



# A SPECIALISED THYLACINID, *THYLACINUS MACKNESSI*, (MARSUPIALIA: THYLACINIDAE) FROM MIOCENE DEPOSITS OF RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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*Thylacinus macknessi* is described from Miocene sediments of Riversleigh, northwestern Queensland. Comparisons with other thylacinids and dasyurids reveal it to be a new species of *Thylacinus*. In most features it is as specialised as *T. cynocephalus* and it is not considered to be ancestral to any other taxon. The presence of such a specialised thylacine in the Riversleigh deposits argues for a pre-Late Oligocene divergence of this group from the Dasyuridae.

Key words: Thylacine, *Thylacinus macknessi*, Thylacinidae, Riversleigh, Tertiary, Queensland, Marsupialia.

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THE Thylacinidae is a small family consisting of a recently extinct form *Thylacinus cynocephalus* Harris, and two Tertiary taxa. Although thylacinid premolars have been recovered from the Miocene Wipajiri Formation of South Australia and the late Pliocene Otibanda Formation of New Guinea (Campbell 1976, Plane 1976, Archer 1982), only two distinct thylacinids have been described from the fossil record: the late Miocene *Thylacinus potens* from the Alcoota Local Fauna (Woodburne 1967) and the late Oligocene to middle Miocene *Nimbacinus dicksoni* from the Henk's Hollow Local Fauna, the Riversleigh Local Fauna and the Bullock Creek Local Fauna (Muirhead and Archer 1990). *Thylacinus potens* is larger than *T. cynocephalus* and slightly less specialised. It was considered by Archer (1982) to represent a sister taxon to the modern form. *Nimbacinus dicksoni* is a small and very plesiomorphic thylacinid, evidently not far removed from the group's dasyuroid origins and a possible ancestor to *Thylacinus*. Material described here as *Thylacinus macknessi* is of comparable age to the plesiomorphic *Nimbacinus dicksoni* but, in contrast, represents a specialised thylacine whose closest relative appears to be the modern *Thylacinus cynocephalus*.

Dental and taxonomic nomenclature follows that of Muirhead and Archer (1990). Dental terminology is also presented in Fig. 1. Catalogue number

abbreviations used are: QMF, Queensland Museum palaeontological collection; AR, temporary catalogue number in School of Biological Science, University of New South Wales. Measurements of tooth dimensions of *T. macknessi* are presented in Table 1. The regions measured are presented in Fig. 1.

## SYSTEMATICS

Thylacinidae Bonaparte, 1838  
*Thylacinus* Temminck, 1827  
*Thylacinus macknessi* n. sp.

### HOLOTYPE

QMF16848a (formerly AR16491), right dentary portion with broken M<sub>3</sub>, complete M<sub>4</sub> and M<sub>5</sub>.

### REFERRED SPECIMENS

QMF16848b (formerly part of AR16491), right canine closely associated but not attached to holotype, QMF16849 formerly (AR11046) isolated left M<sub>4</sub>, and QMF16850 formerly (AR4794), isolated right M<sub>2</sub>.

### TYPE LOCALITY, LOCAL FAUNA AND AGE

QMF16848 Neville's Garden Local Fauna, Neville's Garden Site, Riversleigh Station, northwestern Queensland; early to middle Miocene. QMF16849,

