A NEW GENUS AND SPECIES, *BADJCINUS TURNBULLI* (THYLACINIDAE: MARSUPIALIA), FROM THE LATE OLIGOCENE OF RIVERSLEIGH, NORTHERN AUSTRALIA, AND AN INVESTIGATION OF THYLACINID PHYLOGENY

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ABSTRACT-Badjcinus turnbulli, gen. et sp. nov., is described from dental and incomplete skull material that includes the only pre-Pliocene dasyuromorphian basicranium described to date. Phylogenetic analysis places *B. turnbulli* basally within the Thylacinidae, but with autapomorphies. The relationship of *B. turnbulli* **to** other thylacines is assessed. The breadth of thylacinid diversity evident during the middle Tertiary argues for an earlier origin for the family than that suggested by molecular-based investigations. An amended diagnosis of the Thylacinidae is presented and thylacinid diversity and ecology is discussed.

INTRODUCTION

Known diversity of thylacinids has been greatly expanded over the past few years with five new genera and six new species described from the Oligocene to middle Miocene faunas of the Riversleigh region in northwestern Queensland, Australia (Muirhead and Archer, 1990; Muirhead, 1992; Muirhead and Gillespie, 1995; Wroe, 1996; Muirhead, 1997). *Badjcinus turnbulli,* gen. et sp. nov., described here, is the sixth genus and eighth species of thylacinid known. These new taxa, particularly *B. turnbulli,* provide new insight into the evolution of this clade. Morphology of this species indicates that considerable character convergence or reversal has occurred within the family. Molecular-based investigations have suggested an origin for the family ranging from 7 to 20 million years (Lowenstein et al., 1981; Sarich et al., 1982; Thomas et al., 1989 and Krajewski et al., 1992).

Historically, thylacinids have been allied with either the South American borhyaenoids (Sinclair, 1905, 1906; Wood, 1924; Archer, 1976b), or the Australian dasyuromorphian radiation (Bensley, 1903; Matthew, 1915; Simpson, 1941; Tate, 1947; Marshall, 1977; Archer, 1982; Szalay, 1982). That the Thylacinidae forms part of the dasyuromorphian radiation is now widely accepted on the basis of molecular (Lowenstein et al., 1981; Sarich et al., 1982; Thomas et al., 1989; Krajewski et al., 1992)-and morphological data (Szalay, 1982).

Dental nomenclature used here follows that of Archer (1976b) but differs regarding the molar/premolar boundary, which follows Flower (1869) and Luckett (1993), wherein the adult (unreduced) postcanine cheektooth formula of marsupials is P1-3, M1-4. Basicranial nomenclature follows that of Archer (1976a) and Gaudin et al. (1996). Taxonomic nomenclature follows Aplin and Archer (1987) unless stated other- wise. Specimens are held in the Queensland Museum palaeontological collection and denoted by the prefix QM F.

SYSTEMATIC PALEONTOLOGY

Order DASYUROMORPHIA (Gill, 1872)
Superfamily DASYUROIDEA (Goldfuss, 1820)
Family THYLACINIDAE (Bonaparte, 1838)

BADICINUS, gen. nov.
(Figs. 1-4; Tables 1-2)

Type and Only Known *Species-Badjcinus turnbulli, sp.* nov.
Generic Diagnosis-Differs from all other dasyuromorphians in lacking a squamosal epitympanic sinus. Differs from all

dasyurids in lacking a contribution to the tympanic bulla by the petrosal part of the periotic. *Badjcinus turnbulli* may be distinguished from all known thylacinids by possession of two autapomorphies: m1 and m2-4 metaconid differentially reduced; MI preparacrista parallel to long axis of tooth row. Among thylacinids, *B. turnbulli* differs from *Nimbacinus dicksoni* Muirhead and Archer, 1990 as follows: stylar shelf, protocone and conules further reduced; notched upper cingulum; postmetacristae more elongate; posterior cingulid joining hypocristid at base of hypoconid. *Badjcinus turnbulli* differs from *Wabulacinus ridei* Muirhead, 1997, *Ngamalacinus timmulvaneyi* Muirhead, 1997, and species of *Thylacinus* Temminck, 1824 as follows: entoconid, protocone, protoconule, and metaconule less reduced; m2-4 metaconid less reduced; lacking a camassial notch in cristid obliqua; hypocristid orientation closer to transverse axis of dentary; anterior termination of cristid obliqua less lingually shifted.

Generic Etymology--*Badjcinus*, derived from Wanyi Aboriginal word "badj,"meaning expert hunter, and *kynos, Greek* for dog and stem noun for the family Thylacinidae.

BADJCINUS TURNBULLI, sp. nov.

Holotype--QM F30408, skull fragments including: the premaxilla containing alveoli for I1-4 and a depression for the reception of c1; the maxilla, including an alveolus for C1, P1-2, alveoli for P3, and M1-4 (this bone is broken away dorsally from above the anterior opening of the infraorbital canal); the posterior parts of nasals where they contact the frontals; the frontals except for the anteroventral symphysis with the maxillae; the posterior part of the right jugal where it contacts the squamosal; all basicranial elements; and most of the parietals excepting the dorsal surface.

Referred Specimens--QM F30409, Rm1; QM F30407, incomplete right dentary containing posterior alveolus of p2, alveoli of p3, molar crowns of m1-4; QM F30410, incomplete left dentary containing alveolus of one incisor, canine alveolus, alveoli of p1 and p3 and crowns of p2 and m1-4; QM F30411, dentary fragment containing p2-3 and m1-3.

Type Locality--White Hunter Site, Hall's Hill, D- Site Plateau, Riversleigh Station, northwestern Queensland, Australia. Precise locality data is available from the Queensland Museum.

Age and Stratigraphy--White Hunter Site is one of the oldest Riversleigh sites, chronologically between the Wipajiri and Etadunna formations of South Australia on the basis of biostratigraphic correlation (Archer et al., 1989, 1994). Woodburne et al. (1993) suggested a maximum age of 26 million years for

basal sediments of the Etadunna Formation and a one to perhaps two million year accumulation period for the formation.

Species Diagnosis--As for genus.

Specific Etymology--Named in honour of Dr William D. Turnbull, in recognition of his contributions to Australian vertebrate paleontology.

Description

Cranial Material--The skull is preserved in three parts, each of which is described separately. The anterior fragment preserves the premaxilla including the alveoli for four upper incisors. These decrease in size posteriorly. There is no diastema within the incisor region. A deep depression is present immediately posterior to the incisor region for reception of a tall lower canine. The posterior part of the premaxilla is broken away. The maxilla contains the upper canine alveolus, which is a narrow ovoid cavity, indicating an anteroposteriorly broad but transversely narrow canine. The canine appears to have been quite long. No sutures indicating contact with the nasals or lacrimal are preserved in the maxilla. A narrow infraorbital foramen opens above the posterior alveolus of P3 on the flat surface of the maxilla. The anterior process of the zygomatic arch arises from the region of M2 and preserves the sutural contact with the jugal, which lies obliquely above M1-2 and closely approaches the anterior opening of the infraorbital canal. The interior opening of the infraorbital canal lies immediately medial to the maxillary-jugal suture; the canal is short (5 mm). Part of the palatine is preserved within the orbit and contains a small sphenopalatine foramen near the ventral suture with the maxilla. The secondary palate retains an incisive vacuity between the premaxilla and the maxilla, and a vacuity in the molar region that extends between MI and M3.

The dorsal portion of the skull retains the posterior extent of the nasals and the dorsal exposure of the frontals. Posteriorly, the nasals form a flat surface. They narrow posteriorly, but remain in contact with each other along their length. The anterior limit of the sagittal crest extends to a point level with the well-developed orbital crests. The orbital crest forms a pointed overhang. The skull narrows posteriorly (only 1 cm wide) before quickly widening. Although broken, the frontal appears to have risen into a low ridge along its medial dorsal surface.

Posteriorly, the ventral surface of the skull is well preserved, but the dorsal surface is broken away. The dorsal portion is preserved anteriorly from the alisphenoid suture with the palatine. The alisphenoid boundary of the sphenorbital fissure indicates a tall, but narrow foramen. This foramen lies anterodorsal to the circular foramen rotundum. The alisphenoid bulges posteriorly from the foramen rotundum. The zygomatic arch is preserved posteriorly. In lateral view, the alisphenoid-squamosal suture is oriented anterodorsally away from the glenoid fossa. The postglenoid process is constructed entirely by the squamosal, and the glenoid fossa is medially wide but anteroposteriorly narrow. The anterior part of the jugal is not present. Ventrally, the transverse foramen is located anteromedial to the base of the zygomatic arch. A ridge lies medial to this foramen and forms the medial edge of the entocarotid foramen at the boundary of the basisphenoid and alisphenoid. The suture between the basisphenoid and basioccipital is medial to the petrosal part of the periotic. Anteriorly, the alisphenoid tympanic wing is rounded, but the ventral floor is flat. A thin bridge of bone protrudes anteromedially and dorsally from the tympanic wing of the alisphenoid. The primary foramen ovale lies to the anteromedial side of the alisphenoid tympanic wing and is formed between the alisphenoid and petrosal part of the periotic. An anterodorsal bridge of the alisphenoid forms a secondary foramen ovale, which is confluent with the primary foramen dorsally. The petrosal part of the periotic is small and without

distinct tympanic processes. The fenestra rotundum and fenestra ovalis lie on the lateral and posterolateral wall of the petrosal part of the periotic, respectively. The mastoid part of the periotic forms a small roof of the tympanic sinus. The contact between the alisphenoid and mastoid part of the periotic is flat, and no wall exists between the epitympanic and hypotympanic regions. The ectotympanic is flat ventrally and acts to extend the floor of the tympanic sinus formed by the alisphenoid. Ale ectotympanic is laterally wide. The squamosal is broad and forms a ridge at its contact with the mastoid part of the periotic. There are no epitympanic sinuses on the squamosal or mastoid part of the periotic. The mastoid part of the periotic is bounded by squamosal and paroccipital and does not extend onto the lateral side of the skull. The paroccipital process is long and posteriorly directed. A groove lies on the medial side of the process and leads into the posterior lacerate foramen as well as to the internal jugular foramen. These foramina lie close to one another, with the posterior lacerate foramen the larger. A posterior process of the basioccipital contacts the paroccipital pro- cess. A large foramen opens on the medial side of this contact and connects with the internal jugular foramen. Two hypoglossal foramina lie on the ventrolateral floor of the basioccipital. The subsquamosal fossae open posterior to the zygomatic arch. The squamosal makes an extensive contribution to the lateral side of the skull. The paroccipital-supraoccipital suture is un- clear.

