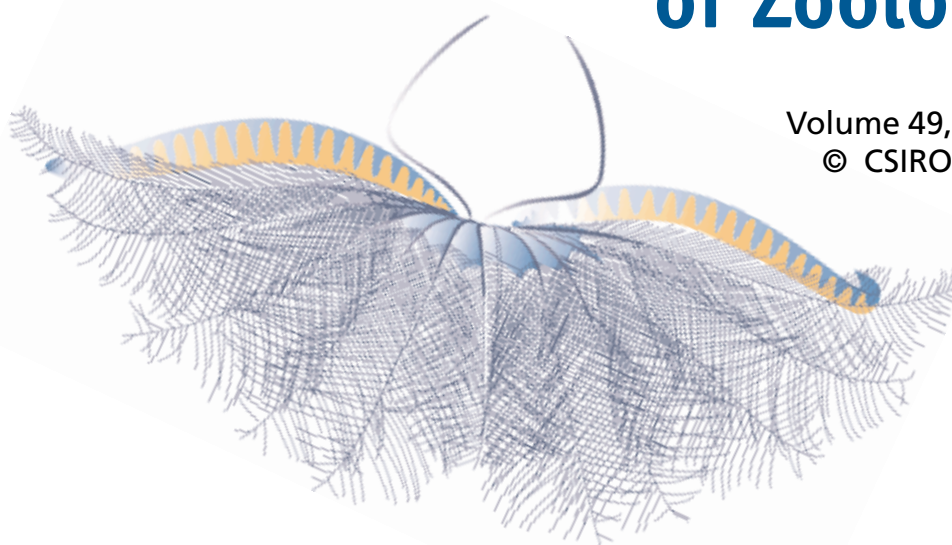


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The skull of *Nimbacinus dicksoni* (Thylacinidae : Marsupialia)

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Abstract

The exceptionally well preserved skull and mandible of the Miocene thylacinid *Nimbacinus dicksoni* is described. Phylogenetic analysis supports the contention that, within the family, the dentition of *N. dicksoni* is unspecialised, less derived than the recent *Thylacinus cynocephalus* for at least 12 features. However, relatively few cranial specialisations evident in *T. cynocephalus* clearly distinguish it from *N. dicksoni*. These two taxa share at least three derived cranial features not present in the most generalised thylacinid known from significant cranial material, the late Oligocene *Badjcinus turnbulli*. On the other hand, where comparison is possible, even the most specialised thylacinid, *T. cynocephalus*, is plesiomorphic for at least 10 cranial features common to modern dasyurids and five present in the Miocene dasyurid, *Barinya wangala*. Two character states found in thylacinids are more derived than in *B. wangala*. Relative to the remaining dasyuromorphian family, Myrmecobiidae, represented by the monotypic *Myrmecobius fasciatus*, thylacinids are derived for five cranial features and plesiomorphic for five. It appears that despite considerable anatomical diversity among the dentitions of thylacinids and the presence of many highly specialised dental features in some species, the crania of thylacinids have remained remarkably conservative. Even with respect to dentition, in terms of overall similarity, the Miocene *Thylacinus macknessi* and late Oligocene material referred to *Thylacinus* does not differ greatly from the recently extinct *T. cynocephalus*. It now also seems probable that *T. macknessi* was also very similar to *T. cynocephalus* with respect to cranial anatomy. Numerical parsimony analysis incorporating this new material produced moderate bootstrap and Bremer support for a monophyletic Thylacinidae. In this same treatment strict consensus placed *Myrmecobius fasciatus* as the sister taxon to Thylacinidae–Dasyuridae, but bootstrap and Bremer support was lacking. Both of these results are *contra* those of the most recent attempt to resolve dasyuromorphian relationships using numerical parsimony and anatomical data. In the present analysis, the early Eocene Australian taxon, *Djarthia murgonensis*, fell outside a clade inclusive of all other Australian taxa and was monophyletic with the borhyaenoid, *Mayulestes ferox*. This latter relationship is based on limited material, poorly supported and considered highly unlikely, but it does strengthen the argument that formal placement of *D. murgonensis* beyond the level of Marsupialia *incertae sedis* is unwarranted at present.

Introduction

Until recently, Australia's fossil record of marsupicarnivores has been poor. However, new discoveries over the last decade have greatly advanced our understanding (Wroe 2002). Prominent among these have been the first pre-Pleistocene skulls referred to Thylacinidae and Dasyuridae by Muirhead and Wroe (1998) and Wroe (1999), respectively. A major and unexpected revelation has been that Thylacinidae, monotypic at the time of European colonisation, was once a relatively diverse clade. Prior to 1990 the pre-Pliocene record for the family consisted of a single species, *Thylacinus potens*, from the late Miocene Alcoota Local Fauna (Woodburne 1967). However, since 1990 the fossil record of the family has grown from one to 11 (Muirhead and Archer 1990; Wroe 1996; Muirhead 1997; Murray

1997; Muirhead and Wroe 1998; Murray and Megirian 2000). Six of these new species have come from the late Oligocene to early–late Miocene deposits of Riversleigh in north-western Queensland (*Muribacinus gadiyuli*, *Badjcinus turnbulli*, *Wabulacinus ridei*, *Ngamalacinus timmulvaneyi*, *Thylacinus macknessi* and *Nimbacinus dicksoni*). The remaining four were discovered in three deposits from the Northern Territory of middle to late Miocene age (*Thylacinus megiriani*, *Mutpuracinus archibaldi*, *Nimbacinus richi* and *Tyarrpecinus rothi*). While this newly discovered material has obviously enriched our understanding of thylacinid diversity and evolution, it has to date included only one species represented by significant cranial remains (*Badjcinus turnbulli*). Below is the description of a second and exceptionally well preserved thylacinid fossil specimen referred to the Miocene species *Nimbacinus dicksoni* (Muirhead and Archer 1990).

Incorporating new data from the study of this skull and some additional taxa, the cladistic investigation of Wroe *et al.* (2000) is re-run. To date relatively few anatomy-based numerical parsimony treatments inclusive of Australian marsupicarnivores have been undertaken (Kirsch and Archer 1982; Springer *et al.* 1997; Rougier *et al.* 1998; Wroe *et al.* 2000). Results of the first three of these are reviewed by Wroe *et al.* (2000) and only the latter is considered here. The analysis of Wroe *et al.* (2000) included a variety of extant and extinct marsupicarnivore species, both Australidelphian and Ameridelphian, achieving resolution in some important respects. These included monophyly for Dasyuromorphia and placement of the *Barinya wangala* as sister taxon to a monophyletic clade containing representatives of each of the three extant dasyurid subfamilies. However, Wroe *et al.* (2000) found Thylacinidae to be paraphyletic and did not resolve the positions of dasyuromorphian families with respect to one another.

Methods

Terminology and institutional abbreviations

Dental nomenclature follows Flower (1867) and Luckett (1993) regarding the molar–premolar boundary, such that the adult (unreduced) post-canine cheektooth formula of marsupials is P1–3 and M1–4. Morphological terminology follows Archer (1976a, 1976b), as modified by Wroe (1997a). Systematic terminology follows that used by Wroe (1996, 1997a) and Wroe *et al.* (2000), adapted from Marshall *et al.* (1990) and Krajewski *et al.* (1994). Institutional abbreviations are: QMF (Queensland Museum Fossil) and NTM (Northern Territory Museum).

General methods

The new specimen of *Nimbacinus dicksoni* (QMF36357; see Figs 1–7) has been directly compared with all described thylacinid material from Riversleigh deposits and the holotype of *Thylacinus potens*. We have not observed the holotypes of *Thylacinus megiriani*, *Mutpuracinus archibaldi*, *Tyarrpecinus rothi* or *Nimbacinus richi* at first hand and any comparisons with these species are based on the comments and figures provided in the descriptions by Murray (1997) and Murray and Megirian (2000).

A primary objective of the numerical parsimony analysis was to study effects of including new data, from the skull of *N. dicksoni*, on the placement of thylacinids with respect to other dasyuromorphians. This is because only three thylacinids are currently represented by significant cranial material and consequently any investigation using both cranial and dental features would have been based on a data set dominated by missing characters for most taxa. Analyses of intrafamilial relationships based primarily or exclusively on dental features have been performed by Muirhead and Wroe (1998), Murray and Megirian (2000) and Wroe (2001).

Taxa included in the present analysis are as used by Wroe *et al.* (2000), but with five additions. These were the peradectid *Alphadon marshii*, the possible microbiotherian *Mirandatherium alipioi*, Australia's oldest marsupicarnivore *Djarthia murgonensis* (Marsupialia *incertae sedis*) and two thylacinids, *Muribacinus gadiyuli* and *Nimbacinus dicksoni*. *Alphadon marshii* was included because, historically, species of *Alphadon* have been treated as generalised, if not stem, marsupials (Clemens 1979) and, within

the genus, *A. marshii* is relatively well represented and unspecialised (Johanson 1996). Inclusion of *Mirandatherium alipioi* was considered appropriate given that it was treated as a microbiotherian with links to the Australian radiation by Marshall (1987). *Alphadon marshii* constituted the outgroup to all remaining taxa. Of these five fossil species, all excepting *N. dicksoni* were known on the basis of dental material only. However, each was represented by complete upper and lower molar rows at least.

A number of significant fossil taxa were not included because they are known only from incomplete molar material and would not have fulfilled minimum requirements for the realistic elucidation of phylogeny (Novacek *et al.* 1988). Among excluded taxa were seven thylacinids: *Thylacinus macknessi* (Muirhead 1992), *Wabulacinus ridei* (Muirhead 1997), *Ngamalacinus timmulvaneyi* (Muirhead 1997), *Nimbacinus richi*, *Tyarrpecinus rothi* and *Mutpuracinus archibaldi* (Murray and Megirian 2000). Other fossil Australian marsupicarnivore taxa that likewise failed to meet this requirement included *Mayigriphus orbus* (Wroe 1997b), *Ganbulanyi djadjinguli* (Wroe 1998), *Ankotarinja tirarensis* (Archer 1976c) and *Keeuna woodburnei* (Archer 1976c).

Character scoring largely follows Wroe *et al.* (2000) with character states given in Appendix 1 for 44 dental and 33 cranial features. Altogether, 29 taxa were included in the input data matrix (Table 1). An additional three thylacinids known from incomplete upper and/or lower molar rows were also scored in this table but were not included in the phylogenetic analysis. Notoryctidae, a possible sister taxon to Dasyuromorphia, was excluded because specialisation in *Notoryctes* is so extreme that for most features it would have been scored either as unknown or as autapomorphic. Diprotodontians were not included for the same reasons.

The analysis employed PAUP 3.1.1 (Swofford 1993), a heuristic search, ACCTRAN character optimisation and TBR branch swapping. The relative stability of clades was assessed using Bremer support (Bremer 1988, 1994) and bootstrap analysis (Felsenstein 1985). Bremer support indices were determined by studying suboptimal trees. Only species that we have examined at first hand were included. Bootstrapping was based on 100 replicates.

Description of new material

Background

The description of *Nimbacinus dicksoni* by Muirhead and Archer (1990) was based on a left M_1 (QMF16802), the holotype and the following paratypes: QMF16803, a right maxillary fragment containing P^3 , M^{1-3} ; QMF16804, a right maxillary fragment containing M^{1-3} ; QMF16805, a right M^3 ; QMF16806, a left M^3 ; QMF16807, a right M^4 ; QMF16809, a broken right M_2 ; and NTMP85553–3, a right dentary fragment containing P_{1-2} and M_1 . Excepting NTMP85553–3 and QMF16809 all material is from Henk's Hollow Site, Riversleigh, north-western Queensland. This deposit is thought to be middle Miocene in age (Creaser 1997). QMF16809 is from D-Site, Riversleigh and NTMP85553–3 is from the Bullock Creek Local Fauna. Respectively, these deposits are considered to be late Oligocene and middle Miocene in age (Black 1997).

