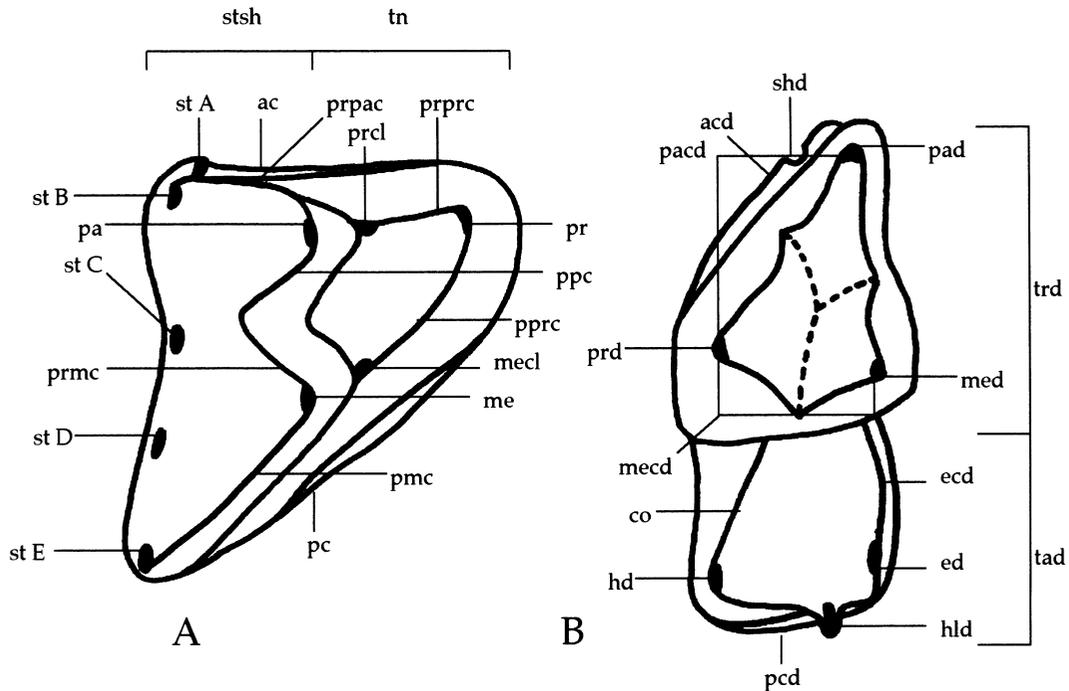


THE GEOLOGICALLY OLDEST DASYURID, FROM THE MIOCENE OF RIVERSLEIGH, NORTH-WEST QUEENSLAND

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ABSTRACT. A new subfamily, genus and species of Dasyuridae is described on the basis of exceptionally well preserved material from the Miocene of Riversleigh, north-west Queensland. Specimens include the only pre-Pleistocene crania known for the family. *Barinya wangala* gen. et sp. nov. (Barinyainae subfam. nov.) is the geologically oldest taxon that can be placed within Dasyuridae on the basis of synapomorphies that are unequivocal within Dasyuomorpha. Four derived cranial features present in *Barinya wangala* are shared only with modern Dasyuridae among dasyuomorphians. These are: development of a tympanic process of the *pars petrosa* to form a distinct periotic hypotympanic sinus; presence of a paroccipital hypotympanic sinus; presence of a deeply invasive sulcus with the posteroventral lip formed by a mesially directed process in the *pars petrosa* for passage of the internal jugular; and presence of a distinct tubal foramen for passage of the Eustachian tube. Additionally, the following four apomorphies are identified that are found in all modern Dasyuridae, but no other Dasyuomorpha, including *Barinya wangala*: presence of a fully enclosed styломastoid foramen that includes a periotic component; contact between the *pars petrosa* and a paroccipital tympanic process that fully encloses the paroccipital hypotympanic sinus ventrally; extensive dorsal enclosure of the internal jugular canal; and contact between the mastoid tympanic process and the *pars petrosa*. *Barinya wangala* represents the sister clade to a monophyletic taxon that includes all extant Dasyuridae. The perception that even basal Dasyuridae may represent morphological approximations of the ancestral australidelphian or dasyuomorphian is strongly refuted.

THE fossil record of Dasyuomorpha has been reviewed by Archer (1982a, 1982b; see Wroe (1996a, 1997a) for a more recent introduction to the literature). Dasyuomorpha consists of three families: Thylacinidae, Myrmecobiidae and Dasyuridae. Thylacinidae is now extinct. Myrmecobiidae is monophyletic and unknown from the fossil record. The 64 recognized extant species of living dasyurid currently dominate marsupial carnivore-insectivore niches in Australasia. Fifty-one are endemic to Australia (Strahan 1995) and 13 to New Guinea (Flannery 1995). Owen (1838) described the first fossil dasyuomorphian, *Sarcophilus laniarius*, a specialized dasyurid of Pleistocene age. Following a 69 year hiatus Stirton (1957) described another fossil dasyurid, *Glaucodon ballaratensis*, and a third fossil taxon was added, *Dasyurus dunmalli* (Bartholomai, 1971), both from Pliocene deposits. *Thylacinus potens* Woodburne, 1967, from the Alcoota Local Fauna (Pliocene), represented the first thylacinid known other than the recently extinct *Thylacinus cynocephalus*. Additional taxa of Pliocene–Pleistocene age include three dasyurids: *Sarcophilus moornaensis* Crabb, 1982, *Sminthopsis floravillensis* Archer, 1982a and *Dasyuroides achilpatna* Archer, 1982a. Descriptions of the first pre-Pliocene dasyuomorphians, *Ankotarinja tirarensis* and *Keeuna woodburnei*, from the late Oligocene to Miocene Etadunna Formation of South Australia, were published by Archer (1976a) and two further Miocene taxa were described from the Namba Formation of central Australia: *Wakamatha tasselli* Archer and Rich, 1979 and *Dasylurinja kokuminola* Archer, 1982a. The pace of new discovery has accelerated following the unearthing of abundant dasyuomorphian material from the late Oligocene and Miocene deposits of Riversleigh in north-west Queensland, with seven new taxa described in recent years. These include six new thylacinid species: *Nimbacinus dicksoni* Muirhead and Archer, 1990, *Thylacinus macknessi* Muirhead, 1992, *Wabulacinus ridei* Muirhead, 1997, *Ngamalacinus timmulvaneyi* Muirhead, 1997, *Badjcinus turnbulli* Muirhead and



TEXT-FIG. 1. Stylized dentition of generalized marsupial. A, upper right molar; B, lower left molar.

Wroe, 1998 and *Muribacinus gadiyuli* Wroe, 1996a. An additional dasyuromorphian of uncertain family level affinity, *Mayigriphus orbus*, has also been described by Wroe (1997b).

Among dasyuromorphians, understanding of the evolution of the dasyurids has been considered to be of particular importance because the taxon has been treated as structurally, if not actually, ancestral to the Australian marsupial radiation (Bensley 1903; Ride 1964; Szalay 1993, 1994). However, the investigation of recently discovered fossil material from the Oligocene and Miocene sediments of Riversleigh has shown the ascendancy of Dasyuridae within Dasyuromorphia to be a relatively recent phenomenon (Wroe 1996a, 1997a; Muirhead and Wroe 1998).

The fossil-rich Oligocene–Miocene sediments of the Riversleigh World Heritage Estate, north-west Queensland, have yielded an unexpected diversity of mammalian taxa, with up to 63 mammal species identified in a single local fauna, i.e. Upper Site (Archer *et al.* 1993). Material described below, from the lower to middle Miocene of Riversleigh, includes the most complete dasyuromorphian, and only dasyurid cranial specimen known to date from any pre-Pliocene deposit. One other pre-Pliocene dasyuromorphian, the thylacinid *Badjcinus turnbulli*, has been described on the basis of partial cranial material (Muirhead and Wroe 1998).

Dental nomenclature follows Flower (1867) and Luckett (1993) regarding the molar-premolar boundary, where the adult (unreduced) postcanine cheektooth formula of marsupials is P1–3 and M1–4. Dental terminology is given in Text-figure 1. Basicranial terminology follows Archer (1976b), excepting that for the V³ foramina (see Gaudin *et al.* 1996; Wroe 1997a). Systematic terminology largely follows Aplin and Archer (1987), but with that used for Dasyuromorphia as amended by Krajewski *et al.* (1994) and Wroe (1996a, 1997a).

Institutional abbreviations. QM F, Queensland Museum fossil collection; YPFB Pal, palaeontology collection of Yacimientos Petroliferos Fiscales de Bolivia in the Centro de Tecnologia Petrolera, Santa Cruz, Bolivia; and MNHN, Institut de Paleontologie, Museum National d’Histoire Naturelle, Paris.

SYSTEMATIC PALAEOLOGY

Order DASYUROMORPHIA Gill, 1872
 Superfamily DASYUROIDEA Goldfuss, 1820
 Family DASYURIDAE Goldfuss, 1820
 Subfamily BARINYAINAE subfam. nov.

Diagnosis. As for the genus.

Genus BARINYA gen. nov.

Derivation of name. Barinya is the Wanyi Aboriginal word for a 'native cat' (Dymock 1993).

Type species. *Barinya wangala* gen. et sp. nov.

Diagnosis. The genus can be clearly distinguished from all other Dasyuridae by the presence of the following derived features: P^3 is a very large bulbous tooth which approaches or exceeds M^1 on the transverse dimension; and P_2 is relatively larger than that of any other dasyurid, being longer than, and almost as wide as M_1 .

Barinya wangala gen. et sp. nov.

Plate 1; Text-figures 2–4

Derivation of name. Wangala is the Wanyi Aboriginal word for dreamtime (Dymock 1993).

Holotype. Nearly complete skull, QM F31408, with only the right ectotympanic, most of the right and left alisphenoid tympanic wings and the anteriormost tips of the nasals missing (Pl. 1, figs 1–3; Text-fig. 2A–C).

Paratypes. QM F31409, skull containing complete left and right dentitions except the canines and incisors. The premaxillae, palatine and transverse palatine processes are broken away (Text-figs 3A, 4A); mandible QM F23889 containing right and left $C_1 P_{1-3} M_{1-4}$ (Text-figs 3B–D, 4B–D); dentary fragments, QM F31410, containing $P_{1-3} M_{1-4}$, QM F 31411 containing $P_{1-3} M_{1-4}$, QM F 31412 containing $P_{2-3} M_{1-3}$, QM F31413 containing $P_{1-3} M_{2-3}$, QM F31425 containing M_{1-4} , QM F31426 containing M_{3-4} , QM F3147 containing M_{3-4} ; isolated lower molars QM F31421 M_4 , QM F31424 M_4 ; maxillary fragments QM F23261 containing $P^{2-3} M^{1-4}$, QM F31414 containing $P^{2-3} M^{1-3}$, QM F31415 containing M^{2-3} , QM F31416 containing M^{2-4} , QM F31417 containing $P^3 M^{1-4}$, QM F31418 containing $P^{2-3} M^{1-4}$ and QM F31419 containing M^{3-4} ; and isolated upper molars QM F31420 M^2 , QM F31422 M^2 and QM F31423 M^3 .

Type locality and age. Neville's Garden Site, Riversleigh World Heritage Estate, north-west Queensland. Estimated to be early to mid Miocene in age (Archer *et al.* 1995).

Locality and age of paratypes. All specimens have been collected from the Riversleigh World Heritage Estate, north-west Queensland and suggested dates are from Archer *et al.* (1995). QM F31409–31410, QM F23889 from Neville's Garden Site; QMF 23261, QM F31411–31412 from Bite's Antennary Site; and QM F31414–31421 from Upper Site are considered to be early Miocene in age. QM F31413 from Jim's Jaw Site; and QM F31422–31427 from Henk's Hollow Site are considered to be mid Miocene in age. Thus, the estimated stratigraphical range of this taxon is early to mid Miocene.

Diagnosis. As for the genus.

Description

The quality of preservation is exceptional, particularly that of the holotype, QM F31408. Minimal deformation is present in this specimen, and is restricted to slight, clockwise torsion of the rostrum in anterior view. Almost all cranial, mandibular and dental morphology is preserved in the holotype and paratypes. Specimens QM F31408 and QM F31409 preserve all cranial elements excepting the anteriormost tip of the nasal and a ventral portion of the premaxilla. The angular process of the dentary is not preserved in any specimen. The complete upper and lower dentitions are known, excepting I_1 and I_2 .

