ADDITIONAL PARTS OF THE TYPE SPECIMEN OF *THYLACINUS MACKNESSI* (MARSUPIALIA: THYLACINIDAE) FROM MIOCENE DEPOSITS OF RIVERSLEIGH, NORTHWESTERN QUEENSLAND

JEANETTE MUIRHEAD AND ANNA K. GILLESPIE

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A revised diagnosis and description of *Thylacinus macknessi* Muirhead, 1992 is presented following recovery of the previously unknown anterior half of the holotype. This provides the most completely represented lower dentition of a species of thylacinid other than *T. cynocephalus*. The new part of the holotype further confirms the thylacinid nature of this taxon by displaying additional features that in combination are only known in that family. The molar and premolar region suggest that selection pressure to elongate the face and shearing crest system were greater at the front of the dentition. This specialisation differs significantly from that of most dasyurids which appear to have been under pressure to shorten the facial region by premolar loss.

Key words: Thylacine, *Thylacinus macknessi*, Thylacinidae, marsupial, carnivore, Miocene.

J. Muirhead and A. Gillespie, School of Biological Science, University of New South Wales, New South Wales, 2052, Australia. *Manuscript received 30 August, 1994*

THYLACINUS macknessi, from Miocene deposits of Riversleigh (northwestern Queensland),was described from a broken right dentary with complete M_4, M_5, a broken M_3 and associated canine collected in 1987 (together comprising the holotype) as well as isolated M_4 and M^2 (paratypes) (Muirhead 1992). This species is the third and oldest known member of the genus *Thylacinus* but is not considered to be directly ancestral to any other species having some features more apomorphic than the remaining two: *T. cynocephalus* Harris, 1808 and *T. potens* Woodburne, 1967. The anterior lower dentition of *T. macknessi* and all of the upper dentition other than the M^2 were unknown. Following the original description, the anterior part of the holotype QMF16848 was recovered and warrants an amended description of the holotype and assessment of the anterior dentition.

Dental and taxonomic nomenclature follows that of Muirhead (1992). QMF catalogue number represents specimens from the palaeontological collection of the Queensland Museum. Tooth dimensions are presented in Table 1.

Tooth	length (mm)	width (mm)	max. crown height (mm)
C_1	n/a	n/a	13.4*
P_1	4.6	2.0	4.0
P_2	7.1	2.6	5.2
P_3	8.1	3.1	6.3
M_2	8.8	4.2	6.4
M_3	9.0	4.3	7.8
M4	9.0	5.0	8.5
M5	8.6	4.7	7.6

Table 1. Tooth measurements of dentition of *T. macknessi*. * above lingual alveolar margin

SYSTEMATICS

Thylacinidae Bonaparte, 1838
Thylacinus Temminck, 1824
Thylacinus macknessi Muirhead, 1992

HOLOTYPE Amended as QMF16848 (including the part previously numbered QMF16848a), right dentary with C, P_{1-3}, M_{2-5} (Fig. 1).

REFERRED SPECIMENS QMF16848b, right canine associated to holotype now removed from the type series. This specimen was previously considered to be the canine for specimen QMF16848a. However, the later find of the anterior portion of this specimen precludes the isolated canine from being part of this specimen. This specimen has been renumbered as a isolated specimen. QMF16849 and QMF16850 are retained as paratypes.

REVISED DIAGNOSIS Revised diagnosis as follows: *Thylacinus macknessi* differs from all other species of *Thylacinus* (i.e. *T. cynocephalus* and *T. potens*) in the following combination of features 1, retension of a distinct entoconid on all lower molars; 2, retension of a vestigial metaconid on M_4 and M_5; 3, long cristid obliqua orientated centrally on the crown and parallel (rather than oblique) to the long axis of the dentary; 4, lack of a stylar shelf on M^2; 5, well developed and unnotched anterior cingulum that is continuous with the protocrista on M^2; 6, retension of a small metaconule on M^2; 7, relatively unreduced paracone on M^2; 8, M_5 anteroposteriorly shorter in length than preceding molar; 9, M_2 protoconid centrally located on crown without lingual curvature - the preprotocristid, postprotocristid and cristid obliqua are almost perfectly in line anteroposteriorly on this tooth whereas they angle on *T. cynocephalus*; 10, anterior cingulum reduced but present on M_2 and larger on all other molars than that of *T. cynocephalus*; 11, no posterior reclination of the protoconid on P_{1-3} -these cusps are anteriorly inclined on P_{1-2} and straight on P_3; 12, anterior cuspule retained on P_{1-3}; and 13, coronoid process departs from the ramus at approximately 120°.while on *T. cynocephalus* it departs at a wider angle (approx. 130°).