General description

The cranium and mandible QMF36357 are from AL90 Site, Riversleigh, north-western Queensland. Black (1997) considers this site to be middle Miocene in age. Overall, the quality of preservation is exceptional. Fine detail is present, including parts commonly not recovered in fossil material such as the pterygoid processes and alisphenoid tympanic processes. There is little distortion, although dorsally the nasals and anterior regions of the frontals are crushed. RI^2 is retained; all other incisors are absent; only the bases of both canines are present; and RP^2 has been lost. From the degree of tooth wear it is clear that the specimen represents a mature adult. QMF36357 is referred to *Nimbacinus dicksoni* because it differs in no way from the holotype or paratypes from the type locality that can not be ascribed to differences in wear. Dental and cranial measurements are given in Table 2.

Table 1. Data matrix showing the distribution of 77 characters among 29 taxa subject to parsimony analysis (PAUP 3.1) in the present study
 0 = the plesiomorphic state; P = polymorphic; n = not applicable; u = state unknown; and ? = missing; three thyllacids denoted by asterisks are shown here for comparative purposes but were not included in the analysis because they were represented by insufficient material

Taxon	Character										
	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777			
<i>Alphadon marshii</i>	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890			
<i>Pucadelphys andinus</i>	??001?000	0000000000	10000?0000	0000000000	00000?0000	??00000000	??00000000	??00000000			
<i>Andinodelphys cochabambensis</i>	0000000101	0010000000	1000100010	0000011002	0000?000010	nm00000000	0000000110	0000000			
<i>Mayulestes ferax</i>	0000000101	0010000000	10?0100010	0000010002	0000101010	nm0000?010	0010000?010	0000000			
<i>Didelphis marsupialis</i>	0000000112	0010000010	1000100010	0010011000	1110100010	nm0030?010	0000100?010	0001001			
<i>Metachirus naudicaudatus</i>	0010000000	0010000000	0000100010	1000021002	0100101001	P110011000	001011000P3	0000000			
<i>Lestodelphys halli</i>	0010000111	0010000000	0000100010	1000011002	0000001010	0210021000	0011100000	0000000			
<i>Dromiciops australis</i>	0000000111	0011100010	0000100010	1000021002	2101001010	0110022000	1010121003	0000000			
<i>Mirandatherium alpiot</i>	0110000020	01011022u0	0000100000	0000021002	0001031010	0003022000	0011302012	0000001			
<i>Djaruthia murgonensis</i>	????0000000	00?00001100	10001?00?0	0000101002	0000?00000	????000000	????000000	????0000			
<i>Yarala burchfieldi</i>	??00000101	0010010000	11001?00?0	00000?0000	00101?0000	????000000	????000000	????0000			
<i>Echymipera kalubu</i>	??00000111	0211100010	0000111111	1000021002	00020?0010	02?00001?0?	001010101?	0000111			
<i>Perameles nasuta</i>	1111000101	1211000000	0000011111	1000021001	0001001010	0100001000	0011101010	1110111			
<i>Myrmecobius fasciatus</i>	011001101	1211000010	0000011111	1000021001	0001031010	0200122000	0011121010	1110111			
<i>Barinya wangala</i>	1010100uuu	0uuuuuuuuu	u001110001	0010u2100u	0000110010	0000122000	0010213010	0000011			
<i>Sminthopsis murina</i>	1100010111	0010010010	1000110010	0000101002	00111?1110	1000112000	1010321012	0000001			
<i>Sminthopsis crassicaudata</i>	1100000111	0011011110	0000110n10	0000001002	2002031110	0002122001	1111332012	1100001			
<i>Planigale maculata</i>	1101000111	0010010010	0000111010	0000001000	0012031110	0002122001	1111332012	1100001			
<i>Murexia longicaudata</i>	1000000121	0111111110	0000110n10	0011001002	2012031110	0002122001	1110332012	0000001			
<i>Phascogale tapoatfa</i>	1100000111	0010010010	0000010010	0000101002	001P011110	1003122001	1110332012	0000001			
<i>Aneides flavipes</i>	1000000111	0010011010	1000010010	0000101002	0000001110	0002122001	1110332012	0000001			
<i>Neophascogale lorentzii</i>	1110100101	0210000010	0000011010	0000101002	0012021110	0002122001	1110332012	1000001			
<i>Dasyurus hallucatus</i>	1000200111	0310011010	0000010010	0101111002	0021101110	00P2122001	1110332012	0000001			
<i>Dasyurus maculatus</i>	1010200122	0310010011	0000110010	0111121102	0022111110	P103122101	1110332012	0000001			
<i>Sarcophilus harrisi</i>	1010210123	0311010011	0000110011	0112121102	1022121110	1102122201	1110332012	0000001			
<i>Murbacinus gadyuli</i>	????0001112	0010011110	00000?00?0	001010?002	00?0?00000	????000000	????000000	????0000			
<i>Badjcinus turnbulli</i>	1?00??112	0710011110	000?010010	0110000000	001111?000	0100012100	0011100000	0000001			
<i>Nimbacinus dicksoni</i>	11?0001112	0010011110	0001010010	00101010?2	0001111111	2100112100	0011100000	0?0000?			
<i>Thylacinus cynocephalus</i>	1110000113	0111112200	0001110010	002011112n	1102121111	2100112100	0011100000	0000001			
* <i>Ngamalacinus timuluaneyi</i>	????00011?2	00?00011210	0000?00?00	0010100102	00?1?00000	????000000	????000000	????0000			
* <i>Wabulacinus ridei</i>	??????01?3	01?111222?	00001?00?0	0?1?11?002	0?0?000000	????000000	????000000	????0000			
* <i>Thylacinus macknessi</i>	??????01?3	01?101?00?	????01?0?0	002011011?	1001?00000	????000000	????000000	????0000			

Table 2. Dental measurements of *Nimbacinus dicksoni* (QMF36357)

Dental measurements are given for the dentition of the left side for upper teeth and right side for lowers. All measurements are in millimetres. Further measurements are as follows: skull length, 132.4 mm; maximum width across zygomatic arches, 80.8 mm; length of upper molar row, 27.4 mm; length of lower molar row, 30.3 mm

Tooth	Upper jaw Length	Width	Tooth	Lower jaw Length	Width
M ¹	7.7	5.7	M ₁	6.2	4.2
M ²	7.9	7.5	M ₂	8.5	5.0
M ³	7.5	8.6	M ₃	8.6	5.2
M ⁴	4.8	6.7	M ₄	8.5	4.7
P ¹	4.5	2.2	P ₁	4.4	2.3
P ²	5.8	2.7	P ₂	7.8	3.5
P ³	7.7	4.2	P ₃	8.1	3.8

Skull

Cranium

Nasal. The nasal flares posteriorly before angling sharply towards the midline at the naso-maxillo-frontal suture. The bone's posterior limit lies just beyond the anterior-most margin of the orbit and the naso-premaxillo-maxillary suture is dorsal to the anterior margin of P³ and the naso-maxillo-frontal suture is approximately dorsal to M². Anteriorly the nasal tapers slightly towards the midline as in *Badjcinus turnbulli*, but not in *Thylacinus cynocephalus* and *Dasyurus maculatus*, where the anterolateral border of the nasal is straight, or in *Barinya wangala* and *D. viverrinus* where this bone is angled laterally. Because of damage, it can not be determined whether the nasal extends beyond the point of contact with the premaxillae. The posterior margin of the right nasal is intact although marginally displaced; it angles obliquely towards its posterior junction with the maxilla, as it does in *T. cynocephalus*, *B. turnbulli* and *B. wangala*, rather than as in *Dasyurus* (in particular *D. viverrinus*), where this suture tends to be more transverse.

Premaxilla. Laterally the premaxilla and maxilla form a near-linear suture, as in *Thylacinus cynocephalus*, *Barinya wangala* and *Dasyurus maculatus*; in *Dasyurus viverrinus* the lateral margin of the premaxilla has a distinct sigmoid curve. The state of this feature can not be ascertained in *Badjcinus turnbulli*. The dorsomedial border of the premaxilla is formed by the nasal and the ventrolateral and ventral borders are formed by the maxilla. Laterally, the premaxillo-maxillary suture is anterior to the canine as in *T. cynocephalus*, *Badjcinus turnbulli*, *B. wangala* and *Dasyurus*. As in *B. turnbulli*, *B. wangala* and *Dasyurus*, but not *T. cynocephalus*, the premaxilla does not contribute to the anteromedial border of the canine alveolus. Ventrally the premaxillo-maxillary suture extends posteromedially from the anteromedial third of the canine alveolus before angling anteromedially to meet the anterolateral border of the premaxillary vacuity (palatal fissure). Medially, the premaxilla runs transversely from the posteromedial margin of the premaxillary vacuity to the median line of the skull. In occlusal view the curvature of the incisal arcade is very slightly convex, as in *T. cynocephalus*, *B. turnbulli* and *D. maculatus*, contrasting with the more obviously convex and V-shaped arcades of *D. viverrinus* and *B. wangala*, respectively. Alveoli for I¹⁻⁴ are contained in the premaxilla and RI² is retained. A well developed depression for the reception of C₁ is present. The paired incisive foramina are bordered anterolaterally and medially by the premaxilla and posterolaterally by the maxilla.



Fig. 1. *Nimbacinus dicksoni*, QMF36357; cranium. (a), lateral view; (b), ventral view; (c), dorsal view. Scale = 2 cm.

Maxilla. Although damage to the skull has obscured some of the relationships of the maxilla, where comparison is possible it appears to have the same borders as in *Thylacinus cynocephalus*, *Badjcinus turnbulli*, *Barinya wangala* and *Dasyurus*. On the rostrum the maxilla is bordered anterodorsally by the premaxilla, posterodorsally by the nasal and briefly by the frontal, and posteriorly by the lachrymal and jugal, the suture between these two bones meeting posterior to the slit-like infraorbital canal. The maxilla floors the orbit and the suture between the maxilla and palatine medial to the orbit floor extends posteriorly before wrapping ventrally onto the palate. In palatal view the maxilla, bordered anteriorly by the premaxilla, forms the posterolateral border of the premaxillary vacuity. C^1 , P^{1-3} , and M^{1-4} are contained within this bone; the anterior border of the canine alveolus is confluent with its anterolateral border. Posteromedially the maxilla abuts the palatine at the posterolateral margin of the conjoined maxillary vacuity. The maxillary vacuities are large and contained mostly within the maxilla, but are bordered posteriorly by the palatine. Where comparable, these vacuities are similar in structure to those of *T. cynocephalus* and *B. turnbulli* (only the lateral border is preserved). They differ from those of *Dasyurus*, where the vacuities are small and variable (*B. wangala* is damaged in this area but the maxillary vacuities appear to have been large and conjoined). A rostral opening of the infraorbital canal, situated anterior to the lachrymal/jugal suture and dorsal to the posterior limit of M^1 , is surrounded by the maxilla as in *B. turnbulli*, *Dasyurus* and *B. wangala*. In *T. cynocephalus* the infraorbital canal is much larger and anteriorly the canal runs through the maxilla, while posterolaterally its margin is formed by the jugal with the maxillo-jugal suture running through its roof. The roughly triangular orbital (posterior) opening of the canal in *Nimbacinus dicksoni* opens dorsal to the posterior root of M^2 . This canal appears to be bordered dorsally by the lachrymal and is floored by the maxilla, which forms the lateral, ventral and medial borders. The palatine has no contact with the infraorbital canal, terminating posterior to the orbital opening. An incomplete posterolateral palatine foramen is present entirely within the palatine and has no border with the maxilla. No accessory posterolateral palatine foramen is evident.

