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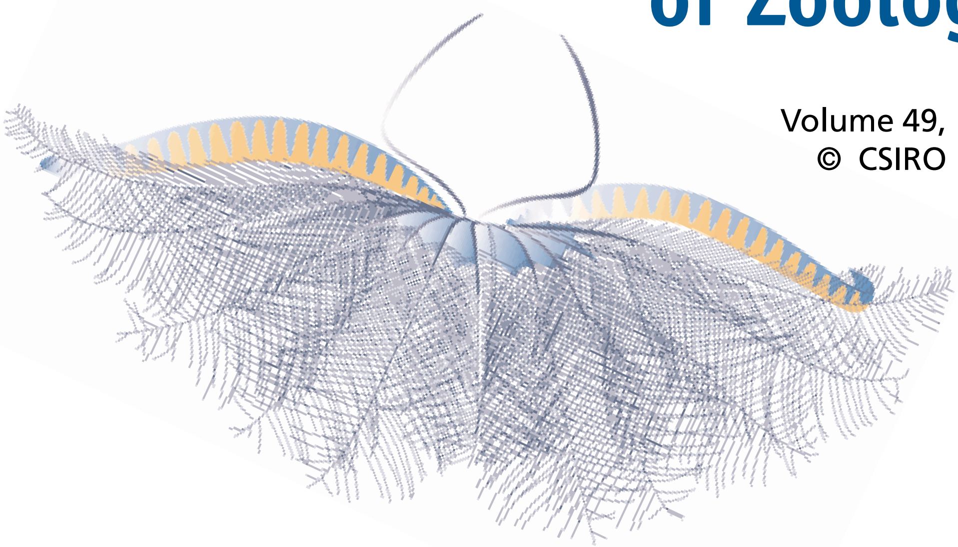

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Maximucinus muirheadae, gen. et sp. nov. (Thylacinidae : Marsupialia), from the Miocene of Riversleigh, north-western Queensland, with estimates of body weights for fossil thylacinids

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Abstract

An eighth genus and twelfth species of Tertiary thylacinid is described. This new taxon represents the seventh member of the family from the fossiliferous Carl Creek limestones of Riversleigh, north-western Queensland. Although plesiomorphic within Thylacinidae regarding most features and lacking synapomorphies that unambiguously unite it with specialised taxa within the family, it possesses two autapomorphies. With an estimated body weight of around 18 kg it is also larger than any previously known thylacinid predating the late Miocene. Body-weight estimates for remaining fossil Thylacinidae span a wide range from just over 1 kg to almost 60 kg. While the smallest species is comparable to the extant *Dasyurus viverrinus* in size, most (i.e. 9 of 12 taxa) are at least twice the average size of the living *Dasyurus maculatus*. These results suggest that trophic diversity among thylacinids is even greater than previously thought and detract from the argument that reptiles have dominated large terrestrial carnivore niches in Australia since at least early Miocene times.

Introduction

For most of the decade following the synonomy of then known Pliocene and Pleistocene thylacinids with the recently extinct *Thylacinus cynocephalus* (Dawson 1982), the family Thylacinidae was represented by only one fossil taxon, the late Miocene *Thylacinus potens*. However, between 1990 and 2000, 10 fossil species were described (Muirhead and Archer 1990; Muirhead 1992, 1997; Wroe 1996; Murray 1997; Muirhead and Wroe 1998; Murray and Megirian 2000). While most of these were based largely on dentitia, two were represented by complete or near-complete cranial material (Muirhead and Wroe 1998; Wroe and Musser 2001). Recent works addressing the phylogeny of fossil thylacinids include Muirhead and Wroe (1998), Murray and Megirian (2000), Wroe *et al.* (2000) and Wroe and Musser (2001). A new genus and species of Miocene fossil thylacinid is described below, further expanding on known taxonomic breadth for the family.

Discoveries over the last decade have not only demonstrated unexpected species richness, but also hint at a considerable breadth of trophic diversity for the family. Body weight is one of the most important influences on a species' biology and ecology (Egi 2001). As a step toward achieving a fuller understanding of fossil thylacinid lifestyles, body weights for all fossil species referred to Thylacinidae are estimated.

