead and Wroe (1998).

37. *Posterior cingulid in m4 present or absent*.-Present (0); absent (1). This feature has been treated as separate from character 37 because loss of a posterior cingulid on m4 occurs in many taxa without concomitant reduction or loss of the posterior cingulid in m1-3.

38. *Presence or absence of 'carnassial notch' in cristid obliqua*.-Absent (0); present (1). See Muirhead and Wroe (1998).

39. *Morphology of postprotocristid in m3-4*.-Postprotocristid continuous with metacristid (0); postprotocristid oriented posteriorly and almost continuous with cristid obliqua (1); postprotocristid oriented posteriorly and continuous with cristid obliqua (2). See Muirhead and Wroe (1998).

40. *Anterior point of termination of the cristid obliqua in m3 with respect to carnassial notch formed by postprotocristid and metacristid*.-Beneath carnassial notch (0); lingual to carnassial notch (1); buccal to carnassial notch (2). See Archer (1976b) and Godthelp et al. (1999).

41. *Entoconid size*.-Large (0); reduced (1); absent (2). See Archer (1976b) and Wroe (1999a).

42. *Anteroposterior dimension of m4 relative to that of m3*.-m4 < m3 (0); m4 > m3 (1). See Muirhead and Wroe (1998).

43. *Height of p3 relative to p2*.-p3 higher

crowned than p2 (0); p3 smaller than p2 (1); p3 absent (2). See Archer (1976b) and Wroe (1996, 1997b).

44. *Number of cusps on m4 talonid*.-3 cusps (0); 2 cusps (1); 1 cusp (2). See Archer (1976b).

45. *Presence or absence of orbital crest*.-Absent (0); present (1). See Muirhead and Wroe (1998).

46. *Morphology of fossa for the lower canine*.-Bordered by anterolateral process of maxilla (0); bordered by anterolateral processes of premaxilla and maxilla (1); bordered by anterolateral process of premaxilla (2); no lateral process (3). See Muizon (1998).

47. *Presence or absence of palatal vacuities*.-Absent (0); present (1). See Marshall and Muizon (1995).

48. *Presence or absence of posterolateral palatine foramen*.-Present (0); absent (1). See Archer (1984) and Wroe (1997b).

49. *Presence or absence of accessory posterolateral palatine foramen*.-Present (0); absent (1). See Wroe (1997b).

50. *Contribution of alisphenoid and periotic to primary foramen ovale*.-Delimited by alisphenoid anteriorly and periotic part of the petrosal posteriorly (0); delimited by alisphenoid only (1). See Gaudin et al. (1996) and Wroe (1997b).

51. *Presence or absence of secondary foramen ovale formed by anteriorly directed strut of alisphenoid tympanic wing*.-Absent (0); present but incomplete (1); present and complete (2). See Wroe (1997b).

52. *Presence or absence of secondary foramen ovale formed by mesial fold in alisphenoid tympanic wing*.-Absent (0); present but incomplete (1); present and complete (2). See Wroe (1997b).

53. *Presence or absence of contribution to secondary foramen ovale by posteriorly directed strut in alisphenoid*.-Absent (0); present but incomplete (1); present and complete (2). See Wroe (1997b).

54. *Morphology of ventral facial nerve canal*.-Absent (0); present but completed anteriorly by squamosal only (1-); present and enclosed within periotic with squamosal contribution to ventral rim (2); present and enclosed wholly within periotic (3). See Archer (1976a) and Wroe (1999a).

55. *Size of squamosal epitympanic sinus*.-

Absent (0); present (1). See Archer (1976a), Wroe (1999a), and Wroe et al. (1998).

56. *Alisphenoid hypotympanic sinus*.-Absent (0); present with periotic component (1); present wholly within alisphenoid, i.e., separated from alisphenoid hypotympanic sinus by distinct petrosal ridge (2); present with alisphenoid, periotic, and squamosal contributions (3). See Archer (1976a).