Palatine. Although sutures are somewhat obscured, relationships of the palatine to other bones appear to largely follow the pattern in *Thylacinus cynocephalus* and *Barinya wangala* (because the maxillary vacuities are small in *Dasyurus* the contribution of the palatine to the secondary palate is greater). The palatine is only partially preserved in *Badjcinus turnbulli*. In palatal view the palatine is bordered laterally by the maxilla, the sutures running posterolaterally from the maxillary vacuities at about a 45° angle as in *T. cynocephalus* and *B. wangala*. Anteriorly the palatine forms the posterior margin of the maxillary vacuity; medially the palatines project to form a median process. Posterior to the palate the palatine meets the pterygoid just anterior to the pterygoid wings. In the orbital region the palatine is bordered laterally by the maxilla, anteriorly by the lachrymal, dorsally by the frontal and posteriorly by the alisphenoid, extending to a point just anterior to the foramen rotundum. The orbitosphenoid may make a small contribution between the frontal and the alisphenoid. A distinct transverse bar of bone, the postpalatine torus, forms the posterior margin of the palate. This torus is thickened and rugose and terminates laterally in small, sharp spines. It is generally similar to that in *Dasyurus*, but is better developed than in *B. wangala* (where a smooth lip is formed). In the *T. cynocephalus* examined a torus, as such, is absent, although there is a raised ridge of bone. The palatal spines are larger in *T. cynocephalus* and are displaced posteriorly. The vomerine/presphenoid region is obscured and interpretation is difficult. On the orbital face just posterior to the palatine-lachrymal suture is an elliptical sphenopalatine foramen, similar in position to that

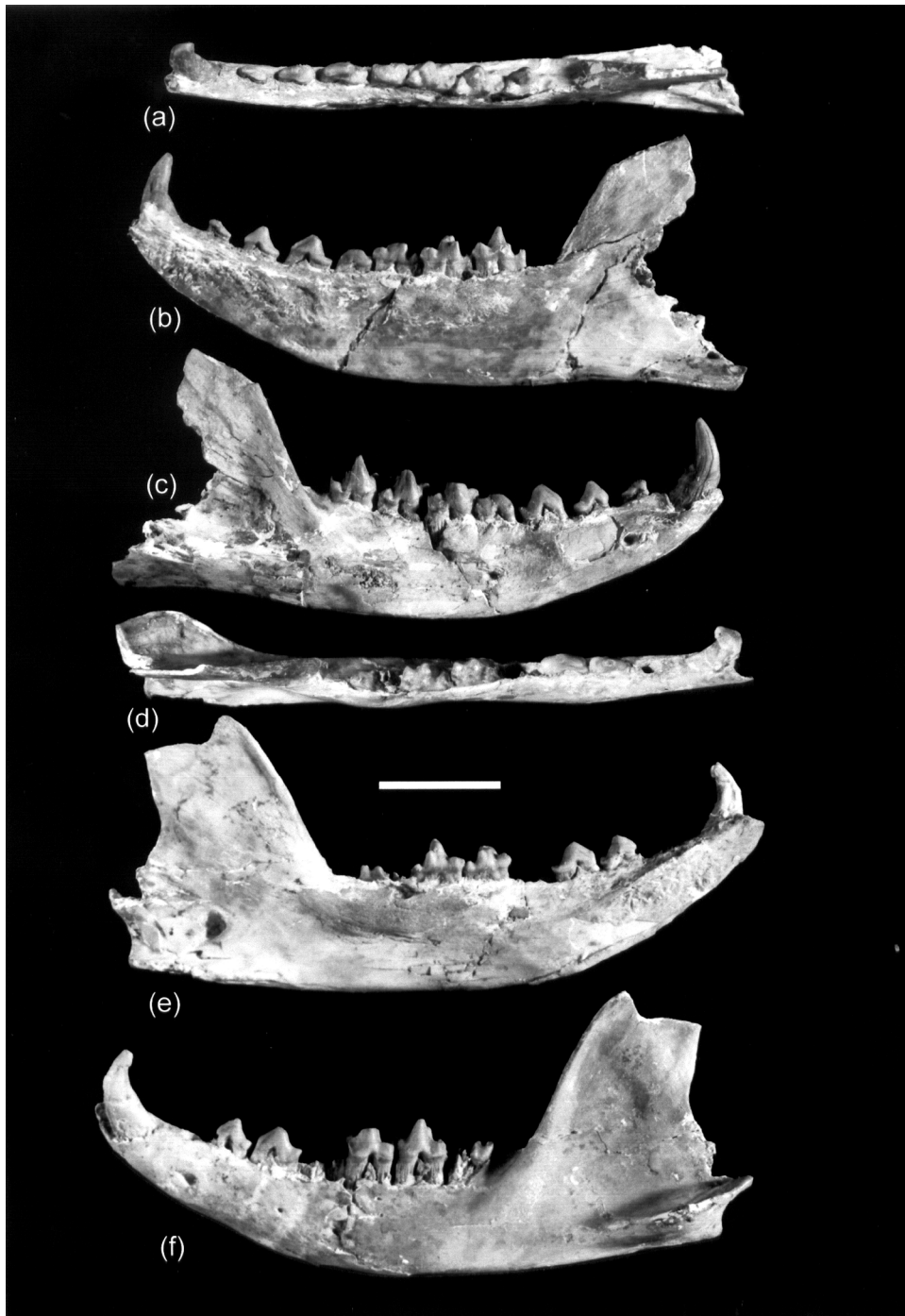


Fig. 2. *Nimbacinus dicksoni*, QMF36357; right and left dentaries. Right dentary: (a), occlusal view (b), lingual view (c), buccal view. Left dentary: (d), occlusal view (e), lingual view (f), buccal view. Scale = 2 cm.

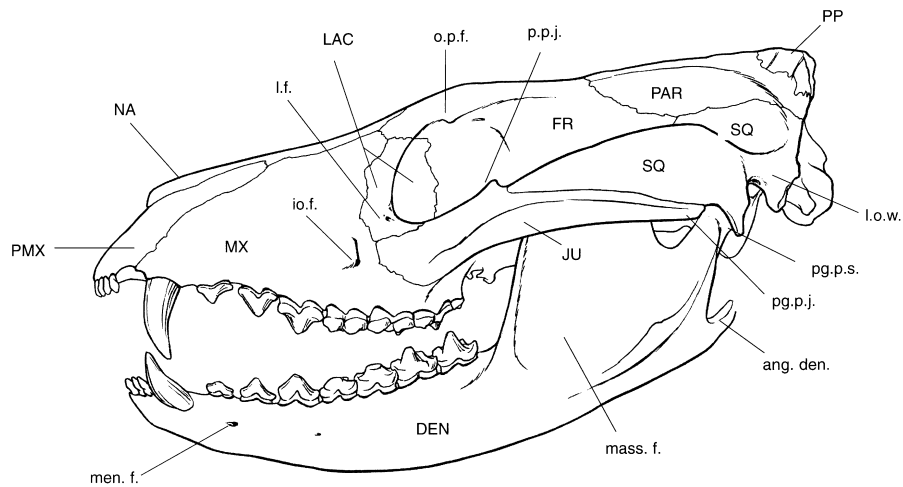


Fig. 3. *Nimbacinus dicksoni*, QMF36357; stylised lateral view of skull and dentary. See Appendix 3 for legend to abbreviations.

of *B. wangala* and *Dasyurus*. In *T. cynocephalus* the sphenopalatine foramen is proportionately slightly larger and lies closer to the maxillopalatine suture.

Lachrymal. The lachrymal, forming the anterior rim of the orbit, is bordered anteriorly by the maxilla, dorsally and posteriorly by the frontal, ventrally by the palatine and maxilla and ventrolaterally by the jugal. Three small lachrymal foramina are present: on the rostral part of the lachrymal just anterior to the rim of the orbit are superior and inferior foramina and a third foramen lies within the orbit. The lachrymal extends onto the face to a greater extent than in *Dasyurus* or *Barinya wangala*, but not to the extent seen in *T. cynocephalus*, in which the rostral extension of the lachrymal overlaps the infraorbital foramen. This bone is not preserved in *Badjcinus turnbulli*.

Jugal. The anterior border of the jugal is formed by broad contact with the maxilla. Dorsal to this the jugal contacts the lachrymal and continues posteriorly to form the remainder of the ventral margin of the orbit, ending in a well developed postorbital process of the jugal (inferior postorbital process). This process terminates just in front of the anterior junction with the squamosal. The squamosal overlies the jugal to form its posterodorsal border. The sulcus for origin of the masseter is well developed. Ventrally the jugal forms the lateral border of the glenoid fossa to produce a preglenoid process of the jugal as in *Dasyurus* and *Barinya wangala*, but not *Thylacinus cynocephalus*, where the jugal terminates prior to the fossa with no distinct process formed. This region is damaged in *B. turnbulli*. The zygomatic arch is relatively deep, as in *D. maculatus*, in contrast to the more slender zygoma in *B. wangala*, *D. viverrinus* and *T. cynocephalus*. Again, damage prohibits direct comparison with *Badjcinus turnbulli* here.

Frontal. Damage to the anterior part of the frontal obscures much of its precise relationships to the nasal and maxilla, and some of the sutural connections, particularly in the orbital region and side wall of the braincase, are damaged or obscured. However, the following relationships are clear. Anteriorly the frontal abuts the nasal at an oblique angle. Anterolaterally the frontal makes brief contact with the maxilla; just posterior to this the frontal is bordered anterolaterally to anteroventrally with the lachrymal, forming the

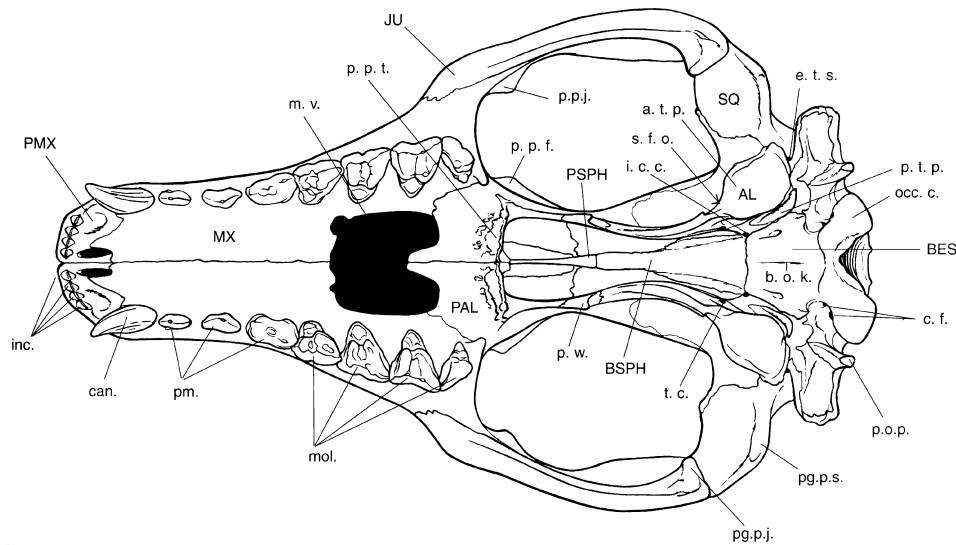


Fig. 4. *Nimbacinus dicksoni*, QMF36357; stylised ventral view. See Appendix 3 for legend to abbreviations.