Methods

Dental nomenclature follows Flower (1867) and Luckett (1993) regarding the molar–premolar boundary, such that the adult (unreduced) postcanine cheektooth formula of marsupials is P1–3 and M1–4. Dental

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terminology is after Wroe (1999*a*). Systematic terminology follows that used by Wroe *et al.* (2000), adapted from Marshall *et al.* (1990) and Krajewski *et al.* (1994). Institutional abbreviations are: AM (Australian Museum), CPC (Commonwealth Palaeontological Collection), NTM (Northern Territory Museum) and QM (Queensland Museum).

Character analysis, adapted from Muirhead and Wroe (1998), was performed and the results are given in Table 1.

The maximum length and width of M^2 in *Maximucinus muirheadae* (gen. et sp. nov.) were measured and plotted relative to those of the same tooth in samples of *Thylacinus cynocephalus*, *Nimbacinus dicksoni* and *Dasyurus maculatus* (Table 2, Fig. 1). The same dimensions for all thylacinids represented by at least one M^2 were measured and are given in Table 3, including averages where applicable. The lower molar row length for samples of three species of *Dasyurus* and *Thylacinus cynocephalus* are provided in Table 4.

Body-weight estimates for 10 of the 12 fossil thylacinids now known were calculated using equations derived by Myers (2001), which were based on analyses that included 29 cranio-dental variables ranked on the basis of accuracy. Myers (2001) determined lower molar row length (LMRL) to be the most reliable indicator of body weight in dasyuromorphians. Where possible, LMRL has been used in the present study, but for three taxa that were not represented by at least one complete lower molar row the next highest ranked variable for which data were available has been substituted. Results are given in Table 5. Predictions include adjustments for logarithmic transformation bias (smearing estimate). Measurements of dental variables for *Thylacinus potens* and *Thylacinus megiriani* exceed any included in the data set of Myers (2001), consequently estimates using this methodology were not attempted. For these two large, late Miocene species, body size was estimated assuming geometric similtude with *Thylacinus cynocephalus*. Neither of these fossil species are represented by complete upper or lower molar rows, and in both the relative dimensions of the molars to each other clearly differ from those of *T. cynocephalus* (Woodburne 1967; Megirian 1997). Estimates were thus based on the combined lengths of M^{1-3}, as given by Woodburne (1967) and Murray (1997), against the average of the same dimension from a sample of *Thylacinus cynocephalus* (see Woodburne 1967). Results are given in Table 6. Tooth dimensions for *Nimbacinus richi*, *Mutpuracinus archibaldi*, *Tyrrapecinus rothi*, *T. megiriani* and *T. potens* are as given by Woodburne (1967), Murray (1997) and Murray and Megirian (2000). Samples of extant and recent taxa constitute all available specimens, male and female, available in the Australian Museum's collections.

Systematics

Dasyuromorphia Gill, 1872

Thylacinidae Bonaparte, 1838

***Maximucinus*, gen. nov.**

(Figs 1–3; Tables 1, 2, 4 and 6)

Type and only species. *Maximucinus muirheadae*, sp. nov.

Generic diagnosis

Large, generalised thylacinid. Well developed, laterally compressed stylar cusps B and D on M^2 distinguished by an unbroken crest running from stylar cusp B to the metastylar corner of the tooth. The anterior cingulum is continuous with the preparacrista. Protoconule and metaconule are minute.

Generic etymology

From the Latin *maximus*, meaning large, and the Greek, *kynos*, meaning dog.

***Maximucinus muirheadae*, sp. nov.**

Holotype. QM F30331, a right M^2.

Type locality and age

Ringtail Site, Riversleigh World Heritage Estate, north-western Queensland. This deposit is thought to be middle Miocene in age (Creaser 1997).

