A Reexamination of Proposed Morphology-based Synapomorphies for the Families of Dasyuromorphia (Marsupialia). 1. Dasyuridae

Stephen Wroe[1]

The validity of eight morphological features previously advanced as synapormorphic for Dasyuridae is investigated in the light of new fossil and molecular data. Results indicate that one of these features (alisphenoid-periotic enclosure of the foramen ovale) is common to outgroups for Dasyuromorphia. Another feature (loss of intestinal cecum) is a likely synapomorphy for Dasyuromorphia. Two features (development of a hypoconulid notch, enlargement of stylar cusp D) may represent shared-derived characters within Dasyuromorphia but not at the family level for Dasyuridae (i.e., probably unite Dasyuridae-Thylacinidae). Another two features (loss of posterolateral palatine foramina, reduction Of P3) are also apomorphic within Dasyuromorphia but unite specialized clades within Dasyuridae. Only two previously treated features are probable synapomorphies for the family (enlargement of the alisphenoid tympanic wing and development of a distinct periotic hypotympanic sinus). An additional feature is identified as a dasyurid synapomorphy (presence of a distinct tubal foramen). Of all putative synapomorphies proposed to date, only the presence of a periotic hypotympanic sinus and tubal foramen are unique for Dasyuridae among dasyuromorphians. Results suggest considerable homoplasy for basicranial features within Dasyuromorphia. Independent acquisition for alisphenoid enclosure of the foramen ovale, development of secondary foramina ovale and loss of posterolateral palatal foramina has occurred in derived thylacinid and dasyurid clades. Convergence is also indicated for hypertrophy of the alisphenoid tympanic wing shown for dasyurids and myrmecobiids, and the development of a squamosal epitympanic sinus in Thylacinidae, Dasyuridae, and Myrmecobiidae. The finding of plesiomorphy for alisphenoid-periotic enclosure of the foramen ovale within Dasyuromorphia undermines the strongest morphology-based synapomorphy uniting a monophyletic Dasyuridae-Myrmecobiidae. Phylogenetic placement for some plesiomorphic fossil dasyuromorphians, known only from dental material, within Dasyuridae is currently untenable, with no dental synapomorphies uniting the family. The value of identifying morphoclines within clades known from robust phylogenetic data for consideration in character analysis is stressed, as is the importance of form-function and ontogenetic data.

INTRODUCTION

Dasyuromorphia constitutes the principle marsupial carnivore-insectivore radiation of Australasia and contains three families: Dasyuridae, Myrmecobiidae, and Thylacinidae. Dasyuridae represents a major element of the modern Australian marsupial fauna. Fifty-one extant Australian species are currently recognized (Strahan, 1995), with a fur-

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-ther 13 species endemic to New Guinea (Flannery, 1995). Myrmecobiidae contains a single taxon *(Myrmecobius fasciatus).* The last surviving thylacinid species, *Thylacinus cynocephalus,* has not been sighted since 1936, but a further seven species are now known from the fossil record (see below). Ten fossil species have been assigned to Dasyuridae by various authors: *Sarcophilus laniarius* (Owen, 1838), *Glaucodon ballaratensis* (Stirton, 1957), *Dasyurus dunmalli* (Bartholomai, 1971), *Ankotarinja tirarensis* and *Keeuna woodburnei* (Archer, 1976a), *Wakamatha tasselli* (Archer and Rich, 1979), *Dasylurinja kokuminola* (Archer 1982a), *Sarcophilus moornaensis* (Crabb, 1982), *Sminthopsis floravillensis* (Archer, 1982a), and *Dasyuroides achilpatna* (Archer, 1982a).

Additional fossil taxa from Pliocene or Pleistocene deposits have 6cen assigned to modern dasyurid genera by Archer (1982a) but, due to the incompleteness of material, have not received specific designation. These are an *Antechinus* species from the early Pliocene Hamilton Fauna of Victoria, a *Planigale* species from the early Pliocene Bluff Downs Fauna of Queensland, *Antechinus and Dasyurus* from the late Pliocene or early Pleistocene Floraville Fauna, and species of *Dasyurus, Sminthopsis, and Antechinus* from the late Pliocene or early Pleistocene Fisherman's Cliff local fauna of New South Wales.

Four of the above fossil taxa have been found in central Australian deposits that predate the earliest Pliocene *(Ankotarinja tirarensis, Keeuna woodburnei, Wakamatha tasselli, and Dasylurinja kokuminola).* Three dasyuromorphians from Miocene deposits of Riversleigh, northwestern Queensland, have been equivocally assigned to Dasyuridae: a possible phascogaline taxon known from a single M' or M2 (Archer, 1982a), an unnamed *"Antechinus-like"* species from Riversleigh (Van Dyck, 1989), and *Mayigriphus orbus* (Wroe, 1996). In contrast to the taxonomic composition of modem Australian faunas, evidence to data suggests that thylacinids dominated late Oligocene and Miocene mammalian carnivore niches of Australia. Six fossil thylacinids have now been described: five from Riversleigh deposits, *Nimbacinus dicksoni* (Muirhead and Archer, *1990), Thylacinus macknessi* (Muirhead, 1992; Muirhead and Gillespie, 1995), *Wabulacinus ridei* (Muirhead, 1997), *Ngamalacinus timmulvaneyi* (Muirhead, 1997), and *Muribacinus gadiyuli* (Wroe, 1996). An additional thylacinid taxon from Riversleigh, hereafter referred to as thylacinid sp., is currently being studied by J. Muirhead and the author. A seventh species, *Thylacinus potens* (Woodbume, 1967), is known from Alcoota (late Miocene).

Perhaps the greatest impediment to unambiguous disclosure of phylogenetic position for the Dasyuridae has been the clade's generally conservative morphology. Many authors have considered dasyurids to be phenetically and/or karyotypically close to the australidelphian common ancestor (Bensley, 1903; Ride, 1964a; Westerman and Woolley, 1990, 1993; Szalay, 1993, 1994). Paradoxically, a growing body of evidence now supports the contention of Archer (1982a) that dasyurids represent a relatively recently derived dasyuromorphian clade. Baverstock *et al.* (1990) forward a date of 20 million years B.P. for the initial radiation of extant dasyurid subfamilies, although the phylogeny produced therein differs in some detail with that accepted here. Krajewski *et al.* (1992) concur with Archer's (1982a) suggestion that Thylacinidae probably represents an older lineage than Dasyuridae. The suggestion by Flannery (1989) that most New Guinean endemic dasyurid lineages are the product of an early Miocene vicariance event might be construed as evidence for a considerably earlier origin for the family. However, the

results of recent molecular studies have indicated late Miocene-early Pliocene divergence dates for New Guinean genera and their proposed Australian sister taxa (Krajewski, *et al*., 1993, 1994; Kirsch and Springer, 1993; Aplin *et al.,* 1993).

Difficulties encountered in the elucidation of dasyurid synapomorphies are considered by Wroe (1995, 1996), with the author inferring that Dasyuridae is not unified by any reliable dental synapomorphies advanced to date. Consequently, Wroe (1996) pro- posed that placement of several plesiomorphic fossil taxa within the Dasyuridae produced a possibly paraphyletic phylogeny. It was suggested that *Ankotarinja tirarensis, Keeuna woodburnei, Wakamatha tasselli, and Dasylurinja kokuminola* be considered Dasyuromorphia *incertae sedis,* until/unless additional material revealed features allying these taxa with a monophyletic clade within the order on the basis of shared derived features. The placement of these four taxa within Dasyuromorphia was based on the presence of australidelphian (small twinned stylar cusps in the "C" position and a V-shaped centrocrista) and dasyuromorphian (reduction of talonids compared to trigon- ids) synapomorphies defined by Marshall *et al.* (1990), as well as on geographic and temporal position.

Recent syntheses addressing the phylogenetic position of Dasyuridae within Dasyuromorphia include those by Archer (1982a, 1984), Aplin and Archer (1987), and Marshall *et al.* (1990). Archer's (1982a, 1984) and Aplin and Archer's (1987) concepts of dasyuromorphian relationships differ from Marshall and co-workers' (1990) in the treatment of dasyurids and myrmecobiids as a monophyletic taxon [i.e., the Dasyuroidea of Archer (1982a, 1984)], proposing that development of a periotic and alisphenoid contribution to the opening (foramen ovale) for the mandibular branch (V3) of the trigeminal nerve was synapornorphous for the clade. Marshall *et al.* (1990) placed the Myrmecobiidae outside of a thylacinid-dasyurid clade. This position reflected the findings of Lowenstein *et al.* (1981), based on albumin serology, and Case's (1989) analysis of cranial isometry for *Thylacinus cynocephalus* and a number of dasyurid species.

In response to these recent developments, and as a prelude to the investigation of new dasyuromorphian fossil material from Riversleigh's Oligocene and Miocene deposits and Eocene deposits in Murgon (Godthelp and Archer, 1995), a character analysis is performed on morphology-based dasyurid synapomorphies advanced by previous authors.

MATERIALS AND METHODS

Outgroup identification (Nixon and Carpenter, 1993), missing data (Cracraft, 198 1; Novacek *et al.,* 1988; Simmons, 1993; Luckett, 1994; Wilkinson and Benton, 1995), major gaps in the fossil record and homoplasy (Felsenstein, 1978, 1983; Felsenstein and Sober, 1986; Harvey and Pagel, 1991; Stewart, 1993; Sundberg and Svensson, 1994) commonly obstruct the resolution of phylogenies. These factors are acute and particularly vexatious for the investigator of dasyuromorphian phylogeny. Some progress in tackling problems imposed by the considerations raised above has been made, or is imminent, following recent fossil discoveries from late Oligocene and Miocene deposits in Riversleigh and Australia's first early Tertiary mammal-bearing deposit in Murgon (Godthelp *et al.,* 1992; Archer *et al.,* 1992; Hand *et al.,* 1994; Godthelp and Archer, 1995).

To date no accepted phylogeny for Dasyuromorphia using morphology has been

produced employing parsimony-based algorithms. The single attempt known to the author (Kirsch and Archer, 1982) produced results grossly incongruent with previously and subsequently presented phylogenies. This outcome indicates problems with either character analysis or the efficacy of parsimony analysis itself. The validity of parsimony in phylogenetic reconstruction is not taken for granted here [arguments abound both for and against (Dunbar, 1980; Friday, 1982, Kirsch, 1982; Sober, 1983, 1986, 1989; Campbell and Barwick, 1990; Faith, 1991; Lipscombe, 1992; Swofford and Maddison, 1992; Stewart, 1993; Kuhner and Felsenstein, 1994; Mishler, 1994; Nixon and Carpenter, 1993; Edwards, 1996)1. But regardless of the investigator's position regarding numerical procedures in phylogenetic studies, it is clear that the analysis of characters relevant to identifying the position of Dasyuridae warrants reconsideration.

Central to problems with determination of character-state polarity for Dasyuromorphia is the appropriate choice and application of outgroup data. The identity of the ancestral dasyuromorphian remains highly contentious. For the purposes of this study, proposed sister taxa to Dasyuromorphia are considered in the determination of a hypothetical ancestral morphotype. Taxa advanced as ancestral or structurally ancestral for the Australian or dasyuromorphian radiations include pleisomorphic peradectids and didelphoids, including species of *Alphadon* (Clemens, 1966; Archer 1976a), *Peratherium* (Bensley, 1903), and *Mirandatherium* (Marshall, 1987), Microbiotheriidae (Szalay, 1982, 1994), and Peramelemorphia [the possibility that this clade may represent a sister taxon to Dasyuromorphia has fuelled a long running debate in the literature (Abbie, 1937; Ride, 1962; Kirsch, 1977; Hall, 1987; Luckett, 1994)1. The interpretation of bandicoot phylogeny has recently taken an unexpected turn, with some authors inferring that Peramelemorphia may be basal to all other Australian marsupials, or possibly the entire marsupial radiation (Kirsch *et al.,* 199 1; Springer *et al.,* 1994; Retief *et al.,* 1995).