anterior region of the orbit. Posteriorly the orbital region is formed by the frontal and orbital part of the palatine, the palatine forming the ventral border of the frontal. On the side wall of the braincase the frontal is bordered posteroventrally by the small orbitosphenoid and, dorsal to this, by the alisphenoid, although portions of the alisphenoid–squamosal–frontal region are damaged. In *Thylacinus cynocephalus* the frontal is bordered posteroventrally by the squamosal, which is probably the case in *Nimbacinus dicksoni*, although there is breakage and flaking of bone in this region. The frontal–squamosal suture is not clear, but the relatively minor contribution of both the parietal and alisphenoid to the braincase excludes the possibility of alisphenoid–parietal contact, in contrast to both *Barinya wangala* and *Dasyurus* where the alisphenoid contacts the parietal dorsally (feature not preserved in *Badjcinus turnbulli*). Posteriorly the frontal is bordered by the parietal. The dorsal fronto-parietal suture in both *N. dicksoni* and *T. cynocephalus* lies more posteriorly than it does in *Dasyurus* and *B. wangala*. A distinct orbital process of the frontal (supraorbital process, zygomatic process of frontal bone) is present. There is a tiny foramen posterior to the orbital process of the frontal, preceded by a narrow sulcus. Both features are present in *T. cynocephalus* examined and this foramen is variably present in *Dasyurus* (absent in *B. wangala*), but is not accompanied by a sulcus or groove. A V-shaped ethmoid foramen is present at the juncture of the frontal, alisphenoid and orbitosphenoid.

Parietal. The paired parietals roof the brain case and form a moderate sagittal crest where they meet along the dorsal midline. The parietal is bordered by the frontal anteriorly at the origin of the sagittal crest. Laterally the parietal is overlain by the squamosal, but damage to this part of the skull makes interpretation difficult. In *Thylacinus cynocephalus* the parietal is bordered ventrally by the squamosal before abutting the frontal, with no parietal–alisphenoid contact, which also appears to be the case in *Nimbacinus dicksoni*. In *Dasyurus* and *Barinya wangala* the parietal contacts the alisphenoid anteroventrally between the squamosal and frontal. The relationships of these bones can not be determined in *Badjcinus turnbulli*. The parietal broadly contacts the postparietal, or interparietal,

posteriorly. Ventral to the postparietal the parietal briefly abuts the supraoccipital, contributing in a minor way to the nuchal crest.

Postparietal (interparietal). The postparietals, contacting the parietals across their anterior margins, form the terminus of the dorsal surface of the skull and contribute to the sagittal crest. The nuchal crest is formed by the posterior margin of the postparietal fused to the anterior border of the supraoccipital (described as part of the fused basioccipital–exoccipital–supraoccipital complex [BES] below). A median V-shaped notch is formed along the posterior margin and is more developed than in *Thylacinus cynocephalus*, *Barinya wangala* or *Dasyurus*.

Orbitosphenoid. The orbitosphenoid is exposed on the skull at the rear of the orbital region, sandwiched between the frontal anteriorly and the alisphenoid posterodorsally. It briefly contacts the palatine ventrally and forms the medial wall of the optic orbital foramen. This foramen is completed by the alisphenoid laterally. A minute foramen communicates with the opposite side of the skull. The orbitosphenoid makes no significant contribution to the orbit.

Alisphenoid. The alisphenoid is bordered anterodorsally by the frontal, anteroventrally by the palatine, and ventromedially by the basisphenoid. Its posterodorsal border is formed by the squamosal, which also delimits the alisphenoid's lateral extent on its ventral surface where it is confluent with the glenoid fossa (forming the medial margin of the glenoid fossa). The dorsal margin of the alisphenoid forms a natural edge and its margin meets the frontal (as in *Thylacinus cynocephalus* but not *Barinya wangala* and *Dasyurus*, where the alisphenoid contacts the parietal). A complete secondary foramen ovale (*sensu* Wroe 1997a) is present, as in *T. cynocephalus*, *B. turnbulli*, some *Dasyurus* and *Sarcophilus*. It is formed by an anteriorly directed strut emanating from the alisphenoid tympanic process. The alisphenoid also forms at least the anteriormost boundary of the primary foramen ovale. A moderately well developed alisphenoid tympanic process is present, enclosing an alisphenoid hypotympanic sinus. This process is proportionately larger and more inflated than in *T. cynocephalus* and *B. turnbulli*, but somewhat smaller than in *D. maculatus*. Posteriorly, the alisphenoid tympanic process is fused to the ectotympanic. Ventromesially, a deep and extensive sulcus is formed at the alisphenoid–basisphenoid boundary. This almost certainly conducted a branch of V_3 as in other dasyuromorphians (Wroe 1997a). The transverse canal is contained within this sulcus.

Basisphenoid. The unpaired basisphenoid floors the anterior two-thirds of the neurocranium. It is roughly triangular in ventral view, with the apex formed anteriorly by articulation with the presphenoid and the base formed by contact with the unpaired basioccipital. The basisphenoid makes a minor contribution to the internal carotid foramen. Bilaterally it is bordered by thin flanges of the alisphenoids.

Squamosal. The dorsal margin of the squamosal is delimited by the parietal. The squamosal meets the frontal anteriorly (as in *Thylacinus cynocephalus*) and not the alisphenoid as in most dasyurids. Anteroventrally the squamosal overlies the alisphenoid; the ventral squamosal–alisphenoid suture runs anteroposteriorly along the medial limits of the glenoid fossa. The squamosal abuts the occipital region posteriorly to form the anteroventral margin of the nuchal crest before terminating in lateral occipital wings. There is a well developed posterior glenoid process. The transverse orientation of the glenoid fossa resembles that of *T. cynocephalus* and *Dasyurus* (but not *Barinya wangala*, where its orientation is more oblique). Laterally the squamosal overlies the jugal, terminating just posterior to the postorbital process of the jugal on the lateral face of the zygomatic arch. The anterior terminus of the squamosal on the zygomatic arch varies within *Dasyurus* –

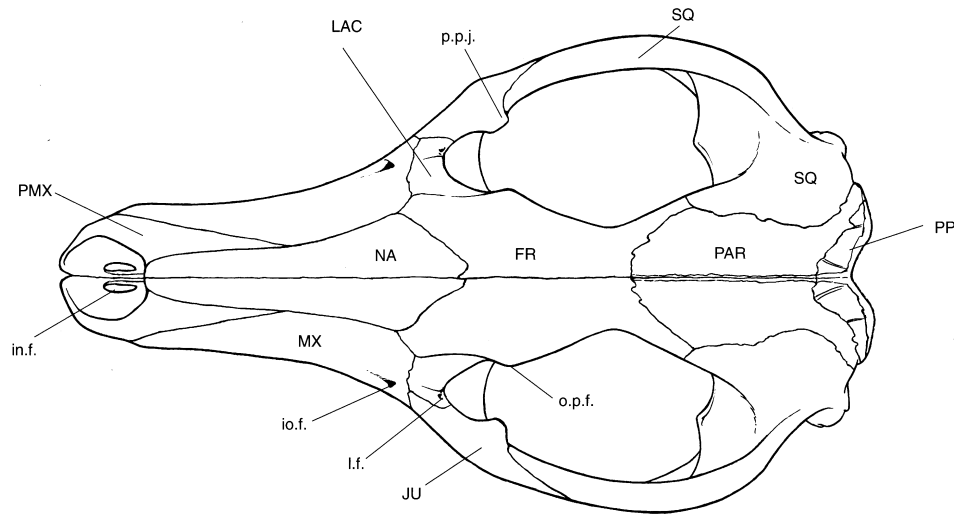


Fig. 5. *Nimbacinus dicksoni*, QMF36357; stylised dorsal view. See Appendix 3 for legend to abbreviations.

B. wangala and *Badjcinus turnbulli* are damaged in this area and can not be assessed, and in *T. cynocephalus* the squamosal extends anteriorly below the infraorbital process. The zygomatic arch is robust, contrasting with the more slender zygomatic arch in *T. cynocephalus* and *B. wangala* and resembling the more robust zygoma in *Dasyurus*. Damage in *B. turnbulli* again precludes comparison. The zygomatic arch is roughly horizontal, terminating posteriorly and somewhat dorsally on the skull (similar to the condition in *Dasyurus*). In *T. cynocephalus* the zygomatic arch curves ventrally to terminate at a more ventral point on the skull, as it does in *B. wangala*. A small subsquamosal foramen is present at the point where the dorsal ridge of the zygomatic arch runs into the skull wall. A distinct squamosal epitympanic sinus is also present.

Basoccipital, exoccipital, and supraoccipital. Sutural boundaries between these bones cannot be distinguished and they are described here as a single unit (BES). The BES is bordered anteriorly by a transverse suture with the basisphenoid. A distinct basoccipital keel is present on the ventral surface anterior to the occipital condyles. On either side of the occipital condyles are paired paroccipital processes whose anterolateral borders are formed by the *pars mastoidea* of the periotic. The internal jugular canal is not fully enclosed although a sulcus for the internal jugular is present, as is an incomplete posterior lacerate foramen. A large condylar foramen is positioned at the base of the ventral condylar lobe, with a smaller foramen immediately anterior to this. In posterior view the BES is bordered by the *pars mastoidea* of the periotic laterally and is fused with the postparietal dorsally.

Periotic. The periotic is composed of two parts: the *pars petrosa* and *pars mastoidea*. The *pars petrosa* contains the inner ear and internal acoustic meatus, while the *pars mastoidea* contributes to the lateral occipital region. Only the external features are described because no isolated periotics are known to reveal endocranial detail. The *pars petrosa* does not abut the basioccipital ventromedially. A small periotic tympanic process is present, but does not contact the alisphenoid tympanic process or the ectotympanic. Neither the *pars mastoidea* nor the paroccipital are contacted posteriorly. No distinct tubal

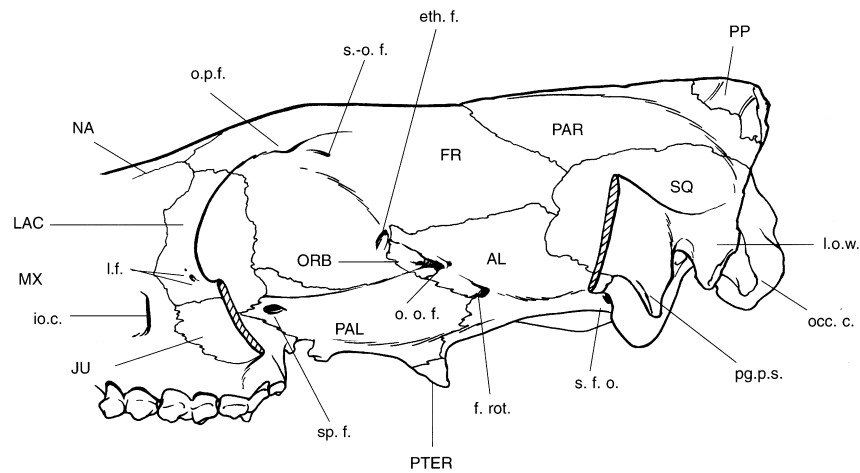


Fig. 6. *Nimbacinus dicksoni*, QMF36357; stylised lateral view of braincase. See Appendix 3 for legend to abbreviations.

foramen for the Eustachian tube is formed. Whether the *pars petrosa* contributes to the posterior rim of the primary foramen ovale can not be determined. Neither a secondary facial canal nor stylomastoid foramen are evident. The fenestra ovalis is not visible in ventral view. The *pars mastoidea* contains no epitympanic recess, nor is there a paroccipital epitympanic sinus. Anteroventrally, a well defined sulcus may be for transmission of the facial nerve. Ventromedially the *pars petrosa* forms the base of the paroccipital process.