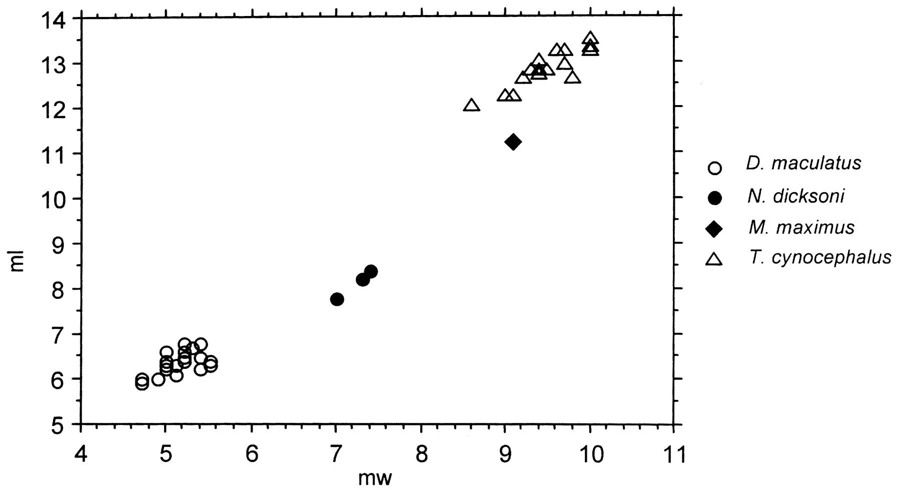

Fig. 1. Bivariate plot of maximum width (mw) against maximum length of M^2 (ml) for *Maximucinus muirheadae* and averages for samples of *Nimbacinus dicksoni*, *Thylacinus cynocephalus* and *Dasyurus maculatus* (see Table 2).

Species diagnosis

As for the genus.

Description of holotype

QMF30331 is unworn, tri-rooted and preserves all aspects of the tooth's morphology excepting the tip of the anterior-most lateral root. The protocone and metastylar corner had

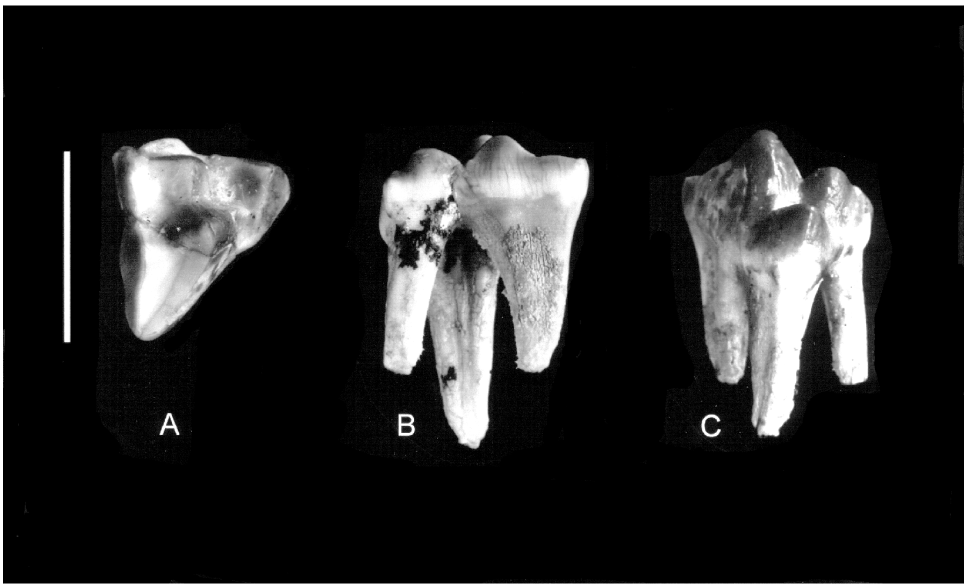

Fig. 2. QM F30331, holotype of *Maximucinus muirheadae*, gen. et sp. nov. *A*, occlusal view. *B*, lateral view. *C*, lingual view.

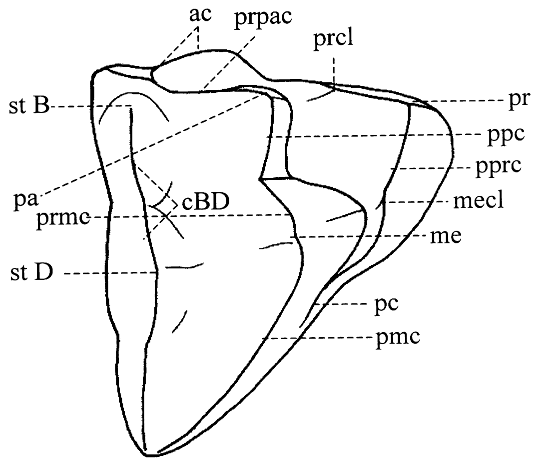

Fig. 3. Stylised line drawing of QM F30331, holotype of *Maximucinus muirheadae*, gen. et sp. nov., occlusal view. ac = anterior cingulum, cBD = crista connecting st B and st D, me = metacone, mecl = metaconule, pa = paracone, pc = posterior cingulum, pmc = postmetacrista, ppc = postparacrista, pprc = postprotocrista, p*r* = protocone, prcl = protoconule, prmc = premetacrista, prpac = preparacrista, st B = stylar cusp B, st D = stylar cusp D.