In addition to outgroup comparison, ontogenetic data are used as a supplement in character polarization where available. A number of investigators have concluded that ontogeny provides a valid and useful means of determining character-state polarity, finding general congruence between phylogenies based on outgroup and ontogenetic meth- ods (Miyazaki and Mickevich, 1982; Krauss, 1988; Wheeler, 1990). Hecht and Hecht (1994) have stressed the importance of developmental data in assessing synapomorphies. Williams *et al.* (1990, p. 106) conclude that recent arguments against the use of ontogenetic evidence may equally apply to outgroup criterion, that is, "that polarity should be contained within the data and not imposed on it." In a review of the literature Kitching (1993) considered the consensus of opinion to hold that ontogenetic criteria provided a viable alternative or adjunct to outgroup comparison for character polarization.

While it has been suggested that study of functional context may not be necessary to produce reliable phylogenies (McKenna, 1987; Sober, 1989), many authors claim that investigation of form and function is desirable, or essential (Campbell and Barwick, 1990; Moore and Gibson, 1993; Szalay, 1994). Szalay (1985, 1994) notes that information regarding form and function is necessary to assess the likelihood of homoplasy. Furthermore, where variation in a character can be shown to correlate consistently with changes in other characters, it can be argued that all should be treated as a single unit in phylogenetic analysis (Kluge and Farris, 1969).

Ordinal- and familial-level taxonomic nomenclature follows Marshall *et al.* (1990) but differs in that the dasyuromorphian taxa *Ankotarinja tirarensis, Keeuna woodburnei,*
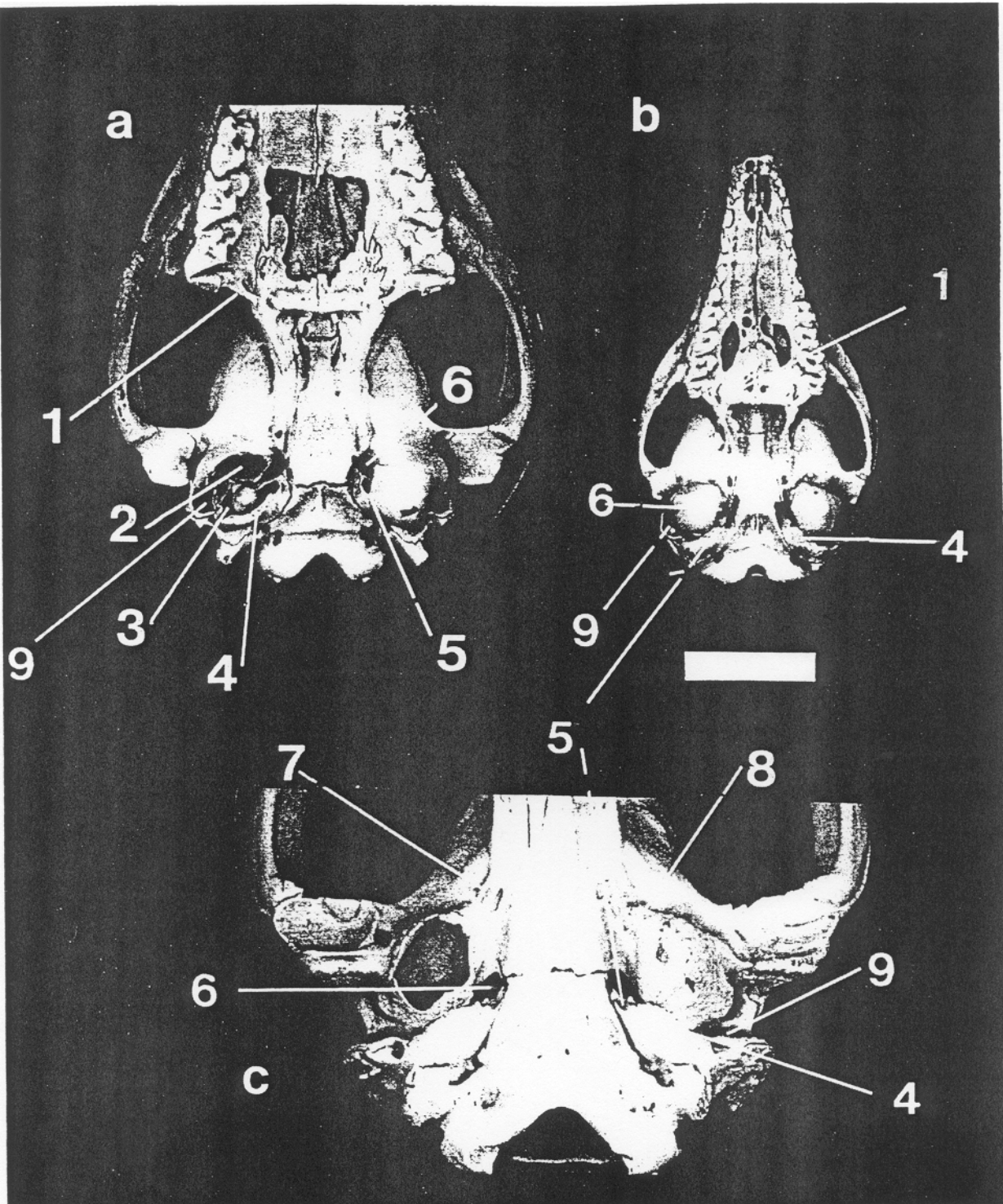
Wakamatha tasselli, and Dasylurinja kokuminola, from Oligocene and Miocene deposits of central Australia (Woodbume *et al.,* 1993), are considered Dasyuromorphia *incertae sedis* following Wroe (1997). Regarding subfamilial systematics of extant dasyurids, Archer's (1989a) synthesis of dasyurid relationships has been largely substantiated (Kirsch *et al.,* 1990; Baverstock *et al.,* 1990). However, recent molecular studies (Baverstock *et al.,* 1990; Krajewski *et al.,* 1992, 1993, 1994, 1996; Aplin *et al.,* 1993; Springer *et al.,* 1994; Painter *et al.,* 1995) have queried the monophyly of some dasyurid subfamilies and tribes therein. Consensus has been reached by these investigations allying *Murexia* with Phascogalinae and *Neophascogale and Phascolosorex* with Dasyurinae. Consequently, three subfamilies are recognized here as suggested by Krajewski *et al*. (1994): Phascogalinae (including *Murexia),* Dasyurinae (including *Neophascogale and Phascolosorex),* and Sminthopsinae (Table 1). Tribal level designations are not used pending the results of 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 PI-P3 and MI-M4. Archer's (1976b) basicranial terminology is fol- lowed excepting that for V3 foramina (Figs. 1 and 2, and see below). For the characters analyzed below, their inferred position in the phylogenies of Marshall et al. (1990), Aplin and Archer (1987), and Wroe (1997) are shown in Fig. 3.

Multiple specimens have been examined for all described genera and most species of extant Dasyuromorphia, excepting *Sminthopsis birds* (Van Dyck *et al., 1994), Smin- thopsis psammophila* (Aitken, 197 *1), Sminthopsis griseoventer, S. aitkeni, S. dolichura, S. gilberti* (Kitchener *et al.,* 1984), and *Pseudantechinus woolleyae* (Kitchener and Caputi, 1988), although the descriptions of these taxa have been considered. The fol- lowing material representing fossil dasyuromorphian taxa has been studied: *7bylacinus potens* (holotype, CPC 6746), *Thylacinus macknessi* (holotype QM F 16848a), thylacinid sp. (QM F30408), *Muribacinus gadiyuli* (holotype QM F30386, paratype QM F30385), *Nimbacinus dicksoni* (holotype QM F 16802, paratype QM F 1*6803), Wabulacinus ridei* (holotype QM F 16851, paratype QM F 16852*), Ngamalacinus timmulvaneyi* (holotype QM F16853, paratype QM F30300), *Glaucodon ballaratensis* (AR 252, cast of holotype)*, Ankotarinja tirarensis* (QM F7331, cast of holotype), *Keeuna woodburnei* (QM

Table 1. Dasyuromorphian Classification Recognized in this Study

Order Dasyuromorphia
  Family Dasyuridae
    Subfamily Sminthopsinae
      Sminthopsis, Ningaui, Antechinomys, Planigale
    Subfamily Phascogalinae
      Antechinus, Murexia, Phascogale
    Subfamily Dasyurinae
      Neophascogale, Phascolosorex, Mvoictis. Parantechinus, Pseudantechinus. Dasykaluta, Dasyuroides, Dasycercus, Dasyurus, Glaucodon, Sarcophilus
  Family Thylacinidae
      Muribacinus, Nimbacinus, Ngamalacinus. Wabulacinus, Thylacinus, thylacinid sp.
  Family Myrmecobiidae
      Myrmecobius
  Order Dasyuromorphia *incertae sedis*
      Ankotarinja, Dasylurinja, Keeuna, Wakamatha

Fig. 1. *(a) Dasyurus viverrinus* skull in anteroventral view. showing posterolateral palatal foramina and with right alisphenoid tympanic wing partially removed to expose alisphenoid and periotic hypotympanic sinuses (AR 6521). (b) *Neophascogale lorentzii* (skull in ventral view, AR 1765). *(c) Dasyurus maculatus* skull in ventral view (AR 17697. adult). (1) Posterolateral palatal foramen. (2) alisphenoid tympanic sinus. (3) periotic hypotympanic sinus., (4) periotic tympanic process (wing)., (5) tubular foramen, (6) foramen ovate; (7) complete anterior strut of alisphenoid tympanic wing forming a secondary foramen ovate dorsally; (8) mesial process of alisphenoid tympanic wing. (9) squamosal epitympanic sinus. (10) basal-mesial process of alisphenoid tympanic wing forming secondary foramen ovate. Scale = 1.0 cm.

F7333, cast of holotype), *Dasylurinja kokuminola* (SAM P23623, cast of holotype), *Wakamatha tasselli* (AR 710, cast of holotype), and *Yarala burchfieldi* (holotype QM F1680, paratypes QM F16861 and QM F16862). A manuscript describing a new thylacinid genus and species has recently been submitted for publication. This late Oligocene species, referred to in the present report as "thylacinid sp.," represents the geologically oldest dasyuromorphian described to date on the basis of cranial material. institutional abbreviations: Queensland Museum collection (JM and QM), Australian Museum (AM), South Australian Museum (SAM), Commonwealth Palaeontological Collection (CPC) and University of New South Wales Vertebrate Palaeontology Laboratory (AR).   1

REVIEW OF PROPOSED MORPHOLOGICAL SYNAPOMORPHIES FOR DASYURIDAE

Position and Morphology of the Foramen Conducting the Mandibular Branch (V3) of the Trigeminal Nerve

