

***Thylacinus* (Marsupialia: Thylacinidae) from the Mio-Pliocene boundary and the diversity of Late Neogene thylacinids in Australia.**

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Thylacinus yorkellus is described as a new, moderately small-bodied species of thylacinid from the latest Miocene or, more likely, earliest Pliocene of South Australia. The new species can be diagnosed by the autapomorphic presence a strongly developed precingulid that terminates in a cuspidule on the anterobuccal face of the paraconid of the lower molars and a tiny basal anterior cuspidule on P_2 , P_3 and the lower molars. It is found by cladistic analysis to be the sister species of the recently extinct *Th. cynocephalus* and distinct from the approximately coeval *Th. megiriani* from the Northern Territory. New dentary material is described and referred to *Th. megiriani*. These add character data and allow this species to be re-diagnosed based on autapomorphic character traits. Each of the three known Late Miocene to Early Pliocene *Thylacinus* species (*Th. potens*, *Th. megiriani* and *Th. yorkellus*) suggest that, instead of declining, there was a modest radiation of *Thylacinus* in the Late Miocene.

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Introduction

The tragic tale of Thylacinidae, or the marsupial wolves, involves a sustained loss of diversity from an early to middle Miocene high (Wroe, 2003) up to the final extermination of the last surviving population of *Thylacinus cynocephalus* at our own hands in the early twentieth century (Thornback and Jenkins, 1982; Fisher and Blomberg, 2011). Just when the Thylacinidae became restricted to a single species is an interesting question that might relate to broadscale changes in Australian terrestrial ecosystems during the latter part of the Cenozoic. It has been noted that the late Miocene diversity of thylacinids is severely depleted (Rich, 1991; Wroe and Muirhead, 1999; Wroe, 2003), although the dearth of fossil deposits from this time is a confounding factor. Nevertheless, has one popular account suggested that the wolf-sized *Th. potens* from the Alcoota Local Fauna (Woodburne, 1967) was the sole surviving lineage by this time and that it was directly ancestral to the modern *Th. cynocephalus* (Archer, Hand and Godthelp, 1991).

Subsequently *Tyarrpecinus rothi*, a small plesiomorphic thylacinid that apparently lay outside the genus *Thylacinus*, was discovered in the Alcoota local fauna demonstrating that at least two thylacinid lineages were surviving at this point in the Late Miocene (Murray and Megirian, 2000). However all thylacinids from younger local faunas belong to *Thylacinus*, indicating that *Ty. rothi* was a late surviving relict that probably died out shortly after the deposition of the Alcoota Local Fauna. The discovery of *Ty. rothi* does not falsify the hypothesis that *Th. potens* was part of a single anagenetic lineage of large-bodied thylacinids that led directly to *Th. cynocephalus*. Therefore the scenario where Thylacinidae was reduced to a single lineage prior to the close of the Miocene remained a viable hypothesis.

A further large-bodied *Thylacinus* species, *Th. megiriani*, was discovered in the Ongeva Local Fauna which derives from a channel-fill in the Waite formation that overlies the Alcoota Local Fauna on Alcoota Station (Murray, 1997). The Ongeva Local Fauna correlates with the Beaumaris Local Fauna from the Black Rock Sandstone in the Port Philip Basin of south-eastern Australia based on the shared presence of *Zygomaturus gilli* (Megirian, Murray and Wells, 1996; Murray, 1997; Megirian et al., 2010). The Black Rock sandstone also preserves a marine invertebrate fauna and has a robustly stratigraphically controlled age of 6.2-5.0 ma, an age that straddles the Mio-Pliocene boundary (Dickinson et al., 2002). *Th. megiriani* shares more derived features with the modern *Th. cynocephalus* than with *Th. potens*. Thus *Th. megiriani* could be interpreted as chronospecies on an anagenetic lineage leading from *Th. potens* to *Th. cynocephalus*. At the time of its description *Th. megiriani* was known only from its holotype which is a single broken maxilla with worn and damaged teeth. However, a couple of large thylacinid dentary fragments have been found in the Ongeva Local Fauna since the initial publication that can be referred to this species. Character data from these specimens has been incorporated into a phylogenetic analysis of thylacinid relationships (Yates, 2014) but they have not been described or adequately illustrated in the scientific literature.