broken away, but have been reattached. Each of the three roots is compressed on the lateral axis. The tip of the mesial root, dorsal to the protocone, is the longest, despite damage to its tip, while the two slightly shorter lateral roots are subequal in length. In occlusal view the tooth's crown is roughly triangular in outline, with a 90° angle formed by the anterior and lateral edges. It is longest mesially, followed in descending order by the lateral and anterior dimensions. The metacone is the tallest cusp. In order of decreasing height the remaining cusps are stylar cusp D, paracone, stylar cusp B and protocone. Minimal ectoflexus is apparent. No distinct stylar cusp C or E is present. The anterior cingulum is continuous with the preparacrista. A very weakly developed notch separates this cingulum from the parastyle. The postmetacrista is the dominant shearing crest of the trigon, followed in order of decreasing length by the premetacrista, preparacrista and postparacrista. No crest unites the paracone and stylar cusp B. Stylar cusps B and D are laterally compressed and an unbroken crest runs from stylar cusp B to the metastylar corner of the tooth. The protocone is a distinct cusp, but the protoconule and metaconule are minute. Dorsally, the protocone is narrow. A short, partial posterior cingulum connects with the postprotocrista.

Etymology

After Dr Jeanette Muirhead, in recognition of her considerable contributions to the study of thylacinid palaeontology.

Discussion

Maximucinus muirheadae possesses the following thylacinid synapomorphies, as identified by Muirhead and Archer (1990), Wroe (1996), Muirhead and Wroe (1998) and Wroe *et al.* (2000): reduction of the protocone and stylar shelf and elongation of the postmetacrista. Each of these features is also common to at least some carnivorous dasyurid taxa. But, *M. muirheadae* and known thylacinids share one derived feature identified by these authors that is not present in carnivorous dasyurids: reduction of stylar cusps B and D without close juxtaposition to the paracone and metacone.

With respect to overall proportions, the holotype of *Maximucinus muirheadae* (QM F30331) does not differ significantly from the M^2 of the only described specimens of

Table 1. Characters and character scoring

Adapted from Muirhead and Wroe (1998). 0 = plesiomorphic. Characters are as follows: 1, size of paracone: unreduced (0), slight reduction (1), significant reduction (2), extreme reduction (3). 2, stylar cusp B: well developed (0), slight reduction (1), significant reduction (2), distinct reduction (3), extreme reduction or loss (4). 3, anterior cingulum: complete (0), incomplete (1). 4, protoconules and metaconules: well developed (0), slightly reduction (1), significant reduction (2), loss of conules (3). 5, length of postmetacrista: not elongate (0), significant elongation (1), pronounced elongation (2). 6, angle of centrocrista: acute (0), obtuse (1), colinear (2). 7, direction of preparacrista: perpendicular (0), slightly oblique (1), parallel to long axis (2), directly anterior to paracone (3). 8, angles formed by paracristae and metacristae: narrow (0), significantly wider (1), wide (2). 9, Anterior cingulum continuous with preparacrista: not present (0); present (1). 10, Continuous crest uniting stylar cusp B and stylar cusp D: not present (0); present (1)

Taxon	Character 1 1234567890
Muribacinus gadiyuli	1100010100
Mutpuracinus archibaldi	1100010100
Badjcinus turnbulli	1201113100
Nimbacinus dicksoni	1100110100
Maximucinus muirheadae	1102110111
Ngamalacinus timmulvaneyi	1201110100
Wabulacinus ridei	1312222200
Tjarrpecinus rothi	2312221200
Thylacinus macknessi	1402221200
Thylacinus potens	2412221200
Thylacinus megiriani	3423221200
Thylacinus cynocephalus	3423221200