Character-State Terminology

Terminology regarding the external foramen for the mandibular branch (V3) of the trigeminal nerve (fifth cranial) varies. Traditionally the opening for V3 has been considered a "foramen ovale." Deviations from what was thought to be the common morphology for this foramen have subsequently been termed "foramina pseudovale" by some authors (Maclntyre, 1966; Archer, 1976b; Muirhead, 1994), while others have maintained the term "foramina ovale" for all V3 exit morphologies (Edinger and Kitts, 1954; Marshall, 1979; Novacek and Wyss, 1986; Marshall and Muizon, 1995; Gaudin *et al.,* 1996). A wide range of morphologies for the external V3 foramen that might be regarded as "foramina pseudoyale" has now been described (Zeller, 1989; Maclntyre, 1966; Muizon 1991). Subsumption of all these variations under one term might be considered an oversimplification and produce confusion. Furthermore, the term "foramen pseudovale" carries an implicit, although not necessarily warranted, message regarding character-state polarity. For these reasons the suggestion of Marshall and Muizon (1995) and Gaudin *et al.* (1996) is followed here, with all primary V3 foramina considered "foramina ovale." For marsupials, in addition to the primary exit for V3, a second external opening for V3, or a branch thereof, may be produced through modification of the alisphenoid tympanic wing (Archer, 1976b; Gaudin *et al.,* 1996). A secondary for- amen ovale may completely enclose V3 (e.g., *Sarcophilus harrisii, Lutreolina crassicaudata,* some *Dasyurus maculatus)* but often only partially bounds the mandibular nerve (e.g., *Marmosa, some D. maculatus).* Muizon (1991, 1994) suggests that the development of an alisphenoid tympanic wing is a derived feature within Metatheria, because it is absent in two early Tertiary marsupials from South America *(Pucadelphys andinus, Mayulestes ferox).* However, Trofimov and Szalay (1994) report that an alisphenoid component to the buila is present in the Late Cretaceous Asian marsupial, *Asiatherium reshetovi. Gaudin et al.* (1996) treat the dorsal V3 exit from the cranial cavity as the primary foramen ovale, with additional ventral V3 foramina considered secondary foramina ovale. As noted by Gaudin *et al.* (1996, p. 50), *"...*True identification of the elements contributing to the enclosure of the foramen ovale in adult skulls
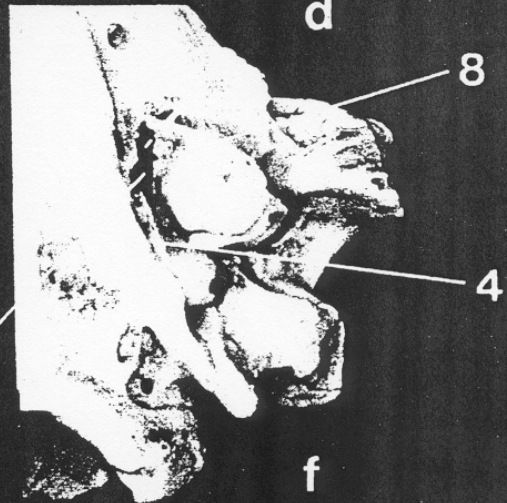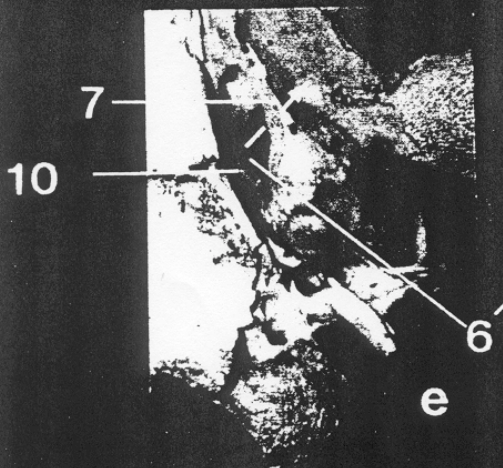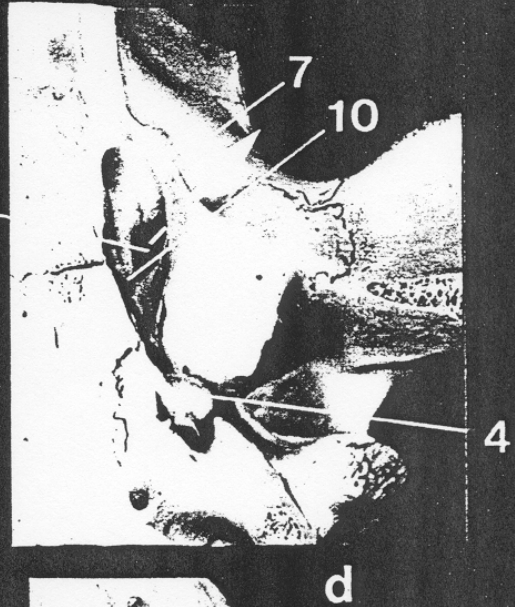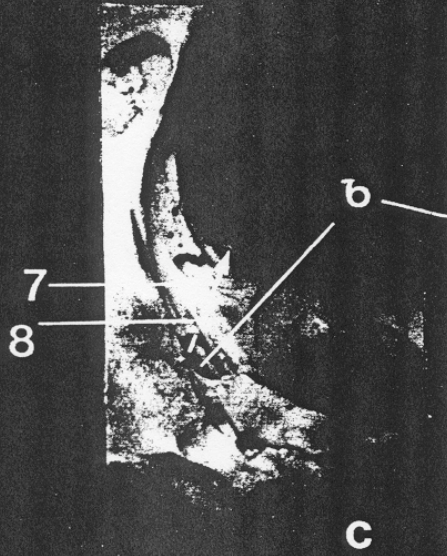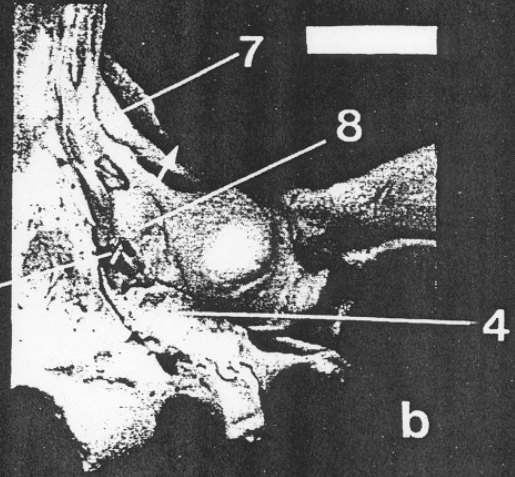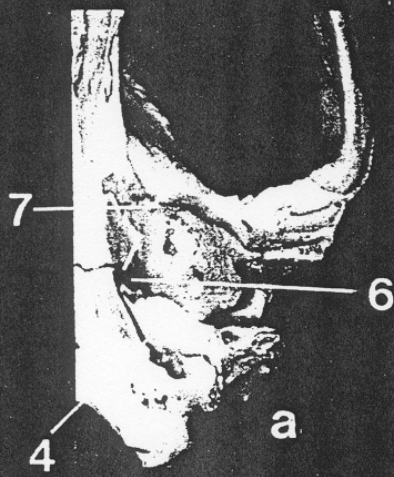
requires information on sutural patterns from both the exo- and the endocranial surfaces. "

Character-State Distributions

The taxonomic distribution of character states for the foramen ovale among non-mammalian cynodonts and mammals is well covered by Gaudin *et al.* (1996). For marsupials, a wide range of morphologies is reported regarding both primary and secondary foramina ovale (Archer, 1976b; Reig *et al.,* 1987; Muirhead, 1994). This variation extends to asymmetry in character states shown by individual specimens for some taxa, including *Phalanger orientalis* (Norris, 1993), *Didelphis albiventris,* and *Sarcophilus harrisii* (Gaudin *et al.,* 1996). Archer (1976b) notes that all marsupial taxa possess an aperture between the alisphenoid and the periotic (his "foramen pseudovale"). However, the V3 trunk does not always exit the skull via this foramen; and for some taxa it is not clear whether this aperture conducts a branch of V3, a blood vessel, or nothing at all (e.g., *7hylacinus cynocephalus).*

For the early Tertiary didelphoids *Pucadelphys andinus* (Marshall and Muizon, 1995) and *Peratherium frequeus* (Muirhead, 1994), V3 is delimited by both the alisphenoid and the periotic. Either alisphenoid-periotic or alisphenoid enclosure of the foramen ovale is shown by extant didelphids (Reig *et al.,* 1987). The basal borhyaenoid *Mayulestes ferox* shows alisphenoid-periotic delimitation of V3 (Muizon, 1994) with alisphenoid enclosure defining derived clades within Borhyaenoidea (Muizon, 1994). Patterson (1965) notes that for *Borhyaena* no specific foramen exists for V3. *Dromiciops australis* shows alisphenoid enclosure of the foramen ovale. Both alisphenoid and alisphenoid-periotic delimitation of V3 are shown by peramelemorphs. Foramen ovale morphology is unknown for all taxa considered Dasyuromorphia *incertae sedis* in this study. Alisphenoid-periotic delimitation of the foramen ovale is present for *Myrmecobius fasciatus.* Among thylacinids, thylacinid sp. shows alisphenoid-periotic delimitation for the foramen ovale and *Thylacinus cynocephalus* shows alisphenoid enclosure. Gaudin *et al.* (1996) report that in dasyurids the foramen ovale may be between the alisphenoid and the periotic or wholly enclosed by the alisphenoid. Following examination of material representing all dasyurid genera and 57 dasyurid species, both this author and Archer (personal communication) have found only one dasyurid for which alisphenoid enclosure of the foramen ovale might be construed, i.e., *Dasyurus spartacus* (Archer, 1976b; Van Dyck, 1987).

Secondary foramina ovale are absent for basal didelphids (*Pucadelphys andinus*), borhyaenoids (*Mayulestes ferox*), peramelemorphians (Muirhead, personal communication), microbiotheriids (*Dromiciops*), and *Myrmecobius fasciatus*; unknown for taxa treated here as Dasyuromorphia *incertae sedis*; and present for the thylacinids *Thylacinus cynocephalus* and thylacinid sp. Secondary foramina ovale are not present in most

Fig. 2. (Opposite) Left basicranial region in ventral view for (a) *Dasyurus maculatus* (adult, AR 17697); (b) *Sarcophilus harrisii* (adult, AR 17698); *(c) Sarcophilus harrisii* (juvenile, AM 5270)., (d) *Thylacinus cynocephalus* (adult, AM 219),, (e) *Thylacinus cynocephalus* (juvenile AM P778)., (f) thylacinid sp. (QM F30408). Arrow: Passage of V3 (for each specimen exit point of arrow shows position of secondary foramen ovale). Numbered traits as in Fig. 1. Scale = 1.0 cm.
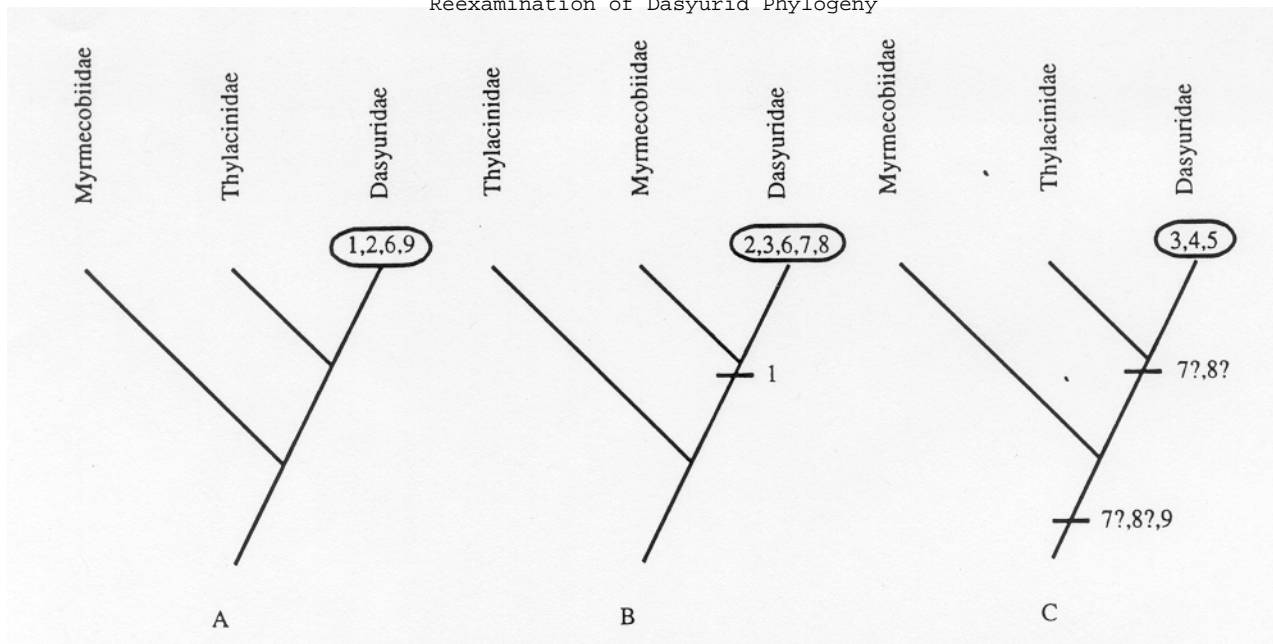
Fig. 3. Position of inferred derived states within Dasyuromorphia for nine characters considered in the text for phylogenies from (A) Marshall *et al.* (1990), (B) Aplin and Archer (1987) and Archer (1982b, 1984), and (C) Wroe (1997) and this study. For numbered apomorphic features, see Table 11. Only features considered synapomorphic at the family level or higher are shown.

dasyurids excepting some specimens of *Dasyurus maculatus* and all specimens of *Sarcophilus harrisii and Dasyurus spartacus* examined.