Thylacinus macknessi differs from the only other known genus of thylacine (*Nimbacinus dicksoni*) in that 1, the centrocrista (postparacrista and premetacrista) is straight rather than angular; 2, extreme reduction of the metaconid with no sign of this cusp on M_2 and M_3; 3, complete loss of anterior stylar cusps on M^2 (total absence of St B); 4, lack of protoconules and reduced metaconule on M^2; and 5, increased diastemata size between premolars, particularly P_2 and P_3.

REVISED DESCRIPTION The anterior portion of the dentary contains three alveoli for I_{1-3}. I_2 is located higher than I_1 and I_3. No diastema between incisors or incisors and canine. Diastemata present between C_1, P_1 and P_2 of approximately equal size. Diastema present between P_2 and P_3 is the largest on the dentary. Two mental foramina are present. The anterior is located directly beneath the posterior root of P_1 and the other is located beneath the anterior root of P_3. Dentary depth increases posteriorly with its greatest depth beneath M_5. The symphysis extends posteriorly to beneath P_3.

The canine departs from the ramus at 130° and strongly recurves posteriorly so that the tip points directly up. The tip of the canine is higher than any cusp of the remaining dentition, being approximately twice as high as the tip of the molars. An extremely large thegotic "wear" facet occurs on the posterobuccal surface of the canine.

The anterior root of P_1 is anteroposteriorly thinner than the posterior root. Both roots incline anteriorly relative to the ramus. A minute anterior cuspule is present directly anterior to the protoconid. A crest continues from the anterior cusp, through the protoconid to a large posterior cuspule. The crown inclines anteriorly with the large protoconid lying over the anterior root. The crown is a narrow ovoid in occlusal view. The protoconid curves slightly towards the lingual side of the crown.

The morphology of P_2 follows that of P_1 except as follows. P_2 has a larger size. The anterior cuspule is larger. The protoconid is larger and the distance between the protoconid and the posterior cuspule has increased with a resultant increase in the size of the posterior crest.

The morphology of P_3 follows that of P_2 except as follows. The crown has no anterior inclination. The protoconid is directed upwards and without any lingual curvature. The protoconid lies in a position directly between the two roots. The anterior and posterior cuspules are larger than on P_2. The crest system between the anterior cuspule, through the protoconid to the posterior cuspule is straight due to the lack of the lingual curvature of the protoconid. Occlusal shape of the crown approximates a thin ovoid except for a bulge of enamel posterolingual to the protoconid.

The M_2 of the paraconid lies almost directly anterior to the protoconid and is very reduced in size. A very reduced anterior cingulum lines the anterobuccal corner of the crown. The paracristid runs anteriorly from the protoconid to connect with the posterobuccal corner of the paraconid. The paracristid is low (relative to the posterior molars). The postprotocristid is directly parallel to the paracristid and continuous through the protoconid.