Upper Incisors--No incisors are preserved, but alveoli indicate that I1 was the largest of the four upper incisors. Alveoli for I2 and I3 are narrow and equal in size. The alveolus of I4 is smaller and subcircular. No diastemata are present between the upper incisor alveoli.

C1-The upper canine is not preserved. The alveolus is large and recurves strongly into the maxilla.

Upper Premolars--The P1 is narrow with a single central cusp. The anterior flank of the cusp is recurved, and a low crest runs posteriorly, terminating in a raised posterior cuspule. Two roots of equal size are present. The crown is oriented parallel to the tooth row. P2 is similar in morphology to P1 but approximately 50% larger in size. The anterior surface of the cusp is convex, while the posterior edge is concave. The two alveoli of P3 are equal in size, circular in cross section, and are larger than those of P2. A small diastema is present between C1 and P1. A diastema almost twice this size is present between PI and P2. No diastema is present between P2 and P3.

M1--The M1 is represented by QM F30409. It is longer on the anteroposterior dimension than on the transverse. The anterior region of the crown contains a paracone, a poorly developed anterior cingulum, and a small cuspule at the anterobuccal corner. No stylar cusps are present on the anterior half of the crown, and no crests run along the buccal shelf. No preparacrista is present. The paracone is conical in shape. The centrocrista is straight in occlusal view. An anterior cingulum is present and continuous with the preprotocrista. The metacone is the largest cusp. Posterobuccal to the metacone is stylar cusp D, which is lower in height than the paracone. Stylar cusp D is rounded on all sides except posteriorly, where a crest runs from its tip to the posterobuccal corner of the crown. A small, partially raised region occurs on this crest at the position normally occupied by stylar cusp E. A deep ectoflexus separates anterior from posterior crown regions on the buccal side; otherwise, the buccal surface of the crown is relatively straight. The talon region of the crown is poorly defined. The protocone is reduced in size, low, and positioned directly lingual to the paracone. Low protocristae are present that diverge around small, raised regions which constitute the protoconule and metaconule.

M2--A distinct anterior cingulum terminates anterobuccal to the paracone. Stylar cusp B is large and distinct at the anterior corner of the crown. It is joined to the low paracone by a low
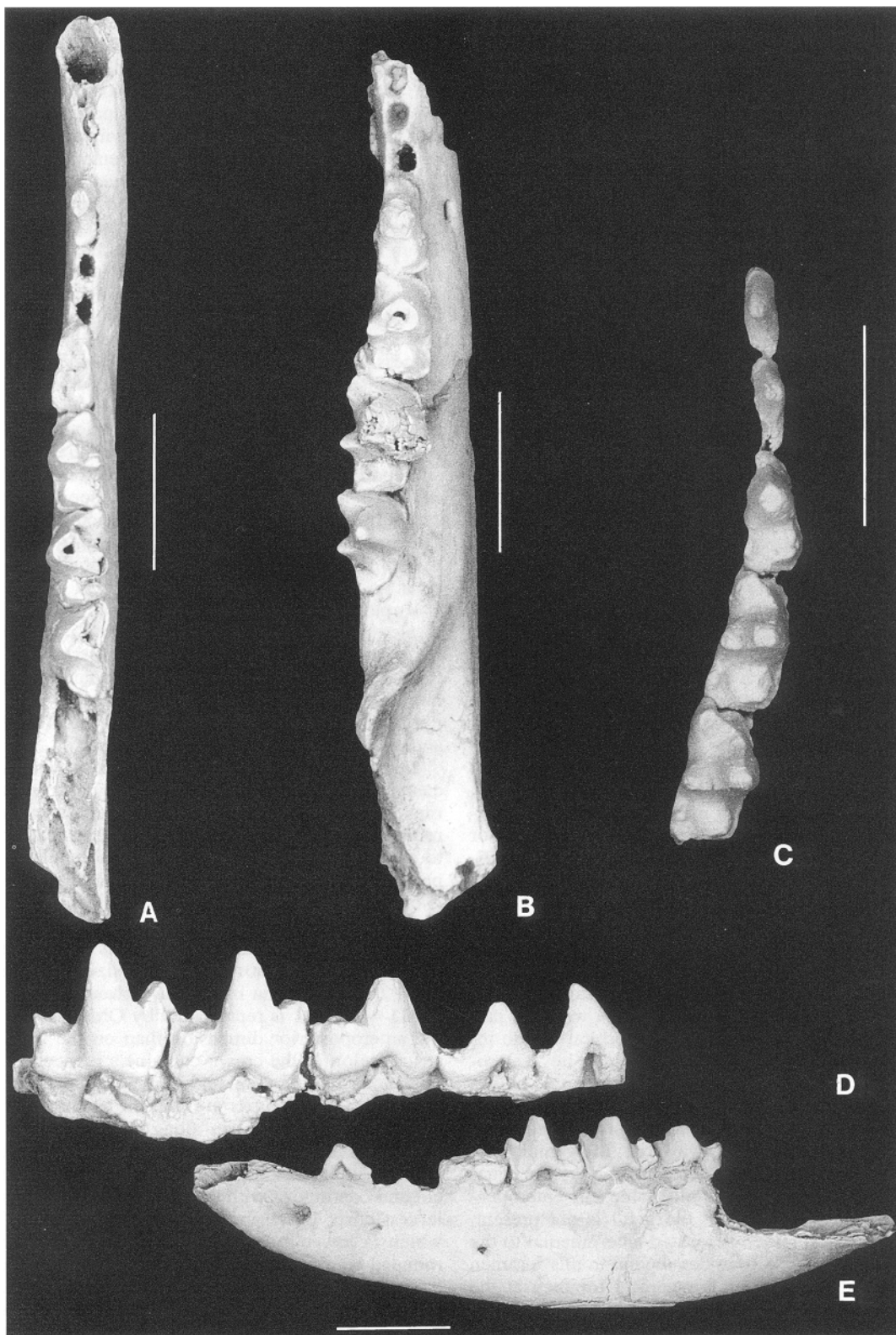
FIGURE *1. Badjcinus turnbulli,* gen. et sp. nov. **A,** QM F30410, left portion of dentary containing p2, M1-4, and alveoli for i3, c1, p1, and p3 (occlusal view). **B,** QM F30407, right dentary fragment containing M1-4, posterior alveolus of p2, and alveoli of p3 (occlusal view). **C,** QM F 30411, right dentary fragment containing p2-3 and M1-3 (occlusal view). **D,** same in buccal view. **E,** QM F30410, left portion of dentary containing p2, M1-4, and alveoli for i3, cl, pl, and p3 (buccal view). Scale bar equals 1 em.
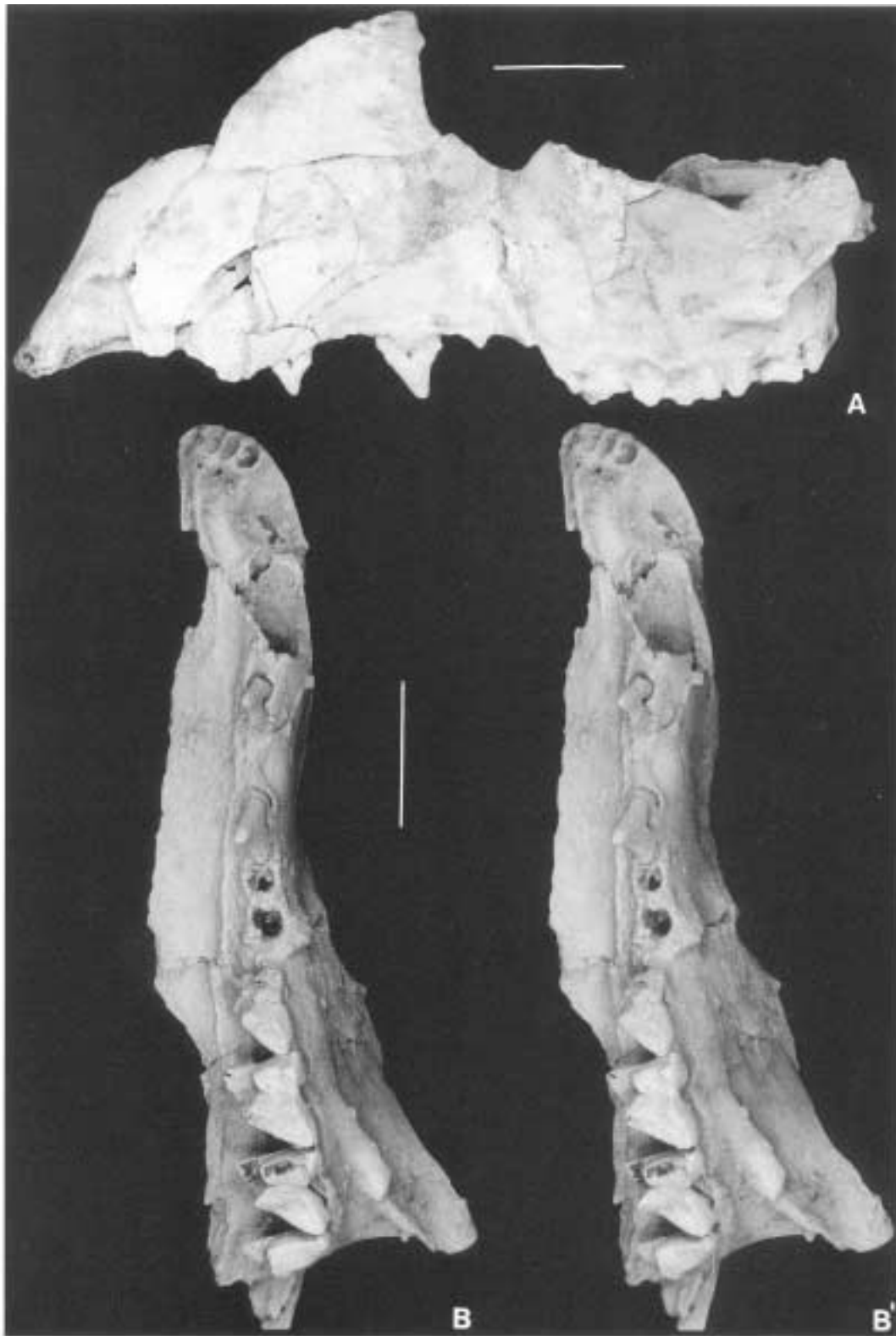
FIGURE 2. *Badjcinus turnbulli* gen.etsp.nov.,QMF30408,holotype.A,leftpremaxilla,maxilia,andupperdentition(P1-2,M1-4) in buccal view. B and B', same in occlusal view (stereo pair). Scale bar equals 1 cm.