Upper dentition

P³ and M¹⁻⁴ are described in detail by Muirhead and Archer (1990). The morphology of these teeth in QMF36357 does not differ in any significant way from that of the material considered by these authors. Consequently, only those elements of the upper dentition not previously described are treated here. All molars, as well as the P³, show moderate wear.

I² is present in the right premaxilla. This tooth is spatulate. From the alveoli it is clear that no diastema are formed between any of the upper incisors. In ventral view the incisal arcade has only a slight convex curvature. The alveoli of I¹⁻³ are similar in size and shape and it seems unlikely that I¹ was procumbent, as in *Barinya wangala*. The alveolus of I⁴ is the largest of the incisal arcade as in *Thylacinus cynocephalus*, but not *Badjcinus turnbulli*, *Dasyurus maculatus* or *D. viverrinus*. Although C¹ is not fully preserved, from its occlusal outline in the less badly damaged left C¹, it was evidently compressed on the transverse axis. It is contained within the maxilla. P¹ is separated from C¹ by a short diastema. It is double rooted, transversely compressed, roughly triangular in lateral view and slightly recurved along the posterior face (although not to the extent evident in *T. cynocephalus*). A poorly developed heel is apparent. P² is preserved in the left side of the skull. It is separated from P¹ by a small but distinct diastema. It differs from P¹ in being higher crowned with a more strongly developed heel. No diastema separates P² and P³.

Dentary

Both dentaries are well preserved although neither is complete posteriorly; the angular processes are not fully preserved and neither of the mandibular condyles is present. The right

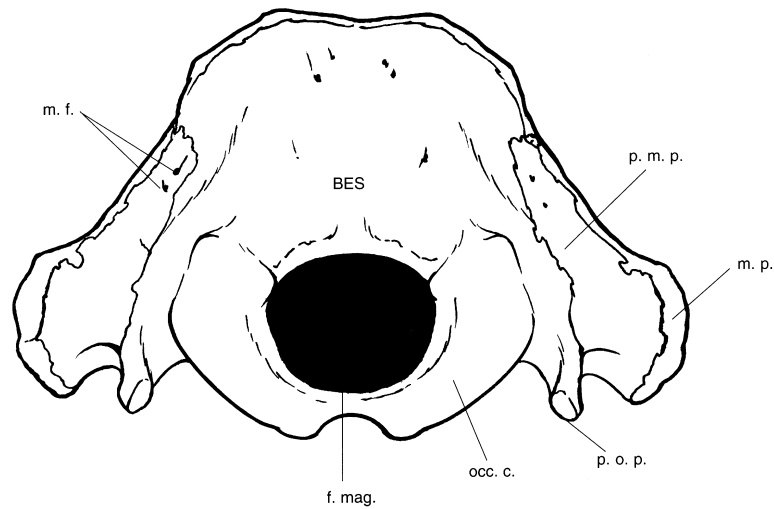


Fig. 7. *Nimbacinus dicksoni*, QMF36357; stylised occipital view. See Appendix 3 for legend to abbreviations.

dentary retains all of the teeth excepting the incisors; the left dentary retains the canine, P_{2-3} and M_{2-4} . In lateral view the dentary is long and slender, similar proportionately to the dentaries of *Badjcinus turnbulli* and *Dasyurus maculatus*, but not as elongate and gracile as in *Thylacinus cynocephalus*. The masseteric fossa is shallow, resembling that of *T. cynocephalus* and *B. turnbulli*, and contrasting with that of *D. maculatus* and *D. viverrinus*, where a distinct lip rimming the fossa is present. The posterolateral shelf of the masseteric fossa is wide, as in *D. maculatus* and *D. viverrinus*; this shelf is less pronounced in *T. cynocephalus* (incompletely preserved in *B. turnbulli*). Two mental foramina are present. On both dentaries the anterior foramina (the larger) are ventral to the posterior roots of P_1 . The more posterior foramina differ in position: the foramen through the left dentary is tiny and lies ventral to the posterior root of P_3 while on the right dentary a more well developed foramen lies ventral to the posterior root of M_1 . In the Bullock Creek specimens, assigned to *N. richi* by Murray and Megirian (2000), the posterior mental foramen is larger and positioned more posteriorly, below the anterior alveolus of P_3 in P85553–3, but present ventral to the posterior root of P_3 in P9612–4. Intraspecific and within-individual variation regarding size, number and position of mental foramina is evident in *D. maculatus*, *D. viverrinus*, *B. turnbulli* and *T. cynocephalus*. On the medial aspect of the dentary the mandibular foramen (inferior alveolar foramen) lies beneath the most dorsal point on the anterior margin of the coronoid process, as it does in *T. cynocephalus*, *D. maculatus*, and *D. viverrinus*. The mandibular foramen is well developed as in *T. cynocephalus* and larger than in *D. maculatus* and *D. viverrinus* (not preserved in *B. turnbulli*). The coronoid process rises from the dentary at an angle of about 80° , which is similar to the inclination of the coronoid process in *D. maculatus* and *D. viverrinus* and more steeply inclined than in *T. cynocephalus*. The angular process is broken away.

Lower dentition

Muirhead and Archer (1990) have described P_1 , P_2 and M_1 (M_2 of these authors) from Riversleigh and Bullock Creek material; P_3 and M_{2-4} (M_{3-5} of these authors) present in the

specimen described here, had not been recovered for *Nimbacinus dicksoni* at that time. Differences between M_1 of the holotype and material referred to *Nimbacinus richi* by Murray and Megirian (2000) are discussed above. Because we have not seen the holotype of *N. richi* at first hand we do not attempt detailed comparisons with this specimen, but reiterate that, based on the description provided by Murray and Megirian (2000), there are no clear differences regarding premolar or molar morphology other than entoconid size.

From the alveoli of the incisal arcade it is inferred that I_3 was crowded or staggered (*sensu* Hershkovitz 1995, 1999). C_1 is large, recurved and transversely compressed. It is separated from P_1 by a diastema almost 3 mm in length. On both the right and left C_1 a distinct wear facet is present, probably formed by occlusion with C^1 . P_1 is recurved, twin rooted, low crowned and shows considerable wear. A well developed heel is evident. P_2 differs from P_1 in being larger, higher crowned and more distinctly recurved, with a poorly defined cristid running from the protoconid to the base of the heel. P_3 is separated from P_2 by a very small diastema of less than 1 mm. In the Bullock Creek dentary described by Muirhead and Archer (1990), the size of the P_3 alveoli suggest that P_3 in *N. dicksoni* was approximately equal in size to P_2 , but P_3 is larger in all dimensions than P_2 . P_3 is only slightly worn in both the right and left dentaries. Although the crown has been somewhat diminished by wear, P_3 in *N. dicksoni* lacks the higher, more triangular cutting blade of the P_3 in *T. cynocephalus*. Its lower crown resembles that of the P_3 in *Dasyurus maculatus* although the P_3 of *N. dicksoni* is more transversely compressed. M_1 is missing from the left dentary. The right M_1 is heavily worn, as is the M_1 in the Bullock Creek dentary (M_2 of Muirhead and Archer 1990). Its talonid is wider than its trigonid. Neither a paraconid (present but poorly developed in the holotype: Muirhead and Archer 1990) nor entoconid (present in holotype: Muirhead and Archer 1990) appear to be present, but this may be the product of wear. M_2 shows less wear than M_1 and can be further distinguished as follows: it is larger in anteroposterior, dorsoventral and transverse dimensions; both a small entoconid and a distinct paraconid are apparent as is an anterior cingulid; the protoconid is more massive and displaced buccally; the metaconid is not positioned as posteriorly relative to the protoconid; the trigonid is only very slightly shorter than the talonid transversely; and the cristid obliqua runs into the posterior face of the protoconid at a point level with the protoconid's centre. M_3 is similar to M_2 but differs in the following ways: the talonid is smaller on both the long and transverse axes of the dentary and is not as wide as the trigonid; the protoconid and paraconid are higher crowned; the entoconid is smaller; and the cristid obliqua terminates anteriorly in a more lingual position. M_4 differs from M_3 as follows: the tooth is less worn; the entoconid is absent; and the talonid is further reduced in overall size relative to the trigonid.

Remarks

As conceded by Muirhead and Archer (1990) and extrapolated upon by Murray and Megirian (2000), there are differences between the holotype of *Nimbacinus dicksoni*, the Bullock Creek paratype and QMF16809 that may be of phylogenetic consequence. In particular, Murray and Megirian (2000) question the status of paratype QMF16809, a broken M_2 now thought to be from a considerably older site than the holotype. This tooth fragment is characterised by marked reduction of the metaconid, leading Murray and Megirian (2000) to suggest that it may not represent *N. dicksoni*. When Muirhead and Archer described *N. dicksoni* it was then only the third thylacinid known. Certainly the species richness of Thylacinidae attested to by subsequent discoveries was then unanticipated. With the benefit of hindsight and new material, we concur with Murray and

Megirian (2000) regarding the taxonomic status of QMF1609, which must now be considered uncertain. However, the basis of the argument advanced by Murray and Megirian (2000) to dispute whether QMF1609 represented *N. dicksoni* eats into the validity of their own distinction between this species and the new taxon, *N. richi*. When described, the lower molar morphology of *N. dicksoni* was known only from two first lower molars and the partial M_2 that Murray and Megirian (2000) suggest is another species. As stated by Murray and Megirian (2000, p. 153) their ‘... proposed revision leaves the states of the M_{2-4} metaconids of *N. dicksoni* in some doubt’. But the presence of relatively well developed metaconids on M_{2-4} in conjunction with a reduced metaconid on M_1 in *N. richi* was one of the two diagnostic features used to distinguish it from *N. dicksoni*. The second feature was the presence of large conical entoconids on M_{1-3} . In QMF36357 the M_{2-4} metaconids are distinct, although clearly reduced on the plesiomorphic dasyuromorphian condition. Comparison with the figures provided by Murray and Megirian (2000) yields no obvious differences with respect to metaconid morphology between QMF36357 and the holotype of *N. richi*. This brings us to another issue, i.e. whether metaconid reduction for these two specimens should be scored as differential (*sensu* Muirhead and Wroe 1998). Confusion over this matter may be attributable to misinterpretation of the character-state descriptions given by Muirhead and Wroe (1998), so here we will attempt clarification. Plesiomorphically, in dasyuromorphians the metaconid of M_1 is smaller than that of M_{2-4} . However, uniquely among thylacinids in *Badjcinus turnbulli* the M_1 metaconid is lost while the M_{2-4} metaconids are only slightly reduced. This character state was treated as a dasyuromorphian apomorphy by Muirhead and Wroe (1998). Despite significant to very heavy wear on all M_1 metaconids referred to *Nimbacinus*, a distinct metaconid is present in each. While the metaconid on M_1 is clearly smaller than that of M_{2-4} in the only two *Nimbacinus* specimens wherein a full molar row is preserved (i.e. QMF36357 and the holotype of *N. richi*), this difference is within the range exhibited by other thylacinids, excepting *B. turnbulli*. In short, *N. dicksoni* and *N. richi* can not be distinguished from each other on the basis of metaconid morphology and neither possesses differential reduction of the metaconids *sensu* Muirhead and Wroe (1998). This leaves one diagnostic feature separating the two species of *Nimbacinus*: M_{1-3} entoconid size. We do not question the fact that in both the holotype of *N. dicksoni* and QMF36357 the entoconids appear to be smaller than in the holotype of *N. richi* and P85553-3. P85553-3 was considered to represent *N. dicksoni* by Muirhead and Archer (1990), but *N. richi* by Murray and Megirian (2000). However, the question here is whether differences in entoconid size alone, particularly given such a small sample size, should be accepted as a basis for the erection of a new taxon. The value of entoconid morphology as a stand-alone diagnostic character among dasyurids has been questioned by Dickman *et al.* (1998). Even the presence or absence of entoconids has been shown to be highly variable among unworn teeth of juvenile *Sminthopsis griseoventor* and *Antechinus flavipes* (Crowther *et al.* 1999). Consequently, we consider the status of *N. richi* to be debatable at present.