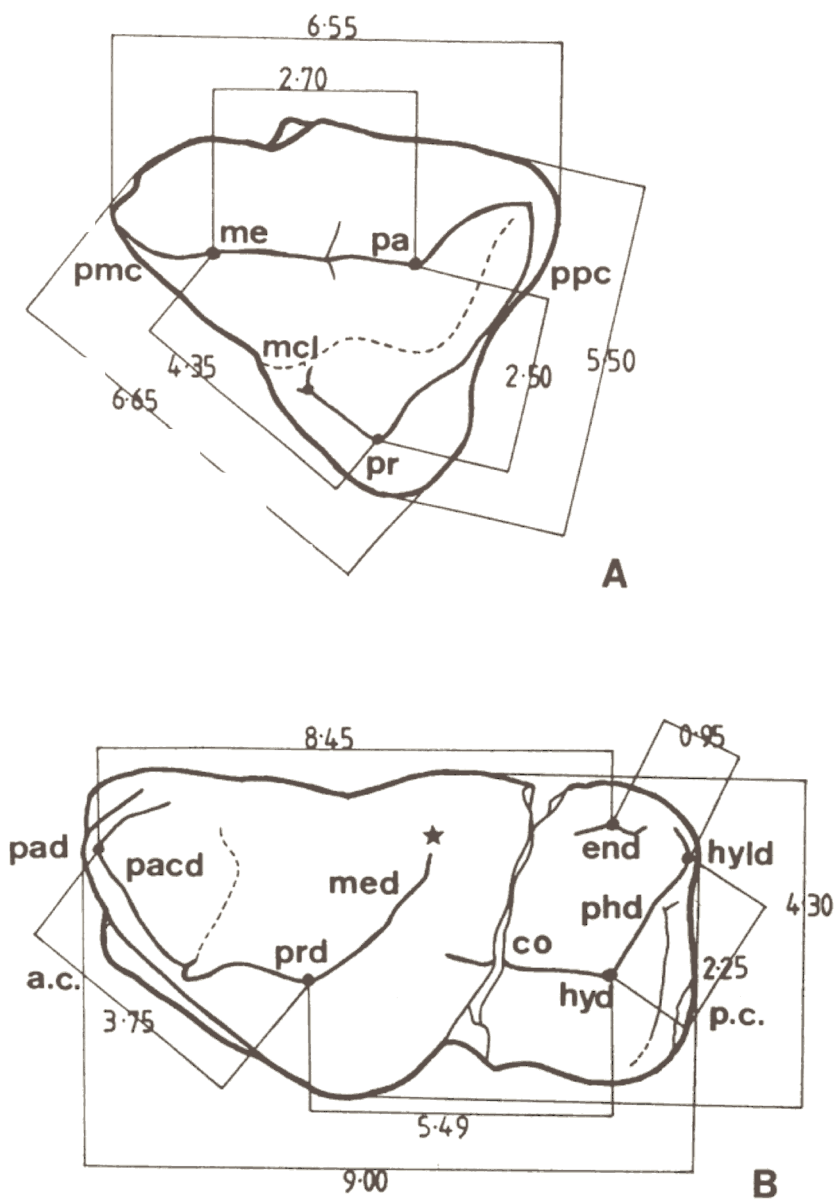


Fig. 1. Diagram showing terminology of morphology on an upper and lower molar of *T. macknessi*. Regions used for measurements in Table 1 are also presented using the measurement for two teeth as examples taken from Table 1. A = QMF16850. B = QMF16849. Arrow indicates anterior of molar. Star indicates region of lost metaconid. Abbreviations: a.c., anterior cingulum; co, cristid obliqua; end, entoconid; hyd, hypoconid; hyld, hypoconulid; mc, metaconid; mcl, metaconule; med, metacristid; pa, paracone; pacd, paracristid; pad, paraconid; p.c., posterior cingulum; phd, posthypoconid; pmc, postmetacrista; ppc, preparacrista; prd, protoconid.

LOWER MOLARS	M <sub>3</sub>		M <sub>4</sub>	M <sub>5</sub>
QMF number	16848	16848	16849	16848
Tooth length		9.10	9.00	8.75
Tooth width	4.38	4.92	4.30	4.66
Proto-hypo		5.08	5.49	6.02
Hypo-hypoconulid	2.09	2.27	2.25	1.01
Hypoconulid-ento	1.10	0.85	0.95	
Proto-para		3.72	3.75	4.17
Proto-para (horizontally)		4.87	5.25	5.04
UPPER MOLARS	M <sup>2</sup>			
QMF number	16850			
Anterior	5.50			
Tooth length	6.55			
Posterolingual dimension	6.65			
Para-meta	2.70			
Meta-proto	4.35			
Proto-para	2.50			

Table 1. Tooth measurements of *Thylacinus macknessi* in mm. All measurements are actual distance between cusps except 'Proto-para (horizontally)' in which measurements are taken from a horizontal plane above these cusps.