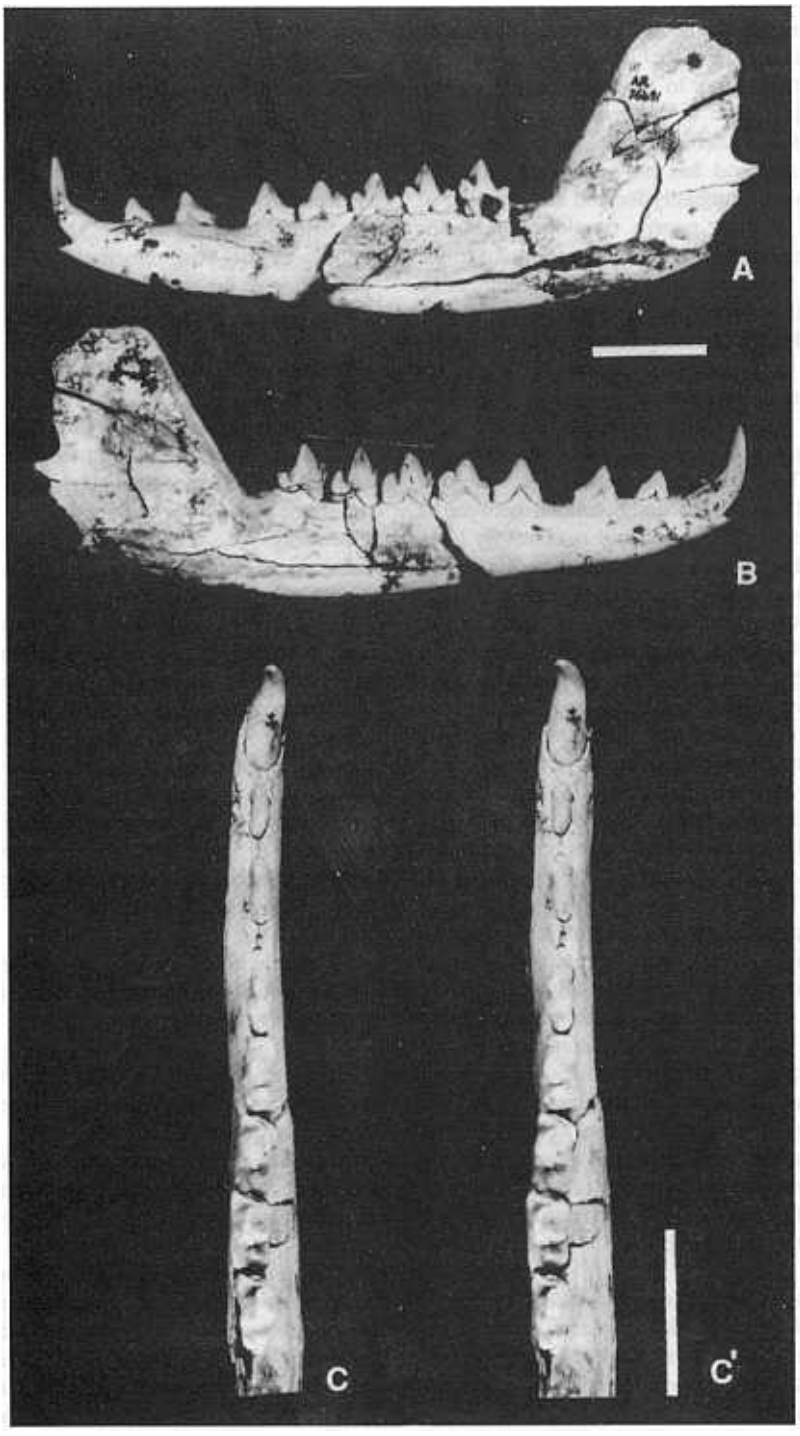

Fig. 1. QMF16848. A = lingual view. B = buccal view. C and C' = stereo occlusal views. Scale = 2cm.

The postprotocristid connects directly with the cristid obliqua. No metaconid or metacristid exists. The posterolingual surface of the protocone is smooth and continuous to the base of the crown. The hypoconid is the largest cusp on the talonid followed by the entoconid and hypconulid. The entoconid is low and has no preentocristid. The entoconid is posterolingually located at the corner of the crown. A low, poorly developed posterior cingulum is present from the low hypoconulid to the base of the hypoconid. The cristid obliqua + postprotocristid + paracristid runs almost parallel to the ramus with the anterior part of this crest system only slightly more lingually located. A distinct posthypocristid is also present.

Morphology of M_3 follows that of M_2 except as follows. The anterior cingulum is strongly developed with a distinct notch formed between it and the paraconid. The paraconid is relatively large compared to that of M_2 and located anterolingual to the protoconid. A distinct cleft exists in the paracristid between the paraconid and protoconid. The crown of the M_3 is not premolariform as it is in M_2, due, in part, to the larger paraconid on this tooth. The paracristid is angled such that it runs directly anterior from the protocone but turns anterolingual at the cleft towards the paraconid. The paracristid is raised high upon the flank of the protoconid as a sharp cristid. The posterior of M_3 is like that of M_2 except that all cusps and crests are slightly larger.