Phylogenetic analysis

Numerical parsimony analysis produced 10 shortest trees of 275 steps. Excluding uninformative characters $CI = 0.379$, $HI = 0.621$, $RI = 0.647$, and $RC = 0.254$. The strict consensus tree is provided in Fig. 8 along with bootstrap and Bremer support indices for resolved nodes. Character-state reconstructions for the first of the 10 most-parsimonious trees are provided in Appendix 2 for the nodes in Fig. 9.

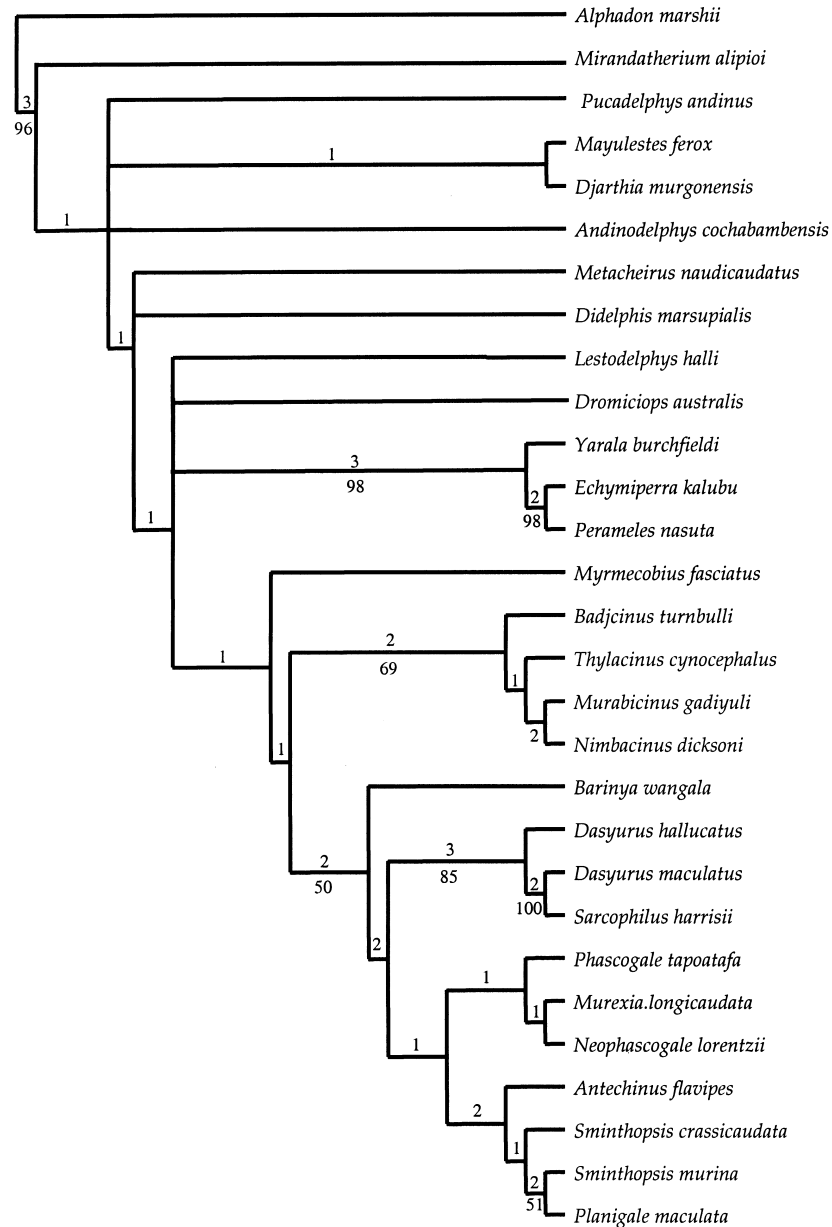


Fig. 8. Strict consensus of 10 most-parsimonious trees of 275 steps. Excluding uninformative characters CI = 0.379, HI = 0.621, RI = 0.647 and RC = 0.254. Bremer support is given above and bootstrap below branches.

In the strict consensus tree the monophyly of Thylacinidae received moderate bootstrap and Bremer support as did that of Dasyuridae (however, among extant dasyurid subfamilies only Sminthopsinae was monophyletic). While both the position of *Myrmecobius fasciatus* as sister taxon to a thylacinid–dasyurid clade and a monophyletic Dasyuromorphia were



Fig. 9. The first of the 10 most-parsimonious trees. See Appendix 2 for character-state changes.

resolved, neither of these results were supported by analysis of suboptimal trees or bootstrap values of over 50. Similarly, the early Eocene Murgon taxon, *Djarthia murgonensis*, and the generalised Palaeocene borhyaenoid, *Mayulestes ferox*, were found to be monophyletic, but this relationship was unsupported.

Within Thylacinidae *Nimbacinus dicksoni* was plesiomorphic for most dental features analysed here. With respect to the generalised *Muribacinus gadiyuli* it was apomorphic for

only one dental feature (absence of an anterior cingulum on M^1 , C 24), but it lacked the following 12 apomorphies of the dentition that were present in the specialised *T. cynocephalus*: M^1 preparacrista oriented anterobuccally relative to long axis of tooth (C 12), protoconule absent (C 14), metaconule absent (C 15), stylar cusp B absent on M^3 (C 17), stylar cusp D absent on M^3 (C 18), posterior cingulum on M^1 absent (C 25), metaconids absent on M^{2-4} (C 33), posterior cingulid absent on M_{1-3} (C 36), presence of carnassial notch in cristid obliqua (C 38), entoconid reduced (C 41), length of M_4 exceeds that of M_3 relative to the long axis of the dentary (C 42) and number of cusps on M_4 talonid reduced to one (C 44).

In contrast to its relatively generalised dentition, the crania of *N. dicksoni* lacked only one apomorphy evident in *T. cynocephalus* (fossa for the lower canine bordered by anterolateral processes of premaxilla and maxilla, C 46). Together, *N. dicksoni* and *T. cynocephalus* shared three derived cranial character states absent in *B. turnbulli*: a primary foramen ovale delimited by the alisphenoid only (C 50), a complete secondary foramen ovale (C 51) and presence of a squamosal epitympanic sinus (C 55).

Relative to Myrmecobiidae, thylacinids were apomorphic for five cranial features: presence of palatal vacuities (C 47), loss of posterolateral palatine foramen (C 48), presence of a complete secondary foramen ovale formed by a mesial fold in the alisphenoid tympanic process (C 52), a laterally extensive U shaped ectotympanic (C 58) and frontal squamosal contact. While five derived cranial features in *Myrmecobius fasciatus* distinguish it from thylacinids: a tympanic wing of the periotic that contacts the alisphenoid tympanic process (C 65), presence of a paroccipital tympanic process that does not contact any other tympanic elements (C 66), a mastoid tympanic wing that contacts the alisphenoid tympanic process (C 67) and a small antorbital fossa (C 76).

Modern dasyurids were distinguished from thylacinids by the presence of 10 cranial specialisations: a ventral facial nerve canal (C 54), an alisphenoid hypotympanic sinus enclosed wholly within the alisphenoid (C 56), an internal jugular canal that extends to the basisphenoid (C 60), a well developed posteroventral lip in the pars petrosa enclosing the internal jugular ventrally (C 61), an internal jugular canal that is fully enclosed dorsally (C 62), a tympanic wing of the periotic that contacts the alisphenoid tympanic process and floors the periotic hypotympanic sinus (C 65), a paroccipital that is fused to the pars petrosa anteriorly and mastoid tympanic process laterally (C 66), a mastoid tympanic process that contacts the pars petrosa (C 67), a foramen lacerum medium that is confluent with the primary foramen ovale (C 69) and a tubal foramen formed by a sulcus in the pars petrosa (C 70).

All thylacinid cranial synapomorphies were also found in at least some modern dasyurids. However, two shared derived cranial features present in thylacinids were not found in *Barinya wangala*: a laterally extensive, U-shaped ectotympanic (C 58) and frontal–squamosal contact (C 64). Five features in the cranium of *B. wangala* were derived with respect to Thylacinidae. These specialisations in characters 65, 66, 67, 69 and 70 were shared with the three extant dasyurid subfamilies.

Discussion

Phylogeny

Overall, the inclusion of new thylacinid material and additional fossil taxa in the analysis improved on the resolution of dasyuromorphian phylogeny provided by Wroe *et al.* (2000), but in general, consistency was low and homoplasy high. Support was weak at most nodes,

but there were exceptions, particularly within Dasyuromorphia. Many possible synapomorphies identifying specific clades were in agreement with those determined in previous analyses. Dasyuromorphia was united by the reduction of upper (C 1) and lower (C 26) incisor numbers (Marshall *et al.* 1990; Wroe *et al.* 2000), while Dasyuridae was unified by the acquisition of basicranial features largely as found by Wroe (1999) and Wroe *et al.* (2000). However, as also found by Wroe *et al.* (2000), clades were often denoted by additional possible synapomorphies not predicted in earlier investigations. For example, at node 13 (Fig. 9) the reduction of upper and lower incisor numbers accounts for only two of 10 synapomorphies that supported monophyly for dasyuromorphians.

Regarding thylacinid phylogeny and evolution, the finding of monophyly for Thylacinidae is in agreement with results of the numerical parsimony analysis performed by Muirhead and Wroe (1998), but *contra* that of Wroe *et al.* (2000). Thylacinidae was united by possession of character states that included previously suggested synapomorphies such as a laterally extensive, tubular ectotympanic (C 58) and squamosal–frontal contact (C 64) (Archer 1982; Muirhead and Wroe 1998). However, homoplasy among middle ear features complicates any interpretation. Of 10 potential synapomorphies for Thylacinidae at node 15 (Appendix 2), two are reversals in middle ear characters (C 65 2 \Rightarrow 1, C 66 1 \Rightarrow 0), while at node 13 another middle ear feature is reversed (C 52 1 \Rightarrow 0). Reversals in this region are treated as most improbable (MacPhee 1981) and consequently, although monophyly for Thylacinidae is supported, it is difficult to take all character-state transformations at face value.