Mike's Menagerie Local Fauna, Mike's Menagerie Site, Godthelp Hill, Riversleigh Station, northwestern Queensland. QMF16850 Dwornamor Local Fauna, Gag Site, Gag Plateau, Riversleigh Station, northwestern Queensland. Neville's Garden Site and Mike's Menagerie Site are part of System B of the Riversleigh Sequence and are estimated to be approximately Early to Middle Miocene in age (Archer, Godthelp, Hand and Megirian, 1989). Gag Site is part of System C estimated at Middle to early? Late Miocene (Archer et al 1989). Precise locality details have been lodged with the Queensland Museum.

#### SPECIFIC NAME

Named in honour of Brian Mackness in recognition of his support for, and long term involvement in Australian vertebrate palaeontology.

#### DIAGNOSIS

Differs from all other species of *Thylacinus* in the following combination of features: 1, distinct entocoid; 2, vestigial metaconid; 3, long cristid obliqua orientated centrally on the crown and parallel to the long axis of the dentary; 4, no styler shelf; 5, well-developed and unnotched anterior cingulum that is continuous with the preparamacrista; 6, centrocrista (postparamacrista plus premetacrista) straight; 7, small metaconule but no paraconule; 8, relatively unreduced paracone; and 9, M<sub>5</sub> antero-posteriorly shorter in length than preceding molar.

#### DESCRIPTION

The dentary is preserved posteriorly from the region of the M<sub>3</sub>. The coronoid process departs from the ramus at approximately 120°. The anterior margin of the coronoid process is very straight. The articular condyle and angular process are absent. The articular condylar appears to have departed from the remaining bone at a level no higher than the ramus. The inferior dental foramen is low lying and directly below the highest dorsal point of the coronoid process.

Lower canine represented by QMF16848b (Fig. 2). Crown broken at tip. Root laterally compressed and striated. Crown thick at base. Thegosed facet on anterior surface (*sensu* Every 1975). M<sub>3</sub> represented by QMF16848a (Fig. 2). Crown broken anteriorly at protoconid. Hypoconid tallest cusp on talonid followed in decreasing height by entoconid and hypoconulid. Well developed posterior cingulum extends from hypoconulid to posterobuccal corner of crown. Cristid obliqua orientated almost perpendicular to antero-posterior dimension of tooth. Both entoconid and hypoconulid high and distinct. M<sub>4</sub> is represented by QMF 16849a (Figs 3A, 3B) and QMF16848 (Figs 1B, 2). Protoconid largest cusp followed in decreasing height by paraconid, hypoconid, entoconid and hypoconulid. Vestigial metaconid represented by slight thickening of enamel in position usually occupied by metaconid on dasyurids and in the plesiomorphic *Nimbacinus*. Anterior cingulum continues to anterobuccal base of protoconid. In