57. *Size of alisphenoid tympanic wing*.-Absent (0); poorly developed, i.e., with alisphenoid hypotympanic sinus visible in external view (1); well developed, i.e., extends posteriorly to reach posterior limit of alisphenoid contribution of alisphenoid hypotympanic sinus in ventral view (2). See Archer (1976a), Wroe (1999a), and Wroe et al. (1998).

58. *Shape of ectotympanic*.-Simple U shape (0); laterally extensive, but simple U shape in lateral view (1); laterally extensive, complex saddle shape (2). See Archer (1976a) and Wroe et al. (1998).

59. *Medial process of the squamosal*.-Absent (0); present (1). See Muizon (1998) and Muizon et al. (1997).

60. *Length of the internal jugular canal*.-Does not extend anteriorly to basisphenoid (0); extends to basisphenoid (1). See Archer (1976a) and Wroe (1999a).

61. *Presence or absence of a well-developed posteroventral lip formed by a mesially directed process in the pars petrosa, enclosing the internal jugular ventrally*.-Absent (0); present (1). See Archer (1976a) and Wroe (1999a).

62. *Dorsal enclosure of internal jugular canal*.-Not fully enclosed dorsally (0); fully enclosed dorsally (1). See Wroe (1999a).

63. *Presence or absence of transverse canal*.-Absent (0); present (1). See Archer (1976a) and Wroe (1999a).

64. *Frontal-squamosal or alisphenoid-parietal contact*.-Alisphenoid-parietal contact (0); frontal-squamosal contact (1). See Muizon @1998 and Wroe (1999a).

65. *Morphology of tympanic wing of periotic*.-Absent (0); present but does not contact alisphenoid tympanic wing (1); present and contacts alisphenoid tympanic wing but does not form periotic hypotympanic sinus (2); present and contacts alisphenoid tympanic wing and floors periotic hypotympanic sinus (3). See Archer (1976a) and Wroe (1999a).

66. *Morphology of paroccipital tympanic pro-*

cess.-Absent (0); present but does not contact any other tympanic elements (1); present and contacts the mastoid tympanic process laterally (2); present and fused to the pars petrosa anteriorly and mastoid tympanic process laterally (3). See Archer (1976a) and Wroe (1999a).

67. *Morphology of mastoid tympanic process.*-Absent (0); present (1); present and contacts pars petrosa (2); present and contacts alisphenoid tympanic wing (3). See Archer (1976a) and Wroe (1999a).

68. *Presence or absence of mastoid contribution to occiput.*-Present (0); absent (1). See Muizon (1998).

69. *Morphology of foramen lacerum medium.*-Distinct from primary foramen ovale (0); confluent with primary foramen ovale (1). See Marshall and Muizon (1995), Muizon (1998), and Wroe et al. (1998).

70. *Morphology of tubal foramen.*-Absent (0); present but slitlike and incomplete anteroventrally (1); present and ovoid, with sulcus in pars petrosa (2); present, with sulcus in alisphenoid tympanic wing (3). See Wroe (1999a).

71. *Shape of nasals.*-Posteriorly expanded (0); not posteriorly expanded (1). See Archer (1981, 1982a).

72. *Maxilla-nasal contact.*-Maxilla-nasal contact longer than premaxilla-nasal contact (0); premaxilla-nasal contact longer than maxilla-nasal contact (1). See Muirhead (1994).

73. *Posterior extension of nasals.*-Extend posteriorly beyond the anterior rim of the orbit (0); do not extend posteriorly beyond level of the orbit (1). See Muirhead (1994).

74. *Frontal-maxillary contact.*-Present (0); absent (1). See Archer (1982b).

75. *Morphology of jugal.*-Jugal not Y-shaped (0); jugal Y-shaped (1). See Muirhead (1994).

76. *Morphology of antorbital fossa.*-Antorbital fossa absent (0); antorbital fossa small or incomplete (1); antorbital fossa deep (2). See Muirhead (1994).

77. *Presence or absence of prootic canal.*-Present (0); absent (1). See Wible and Hopson (1995) and Muizon et al. (1997). A prootic canal was observed in 2 dasyurid specimens, *Antechinus* (AMNH 183455) and *M. longicaudata* (AMNH 198721), by J. R. Wible (pers. commun.). Presence of this feature is certainly rare among dasyurids and has not been observed in any other specimens studied by J. R. Wible (pers. comm.), Archer (1976a), or us.