FIGURE 3. *Badjcinus turnbulli,* gen. et sp. nov., QM F30408, holotype. A, basicranium in occlusal view. **A,** left half of basicranium (stereo pair in occlusal view). **B,** skull fragment showing the posterior portion of the nasals and the dorsal portion of the frontals (dorsal view). Scale bar equals 1 cm.

preparacrista, which lies almost perpendicular to the long axis of the tooth row. The metacone is the largest cusp, followed (in orderof decreasing height) by stylar cusp D, stylar cusp E, stylar cusp B, paracone, protoconule, metaconule, and protocone. A V-shaped centrocrista is formed in occlusal view by the postparacrista and premetacrista, which meet at an angle of approximately 100°. The morphology of the posterior half of the crown resembles that of M1 except as follows: 1) a possible stylar cusp C is present between stylar cusps B and D; 2) a distinct ectoflexus is present; 3) the metaconule and protoconule are larger; 4) the protocone is larger and more lingually positioned; 5) the angle formed between the preprotocrista and postprotocrista is more acute, forming an anteroposteriorly shorter talon; 6) crests on the lingual flanks of the metacone and paracone connect to the metaconule and protoconule respectively.

   M3--The morphology of M3 is similar to that of M2 except

as follows: 1) the paracone is more lingually positioned; 2) the distance between the paracone and metacone is reduced, and the angle at the centrocrista is approximately 90 ; 3) the postmetacrista is indistinguishable at the base of the metacone, but it becomes distinct towards the posterobuccal corner of crown; 4) stylar cusp D is minute, although a distinct stylar crest continues from stylar cusp B to the posterior tip of the crown; 5) the occlusal surface of the crown buccal to the paracone and metacone is flat, continuing to the posterior tip of the crown; 6) no sharp division exists between the anterior and posterior halves of the crown, as on M1 and incompletely developed on M2; 7) the talon basin is further reduced in size from the condition of M2.

   M4--The M4 is represented by QM F30408. The morphology of M4 is similar to that of M3 except as follows: 1) all cusps are relatively reduced in size, and only stylar cusp B, the
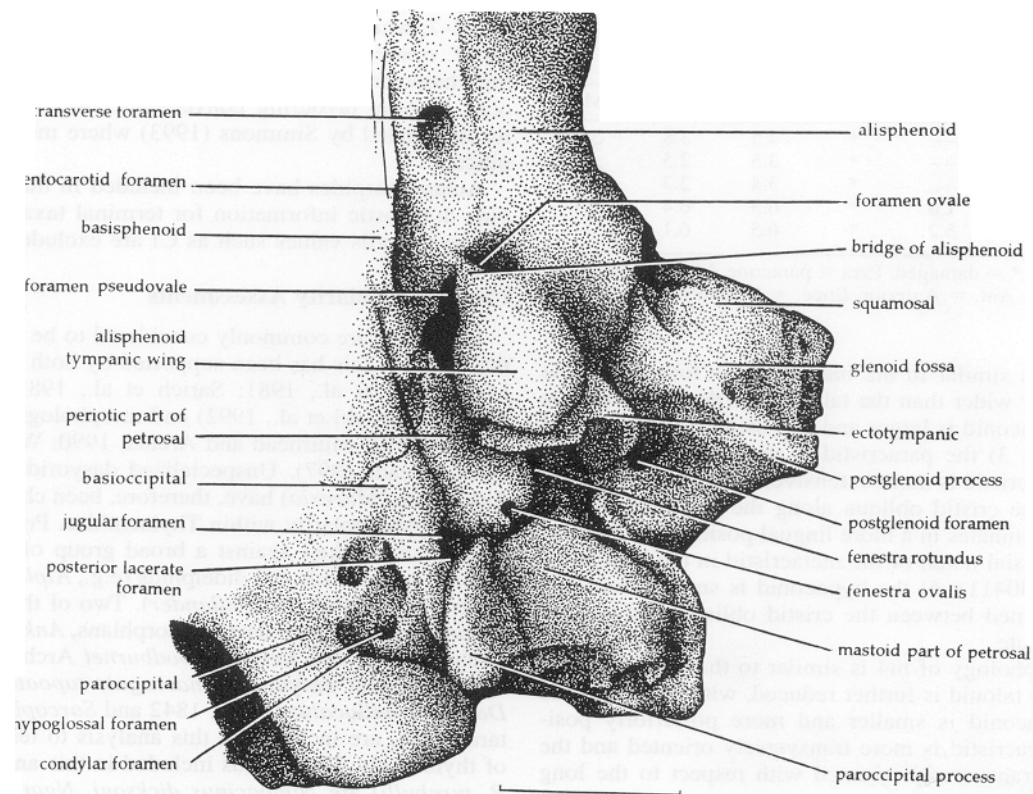
FIGURE 4. *Badjcinus turnbulli* basicranium drawn from QM F30408, holotype, with labelled morphology. Scale bar equals 1 cm

paracone, protoconule, and protocone are present; 2) all crests are poorly defined, except on the anterobuccal corner; 3) the preparacrista is longer and the paracone is more lingually positioned; 4) the postparacrista runs parallel to the tooth row; 5) the talon is reduced on the anteroposterior axis; 6) the protoconule is present but minute, and the posterior crest ascends the lingual flank of the paracone.

Meristic Gradients from M1 to M4--The talon narrows on the anteroposterior dimension. The paracone occupies an increasingly lingual position. The distance between the paracone and metacone decreases and an increasingly acute angle is formed between the postparacrista and premetacrista. The depth of the ectoflexus increases.

Dentary--Most of the dentary is represented by QM F30410 and QM F30407. Anteriorly, only the tip is broken away on QM F30410, with the alveoli for c1, p1 and a single incisor of uncertain homology remaining. The posterior parts of the dentary are best represented by QM F30407. Although the condyle and coronoid process are missing from this specimen, most of the angular process remains. In buccal view, the dentary is slightly convex, deepest beneath the anterior root of m3, and tapers markedly toward the anterior tip.

The entire postcanine tooth row of the dentary is represented by referred specimens QM F30407, QM F30410, and QM F3041 1, excepting p1, for which only the alveolus is known.

c1--From the alveolus (QM F30410), it is clear that cl was a large tooth with a basal diameter of about 4 nun.

p1--From the two alveoli in QM F30410, p1 was small, less than half the anteroposterior length of p2. A diastema of about 3 mm separates p1 from p2. No diastema separates p1 and c1. From the alignment of its alveoli, p1 was oriented at an angle of approximately 30° to the long axis of the dentary.

p2--The p2 is represented by QM F30411 and QM F30410. This tooth is gently recurved in lateral view, with a weakly

defined cristid running from the protoconid to about halfway along the posterior face. The p2 is ellipsoid in occlusal view. There is no diastema between p2-p3.

p3--The p3 is known only from QM F30411. It is similar to p2 except that p3 is lower, anteroposteriorly longer, the protoconid is not recurved, and the heel is relatively larger.

m1-No diastema separates p3 and m1. The principal cusps, in order of decreasing height, are the protoconid, hypoconid, entoconid, paraconid, and hypoconulid. No metaconid is present. The protoconid is large and centrally positioned in occlusal view with respect to both long and transverse axes. A cristid runs from beneath the protoconid tip to connect with the cristid obliqua. Although worn on all specimens, the entoconid of mi is. evidently a well-developed cusp, showing slight compression in the transverse axis. The hypoconid is also worn on all specimens. However, judging from its basal width, the m1 hypoconid was probably taller than the entoconid and clearly more massive. The well-defined posterior cingulid and hypocristid meet at the buccal side of the hypoconulid. The hypoconulid slots into a notch in the anterior cristid of m2. An angle of approximately 45° is formed between the transverse axis of the dentary and the hypocristid. The cristid obliqua is nearly parallel to the long axis of the dentary but with a slight lingual inflection. A variably developed cingulid runs buccally from the paraconid to the base of the crown below the protoconid. Another cingulid circumscribes the base of the hypoconid.

m2--The m2 differs from m1 as follows: 1) a small but distinct metaconid is present; 2) the paraconid is much wider and taller, but it remains the lowest cusp on the trigonid; 3) the protoconid is more massive, taller and located on the buccal side of the crown; 4) the cristid running vertically from the cristid obliqua along the posterior face of the protoconid terminates lingual relative to the protoconid tip; 5) the cristid obliqua forms a more acute angle with the hypocristid.