Skull. The skull is markedly dolichocephalic, with the pre-orbital region elongate with respect to the postorbital region. Posterodorsally, well developed sagittal and nuchal crests are present. Postorbital constriction is pronounced. In ventral view enclosure of the middle ear is near-complete. The alisphenoid and periotic tympanic wings contact, as do those of the paroccipital and mastoid, but posteriorly the mastoid tympanic wing does not contact the *pars petrosa*.

The nasal is elongate, almost half the total skull length and is roughly wedge-shaped in dorsal view. It is delimited by the premaxilla anteriorly, the maxilla laterally and the frontal posteriorly. The posteriormost limit of the nasal-frontal suture is dorsal to the juncture of M^3 and M^4 .

The premaxilla contains I^{1-4} . In lateral view the ascending process forms a right angled triangle between the nasal and maxilla. In dorsal view a distinct U-shape is produced. Ventrally and immediately posterior to I^4 a circular depression is present for the reception of C_1 .

The maxilla largely contains C^1 , but a small sulcus in the posteroventral rim of the premaxilla delimits this tooth anteriorly. In ventral view a vacuity which extends from a point level with the protocone of M^1 to that of M^4 is bordered by the maxillae and completed by the palatine posteriorly. The rostral opening of the infraorbital canal is laterally compressed and positioned *c.* 3 mm above the M^{1-2} juncture. The posterior rim of this opening is *c.* 1 mm anterior to the maxilla-lacrimal suture. Posterodorsally there is narrow contact between the maxilla and frontal. Within the orbit the maxilla is wedge-shaped, tapering anteriorly and contributing to the internal opening of the infraorbital canal which is completed by the lacrimal dorsally.

In ventral view the palatine terminates posteriorly in a slightly thickened rim. Laterally this rim contains a sulcus for vestigial posterolateral palatine and accessory posterolateral palatine foramina. The accessory posterolateral palatine sulcus is the more mesially positioned. The anterior rim of the posterolateral palatine sulcus is contributed to by the maxilla. A thin sliver of the palatine extends anteriorly to the internal opening of the infraorbital canal, and a large elliptical sphenopalatine foramen is positioned in the anteroventral corner of the bone's orbital face.

The lacrimal forms the anterior rim of the orbit within which it is bordered by the frontal dorsally, the maxilla anteriorly, the palatine posteriorly and the jugal laterally. Superior and inferior lacrimal foramina are positioned near the rostral-maxillary suture.

In lateral view the jugal extends anteriorly to a point immediately beneath the inferior lacrimal foramen. This bone delimits the lateral border of the glenoid fossa forming a distinct lateral glenoid process. Anterodorsally, a V-shaped intrusion of the nasals extends down along the midline of the skull and is bordered by the frontals.

The frontal-maxilla suture is *c.* 3 mm long. Dorsolaterally the frontal is bordered by the lacrimal and a strongly developed supraorbital process is present. Posterodorsally the frontal meets the parietal, forming the anteriormost extent of the sagittal crest. Posterolaterally this bone has a broad contact with the alisphenoid, and ventromesially it is delimited by the sphenorbital. At the anterodorsal boundary of the frontal-sphenorbital suture a sulcus within the frontal is continuous with the ethmoidal foramen of the sphenorbital. Within the orbit the frontal is bounded by the palatine ventrally and the lacrimal anteriorly.

The parietals meet dorsally to form a well-developed sagittal crest and the parietal-alisphenoid contact is extensive. Posterolaterally the parietal extends to the posterior face of the cranium and contributes to the nuchal crest, but is met by the wedge-shaped interparietal dorsally.

A well defined interparietal-parietal suture extends anteriorly to a point dorsal to the subsquamosal foramen. Posteriorly the interparietal forms most of the anterior face of the nuchal crest and has a broad contact with the supraoccipital.

The sphenorbital is small, only a minor contributor to the orbit and roughly saddle-shaped. It is bordered by the

EXPLANATION OF PLATE I

Figs 1–3. *Barinya wangala* gen. et sp. nov.; holotype, QM F31408; skull. 1, ventral view; 2, dorsal view; 3, lateral view. All $\times 2$.



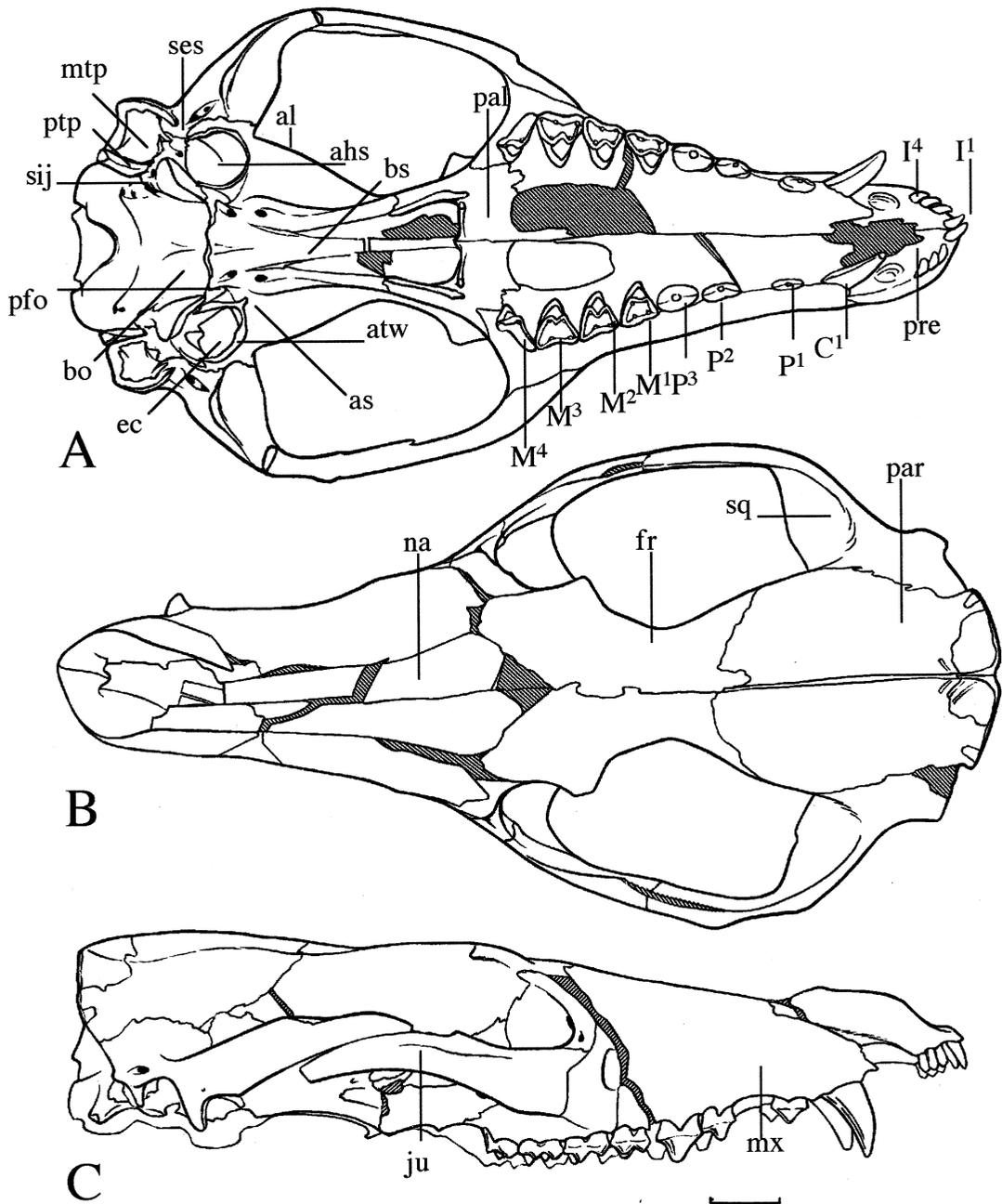
1



2



3



TEXT-FIG. 2. *Barinya wangala* gen. et sp. nov.; holotype, QM F31408; skull. A, ventral view; B, dorsal view; C, lateral view. Scale bar represents 5 mm.

frontals anterodorsally, the palatines anteroventrally and the alisphenoid and basisphenoid posteriorly. A distinct sulcus in this bone forms the mesial wall of the ethmoidal foramen which is completed by the frontal laterally. This bone forms the anteromesial wall of the optic foramen.

The alisphenoid contacts the frontal anterodorsally, the parietal dorsally and the squamosal posterodorsally. In lateral view this bone contacts the palatine anteriorly, bounds the posterior wall of the optic foramen and contains the foramen rotundum which is confluent with a smaller, secondary foramen rotundum anterodorsally. In ventral view this bone abuts the basisphenoid mesially. Posteromesially the alisphenoid and basisphenoid are fused to form a distinct keel, and their sutures are indistinct. The alisphenoid encloses the transverse canal foramen and posterior to this foramen it contributes to the lateral wall of the internal carotid foramen. Posterolateral to the internal carotid foramen the alisphenoid bounds the primary foramen ovale, which is delimited by the petrosal part of the periotic (*pars petrosa*) posteriorly. A well developed alisphenoid tympanic process encloses the large alisphenoid hypotympanic sinus and has a broad contact with the tympanic wing of the *pars petrosa* posteriorly.

The basisphenoid forms an elongate wedge-shape that tapers anteriorly and contacts the presphenoid ventral to the optic orbital foramen and the basioccipital posteriorly.

The basioccipital, exoccipital and supraoccipital are not clearly differentiated and for the purposes of description will be considered together (BES). In ventral view the BES is bordered by the basisphenoid anteriorly, the *pars petrosa* mesially and the tympanic process of the mastoid part of the periotic (*pars mastoidea*) posteromesially. A well developed laterally directed process contacts the mesially oriented process of the promontorium of the periotic. A well defined sulcus in the basioccipital forms the mesial border of the internal jugular canal which is delimited laterally by a sulcus in the *pars petrosa*. Another sulcus, immediately posterior to the foramina for the internal jugular canal, constitutes the posterior rim of the posterior lacerate foramen. The paraoccipital process is large with a minor contribution to the base formed by the *pars mastoidea*. A well defined condylar foramen is positioned at the base of the ventral condylar lobe. The smaller hypoglossal foramen is slightly ventral and anterior to the condylar foramen. In posterior view the BES is bordered laterally by the *pars mastoidea* and dorsally by the interparietal.

In lateral view the squamosal contribution to the brain case is bordered by the parietal dorsally, the alisphenoid ventrally and the mastoid part of the periotic posteriorly. The squamosal overlies the jugal from the lateral edge of the glenoid fossa to a point level with the ethmoidal foramen. The subsquamosal foramen is well developed and positioned dorsal to the small posterior squamosal epitympanic sinus. In ventral view the ventral postglenoid foramen is large and posterior to the postglenoid process. At the base of the postglenoid process is a small post zygomatic foramen. The postglenoid process is well developed along the dorsoventral axis, but is not extensive in the transverse plane. A very small preglenoid process is discernible.

The periotic is here considered in two parts: the *pars petrosa*, which houses the inner ear and internal acoustic meatus, and the *pars mastoidea*, which contributes to the lateral occipital region and a tympanic process in lateral view. No isolated periotics are known and only the exocranial features are described. The *pars petrosa* abuts the basisphenoid anteromesially, the alisphenoid and squamosal dorsolaterally and the basioccipital along its entire ventromesial edge. In ventral view a strongly developed, wedge-shaped tympanic process of the promontorium makes broad contact with the alisphenoid tympanic wing. A sulcus in the anterior tip of the *pars petrosa* forms the mesial rim of the tubal foramen which is completed laterally by the alisphenoid tympanic process. This foramen carries the Eustachian tube. A weakly developed mesially oriented process contacts the basioccipital. Ventral to this process a sulcus runs anteroposteriorly, providing a lateral contribution to the internal jugular canal. This canal is fully enclosed ventrally for a short distance (*c.* 3 mm). Posteriorly, a sulcus in the *pars petrosa* forms the anterior rim of the posterior lacerate foramen. Posteroventrally there is no contact between the promontorium and the paroccipital or *pars mastoidea* and no secondary facial canal or stylomastoid foramen is evident. The fenestra ovalis is clearly visible in ventral view and the fenestra rotunda is visible in ventrolateral view. Immediately anterodorsal to the fenestra ovalis is the secondary facial foramen (*sensu* Wible 1990) which runs into a well defined sulcus for the facial nerve. In posterior view a small mastoid foramen is present just lateral to the mastoid supraoccipital suture. A distinct mastoid tympanic process abuts the paroccipital process and floors the mastoid epitympanic sinus. This sinus is continuous with a small paroccipital hypotympanic sinus. An anteriorly projecting septum delimits the lateral limit of the mastoid hypotympanic sinus and abuts the mesial wall of the squamosal epitympanic sinus. A sulcus in this septum delimits the ventral point of exit for the facial nerve.