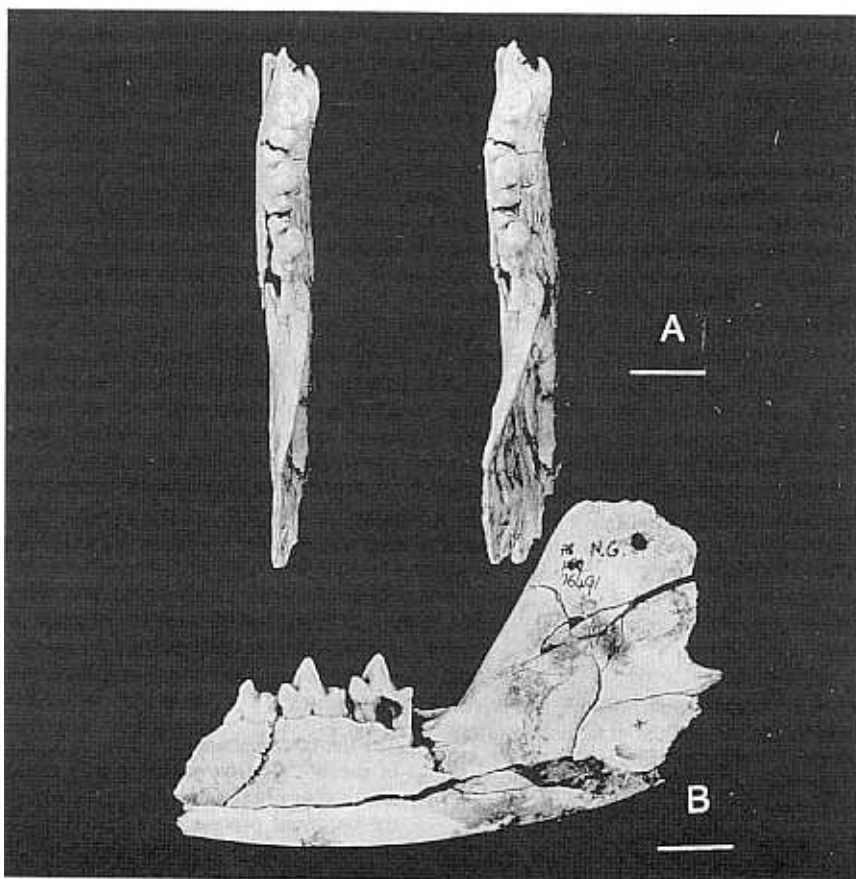


Fig. 2. *Thylacinus macknessi* holotype QMF16848a. Bar = 1 cm. A, occlusal view stereo pair, anterior at top. B, lingual view, anterior to left.

occlusal view the protocristid is the longest crest. It is 'V'-shaped and almost vertical in the valley between the paraconid and protoconid. Cristid obliqua slightly shorter, terminating on flank of protoconid. Remaining crests (in decreasing length): metacristid, posthypocristid, pre-entocristid. Metacristid terminates at vestigial metaconid.  $M_5$  represented by QMF16848a (Fig. 2). Morphology follows that of  $M_4$  except as follows. Talonid reduced in size by lingual shift in hypoconid and reduction of height, loss of entoconid and reduction in posterior cingulum.

$M^2$  represented by QMF16850 (Figs 1A, 3C, 3D). Anterior width of crown less than buccal length which is less than posterior width. Major cusps present (in decreasing height): metacone, paracone, protocone. Minuscule metaconule present. No cusps or crests present on stylar shelf which is represented by steep regular slope to buccal flank of crown. Posterobuccal region of crown missing (may or may not have

retained St E). Although postmetacrista broken, posteriorly it appears to have been the longest crest on crown, followed (in decreasing order) by preparacrista, postprotocrista, preprotocrista, premetacrista, postparacrista. Preprotocrista connects with anterior cingulum and extends continually up anterior face of crown. Angle formed at junction of crests at protocone approximately  $90^\circ$ . Postparacrista and premetacrista connect in straight line as centrocrista and forms sharp valley between cusps. Postmetacrista departs from metacone almost parallel to premetacrista and then bends. Preparacrista forms sharper angle with postparacrista.

#### COMPARISON

*Thylacinus macknessi* is a very specialised thylacinid sharing many derived features with *T. cynocephalus*. It is in some respects more plesiomorphic than *T. cynocephalus* and, in most features, far more special-