There is a further thylacinid from the penecontemporaneous Curramulka Local Fauna of South Australia (Pledge, 1992) that sheds light on the number of thylacinid lineages present in Australia during the latest Miocene and earliest Pliocene. This thylacinid is described here as a new species. In addition the new mandibular specimens of *Th. megiriani* are described and the species diagnosed with autapomorphic characters. This new data casts strong doubt on the hypothesis of a single anagenetic lineage of *Thylacinus* in the late Neogene of Australia.

50 Systematic Palaeontology

51

52 *Dasyuromorphia* Gill, 1872

53 *Thylacinidae* Bonaparte, 1838

54 *Thylacinus* Temminck, 1824

55 *Thylacinus yorkellus* sp. nov.

56 urn:lsid:zoobank.org:act:D176F98E-740B-4E37-A491-3AFDCCC1CD50

57 *Holotype*. South Australian Museum (hereafter SAM) P29807, incomplete left dentary with C, P₁₋₃ and M₂₋₃ (Fig.
58 1-2, Table 1-2).

59 *Referred specimen*. SAM P38799, crown of right M₃ (Fig. 3-4, Table 2).

60 *Locality and stratigraphic age*. Corra-Lynn Cave, approximately 3km south of Curramulka, York Peninsula,
61 South Australia. Late Miocene or, more likely, early Pliocene in age.

62 *Etymology*. From York Peninsula and the diminutive suffix –ellus (Latin), referring to its small size relative to *Th.*
63 *cynocephalus*.

64 *Diagnosis*. Differs from all thylacinids by the presence of the following autapomorphies: Lower molars with a
65 strongly developed precingulid that terminates in a cuspidule on the anterobuccal face of the paraconid and a
66 tiny basal anterior cuspidule on P₂, P₃ and the lower molars. It can be further distinguished from *Th. macknessi*
67 and all thylacinids not in the genus *Thylacinus* by the complete absence of metaconids on M₂, M₃ and,
68 presumably, M₄. It can be further distinguished from *Th. potens* by its smaller size (estimated adult body mass
69 of 16-18 kg vs. 39-56 kg for *Th. potens*; Yates, 2014), by the presence of wide diastemata between each of the
70 lower premolars as well between P₃ and M₁, and by the presence of deep cleft-like carnassial notches on the
71 lower molars. It can be further distinguished from *Th. megiriani* by its smaller size (estimated body mass of *Th.*
72 *megiriani* is 57 kg; Wroe, 2001), wider diastemata separating P₃ from M₁ and P₂ from P₃, its relatively gracile and
73 buccolingually compressed anterior dentary lacking a ventrolateral torus, the complete absence of any trace of
74 the metaconid on the lower molars, and by the presence of deep cleft-like carnassial notches on the lower
75 molars. Lastly it can be further distinguished from *Th. cynocephalus* by the lengths of both P₂ and P₃ exceeding
76 that of M₁ and the presence of a diastema between the canine and P₁.

77 *Remarks*. Pledge (1992) figured and briefly described the holotype specimen in his description of the
78 Curramulka Local Fauna. He suggested that it may belong to an undescribed species but declined to name it.
79 With our improved knowledge of thylacinid diversity and the addition of a second specimen showing the same
80 autapomorphic characters of the molars as the holotype, there is now sufficient evidence to warrant the
81 naming of a new species.

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83 Description

84 The holotype includes the incisor alveoli, the canine, all three premolars, M_2 , M_3 and the alveolus for M_1 (Fig. 1-
85 2, Table 1-2). Posteriorly the dentary has broken off at the level of the posterior end of M_3 , so that M_4 is
86 missing. The dentary is transversely compressed, as it is in *Th. cynocephalus* but unlike the transversely broad,
87 robust dentaries of *Th. megiriani* and some *Th. potens*. It differs further from *Th. megiriani* and *Th. potens* in
88 lacking a thickened torus along the ventrolateral margin, below the mental foramina. The dentary depth below
89 the anterior root of M_2 (the posteriormost level at which this measurement can be made) is 24.5 mm which
90 lies within the range of *Th. cynocephalus*. Given that the length of the lower molar row and the heights of the
91 individual molars lie below the range seen in *Th. cynocephalus*, it would seem that the holotype *Th. yorkellus*
92 has a deeper jaw relative to tooth size in comparison to the former species. A relatively deep dentary is also
93 seen in some, but not all, specimens of *Th. potens* (Yates, 2014). The lateral surface of the dentary is pierced by
94 three mental foramina set approximately at the mid height of the dentary, although it is possible that a fourth
95 was present in what is now a large area of missing bone below P_3 (Fig. 2). The anterior mental foramen is large
96 anteriorly facing opening with a diameter of 3.2 mm located below the anterior root of P_2 . The two close-set
97 posterior mental foramina are placed below M_2 and the anterior margin of M_3 , respectively. These openings
98 are smaller, with anteroposterior diameters of 2.1 and 1.4 mm, respectively. In lateral view the alveolar margin
99 is concave with P_3 set lower than the rest of the preserved tooth row. The medial symphyseal surface extends
100 posteriorly to the level of the anterior margin of P_3 .