Within Thylacinidae a point of interest borne out in this study is that although considerable variation is apparent among the dentitions of thylacinid species, the family's skull anatomy appears to be have been characterised by marked conservatism. Thus, despite a prevalence of relatively plesiomorphic dental features, the cranium of *Nimbacinus dicksoni* is remarkably similar to that of the recent *Thylacinus cynocephalus*. Among characters analysed, *N. dicksoni* lacks only one apomorphy present in *T. cynocephalus*, i.e. a fossa for the lower canine bordered by an anterolateral process of the premaxilla (C 46). Because dentally generalised *Nimbacinus* and dentally specialised *Thylacinus* are both now known from late Oligocene deposits (Wroe 2002), it now appears likely that much of the gamut of thylacinid specialisation, both cranial and dental, had appeared prior to the earliest Miocene.

As regards higher-level relationships among dasyuromorphians, placement of *Myrmecobius fasciatus* as the immediate outgroup to a clade comprising thylacinids and dasyurids is in agreement with two previous studies based on morphology (Archer 1984; Aplin and Archer 1987), but not Wroe (1997a). Of three molecular investigations addressing this issue two concur with this interpretation, Lowenstein *et al.* (1981) and Krajewski *et al.* (2000a), while another places *M. fasciatus* within Dasyuridae (Krajewski *et al.* 1997). However, the results of neither the present nor any previous investigations have received strong support.

With respect to the position of dasyuromorphians within Marsupialia, results differ from those of Wroe *et al.* (2000) in that potential sister taxa are reduced from seven to three (*Lestodelphys halli*, *Dromiciops australis* and Peramelemorphia). Both *Dromiciops australis* (Rougier *et al.* 1998) and peramelemorphians (Kirsch 1968; Baverstock *et al.* 1990; Westerman 1991) have been advanced as possible sister taxa to Dasyuromorphia. But while historically Didelphidae has been considered as possibly ancestral to Australian marsupicarnivores (Archer 1976a), this is not a position accepted by any recent authors including ourselves. In this context, the placement of the relatively derived didelphid *L. halli* as a potential sister taxon to dasyuromorphians seems unlikely in the extreme.

The position of Australia's oldest marsupicarnivore, *Djarthia murgonensis*, as monophyletic with the generalised borhyaenoid *Mayulestes ferox* appears most improbable. However, this result does highlight the need for circumspection regarding both the classification of *D. murgonensis* beyond the level of *Marsupialia incertae sedis* and decisions over whether Australian and South American marsupial radiations are fundamentally disjunct (excepting microbiotheriids), as has been suggested by Woodburne and Case (1996).

Trends in thylacinid evolution

Three thylacinids are now known to have existed in the late Oligocene (Wroe 2002), while as many as 10 are known from Miocene sites. All of these have been collected within a somewhat restricted geographical area including Riversleigh, north-western Queensland, and three sites in the Northern Territory. By way of contrast, only one species is widely recognised in Pliocene and Pleistocene deposits. At present, no more than two species have been shown to have existed sympatrically, but given the species richness evident in Riversleigh in particular, it is probable that at least three, and possibly as many as five, thylacinids coexisted in late Oligocene–Miocene times (Murray and Megirian 2000). Exactly how sympatric thylacinids may have carved out niche space in these northern Australian habitats is at present unclear. Moreover, Tertiary thylacinid ecology must be seen against a backdrop of increasingly complex interaction and competition with other marsupial carnivores. For example, in Riversleigh sites these now include four thylacoleonids, two giant rat-kangaroos and at least one bone-cracking dasyurid (Wroe 2002). Detailed, quantitative analyses are needed to more accurately predict the ecology of different thylacinid species. However, it is already apparent that considerable variation existed, although all share at least some apomorphies associated with a carnivorous habitus. The smallest, *Muribacinus gadiyuli*, is about the size of *Dasyurus maculatus* (Wroe 1996), while the biggest, *Thylacinus megiriani* and *Thylacinus potens*, are significantly larger than the recently extinct *Thylacinus cynocephalus* (Murray 1997). On the basis of both dentition and body size it is likely that smaller, less specialised species, such as *M. gadiyuli* and *Badjcinus turnbulli*, took small to medium-sized vertebrate prey and probably supplemented their diets with invertebrates. The near total dominance of vertical shear and extreme reduction of styler cusps in the molars of more specialised *Thylacinus* and *Wabulacinus* suggests that these taxa were fully carnivorous.

A combination of evolutionary stagnation with respect to cranial anatomy and specialisation of the dentition among thylacinids stands in marked contrast to the emerging picture of dasyurid evolution, characterised by the retention of dental plesiomorphies (in most taxa) stacked against a plethora of new adaptations in the middle ear region. Wroe (1997a) speculates that the development of key adaptations of the middle ear in dasyurids may at least partly account for the apparent reversal of thylacinid and dasyurid fortunes in the late Tertiary. Expansion and full enclosure of the middle ear can significantly enhance the reception of low-frequency sound (Webster and Webster 1975, 1980). However, this is an allometric function and there is an absolute maximum size beyond which further increases impart no advantage (Webster and Webster 1975, 1980). This may have produced differential selection in favour of larger thylacinids, with smaller members of the family being out-competed by large, carnivorous dasyurids (Wroe 1997a; Krajewski *et al.* 2000b). Similarly, in the middle Miocene, small dasyurids may have attained an adaptive edge over diminutive peramelemorphian insectivores such as *Yarala burchfieldi* (Muirhead 2000).

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Appendix 1. Character states (character analysis given by Wroe *et al.* 2000)

1. Upper incisor number. 5 (0); 4 (1).
2. Shape of upper incisors. Peg-shaped (0); spatulate (1).
3. Height of I¹. Not hypsodont (0); hypsodont (1).
4. Morphology of C¹. Caniform (0); premolariform (1).
5. Height of P³. Higher crowned than P² (0); lower crowned than P² (1); absent (2).
6. Shape of P³. Laterally compressed in occlusal view (0); bulbous and ovate in occlusal view (1).
7. Posterolingual cuspule present or absent on P³. Absent (0); present (1).
8. Relative size of paracone and metacone M¹⁻³. Paracone and metacone equal or almost equal in size to metacone (0); metacone much larger than paracone (1).
9. Metacone on M⁴. Present and distinct from metastylar corner of tooth (0); present but not distinct from metastylar corner of tooth (1); absent (2).
10. Shape and orientation of the centrocrista (unordered). Centrocrista straight, with apex of postparacrista and premetacrista oriented dorsoventrally terminating dorsally at or almost level with the talon basin (0); apex of centrocrista oriented buccally and well above talon basin, with an acute angle evident between the postparacrista and premetacrista, and a distinct V-shape in occlusal view (1); apex of centrocrista oriented buccally and well above protocone basin, with an oblique angle apparent between the postparacrista and premetacrista (2); and apex of centrocrista positioned well above protocone basin with linear centrocrista (3).
11. Proximity of apex of centrocrista to ectoloph in dilambdodont taxa. Does not approach or breech ectoloph (0); approaches or breeches ectoloph (1).
12. Orientation of preparacrista on M¹. M¹ preparacrista forms a near perpendicular angle with respect to the long axis of the tooth (0); M¹ preparacrista oriented anterobuccally relative to long axis of the tooth (1). M¹ preparacrista runs posterobuccally relative to long axis of the tooth (2); M¹ preparacrista absent (3).
13. Relative lengths of M³ and M⁴ preparacristae. M⁴ preparacristae shorter than or equal to that of M³ (0); M⁴ preparacristae longer than that of M³ (1).
14. Protoconule present or absent. Present (0); absent (1).
15. Metaconule present or absent. Present (0); absent (1).
16. Styler cusp A distinct or indistinct from parastylar corner of tooth. Distinct (0); indistinct (1).
17. Size of styler cusp B on M³. Large (0); small (1); absent (2).
18. Size of styler cusp D on M³. Large (0); small (1); absent (2).
19. Relative size of styler cusp B and styler cusp D on M². Styler cusp B > styler cusp D (0); styler cusp D > styler cusp B (1).
20. Relationship of styler cusp D to metacone. Not appressed (0); appressed (1).
21. Presence or absence of styler cusp C. Styler cusp C absent (0); styler cusp C present (1).
22. 'Central cusp'. Absent (0); present (1).
23. Twinned cusps in the 'C' position. Absent (0); present (1).
24. Presence or absence of anterior cingulum on M¹. Present (0); absent (1).
25. Presence or absence of posterior cingulum on M¹. Present (0); absent (1).
26. Lower incisor number. 4 (0); 3 (1).
27. I₃ bilobed or not bilobed. Not bilobed (0); bilobed (1).
28. Position of hypoconulid. Hypoconulid positioned posterolingual to entoconid (0); positioned posterior to entoconid (1).
29. I₃ morphology. Not staggered (0); staggered (1).
30. Presence or absence of hypoconulid notch. Present (0); absent (1).
31. Presence or absence of well developed sulcus formed by anterior cingulid. Absent (0); present (1).
32. Size of metaconid on M₁ relative to that of M₂₋₄. Metaconid in M₁ not reduced relative to M₂₋₄ (0); reduced relative to M₂₋₄ (1).
33. Size of metaconid in M₂₋₄. Large (0); reduced (1); absent (2).
34. Size of paraconid in M₁. Large (0); reduced (1); absent (2).
35. Orientation of postprotocristid with respect to long axis of dentary. Transverse (0); oblique (1).
36. Size of posterior cingulid in M₁₋₃. Posterior cingulid present and well developed on M₁₋₃ (0); reduced (1); absent (2).