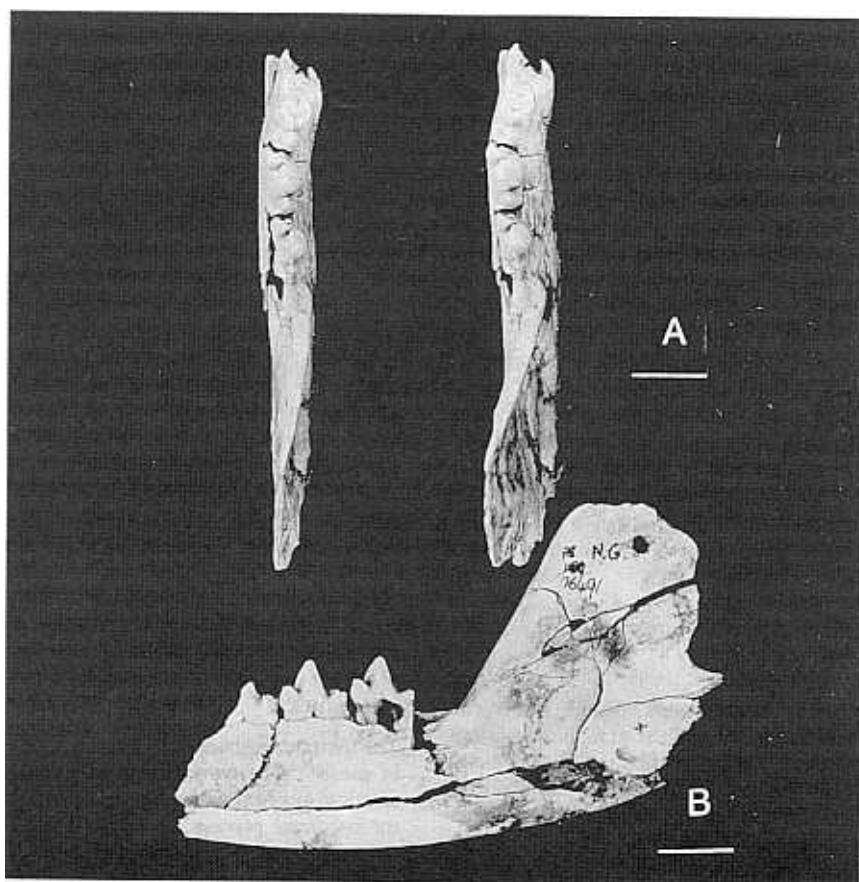


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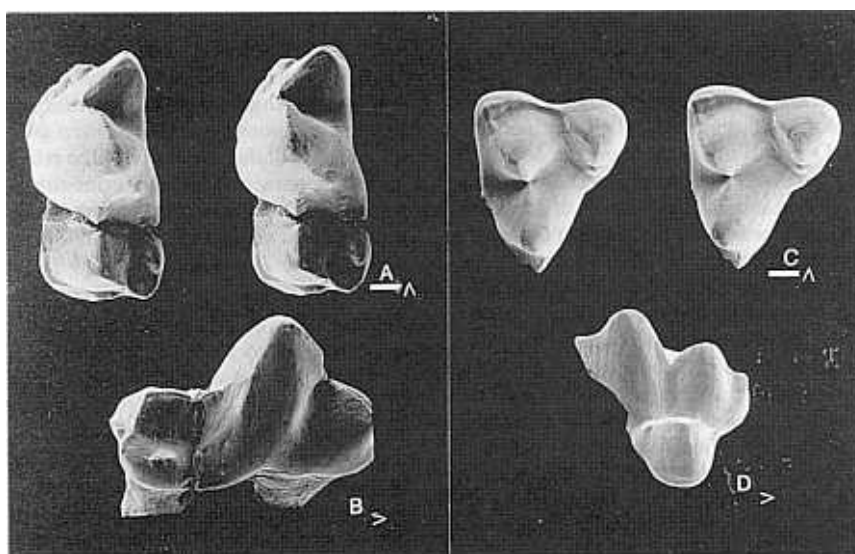


Fig. 3. *Thylacinus macknessi* paratypes QMF16849 and QMF16850. Arrows point anteriorly. Bar = 1 mm. A, QMF16849 occlusal view stereo pair. B, QMF16849 lingual view showing lack of metaconid. C, QMF16850 occlusal view stereo pair. D, QMF16850 lingual view.

ised than *N. dicksoni*. Comparison to *T. potens* is restricted because of the poor preservation of known teeth in *T. potens*. The features that set *T. macknessi* apart from other species of *Thylacinus* are discussed below.

**Metaconid:** *Thylacinus macknessi* has a slight thickening of the enamel on the posterolingual flank of the protoconid at the position where the metacristid terminates. This appears to represent a remnant metaconid (Fig. 3B). A distinct metacristid continues from this region to the tip of the protoconid. Marked reduction and posterior shift in position of the metaconid is a synapomorphic feature of the Thylacinidae while the retention of the metaconid and metacristid is the plesiomorphic condition. *Nimbarcinus dicksoni* displays the extreme plesiomorphic condition for thylacinids with a distinct metaconid on  $M_2$  while *T. cynocephalus* has lost all traces of the metaconid and metacristid.