Previous Phylogenetic Interpretations

Archer (1976b) considered that the development of alisphenoid-periotic delimitation for the foramen ovale was a derived character among some marsupial clades. This was interpreted as a synapomorphy uniting Dasyuridae and Myrmecobiidae by Archer (1982a, 1984). Marshall *et al.* (1990) treat the development of alisphenoid-periotic delimitation of the foramen ovale as a dasyurid synapomorphy (Tables 11 and 111) but do not recognize Myrmecobiidae as the sister taxa to Dasyuridae, implying that a foramen

Table II. Character Analysis for Dasyuromorphian Features Considered in Phylogenetic Analysis of Dasyuridae

Primitive	Derived
1. V3 bounded by alisphenoid-periotic	V3 bounded by alisphenoid only
2. Posterolateral palatal foramen present	Posterolateral palatal foramen absent
3. Alisphenoid tympanic wing absent	Alisphenoid tympanic wing present
4. Periotic hypotympanic sinus absent	Periotic hypotympanic sinus present
5. Tubal foramen absent	Tubal foramen present
6. P3 larger than P2	P3 smaller than P2
7. Stylar cusp D small	Stylar cusp D large
8. Hypoconulid notch present'	Hypoconulid notch absent
9. Cecum present	Cecum absent

'Reversed polarity decision on that of Archer (1984), Aplin and Archer (1987), and Marshall *et al.* (1990).

Table III. Proposed Synapomorphies for Dasyuridae.

Marshall *et al.* (1990)	Archer (1982b, 1984) and Aplin and Archer (1987)	Wroe (1997) or on basis of current study
Alisphenoid-periotic enclosure for V3, posterior palatal foramina lost; P3 reduced, intestine lacks cecum	Alisphenoid-periotic enclosure for V3, loss of a complete posterolateral foramen, reduction Of P3; development of a hypoconulid notch in the anterior cingulum, enlargement of stylar cusp D; development of a large alisphenoid tympanic wing	Development of a periotic hypotympanic sinus with periotic tympanic wing contacting the alisphenoid tympanic process; development of a large alisphenoid tympanic wing; development of a tubal foiamen

ovale bounded by the alisphenoid and periotic is independently derived for both clades. Marshall and Muizon (1995) note some confusion regarding the interpretations of foramen ovale morphology/homology by Archer (1976b) and Maclntyre (1966), further suggesting that phylogenetic conclusions based on this feature should be reconsidered. Novacek and Wyss (1986) consider alisphenoid-periotic delimitation of the foramen ovale to be plesiomorphic for mammals and alisphenoid enclosure to be synapomorphous for a monophyletic clade which included all eutherians except edentates. Gaudin *et al.* (1996) observed a variety of character states for foramen ovale morphology in outgroups to Recent Theria and were unable to determined whether or not the development of a V3 foramen encircled by the alisphenoid constituted a synapomorphy for Recent Theria or Eutheria. Both Case (1989) and Muirhead (1994) suggest that development of a V3 foramen bounded by the alisphenoid and periotic is plesiomorphic for marsupials and that enclosure of the foramen ovale by the alisphenoid is derived within the clade. Griffiths (1978) considers that variability in the composition of bones delimiting the V3 foramen precludes unambiguous phylogenetic interpretation for monotremes, placentals, or marsupials.

Although most authors identify a foramen ovale bounded by the alisphenoid and periotic in outgroups to Recent Theria *(sensu Gaudin et al.,* 1996), opinion is divided regarding the morphology of the foramen ovale shown by the common ancestor of marsupials (i.e, whether alisphenoid enclosure of V3 is a synapomorphy of Eutheria or of Metatheria-Eutheria). However, at the ordinal and familial levels within Metatheria, recent authors have considered alisphenoid-periotic contribution to the foramen ovale to be plesiomorphic for didelphids (Marshall and Muizon, 1995), peramelemorphians (Muirhead, 1994), borhyaenoids (Muizon, 1994), and thylacinids (Muirhead and Wroe, submitted).

Outgroups, Homology, and the "Foramina Ovale " of Dasyurids and 7hylacinids

If the Paleocene didelphid *Pucadelphys andinus* (with V3 bordered posteriorly by the periotic and anteriorly by the alisphenoid) shows the plesiomorphic marsupial state for all cranial features as suggested by Marshall and Muizon (1995), then a foramen ovale delimited solely by the alisphenoid cannot be a synapomorphy uniting marsupials or Metatheria-Eutheria. Consideration of findings by Marshall and Muizon (1995) sup-

ports the contention that alisphenoid enclosure of the foramen ovale represents a derived feature within some marsupial clades and a likely eutherian synapomorphy. Of particular interest here is the V3 foramen morphology shown in asiadelphians. Elucidation of the character state shown by this taxon would be of considerable value.

Further relevant material is available for three taxa considered as sources of out-group data for Dasyuromorphia: *Peratherium frequeus,* Microbiotheriidae, and Peramelemorphia. For *P. frequeus* the foramen ovale is bounded by both the alisphenoid and the periotic (Muirhead, 1994). For adult *Dromiciops australis* V3 is enclosed by the alisphenoid. However, the otherwise highly autapomorphic auditory region of *D. australis (Reig et al.,* 1987; Hershkovitz, 1992a) renders the taxon a poor model for out-group comparison. Muirhead (1994) concludes that an alisphenoid-periotic enclosed foramen ovale is plesiomorphic for peramelemorphians, based on a study of Oligocene and Miocene bandicoots. An additional taxon considered here, *Yalkaparidon,* shows alisphenoid-periotic delimitation of V3. The phylogenetic position of *Yalkaparidon* (sole taxon within the new marsupial order Yalkaparidontia) is uncertain, but Archer *et al.* (1988) note that this taxon is highly plesiomorphic within the Australian marsupial radiation regarding basicranial features. Because an alisphenoid-periotic contribution to the foramen is found in Myrmecobiidae, and basal thylacinids and dasyurids, in outgroups to Recent Theria, as well as in most taxa considered as possible dasyuromorphian out-groups, it is concluded here that alisphenoid-periotic delimitation of the foramen ovale represents a plesiomorphy for Dasyuromorphia. Consequently, the alisphenoid-periotic enclosed foramen ovale of Dasyuridae and Myrmecobiidae is treated as a retained plesiomorphy, contra Archer (1976b), Aplin and Archer (1987), and Marshall *et al.* (1990). The alisphenoid-enclosed foramen ovale reported for *7hylacinus cynocephalus (Archer,* 1976b; Gaudin *et al., 1996), Dasyurus spartacus* (Archer, 1976b; Van Dyck, 1987), and one side of a specimen of *Sarcophilus harrisii* (FMNH 46006) (Gaudin *et al.,* 1996) are considered derived features within Thylacinidae and Dasyuridae, respectively. Following the investigation of specialized clades within Dasyuromorphia, three inferred morphoclines documenting transitions to alisphenoid delimitation of V3 foramina are identified below (Figs. 4 and 5).

(1) Secondary development of alisphenoid enclosure of V3 can occur through hypertrophy of a mesial process of the alisphenoid tympanic wing (Figs. 4A-D). Both morphological and molecular evidence suggests that *Dasyurus maculatus* represents the immediate extant sister taxon to *Sarcophilus harrisii* (Butler, 1946; Ride, 1964a; Archer, 1976c, 1982a; Crabb, 1982; Krajewski *et al.,* 1992, 1993, 1994). *Dasyurus maculatus* shows alisphenoid-periotic enclosure of the foramen ovale. In addition, a complete secondary V3 foramen was also apparent in 9 of 21 specimens of *D. maculatus* examined, while the remaining specimens showed an incomplete secondary V3 foramen. This secondary V3 foramen occurs as a strut running from the anterior of the alisphenoid tympanic wing to a point anterior to the foramen for the transverse canal. In all *D. maculatus* showing a complete anteriorly directed strut, a variably developed mesial process of the alisphenoid is also apparent (Figs. lc and 2a). Among material examined, the phenomenon is peculiar to larger and/or older individuals (judging by degrees of tooth wear). All 41 *S. harrisii* observed in this study show a foramen ovale bounded by the alisphenoid and periotic. All specimens also showed a strut connecting the alisphenoid wing to a point anterior to the transverse canal foramen (Fig. 2b), as for some *D. maculatus.*
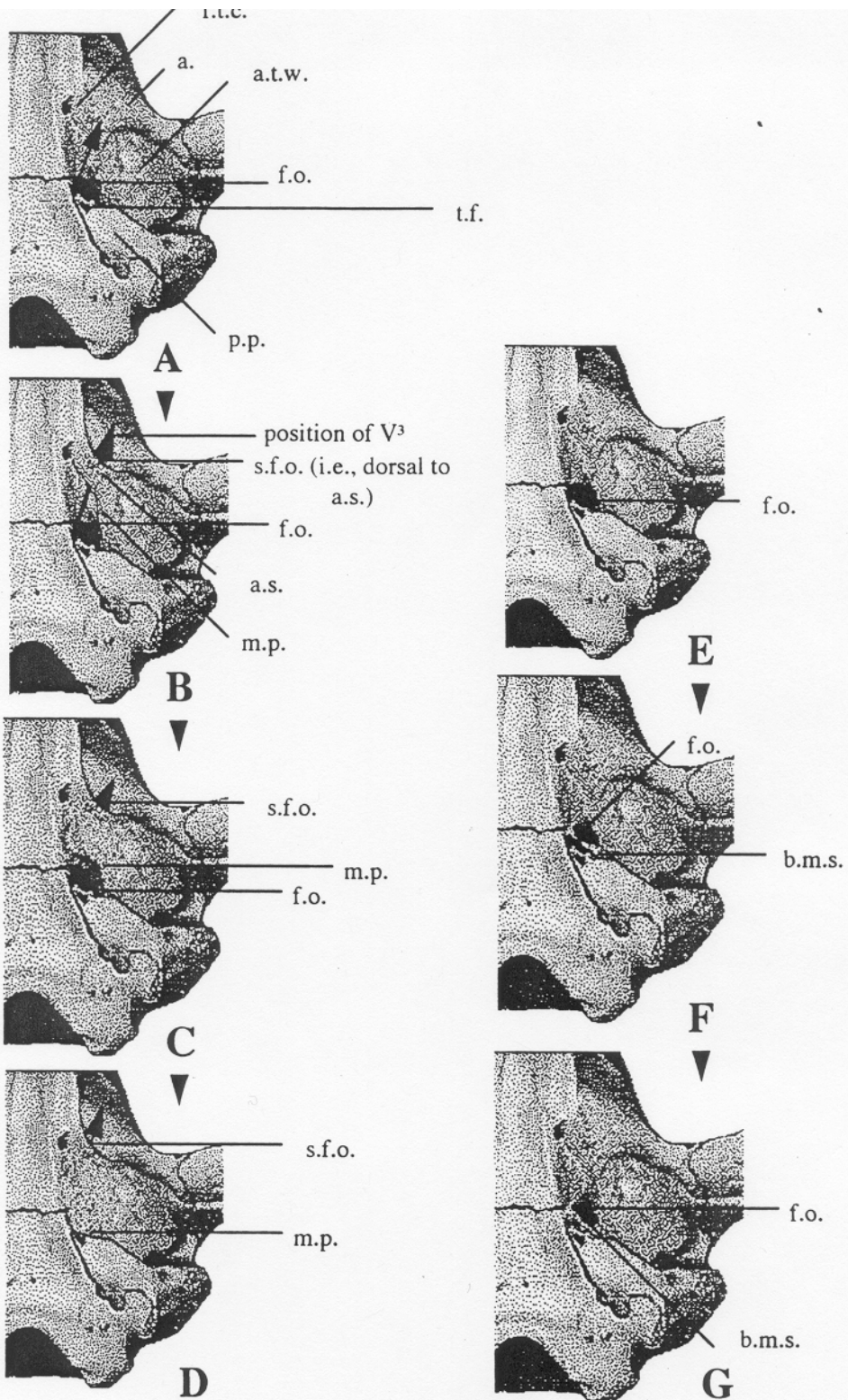
Fig. 4. Proposed morphoclines secondarily producing alisphenoid enclosure of the foramen ovale. A - B - C - D; Development of an anteriorly directed strut and mesial fold of the alisphenoid tympanic wing (exit point of arrow indicates position of secondary foramen ovale). E - F - G: Development of a basal-mesial strut in the alisphenoid tympanic wing. a, alisphenoid, a.s., anterior strut of alisphenoid tympanic wing; a.t.w., alisphenoid tympanic wing., b.m.s. basal-mesial strut of alisphenoid tympanic wing; f.o., foramen ovale; f.t.c., foramen for the transverse canal; M.p., mesial process of alisphenoid tympanic wing; p.p., petrosal part of the periotic; s.f.o, secondary foramen ovale; t.f., tubal foramen.
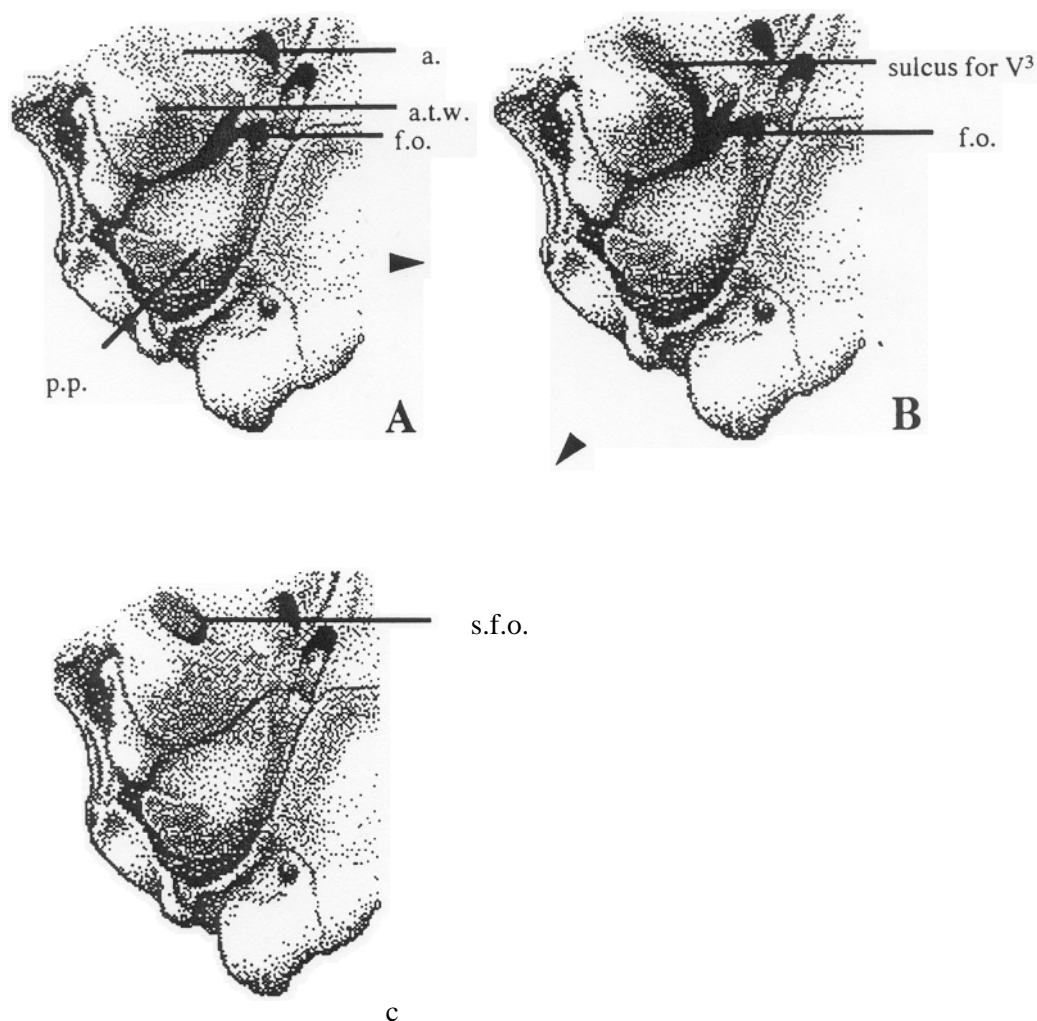
Fig. 5. Proposed morphocline secondarily producing alisphenoid enclosure of the foramen ovale: A - B - C: Development of a sulcus along the dorsal-rnesial margin of the alisphenoid tympanic wing. Abbreviations as in the legend to Fig. 4.