101 The canine has a procumbent root and a vertically projecting crown. The tip is gently recurved so that the
102 mesial margin in lateral view is convex and the distal margin is concave. In anterior view the crown has a weak
103 lingual curvature. The cross-section of the crown is a slightly bucco-lingually compressed oval. A weakly
104 developed carina extends along the anterolingual margin of the crown, from base to apex. The distal surface is
105 rounded and smooth. The measurements of the canine are given in table 1.

106 A diastema of 3.3 mm separates the canine alveolus from that of P_1 . P_1 is a small, low-crowned tooth. In
107 occlusal view is elongately ovoid with the long axis oriented anteroposteriorly. Although the tip of the
108 protoconid is well worn, it is clear that the unworn tooth would have had a height less than its anterior-
109 posterior length. The apex of the protocone is located in the anterior half with an elongate heel extending
110 posterior to it. The heel has a sharp posterior corner which forms an incipient cuspidule. In lateral view the
111 distal margin of the protoconid curves gently down to the distal heel. A weakly developed cristid extends along
112 the mesial margin of the protoconid. The tooth has no other cristids or cuspidules.

113 A diastema of 2.8 mm separates P_1 from P_2 . P_2 differs from P_1 in being larger (Table 2) and proportionately
114 taller. The apex of large triangular protoconid is less skewed to the mesial side of the tooth, being placed
115 slightly mesial to the mid length. A weak cristid extend up the mesial side of the protoconid. There is a minute
116 tubercle-like cuspidule developed at the base of this mesial cristid. A distal cristid extends from the apex of the
117 protoconid to the distal corner of the basal heel. A distinct inflection in the lateral profile marks the change
118 from the heel to the distal margin of the protoconid.

119 A long diastema of 6.4 mm separates P_2 from P_3 . P_3 is larger than, P_2 and differs from it in a number of subtle
120 features. P_3 shows a greater development of the mesial basal cuspidule than in P_2 . The large protoconid is

centrally located and triangular in lateral view. Both medial and distal margins bear cristids. In occlusal view the crown is widest distally, where the heel now forms an incipient talonid basin. A shallow notch in the lateral profile now separates the distal heel from the protoconid, and the distal heel now forms a protrusive cuspidule with a worn tip.

M_1 is missing, and the lingual alveolar margin of the dentary is missing from the level of the distal root of P_3 , posteriorly. Nevertheless the buccal side of the M_1 alveolus is separated from P_3 by a diastema of 3.0 mm, whereas there is no diastema between the alveolus of M_1 and M_2 .

M_2 consists of two large trigonid cusps (paraconid and protoconid) and three far smaller cusps (hypoconid, hypoconulid and entoconid) surrounding the talonid basin. The most remarkable feature of M_2 (and M_3) is the strength of the short precingulid, which forms a sharp-edged shelf that terminates in a well-developed cuspidule on the anterobuccal face of the base of the paraconid. The precingulid slopes steeply distalobuccally from this cuspidule and terminates near the base of the crown level with the mesial margin of the protoconid. The paraconid is well developed and triangular in occlusal view. A minute cuspidule is developed on the anterior slope of the paraconid, near the base of the crown, at about the same level as the anterobuccal cuspidule of the precingulid. The protoconid forms the largest cusp of M_2 . In lateral view the mesial margin of the protoconid curves distally towards the apex, however this shape has been created by wear. A distinct, tear-drop shaped wear facet is developed at the tip of the protoconid and extending down its anterior side, along the course of the paracristid. A deep carnassial notch is developed between the paraconid and protoconid, dividing the paracristid into two sections. There is no trace of a protocristid or a metaconid on the posterior side of the protoconid, although the cristid obliqua extends approximately half way up this surface. The cristid obliqua is also divided into two sections by a deep carnassial notch, this time separating the protoconid from the hypoconid. In buccal and lingual view the talonid is set distinctly lower than the trigonid. In occlusal view its transverse width is slightly greater than that of the trigonid. All of the cusps of the talonid are highly worn and flat-topped. The largest of these and the most strongly projecting is the buccally placed hypoconid. The posteriorly located hypoconulid has been virtually obliterated by wear and is only recognisable as a slight thickening of the enamel around the posterior rim of the wear facet. The very small entoconid is placed on the lingual side of the talonid, slightly inset from the lingual margin of the crown. A short ridge extends posterobuccally from its apex towards the hypoconulid. A short postcingulid extends obliquely up the posterior surface of the hypoconid from a basally located point on the buccal side to a more apical point on the lingual side.