TABLE 1.　Measurements (in mm) of upper dentition of *B. turnbulli* (holotype, QM F30408).

	P1	P2	M1	M2	M3	M4
Para-Meta	—	—	*	4.5	3.8	3.3
Meta-Proto	—	—	*	3.5	2.5	—
Proto-Para	—	—	*	3.4	2.3	2.3
Ant. width	1.3	1.6	*	6.3	6.4	6.5
Bucc. length	3.6	5.2	*	6.5	6.1	—

— = not applicable, * = damaged, Para = paracone, Meta = metacone, Proto = Protocone, Ant. = Anterior, Bucc. = Buccal.

m3--The m3 is similar to m2 but differs as follows: 1) the trigonid is slightly wider than the talonid and the protoconid is larger; 2) the metaconid is larger and less closely approximated to the protoconid; 3) the paracristid is more transversely oriented; 4) the metacristid is more extensive; 5) the vertical cristid extending from the cristid obliqua along the posterior face of the protoconid terminates in a more lingual position, and almost reaches the carnassial notch of the metacristid in the least worn specimen (QM F30411); 6) the hypoconid is smaller, with the interior angle formed between the cristid obliqua and the hypocristid more acute.

m4--The morphology of m4 is similar to that of m3 except as follows: 1) the talonid is further reduced, with the entoconid lost; 2) the metaconid is smaller and more posteriorly positioned; 3) the paracristid is more transversely oriented and the metacristid less transversely oriented with respect to the long axis of the dentary.

Meristic Gradients from M1-4--Orientation of the paracristid becomes increasingly transverse to the long axis of the dentary. No metacristid is apparent on m1, but it is increasingly transverse in orientation from m2-4. The interior angle between the paracristid and metacristid is increasingly acute. The size of the protoconid increases from m1-3, then decreases in m4. The height of the metaconid increases from m1-4. The size of the metaconid increases from m1-3, and decreases in m4.

PHYLOGENETIC ANALYSIS

Method

The relationships of *B. turnbulli* to other thylacinids were analysed. The monophyly of the family Thylacinidae was also assessed in light of this new species. Thirty-two characters, including 15 multistate characters, were scored for seven thylacinid taxa. Dasyuromorphians were used as the sister group to thylacinids (see below), and polarity decisions based on the sister group were checked relative to the out-group of plesiomorphic didelphimorphian marsupials. These data were analysed using PAUP version 3.1 (Swofford, 1993). Characters were considered to be ordered when directed in a linear additive transformation series following the reasoning of Mickevick and Weller (1990). Characters were analysed using Wagner parsimony with the Branch and Bound algorithm. A number of character states were unknown for some taxa (particularly charac-

ters 2-7, which were missing for species other than *B. turnbulli* and *T. cynocephalus*). DELTRAN optimization was used, placing character state changes further down the tree when equivocal, thereby favouring convergence over reversal, an option recommended by Simmons (1993) where missing data are significant.

Autapomorphies have been included in this analysis to provide diagnostic information for terminal taxa, but their contribution towards values such as CI are excluded.

Character Polarity Assessments

Dasyurids are commonly considered to be the sister-taxon to thylacinids. This has been supported by both biochemical (e.g., Lowenstein et al., 1981; Sarich et al., 1982; Thomas et al., 1989; Krajewski et al., 1992) and morphological research (e.g., Archer, 1982; Muirhead and Archer, 1990; Wroe, 1996, 1997a, b; Muirhead, 1997). Unspecialized dasyurids (e.g., species of *Antechinus, Murexia*) have, therefore, been chosen as outgroups to determine polarity within Thylacinidae. Polarity assessments have been checked against a broad group of relatively unspecialized peradectids and didelphids (e.g., *Alphadon, Peradectes, Didelphis, Metachirus, Philander*). Two of the oldest and most plesiomorphic known dasyuromorphians, *Ankotarinja tirarensis* Archer, 1976e and *Keeuna woodburnei* Archer, 1976c, as well as three extant dasyurids, *Phascogale tapoatafa* Meyer, 1793, *Dasyurus hallucatus* Gould, 1842 and *Sarcophilus harrisii* Boitard, 1841, are included in this analysis to test the monophyly of thylacinids. Thylacinids included in this analysis (other than *B. turnbulli*) are *Nimbacinus dicksoni, Ngamalacinus timmulvaneyi, Wabulacinus ridei, Thylacinus macknessi* Muirhead, 1992, *T. potens* Woodburne, 1967, and *T. cynocephalus* Harris, 1808.

Of all known thylacines, reasonably complete skull material is only known for *T. cynocephalus* and *B. turnbulli*. No cranial material is known for *A. tirarensis* or *K. woodburnei*.

1. **Mastoid Epitympanic Sinus**--Absence of a mastoid epitympanic sinus is plesiomorphic for Marsupialia (0). This is the case in *Metachirus, Philander,* and most didelphimorphian taxa investigated by Reig et al. (1987). In both *T. cynocephalus* and *B. turnbulli,* the mastoid part of the periotic shows no sinus development (0). Many dasyurids, in contrast, show well-developed epitympanic sinuses in the mastoid part of the periotic. This is the case for *P. tapoatafa, D. hallucatus,* and *S. harrisii* (1).

2. **Orbital Crest**--This apomorphic feature is typical of marsupial carnivores. *Badjcinus turnbulli* has a prominent orbital crest similar to that of *T. cynocephalus* (1). A similar crest also occurs in larger species of *Dasyurus, Sarcophilus, and Didelphis* but is absent for smaller and less carnivorous dasyurids and didelphimorphians (e.g., *P. tapoatafa*) (0).

3. **Infraorbital Foramina**--The infraorbital foramen is preserved in maxillary fragments of *N. dicksoni, W. ridei, Ng. timmulvaneyi, T. potens, B. turnbulli,* and *T. cynocephalus*. In *T. cynocephalus, T. potens, Ng. timmulvaneyi, and N. dicksoni,* the infraorbital foramen is bounded posteriorly by the jugal (1).

TABLE 2.　Measurements (in mm) of lower dentitions of *B. turnbulli*. Paratypes QM F30411, QM F30410 and QM F30407 shown from left to right in columns in the above order.

	p2	p3	m1	m2	m3	m4
Para-Meta	—, —, —	—, —, —	—, —, —	3.8, 4.2, *	4.1, *, *	*, *, 3.5
Meta-Proto	—, —, —	—, —, —	—, —, —	3.4, 3.2, *	3.6, *, *	*, *, 3.4
Proto-Para	—, —, —	—, —, —	—, —, —	4.0, 4.0, *	4.8, *, *	*, *, 4.2
Post. width	1.5, 1.7, *	1.6, *, *	3.0, *, *	3.5, 2.9, *	3.3, *, 3.0	*, 2.3, 2.0
Ling. length	4.2, 4.2, *	5.2, *, *	5.4, 5.7, *	6.2, 6.4, *	6.8, *, *	*, 6.1, 6.2

— = not applicable, * = damaged, Para = paraconid, Meta = metaconid, Proto = protoconid, Post. = posterior, Ling. = lingual.

The posterior position of the foramen is considered apomorphic, because in dasyurids, peramelemorphians, and many didelphimorphians examined, this foramen is not delimited posteriorly by the jugal (0). In *W. ridei and B. turnbulli,* the infraorbital foramen is positioned anterior to the jugal (0).

4. Nasal--In *B. turnbulli,* the nasal extends posteriorly as far as the orbital crest, as in dasyurids and many didelphimorphians. In *T. cynocephalus,* the nasal is less extensive posteriorly. This may be related to the apomorphic elongation of the snout (1), while the greater posterior development of the nasal in *B. turnbulli* (0) is likely to be a plesiomorphy.

5. Primary Foramen Ovale--*Thylacinus cynocephalus has* the primary foramen ovale completely enclosed within the alisphenoid (1) (termed the foramen ovale sensu Archer 1976a). Contrary to earlier opinion (e.g., Archer, 1976a, 1982; Marshall, 1977), the morphology of this foramen evident in *T. cynocephalus* is considered to be apomorphic for Australian polyprotodonts based on comparison with didelphimorphians (Case, 1989; Muirhead, 1994; Wroe, 1997b). Medially, part of the alisphenoid tympanic wing is broken away in the holotype of *B. turnbulli.* However, where present, this wall is similar to that *of Didelphis,* although it does not appear to have completely separated the foramen from the periotic. There is little to no development of an alisphenoid partition projecting from the anterior of the foramen margin, and it is concluded that the primary foramen ovale of *B. turnbulli* was not completely enclosed within the alisphenoid (0) (and therefore considered to be a foramen pseudovale sensu Archer, 1976a). This morphology of the primary foramen ovale is considered to be plesiomorphic for thylacinids. All dasyurids have a foramen pseudovale (0) (sensu Archer, 1976a); however, Gaudin et al. (1996) have reported a primary foramen ovale completely enclosed by alisphenoid for a single specimen of *S. harrisii.*

6. Postglenoid Foramen--The mastoid part of the periotic bounds the median surface of the postglenoid foramen in *T. cynocephalus* (1*).* This is the apomorphic state. In most dasyurids and most didelphoids, this foramen is bounded completely by the squamosal or a combination of squamosal and alisphenoid (the dasyurid exception is shown in *Planigale,* in which the mastoid part of the periotic also contributes to for mation of the postglenoid foramen [Archer, 1976a]). This is considered to be the plesiomorphic condition (Muirhead, 1994). *Badjcinus turnbulli* shows the plesiomorphic state in that the postglenoid foramen is bounded entirely by squamosal (0).