For all *S. harrisii* examined, the mesial process extends to connect the alisphenoid tympanic wing with the alisphenoid between the foramina for the transverse canal and the internal carotid (Fig. 2b). All 37 adult specimens show further mesial and posterior extension of this second process. For all adult specimens this mesial process of the alisphenoid tympanic wing extends posteriorly to almost obscure the foramen ovate. As for *D. maculatus,* development of this process advances with age, and for the four juvenile specimens examined (AM M5270, 10765, 2758, 1182) a large alisphenoid/periotic-bounded foramen ovate is clearly visible (Fig. 2c). It is concluded that the well-developed secondary foramen ovate for *5. harrisii* represents the terminal point of a transformation series, the beginning of which is exemplified by its sister taxon *D. maculatus.* Slight, continued hypertrophy of the mesial process shown by some *S. harrisii* would completely obscure the alisphenoid/periotic-delimited foramen ovate, producing a secondarily derived V3 exit bounded solely by the alisphenoid in ventral view (Fig. 4D).

(2) Secondary development of alisphenoid enclosure of the foramen ovale can occur

through development of a basal-mesial strut in the alisphenoid tympanic wing (Figs. *4E-G*). *Dasyurus spartacus* shows alisphenoid enclosure of the foramen ovale. Archer (1976b, p. 252), in reference to a specimen considered *Dasyurus* sp. nov. [subsequently included within *D. spartacus* by Van Dyck (1987)], notes that the V3 "has distinct bony wall of alisphenoid as posterior wall of foramen. " This is confirmed by Van Dyck (1987), who observes the presence of a thin strut of the alisphenoid bisecting the foramen ovale. *Dasyurus spartacus* is a specialized carnivorous dasyurine. All taxa that might be considered as outgroups to *D. spartacus* (i.e., all other Dasyuridae) show alisphenoid-periotic delimitation of V3, and the occurrence of alisphenoid enclosure of the foramen ovale for this taxon must be treated as apomorphic within Dasyuridae.

Similarly, secondary development of a basal-mesial strut in the alisphenoid tympanic process is considered the probable method of foramen ovale enclosure for *Thylacinus cynocephalus.* The demonstration of a transformation series secondarily producing alisphenoid enclosure of V3 for *Thylacinus cynocephalus* must be considered less robust than for *Sarcophilus harrisii or Dasyurus spartacus.* A considerable temporal and morphological distance separates *T. cynocephalus* from thylacinid sp., the only other thylacinid species for which basicranial material is known. For thylacinid sp., the foramen ovale is bounded by the alisphenoid-periotic, and an incomplete secondary foramen ovale is evident in the form of a mesial fold in the alisphenoid tympanic wing (Fig. 2f). V3 foramen morphology differs for *T. cynocephalus,* with a moderate extension of the alisphenoid tympanic wing extending mesially, associated with the anterior alisphenoid strut (Fig. 2d). Thylacinid sp. lacks this anterior alisphenoid strut (present in *T. cynocephalus, S. harrisii,* and some adult *D. maculatus).* For all adult *T. cynocephalus,* V3 exits the skull, first through a foramen ovale completely enclosed by the alisphenoid and then through a secondary foramen ovale, also enclosed by the alisphenoid (Fig. 2d). In showing this primary exit for V3 bounded solely by the alisphenoid, *T. cynocephalus is* rare among dasyuromorphians, with the exception of *D. spartacus* and the single *S. harrisii* specimen reported by Gaudin *et al.* (1996). This is considered a derived feature within Thylacinidae, with polarity inferred from outgroup comparison with thylacinid sp. Additional evidence for apomorphy of the alisphenoid-enclosed primary V3 foramen for *Thylacinus cynocephalus* is provided by ontogenetic data. For all adult *T. cynocephalus* examined (24) a tiny aperture is present between the alisphenoid and the periotic (Fig. 2d), but for the four juvenile specimens (AM P778, AM S403, AM P774, AM M27836) examined this aperture is much larger and separated from an alisphenoid enclosed foramen by a thin strut of bone (Fig. 2e). For older individuals this strut is enlarged and almost completely obscures the posterior alisphenoid/periotic-delimited aperture. Unfortunately a complete record of the ontogeny for this feature could not be made, with the youngest individual available showing M3 partially erupted.

(3) Secondary development of alisphenoid enclosure of V3 can occur through development of a sulcus along the dorsal-mesial margin of the alisphenoid tympanic wing (Figs. SA-C): Archer (1976b) notes that for many *Dasyurus* a sulcus is formed in this region of the alisphenoid tympanic wing. Similar sulci are found in some didelphids *(e.g., Caluromys philander, Micoureus cinereus).* For one *Dasyurus* specimen observed by Archer (1976b), this groove is completely enclosed within the alisphenoid, forming a complete secondary V3 foramen continuous with the foramen ovale. Posterior elaboration and enclosure of this sulcus could obscure the foramen ovale, producing a single

exocranial foramen for V3 bounded solely by the alisphenoid (i.e., a secondary foramen ovale).

Ontogenetic and Form-Function Data Bearing on the Phylogenetic Value of the Foramina Ovale

As noted above, in the geologically oldest marsupials for which the structure is known, the foramen ovale is a simple perforation of the basicranium bounded by the alisphenoid-periotic (*Mayulestes ferox*), *Pucadelphys andinus*). Ontogenetically in therians, the mandibular branch of the trigeminal nerve forms before the surrounding bone (Broom, 1909; Presley and Steel, 1976; Zeller, 1987; Clark and Smith, 1993). Clark and Smith (1993) observed that the alisphenoid for *Monodelphis domestica* originates from two cartilaginous processes, between V1 and V2 and between V2 and V3, respectively. Alisphenoid hypertrophy or slight shifts in the position of the mandibular branch of the trigeminal nerve would transform an alisphenoid/pedotic-bounded foramen ovale into an alisphenoid-enclosed V3 foramen.

Selective pressures which might produce a secondary foramen ovale or result in its reduction or loss can only be the subject of speculation at present. Among dasyuromorphians there is an apparent correlation between the evolution of a secondary foramen ovale, advanced carnassialization, and large size, with the most specialized taxa of both thylacinid and dasyurid clades showing the most advanced development. In this context the buttressing provided by a secondary foramen ovale may be necessary for protection of V3 from forces of compression generated by these carnivores in killing and chewing. Damage to V3 can result in paralysis, atrophy, and loss of bite strength (Wilson-Pauwels *et al.,* 1988). The inflated bulla provides a site for the anchorage of the external (lateral) and internal (medial) pterygoids for bandicoots (Filan, 1990). Rosenburg and Richard- son (1995) note the insertion of the pterygoid, stylohyoid, and digastic muscles on the alisphenoid tympanic wing of the small dasyurid *Sminthopsis crassicaudata.* Development of the strut or fold containing V3 may also provide additional anchorage for masticatory musculature.

Another evolutionary scenario involves the loss of a secondarily produced foramen ovale. Hershkovitz (1992b) notes that for the species of *Gracilinanus* the size of the alisphenoid tympanic strut inversely correlates with bulla inflation, completely disappearing in species with large alisphenoid tympanic wings. As the alisphenoid tympanic wing of all dasyurids is relatively large, it is possible that the absence of a secondary foramen ovale represents an apomorphy associated with enlargement of the auditory bulla. The independent expansion and evolution of a floor to the middle ear in numerous mammalian lineages demonstrate an almost-universal adaptive advantage (Novacek, 1977). Hypertrophy of the alisphenoid tympanic wing and other processes contributing to the floor of the middle ear probably acts to maintain an optimal constant volume (Fleischer, 1978). For small nocturnal animals a large middle ear cavity may be of great importance for predator avoidance (Webster and Webster, 1975, 1980). Webster (1966) identified a minimum volume for the middle ear that will enable efficient low-frequency hearing. Because this volume is constant, small taxa are likely to possess relatively large auditory bulla. If the stem dasyurid did posses a partial or complete secondary foramen ovale, it is possible that this character could have been lost with expansion of the alis-

tympanic wing. At present there is insufficient evidence to allow further speculation on this issue.