M_3 is very much like M_2 , differing in the following respects. The minute anterior cuspidule at the base of the paraconid is even less well-developed. The protoconid is taller, and the cristid obliqua extends for less than half its height up the posterior surface. The talonid is slightly narrower than the trigonid and the hypoconulid forms a low conical cuspid. The posterobuccal ridge extending from the apex of the entoconid joins the anterior base of the hypoconulid, thus creating a small oval basin that is separated from the main talonid basin. A low but sharp postcristid between the hypoconulid and the entoconid forms the posterolingual margin of this small oval basin. The postcingulid is very reduced, and is little more than a shallow depression on the posterior surface of the hypoconid.

The M₃ of SAM P38799 shows some minor differences from the holotype but the main features are the same, including the distinctive precingulid terminating in an anterobuccal cuspidule (Fig. 3-4, Table 2). In this specimen the anterior cuspidule at the base of the paraconid is better developed than in either of the two molars of the holotype, and has an incipient preparacristid leading from it towards the apex of the paraconid. The talonid is as wide as the trigonid and the entoconid appears to lack the posterobuccal ridge that links it to the hypoconulid.

Size estimate

Calculating from the third lower molar length regression formula, derived from the dasyuromorphian-only data set of Myers (2001), a body mass estimate of 17.8 kg is obtained for the holotype and 15.9 kg for SAM P38799. These estimates are well below the average body mass of 29.5 kg for recent Tasmanian *Th. cynocephalus* (Paddle, 2000) but are not outside the range estimated for mainland Holocene samples of this species (Letnic, Fillios and Crowther, 2012). However, it is clear that *Th. yorkellus* was a far smaller species than either *Th. potens* or *Th. megiriani* which have estimated body masses ranging between 38.7 and 57.3 kg (Wroe, 2001; Yates, 2014).

Thylacinus megiriani Murray, 1997

Holotype. NTM P9618, fragmentary left maxilla with P¹⁻³ and M¹⁻³

Referred specimens. NTM P4376, anterior fragment of a right dentary containing the alveoli with broken roots for P₂, P₃ and M₁ and the empty alveolus for M₂ (Fig. 5-7). NTM P4377, posterior fragment of a right dentary containing an incomplete M₄ (Fig. 8-10).

Locality and stratigraphic age. ‘South Quarry’, an excavation on the south-western side of ‘Hill 1’ (Woodburne 1967) an erosional remnant of the upper Waite Formation on the Alcoota Fossil Reserve. Ongeva Local Fauna, latest Miocene or earliest Pliocene in age.

Diagnosis. Differs from all thylacinids by the presence of the following autapomorphies: a short, lobe-like postcingulum between the metastyle and protocone of M₂; hypertrophied ventrolateral torus of the dentary with the buccolingual width of the dentary at the level of P₃ that is greater than 75% its depth at the same level. The presence of a small stylar cusp E on M₂ and M₃ might also be an autapomorphic reversal within the genus *Thylacinus* but the optimisation of the character is ambiguous due to its presence in the closely related outgroup, *Wabulacinus ridei*, and the absence of a preserved M² or M³ for *Th. macknessi*. Similarly the presence of a vestigial metaconid and metacristid on M₄ (and presumably the other lower molars) is ambiguous due to the presence of metaconids in *Th. macknessi* and their absence in *Th. potens*. This may represent an autapomorphic reversal in *Th. megiriani* or a case of convergent loss in *Th. potens* and the *Th. yorkellus* + *Th. cynocephalus* clade. It can be further distinguished from *Th. macknessi* and all non-*Thylacinus* thylacinids by: its greater size; the great reduction of the size of the paracone relative to the metacone; elongation of the postmetacrista, so that it is greater than 52% the length of the tooth in M² and M³. It can be further distinguished from *Th. potens* by: the long axis of P¹ aligned with those of the other upper premolars; the length of M¹ is greater than its width; the complete absence of a precingulum on M¹ and M³; the absence