37. Posterior cingulid in M_4 present or absent. Present (0); absent (1). [This feature has been treated as separate from character 36 because loss of a posterior cingulid on M_4 occurs in many taxa without concomitant reduction or loss of the posterior cingulid in M_{1-3} .]
38. Presence or absence of carnassial notch in cristid obliqua. Absent (0); present (1).
39. Morphology of postprotocristid in M_{3-4} . Postprotocristid continuous with metacristid (0); oriented posteriorly and almost continuous with cristid obliqua (1); oriented posteriorly and continuous with cristid obliqua (2).
40. Anterior point of termination of the cristid obliqua in M_3 with respect to carnassial notch formed by postprotocristid and metacristid (unordered). Beneath carnassial notch (0); lingual to carnassial notch (1); buccal to carnassial notch (2).
41. Entoconid size. Large (0); reduced (1); absent (2).
42. Anteroposterior dimension of M_4 relative to that of M_3 . $M_4 < M_3$ (0); $M_4 > M_3$ (1).
43. Height of P_3 relative to P_2 . P_3 higher crowned than P_2 (0); smaller than P_2 (1); absent (2).
44. Number of cusps on M_4 talonid. Three cusps (0); two cusps (1); 1 cusp (2).
45. Presence or absence of orbital crest. Absent (0); present (1).
46. Morphology of fossa for the lower canine. Bordered by anterolateral process of maxilla (0); bordered by anterolateral processes of premaxilla and maxilla (1) bordered by anterolateral process of premaxilla (2); no lateral process (3).
47. Presence or absence of palatal vacuities. Absent (0); present (1).
48. Presence or absence of posterolateral palatine foramen. Present (0); absent (1).
49. Presence or absence of accessory posterolateral palatine foramen. Present (0); absent (1).
50. Contribution of alisphenoid and periotic to primary foramen ovale. Delimited by alisphenoid anteriorly and periotic part of the petrosal posteriorly (0); delimited by alisphenoid only (1).
51. Presence or absence of secondary foramen ovale formed by anteriorly directed strut of alisphenoid tympanic process. Absent (0); present but incomplete (1); present and complete (2).
52. Presence or absence of secondary foramen ovale formed by mesial fold in alisphenoid tympanic process. Absent (0); present but incomplete (1); present and complete (2).
53. Presence or absence of contribution to secondary foramen ovale by posteriorly directed strut in alisphenoid. Absent (0); present but incomplete (1); present and complete (2).
54. Morphology of ventral facial nerve canal (unordered). Absent (0); present but completed anteriorly by squamosal only (1); present and enclosed within periotic with squamosal contribution to ventral rim (2); present and enclosed wholly within periotic.
55. Size of squamosal epitympanic sinus. Absent (0); present (1).
56. Alisphenoid hypotympanic sinus (unordered). Absent (0); present with periotic component (1); present wholly within alisphenoid, i.e. separated from alisphenoid hypotympanic sinus by distinct petrosal ridge (2); present with alisphenoid, periotic and squamosal contributions (3).
57. Size of alisphenoid tympanic process. Absent (0); poorly developed, i.e. with alisphenoid hypotympanic sinus visible in external view (1); well developed, i.e. extends posteriorly to reach posterior limit of alisphenoid contribution of alisphenoid hypotympanic sinus in ventral view (2).
58. Shape of ectotympanic (unordered). Simple 'U-shape' (0); laterally extensive, but simple 'U-shape' in lateral view (1); laterally extensive, complex 'saddle-shape' (2).
59. Medial process of the squamosal. Absent (0); present (1).
60. Length of the internal jugular canal. Does not extend anteriorly to the basisphenoid (0); extends to basisphenoid (1).
61. Presence or absence of a well developed posteroventral lip formed by a mesially directed process in the *pars petrosa*, enclosing the internal jugular ventrally. Absent (0); present (1).
62. Dorsal enclosure of internal jugular canal. Not fully enclosed dorsally (0); fully enclosed dorsally (1).
63. Presence or absence of transverse canal. Absent (0); present (1).
64. Frontal–squamosal or alisphenoid–parietal contact. Alisphenoid–parietal contact (0); frontal–squamosal contact (1).
65. Morphology of tympanic wing of periotic. Absent (0); present but does not contact alisphenoid tympanic process (1); present and contacts alisphenoid tympanic process, but does not form periotic hypotympanic sinus (2); present contacts alisphenoid tympanic process and floors periotic hypotympanic sinus (3).
66. Morphology of paroccipital tympanic process. Absent (0); present but does not contact any other tympanic elements (1); present and contacts the mastoid tympanic process laterally (2); present and fused to the *pars petrosa* anteriorly and mastoid tympanic process laterally (3).

67. Morphology of mastoid tympanic process (unordered). Absent (0); present (1); present and contacts *pars petrosa* (2); present and contacts alisphenoid tympanic process (3).
68. Presence or absence of mastoid contribution to occiput. Present (0); absent (1).
69. Morphology of foramen lacerum medium. Distinct from primary foramen ovale (0); confluent with primary foramen ovale (1).
70. Morphology of tubal foramen (unordered). Absent (0); present but slit-like and incomplete anteroventrally (1); present and ovoid, with sulcus in *pars petrosa* (2); present, with sulcus in alisphenoid tympanic process (3).
71. Shape of nasals. Nasals posteriorly expanded (0); not posteriorly expanded (1).
72. Maxilla–nasal contact. Maxilla–nasal contact longer than premaxilla–nasal contact (0); premaxilla contact longer than maxilla–nasal contact (1).
73. Posterior extension of nasals. Nasals extend posteriorly beyond the anterior rim of the orbit (0); do not extend posteriorly beyond the orbit (1).
74. Frontal–maxillary contact. Present (0); absent (1).
75. Morphology of jugal. Jugal not Y-shaped (0); jugal Y-shaped (1).
76. Morphology of antorbital fossa. Antorbital fossa absent (0); small or incomplete (1); deep (2).
77. Presence or absence of prootic canal. Present (0); absent (1).

Appendix 2. Character-state changes for Nodes 1–27 in the first of 10 most-parsimonious trees

See Fig. 9

- Node 1: C6 1 \Rightarrow 0; C13 0 \Rightarrow 1; C25 0 \Rightarrow 1; C37 0 \Rightarrow 1; C40 0 \Rightarrow 2
Node 2: C8 0 \Rightarrow 1; C10 0 \Rightarrow 1; C36 0 \Rightarrow 1
Node 3: C45 0 \Rightarrow 1; C59 0 \Rightarrow 1; C65 0 \Rightarrow 1
Node 4: C40 2 \Rightarrow 0; C43 0 \Rightarrow 1; C74 0 \Rightarrow 1; C77 0 \Rightarrow 1
Node 5: C47 0 \Rightarrow 1; C63 0 \Rightarrow 1
Node 6: C9 0 \Rightarrow 1; C21 1 \Rightarrow 0; C31 0 \Rightarrow 1; C56 0 \Rightarrow 2; C57 0 \Rightarrow 1; C59 1 \Rightarrow 0
Node 7: C36 1 \Rightarrow 2; C66 0 \Rightarrow 1
Node 8: C19 0 \Rightarrow 1; C44 0 \Rightarrow 1; C53 1 \Rightarrow 0; C57 1 \Rightarrow 2; C67 0 \Rightarrow 1; C77 0 \Rightarrow 1
Node 9: C14 0 \Rightarrow 1; C15 0 \Rightarrow 1; C45 1 \Rightarrow 0
Node 10: C2 0 \Rightarrow 1; C3 0 \Rightarrow 1; C12; 0 \Rightarrow 1; C46 0 \Rightarrow 3; C64 0 \Rightarrow 1; C66 1 \Rightarrow 0
Node 11: C12 1 \Rightarrow 2; C26 0 \Rightarrow 1; C27 0 \Rightarrow 1; C28 0 \Rightarrow 1; C30 0 \Rightarrow 1; C52 1 \Rightarrow 2; C56 2 \Rightarrow 0; C57 2 \Rightarrow 1; C75 0 \Rightarrow 1; C76 0 \Rightarrow 1
Node 12: C4 0 \Rightarrow 1; C9 1 \Rightarrow 0; C11 0 \Rightarrow 1; C25 1 \Rightarrow 0; C40 2 \Rightarrow 1; C71 0 \Rightarrow 1; C72 0 \Rightarrow 1; C73 0 \Rightarrow 1
Node 13: C1 0 \Rightarrow 1; C16 0 \Rightarrow 1; C26 0 \Rightarrow 1; C31 1 \Rightarrow 0; C33 0 \Rightarrow 1; C35 0 \Rightarrow 1; C46 0 \Rightarrow 1; C52 1 \Rightarrow 0; C55 0 \Rightarrow 1; C65 1 \Rightarrow 2
Node 14: C25 1 \Rightarrow 0; C36 2 \Rightarrow 1; C43 0 \Rightarrow 1; C48 0 \Rightarrow 1; C56 2 \Rightarrow 1
Node 15: C10 1 \Rightarrow 2; C17 0 \Rightarrow 1; C18 0 \Rightarrow 1; C34 0 \Rightarrow 1; C52 0 \Rightarrow 1; C58 0 \Rightarrow 1; C64 0 \Rightarrow 1; C65 2 \Rightarrow 1; C66 1 \Rightarrow 0; C69 1 \Rightarrow 0
Node 16: C43 1 \Rightarrow 0; C50 0 \Rightarrow 1; C51 0 \Rightarrow 3; C67 1 \Rightarrow 0
Node 17: C7 0 \Rightarrow 1; C26 1 \Rightarrow 0
Node 18: C33 1 \Rightarrow 0; C61 0 \Rightarrow 1; C65 2 \Rightarrow 3; C66 1 \Rightarrow 2
Node 19: C54 0 \Rightarrow 2; C56 1 \Rightarrow 2; C 60 0 \Rightarrow 1; C62 0 \Rightarrow 1; C66 2 \Rightarrow 3; C67 1 \Rightarrow 2; C70 0 \Rightarrow 2
Node 20: C5 0 \Rightarrow 1; C12 0 \Rightarrow 3; C32 0 \Rightarrow 1; C36 0 \Rightarrow 1; C43 1 \Rightarrow 2
Node 21: C3 0 \Rightarrow 1; C9 1 \Rightarrow 2; C10 1 \Rightarrow 2; C20 0 \Rightarrow 1; C25 0 \Rightarrow 1; C36 1 \Rightarrow 2; C38 0 \Rightarrow 1; C44 1 \Rightarrow 2; C51 0 \Rightarrow 1; C52 0 \Rightarrow 1; C58 0 \Rightarrow 1
Node 22: C45 1 \Rightarrow 0
Node 23: C44 1 \Rightarrow 0
Node 24: C2 0 \Rightarrow 1; C54 2 \Rightarrow 3
Node 25: C44 1 \Rightarrow 2; C46 1 \Rightarrow 2; C71 0 \Rightarrow 1; C72 0 \Rightarrow 1
Node 26: C2 0 \Rightarrow 1; C25 0 \Rightarrow 1; C35 1 \Rightarrow 0; C46 2 \Rightarrow 3; C64 0 \Rightarrow 1
Node 27: C14 0 \Rightarrow 1; C17 0 \Rightarrow 1; C41 0 \Rightarrow 2

Appendix 3. Abbreviations for cranial features

AL , alisphenoid	o.p.f. , orbital process of frontal
a.t.p. , alisphenoid tympanic process	ORB , orbital
BES , basioccipital–exoccipital–supraoccipital complex	PA , parietal
bo.k. , basioccipital keel	PAL , palatine
BS , basisphenoid	pal.f. , palatine foramen
c.f. , condylar foramina	pgf , postglenoid foramen
eth.f. , ethmoid foramen	PL , palatine
et.s. , epitympanic sinus	PM(pm) , pars mastoidea of petromastoid (= mastoid s.s.)
f.l.c. , fossa for lower canine	PM(pp) , pars petrosa of petromastoid (= petrosal s.s.)
f.m. , foramen magnum	PMX , premaxilla
fo , foramen ovale	PP , postparietal
FR , frontal	p.p.f. , posterolateral palatine foramen
f.rot. , foramen rotundum	p.p.j. , postorbital process of jugal
g.f. , glenoid fossa	p.p.t. , postpalatine torus
i.c.c. , internal carotid canal;	pg.p.j. , preglenoid process of jugal
in.f. , incisive foramen	pg.p.s. , postglenoid process of squamosal
io.c. , infraorbital canal	po.p. , paroccipital process
io.f. , infraorbital foramen	prgps , preglenoid process of squamosal
JU , jugal	ptc , pterygoid canal
LA , lacrimal	p.t.p. , periotic tympanic process
l.f. , lacrimal foramen	p.w. , pterygoid wing
l.o.w. , lateral occipital wings	s.c. , sagittal crest
lpps , lateral postpalatine spine	s.f.ov. , secondary foramen ovale
mp , mastoid process	sof , supraorbital foramen
mpf , middle palatine foramen	s.o.m. , sulcus for origin of masseter
mpps , medial postpalatine spine	sp.f. , sphenopalatine foramen
max.v. , maxillary vacuity	SQ , squamosal
MX , maxilla	ssf , subsquamosal foramen (= suprameatal, post-squamosal)
NA , nasal	tr.c. , transverse canal
nuc.c. , nuchal crest	
o.c. , occipital condyles	
o-o.f. , optic–orbital foramen	

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