Summary

Within Dasyuromorphia alisphenoid-periotic delimitation of the foramen ovale is considered pleisomorphic for known families. Secondary foramina ovale and/or alisphenoid enclosure of the foramen ovale are derived within Marsupialia. Among dasyuromorphians derived V3 foramina are manifested as anterior struts, mesial folds, basal-mesial struts in the alisphenoid tympanic wing, or sulci circumscribing the alisphenoid tympanic wing along the dorsal-mesial margin. The development of two or more of these processes may occur simultaneously. For example, *Thylacinus cynocephalus* shows both a mesial fold in the alisphenoid wing and a basal-mesial strut. Alisphenoid enclosure of the foramen ovale in *7hylacinus cynocephalus* and some carnivorous dasyurids represents a derived character within Dasyuridae and Thylacinidae, produced through hypertrophy of alisphenoid tympanic wing elements. The consideration of postulated morphoclines (shown above) may be of value in polarity determination for foramen ovale morphology in other marsupial taxa.

Morphology of Posterolateral Palatal Foramina

The posterolateral palatal foramen (p.p.f.) carries the minor palatine artery from the maxillary artery to the ventral surface of the palate and/or the posterior palatine nerve in therians (Gregory, 1910; Miller *et al.,* 1964). The p.p.f. is formed by a bridge com- posed of an anteriorly directed process from the lateral margin of the palatine, and a posteriorly directed process from the posterolateral border of the maxilla. An accessory posterolateral palatal foramen (a.p.p.f.) may also be present, which is contained wholly within the posteroventral rim of the palatine (palatine ridge). It is not clear which vessel(s) passes through the a.p.p.f. For some marsupial species the p.p.f. is incomplete posteriorly, forming a notch at the posterolateral symphysis of palatine and maxilla, or is lost. Loss (or reduction; i.e., incomplete) of the p.p.f. has been proposed as a synapomorphy of the Dasyuridae by Archer (1982a, b, 1984) and Marshall *et al.* (1990), although Marshall (1977a) considered this character to be of questionable phylogenetic value in a cladistic analysis of marsupicamivores.

For the plesiomorphic didelphoid *Pucadelphys andinus* both the p.p.f. and the a.p.p.f. are present; this is also the case for many didelphids (e.g., *Didelphis marsupialis, Marmosa chapmani, Metachirus* spp., and *Caluromys derbianus*). Accessory posterolateral palatal foramina are lost in some didelphoid taxa including *Chironectes minimum.* For the derived sparassocynid, *Sparassocynus deriatus,* the a.p.p.f. is lost and the p. p. f. is incomplete. In the basal borhyaenoid *Mayulestes ferox* both posterolateral palatine foramina are present; however, derived representatives of this clade show loss of the p.p.f. and a.p.p.f. (Simpson, 1941). Accessory posterolateral palatal foramina are lost in *Dromiciops australis,* but complete posterolateral palatal foramina are present. Among peramelemorphians both a.p.p.f. and p.p.f. are present in many taxa (e.g., some species of *Isoodon, Echymipera),* but a.p.p.f. are lost in *Macrotis* and *Perameles. The* morphology of this region is unknown for *Ankotarinja tirarensis, Keeuna woodburnei, Wakamatha tasselli, and Dasylurinja kokuminola.* Only for *Thylacinus potens* and Thy-

-lacinus cynocephalus is posterolateral palatal foramina morphology known among thylacinids. An a.p.p.f. is not present in either taxon. An incomplete p.p.f. is variably present in *T. cynocephalus.* For the single specimen of *T. potens* the p. p. f. is large and complete. *Myrmecobius fasciatus* has a complete p.p.f. but no a.p.p.f. Accessory posterolateral palatal foramina are lost for all Dasyuridae. Posterolateral palatal foramina are incomplete or lost in all dasyurids excepting *Neophascogale* and some *Dasyurus viverrinus.*

Becht (1953) notes that the pterygoid is both small and inefficiently oriented in carnivorans and concludes that this arrangement is necessary to increase the size of the gullet. Loss of the posterolateral foramina and accessory posterolateral foramina correlates with increased carnassialization in marsupicamivores. This phenomenon is related to a general reduction in the transverse and ventral dimensions of the palatine ridge. Reduction of this ridge may permit the ingestion of larger food chunks and may also represent a response to the diminished importance of lateral shear in carnivorous taxa. For specialized mammalian carnivores jaw movement is restricted largely to the vertical plane (Mellet, 1984) and the internal pterygoid, a major contributor to lateral movement, is relatively small (Tumbull, 1970; Hiiemae, 1978). The internal pterygoid muscle attaches anteriorly to the palatine ridge in dasyurids (Rosenberg and Richardson, 1995), and reduction in the size of the muscle would diminish the required dimensions of muscle attachment sites.

The contention that complete posterolateral palatal foramina are lost in all dasyurids (Archer, 1982a,b, 1984; Marshall *et al.,* 1990) is incorrect. *Neophascogale* shows fully formed p.p.f. (Fig. lb). Complete p.p.f. are also present in some specimens of *Dasyrus viverrinus* (Fig. la). Given the appearance of posterolateral palatal foramina in the basal dasyurine *Neophascogale,* a high degree of variation at all taxonomic levels, and demonstrable correlation of p.p.f. loss with carnassialization in independent lineages, it is suggested that loss of this character can no longer be applied as a dasyurid synapornorphy.

Alisphenoid Tympanic Wing Morphology

For most metatherians development and posterior expansion of a process (wing) of the alisphenoid produces the alisphenoid hypotympanic sinus. Archer (1982b) considers a well-developed alisphenoid tympanic wing to represent a possible synapomorphy for the Dasyuridae. No alisphenoid tympanic process is present in *Pucadelphys andinus* (Muizon, 1994; Marshall and Muizon, 1995). Limited development of an alisphenoid tympanic wing is common to most didelphoids, although in some taxa, such as *Sparassocynus, Lutreolina, and Lestodelphys,* elaboration is pronounced (Marshall, 1977b; Reig *et al.,* 1987). Among borhyaenoids, *Mayulestes, Borhyaena, Prothylacinus, Proborhyaena, Lycopsis,* and *Thylacosmilus* lack an alisphenoid tympanic process, with only *Sipalocyon* and *Cladosictis* showing this feature (Patterson, 1965; Muizon, 1994). A well-developed alisphenoid tympanic wing is present in microbiotheriids. Among peramelemorphians the alisphenoid tympanic wing is small in *Microperoryctes longicauda* and *Peroryctes raffrayana* but large for other extant taxa. The basicranial region is unknown for all dasyuromorphians considered *incertae sedis here. Myrmecobius fasciatus* shows a large alisphenoid tympanic process. For thylacinid sp. this process is very poorly developed and comparable to those of unspecialized didelphids (e.g., *Didelphis, Metachirus).* Thylacinid sp. is less derived for this character than any other dasyuromorphian.

Development of this process is only slightly greater in *Thylacinus cynocephalus.* All dasyurids possess a well-developed alisphenoid tympanic contribution to the tympanic bulla (Archer, 1976b). Among dasyurids the smallest alisphenoid tympanic processes are shown by the species of *Murexia, Neophascogale,* and *Phascolosorex*; *the* largest, by *Dasycercus* and *Dasyuroides* (Figs. 1 and 2).

As noted above, expansion of the alisphenoid tympanic process is clearly linked to increased auditory efficiency, with allometric and ecological factors imposing the strongest selective pressure on small taxa. For marsupials the development of an alisphenoid tympanic wing has undoubtedly occurred in various independent lineages (Reig and Simpson, 1972; Reig *et al.,* 1987). Among dasyuromorphians hyptertrophy of this process is found in *Myrmecobius fasciatus,* as well as in dasyurids. This feature may constitute a myrmecobiid-dasyurid synapomorphy or an independently derived character for both clades.

Morphology of the Periotic Hypotympanic Sinus and Tympanic Wing of the Periotic

For many marsupial taxa a process is present on the promontorium of the petrosal part of the periotic (pars petrosa). Some clades show expansion of this process to produce a distinct tympanic wing (rostral tympanic process). At which point expansion of the petrosal tympanic wing produces a periotic hypotympanic sinus is open to a degree of interpretation. To avoid confusion, for this study a periotic hypotympanic sinus is acknowledged only where the anterior part of the petrosal tympanic wing contacts the posterior margin of the alisphenoid tympanic wing and a distinct cavity is produced within the expanded promontorium of the periotic. Wroe (1996) suggests that the development of a periotic hypotympanic sinus may constitute a dasyurid synapomorphy.

The rostral tympanic process is tiny or absent in Late Cretaceous North American marsupials (Wible, 1990), all didelphids excepting *Caluromys* and *Caluromysiops* [petrosal tympanic wing well developed and contacts alisphenoid tympanic wing (Reig *et al.,* 1987). No periotic hypotympanic sinus is present for borhyaenoids (Archer, 1976b; Muizon, 1994). *Dromiciops australis* shows a well-developed petrosal tympanic wing contacting the alisphenoid and enclosing a distinct sinus. Among peramelemorphians the petrosal tympanic process is very small for basal taxa with no sinus formed *(Peroryctes, Echymipera)* but well-developed in some specialized taxa (*Perameles, Macrotis, Isoodon*). *Myrmecobius fasciatus* shows a small periotic tympanic process (a ventrally directed extension with no marked anterior development) but the alisphenoid and petrosal tympanic wings do contact. However, within the limits defined above *M. fasciatus* shows no periotic hypotympanic sinus, as no cavity is delimited within the petrosal itself. For *Thylacinus cynocephalus* and thylacinid sp. the periotic tympanic crests are small and tiny, respectively, with no contact between the process of the promontorium and the alisphenoid tympanic process (Fig. 2). All dasyurids show an anteriorly directed tympanic process of the promontorium which contacts the posterior edge of the alisphenoid tympanic wing, forming a clearly defined periotic hypotympanic sinus (Fig. 1). The extent of development of these features is variable within the clade. Some dasyurid taxa (e.g., *Murexia, Neophascogale, Planigale*) show limited elaboration of the periotic tympanic wing and the associated sinus is small, while for others (e.g., *Dasycercus, Dasyuroides)* both features are greatly expanded.

As for the expansion of the alisphenoid tympanic wing, the development of a periotic hypotympanic sinus is associated with increased auditory efficiency. Lack of a petrosal tympanic wing and periotic hypotympanic sinus is plesiomorphic for marsupials. Dasyurids are unique among dasyuromorphians in showing, a periotic hypotympanic sinus and marked development of the petrosal tympanic wing (Fig. 1). The only marsupial taxa showing comparable morphology are some derived didelphids, specialized peramelemorphians, and microbiotheriids. Dismissal of these features as synapomorphies for Dasyuridae requires the acceptance of either a special relationship between dasyurids and one of these clades or apomorphic loss of a well-developed petrosal tympanic wing and periotic hypotympanic sinus in Thylacinidae and/or Myrmecobiidae.

An additional possible dasyurid synapomorphy associated with the petrosal part of the periotic does not appear to have been considered in previous literature. Ubiquitous for Dasyuridae is a well-developed tubular foramen immediately posterior and ventral to the foramen ovale (Fig. 1). This foramen is largely contained (anteroventrally) within the petrosal part of the periotic and floored by the periotic tympanic wing but is completed laterally by the alisphenoid tympanic wing. The tubal foramen carries the Eustachian canal (Aplin, 1990). Specific data for Dasyuridae regarding soft tissue morphology associated with the tubal foramen are unavailable. Aplin (1990) reports that for macropodoids a number of neurovascular elements are carried by this foramen, including the nerve to the tensor tympani muscle, the lesser petrosal nerve, and a branch of the anterior ramus of the internal carotid artery. As defined above for Dasyuridae, the tubal foramen cannot be present in any taxon which lacks a well-developed periotic tympanic wing, and it is absent for all didelphoids observed. Unfortunately, specimens *of Caluromys and Caluromysiops,* the only didelphoids reported to show well-developed periotic tympanic wings by Reig *et al*. (1987), are not available for comparison in this investigation. As no borhyaenids show distinct periotic tympanic wings (Archer, 1976b), it is presumed that a periotic-alisphenoid bounded tubal foramen is not present for the clade. A distinct tubal foramen is present for *Dromiciops australis.* No distinct foramen is present in this position for peramelemorphians, thylacinids, or *Myrmecobius fasciatus.*

A distinct tubal foramen is a derived feature present for all dasyurids, but no other dasyuromorphian taxa. Dismissal of this feature as a dasyurid synapomorphy requires acceptance of apomorphic reversal for known Thylacinidae and Myrmecobiidae or monophyly for Microbiotheriidae-Dasyuridae, to the exclusion of thylacinids and myr-rnecobiids.