Upper dentition. I¹ is simple and peg-like, hypsodont relative to the posterior incisors, procumbent and roughly circular in cross section. The I¹ alveolus is about twice the diameter of the I² alveolus and separated from I² by a short diastema. I² is mesodistally broadened and gently recurved lingually. A single crest bisects the tooth on the long axis and there is no diastema between I² and I³. I³ is indistinguishable from I² in size or morphology. I⁴ is similar to I²⁻³, but slightly larger and more compressed mesodistally. C¹ is large, slightly compressed on the transverse axis around the base, strongly recurved and tapered in buccal view. No obvious wear facets are apparent and the tooth is well separated

anteriorly from I^4 by a marked depression in the premaxilla for the C_1 tip and posteriorly from P^1 by a diastema. P^1 is twin rooted, low crowned and compressed on the transverse axis. The crown is straight on the anterior face with the posterior face clearly recurved in buccal view. Posteriorly, the crown terminates in a small heel and the tooth is separated from P^2 by a large diastema exceeding the anteroposterior length of P^1 . P^2 is twin-rooted, about twice the dimension on the transverse axis and one-and-a-half times the height of P^1 . The protocone is bulbous and worn in all specimens. In buccal view the anterior face is about one-and-a-half times the length of the concave posterior face of the crown. A weak crista runs posteriorly from the protocone to a tiny cuspule on the heel which abuts P^3 . P^3 is twin-rooted, extremely large and bulbous and is more than twice the dimension of P^2 on the transverse axis. This tooth exceeds twice the height of the highest crowned molar and presents an almost circular outline in occlusal view. The crown tip is well worn and the heel greatly reduced in all specimens. Cristae are absent in most specimens, but a very weak crista runs from the paracone to the posterior tip of the heel in QMF 23261. M^1 is tri-rooted with the anterior-buccal root the smallest and the posterior-buccal root the largest. In order of decreasing height the principal cusps are: metacone, stylar cusp D, stylar cusp B, paracone, and protocone. The protocone is robust, basally broad and tapers toward the occlusal surface of the talon. The metaconule and stylar cusps C and E are absent and the protoconule is tiny. Stylar cusp D is equidistant from the metacone and the metastylar corner. Stylar cusps B and D are displaced lingually from the buccal margin to produce a gentle slope from these cusps to the buccal border of the tooth. The postmetacrista is the longest shearing crest, about twice the length of the preparacrista and oriented at *c.* 45° to the long axis of the tooth row. The postprotocrista is longer than the preprotocrista and the ectoflexus is minimal. A weakly developed anterior cingulum connects with the protoconule. M^2 differs from M^1 in the following ways: it is larger than M^1 ; the postmetacrista is aligned closer to the long axis of the tooth row; stylar cusp D sits further above the occlusal plane than the metacone; both these cusps are relatively larger and more widely separated than in M^1 ; there is a greater differential in height between stylar cusp B and the paracone; the anterior cingula is more clearly defined; a tiny stylar cusp E is present near the metastylar corner; the protoconule is better developed and the ectoflexus of M^2 is deeper and more anteriorly positioned. M^3 can be distinguished from M^2 as follows: the preparacrista is longer relative to the postmetacrista; both of these crista are longer than for M^2 ; the paracone is larger; M^3 stylar cusp D is smaller than for M^{1-2} and lower than the metacone; stylar cusp D is twinned with a tiny stylar cusp C in unworn specimens (e.g. QMF 23261); stylar cusp E is absent; the anterior cingula is better developed than in M^2 ; the stylar shelf is further reduced evidently with a deeper ectoflexus; the protoconule and metaconule are slightly larger; less distance separates the metacone and paracone producing a straighter centrocrista in occlusal view and the protocone is smaller both in height and occlusal surface area. M^4 differs from M^{1-3} as follows: the stylar shelf is greatly reduced; the metacone is much smaller, although a dilamodont structure is still retained; no metaconule or protoconule is present; the preparacrista is the only remaining crest of the trigon and it is longer than the M^3 preparacrista; and the anterior cingulum is smaller. Meristic gradients from M^{1-4} are: the preparacrista length increases from M^{1-4} ; the postmetacrista length increases from M^{1-3} (not present on M^4); paracone height increases from M^{1-4} ; metacone height increases from M^{1-3} ; protocone height increases from M^{1-2} and decreases from M^{3-4} ; in occlusal view the surface area of the talon increases from M^{1-3} and decreases from M^{3-4} ; stylar cusp B height increases from M^{1-2} then decreases for M^3 (not present on M^4); development of the anterior cingula increases from M^{1-3} and is about equal for M^{3-4} ; and the ectoflexus is weakly developed on M^{1-2} , but well developed on M^3 . The angle formed by the postparacrista and premetacrista (centrocrista) is *c.* 90° for M^{1-2} , slightly more acute in M^3 and obtuse on M^4 .

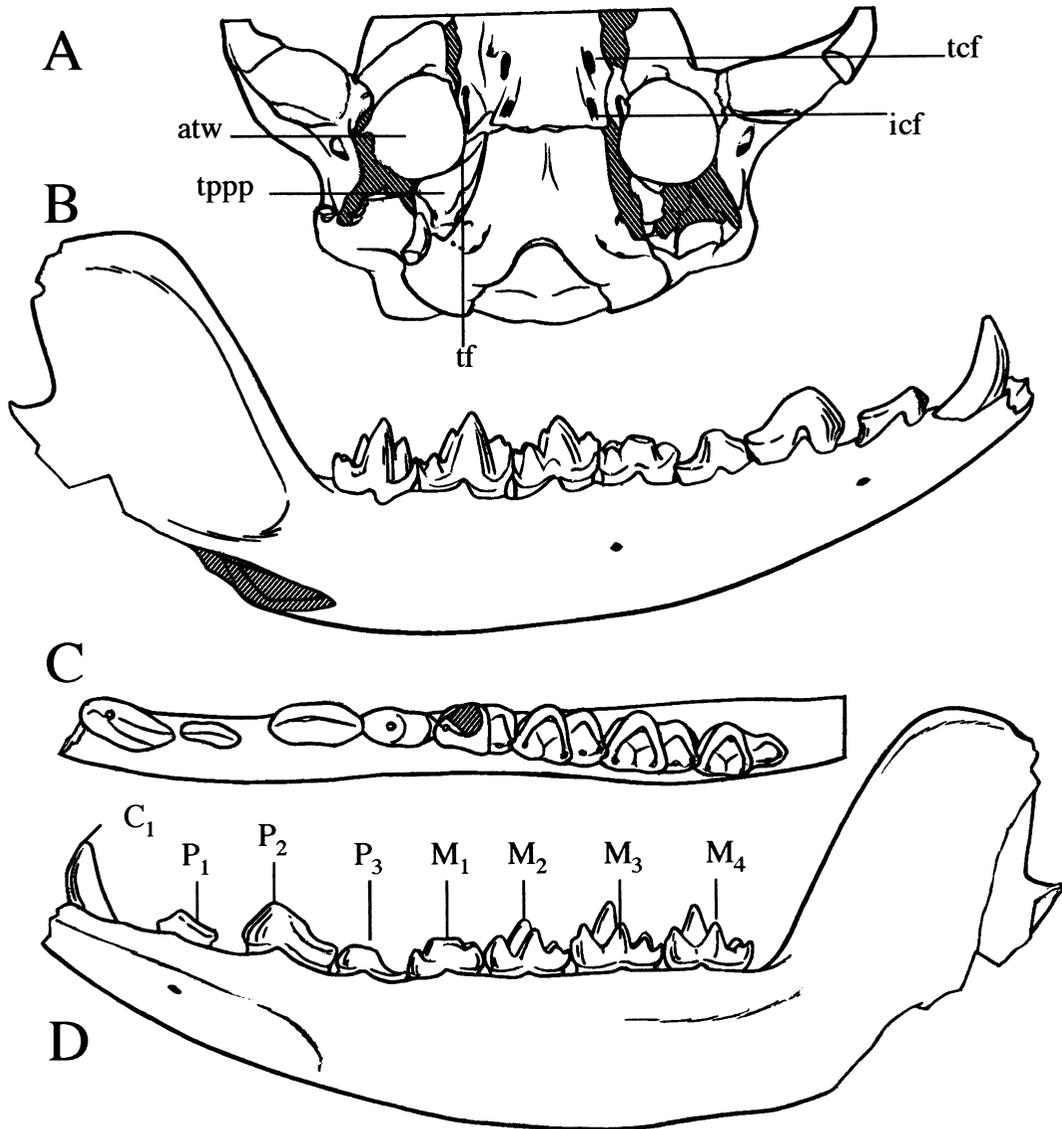
Dentary. The dentary is slightly convex along the ventral margin in buccal view (Text-figs 3–4). It is deepest below the M_3 protoconid and tapers anteriorly. Two dental foramina are present, one beneath the M_1 talonid and other ventral to the diastema separating P_1 and P_2 . The coronoid crest ascends from the body of the dentary at an angle of *c.* 75° with the condyle just higher than the principal cusps of the molars.

By inference from the alveoli preserved in QMF 12463, I_1 is the smallest incisor and the tooth probably projected anteriorly from a position directly ventral to I_2 . Judging from alveoli morphology preserved in QMF 12463 and QMF 23889 the I_2 alveolus was slightly larger and dorsoposterior to that for I_1 . I_3 is represented by QMF 12436, and projects anteriorly from a position buccal to I_2 . The lingual edge of the I_2 crown contacts C_1 about half way along the buccal surface. A cristid bisects the tooth transversely and lingually the crown is concave, descending to a posterior shelf or heel. Posteriorly, the I_3 crown contacts the anterior surface of C_1 . C_1 , known for QMF 12463 and QMF 23889, is the highest crowned tooth in the dentary and *c.* 50 per cent. higher than P_2 . The posterior face of the crown is recurved, the buccal face is more rounded than the lingual face and slight lateral compression is evident. P_1 is twin rooted, very low crowned, slightly recurved on the posterior face and greatly compressed laterally. A cristid emanates from the principal cusp posterior to the P_1 heel and bisects the tooth on the long axis. The tooth is separated anteriorly and posteriorly from C_1 and P_2 respectively by short diastemata. P_2 is the largest lower premolar, slightly lower crowned than C_1 and compressed transversely with the maximum transverse dimension around one-third of that for the longitudinal. This tooth is slightly wider posteriorly than anteriorly and its dimension on the long axis is equal to, or



TEXT-FIG. 3. *Barinya wangala* gen. et sp. nov. A, paratype, QM F31409; basicranial region; $\times 2.55$. B–D, paratype, QM F23889; right dentary containing C₁ P_{1–3} M_{1–4} in B lateral view; $\times 3.34$; C, occlusal view; $\times 2.58$; and D, lingual view; $\times 3.34$.

greater than that of any other tooth in the dentary. A small posteroconule and tiny posterolingual cuspule are present on the heel. P₃ is very similar to P₂ in morphology but about 50 per cent. smaller on the long and dorsoventral axes. The talonid of M₁ is wider than the trigonid. In order of decreasing height the principal cusps are: the protoconid, metaconid, hypoconid, paraconid, entoconid and hypoconulid. The principal cusps in order of decreasing size are: protoconid, hypoconid, paraconid, metaconid, entoconid and hypoconulid. The protoconid is positioned centrally on the transverse axis and is the most heavily worn cusp in the lower dentition of all specimens examined. The metaconid



TEXT-FIG. 4. *Barinya wangala* gen. et sp. nov. A, paratype, QM F31409; basicranial region. B–D, paratype, QM F23889; right dentary containing C₁ P_{1–3} M_{1–4} in B, lateral view, C, occlusal view and D, lingual view. Same magnifications as for Text-figure 3.

is closely twinned with, and slightly posterolingual to the protoconid. The paracristid represents the principal shearing crest and is aligned almost parallel to the long axis of the dentary. An interior angle of *c.* 120° is formed by the paracristid and metacristid. The cristid obliqua terminates on the buccal side of the of the protoconid's posterior face and forms a right angle with the cristid obliqua. The hypocristid is oriented at *c.* 45° to the transverse axis of the dentary. A robust and transversely broad hypoconulid lies posterobuccal to the entoconid. The entoconid is transversely compressed with a distinct preentocristid present. A small carnassial notch divides the preentocristid and postmetacristid. Anterior and posterior cingulids are present. The hypoconulid is secured posteriorly by a hypoconulid notch in the anterior cingulid of M₂. M₂ is similar to M₁ except as follows: the talonid is only slightly wider than the trigonid; the metaconid is larger, both absolutely and relative to the protoconid; the metaconid is less

posteriorly positioned; the paracristid is oriented at *c.* 45° to the transverse axis of the dentary; the metacristid is longer and aligned more closely with the transverse axis; the interior angle between the paracristid and metacristid is more acute; the hypoconid is slightly larger; the entoconid is slightly smaller and the anterior and posterior cingulids are better defined. M_3 is distinguished from M_2 as follows: the talonid is shorter on the transverse dimension than the trigonid; the protoconid is larger; the metaconid is smaller relative to both the protoconid and the paraconid; the metacristid is longer relative to the paracristid; both the paracristid and metacristid are more closely aligned with the transverse axis of the dentary; the interior angle formed between the metacristid and the paracristid is more acute and the anterior and posterior cingulids are better defined. M_4 is similar to M_3 except as follows: the talonid is further reduced on both the long and transverse axes; all principal cusps are smaller (but none is absent); the metaconid is lower than the paraconid; the cristid obliqua terminates anteriorly beneath the carnassial notch of the metacristid and no posterior cingulid is present.