Nimbacinus dicksoni in which this tooth is preserved (QM F36357, QM F16804 and QM F16803). For this reason QM F30331 is considered to be an M^2. But, despite similarities, very distinct morphological differences are evident between QM F30331 and the M^2 or any other upper molar of *N. dicksoni* (Table 1). These include the presence in *M. muirheadae* of a continuous preparacrista–anterior cingulum, a continuous stylar crest uniting stylar cusp B, stylar cusp D and the metastylar corner of the tooth, as well as the near-complete loss of the protoconule and metaconule. The first two of these three features are autapomorphic for *M. muirheadae* and not present in any other thylacinid or dasyuromorphian known to me. Nor is similar morphology reported among any specimen considered by Archer (1975) in a review of unusual and abnormal dental development among marsupials. Regarding reduction of the protoconule and metaconule, *M. muirheadae* is comparable with, or more specialised than, *N. dicksoni*, *Mutpuracinus*, *Badjcinus*, *Ngamalacinus* and *Muribacinus*, but less derived than *Wabulacinus*, *Tjarrpecinus* and *Thylacinus*. Similarly, *M. muirheadae* is plesiomorphic relative to *Wabulacinus*, *Tjarrpecinus* and *Thylacinus* with respect to other features typically associated with carnassialisation. For example, its stylar cusps are less reduced, a less obtuse angle is formed between the paracristae and metacristae and the postmetacrista is not as elongate (Table 1).

Maximucinus muirheadae is clearly a much larger species than *N. dicksoni* (Fig. 1, Tables 2, 3). A second species of *Nimbacinus*, *N. richi*, has recently been described by Murray and Megirian (2000). This taxon is not represented by upper molars, but does not

Table 2. Dimensions of M^2 for three thylacinid species (*T. cynocephalus*, *Nimbacinus dicksoni* and *Maximucinus muirheadae*) and the dasyurid *Dasyurus maculatus*

No. = specimen number, ml = maximum length (anteroposterior). mw = maximum width (transverse). Q = QMF. Measurements are in millimetres

T. cynocephalus			*D. maculatus*			*N. dicksoni*			*M. muirheadae*		
No.	ml	mw	No.	ml	mw	No.	ml	mw	No.	ml	mw
S383	12.9	9.7	S1146	6.3	5.5	Q16804	7.8	7.0	Q30331	11.2	9.1
AM774	12.6	9.8	S897	6.0	4.7	Q16803	8.2	7.3			
AM768	13.2	9.7	M23948	6.8	5.2	Q36357	8.4	7.4			
AM775	12.2	9.0	M21106	6.4	5.5						
M882	12.7	9.4	M11137	6.1	5.1						
S1730	12.8	9.3	M9105	6.2	5.4						
S789	12.6	9.2	M9080	6.0	4.9						
M1821	13.5	10.0	M725	5.9	4.7						
M606	13.2	9.6	A6379	6.5	5.4						
AM770	13.3	10.0	M9076	6.0	4.9						
M823	12.0	8.6	M8262	6.5	5.2						
AM776	13.2	10.0	M8343	6.6	5.2						
AM771	12.2	9.1	M80486	6.5	5.2						
S402	13.0	9.4	M7533	6.7	5.3						
S788	12.8	9.4	M7399	6.5	5.2						
M19465	12.8	9.5	M6523	6.6	5.2						
			M5376	6.3	5.1						
			M6748	6.2	5.0						
			M4720	6.4	5.0						
			M3766	6.6	5.0						
			M1666	6.4	5.2						
			S1770	6.2	5.0						
			S1740	6.8	5.4						
			S1561	6.3	5.1						
			S2078	6.3	5.0						
			S1769	6.6	5.2						
Max.	13.5	10.0	Max.	6.8	5.5	Max.	8.4	7.4	Max.	–	–
Min.	12.0	8.6	Min.	5.9	4.7	Min.	7.8	7.0	Min.	–	–
Mean	12.8	9.5	Mean	6.4	5.1	Mean	8.1	7.2	Mean	–	–

differ significantly in size from *N. dicksoni* on the basis of lower molar dimensions. The only complete molar row of *N. dicksoni* (QMF36357) is 29.9 mm long (Wroe and Musser 2001), while that of *N. richi*, as determined from Murray and Megirian (2000, fig. 5, p. 152), is approximately 30.2 mm long.