P3 Morphology

Archer (1982a, b, 1984) and Marshall *et al.* (1990) have considered a "tendency" to reduce P3 as a shared derived character uniting Dasyuridae. A "tendency" for P3 reduction represents 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 criticized by a number of authors (Farris, 1986; Kitching, 1993) and is not accepted here.

P3 either is higher crowned or closely approximates the height of P2 for peradectids and many didelphoids. Goin (1993) notes moderate P3 reduction for most didelphids,

but a P3 larger than P2 is shown by basal fossil taxa within the clade (e.g., *Pucadelphys*) Marshall *et al.* (1990) consider hypertrophy Of P3 to be a borhyaenoid synapomorphy. P3 is larger than P2 for *Dromiciops australis* and for all peramelemorphians. For *Ankotarinja tirarensis,* P3 is slightly smaller than P2. *Wakamatha tasselli* shows a P3 much larger than P2. Premolar morphology is unknown for *Keeuna woodburnei or Dasylurinja kokuminola.* P3 morphology for *Myrmecobius fasciatus* is similar to that of P2. Thylacinid sp. shows P3 slight smaller than P2. The remaining thylacinid taxa for which P3 is known or can be reasonably estimated from alveolar dimensions (*Wabulacinus ridei, Thylacinus macknessi, Thylacinus potens, Thylacinus cynocephalus*) show a P3 much larger than P2. For most dasyurids P3 is smaller and lower crowned than P2 (Thomas, 1888; Bensley, 1903; Tate, 1947; Archer, 1976b). In a few dasyurid taxa P3 is not reduced (e.g., Murexia, many species of *Sminthopsis).* A number of dasyurid taxa show loss of P3, including *Planigale gilesi, Dasyuroides, Dasycercus, Dasykaluta,* and all *Dasyurus* excepting *D. dunmalli* [Luckett (1993) presents ontogenetic evidence suggesting that, for *Dasyurus viverrinus,* dP2 may be lost instead of P3]. Reduction or loss of P3 has evidently occurred independently within several marsupicarnivore lineages including most didelphids (Goin, 1993), some borhyaenoids (Marshall, 1977a), and several dasyurid genera including *Ningaui, Planigale, and Antechinus* (Ride, 1964b; Archer, 1976a).

Functionally P3 reduction may act 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). Russell *et al.* (1995) show that premolar loss need not correlate with shortening of the face and demonstrate that loss of P2 in *Lynx* may be a phenomenon associated with changing proportions within the deciduous tooth row. Whether or not the latter suggestion might apply to marsupial clades requires further investigation.

A P3 larger than P2 is plesiomorphic for all taxa considered in outgroup analysis for Dasyuromorphia. Dasyurid taxa considered to be actually or structurally plesiomorphic for most features within the three dasyurid subfamilies show a P3 larger than P2 (e.g., *Murexia* for Phascogalinae and nearly all Sminthopsinae) or a P3 Only slightly smaller than P2 (e.g., *Neophascogale* for Dasyurinae). It is concluded that marked P3 reduction is a synapomorphy uniting some taxa within Dasyuridae, but it is not a derived character uniting the family.

Stylar Cusp D Morphology

Cifelli (1993) advanced the consistent presence of a molar stylar cusp in the D position (i.e., between stylar cusps C and E on the stylar shelf) as a synapomorphy uniting early marsupial clades. A meristic gradient, with stylar cusp D increasing from Ml-2 and decreasing from M3-4, is almost-universal for marsupial carnivores and insectivores. Archer (1984) suggests that stylar cusp D hypertrophy may represent a dasyurid synapomorphy [cusp homology *sensu* Archer (1976c)].

For some peradectids (*Alphadon, Albertatherium*) stylar cusp D is distinct but smaller than stylar cusp B. Peradectines (e.g, *Peradectes)* show reduction of all stylar cusps (Marshall *et al.,* 1990). Among didelphoids, *Pucadelphys andinus* (Marshall and Muizon, 1988, 1995) and *Mirandatherium* (Marshall, 1987) show moderate development of stylar cusp D, with stylar cusp B the largest and highest cusp. For Didelphidae

stylar cusp D is generally present, but of comparable size or smaller than stylar cusp B. Some derived didelphids show marked reduction of stylar cusp D (e.g., *Lutreolina*). Among borhyaenoids stylar cusp D is either smaller than stylar cusp B (e.g., *Mayulestes ferox)* or lost (Marshall, 1981; Muizon, 1994), Microbiotheriids show marked reduction of all stylar cusps. The middle Miocene peramelemorphian *Yarala burchfieldi* shows a stylar cusp D markedly larger than stylar cusp B on M^{1-4} (Muirhead, 1995). For other bandicoot taxa stylar cusp D is of comparable size to, or slightly larger than, stylar cusp B.

For the fossil taxa *Ankotarinja tirarensis* and *Keeuna woodburnei,* stylar cusp D is slightly larger than stylar cusp B, but all stylar cusps are very poorly developed. *Dasylurinja kokuminola* shows stylar cusp D larger than stylar cusp B for the holotype and only specimen   (M3), with both cusps much larger than for *A. tirarensis* and *K. woodburnei.* For *Myrmecobius fasciatus* both upper and lower dentitions are greatly reduced, with no clear homologues for stylar cusps apparent. For basal thylacinids (i.e., *Muribacinus gadiyuli,* thylacinid sp., *Nimbacinus dicksoni),* stylar cusp D is well developed on M1-2, but tiny on M3 . For the remaining thylacinid taxa all stylar cusps are greatly reduced or absent. Nearly all dasyurids show a large stylar cusp D which exceeds stylar cusp B in height. Reduction of stylar cusp D occurs in specialized carnivorous taxa, particularly *Dasyurus and Sarcophilus.* For these large dasyurid carnivores reduction of stylar cusp D is accompanied by its close juxtaposition to the metacone (not shown in thylacinids).

Stylar cusp D size diminishes with increases in both overall body size and carnassialization for dasyurids and thylacinids. A large stylar cusp D may have adaptive value as an accessory in the mastication of tough insect exoskeletons. This cusp has no direct occlusal partner in the lower dentition when the mandible is fully elevated. Crompton and Hiiemae (1970) demonstrated that lateral movement of the mandible precedes a preparatory stroke, followed by the "power stroke" in *Didelphis marsupialis.* It appears that in dasyurids and plesiomorphic thylacinids, stylar cusp D may help to contain food within the stylar shelf, as it is punctured/crushed by the hypoconid of the lower molar in the preparatory stroke (unpublished data). Actual occlusion between dental elements is not necessary for efficient puncturing/crushing (Young *et al.,* 1989), although Moore and Sanson (1995) suggest that puncture/crushing should be complemented by a strong vertical shear component for optimum performance. In specialized carnivorous dasyurids (*Dasyurus, Sarcophilus),* stylar cusp D is positioned increasingly anteriorly from M^{1-4}, while in specialized thylacinids stylar cusp D migrates posteriorly (M^{1-4})**.** This phenomenon might be explained as a function of brachycephalization and dolichocephalization, which characterize dasyurids and thylacinids, respectively. In specialized dasyurids shortening of the face is accompanied by a marked reduction of the talonid on the long axis and anterior shifting of the hypoconid relative to the metacone and stylar cusp D. In order to maintain a relationship with the hypoconid, stylar cusp D must also be shifted anteriorly. For basal thylacinids (e.g., *Muribacinus,* thylacinid sp.), although the talonids are reduced in terms of complexity, they are little diminished on the long axis, and stylar cusp D must remain in a posterior position if it is to act as a brace for hypoconid puncturing. It is not clear whether the demonstrable reduction in stylar cusp D size with increasing carnassialization and overall body size in both taxa is related to decreased reliance on insects as prey, mechanical constraint (lateral movement of the

mandible is typically reduced in carnivorous mammals), allometric phenomena, or a combination thereof. However, the presence of a large stylar cusp D in all insectivorous dasyurids, less specialized thylacinids, and plesiomorphic insectivorous bandicoots (Muirhead and Filan, 1995) suggests that the cusp plays some role in cuticle puncturing. On the basis of outgroup data the acquisition of a large stylar cusp D (both in absolute terms and relative to stylar cusp B) may be synapomorphic for Peramelemorphia-Dasyuromorphia, or Thylacinidae-Dasyuridae, or may represent an independently derived shared character for each of these clades.

Hypoconulid Notch Morphology

Many marsupial carnivore and insectivore taxa show an anterior cingulid on the lower molars. For some species the anterior cingulid is interrupted by a notch which receives the hypoconulid of the preceding molar. Archer (1982b, 1984) regards the development of a hypoconulid notch in the anterior cingulum as a possible dasyurid synapomorphy.

For peradectids the single representative lower dentition available to the author *(Alphadon marshii)* shows a well-developed anterior cingulid and hypoconulid notch. Didelphoids show variable morphology for this feature, but a well-developed hypoconulid notch is present in some taxa (e.g., *Didelphis).* Among borhyaenoids a hypoconulid notch is shown by *Patene simpsoni,* but reduced or absent for other taxa (with the possible exception of *M. ferox).* This feature is absent for microbiotheriids, peramelemorphians, and *Myrmecobius fasciatus* and present for *Ankotarinja tirarensis, Keeuna woodburnei, and Wakamatha tasselli* (poorly defined for *W. tasselli).* Among thylacinids, a well-developed hypoconulid notch is present for *Muribacinus* and thylacinid sp., weakly defined in *Ngamalacinus,* and lost in all other taxa. A well-developed hypoconulid notch is present for all dasyurids excepting *Dasyurus maculatus* (reduced), *Glaucodon* and *Sarcophilus* (absent).

The hypoconulid notch forms a functional complex with the hypoconulid of the preceding molar. Changes in the size and/or position of the hypoconulid are intimately linked with the morphology of the notch. No single form-function rationale explains the distribution of the hypoconulid notch among metatherian taxa, but some trends are apparent. Within Dasyuromorphia a correlation exists among increasing size, carnassialization, and reduction or loss of this feature. In the largest and most specialized clades of both the Thylacinidae and the Dasyuridae (*Thylacinus* and *Sarcophilus,* respectively), the hypoconulid notch is absent. A similar morphocline is shown for the Borhyaenoidea, with the greatest reduction shown in the most derived carnivorous taxa (e.g., *Pharsophorus cretaceus, Proborhyaena gigantea).* For marsupial obligate-carnivores reduction/loss of the hypoconulid and hypoconulid notch may simply be an incidental product of carnassialization, associated with the diminished importance of horizontal shear for the dentition (i.e., a general reduction of the talonid and protocone). Other causal mechanisms include a relaxation of selective pressures which originally produced and maintained the feature. As the hypoconulid and hypoconulid notch together form a brace against transverse movement of the molars, their reduction implies a diminution of transverse forces applied to the tooth row. This interpretation is consistent with the general reduction in transverse jaw movement apparent in mammalian carnivores. Allometric

factors may also produce reduction of the hypoconulid notch. Legendre and Roth (1988) show that relative tooth size correlates inversely with body mass in carnivores. It may be that as the jaw becomes relatively more robust, additional room is provided for more extensive root development, detracting from the requirement for an accessory buttress against transverse movement. For some marsupial taxa, however, loss of the hypoconulid notch is difficult to explain in a functional context. For example, all bandicoots completely lack this character, including the small plesiomorphic insectivore *Yarala burchfieldi* (Muirhead and Filan, 1995).