Meristic gradients from M_{1-4} are: the orientation of the paracristid and metacristid becomes increasingly transverse to the long axis of dentary; an increasingly acute interior angle is produced between the paracristid and metacristid; protoconid, metaconid, paraconid, hypoconid and entoconid size increases from M_{1-3} , then decreases for M_4 .

CHARACTER ANALYSIS

Method and background. The elucidation of marsupicarnivore phylogeny has proved to be problematical, particularly with respect to interordinal level relationships, with the results of both morphology- and molecular-based studies failing to achieve consensus on a number of important issues. For example, whilst most authors now concur on the placement of *Dromiciops australis* within Australidelphia (see Hershkovitz 1995 for an alternative view), its position within the clade remains contentious. Competing theories include its placement as sister taxon to the Australian marsupial radiation (Marshall *et al.* 1990), Dasyuomorpha (Szalay 1994) and Diprotodontia (Kirsch *et al.* 1991). The relationships of peramelemorphians to other marsupials are also the subject of much dispute. A long running debate over whether peramelemorphians are more closely related to dasyuomorphians or diprotodontians has recently been eclipsed by doubts as to whether or not they represent the sister group to all Australian marsupials, or even all other marsupials (Kirsch *et al.* 1991; Springer *et al.* 1994; Retief *et al.* 1995). Similarly, there is no consensus on the identity of the sister taxon to Dasyuomorpha. Didelphimorphians (Ride 1964), microbiotheriids (Szalay 1994) and a monophyletic clade inclusive of peramelemorphians and diprotodontians (Kirsch *et al.* 1991) have all been proposed as potential sister taxa. Moreover, there is no agreement with respect to the relationships of dasyuomorphian families to each other. Thus, Archer (1982a) considers Thylacinidae to be the sister group to myrmecobiids and dasyurids, Lowenstein *et al.* (1981) treat myrmecobiids as the sister clade to thylacinids and dasyurids, while results presented by Krajewski *et al.* (1997) place Thylacinidae as the sister taxon to a dasyurid clade that includes *Myrmecobius*. Because there does not appear to be any strong evidence supporting the primacy of any single interpretation of marsupicarnivore phylogeny over all others, a cladogram representing higher level phylogeny is not presented here. A classification of taxa referred to in the present study is given in Table 1.

The determination of character state polarities for Marsupialia largely follows that proposed by previous authors. For Dasyuomorpha, the determination of polarities presents considerable difficulties. Because of the wide range of dasyuomorphian sister taxa hypotheses available, the advancement of any single taxon as a preferred outgroup cannot be supported. Furthermore, to the best of my knowledge, each marsupial apomorphy that is shared between two or more dasyuomorphians, is found in at least one representative of a potential dasyuomorphian sister taxon. With respect to didelphids, for example, this applies to almost every derived marsupial feature considered in the present investigation. The only morphology-based attempt, known to me, to resolve interordinal level marsupicarnivore phylogeny using parsimony (Kirsch and Archer 1982), produced many results that were remarkably inconsistent with those of all previous and subsequent studies, both morphological and molecular. All other attempts, based on, or including, morphological data and inclusive of both American and Australian marsupicarnivore taxa, have been subjective (e.g. Archer 1976b; Marshall *et al.* 1990; Luckett 1994), although parsimony-based methodology has been applied to some groups at lower taxonomic levels (e.g. Reig *et al.* 1987; Muirhead and Wroe 1998). An investigation that will re-examine marsupicarnivore relationships using an algorithm-based

TABLE 1. Classification of marsupicarnivoran and peramelemorphian taxa referred to in the present study. From Aplin and Archer (1987), except for Dasyuromorphia (see Krajewski *et al.* 1994, Wroe 1996a and results of the present study).

Supercohort Marsupialia
Cohort Ameridelphia
Order Didelphimorphia
Family Didelphidae
Order Sparassodonta
Family Borhyaenidae
Family Mayulestidae
Cohort Australidelphia
Order Microbiotheria
Family Microbiotheriidae
Order Dasyuromorphia
Family Thylacinidae
Family Myrmecobiidae
Family Dasyuridae
Subfamily Barinyainae
Subfamily Sminthopsinae
Subfamily Dasyurinae
Subfamily Phascogalinae
Order Peramelemorphia
Family Peramelidae
Family Thylacomyidae
Dasyuromorphia: order <i>incertae sedis</i>
<i>Ankotarinja tirarensis</i>
<i>Keeuna woodburnei</i>
<i>Wakamatha tasselli</i>
<i>Dasyurinja kokuminola</i>
<i>Mayigriphus orbus</i>
Marsupialia: cohort <i>incertae sedis</i> Peradectidae

treatment is in preparation, but this work is well beyond the scope of the present study. The polarity decisions, as well as the interpretation of dasyuromorphian relationships presented below, have been determined subjectively following the methodology of Luckett (1994) and Wroe (1996a), i.e. on the basis of commonality, outgroup comparisons, ontogeny, form function data and stratigraphical position. Taxa examined in the present study include all those listed by Wroe (1997a), i.e. all genera and most species of Australian marsupicarnivore as well as representatives of most American genera. Additional material examined includes the holotypes of the Paleocene didelphimorphian taxa, *Pucadelphys andinus* (YFPB Pal 6105) and *Mayulestes ferox* (MNHC 1249).

Character analysis

Secondary facial nerve canal. In marsupicarnivores the facial nerve passes through a foramen in the petrosal part of the periotic endocranially which leads into a facial nerve canal (Archer 1976b). Ventrally, this nerve exits the facial nerve canal, running posteriorly in an open sulcus. This sulcus may remain open as it continues dorsoventrally, but in many taxa it becomes fully enclosed (whereupon it is referred to here as the secondary facial nerve canal) before exiting the skull ventrally via the stylomastoid foramen. The morphology of elements surrounding the secondary facial nerve canal and stylomastoid foramen varies considerably among marsupials. A secondary facial nerve canal and stylomastoid foramen is absent for basal didelphids, e.g. *Pucadelphys andinus* (Marshall and de Muizon 1995), *Mayulestes ferox* (de Muizon 1994), peramelemorphians, *Myrmecobius fasciatus* (Myrmecobiidae) and the two thylacinid taxa represented by basicranial material (*Thylacinus cynocephalus*, *Badjcinus turnbulli*). In derived sparassodonts

(*Notogale mitis* and *Cladosictis patagonica*) a condition unique among marsupicarnivores may exist in that a secondary facial sulcus is oriented ventromedially and appears to exit the skull via the posterior lacerate foramen. Archer (1976b) reported the presence of a stylomastoid foramen in *Caluromys* among extant didelphids. For this taxon the anterior rim of the foramen is bound by the squamosal only and no canal is present dorsal to it. In *Dromiciops australis* there is no foramen in the topographically equivalent position to that of other marsupials in which the middle ear is fully enclosed. The basicranial region is unknown for all taxa considered Dasyuromorphia *incertae sedis* here. A secondary facial nerve canal enclosed anterodorsally by the *pars petrosa* and by the *pars mastoidea* posteriorly is present in all modern Dasyuridae. Some contribution to the rim of the stylomastoid foramen from the squamosal is also variably present in most modern dasyurids (Archer 1976b). In *Barinya wangala* there is no secondary facial nerve canal or stylomastoid foramen.

The secondary facial nerve canal and stylomastoid foramen are specialized features within Marsupialia (Archer 1976b). Structural differences between the stylomastoid foramen of living dasyurids and *Caluromys* suggest independent acquisition. A secondary facial nerve canal enclosed anterodorsally by the *pars petrosa* and by the *pars mastoidea* posteriorly is a derived feature within Marsupialia that is unique to extant dasyurids.

Internal jugular canal. Two elements of internal jugular canal morphology are considered here: the extent of dorsal enclosure of the canal and the degree to which a sulcus which contributes to the wall of the canal invades the *pars petrosal* laterally. Archer (1982b, p. 463) reported that ‘... the internal jugular canal is short and poorly-enclosed dorsally in didelphids. It is similarly short but enclosed for a short distance in thylacinids. In dasyuroids it is also well-enclosed but very long, extending forward to the basisphenoid.’ Results of the present character analysis are largely in agreement with those of Archer (1982b). However, ‘dasyuroid’ *sensu* Archer (1982b) includes Myrmecobiidae. Specimens of *Myrmecobius* available in the present study show a short dorsally enclosed internal jugular canal (AM M1215, AR 17589) and not a long canal as implied in the previous study. Archer (1976b, p. 309) defined a long dorsal enclosure of the internal jugular canal as extending anteriorly to, or almost to, the basisphenoid. As further defined here, a short internal canal is one in which dorsal enclosure does not extend anteriorly beyond half way between the canal’s ventral opening and the basisphenoid. Additional data has become available since the publication of Archer’s analysis. Basal fossil Peramelemorphia (J. Muirhead, pers. comm.) show a short and poorly enclosed internal jugular as for Didelphidae, but a short, dorsally enclosed canal as seen in *Thylacinus cynocephalus* is evident in some derived taxa. In the holotype of *Badjcinus turnbulli* this feature is similar to that in didelphids. For *Barinya wangala* the internal jugular canal is also short, but fully enclosed dorsally. A deeply invasive sulcus with the posteroventral lip formed by a mesially directed process in the *pars petrosa* is not present in *Pucadelphys andinus*, most Didelphidae, *Dromiciops australis*, Peramelemorphia, Thylacinidae or Myrmecobiidae. This feature is present in *Barinya wangala*, some specialized Didelphidae (e.g. *Lestodelphys*) and all Dasyuridae except some taxa in which the tympanic wing of the *pars petrosa* is greatly inflated (e.g. *Pseudantechinus macdonnellensis*). The absence of this feature in some specialized Dasyuridae is treated as a secondary loss in the present study because it is correlated with hypertrophy of a feature that is clearly derived within Dasyuridae.

A short internal jugular canal that shows incomplete dorsal enclosure is plesiomorphic for marsupials (Archer 1976b). Among dasyuromorphians, Thylacinidae, Myrmecobiidae and *Barinya wangala* are moderately derived from the plesiomorphic state for Marsupialia in showing complete dorsal enclosure of this canal. The long fully enclosed internal jugular canal of modern dasyurids is clearly apomorphic within the order. A deeply invasive sulcus with the posteroventral lip formed by a mesially directed process in the *pars petrosa*, for passage of the internal jugular, is absent in almost all possible sister taxa to Dasyuromorphia as well as in thylacinids and myrmecobiids within the order. Consequently, its presence in *Barinya wangala* and living dasyurids is considered to be a potential synapomorphy uniting these taxa.

