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

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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.

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THYLACINUS macknessi, from Miocene deposits of Riversleigh (northwestern Queensland), was described from a broken right dentary with complete M4, M5, a broken M3 and associated canine collected in 1987 (together comprising the holotype) as well as isolated M4 and M2 (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 M2 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.

<table>
<thead>
<tr>
<th>Tooth</th>
<th>length (mm)</th>
<th>width (mm)</th>
<th>max. crown height (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C1</td>
<td>n/a</td>
<td>n/a</td>
<td>13.4*</td>
</tr>
<tr>
<td>P1</td>
<td>4.6</td>
<td>2.0</td>
<td>4.0</td>
</tr>
<tr>
<td>P2</td>
<td>7.1</td>
<td>2.6</td>
<td>5.2</td>
</tr>
<tr>
<td>P3</td>
<td>8.1</td>
<td>3.1</td>
<td>6.3</td>
</tr>
<tr>
<td>M2</td>
<td>8.8</td>
<td>4.2</td>
<td>6.4</td>
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<tr>
<td>M3</td>
<td>9.0</td>
<td>4.3</td>
<td>7.8</td>
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<tr>
<td>M4</td>
<td>9.0</td>
<td>5.0</td>
<td>8.5</td>
</tr>
<tr>
<td>M5</td>
<td>8.6</td>
<td>4.7</td>
<td>7.6</td>
</tr>
</tbody>
</table>

* above lingual alveolar margin

Table 1. Tooth measurements of dentition of T. macknessi.

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, P1-3, M2-5 (Fig. 1).
REFERRRED 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, retention of a distinct entoconid on all lower molars; 2, retention of a vestigial metaconid on M4 and M5; 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 M2; 5, well developed and unnotched anterior cingulum that is continuous with the protocrista on M2; 6, retention of a small metacone on M2; 7, relatively unreduced paracone on M2; 8, M5 anteroposteriorly shorter in length than preceding molar; 9, M2 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 M2 and larger on all other molars than that of T. cynocephalus; 11, no posterior reinclination of the protoconid on P1-3 - these cusps are anteriorly inclined on P1-2 and straight on P3; 12, anterior cuspule retained on P1-3; 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 M2 and M3; 3, complete loss of anterior stylar cusps on M2 (total absence of St B); 4, lack of protoconules and reduced metacone on M2; and 5, increased diastemata size between premolars, particularly P2 and P3.

REVISED DESCRIPTION The anterior portion of the dentary contains three alveoli for I1-3. I2 is located higher than I1 and I3. No diastema between incisors or incisors and canine. Diastemata present between C1, P1 and P2 of approximately equal size. Diastema present between P2 and P3 is the largest on the dentary. Two mental foramina are present. The anterior is located directly beneath the posterior root of P1 and the other is located beneath the anterior root of P3. Dentary depth increases posteriorly with its greatest depth beneath M5. The symphysis extends posteriorly to beneath P3.

The canine departs from the ramus at 130° and strongly recures 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 P1 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 P2 follows that of P1 except as follows. P2 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 P3 follows that of P2 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 P2. 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 M2 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 protoconid. 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 hypoconulid. 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 linguallly located. A distinct posthypocristid is also present.

Meristic gradients: The angle formed at the paracristid increases between M2 to M5. The size of the paraconid increases from M2 to M5. The anterior cingulum and notch is less reduced from M2 to M5. 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 M4 to M5. The entoconid is largest on M3. 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 dasyuroids 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 dasyuroids 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 metastylid) 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 metastylid 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 metastylid and the postprotocristid. The retention of the metastylid (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°) than *T. macknessi* (approximately 120°). 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 anterior 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 M2 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 M2-5. Dasyurids, in contrast, retain a metaconid consistent in size from M3 to M5. Dasyurids therefore appear to be convergent on thylacinids in the loss of the metaconid on M2 and do not represent an intermediate state towards a thylacinid dentition.

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REFERENCES