7. Ectotympanic--In *T. cynocephalus,* the ectotympanic shows extreme lateral broadening such that it projects well over the mastoid part of the periotic, a condition that increases with age (Archer, 1976a) to twice the width of the alisphenoid tympanic wing in mature adults. Extreme lateral broadening of the ectotympanic is unique to *T. cynocephalus* (2). In *B. turnbulli,* lateral broadening of the ectotympanic is also evident (1), although less derived than in *T. cynocephalus.* For dasyurids and didelphimorphians, lateral broadening is not comparable with these two thylacinids (0).

8. Squamosal Epitympanic Sinus--The squamosal epitympanic sinus is relatively large in *T. cynocephalus,* lying directly over the broadened ectotympanic (1). This is an apomorphic state in dasyuromorphians (Archer, 1976a). In *B. turnbulli,* there is no sinus (0). Many dasyurids show well-developed epitympanic sinuses (1). This is considered to be a derived feature, because in most didelphimorphians the epitympanic sinus is absent or very poorly developed (Reig et al., 1987).

9. Contact of the Petrosal Tympanic Wing and Alisphenoid Tympanic Wing--A tympanic wing of the periotic is not formed in *T. cynocephalus* (0). In this species, a homologous crest runs the length of the petrosal part of the periotic (Archer, 1976a). This crest is entirely absent in *B. turnbulli* (0); however, a small projection of bone is present that is likely to be a lesser developed equivalent. Extant dasyurids have a well-developed tympanic wing on the petrosal part of the periotic, which contacts the alisphenoid tympanic wing (1). Plesiomorphic forest-dwelling dasyurids (e.g., *Neophascogale)* show a lesser degree of development of this feature. It, therefore, appears that dasyurids are generally specialized in this regard. Bandicoots show the same trend, with a well-developed tympanic wing in specialized forms that inhabit and regions, while otherwise plesiomorphic species show little development of this region (Muirhead, 1994). Reig et al. (1987) considered that species of *Philander and Metachirus* approximate the primitive condition for the auditory region of marsupials. In these species, the tympanic processes of the periotic are small compared to those of most dasyurids. These processes also appear to occur predominantly at the posterior region of the periotic in support of the ectotympanic rather than forming a tympanic sinus along the length of the periotic. Among didelphimorphians, *Dromiciops* appears to be an exception, with a well-developed periotic tympanic sinus that contacts the alisphenoid tympanic sinus, as in many dasyurids.

10. Size of Paracone--There is debate regarding whether or not a paracone slightly smaller than or equal in height to the metacone is the plesiomorphic state for marsupials (Reig et al., 1987; Cifelli, 1993; Szalay and Trofimov, 1996). In plesiomorphic dasyurids, the paracone is slightly lower than the metacone. A lower paracone, compared to paracone height in these taxa, is therefore considered to be the apomorphic condition among dasyurids and thylacinids. Among thylacinids, *T. cynocephalus* shows the greatest degree of paracone reduction (3), while *T. potens* shows reduction of this cusp but to a lesser degree (2) than *T. cynocephalus* (Muirhead and Archer, 1990). *Nimbacinus dicksoni, Ng. timmulvaneyi, W. ridei, and T. macknessi* show paracone reduction (1) (at least on M1) compared to more plesiomorphic dasyurids; however, the reduction is not as extreme as in either *T. cynocephalus* or *T. potens* (Muirhead and Archer, 1990; Muirhead, 1992). There is a significant degree of difference in the size of the paracone relative to the metacone on *B. turnbulli* (2), and this species is, therefore, more apomorphic in this regard than *N. dicksoni, Ng. timmulvaneyi,* and *W. ridei.* Because the size disparity between the paracone and metacone is most extreme on M2, the condition of this character in species that do not have this tooth preserved (e.g., *T. macknessi)* is less certain. Paracone height relative to metacone height in *B. turnbulli* is comparable to that in *T. potens* (2), and not as extreme as in *T. cynocephalus.* The size of the paracone in dasyurids is similarly varied, with the most carnivorous forms showing greater paracone reduction [e.g., *S. harrisii* (3)].

11. Size of Stylar Cusp B on M1-2--A well-developed stylar cusp B is considered to he plesiomorphic for didelphimorphians (Reig et al., 1987; Marshall and Muizon, 1995). Plesiomorphic dasyurids show a well-developed stylar cusp B (0); however, reduction of this cusp is evident in two otherwise plesiomorphic dasyuromorphians, *Keeuna* (2) and *Ankotarinja* (4). Stylar shelf reduction is a characteristic of thylacinids (Muirhead, 1992). Stylar cusp B and D are the largest cusps present in members of the family. In all species of *Thylacinus,* these cusps are dramatically reduced (4) (Muirhead, 1992). *Wabulacinus ridei* (3) shows slightly less reduction than seen in species of *Thylacinus, while Ng. timmulvaneyi* (2) is more plesiomorphic again in the degree of reduction (2) (Muirhead, 1997). *Nimbacinus dicksoni* is the most plesiomorphic thylacinid in respect to stylar shelf reduction (1), but still derived compared to most dasyurids (0) (Muirhead and Archer, 1990). *Badjcinus turnbulli* shows a degree of stylar shelf reduction similar to that of *Ng. timmulvaneyi* (2).

12. Anterior Cingulum on Upper Molars (based on M1)--Presence of an anterior cingulum that continues around the an-

teromedial face of the paracone to connect with the prepara-crista (0) is the plesiomorphic state, because of the presence of this morphology in relatively unspecialized dasyurids (e.g., species of *Antechinus, Phascogale).* Anterior cingulum morphology is variable among thylacinids. *Nimbacinus dicksoni* shows the plesiomorphic condition of complete cingula (0). The only known MI specimen of *Ng. timmulvaneyi* is damaged. An anterior cingulum is present, but it is unclear if this cingulum is complete (0 or 1). *Wabulacinus ridei* has incomplete anterior cingula on all upper molars (1). The upper dentition of *T. macknessi* is only known from M1. This tooth has a complete anteripr cingulum (0). The anterior upper dentition of *T. potens* is damaged, and the state of the cingulum on M1 is unknown. The M2 of this species, however, has an incomplete anterior cingulum, indicating that a complete or incomplete cingulum was probably present on MI (0 or 1). *Thylacinus cynocephalus* has lost all anterior cingula on the upper molars (2). *Badjcinus turnbulli and T. macknessi* are similar in anterior cingulum morphology, i.e., complete cingulum on M1 (0), with incomplete cingula on more posterior molars.

13. Size of Protocone and Conules--The size of the protocone varies among thylacinids. Because this cusp is large and usually defined by distinct pre- and postprotocristae on plesiomorphic dasyurids, this condition is considered to be the plesiomorphic state. The presence of a protoconule and metaconule is the plesiomorphic condition for thylacinids (Muirhead and Archer, 1990). *Nimbacinus dicksoni* is plesiomorphic among thylacinids in its retention of large protocones with crests and well-developed conules (0). *Ngamalacinus timmulvaneyi* and *W. ridei* show a reduction of these features relative to *N. dicksoni* and are therefore more apomorphic in this regard (1). *Sarcophilus harrisii* shows a similar degree of reduction (1). The protocone shows significant reduction in size in *T. macknessi, T. potens,* and *B. turnbulli* (2), while *T. cynocephalus shows* the greatest reduction in size of the protocone, with complete loss of conules and protocristae (3).

14. Length of Postmetacrista--Elongation of the postmetacrista is an apomorphic carnivorous specialization in thylacinids, resulting in a relatively longer primary cutting blade (Muirhead, 1992). The postmetacrista shows no elongation in piesiomorphic dasyurids and dasyuromorphians (e.g., *Phascogale, Ankotarinja,* and *Keeuna)* (0). *Nimbacinus dicksoni* has a postmetacrista of approximately equal relative size to that of dasyurids, such as *Murexia* and some didelphimorphians (Muirhead and Archer, 1990) *(0). Badjcinus turnbulli* and *Ng. timmulvaneyi* have a slightly elongated postmetacrista compared to that in *N. dicksoni* (1). All other thylacinid species show greater elongation of the postmetacrista (2). Among dasyurids, more carnivorous taxa show progressively longer postmetacristae: *D. hallucatus* (1), *S. harrisii* (2).

15. Angle at Centrocrista (angle formed by the postparacrbta and premetacrista)--A linear centrocrista, in occlusal view, is present in most Peradectidae and has commonly been treated as a marsupial plesiomorphy (Reig et al., 1987; Marshall et al.,, 1990). As observed by Cifelli (1990), a 'V'-shaped centrocrista is present in at least one taxon referred to *Alphadon.* This may represent a synapomorphy with lower clades, or a homoplasious feature. Although a linear centrocrista has been considered plesiomorphic for Marsupialia, in the closest probable outgroup taxa to Thylacinidae, i.e., peramelemorphians (Muirhead and Filan, 1995) and plesiomorphic dasyurids and dasyuromorphians, the postparacrista and premetacrista meet to form an acute angle (0), while a more obtuse angle is formed in some derived dasyurids (e.g., *S. harrisii*) (1). Species of *Thylacinus* have a linear centrocrista (2). This is also the condition in *W. ridei* (2). An intermediate state for this feature is present *in Nimbacinus dicksoni, Ng. timmulvaneyi,* and *B. turnbulli* (1), which show a widely angled centrocrista.