Transverse canal. A transverse canal is not present in *Pucadelphys andinus* (Marshall and de Muizon 1995), some extant Didelphidae (e.g. *Caluromys*), sparassodonts and some dasyurids (e.g. *Planigale*). This

feature is present in the late Cretaceous metatherian *Asiatherium reshetovi* (Szalay and Trofimov 1996), *Dromiciops australis*, Peramelemorphia, Myrmecobiidae, Thylacinidae, most Dasyuridae and Didelphidae and *Barinya wangala*.

Archer (1976b, 1982b) considered the presence of a transverse canal to be plesiomorphic for Marsupialia. But, as noted by Marshall and Muizon (1995), the absence of this feature in *Pucadelphys andinus*, and metatherian outgroup taxa such as *Morganucodon* and late Cretaceous eutherians from Asia (*Asioryctes*, *Barunlestes*, *Kennalestes*, *Zalambdalestes*), suggests that the absence of a transverse canal may represent the plesiomorphic marsupial condition. The presence of this feature in *Asiatherium* indicates that independent acquisition may have occurred at least twice within Marsupialia, unless apomorphic loss is accepted for the otherwise generalized Paleocene taxa such as *Pucadelphys andinus* and *Mayulestes ferox*. The ubiquitous distribution of this feature among Peramelemorphia, Myrmecobiidae, Thylacinidae and all Dasyuridae, excepting some species of *Planigale* (Archer 1976b), suggests that this feature was present in the ancestral australidelphian and dasyuromorphian. *Barinya wangala* shows the plesiomorphic state for Dasyuromorphia regarding transverse canal morphology.

Alisphenoid and parietal relations. Extensive contact between the alisphenoid and parietal is common to all Didelphidae and some Sparassodonta (Archer 1976b; Marshall and de Muizon 1995). Conclusive determination of the character state shown in specimens of *Dromiciops australis* available for the present study has not been possible because of fusion of elements in this region. Among remaining Australidelphia, squamosal-frontal contact is present in all extant Peramelemorphia and the only thylacinid for which this feature is known, *Thylacinus cynocephalus*, whilst fossil peramelemorphians (Muirhead 1994), *Myrmecobius*, *Barinya wangala* and most dasyurids show an alisphenoid-parietal contact. Within Dasyuridae, *Sminthopsis* shows a frontal-squamosal contact (Archer 1976b).

An alisphenoid-parietal contact is plesiomorphic for Marsupialia (Kirsch and Archer 1982; de Muizon 1998), and *Barinya wangala* exhibits the plesiomorphic state for this feature.

Alisphenoid tympanic wing. An alisphenoid tympanic wing is probably present in the late Cretaceous *Asiatherium reshetovi* (Trofimov and Szalay 1994; Szalay and Trofimov 1996). Among Didelphidae an alisphenoid tympanic wing is absent in *Pucadelphys andinus* (de Muizon 1991; Marshall and de Muizon 1995), and although small in most taxa, is well developed in some, e.g. *Sparassocynus* (Reig *et al.* 1987). This feature is absent in the basal sparassodont *Mayulestes ferox* and in most other members of the order (de Muizon 1994). However, an alisphenoid tympanic process is present in Hathliacynidae (Marshall 1977; de Muizon 1994). A large alisphenoid contribution to the tympanic bulla is present in Microbiotheriidae. All Australidelphia show an alisphenoid tympanic wing, but the degree of development varies greatly both between and within families. Within Peramelemorphia this feature is very poorly developed in basal fossil and extant taxa, but well developed in some derived extant species (Muirhead 1994). The alisphenoid tympanic wing is small in *Badjcinus turnbulli* and *Thylacinus cynocephalus*. In *Myrmecobius* and all modern dasyurids this feature is well developed relative to the condition shown in thylacinids and basal peramelemorphs, with some dasyurids showing extreme hypertrophy of the alisphenoid tympanic wing (e.g. *Dasyercus*). *Barinya wangala* shows a degree of hypertrophy comparable to that of unspecialized dasyurids such as *Murexia* and *Neophascogale*.

Until recently the presence of an alisphenoid tympanic wing was widely regarded as a marsupial synapomorphy. However, with the description of *Pucadelphys andinus* (de Muizon 1991; Marshall and de Muizon 1995) and *Mayulestes ferox* (de Muizon 1994), a strong argument can be made for the absence of this feature in the ancestral metatherian. This interpretation is complicated by the apparent presence of an alisphenoid tympanic wing in the late Cretaceous *Asiatherium reshetovi*, although Szalay and Trofimov (1996) could not conclude definitively that this process was present. Because an alisphenoid tympanic wing is evident in all Australidelphia its presence is probably plesiomorphic for Dasyuromorphia. Within the clade, thylacinids are the least derived for this feature and remaining taxa are variably specialized. *Barinya wangala* exhibits an apomorphic condition within the order, but this is less derived than in some Dasyuridae and *Myrmecobius*. The presence of an expanded alisphenoid tympanic wing may represent a synapomorphy uniting *Barinya wangala*, modern Dasyuridae and Myrmecobiidae. However, because this

feature is better developed in *Myrmecobius* than in unspecialized modern dasyurids, at least some homoplasy must be accepted unless a special relationship is acknowledged for *Myrmecobius* and modern Dasyuridae to the exclusion of less derived dasyurids.

Squamosal epitympanic sinus. A squamosal epitympanic sinus is entirely absent in most ameridelphians. Archer (1976b, 1982b) noted that this feature is present, but very small in some didelphids (e.g. *Monodelphis domestica*, *Lutreolina crassicaudata*) and one borhyaenoid (*Borhyaena excavata*). Within Australidelphia, squamosal epitympanic sinuses are absent in *Dromiciops australis*, basal peramelemorphs (Archer 1982b; Muirhead 1994), *Yalkaparidon coheni* (Archer *et al.* 1988) and the basal thylacinid *Badjcinus turnbulli* (Muirhead and Wroe 1998). A squamosal epitympanic sinus is present, but small, in *Myrmecobius*, *Barinya wangala* and most modern Dasyuridae, but large to very large in some specialized dasyurids (e.g. *Dasymercus*).

Marshall (1977) and Marshall *et al.* (1990) considered the presence of a squamosal epitympanic sinus to be an australidelphian synapomorphy, although Archer (1982b) disagreed with this interpretation. With the discovery of *Yalkaparidon coheni* (Yalkaparidontidae) and the thylacinid *Badjcinus turnbulli*, which, along with generalized peramelemorphs, completely lack this sinus, Archer's position is strongly supported, unless apomorphic reversal to the plesiomorphic state is accepted for taxa which otherwise represent highly generalized elements of Australidelphia. It is likely that there have been multiple independent derivations of a squamosal epitympanic sinus within the Australian marsupial radiation and it is probable that the basal dasyuromorphian lacked this feature. This character may have been acquired independently at least twice within Dasyuromorphia and it could represent a synapomorphy uniting Dasyuridae and Myrmecobiidae to the exclusion of Thylacinidae, or an independently acquired apomorphy within each family. The squamosal epitympanic sinus evident in *Barinya wangala* is probably derived within the order, but this may support affinity with any of the three dasyuromorphian families.

Periotic tympanic process and hypotympanic sinus. The distribution of this feature among marsupials was reviewed by Wroe (1997a). A periotic tympanic process is absent in *Pucadelphys andinus* (Marshall and de Muizon 1995), but is moderately developed in some didelphids (e.g. *Caluromys philander*), projecting anteriorly to contact the posterior rim of the alisphenoid tympanic wing, resulting in an enclosed periotic hypotympanic sinus. A similar condition is shown by *Dromiciops australis*. For unspecialized peramelemorphs (e.g. *Peroryctes*) the periotic tympanic wing is poorly developed and does not approach the alisphenoid tympanic process. Within Dasyuromorphia *Badjcinus turnbulli* and *Thylacinus cynocephalus* show tiny periotic tympanic processes. In *Myrmecobius* this process is larger than for thylacinids and contacts the alisphenoid tympanic wing. However, as noted by Archer and Kirsch (1977) and Wroe (1997a), the periotic tympanic process projects ventrally in this taxon and no hypotympanic sinus is produced dorsal to it. All modern Dasyuridae show a well developed periotic tympanic wing that projects anteriorly and contacts the alisphenoid. In unspecialized taxa such as *Murexia* the process and sinus are small, whilst some taxa (e.g. *Dasyuroides*) show marked hypertrophy of these features. *Barinya wangala* is similar to modern Dasyuridae regarding these features, with the tympanic process contacting the alisphenoid, but the process and resultant sinus are smaller than in any extant dasyurid.

Absence of a periotic tympanic wing and periotic hypotympanic sinus are plesiomorphic for Marsupialia (Kirsch and Archer 1982; de Muizon 1998). These features may have evolved independently within a number of lineages (Wible 1990; de Muizon 1998). A tiny, uninflated periotic tympanic process was probably present in the basal dasyuromorphian. This finding contradicts the assertion of Szalay (1994, p. 346) who considered that a '... small inflated tympanic wing of the petrosal' was probably present in the stem australidelphian. The presence of a ventrally projecting periotic tympanic wing contacting the alisphenoid, but not producing a periotic hypotympanic sinus is autapomorphic for *Myrmecobius*. The anteriorly oriented tympanic wing and distinct hypotympanic sinus of the periotic present in *Barinya wangala* and modern Dasyuridae are derived within Dasyuromorphia and may represent synapomorphies uniting the two taxa.

Paroccipital hypotympanic sinus. A distinct depression within the paroccipital forming a paroccipital

hypotympanic sinus is absent in *Pucadelphys andinus*. Archer (1976b) observed that this sinus is absent or poorly developed in didelphids and sparassodonts, with the possible exception of *Borhyaena*. Within Australidelphia a paroccipital sinus is absent in *Dromiciops australis*, Peramelemorphia, *Myrmecobius* and Thylacinidae. In *Barinya wangala* a process projects anteriorly from the base of the paroccipital process and floors a small paroccipital hypotympanic sinus that is also present in all modern Dasyuridae. Within the family both the size of the process and the hypotympanic sinus vary greatly between taxa. In unspecialized forms, such as *Murexia*, these features are only marginally better developed than in *Barinya wangala*, but some modern Dasyuridae (e.g. *Dasyercus*, *Antechinomys* and *Sarcophilus*) show hypertrophy of these features. In all modern Dasyuridae, but no other outgroup taxa considered here, the paroccipital tympanic process is partially fused with the both the mastoid tympanic wing laterally and the posteroventral portion of the *pars petrosa* anteromesially. *Barinya wangala* shows intimate association of the paroccipital tympanic wing with the mastoid tympanic wing laterally, but no contact with the *pars petrosa*.

The presence of a paroccipital hypotympanic sinus and tympanic process is plesiomorphic for Marsupialia (Marshall and Muizon 1995). Within Dasyuromorphia *Barinya wangala* is apomorphic relative to Thylacinidae and Myrmecobiidae in showing a small but distinct paroccipital sinus and an anteriorly oriented paroccipital tympanic process which contacts the mastoid tympanic process laterally. These derived features are shared with all modern Dasyuridae although the latter show further derivations of these states with the paroccipital tympanic process fused to the *pars petrosa* anteriorly and mastoid tympanic process laterally.

Mastoid tympanic process and epitympanic sinus. A small mastoid tympanic process and epitympanic sinus are present in *Pucadelphys andinus* (Marshall and de Muizon 1995). These features are small or absent in other ameridelphians (Archer 1976b), but hypertrophied in *Dromiciops australis*, in which the mastoid tympanic process is fused with the tympanic process of the *pars petrosa*. Mastoid tympanic processes and epitympanic sinuses are absent in *Thylacinus cynocephalus*, and present but small in Peramelemorphia, *Badjcinus turnbulli*, *Barinya wangala* and some modern dasyurids (e.g. *Murexia*). These features are well developed in some derived bandicoots (e.g. *Macrotis*), dasyurids (e.g. *Dasyercus*) and *Myrmecobius*. The mastoid tympanic process contacts the petrosal wing of the *pars petrosa* only in some specialized didelphids (e.g. *Caluromysiops*), Microbiotheriidae, some derived peramelemorphians (e.g. *Macrotis*), and all modern Dasyuridae.