**Entoconid:** The entoconids on the molars of *T. cynocephalus* occur only on  $M_3$  and  $M_4$  and increase in size posteriorly. They are the smallest cusps on the crowns and lack any linking crests. No entoconid is present on the  $M_2$  of *N. dicksoni* and the talonid region of this species is not preserved for any other molar. The entoconid is typically smaller on the  $M_2$  compared to all other molars in dasyroids and therefore the size of this cusp on a tooth comparable with other species is not known. The entoconid on the

$M_4$  of *T. macknessi* is taller than the hypoconulid. It also has a well defined pre-entocristid which defines the lingual side of the talonid basin. In this respect *T. macknessi* is more plesiomorphic than *T. cynocephalus*.

**Length of  $M_5$ :** *Thylacinus macknessi* differs from both *T. cynocephalus* and *T. potens* in the lack of elongation of the  $M_5$ . On *T. cynocephalus* and *T. potens*, the length of the lower molars increase posteriorly such that each molar is antero-posteriorly longer than the preceding tooth. This may be related to facial elongation, a feature that is characteristic of these species (D. Ride pers. comm.) and as such is a apomorphic specialisation away from the shorter faced and reduced  $M_5$ s of dasyurids. *Thylacinus macknessi* is therefore more plesiomorphic than these two species of *Thylacinus* in retaining the short  $M_5$ . Unfortunately, the premolar region of this species is unknown and the anterior elongation of the snout also typical to species of *Thylacinus* remains unknown for this species.

**Stylar shelf:** Reduction of the stylar shelf is a typical thylacinid feature. Stylar shelf reduction occurs in derived thylacinids and dasyurids (for example, *T. cynocephalus*, *T. potens*, *Sarcophilus harrisii*). However, this specialisation is achieved in different ways in thylacinid and dasyurid lineages. The stylar shelf region of  $M^4$  in specialised thylacinids is distinctly different from that on  $M^{2-3}$ . *Thylacinus macknessi* is

represented only by an M<sup>2</sup> which limits comparisons and *T. potens* cannot be compared to *T. macknessi* because of the poor preservation of this tooth. *Thylacinus macknessi* compares closely with the M<sup>2</sup> of *T. cynocephalus* in lacking stylar shelf development. Stylar cusps D and B are present on the M<sup>2</sup> of *T. cynocephalus* but no crests are developed. Stylar cusp B is present on *T. macknessi* but because of damage it is not known if St D was present. One clear difference between these two species is that *T. cynocephalus* has a distinct bulge of enamel in the area of the stylar shelf while in *T. macknessi* the surface is a steep constant slope from the tips of the paracone and metacone to the buccal edge of the tooth. Reduction of the stylar shelf is an apomorphic feature that contrasts with the plesiomorphic state in most dasyurids where stylar cusps and crests are often prominent and well developed. Thus it appears that *T. macknessi* is slightly more specialised in this feature than *T. cynocephalus*.

The stylar shelf region of the M<sup>2</sup> of *S. harrisii* is unlike that of species of *Thylacinus*. In *S. harrisii* St B and D are always prominent and connected to the paracone and metacone (respectively) by short transverse crests. A crest is also present connecting St D to the posterobuccal corner of the crown. These stylar cusps have moved lingually and are very close to the paracone and metacone. This shift in position has the same function as loss of these cusps in that incorporation of these cusps into the major cones produces a single large cutting blade with an unobstructed buccal face. This carnivorous blade has therefore been achieved in two different ways — by loss of stylar cusps in thylacinids and by the lingual shift in stylar cusps in dasyurids. It is possible that a further lingual shift of stylar cusps to a point of entirely combining with the paracones and metacones could produce a condition similar to that seen in *T. macknessi*. It is therefore possible that *T. macknessi* is a product of this *Sarcophilus*-type specialisation rather than that of the thylacinid-type.

**Postparacrista and Premetacrista:** Many marsupial carnivores (for example, species of *Sarcophilus*, *Thylacinus*, *Borhyaena*) have the paracone and metacone close together with the paracone lying directly anterior to the metacone. As a result, the crests linking these cusps (the postparacrista and premetacrista) are shortened and connect at a more lingual point, producing a linear centrocrista. *Thylacinus cynocephalus* has these crests connecting almost in a straight line, a condition very similar to that in *T. macknessi*. The difference between these two thylacinids is that in *T. cynocephalus*, these crests connect well above the crown basin, thereby forming a lingual wall. In *T. macknessi* the connection is low

and no wall is formed. *Nimbacinus dicksoni* and *S. harrisii* do not have straight centrocristae. A sharper angle is formed, and in both the centrocristae are high and form a lingual wall. *Sarcophilus harrisii* differs from *N. dicksoni* by having a sharp groove running up the flank of the centrocrista. The relative positioning of the paracone and metacone together with the short, straight centrocrista is an apomorphic specialisation culminating in the condition in *T. cynocephalus* and *T. macknessi*.