16. Direction of Preparacrista on M1--The direction of the preparacrista on MI is variable within thylacinids and does not appear to be directly related to other features of the dentition. Plesiomorphically, as in relatively unspecialized dasyurids (e.g., species of *Antechinus and Murexia),* the preparacrista on M1 is aligned at a sharp angle to the long axis of the tooth such that it is almost perpendicular to the long axis (0). It usually forms a 90' angle with the postparacrista. This is also the condition in *N. dicksoni* and *Ng. timmulvaneyi* (0). Species of *Thylacinus* show a more apomorphic state, with the preparacrista aligned more obliquely relative to the long axis of the tooth (1). This is also the condition evident in *S. harrisii* (1). In *T. potens,* this feature is poorly preserved and therefore scored as (?). *Wabulacinus ridei* is unique among thylacinids in that the preparacrista on MI is aligned parallel to the long axis of the tooth, forming a continuous crest with the straight centrocrista (2) (Muirhead, 1997). *Badjcinus turnbulli* is also unique in that the preparacrista on MI is lost, the paracone is conical, with only a postparacrista connecting to it. The polarity of this condition is uncertain. However, it appears that this condition is highly derived and unlike that of most dasyurids. It is considered here to represent a further specialization from the condition in *W. ridei* because, as in *W. rides,* the centrocrista is straight, and the parastylar tip (in the form of the anterior cingulum tip) lies almost directly anterior to the paracone of this tooth (3).

17. Angles formed by Paracristae and Metacristae on M1-3 (including centrocrista)--The angles formed by crests at the paracone and metacone (particularly the angle formed by the metacristae) are narrow on plesiomorphic dasyurids (e.g., species of *Antechinus, Murexia, Phascogale,* as well as the dasyuromorphians *Ankotarinja* and *Keeuna).* *Nimbacinus dicksoni, Ng. timmulvaneyi,* and *B. turnbulli* show a more apomorphic condition: the angle formed by these crests widens, orienting the crests more closely to the long axis of the tooth row (1). *Wabulacinus rides,* as well as *T. cynocephalus* and *T. potens,* have this angle of crests even wider (2). M2-3 are not known for *T. macknessi;* however, the straight centrocrista shown on M1 of this species strongly implies a like condition for M2-3 (2). The derived character state is also found in some derived carnivorous dasyurids, particularly some species of *Dasyurus* (e.g., *D. maculatus,* but not *D. hallucatus*) and *Sarcophilus.*

18. Size of the Metaconid in m1 Relative to that of m2-4--Among thylacinids, most dasyurids, and didelphimorphians, reduction of the metaconid on m1-4 is usually uniform along the molar row (0). *Badjcinus turnbulli* is the single exception within the Thylacinidae for this character, with the m1 metaconid lost, while the size of the metaconid on m2-4 is approximately uniform (1). The character state shown by *B. turnbulli* is also found in some derived carnivorous dasyurids, particularly species of *Dasyurus* and *Sarcophilus.*

19. Size of Metaconid on m2-4.--Metaconid reduction is recognized as the apomorphic condition among didelphimorphians (Reig et al., 1987). In A thylacinids, there is some reduction of the metaconids on m2-4 compared to plesiomorphic dasyurids and didelphimorphlans. For thylacinids, reduction of this cusp is least pronounced in *B. turnbulli* and *N. dicksoni* (1). Reduction is progressively more developed in *Ng. timmulvaneyi* (2) and *W. ridei* (3), culminating in the complete loss of the metaconid in highly derived species of *Thylacinus* (4).

20. Size of the Entoconid--Among plesiomorphic dasyurids and didelphimorphians, the entoconid on the lower molars is large (0). *Ngamalacinus timmulvaneyi* is unique among thylacinids in possessing a large entoconid (0). For *B. turnbulli,* the entoconid is slightly reduced (1). Entoconid diminution is progressively more distinct in *N. dicksoni* (2) and the species of *Thylacinus* (3). This morphocline terminates in complete loss of the entoconid on *W. ridei* (4).

21. Morphology of the Entoconid--The size of the ento-

conid has been used as a character in this analysis (Character 20). In *Ng. timmulvaneyi,* the entoconid is large, a state scored as plesiomorphic. However, the extreme lateral compression and presence of a prominent carnassial notch in the entocristid is unique to this taxon among thylacinids and is derived compared to that in dasyurids and didelphimorphians. The well-developed lateral compression of the entoconid in *Ng. timmulvaneyi* has been treated as derived (1).

22. Diastema between p1-2--A diastema between p1 and p2 is found in the majority of plesiomorphic dasyurids, didelphimorphians, and most thylacinids (0). The exception is *W. ridei* for which the lack of a diastema in this position has been considered apomorphic (1). *Ankotarinja* also displays a diastema in this position.

23. Diastema between p2-3--A distinct diastema between p2-3 is rare among dasyurids and didelphiniorphians. *Badjcinus turnbulli* and *N. dicksoni* also lack a diastema in this position (0). For *Ng. timmulvaneyi,* this region of the dentary has not been preserved (?). In all species of *Thylacinus,* p2 and p3 are well separated, and the character state shown by these taxa has been treated as apomorphic (1).

24. Morphology of the Hypoconulid and Hypoconulid Notch--In all dasyurids, a distinct hypoconulid notch in the anterior cingulid on m2-4 accommodates the posteriorly protruding hypoconulid of the preceding molar (0). Wroe (1996) treats this as a dasyuromorphian plesiomorphy, contra Archer (1982). Some diminution of the hypoconulid notch is apparent in *B. turnbulli* and *N. dicksoni* (1), with progressively more obvious reduction in *Ng. timmulvaneyi* (2), *W. ridei* (3), and *T. macknessi* (4). The most apomorphic state for this character is seen in *T. potens* and *T. cynocephalus,* in which no notch exists (5). The carnivorous *S. harrisii* shows the most derived state among dasyurids (4).

25. Morphology of the Posterior Cingulid/Hypocristid--In *Ng. timmulvaneyi* and *B. turnbulli,* the posterior cingulid and hypocristid meet at the base of the hypoconulid on the buccal side (1). In all other Dasyuromorphia, these crests do not meet (0).

26. Morphology of the Cristid Obliqua--In *Ng. timmulvaneyi* and all species of *Thylacinus,* a well-developed carnassial notch is present on the cristid obliqua of the lower molars (1). This notch is not found in any other thylacinids, and among dasyurids and didelphimorphians is only present in some specialized, carnivorous taxa. A carnassial notch on the cristid obliqua was determined to be derived for thylacinids.

27. Angle of Hypocristid Relative to the Transverse Axis of the Dentary--A hypocristid running nearly parallel to the transverse axis of the dentary has been considered plesiomorphic for both dasyurids and didelphimorphians (0) (Archer, 1976b). Among thylacinids, the hypocristid clearly departs from this condition. The angle formed between the hypocristid and the transverse axis of the dentary is moderate in *B. turnbulli, N. dicksoni, and W. ridei* (1), intermediate in *Ng. timmulvaneyi* (2), and most pronounced in the species of *Thylacinus* (3). Some carnivorous dasyurids, e.g., species of *Dasyurus* and *Sarcophilus,* are also derived regarding this feature (1).

28. Carnassial Notch in Hypocristid--Among thylacinids, a distinct carnassial notch on the hypocristid is known only in *Ng. timmulvaneyi* and *B. turnbulli* (1). This character state is unknown among dasyurids or didelphimorphians (except species of *Didelphis)* and has been determined as apomorphic.

29. Anterior Point of Termination for the Cristid Obliqua--In plesiomorphic dasyurids and didelphids, the cristid obliqua ends well below and buccal to the carnassial notch in the protocristid (Archer, 1976b) (0). A morphocline for this character is shown by thylacinids, with the cristid obliqua progressively shifted buccally and ascending the posterior face of the trigonid in more derived species to become the principal pos-
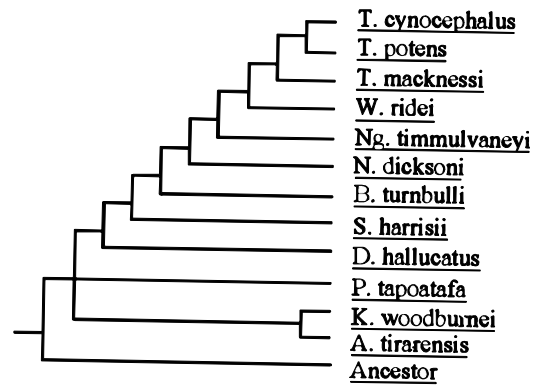

FIGURE 5. The least resolved of the three equally parsimonious cladograms produced by Wagner analysis.

terior shearing crest. This character state is least developed in *B. turnbulli* and *N. dicksoni* (1), more distinctive in *Ng. timmulvaneyi* (2) and *W. ridei* (2), with the most apomorphic condition shown by the species of *Thylacinus* (3). Among dasyurids, *Phascogale* and *Dasyurus* show the plesiomorphic state *(0). Sarcophilus* shows moderate specialization for this feature, but as shown by Ride (1964), the protocristid represents the principal posterior shearing crest for this taxon (1).

30-31. Size of p3--A tendency to reduce the size of p3 relative to p2 has been considered a possible synapomorphy of dasyurids (Archer, 1976b; Marshall et a]., 1990) but, as discussed by Wroe (1996), not all dasyurids show this condition. In many didelphids, the p3 is slightly smaller than p2 (Goin, 1993). This is also the case in *Ankotarinja tirarensis. Further-* more, the greatest relative size of p3 among thylacinids is shown in the most derived species, *T. cynocephalus,* with the differential between these two premolars less distinct in other- wise less specialized thylacinids. In the plesiomorphic *B. turnbulli,* p3 is slightly smaller than p2. In this analysis, a p3 slightly smaller than p2 has been treated as a plesiomorphy (00) following Wroe (1996). The specialized condition can be along two separate pathways: (10) represents the condition in which p3 is greatly reduced or entirely lost, associated with facial shortening (e.g., species of *Dasyurus* and *Sarcophilus)*; while (01) represents the condition shown in apomorphic thylacines, in which the face and p3 are elongated. The possession of a p3 larger than p2 is found in all thylacine taxa other than *B. turnbulli* (and *Ng. timmulvaneyi,* for which this character is unknown).

32. Length of m4--Among dasyurids and didelphids, m4 is anteroposteriorly shorter than m3 (0). This is also the case in all thylacinids except *T. potens* and *T. cynocephalus.* The m4 is not known for *W. ridei (?).* A m4 longer than m3 has been treated as apomorphic in this study (1).