Morphology of M_4 follows that of M_3 except as follows. Vestigial metaconid is represented by slight thickening of enamel in position usually occupied by metaconid on dasyurids and in the plesiomorphic *Nimbacinus*. Anterior cingulum continues to the anterobuccal base of the protoconid. In occlusal view the paracristid is the longest crest. It is 'V'-shaped in lateral view and almost vertical in the valley between the paraconid and protoconid. A metacristid is present and connects the protoconid to the position of the metaconid. A crest connects the metacristid to the cristid obliqua.

Morphology of M_5 follows that of M_4 except as follows. The talonid is reduced in size by the more lingual position of the hypoconid and reduction of height, loss of the entoconid and reduction in posterior cingulum.

Morphology of M^2 follows that of Muirhead (1992).

Meristic gradients: The angle formed at the paracristid increases between M_2 to M_5. The size of the paraconid increases from M_2 to M_5. The anterior cingulum and notch is less reduced from M_2 to M_5. The angle formed by the cristid obliqua + postprotocristid + preprotocristid (as the posterior part of the paracristid) is straight on all molars. The metacristid and metaconid increase in size posteriorly from M_4 to M_5. The entoconid is largest on M_3. The postprotocristid is less pronounced posteriorly as the metacristid increases.

COMPARISON AND DISCUSSION

The Neville's Garden Site (the type locality of *T. macknessi*) was discovered in 1987. Because the site appeared to be exceedingly rich, a large quantity of limestone was brought back to the laboratory for processing. Acid etching of this material commenced immediately and continues.

The posterior half of QMF16848 was discovered and prepared approximately a year after the processing of the Neville's Garden material began. The broken, proximal edge of this specimen was exposed at the sharp, freshly broken edge of a limestone block suggesting the posterior half of the dentary would probably be in the adjoining limestone. The anterior portion of this dentary was recovered in late 1993. When preparation of the anterior portion was completed it perfectly matched the posterior portion QMF16848.

This additional material of *T. macknessi* enables comparison of the anterior dentition and dentary to that of other thylacinids.

The canine is large and severely thegosed on the posterobuccal side. This is consistent with other large dasyuroids such as *T. cynocephalus*, *Sarcophilus harrisii* and species of *Dasyurus* where the lower canine is able to thegose the anterior flank of the upper canine.

The premolars of *T. macknessi* increase in size posteriorly which is a plesiomorphic feature of dasyuroids retained in thylacines but lost in most dasyurids which, in contrast. This retention of all premolars and lack of reduction of the premolars in *T. macknessi* is consistent with the elongation of the face typical of thylacines but not dasyurids which tend to reduce the premolar region by reduction in size of the premolars or premolar loss. The diastemata between the premolars of *T. macknessi* do

not differ significantly from those of *T. cynocephalus* although the distance between P_1 and P_2 appears slightly shorter in *T. macknessi*. The diastemata of *T. macknessi*, however, are much greater and therefore more derived than those shown by *Nimbacinus dicksoni* (Bullock Creek specimen P85553-3) where small diastema are present between the canine and P_1 as well as between P_1 and P_2 but not between P_2 and P_3. Elongation of the premolar region is a feature typical of thylacinids but rare in dasyurids. This condition in *T. macknessi* further supports its inclusion into the Thylacinidae.

The M_2 of *T. macknessi* is in some ways more apomorphic than that in *T. cynocephalus* by being more premolariform in shape. This tooth in *T. macknessi* has the cusps and crests straighter, therefore exhibiting a more carnivorous condition by forming a single, composite straight shearing crest in contrast to the curved one seen in *T. cynocephalus*. This feature, in addition to other autapomorphies discussed by Muirhead (1992) such as the derived anterior cingulum and extremely reduced stylar shelf on the M^2, prevents this thylacine from being considered ancestral to *T. cynocephalus*.