**Elongation of postmetacrista:** *Thylacinus macknessi* appears to have the thylacinid feature of an elongated postmetacrista to a degree similar to that of *T. cynocephalus*. Absolute length of this crest, however, can only be approximated because of damage to the posterobuccal corner of the crown. Elongation of the postmetacrista is an apomorphic carnivorous specialisation resulting in a relatively longer primary cutting blade. This elongation occurs to a similar degree in species of *Sarcophilus*.

**Metaconule and protoconule:** The presence of a metaconule and protoconule is considered to be the plesiomorphic condition among dasyurids (Archer 1976). Neither is present in *T. cynocephalus* while the condition of these cusps is unknown for the M<sup>2</sup> and M<sup>3</sup> of *T. potens*. *Thylacinus macknessi* has a vestigial metaconule but no trace of a protoconule. *Thylacinus macknessi* would therefore be more plesiomorphic than *T. cynocephalus* in this character. *Nimbacinus dicksoni* is more plesiomorphic in having a well-developed metaconule and protoconule on all upper molars.

**Reduction of the paracone:** Reduction of the paracone is an apomorphic feature displayed in the greatest degree in *T. cynocephalus*, *T. potens* and *S. harrisii*. *Nimbacinus dicksoni* shows no such reduction. The condition of the paracone in *T. macknessi* is similarly unreduced and thus plesiomorphic among thylacinids.

**Upper anterior cingulum:** A notched anterior cingulum is a feature common to all dasyurids. *Nimbacinus dicksoni* has a notched anterior cingulum on all upper molars. In these the cingulum does not continue lingually past the paracone. *Thylacinus cynocephalus* has no anterior cingulum on any upper molars. *Thylacinus potens* has a small notched anterior cingulum on M<sup>4</sup>. *Thylacinus macknessi* has a prominent but unnotched anterior cingulum which is unusual because it continues lingually past the paracone to connect with the preprotocrista. It is considered here that the conditions in *T. cynocephalus* and *T. macknessi* are autapomorphic for each.

## DISCUSSION

The family Thylacinidae has very low diversity with two genera, *Thylacinus* (containing *T. cynocephalus*, *T. potens* and *T. macknessi*) and *Nimbacinus dicksoni*. These two genera represent morphological extremes within the family, the species of *Thylacinus* being highly specialised while *N. dicksoni* exhibits many plesiomorphic features that provide a structural link to plesiomorphic dasyurids. *Nimbacinus dicksoni* was considered to be a possible ancestor to species of *Thylacinus* (Muirhead and Archer 1990).

*Thylacinus macknessi* is currently known from early to middle Miocene sediments. Although sharing apomorphic features with some dasyurids, these are considered here to be convergent carnivorous specialisations. Among dasyurids, *T. macknessi* is most similar to the Late Pleistocene–Recent *Sarcophilus harrisii*, however, in some characters it shows a degree of specialisation unattained by any dasyurid, including the very specialised *S. harrisii*. It is unlikely to be related to species of *Sarcophilus* because it does not show specialisations typical to this dasyurid lineage (for example, reduction in size of the talonid basin with loss of the hypoconulid, substitution of entoconid by metaconid on posterior molars) while showing apomorphies unknown to *Sarcophilus*. *Thylacinus macknessi* is further unlikely to represent a dasyurid of the *Sarcophilus* grade, because it shows a much greater degree of specialisation in some characters while occurring prior to first known occurrence of the *Glaucodon*–*Sarcophilus* lineage (Stirton 1957, Ride 1964) which makes its earliest known appearance in the Late Pliocene–Early Pleistocene (Gill 1957, Bartholomai and Marshall 1973). If considered a dasyurid, this species must represent an otherwise unknown lineage with a combination of plesiomorphies (for example, relatively large talonid basin, large hypoconulid) and apomorphies (for example, lost metaconid, lost stylar shelf) unknown to any other species but convergent on both *Sarcophilus* and *Thylacinus*. Although extreme convergence to thylacinids has been demonstrated in other forms such as borhyaenids, *T. macknessi* shows a combination of characters mostly considered to be morphologically intermediate on a lineage between the plesiomorphic *N. dicksoni* and the apomorphic *T. cynocephalus*. Thus phylogenetic placement within the Thylacinidae is the most parsimonious placement, evoking fewer character conflicts than if this taxon is considered to be a dasyurid.