Thylacinus cynocephalus and many dasyurid species are known to show marked sexual dimorphism. However, differences in molar dimensions between *M. muirheadae* and *Nimbacinus* greatly exceed those evident within *T. cynocephalus* or *D. maculatus* present in the Australian Museum's collections (samples of both were inclusive of all available specimens, male and female). For instance, in terms of molar length, *M. muirheadae* was 44% longer than the smallest of three specimens of *N. dicksoni*, while on the same dimension, the largest *T. cynocephalus* was only 11% longer than the smallest of 16 conspecifics. Similarly, on this dimension the largest of 26 *D. maculatus* was only 15% larger than the smallest (Table 2). The difference in size between *M. muirheadae* and the

Table 3. Dimensions of M^2 from 10 species of thylacinid
Asterisks indicate that the dimension is the average given in Table 2. No. = specimen catalogue number, ml = maximum length (anteroposterior). mw = maximum width (transverse). Measurements are in millimetres

Species	No.	ml	mw
Thylacinus cynocephalus	*	12.8	9.5
Thylacinus potens	CPC 6746	15.7	13.9
Thylacinus megiriani	NTM 9618	16.8	15.0
Nimbacinus dicksoni	*	8.1	7.2
Wabulacinus ridei	QM F16851	9.1	6.5
Maximucinus muirheadae	QM F30331	11.2	9.1
Ngamalacinus timmulvaneyi	QM F30300	8.3	7.1
Muribacinus gadiyuli	QM F30386	5.9	5.2
Mutpuracinus archibaldi	NTM 9612–5	5.7	5.0
Badjcinus turnbulli	QM F30408	6.9	6.3

only other generalised thylacinid with which it might possibly be confused, *Ngamalacinus timmulvaneyi*, is comparable to that between it and *Nimbacinus* (Table 3).

On the basis of the dimensions of M^2, *M. muirheadae* is the biggest thylacinid known from late Oligocene to middle Miocene deposits (Fig. 1, Tables 2, 3) and is comparable with small *Thylacinus cynocephalus*. The only larger fossil species, *Thylacinus potens* and *Thylacinus megiriani*, do not appear until the late Miocene.

Applying the equations of Myers (2001) gives a broad range of body weight estimates for the 10 fossil thylacinids to which this methodology can be applied (Table 5). *M. muirheadae* was 3.7 times heavier than the average determined for three specimens of *N. dicksoni*, and larger still with respect to the single specimen of *N. richi*.

Overall, results for extant species and *T. cynocephalus* support the efficacy of Myer's (2001) methods. Estimates based on average measurements for extant dasyurids and the recently extinct *T. cynocephalus* (Table 3) are very close to those reported in the literature (Green and Scarborough 1990; Strahan 1995; Paddle 2000), at least with respect to results based on lower molar row length (LMRL). The equation for estimating weight on the basis of M^2 width, as used here for *M. muirheadae*, may be less reliable, giving an estimate for a *T. cynocephalus* of 2187.2 g using the average for 16 specimens given in Table 2. This result is well under the 2950 g given as an average for *T. cynocephalus* by Paddle (2000). However, this figure was derived from values for the only four wild-caught specimens whose weights have been recorded and could clearly be significantly over, or under, the actual average for the species.

The smallest fossil thylacinid is *Mutpuracinus archibaldi*, which, at 1081.4 g, is comparable to *Dasyurus viverrinus*. Strahan (1995) gives average adult body weights for *D. viverrinus* as 1300 g for males and 880 g for females. At 1563.3 g, *Muribacinus gadiyuli* is intermediate in size between *D. viverrinus* and *Dasyurus maculatus*. The next largest thylacinid, *Badjcinus turnbulli*, is very close to *D. maculatus* at 2422.4 g. The remaining taxa, excepting *T. potens* and *T. megiriani*, are all at least twice the size of *D. maculatus*, but smaller than *T. cynocephalus*. They range from 4918.0 g (*N. richi*) to 18 384.3 g (*M. muirheadae*).