A small mastoid process that does not fuse with a tympanic wing of the *pars petrosa* is plesiomorphic for marsupials (de Muizon 1998). Either the presence of a small mastoid epitympanic sinus and tympanic process, or absence of both features, could be plesiomorphic for Dasyuromorphia. However, contact between the mastoid tympanic process and the *pars petrosa* is a derived feature uniting modern Dasyuridae, to the exclusion of *Barinya wangala* and all other dasyuromorphians.

Posterolateral and accessory posterolateral palatal foramina. The morphology of both the posterolateral palatal foramen (p.p.f.) and the accessory posterolateral palatal foramen (a.p.p.f.) among Marsupialia was considered by Wroe (1997a), Archer (1982a, 1982b, 1984) and Marshall *et al.* (1990) who suggested that loss of the p.p.f. constitutes a dasyurid synapomorphy.

In many extant didelphids (e.g. *Didelphis marsupialis*, *Marmosa*, *Metachirus*) both the p.p.f. and a.p.p.f. are present. Accessory posterolateral palatal foramina are absent in some didelphoid taxa (e.g. *Chironectes minimus*) and both foramina are absent in the derived sparassocynid *Sparassocynus deriatus*. Both foramina are present in the basal sparassodont *Mayulestes ferox* (de Muizon 1998), but specialized sparassodonts show loss of the p.p.f. and a.p.p.f. (Simpson 1941). Accessory posterolateral palatal foramina are absent in *Dromiciops australis*, but complete posterolateral palatal foramina are present. Both foramina are present in basal Peramelemorphia (e.g. *Echymiperra*), but a.p.p.f. are absent in some derived taxa (e.g. *Macrotis*, *Perameles*). Within Thylacinidae this region is known only for *Thylacinus potens* and *Thylacinus cynocephalus*. Neither taxon shows an a.p.p.f., but a large p.p.f. is present in *Thylacinus potens*. Accessory posterolateral palatal foramina are absent for *Myrmecobius*, *Barinya wangala* and all modern Dasyuridae. Among these three taxa p.p.f. are present in *Myrmecobius*, some *Neophascogale* and *Dasyurus viverrinus*, but lost in other taxa.

Presence of the p.p.f. and a.p.p.f. is plesiomorphic for Marsupialia (Archer 1984; Wroe 1997a). Loss of the a.p.p.f. is common to all Dasyuromorphia and may represent a synapomorphy for the order. Within Dasyuromorphia, loss of both foramina has occurred independently within Dasyuridae and Thylacinidae (Wroe 1997). The absence of posterolateral palatal foramina in *Barinya wangala* represents a potential synapomorphy with either derived dasyurid or thylacinid clades.

Primary foramen ovale. The mandibular branch of the fifth cranial nerve (V^3) exits via the foramen ovale. Following the terminology of Gaudin *et al.* (1996) the endocranial and exocranial exits for this nerve are considered the primary foramen ovale and the secondary foramina ovale respectively in the present study. The distribution of the primary foramen ovale among marsupials is reviewed by Gaudin *et al.* (1996) and Wroe (1997a). In early Tertiary didelphoids and sparassodonts the primary foramen ovale is delimited by both the alisphenoid and periotic (Muirhead 1994; de Muizon 1994; Marshall and de Muizon 1995). This is also true for many ameridelphians, but in some taxa, including *Dromiciops australis*, V^3 is delimited solely by the alisphenoid (Reig *et al.* 1987). Fossil peramelemorphian taxa show alisphenoid-periotic enclosure of V^3 , but both character states are present among extant taxa. Within Dasyuromorphia alisphenoid-periotic delimitation of the foramen ovale is present for *Myrmecobius fasciatus*, *Badjcinus turnbulli*, *Barinya wangala* and most Dasyuridae. A primary V^3 foramen bound entirely by the alisphenoid has been reported in the following specialized carnivorous dasyuromorphians: *Thylacinus cynocephalus* (Archer 1976b), *Dasyurus spartacus* (Van Dyck 1987) and a single specimen of *Sarcophilus harrisii* (Gaudin *et al.* 1996).

Novacek and Wyss (1986), Case (1989), Muirhead (1994) and Wroe (1997a) have concluded that alisphenoid-periotic enclosure of the foramen ovale is plesiomorphic for Marsupialia. In the light of this finding and the restriction of alisphenoid delimitation of V^3 to specialized taxa within Thylacinidae and Dasyuridae it is concluded that alisphenoid-periotic enclosure of this foramen is plesiomorphic for Dasyuromorphia. *Barinya wangala* shows the plesiomorphic state for the order.

Secondary foramen ovale. The morphology and distribution of this feature among marsupials was considered by Gaudin *et al.* (1996) and Wroe (1997a). Terminology follows that of Gaudin *et al.* (1996). Secondary foramina ovale are absent in basal didelphoids and sparassodonts, fossil peramelemorphians (J. Muirhead, pers. comm.), microbiotheriids, *Myrmecobius* and most living dasyurids. This feature is present in some extant Didelphidae, extant Peramelemorphia, Thylacinidae, *Sarcophilus harrisii*, *Dasyurus spartacus* and some *Dasyurus maculatus*. In *Barinya wangala* the left alisphenoid tympanic wing of QM F31408 shows an anteriorly directed strut which constitutes an incomplete secondary foramen ovale. This process is absent on QM F31409.

Wroe (1997a) concluded that secondary foramina ovale are produced in a number of ways within Dasyuromorphia. The incomplete secondary foramina ovale evident in one side of one specimen of *Barinya wangala* is apomorphic within the order and morphologically similar to that found in some *Dasyurus maculatus*. This feature has been derived independently at least twice within Dasyuromorphia.

Sigmoid sinus. A well defined sulcus for the sigmoid sinus is present in the posteroventral endocranial surface of the *pars petrosa* in *Pucadelphys andinus* (Marshall and de Muizon 1995), most extant Didelphidae, Peramelemorphia, *Myrmecobius*, *Badjcinus turnbulli* and Dasyuridae (Archer 1976b). Endocranial examination is difficult in specimens of *Barinya wangala*, but a sulcus for this feature appears to be present.

Among australidelphian taxa, *Thylacinus cynocephalus* appears to be unique in showing no sulcus for the sigmoid sinus (Archer 1976b). Presence of this feature in *Barinya wangala* probably represents a retained dasyuromorphian plesiomorphy.

Anterior carotid canal. Some dorsal enclosure of the anterior carotid canal is present in all Didelphidae except *Monodelphis* (Archer 1976b). Marshall and de Muizon (1995) did not comment on the morphology of this canal in *Pucadelphys andinus*. In all didelphids available for comparison the extent of dorsal enclosure is not sufficient to obscure the endocranial aperture of this canal in external view. This is also true of *Dromiciops australis*, all Peramelemorphia, *Myrmecobius*, *Barinya wangala*, and extant dasyurids,

in some of which, e.g. *Planigale* (Archer (1976b)), the anterior carotid canal is almost non-existent. In *Badjcinus turnbulli* and *Thylacinus cynocephalus* dorsal enclosure of the anterior carotid canal is longer than for any other taxa examined and the endocranial aperture for this canal cannot be seen in external view. This feature is particularly well developed in *Thylacinus cynocephalus*.

The presence of some dorsal enclosure of the anterior carotid canal is probably plesiomorphic for Dasyuromorphia. Consequently, both extensive enclosure, as shown by Thylacinidae, and major reduction of this canal, as shown by *Planigale*, are probably apomorphic within the clade. *Barinya wangala* shows the plesiomorphic condition for Dasyuromorphia.

Ectotympanic. No ectotympanic is preserved for *Pucadelphys andinus* (Marshall and de Muizon 1995). A simple horseshoe-shaped ectotympanic that is not laterally extended is common to most Didelphidae (Reig *et al.* 1987) and basal extant peramelemorphians (e.g. *Peroryctes*). Moderate lateral extension of this feature is found in some didelphids (e.g. *Marmosa*), *Barinya wangala*, *Myrmecobius* and some bandicoots. Among extant Dasyuromorphia similar development of this feature is found in most taxa except *Planigale*, *Sarcophilus*, *Badjcinus turnbulli* and *Thylacinus cynocephalus* which show marked hypertrophy in this regard. Thickening of the lateral rim of the ectotympanic and marked lateral extension is shown in *Badjcinus turnbulli*, *Thylacinus cynocephalus*, *Sarcophilus harrisii* and some Peramelemorphia (Archer 1976b). *Sarcophilus harrisii* is uniquely derived among marsupials in exhibiting a well-defined, saddle-shaped ectotympanic in anterior or posterior view (Archer (1976b)).

A simple horseshoe-shaped ectotympanic is plesiomorphic for marsupials (Reig *et al.* 1987). Moderate lateral extension of the ectotympanic, as evident in *Barinya wangala*, is apomorphic within Marsupialia.

Tubal foramen. A distinct tubal foramen for carriage of the Eustachian tube is absent in *Pucadelphys andinus*, all other ameridelphian taxon available for the present study and Thylacinidae. In *Dromiciops australis*, *Barinya wangala* and all modern Dasyuridae a well defined tubal foramen is present and is formed by a sulcus in the anterior limb of the *pars petrosa* and the mesial wall of the alisphenoid tympanic wing. *Myrmecobius* shows a poorly defined slit-like tubal foramen. This foramen is ovoid and better defined in *Barinya wangala*. *Dromiciops* and modern Dasyuridae also show ovoid tubal foramina with further development of the sulcus in the *pars petrosa*.

Tubal foramina are derived within Marsupialia (Wroe 1997a). Wroe (1997a) considered the presence of a distinct tubal foramen as a possible dasyurid synapomorphy, but the presence of this feature in a possible dasyuromorphian outgroup (*Dromiciops*) complicates this issue, and unless apomorphic reversal to a plesiomorphic state for basal peramelemorphians, thylacinids and *Myrmecobius* is accepted, this feature must be considered convergent in Dasyuridae and Microbiotheriidae. The condition shown in *Barinya wangala* represents a possible synapomorphy with modern Dasyuridae.

Incisors. All Didelphidae, Microbiotheriidae and both fossil and basal extant Peramelemorphia show an incisal formula of 5/4. Some sparassodonts, *Barinya wangala*, all Dasyuromorphia and some extant bandicoots show an incisal formula of 4/3. In *Pucadelphys andinus* and most extant Didelphidae the incisors are 'peg-like', whilst *Dromiciops australis*, Peramelemorphia, *Barinya wangala* and most Dasyuromorphia have mesodistally broadened incisors (Reig *et al.* 1987; Szalay 1994; Marshall and de Muizon 1995). In some extant Didelphidae (Archer 1976b), *Dromiciops australis*, Peramelemorphia, *Thylacinus cynocephalus*, *Myrmecobius* and some Dasyuridae (e.g. *Dasyurus viverrinus*, *Dasyurus maculatus*, *Sarcophilus harrisii*), I¹ is not hypsodont relative to the posterior incisors. By contrast, *Pucadelphys andinus*, some extant didelphids, *Barinya wangala* and most modern dasyurids show a markedly hypsodont I¹.

Reduction in the number of incisors, as evident in *Barinya wangala*, is widely acknowledged as a dasyuromorphian synapomorphy (Archer 1976b; Marshall *et al.* 1990). Mesodistal broadening of the incisors, also evident in *Barinya wangala*, is probably derived for Marsupialia and its presence has been treated as a derived feature uniting Australidelphia (Szalay 1994). Archer (1976c) considered the presence of a hypsodont I¹, evident in *Barinya wangala*, to be plesiomorphic for Marsupialia. The loss of this feature is commonly associated with a carnivorous diet (e.g. thylacinids, *Dasyurus maculatus*), but is also absent in some otherwise generalized taxa such as *Neophascogale lorentzii*.

Morphology of P³. P³ is higher crowned than P² in unspecialized ameridelphians (Archer 1976c; Reig *et al.* 1987), *Dromiciops australis*, Peramelemorphia, Thylacinidae, *Barinya wangala* and most modern Dasyuridae. In some derived carnivorous dasyurids P³ is greatly reduced or lost (e.g. *Dasyurus*, *Sarcophilus*). A transversely narrow P³ is present in *Pucadelphys andinus*, most extant Didelphidae, *Dromiciops australis*, most Peramelemorphia, including the basal fossil taxon *Yarala burchfieldi* (Muirhead and Filan 1995), *Myrmecobius*, all Thylacinidae, and most Dasyuridae in which the tooth has not been lost. A massive, transversely broad P³ is apparent in *Barinya wangala* and the peramelemorphian *Echymipera clara*. In *Echymipera clara*, however, this morphology is restricted to males. By contrast, a massive P³ is present in all specimens of *Barinya wangala* for which this region is known, thus there does not appear to be sexual dimorphism of this feature in this taxon.