Appendix II

Character state changes for nodes 1-22 in 1 of the 64 equally parsimonious trees

Node 1.-C59 0 ---> 1.

Node 2.-C9 0 ---> 1; C42 0 ---> 1; C56 0 ---> 1; C65 0 ---> 1.

Node 3.-C21 1 ---> 0; C31 0 ---> 1; C36 1 2; C47 0 ---> 1; C57 0 ---> 1; C63 0 ---> 1; C69 1 ---> 0.

Node 4.-C3 0 ---> 1; C42 1 ---> 0.; C45 1 ---> 0; C52 1 ---> 2; C56 1 ---> 2.

Node 5.-C 14 0 ---> 1; C19 0 ---> 1; C44 0 ---> 1; C57 1 ---> 2; C67 0 ---> 1.

Node 6.-C2 0 ---> 1; C12 0 ---> 1; C26 0 ---> 1; C46 0 ---> 3.; C53 1 ---> 0; C69 0 ---> 1; C77 0 ---> 1.

Node 7.-C12 1 ---> 2; C27 0 ---> 1; C28 0 ---> 1; C30 0 ---> 1; C 56 2 ---> 0; C57 2 ---> 1; C75 0 ---> 1; C76 0 ---> 1.

Node 8.-C4 0 ---> 1.; C9 1 ---> 0; C11 0 ---> 1; C15 1 ---> 0; C25 1 ---> 0; C40 2 ---> 1; C64 0 1; C71 0 ---> 1; C72 0 ---> 1; C73 0 ---> 1.

Node 9.-C17 0 ---> 2; C18 0 ---> 2; C29 1 ---> 0; C31 1 ---> 0; C52 2 ---> 0.

Node 10.-C1 0 ---> 1; C2 1 ---> 0; C16 0 ---> 1; C24 0 ---> 1; C33 0 ---> 1; C35 0 ---> 1; C45 0 ---> 1; C46 3 ---> 1; C55 0 ---> 1.

Node 11.-C29 0 ---> 1; C36 2 ---> 1; C48 0 ---> 1; C52 0 ---> 1; C56 2 ---> 1; C58 0 ---> 1.

Node 12.-C3 1 ---> 0; C12 1 ---> 0; C14 1 0; C15 1 ---> 0; C17 2 ---> 0; C18 2 ---> 0; C24 1 ---> 0; C25 1 ---> 0; C43 0 ---> 1.

Node 13.-C33 1 ---> 0; C52 1 ---> 0; C58 1 ---> 0; C61 0 ---> 1; C65 1 ---> 3; C66 0 ---> 2; C70 0 ---> 2.

Node 14.-C54 0 ---> 1; C56 1 ---> 2; C60 0 ---> 1; C62 0 ---> 1; C66 2 ---> 3; C67 1 ---> 2.

Node 15.-C5 0 ---> 2; C12 0 ---> 3; C32 0 1; C34 0 ---> 1; C36 0 ---> 1; C43 1 ---> 2.

Node 16.-C3 0 ---> 1; C9 1 ---> 2; C10 1 ---> 2; C20 0 ---> 1; C25 0 ---> 1; C33 0 ---> 1; C36 1 ---> 2; C38 0 ---> 1; C44 1 ---> 2; C51 0 ---> 1; C52 0 ---> 1; C58 0 ---> 1.

Node 17.-C44 0 ---> 1; C45 1 ---> 0.

Node 18.-C2 0 ---> 1; C71 0 ---> 1.

Node 19.-C54 1 ---> 2.

Node 20.-C44 0 ---> 2; C46 1 ---> 2; C72 0 ---> 1.

Node 21.-C25 0 ---> 1; C35 1 ---> 0; C46 2 ---> 3; C64 0 ---> 1.

Node 22.-C14 0 ---> 1; C17 0 ---> 1; C18 0 ---> 1; C41 0 ---> 2.