Outgroup data are equivocal regarding hypoconulid notch morphology for Dasyuromorphia. This feature is present for some putative outgroup taxa (e.g., some peradectids and didelphids) but absent for others (microbiotheriids, peramelemorphians). Microbiotherians are dentally specialized (Reig *et al.,* 1987) and bandicoots are derived regarding hypoconulid morphology for metatherians (Muirhead and Filan, 1995), showing reduction, lowering, and an extreme labial position of this cusp. It is probable that this complex of apomorphies for the ancestral peramelemorphian hypoconulid would have been accompanied by loss of the hypoconulid notch. The presence of a hypoconulid notch may be symplesiomorphous or synapomorphous for Dasyuromorphia. Within Dasyuromorphia all unspecialized taxa considered Dasyuromorphia *incertae sedis,* dasyurids (excepting *Sarcophilus* and *Glaucodon*), and basal thylacinids *(Muribacinus,* thylacinid sp.) show a well-developed hypoconulid notch. This feature is lost only in dasyurid and thylacinid taxa showing advanced carnassialization and the termite-eating *Myrmecobius fasciatus.* It is considered likely that a hypoconulid notch was present in the common ancestor of all three families and does not represent a dasyurid synapomorphy.

Based on outgroup analysis and form-function data, loss or reduction of the hypoconulid notch is homoplasious for carnivorous dasyurids and thylacinids and the termite-eating *Myrmecobius fasciatus.* Loss of the hypoconulid notch is common to large metatherian carnivores; its loss in *M. fasciatus* is probably the product of a different selective regime which accompanied general atrophy of the dentition.

Intestinal Cecum

Marshall *et al.* (1990) cite loss of the intestinal cecum as a dasyurid synapomorphy. Aplin and Archer (1987) consider loss of this character to represent a possible dasyuromorphian synapomorphy. Hume (1982) notes that a small but distinct intestinal cecum is present for didelphoids examined (species of *Marmosa, Chironectes, Philander)* and in *Caenolestes.* The microbiotheriid *Dromiciops australis* also shows an intestinal cecum (Hershkovitz, personal communication). For extant Australidelphia the intestinal cecum is present for all taxa excepting Notoryctidae, Thylacinidae, Myrmecobiidae, Dasyuridae, and a single diprotodontian taxon, *Tarsipes* (Mitchell, 1905; Hume, 1982).

Loss of the intestinal cecum is ubiquitous for specialized insectivorous and carnivorous mammalian clades (Hume, 1982). From the distribution of this feature among extant marsupial taxa, it is likely that loss of the intestinal cecum appeared early in dasyuromorphian evolution and probably represents a synapomorphy for the order, rather than just for Dasyuridae.

DISCUSSION

Paleobiology

Niches filled by small to medium-sized thylacinids during Miocene times have since been occupied by specialized dasyurids. Three possible explanations for this phenomenon are proposed: (1) dasyurids out competed thylacinids for existing niche spaces following the derivation of "key innovations" which conferred an adaptive advantage on Dasyuridae; (2) changing extrinsic factors differentially selected the relatively specialized Thylacinidae for extinction over generalist, less ecologically constrained, Dasyuddae; or (3) changing extrinsic factors provided new niche spaces for which dasyurids were preadapted. Each of these hypotheses may stand as an explanation singularly or in some combination with the remaining factor(s).

Wroe (1997) speculates that the derivation of specialized features associated with increased auditory efficiency may have provided an adaptive advantage which precipitated the ascendancy of apomorphic dasyurines over Thylacinidae. Heard and Hauser (1995) suggest that "key innovation" hypotheses must be founded on evidence of both ecological mechanism and comparative analysis. The suggestion of competitive exclusion of Thylacinidae by Dasyuridae (Wroe, 1996) has remained purely conjectural in the absence of comparative data from pre-Pliocene deposits (i.e., regarding basicranial features for both taxa). However, recent fossil discoveries from early to middle Miocene deposits in Riversleigh, including the oldest undisputed representatives of both families (Muirhead and Wroe, submitted; Wroe, unpublished data) have furnished relevant material. Available evidence now shows that the most fundamental morphological differences between plesiomorphic thylacinids and dasyurids are in the auditory region and that apomorphies peculiar to dasyurids among dasyuromorphians have been associated with adaptive advantage in other mammalian taxa. Thylacinid sp. is very plesiomorphic for features of the middle ear (e.g., tiny petrosal tympanic wing), while newly discovered dasyurids from Miocene deposits show fully enclosed hypotympanic and epitympanic regions, as for all Recent Dasyuridae. As discussed above, the improved low-frequency hearing delivered by maintenance of a large and stable middle ear volume (facilitated by the expansion of tympanic processes in dasyurids) is an allometric function. Provision of a minimally effective middle ear volume may also be achieved through increased overall size, without the development of new morphological features. Thus, the advantage imparted by flooring the middle ear is less obvious for large taxa. This may explain differential extinction within Thylacinidae. Smaller thylacinids are unknown from deposits younger than mid-Miocene in age, while the large specialized *Thylacinus cynocephalus* has persisted until Recent times. More conclusive demonstration of competitive exclusion as the agent for thylacinid extinction requires evidence for contemporaneous existence of carnivorous representatives for both clades during the period in question (late Miocene to early Pliocene). If it is shown that contemporaneous thylacinid and dasyurid taxa contested the same adaptive zones, then competitive exclusion is strongly implicated.

Mammalian diversity has decreased in post-Miocene times on the Australian continent (Archer *et al.,* 1994, 1995). Large specialized taxa are particularly vulnerable to extinction associated with environmental change. The onset of prolonged aridity for

Australia by the late Miocene (Greenwood, 1994; Martin and McMinn, 1994; Archer *et al.*, 1995; Macphail, 1996) may have selected apomorphic carnivorous Thylacinidae for extinction over smaller, less ecologically constrained, Dasyuridae. Subsequently, dasyurids may have assumed dominance by default and simply adapted to fill vacated positions, i.e., replacement was not correlated with any intrinsic advantage other than a lack of specialization.

As with the first hypothesis, the third hypothesis also invokes "key adaptation" in the explanation of reversed diversity for Thylacinidae and Dasyuridae, but not competitive exclusion for existing niches. The acquisition of a complete floor to the middle ear must be considered in hypotheses explaining the successful diversification of dasyurids into semiarid habitats. Webster and Webster (1975, 1980) propose that efficient low-frequency hearing is of particular importance regarding predator avoidance for small taxa occupying and habitats. If this hypothesis is correct, then ancestral dasyurid lineages, showing enclosed hypotympanic and epitympanic recesses, may have been admirably preadapted to fill new niches on the increasingly xeric Australian continent of the late Tertiary.

Phylogeny

Synthesis of new data from fossil material and ontogeny shows that six of eight previously proposed dasyurid synapomorphies are likely to be of differing evolutionary significance. Thus, alisphenoid-periotic enclosure of the foramen ovale is present in dasyuromorphian outgroups, loss of the intestinal cecum is considered a likely dasyuromorphian synapomorphy, development of a hypoconulid notch and enlargement of stylar cusp D may represent synapomorphies uniting Thylacinidae-Dasyuridae, and loss of posterolateral palatine foramina and reduction of P3 unify specialized clades within Dasyuridae but not the family itself. Only two features, enlargement of alisphenoid tympanic wing and development of a distinct periotic hypotympanic sinus, are considered to be likely synapomorphies for Dasyuridae. An additional apomorphy identified during this investigation, shared by all Dasyuridae, is the presence of a tubal foramen. Of these three features, only the presence of a periotic hypotympanic sinus and a distinct tubal foramen are unique for Dasyuridae among dasyuromorphians. Basicranial features have often been advanced as less subject to homoplasy than dental character states and there- fore more reliable indicators of relationship. Novacek (1977) and Fleischer (1978) have hypothesized that the selective regime which produces a floor to the middle ear does not favor the development of any individual elements or any combination of elements over another. MacPhee (198 1) considers that tympanic processes are not easily lost or gained. However, evidence contra these assertions has been forwarded, at least with regard to Diprotodontia (Aplin, 1990; Norris, 1993).

Archer (1982a) considered Dasyuridae a more recently derived taxon than Thylacinidae. Accumulating paleontological and molecular data support this tenet of Archer's (1982a, 1984) concept of relationships within Dasyuromorphia. A diverse thylacinid clade has been identified in Oligocene and Miocene deposits of Riversleigh (Muirhead and Archer, 1990; Muirhead, 1992, 1997; Muirhead and Gillespie, 1995; Muirhead and Wroe, submitted; Wroe, 1996), including highly derived *Thylacinus;* although dasyurids are present in these deposits, they are relatively scarce (unpublished data).

The results of this study emphasize the need for more extensive morphological and molecular investigations aimed at resolving interfamilial relationships for Dasyurornorphia. On the basis of morphological features considered in this treatment, the phylogenetic position of the three dasyuromorphian families is equivocal. Hypertrophy of the alisphenoid tympanic wing may unite Dasyuridae and Myrmecobiidae to the exclusion of Thylacinidae. Alternatively, enlargement of stylar cusp D may unite Dasyuridae and Thylacinidae to the exclusion of Myrmecobiidae. At present there is little to recommend ascendancy of either sister-group hypothesis over the other. Alisphenoid tympanic expansion has been independently derived in a number of marsupial taxa. For *Myrmecobius fasciatus* the alisphenoid tympanic wing is anteromesially extended add contacts the mastoid tympanic process (Archer and Kirsch, 1977). These features are autapomorphic for *M. fasciatus* and led Archer (1982b, p. 448) to remark, "Details of the construction of the floor of the middle ear suggest that acquisition of the enlarged alisphenoid hypotympanic sinus in myrmecobiids occurred in parallel with the similar but different enlargement in dasyurids." Following reexamination, the strongest morphological indicator of monophyly for Dasyuridae and Myrmecobiidae proposed by previous authors (alisphenoid-periotic enclosure of the foramen ovale) is considered a marsupial and dasyuromorphian plesiomorphy. Recent investigations of phylogeny within Dasyuddae using molecular data have employed *Thylacinus* (Krajewski *et al.,* 1992) or *Myrmecobius (Baverstock et al.,* 1990; Krajewski *et al.,* 1993) as the outgroup taxon, but only one molecular investigation has addressed intraordinal relationships for the three dasyuromorphian families (Lowenstein *et al.,* 198 1). In the absence of strong conflicting data from any other character system, the suggested phylogeny of Lowenstein *et al.* (1981), wherein Myrmecobiidae was considered the sister taxon to Thylacinidae-Dasyuridae, is very tentatively accepted. However, a less equivocal basis for identifying the sister taxon to Dasyuridae would clearly be of great value.

Considerable homoplasy within Dasyuromorphia is suggested by the results of the present analysis. Alisphenoid enclosure of the foramen ovale has occurred independently in specialized thylacinid and dasyurid clades, as have the development of secondary foramina ovale and loss of posterolateral palatal foramina. Hypertrophy of the alisphenoid tympanic wing for dasyurids and myrmecobiids is likewise probably attributable to convergence. A further problem centers on the development of the squamosal epitympanic sinus within Dasyuromorphia, considered a dasyuromorphian synapomorphy by Aplin and Archer (1987) and a synapomorphy uniting Australian marsupials by Marshall *et al.* (1990). For the phylogeny accepted here, this feature must have been independently derived within all three dasyuromorphian families, unless absence of a squamosal epitympanic sinus is treated as an apomorphic reversal for thylacinid sp. Two Australian marsupial taxa have now been described which lack this feature (thylacinid sp., *Yalkaparidon coheni).* Because these two taxa, considered plesiomorphic for basicranial characters, both lack a squamosal epitympanic sinus, the possibility that development of this sinus represents a synapomorphy for Australian marsupials is unlikely, contra Marshall *et al.* (1990).

The fossil dasyuromorphians *(Ankotarinja tirarensis, Keeuna woodburnei, Wakanwtha tasselli, and Dasylurinja kokuminola),* currently known from dental material alone, show no features that can be considered synapomorphic for Dasyuridae or any other dasyuromorphian family. The position of Wroe (1996) is reiterated: these taxa should

be considered Dasyuromorphia *incertae sedis* until/unless derived features are identified permitting their placement at the family level on the basis of synapomorphy.

The present inability to define Dasyuridae on the basis of derived dental features presents a considerable challenge to students of the clade's paleontology and evolution. Further detailed character analyses incorporating new data from Eocene (Murgon), Oligocene, and Miocene (Riversleigh) fossil deposits, and the results of molecular analyses, will provide a more robust basis for the understanding of dasyuromorphian phylogeny.

ACKNOWLEDGMENTS

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