The high crowned morphology of P³ evident in *Barinya wangala* is plesiomorphic for Marsupialia and Dasyuromorphia (Archer 1976c). Consequently, the massive construction of P³ in this taxon is treated here as a unique derived feature among dasyuromorphians.

Morphology of P₂₋₃. Archer (1976c) considered the presence of a P₃ unreduced relative to P₂ to be plesiomorphic for Marsupialia. P₃ is larger or very similar in size to P₂ among unspecialized Didelphidae, such as *Pucadelphys andinus*, Microbiotheriidae, Peramelemorphia, *Wakamatha tasselli* (Archer and Rich 1979) and some modern Dasyuridae, but in many other marsupial taxa P₃ is markedly reduced or absent. Goin (1993) considered P₃ reduction as a derived feature in a number of extant Didelphidae. Within Dasyuromorphia two taxa considered as *Dasyuromorphia incertae sedis* in the present study, *Ankotarinja tirarensis* and *Mayigriphus orbus* (Wroe 1997b), show moderate P₃ reduction relative to P₂. Reduction of this tooth is also present in the basal thylacinid *Badjcinus turnbulli*. Extreme reduction or loss of P₃ is common to some modern Dasyuridae, particularly dasyurine taxa. Some dasyuromorphians including *Wakamatha tasselli* (judging from alveolus size) and species of *Thylacinus* (Muirhead and Gillespie 1995), exhibit distinctive hypertrophy of this tooth. By inference from alveolus size, the P₃ of *W. tasselli* was enormous and relatively larger than for any other known dasyuromorphian. In *Barinya wangala* P₃ is small relative to P₂, but this is the product of hypertrophy of P₂, which is larger than that of any other Dasyuromorphia.

Both pronounced reduction and hypertrophy of P₃ are apomorphic for Marsupialia. Several authors have treated a 'tendency' for reduction of P₃ as a dasyurid synapomorphy (Tate 1947; Archer 1982b; Marshall *et al.* 1990), but Wroe (1996a, 1997a, 1997b) has argued against this for the following reasons: P₃ reduction is not present in structurally unspecialized Dasyuridae (*Murexia*) and the use of 'tendency' or 'canalised evolutionary potential' (*sensu* Saether 1983, 1986) has been strongly rejected by a number of authors (Farris 1986; Forey *et al.* 1994). This view is maintained here. Within Dasyuromorphia *Barinya wangala* is derived regarding P₂ hypertrophy and plesiomorphic for P₃ size.

M¹ stylar cusp B. Stylar cusp B on M¹ is a distinct cusp in *Pucadelphys andinus*, most extant Didelphidae (Reig *et al.* 1987; Marshall and Muizon 1995), Peramelemorphia, *Keeuna woodburnei*, *Dasyurinja kokuminola*, some Thylacinidae, *Barinya wangala* and most modern Dasyuridae. M¹ morphology is not known for *Ankotarinja tirarensis*. The M¹ stylar cusp B is small or absent in Microbiotheriidae, *Myrmecobius*, specialized Thylacinidae (Muirhead 1992, 1997) and carnivorous Dasyuridae.

The presence of a well developed M¹ stylar cusp B is a marsupial plesiomorphy (Archer 1976c) and probably represents a retained dasyuromorphian plesiomorphy in *Barinya wangala*. Reduction or loss of this cusp has occurred independently in Microbiotheriidae, Myrmecobiidae and specialized carnivorous Dasyuridae and Thylacinidae.

M¹ anterior cingulum. The anterior cingulum of M¹ is continuous with the preprotocrista in *Alphadon*, basal didelphids, Microbiotheriidae, the basal peramelemorphian *Yarala burchfieldi*, *K. woodburnei*, the basal thylacinid *Muribacinus gadiyuli*, *Barinya wangala* and unspecialized modern dasyurids (e.g. *Murexia*, *Phascogale*), but is incomplete or absent in some didelphids, *Myrmecobius*, some dasyurids (*Dasyurus maculatus*, *Dasyuroides byrnei*, *Sarcophilus harrisii*) and most Thylacinidae.

This feature was probably present in the ancestral dasyuromorphian and has been lost independently in various lineages (Muirhead and Wroe 1998). *Barinya wangala* retains the plesiomorphic state for the order.

*M*¹ *stylar cusp D*. In taxa not showing advanced reduction of the stylar shelf the *M*¹ stylar cup D is clearly smaller than, or subequal to stylar cusp B in most Ameridelphia, including generalized Peradectidae and Didelphidae, and Peramelemorphia (except *Yarala burchfieldi*). In all Dasyuromorphia in which the stylar shelf remains, the *M*¹ stylar cusp D is markedly larger than stylar cusp B.

Cifelli (1993) considered the presence of a stylar cusp D to be a synapomorphy uniting early marsupial clades. Archer (1984) treated hypertrophy of this cusp, relative to stylar cusp B, as a possible dasyurid synapomorphy. Evidence from recently discovered fossil material (*Yarala burchfieldi*, *Muribacinus gadiyuli*) casts doubt on Archer's proposal. It is agreed that this feature is derived within Marsupialia, but because the generalized peramelemorphian *Yarala burchfieldi* and basal thylacinids, such as *Muribacinus gadiyuli*, also show stylar cusp D hypertrophy relative to stylar cusp B, it seems equally likely that this feature is synapomorphic for Peramelemorphia and Dasyuromorphia, or for Dasyuridae and Thylacinidae. Consequently, although *Barinya wangala* shows the derived state within Marsupialia, its presence could be interpreted as supportive of a special relationship with various clades.

*M*³ *stylar cusp D*. Stylar cusp D is well separated from the metacone on all upper molars in basal didelphids, Peramelemorphia, *Barinya wangala* and all Dasyuromorphia except specialized carnivorous dasyurids such as *Dasyurus maculatus* and *Sarcophilus harrisii*. In these carnivorous taxa the *M*³ stylar cusp D and metacone are either very close together, such that the bases of the two cusps are in close contact (*D. maculatus*), or have merged to form a single cusp (*S. harrisii*).

Muirhead and Archer (1990) and Wroe (1996a) considered this distinction to be of value in separating derived thylacinids and dasyurids. *Barinya wangala* exhibits the plesiomorphic condition.

*M*³ *postmetacrista*. The *M*³ postmetacrista is shorter than or subequal to that of *M*² in most Didelphidae, Microbiotheriidae, Peramelemorphia, *Barinya wangala*, basal Thylacinidae and most Dasyuridae. This represents the plesiomorphic condition within Marsupialia and Dasyuromorphia (Archer 1976c), whilst many carnivorous thylacinid and dasyurid taxa show hypertrophy of the *M*³ postmetacrista. *Barinya wangala* retains the plesiomorphic condition for marsupials and dasyuromorphians.

*M*⁴ *metacone*. The *M*⁴ metacone forms a cusp distinct from the metastylar corner of the tooth and a dilambdodont structure is retained in peradectids, unspecialized ameridelphians, Microbiotheriidae, *Barinya wangala*, basal Thylacinidae (*Muribacinus*) and structurally unspecialized living dasyurids (*Murexia*, *Neophascogale*). In some didelphids, Peramelemorphia (including *Yarala burchfieldi*), and most Dasyuridae and Thylacinidae the *M*⁴ metacone is greatly reduced or absent and the tooth is not dilambdodont.

A dilambdodont *M*⁴ is plesiomorphic for Marsupialia (Archer 1976c; Reig *et al.* 1987; Marshall *et al.* 1990). Because this feature is present in basal Ameridelphia, Dasyuridae and Thylacinidae the presence of a dilambdodont *M*⁴ in *Barinya wangala* is treated as a probable dasyuromorphian plesiomorphy in the present study.

Protoconules. Distinct protoconules are present in unspecialized peradectids, generalized didelphids (*Pucadelphys*), some Peramelemorphia, *Barinya wangala*, basal Thylacinidae and some extant dasyurids. In some Didelphidae, Peramelemorphia (including *Yarala burchfieldi*), *Dromiciops australis*, derived thylacinids and dasyurids protoconules are absent.

Well defined protoconules are almost certainly plesiomorphic for Marsupialia (Archer 1976c; Reig *et al.* 1987) and probably represent a retained plesiomorphy in *Barinya wangala*.

Hypoconulid. An anterior cingulid notch is formed when the anterior cingulid of lower molars is interrupted by an indentation for embrasure of the preceding molar's hypoconulid. The distribution and

form-function data for this feature among Marsupialia were considered in detail by Wroe (1997a). A hypoconulid notch is present in peradectids, basal ameridelphian taxa, some extant Didelphidae, all Dasyuromorphia *incertae sedis* for which the feature is known, *Barinya wangala*, basal Thylacinidae and most modern Dasyuridae. This feature is absent in microbiotheriids, all peramelemorphians, *Myrmecobius*, and specialized carnivorous Thylacinidae and Dasyuridae.

Archer (1984) considered the presence of a hypoconulid notch as a possible dasyurid synapomorphy. However, this interpretation requires that this feature was acquired independently in dasyurids and peradectids. Archer's (1984) view has been further complicated by the discovery of basal thylacinids (e.g. *Muribacinus gadiyuli*) that possess a distinct hypoconulid notch. Wroe (1997a) argued that absence of this feature in peramelemorphians and specialized thylacinids was derived. Peramelemorphians show a hypoconulid morphology that is derived from the plesiomorphic marsupial condition compared with that of Dasyuromorphia (Muirhead and Filan 1995) and it is likely that changes in hypoconulid position were necessarily linked with loss of the hypoconulid notch. In hypercarnivorous thylacinids it is likely that loss of this feature was related to allometric factors, as well as a shift in the dominant orientation of force transmission in the jaws (Wroe 1997a). Even if the development of this notch is accepted as a derived condition for Dasyuromorphia, then the presence of a hypoconulid notch in plesiomorphic Dasyuromorphia *incertae sedis* and basal representatives of both modern Dasyuridae and Thylacinidae suggests that this feature appeared early in the clade's evolutionary history and does not represent a dasyurid synapomorphy. The presence of this feature in *Barinya wangala* may be a retained marsupial, dasyuromorphian, or dasyurid-thylacinid plesiomorphy, but is unlikely to represent a synapomorphy with dasyurids.

M₁ paraconid. A well developed M₁ paraconid is present in peradectids, basal ameridelphian taxa, Microbiotheriidae, Peramelemorphia, *Ankotarinja tirarensis*, *Barinya wangala*, and basal Thylacinidae and Dasyuridae. The M₁ paraconid is greatly reduced or absent in *Mayigriphus orbus*, *Myrmecobius*, *Badjcinus turnbulli* and many Dasyuridae (particularly among carnivorous taxa).

I agree with Archer (1976c), who considered the presence of a large M₁ paraconid to be plesiomorphic within Dasyuromorphia, but add that, following the discovery of *Badjcinus turnbulli*, it seems probable that marked reduction or loss of this cusp has occurred independently within all three dasyuromorphian families.

Metacristid. Metacristids are transversely oriented with respect to the long axis of the dentary in Cretaceous Ameridelphia, most Didelphidae including *Pucadelphys andinus*, Microbiotheriidae, Peramelemorphia, Dasyuromorphia *incertae sedis* (except *Mayigriphus orbus*) and some modern Dasyuridae (Sminthopsinae). Considerable variation in the degree of deviance from transverse metacristid alignment to a more anteroposterior orientation is shown within Dasyuromorphia. In *Barinya wangala*, *Myrmecobius fasciatus*, basal Thylacinidae (*Muribacinus*) and most modern Dasyuridae the metacristid shows slight anteroposterior orientation, but in more derived thylacinids (e.g. *Ngamalacinus timmulvaneyi*) and dasyurids (e.g. *Sarcophilus harrisii*) anteroposterior alignment is marked.

Archer (1976c) considered transverse orientation of the metacristids to be plesiomorphic for Marsupialia, Dasyuromorphia and Dasyuridae. I concur with Archer's interpretation with respect to Marsupialia, but, because the derived condition is common to generalized representatives of both Thylacinidae and Dasyuridae, as well as *Myrmecobius fasciatus*, it seems likely that alignment of this crest away from the transverse could represent either a dasyuromorphian synapomorphy or a feature derived independently within two or more dasyuromorphian clades. *Barinya wangala* is probably apomorphic within Dasyuromorphia regarding this feature.