Results

Three equally parsimonious trees of 94 steps were produced by Wagner analysis (excluding uninformative characters: CI = 0.611, HI = 0.389, RI = 0.746, RC = 0.468). The tree of poorest resolution among the three most parsimonious trees is shown in Figure 5. Differences between the three most parsimonious trees are described below.

Thylacines form a clade exclusive of dasyurids. The thylacinid clade is supported by six characters. These are: (1) absence of the mastoid epitympanic sinus, a loss from the dasyurid condition, (7) lateral broadening of the ectotympanic, (9) lack of contact of the petrosal tympanic wing with the alisphenoid tympanic wing, apomorphic loss from the dasyurid

condition, (11) reduction in size of the stylar cusp B, (20) reduction in size of the entoconid, and (31) elongation of P/p3.

Relationships among thylacinids are consistent in the three equally parsimonious trees with species of *Thylacinus* forming a clade followed by consecutive sister-taxa of *W. rides, Ng. timrnulvaneyi,* and *N. dicksoni. Badjcinus trnbulli* is considered to be the most plesiomorphic thylacine and excluded from a clade containing all others by the position of the infraorbital canal (3) and the differential of the metaconid size between M1 and m2-4 (18).

The plesiomorphic and extinct dasyuromorphians *K. woodburnei* and *A. tirarensis* are considered to be sister taxa based on their reduction of stylar cusp B and diastema between p1 and p2 (the analysis presumes this condition for *K. woodburnei*). The extant and relatively derived dasyurids *S. harrisii* and *D. hallucatus* (respectively) are consistently placed as sister-taxa to the thylacinid clade. The difference between the three most parsimonious trees is the position of plesiomorphic dasyurids. *Phascogale tapoatafa* is either considered as: 1) a sister-taxon to the thylacine + *S. harrisii* + *D. hallucatus* clade, excluding the extinct dasyurids; 2) outside of a clade made up of all other dasyurids and thylacinids; or 3) unresolved relative to the extinct dasyurids, but outside of a clade of thylacines and other living dasyurids (Fig. 5).

DISCUSSION

For most analyzed features, *Badjcinus turnbulli* is the least derived thylacine examined here. Regarding cranial features considered, *B. turnbulli* is more plesiomorphic than, or similar to, *T. cynocephalus.* There is no feature of the skull that would indicate it is other than intermediate between a plesiomorphic dasyuromorphian (as currently recognized) and the apomorphic *T. cynocephalus.* Comparison of skull morphology, however, is limited to *B. tumbuili* and *T. cynocephalus* among thylacines.

The dentition enables greater comparison among thylacinids. Five dental characters show a transformation series from the most plesiomorphic state in *B. turnbulli* to the most apomorphic in *T. cynocephalus.* These are the angle at the centrocrista (15), angle formed by crests at the paracone and metacone (17), M2-4 metaconid size (19) and the hypoconulid morphology (24). There is only one character in which *B. turnbulli* displays the plesiomorphic condition exclusive of all other thylacines: length of p3 (31). Two characters, the size of stylar cusp B (11) and the length of the postmetacrista (14), would otherwise suggest a more plesiomorphic position for *N. dicksoni* outside of all other thylacines, including *B. turnbulli.* A basal position for *N. dicksoni* among thylacinids, however, conflicts with a greater number of characters than does a basal position for *B. turnbulli.*

Some characters of *B. turnbulli* show a more specialized condition than expected for its basal position among thylacines. The reduction in paracone size (10) of *B. turnbulli* is derived compared to that of most other thylacinids, suggesting a position between *T. macknessi* and *T. cynocephalus.* The greater length of the postmetacrista (14) is also more apomorphic than in many other thylacines and similar to that exhibited within *Thylacinus.*

Among thylacines, *B. turnbulli* is unique in the greater relative reduction of the metaconid on m1 compared to the remaining molars (18) and in its highly derived preparacrista orientation, parallel to the long axis of the tooth row (16). *Badjcinus turnbulli* and *Ng. timmulvaneyi* exclusively share aponiorphic morphology of the posterior cingulid and hypocristid (25), and a carnassial notch in the hypocristid (28).

Badjcinus turnbulli possesses a combination of derived and plesiomorphic character states that exclude its referral to any previously recognized thylacinid genus. It cannot be considered as directly ancestral to any other known taxon.

Badjcinus in Relation to other Australian Marsupial Groups

All dasyurids included in this analysis lie outside the thylacinid clade, including the carnivorous *S. harrisii.* Although many thylacines share carnivorous features with some carnivorous dasyurids, thylacines are distinguished by a unique combination of derived features. Interestingly, modem dasyurids are not monophyletic on the basis of results of the present study. Elucidation of dasyurid phylogeny is the subject of work in progress by the second author and this topic is not pursued further in this investigation.

Possession of the following combination of characters define *B. turnbulli* as a thylacinid: lateral broadening of the ectotympanic, reduction of the stylar shelf-particularly stylar cusp B, widening of the angle of the centrocrista, widening of the angle formed by crests at the paracone and metacone (thereby extending the anteroposterior dimension of the tooth), reduction in height of the metacristid along the lower molar row, reduction in the size of the entoconid, and reduction of the hypoconulid and associated notch for interlocking with the following lower molar.

The combination of apomorphic and plesiomorphic characters in *B. turnbulli* exclude it from consideration as an ancestor to any known dasyurid clade without the acceptance of multiple homoplasies. Metaconid reduction on m1 in *B. turnbulli* (i.e., complete loss) exceeds that of even the most specialized dasyurid, with the possible exception of *'Apoktesis cuspis'* (Campbell, 1976). This material, however, is not available for comparison. Reduction of the metaconid on m2-4 is greater than that in all dasyurids, except *S. harrisii* and *D. maculatus.* These apomorphies in *B. turnbulli,* concurrent with plesiomorphic features including relatively large p3 and m4 talonids, lack of both a squamosal epitympanic sinus and significant contribution of the periotic to the tympanic sinus, as well as the presence of a diastema between p1-2 (in carnivorous dasyurids, this diastema is never present unless p3 is lost), are unknown in any dasyurid. The morphology of m1 in *B. turnbulli* also differs from that seen in nearly all unworn specimens of *Dasyurus* species in lacking a paracristid.

A possible alliance of *B. turnbulli* with specialized caniivorous dasyurid taxa is further contradicted by the latest molecular evidence suggesting a recent origin for *Dasyurus* and *Sarcophilus* species (Krajewski et al., 1992, 1993). If *B. turnbulli* is a dasyurid, it must represent an ancient but ultimately sterile branch of the phylogenetic tree. Alternatively, only two apomorphies of *B. turnbulli* might exclude it from a structurally ancestral position within the Thylacinidae: reduction of the paraconid on m1 and the orientation of the preparacrista on M1. Both of these features are considered here to represent variations on the basic thylacinid theme, and on the basis of parsimony, *B. turnbulli* is most correctly placed within the Thylacinidae.

Convergence Between Thylacinids and Borhyaenids

Historically, the morphological similarity noted between thylacinids and South American borhyaenids has been based on comparisons with a limited sample of highly specialized thylacinid taxa (*T. cynocephalus* and *T. potens*). The many potential synapomorphies between these two derived thylacinids and apomorphic borhyaenids provided a basis for serious debate regarding their relationships. Given the lack of structural intermediates bridging the gap between plesiomorphic dasyurids and *Thylacinus,* in conjunction with mounting evidence placing *Thylacinus* outside of the Dasyuridae, the evidence for a thylacinid-borhyaenoid relationship was considerable.

New thylacinid specimens from Oligo-Miocene deposits of Riversleigh (e.g., Muirhead and Archer, 1990; Muirhead, 1992;

Muirhead and Gillespie, 1995; Muirhead, 1997) provide structural intermediates along a morphocline between plesiomorphic dasyurids and derived thylacinids. These taxa, as well as new cranial data provided by the plesiomorphic *B. turnbulli,* provide morphological information to supplement biochemical data in supporting distinctly separate origins for the Borhyaenidae and the Thylacinidae. Wroe (1996, 1997a, b, in press) has suggested that Dasyuridae is not presently defined on the basis of derived dental features, indicating possible paraphyly for a number of plesiomorphic fossil ?Dasyuridae known only from dental ma- terial (e.g., *Ankotarinja, Keeuna, Wakamatha*).

Borhyaenidae (sensu Marshall, 1978) includes the subfamilies Hathlyacyninae, Proborhyaeninae, Prothylacyninae, and Borhyaeninae, which are defined by possession of the following characters: molars increase in size from m1 to m4; paracone often reduced; metaconids often absent and always smaller than paraconids; distinct nasal-lacrimal contact; the basisphenoid and basioccipital progressively increase in width posteriorly and are relatively flat transversely, forming a prominent transverse ridge at their suture; petrosal part of the periotic lacks a tympanic process; large hypoglossal foramina, postsquamosal, and postglenoid foramina present. Another character present in all borhyaenid taxa known from cranial material is the reduction or loss of the transverse foramina (Archer, 1976a).

Of these characters, nasal-lacrimal contact and the reduction of the transverse foramina are unique to borhyaenids. There is no nasal-lacrimal contact in *Thylacinus* (the only thylacinid in which this feature is known), and the transverse and entocarotid foramina are present and unreduced in *T. cynocephalus* and *B. turnbulli.*

Many features that distinguish *B. turnbulli* from *T. cynocephalus* are marsupial plesiomorphies shared with less derived borhyaenid taxa, including the possession of an anteriorly positioned infraorbital foramen and the lack of a squamosal epitympanic sinus.