*Thylacinus macknessi* falls outside of the currently known species of *Thylacinus* in the lack of elongation of the M<sub>5</sub>, unreduced paracone, lesser reduction of the

entoconid and the presence of remnant conules. Some of these characters, however, cannot be compared to *T. potens* and therefore the typical condition for the genus in these characters is unknown. *Thylacinus macknessi* is referred to the genus *Thylacinus* because it shares many apomorphic states unique only to other species of this genus. In these features *T. macknessi* is clearly more similar to *T. cynocephalus* and *T. potens* than it is to *N. dicksoni*. Due to these synapomorphies with species of *Thylacinus*, *T. macknessi* is conservatively placed within this genus. The presence of these 'Thylacinus' apomorphies in combination with the plesiomorphic retention of some features is, at present, inadequate justification for erection of a new monotypic genus.

Despite the consequent expansion of the concept of *Thylacinus*, morphological variation within this genus is no greater than it is within many dasyurid genera, such as *Dasyurus* or *Antechinus*. *Thylacinus macknessi* is less apomorphic in a number of respects than *T. cynocephalus* and is therefore positioned as the sister taxon of a combined *T. cynocephalus*/*T. potens* clade. It cannot itself be considered ancestral to *T. cynocephalus* because of the derived character states of its anterior cingulum, cristid obliqua orientation and specialised stylar shelf.

Archer et al (1989) have summarised current understanding about the biostratigraphic relationships of Riversleigh's local faunas. Neville's Garden Local Fauna and Mike's Menagerie Local Fauna (the type and one paratype locality of *T. macknessi*) is part of System B and thus interpreted to be early to middle Miocene in age. The Gag Local Fauna (other paratype locality of *T. macknessi*) and Henk's Hollow Local Fauna (type locality of *N. dicksoni*) are System C local faunas currently interpreted to be middle to early Late Miocene in age. Presuming the stratigraphic relationships to be correctly interpreted, *T. macknessi* may span early to middle Miocene time while the time range for *N. dicksoni* remains unclear. Although a single tooth from the Site D Local Fauna (a System A local fauna interpreted to be late Oligocene to early Miocene in age) was statistically unable to be distinguished from *N. dicksoni* from the Henk's Hollow Local Fauna (Muirhead and Archer 1990), it was in fact smaller in size and only doubtfully referred to *N. dicksoni*. Nevertheless, such a time range for a Tertiary thylacinid probably would not be extraordinary considering that *T. cynocephalus* appears to span at least early Pliocene to Holocene time (Archer 1982, Dawson 1982), an interval of 5 million years.

The presence of a variety of thylacinids in late Oligocene to middle Miocene sediments (Archer 1982, Muirhead and Archer 1990) rejects the



molecular clock date of 7 million years given by Sarich, Lowenstein and Richardson (1982) and of 6–10 million years estimated by Lowenstein, Sarich and Richardson (1981) for the divergence of thylacines from dasyurids. It now also seems probable that this dichotomy occurred well prior to 10–20 million years ago date suggested by Thomas, Schaffner, Wilson and Paabo (1989). An early separation date is supported here by the demonstration that highly derived thylacinids (*T. macknessi*) were present in middle Miocene sediments as contemporaries of very plesiomorphic taxa (*N. dicksoni*). Clearly a common ancestral stock for both must significantly predate the presently oldest known occurrence of either.

Presuming that the *Nimbacinus* lineage (not specifically *N. dicksoni*) was ancestral to that of *Thylacinus*, its occurrence with the specialised *T. macknessi* represents persistence of this archaic lineage beyond the time of the *Nimbacinus/Thylacinus* dichotomy.

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