Metaconid (M₁). The M₁ metaconid is comparable in size to, or only slightly smaller than, that of M₂ in basal Ameridelphia and Didelphidae, Microbiotheriidae, Peramelemorphia, Dasyuromorphia *incertae sedis*, *Barinya wangala*, basal Thylacinidae (*Muribacinus gadiyuli*) and most modern Dasyuridae. This cusp is greatly reduced or absent in some modern Dasyuridae (*Dasyurus*, *Sarcophilus*) and most Thylacinidae.

Archer (1976c) and Wroe (1996a) treated the condition apparent in *Barinya wangala*, an M₁ metaconid that is unreduced relative to that of M₂, as plesiomorphic for marsupials and dasyuromorphians.

Entoconid. The entoconid is well defined, exceeding or approaching the height of the hypoconid and with a distinct preentocristid present in unspecialized Ameridelphia, Microbiotheriidae, basal peramelemorphians, Dasyuromorphia *incertae sedis* (excepting *Mayigriphus orbus*), *Barinya wangala*, basal Thylacinidae and Dasyuridae. Variation in this morphology is shown by some taxa and takes the form of overall reduction or loss, often accompanied by loss of the preentocristid, resulting in a more conical cusp. Examples of these character states are found among derived Dasyuridae, Thylacinidae and Peramelemorphia.

A large entoconid and distinct preentocristid, such as is evident in *Barinya wangala*, is plesiomorphic for Marsupialia (Muirhead 1994).

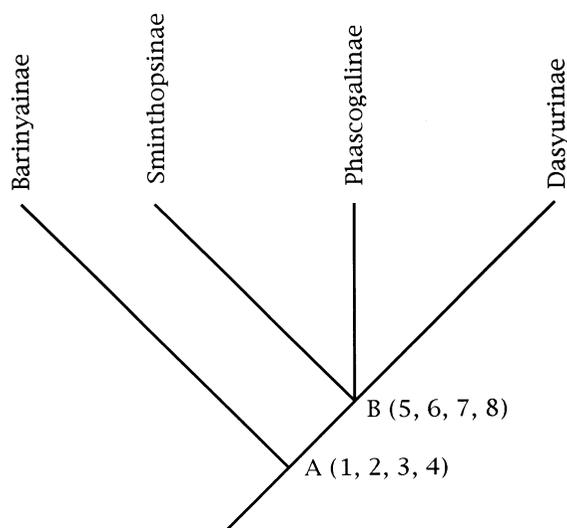
DISCUSSION

The single dental feature that has been commonly held to be a synapomorphy for Dasyuromorphia, reduction of incisor number to 4/3 (Archer 1976c; Marshall *et al.* 1990), is present in *Barinya wangala*. From the results of character analysis it is inferred that *Barinya wangala* is plesiomorphic within Marsupialia and Dasyuromorphia for most of the dental features considered in the present study, but two dental autapomorphies, extreme hypertrophy of both P³ and P₂, clearly distinguish this taxon within the order. However, neither of these features suggest a special relationship with any other dasyuromorphian taxon. One other dental feature in *Barinya wangala* that is considered to be apomorphic within Marsupialia, oblique orientation of the metacristid, is common to some, or all, representatives of each dasyuromorphian family. However, it is unclear whether this feature is a dasyuromorphian synapomorphy, or independently derived in two or more clades.

In contrast with the situation regarding dental character states, *Barinya wangala* shows eight cranial features that are derived within Dasyuromorphia. Four of these are equivocal indicators of relationship within the order and are shared with representatives of at least two of the three recognized dasyuromorphian families. Marked inflation of the alisphenoid tympanic wing is apparent in both extant dasyurids and Myrmecobiidae. The loss of complete posterolateral palatal foramina and the presence of a secondary foramina ovale (a variable feature for *Barinya wangala*) is common to representatives of both derived dasyurine and thylacinid clades, and the development of a squamosal epitympanic sinus is common to all Dasyuridae, *Myrmecobius* and *Thylacinus cynocephalus*. However, four cranial features in *Barinya wangala* are shared only with extant dasyurids (Text-fig. 5). These are: development of a tympanic process of the *pars petrosa* to form a distinct periotic hypotympanic sinus; presence of a paroccipital hypotympanic sinus; presence of a deeply invasive sulcus with the posteroventral lip formed by a mesially directed process in the *pars petrosa* for passage of the internal jugular; and presence of a distinct tubal foramen for passage of the Eustachian tube. Of additional interest is the identification of the following four apomorphies that are found in all living dasyurids, but no other Dasyuromorphia: presence of a secondary facial canal which is fully enclosed by the periotic dorsally; contact between the *pars petrosa* and a paroccipital tympanic process which fully encloses the paroccipital hypotympanic sinus ventrally; extensive dorsal enclosure of the internal jugular canal; and contact between the mastoid tympanic process and the *pars petrosa* (Text-fig. 5).

Because eight potential synapomorphies unite *Barinya wangala* with dasyurids, including four that are unequivocal within Dasyuromorphia, this new species is placed within Dasyuridae. Furthermore, the additional four apomorphies, also unequivocal within Dasyuromorphia, shared only by representatives of the extant dasyurid subfamilies are interpreted as strong evidence for the monophyly of Sminthopsinae, Phascogalinae and Dasyurinae. In further support for both these conclusions it is noted that most of these features are related to the acquisition and development of auditory specializations that have commonly been accorded a high value in phylogenetic analysis (Novacek 1977; Fleischer 1978; MacPhee 1981). Because *Barinya wangala* shares some synapomorphies of the basicranium with living dasyurids, but lacks others (Text-fig. 5), while showing distinctive dental autapomorphies, it is considered to be the sister taxon to a monophyletic clade which includes all extant dasyurids. Consequently, *Barinya wangala* is placed in the new subfamily Barinyinae.

Wroe (1996a, 1997a, 1997b) concluded that no well supported dental synapomorphies define Dasyuridae and recommended that a number of Oligocene–Miocene taxa, previously placed in the



TEXT-FIG. 5. Phylogenetic position of *Barinya wangala* gen. et sp. nov. (Barinyainae, Dasyuridae) and modern Dasyuridae. Synapomorphies at node A (Dasyuridae): 1, development of a tympanic process of the *pars petrosa* to form a distinct periotic hypotympanic sinus; 2, presence of a *paroccipital hypotympanic sinus*; 3, presence of a deeply invasive sulcus with the posteroventral lip formed by a mesially directed process in the *pars petrosa* for passage of the internal jugular; 4, presence of a distinct tubal foramen for passage of the Eustachian tube. Synapomorphies at node B (extant Dasyuridae): 5, presence of a secondary facial canal fully enclosed dorsally by the periotic component; 6, contact between the *pars petrosa* and an a paroccipital tympanic process which fully encloses the paroccipital hypotympanic sinus ventrally; 7, extensive dorsal enclosure of the internal jugular canal; 8, contact between the mastoid tympanic process and the *pars petrosa*.

family, but known only on the basis of dental evidence, should be treated as *Dasyuromorphia incertae sedis*. These taxa, *Ankotarinja tirarensis*, *Keeuna woodburnei*, *Wakamatha tasselli* and *Dasyulurinja kokuminola*, are plesiomorphic among dasyuromorphians for almost all dental features and none of the derived features that they exhibit convincingly demonstrates a special relationship with any known dasyurid taxon. In short, although the central Australian taxa listed above are very similar to generalized dasyurids regarding dental features, all of these shared features appear to be dasyuromorphian or marsupial plesiomorphies. Thus, they might be monophyletic with any dasyuromorphian family or members of a sister clade to Dasyuromorphia, as currently recognized. Consequently, it is argued that the early to mid Miocene *Barinya wangala* represents the oldest known dasyurid that can be placed within the family with any confidence.

The common perception of Dasyuridae as a generalized marsupial clade, representing a possible structural morphotype for the Australian radiation is contradicted, at least by basicranial features. *Barinya wangala* and, in particular, extant dasyurids, show many specializations of the auditory region that are clearly apomorphic within Dasyuromorphia. Wroe (1997a) suggested that the development of a derived middle ear morphology, present in all extant dasyurids, may have played a rôle in the family's spectacular radiation, at the expense of Thylacinidae and Peramelemorphia. That these latter two clades have suffered a dramatic decline in diversity since the mid Miocene is well demonstrated by Muirhead (1994), Wroe (1996a) and Muirhead and Wroe (1998). Wroe (1996a) further argued that the niches of smaller thylacinids may have subsequently been occupied by dasyurids of the genus *Dasyurus*, while the niches of insectivorous-omnivorous bandicoots have since been occupied by smaller dasyurids (Muirhead 1994). The decline of thylacinids has been especially dramatic. The family was represented by a single, now extinct species, *Thylacinus cynocephalus*, at the time of European colonization. By contrast, at least five thylacinid species are known from the Miocene of Riversleigh and these taxa dominated a wide variety of

carnivorous niches. It is surprising that among the eminently productive Oligocene–Miocene deposits of Riversleigh, *Barinya wangala* constitutes the only confirmed representative of the now ubiquitous dasyurid clade. Even if the remaining Miocene Riversleigh dasyuromorphian, *Mayigriphus orbus*, currently classified as *Dasyuromorphia incertae sedis*, is ultimately shown to be dasyurid, representation of the family in Oligocene–Miocene deposits of Riversleigh remains very poor compared with that of modern faunas. This finding is all the more remarkable given the relative abundance of large, specialized carnivorous mammalian taxa, which in addition to the diversity of thylacinids present in the Oligocene–Miocene of Riversleigh, also included at least two thylacoleonids (Archer *et al.* 1997) and two possibly carnivorous kangaroo taxa (Wroe and Archer 1995; Wroe 1996b; Wroe *et al.* 1998). Large carnivores are generally found in low abundance compared with smaller, less specialized taxa (Damuth 1981). A further unexpected outcome of research accomplished to date has been the failure to find support for the existence of extant dasyurid subfamilies in pre-Pliocene sites of Riversleigh, or elsewhere (Wroe 1996a). The rarity of dasyurids and the absence of any representatives of the monophyletic clade, inclusive of all living dasyurids (Sminthopsinae, Phascogalinae, Dasyurinae), in pre-Pliocene faunas, might be explained as a serendipitous artefact of the fossilization process. However, it now seems equally tenable that these findings are truly reflective of dasyurid diversity at the time and that the monophyletic clade inclusive of extant subfamilies may not have existed prior to the late Miocene. Certainly, given the insubstantial record of Dasyuridae from the otherwise fossil-rich Miocene deposits of Riversleigh, it seems likely that dasyurid diversity was low during this time and that the evidently explosive radiation of the modern subfamilies was only in its early stages, if it had commenced at all.

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APPENDIX: ABBREVIATIONS USED IN TEXT-FIGURES

Cranial features: al, alisphenoid; atw, alisphenoid tympanic wing; ahs, alisphenoid hypotympanic sinus; as, alisphenoid strut; bo, basoccipital; bs, basisphenoid; ec, ectotympanic; fr, frontal; icf, internal carotid foramen; ju, jugal; mtp, mastoid tympanic process; mx, maxillary; na, nasal; pal, palatine; par, parietal; pfo, primary foramen ovale; pre, premaxilla; ptp, paroccipital tympanic process; ses, squamosal epitympanic sinus; sij, sulcus for internal jugular; sq, squamosal; tcf, transverse canal foramen; tf, tubal foramen; tppp, tympanic process of the *pars petrosa*. Dental features: ac, anterior cingulum; acd, anterior cingulid; co, cristid obliqua; ecd, entocristid; ed, entoconid; hd, hypoconid; hld, hypoconulid; me, metacone; mecd, metacristid; mecl, metaconule; med, metaconid; pa, paracone; pacd, paracristid; pad, paraconid; pc, posterior cingulum; pcd, posterior cristid; pmc, postmetacrista; ppc, postparacrista; pprc, postprotocrista; pr, protocone; prcl, protoconule; prd, protoconid; prmc, premetacrista; prpac, preparacrista; ppprc, postprotocrista; shd, sulcus for hypoconulid of preceding molar; st A, stylar cusp A; st B, stylar cusp B; st C, stylar cusp C; st D, stylar cusp D; st E, stylar cusp E; stsh, stylar shelf; ta, talonid; trd, trigonid; tn, talon.