In thylacinids, the transformation of a primary foramen ovale enclosed by the alisphenoid and periotic into a foramen enclosed wholly by the alisphenoid is mirrored in borhyaenids. In borhyaenids, a primary foramen ovale enclosed by the alisphenoid is common to most derived taxa. Muizon (1994) considers the location of this foramen wholly within the alisphenoid to be an apomorphy for borhyaenids, while its location between the alisphenoid and periotic is the condition in the basal *taxa Mayulestes* and *Sallacyon.* The lack of a mastoid epitympanic sinus shared by all known thylacinids and borhyaenids is a symplesiomorphy among marsupials.

Most cranial and dental similarities between thylacinids and borhyaenids are associated with carnivory. Characters correlated with carnassialization in both borhyaenids and thylacinids include snout elongation, metaconid reduction to loss, talon and talonid reduction, orientation and elongation of principal sectorial blades of upper and lower molars in line with the long axis of the dentary, the trend toward unification of paracone and metacone, and reduction in size of paracone, reduction to loss of conules, and loss of ectoflexus on upper molars.

The discovery of structural intermediates within the thylacinid lineage has revealed subtle differences in some transformation series terminating in derived thylacinids and borhyaenids, respectively.

Relative Size of Paracone and Metacone--Reduction in the size of the paracone differs between thylacinids and borhyaenids. The trend in borhyaenids is for the paracone to show a greater reduction in posterior molars compared to anterior molars. Thylacinids, in contrast, undergo a relative consistent degree of paracone reduction (compared to the size of the metacone) along the entire tooth row.

P/p3 1-lypertrophy--Marshall et al. (1990) consider enlargement of P/p3 to be a borhyaenid synapomorphy. In species of *Thylacinus,* P/p3 is also large compared to P/p2. Prior to the description of *B. turnbulli,* this character in *Thylacinus* was considered a plesiomorphy for thylacines (Archer, 1976b, 1982). Because it is now clear that P/p3 hypertrophy represents an apomorphy for *Thylacinus,* this character must be consider convergent in derived borhyaenid and thylacinid clades.

Principle Posterior Shearing Crest--As noted by Rieg (1964) for the most derived species of thylacinids (e.g., species of *Thylacinus),* the principal posterior shearing crest connects the protoconid and hypoconid (incorporating the postprotocristid and cristid obliqua, terminating at the hypoconid). A carnassial notch delineates the postprotocristid and cristid obliqua components of this crest. The postprotocristid runs vertical from the carnassial notch with a lingual inflection. Ride used this character to separate *Thylacinus* from the apomorphic dasyurid *Sarcophilus,* in which the posterior shearing crest incorporates the greatly reduced metaconid.

Some borhyaenid taxa have no posterior shearing crest on the lower molars (e.g., *Prothylacinus patagonicus, Cladosictis centralis),* while most possess one or two distinct posterior shearing crests. In all borhyaenid specimens available for study (i.e., representatives of 25 genera) in which a single posterior shearing crest is evident, it runs from the protoconid to a cusp on the lingual margin of the talonid, bypassing the hypoconid (e.g., *Acrocyon sectoris),* as in *Sarcophilus.*

For borhyaenids in which the metaconid has not been lost the posterior shearing crest runs from the protoconid to the metaconid and then from the metaconid to the entoconid (e.g. *Pharsophorus cretaceus, Stylocynus paranensis.* Some borhyaenids (e.g., *Borhyaena sp., Palaeothent aratae)* possess an additional posterior shearing crest that is homologous with that in *Thylacinus* species. However, in the borhyaenoids with two crests connecting the protoconid with the talonid, the crest that runs through the metaconid and bypasses the hypoconid is the larger. In species of *Thylacinus,* this crest does not exist. For plesiomorphic thylacinids, as for less derived borhyaenids, both posterior crests may be present, although relatively small (*B. turnbulli, Ng. timmulvaneyi),* but in these thylacinids, the crest that connects the protoconid to the hypoconid is the more distinct (i.e., the crest homologous with the posterior shearing crest of *Thylacinus).* Furthermore, in *B. turnbulli* and *Ng. timmulvaneyi,* the hypoconid-protoconid crest ascends the posterior face of the protoconid with a lingual inflection, as in *Thylacinus* species. In summary, morphology of the posterior shearing crest in species of *Thylacinus* distinguishes this taxon from borhyaenids and establishes *B. turnbulli* and *Ng. timmulvaneyi* as more likely structural ancestors to apomorphic thylacinids.

Orientation of Metacristid--Reduction and posterior shifting of the metaconid is common to borhyaenids and thylacinid However, differences in orientation of the metaconid in less derived species of both taxa suggest discrete points of origin. In plesiomorphic thylacinids, in which the metaconid has not been lost (*N. dicksoni, B. turnbulli, Ng. timmulvaneyi),* reduction and posterior displacement of this cusp is concurrent with a re-orientation of the complete metacristid, which is oriented away from the transverse axis of the dentary in occlusal view. For plesiomorphic borhyaenids (e.g., *Palaeothentes aratae)* and borhyaenids considered likely structural ancestors for groups such as *Patene* (Marshall, 1981), reduction and displacement of the metaconid is achieved without re-orientation of the metacristid. In these taxa, only that portion of the metacristid connecting the metaconid to the carnassial notch is inflected posteriorly from the transverse axis of the dentary, while the section running from the carnassial notch to the protoconid tip remains transversely oriented, producing a distinct "kink" in occlusal view. In carnivorous didelphoids (e.g., species of *Lutreolina* and *Thylophorops),* metaconid reduction is achieve

without posterior shifting of the cusp and the entire metacristid remains transversely oriented.

This evidence suggests that thylacinids are derived from a taxon in which the metacristid was already oriented obliquely to the long axis of the dentary (as is the case for most dasyurids), while the immediate ancestral taxa to the South American clades possessed a transversely oriented metacristid.

Relative Size of m4--Marshall (1981) and Marshall et al. (1990) considered marked lower molar size increase from M1-4 to be a synapomorphy of the Borhyaenoidea. This character is also shared by *T. cynocephalus* and *T. potens,* with m4 being both longer and higher crowned than all preceding molars.

Analysis of new material clearly shows that in thylacinids, the possession of this gradient in M1-4, is a synapomorphy uniting these two species of *Thylacinus* only, indicating no special relationship with borhyaenids. In all Oligo-Miocene thylacinids from Riversleigh, including *T. macknessi,* m4 is clearly shorter than m3, as it is in all dasyurids.

Re-diagnosis of the Thylacinidae

Thylacinids can be distinguished from all other polyprotodont marsupials by the following combination of features: snout elongation such that the nasals posteriorly terminate anterior to or at the position of the orbital crest, presence of palatal fenestrae, laterally broadened 'U'-shaped ectotympanic, squamosal-frontal contact, lack of a mastoid epitympanic sinus, little to no development of a petrosal tympanic wing, posteriorly projecting paroccipital process, presence of the transverse canal foramen, reduction of the paracone, reduction of the stylar shelf, elongation of the postmetacrista, widening of angle of crests at the paracone, metacone and centrocrista, orientation of tooth crests more anteroposteriorly, reduction to loss of the metaconid height along the entire tooth row, dominance of the postprotocristid-cristid obliqua as the principal posterior shearing crest, and reduction of the hypoconulid. Among these features, squamosal-frontal contact is only tentatively forwarded as diagnostically useful for the family, as this region is only known for *T. cynocephalus.*

Thylacinids differ from borhyaenids in the lack of nasal-lacrimal contact (again verifiable for *T. cynocephalus* only, among thylacines), presence of the transverse foramen, and reduction of the paracone on all molars to a consistent degree, m4 shorter than m3 in all species other than *T. cynocephalus and T. potens,* and postprotocristid (sensu Muirhead and Gillespie, 1995) hypertrophy.

Thylacinids differ from dasyurids in showing lateral broadening of the ectotympanic, uniform reduction of the metaconid along the entire tooth row, elongation of the snout and retention of three premolars, in combination with other features of the dentition associated with carnassialization.

Diversity and Ecology of the Thylacinidae

The presence of thylacinids in Tertiary Riversleigh deposits, aged between the late Oligocene to early late Miocene (Archer et al., 1994), implies a minimum age for the lineage of 25 million years. The considerable thylacinid diversity in Tertiary Riversleigh deposits, including highly specialized taxa (e.g., *T. macknessi, W. ridei),* indicates that the origins of the clade may extend well into the Oligocene (Muirhead and Archer, 1990; Muirhead, 1992, 1997). Almost certainly the antiquity of the thylacinid clade exceeds that inferred from molecular data (Lowenstein et al., 1981; Sarich et al., 1982; Thomas et al., 1989; Krajewski et al., 1992), which range from around seven to twenty million years.

The family has suffered a dramatic decline in diversity since the middle Miocene. In Pliocene and subsequent times, there was only one species of thylacine known at any time *(T. potens*

during the Pliocene and *T. cynocephalus* in Pleistocene to Recent times). This decline in thylacinid diversity may have been related to late Miocene climate change (Martin and McMinn, 1994) that appears to have affected much of the biota of the continent.

Contemporaneous with thylacinids in the late Oligocene to middle Miocene Riversleigh deposits are a number of small to medium-sized 'dasyurid' taxa (Wroe, 1995). However, none of these represent large, specialized carnivores in the size range occupied by thylacinids or extant carnivorous dasyurids. Large carnivorous dasyurids do not appear in the record until the Pliocene, after the decline in diversity of thylacinids. Wroe (1997b) speculates that derived features of the middle ear in dasyurids may have given the clade an adaptive edge over thylacinids.

Smaller, less derived thylacinids, such as *B. turnbulli,* were similar in size and general cranial morphology to large extant dasyurids and probably filled similar carnivorous to insectivorous niches. As many of the Riversleigh local faunas include taxa adapted to 'rainforest' environments (Archer et al., 1994), this parallel may have extended to include the arboreal habits of some extant *Dasyurus* species (e.g., *D. maculatus).* Posteranial elements of *B. turnbulli* are required to test this possibility.

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