Estimating body weight for *T. megiriani* and *T. potens* is problematic. The authors of both species consider them to be larger than *T. cynocephalus*, but actual weight estimates

Table 4. Measurements of lower molar row length (LMRL) for *Thylacinus cynocephalus* (*n* = 14), *Dasyurus maculatus* (*n* = 25), *Dasyurus viverrinus* (*n* = 16) and *Dasyurus hallucatus* (*n* = 15)
Measurements are in millimetres

Thylacinus cynocephalus		*Dasyurus maculatus*		*Dasyurus viverrinus*		*Dasyurus hallucatus*	
AM S789	48.0	AM S1740	25.6	AM M1765	20.0	AM M6371	16.2
AM P767	53.0	AM S1770	23.3	AM M1734	17.8	AM M8096	16.7
AM S788	51.9	AM M8048	23.8	AM S2061	16.7	AM M25571	15.5
AM S1730	50.6	AM M7646	24	AM M2600	17.7	AM M22092	16.6
AM M822	48.2	AM M7659	22.8	AM M3776	19.7	AM M21231	15.9
AM 775	46.7	AM M3766	25	AM M3775	21.6	AM M26350	15.5
AM M823	45.2	AM M8343	25.1	AM M4280	19.6	AM M21230	16.8
AM M606	51.8	AM M7399	25.4	AM M5093	18.2	AM M9081	15.7
AM M19465	51.3	AM M5376	24.5	AM M6524	18	AM M1965	17
AM S402	47.5	AM S1769	23.6	AM M5269	19.5	AM M3789	15.5
AM M1821	52.4	AM M4720	24.6	AM M4484	18.4	AM M8673	16.5
AM 771	49.2	AM M8262	25.4	AM M9944	15.9	AM M8097	17
AM 769	52.4	AM M7533	25.1	AM M7389	16.7	AM M8615	15.3
AM 763	53.9	AM M4719	23.8	AM M6525	17.7	AM M5044	15.9
		AM M4330	24.5	AM 752	19.2	AM M8619	15.7
		AM S2124	25	AM S1103	17.4		
		AM M1666	25				
		AM M9072	24.4				
		AM M9076	23.5				
		AM M23948	25.5				
		AM M11137	23.5				
		AM M21106	24.5				
		AM M9105	24.9				
		AM M9080	23.1				
		AM S1146	25.2				
Mean	51.2	Mean	24.4	Mean	18.4	Mean	16.1

are not given. Murray (1997) observes that *T. megiriani* is around 10% larger than *T. cynocephalus*, but it is not clear whether this deduction refers to linear dimensions or body weight, two variables that are geometrically related (Wroe *et al.* 1999). Using the methodology described above gives body-weight estimates for *T. potens* and *T. megiriani* that greatly exceed that of *T. cynocephalus*, with *T. potens* at 38 700 g and *T. megiriani* at 57 300 g (Table 6). At almost double the average body weight of *T. cynocephalus* this estimate for *T. megiriani* seems high. It is, of course, possible that the only known specimen is exceptional. Furthermore, the methodology used here rests on the assumption that both fossil taxa are identical to the recent species regarding body shape and relative tooth size. The molars of *T. megiriani* and *T. potens* may be relatively large compared with those of their recent cogeneric. However, on the other hand, there is general agreement that both of these fossil species are significantly more robust than *T. cynocephalus* on the basis of preserved cranial material (Woodburne 1967; Murray 1997). If so, the methodology employed in the present study would translate into significant underestimates for *T. potens* and *T. megiriani*.

Eleven of the 12 known thylacinid fossil species have been described since 1989. This species diversity might be considered surprising given the paucity of middle-to-late-Tertiary mammal-bearing localities in Australia (Savage and Russell 1983). All of these

Table 5. Estimated body weights for 10 fossil thylacinid species as well as samples of *Thylacinus cynocephalus* and three species of *Dasyurus* from dental dimensions using equations derived by Myers (2001)

Estimate includes smearing factor. Measurements for *T. cynocephalus*, *D. maculatus*, *D. viverrinus* and *D. hallucatus* are averages from Table 3. LMRL = lower molar row length. 2UMW = M^2 width. 1UML = M^1 width. Linear dimensions are in millimetres. Weight is in grams