The M_2 and M_3 show no sign of a metaconid. *Thylacinus macknessi* is therefore more specialised than *N. dicksoni* in this regard. Remnants of the metaconid are retained on the posterior molars of *T. macknessi* (by the presence of the metacristid) and this species is therefore more plesiomorphic than *T. cynocephalus* (Muirhead 1992). In *T. macknessi*, the most posterior shearing crest, the posterior crest from the protoconid (the postprotocristid), runs directly to the hypoconid and joins the cristid obliqua on M_2 and M_3 (the postprotocristid connects the protoconid to the cristid obliqua as opposed to the metacristid which connects the protoconid to the metaconid). Loss of the metaconid and a straight posterior shearing crest on all molars are features also found in *T. cynocephalus* and are unknown in combination in any dasyurid (Ride 1964). *Thylacinus macknessi*, however, differs from *T. cynocephalus* in that the angle of the postprotocristid changes in posterior molars instead of being consistent and straight in all molars as in *T. cynocephalus*. On anterior molars of *T. macknessi* this crest is parallel with the long axis of the teeth and connect directly to the cristid obliqua. On M_4 and M_5, the postprotocrista runs posterolingually to the position normally (in dasyurids) occupied by the metaconid where it then terminates. There is a small swelling in this crest which is considered to represent the remnant metaconid (Muirhead 1992). On these teeth, the cristid obliqua connects to the postprotocristid which runs obliquely down the posterior face of the protoconid (see figs 3A and B in Muirhead 1992). This results in an angular posterior shearing crest (postprotocristid+cristid obliqua) on M_4 and M_5 while M_3 and M_2 have relatively straight posterior shearing crests. The M_4 and M_5 therefore have two crests emanating posteriorly from the protoconid: the metacristid and the postprotocristid. The retention of the metacristid (and its posterolingual orientation) on the posterior molars is a condition of *T. macknessi* more plesiomorphic than found in *T. cynocephalus*. The single straight shearing crest created by the combination of the preprotocrista + postprotocrista + cristid obliqua (found on the anterior molars of *T. macknessi* and all molars of *T. cynocephalus*) is the more specialised condition.

Facial elongation appears to be greater in *T. cynocephalus* than *T. macknessi*. In *T. cynocephalus*, the face has elongated by diastemata between the premolars and elongation of M_5. The M_5 of *T. macknessi*, however, is not as elongated as it is in *T. cynocephalus* and remains smaller than M_4 (Muirhead 1992). The angle of the coronoid process (relative to the ramus of the dentary) is greater in *T. cynocephalus* (approximately 130^o) than *T. macknessi* (approximately 120^o). Possibly associated with the facial extension is the more posterior location of the mental foramen in *T. cynocephalus* compared to *T. macknessi*. In *T. macknessi*, the anterior mental foramen is situated under the posterior root of P_1 and the posterior mental foramen is situated under the anterior root of P_3. In *T. cynocephalus*, these foramina are more posteriorly located.

Thylacinus macknessi is the only thylacine taxon other than *T. cynocephalus* that has a complete representation of lower molars. Lack of the metaconid on M_2 and M_3, while retaining an albeit extremely reduced metaconid on M_4, may represent a trend typical to all thylacinids where loss of this cusp occurs initially from the anterior molars and progresses posteriorly. This progression in cusp loss from anterior to posterior in thylacinids may suggest that those dasyurids in which the metaconid is lost on M_2 may represent an intermediate or convergent state in the development of a thylacinid-type dentition.

All dasyurids in which metaconid loss of M_2 occurs (e.g. *Sarcophilus, Dasyurus,* etc. see Archer 1976) have also undergone reduction in the premolar

region by reduction or loss of a premolar. Although the M_2 morphology of these dasyurids is showing specialisations similar to thylacinids, the anterior dentition is specialising in a different direction than that taken by thylacines and these dasyurids cannot, therefore, be considered as in any way a lineage closely related to thylacinids. In addition, thylacines show a progressive reduction in size of this cusp on M_{2-5}. Dasyurids, in contrast, retain a metaconid consistent in size from M_3 to M_5 Dasyurids therefore appear to be convergent on thylacinids in the loss of the metaconid on M_2 and do not represent an intermediate state towards a thylacinid dentition.

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