Species	Specimen no.	Variable	Dimension	Body weight	Percentage error
Maximucinus muirheadae	QM F30331	2UMW	9.1	18384.3	21
Muribacinus gadiyuli	QM F30385	LMRL	21.2	1563.3	13
Wabulacinus ridei	QM F16851	2UMW	6.7	5339.8	21
Badjcinus turnbulli	QM F30407	LMRL	24.3	2422.4	13
Thylacinus macknessi	QM F16048	LMRL	36.6	9016.7	13
Ngamalacinus timmulvaneyi	QM F16853	LMRL	31.8	5742.8	13
Nimbacinus dicksoni	QM F3657	LMRL	30.5	5022.9	13
Nimbacinus richi	NTM P9612-4	LMRL	30.3	4918.0	13
Mutpuracinus archibaldi	NTM P907-3	LMRL	18.9	1081.5	13
Tyrrapecinus rothi	NTM P98211	1UML	7.4	5394.6	22
Thylacinus cynocephalus	*	LMRL	51.2	26478.0	13
Dasyurus maculatus	*	LMRL	24.4	2454.5	13
Dasyurus viverrinus	*	LMRL	18.4	992.3	13
Dasyurus hallucatus	*	LMRL	16.2	659.4	13

fossil species are restricted to deposits of late Oligocene to late Miocene or early Pliocene age from three geographic locations in northern and central Australia: Riversleigh (Queensland), Alcoota (Northern Territory) and Bullock Creek (Northern Territory). The results of the present study draw attention to the fact that, in addition to considerable species richness, the family was also diverse with respect to body weight and, by inference, ecological niche. Indeed, the range of body weights estimated here for Thylacinidae (1081.5–57 300 g) exceeds that of average body weights for extant Canidae, i.e. 1500–33 200 g (Gittleman 1985).

Wroe (1999*b*), Wroe *et al.* (1999) and Wroe (2002) question the assertion that Australia's large terrestrial carnivore niches have long been dominated by reptiles (Hecht 1975; Archer and Bartholomai 1978; Lee and Cockburn 1985; Flannery 1991, 1994). This argument has rested, at least in part, on the assumption that the relatively few species of large, mammalian carnivores then evidenced by the fossil record, constituted a reasonable reflection of actual diversity. This hypothesis appears to have gained wide acceptance (Diamond 1992). However, almost all body-weight estimates for relevant taxa, reptilian and mammalian, have been the product of educated guesswork only. Thus, among fossil reptiles, only for the giant varanid, *Megalania prisca*, has a figure been founded on quantitative methodology (Hecht 1975). As pointed out by Wroe (2002), the widely cited estimate of maximum weight for this species (620 kg), based on extrapolation from a toe bone, is likely to vastly exceed that of the average for this species. On the other hand, using equations derived on the basis of large data sets, the average body weight of Australia's largest mammalian carnivore, *Thylacoleo carnifex*, has recently been estimated at 101–130 kg (Wroe *et al.* 1999), much larger than posited by most recent investigators.

Flannery (1991, 1994) defines mammalian carnivores the size of *Dasyurus maculatus* or bigger as large. The evidence presented here contributes to what is now a six-fold

Table 6. Estimated body weights for *Thylacinus megiriani* and *Thylacinus potens* (BW) based on the length of $M^{1–3}$ ($M^{1–3}$ l) and assuming geometric simiItude with *Thylacinus cynocephalus*
Average body weight for *T. cynocephalus* is taken from Paddle (2000). Dental measurements, including average for *T. cynocephalus* *, are compiled from data provided by Woodburne (1967) and Murray (1997). Linear dimensions are in millimetres. Weight is in kilograms

Species	Specimen no.	$M^{1–3}$ l	BW
Thylacinus potens	CPC 6746	42.9	38.7
Thylacinus megiriani	NTM P9618	48.9	57.3
Thylacinus cynocephalus	–	39.2*	29.5

increase in the number of fossil thylacinid species over the last decade and demonstrates that three-quarters of these were probably at least twice as heavy as *Dasyurus maculatus*. At the very least, this detracts from the hypothesis that reptiles dominated large terrestrial carnivore niches in Australia.

It might be argued that I have provided insufficient evidence to overturn the assertion of long-standing reptilian domination of Australia's large terrestrial carnivore niches. I would turn this on its head. There was never sufficient evidence to present the case for reptilian supremacy as anything more than an undeveloped and largely unsubstantiated hypothesis. Data presented here and elsewhere (Wroe *et al.* 1999) demonstrate that Australia was home to a far greater number of large fossil marsupial carnivore species than previously thought. Consequently, it behooves advocates of reptilian domination to present arguments based on more than educated guesswork if their hypothesis is to be validated. To date, it is not yet even clear whether key reptilian taxa in this debate were, in fact, terrestrial (Molnar 1981; Barrie 1990; Willis 1997).

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