of a metaconule on all upper molars; M^3 much longer (>5%) than M^2 ; M^3 longer than wide; presence of a diastema between P_3 and M_1 .

Remarks. The new dentary specimens cannot be referred to *Th. megiriani* on the basis of autapomorphic characteristics due to their fragmentary nature and lack of overlap with the holotype maxilla. However the apparent reversal to the presence of an, albeit vestigial, metaconid parallels the reappearance of a tiny tubercular styler cusp on the upper molars of the holotype.

Furthermore they derive from the same level in the same quarry as the holotype, are of an appropriately large size, and can be distinguished from *Th. potens*, which is the only other large-bodied thylacinid known from a similar time and place. For these reasons it is reasonable to refer them to *Th. megiriani*.

Description of the new material

The anterior dentary fragment (NTM P4376; Fig. 5-7, Table 3) has only broken roots and empty alveoli and does not contain any tooth crowns. This coupled with poor preservation means that it is not immediately obvious exactly which teeth the roots and alveoli belong to and therefore the disposition of the teeth in the jaw. However several lines of evidence indicate that the posterior two empty alveoli are for the anterior and posterior roots of M_2 , respectively, while the posterior two projecting root stumps are the mesial and distal roots of M_1 . Anterior to the molar alveoli there are the broken roots and alveoli of P_2 and P_3 (Fig. 7). Evidence for this interpretation comes from a partial bridge of finished bone between the second and third preserved alveoli, indicating that there was a diastema between two different teeth in this position, rather than these alveoli representing the anterior and posterior alveoli of the same tooth. The posterior limit of medial symphyseal surface is level with the front margin of the fourth alveolus. As the posterior end of the symphysis draws level with P_3 , or at least the diastema between P_2 and P_3 in all thylacinid specimens examined, the third and fourth alveoli in NTM P4376 should represent the anterior and posterior alveoli for P_3 . From the alveoli it can be seen that there was no diastema between M_1 and M_2 , but there was a short diastema of 3.6 mm between P_3 and M_1 , and a slightly longer diastema of 4.0 mm between P_2 and P_3 .

The dentary is dorsoventrally shallow but mediolaterally thickened, giving it a distinctly robust appearance. Adding to the thickness of the jaw is a strong torus developed along the ventrolateral margin of the dentary from a point level with the midlength of P_2 to one level with the distal end of M_1 . At the maximum thickness of the torus (level with the posterior root of P_3) the dentary measures 20.8 mm wide, which approaches the dorsoventral depth of the dentary at the same level (27.0 mm). The lateral surface of the dentary, above the ventrolateral torus, is pierced by three mental foramina. The anterior-most mental foramen lies anterior to the alveoli for P_2 , the middle foramen lies level with the anterior end of P_3 , and the posterior foramen lies level with the posterior end of M_1 .

The second specimen (NTM P4377; Fig. 8-10, Table 4) is a small fragment from the posterior end of a right dentary including a partial M_4 and the anterior base of the coronoid process. The medial surface of the dentary is gently convex dorsoventrally, whereas the lateral surface bears a ridge that slopes posterodorsally to merge with the leading margin of the coronoid process. The lateral ridge forms the lower border of a flat

dorsomedially facing surface that occurs below the fourth lower molar. The ventral part of the dentary is missing so the depth to height ratio cannot be measured. The incomplete M_4 includes the talonid and the posterior side of the protoconid. The protoconid is tall with an almost vertically oriented posterior margin. The protocristid extends from the apical tip of protoconid to a small tubercle about half-way down the posterior face of the protoconid (Fig. 10). This tiny tubercle appears to be a vestigial remnant of the metaconid which is usually absent in derived species of *Thylacinus*. Two weakly developed cristids extend ventrally from the tubercle. The two cristids diverge at a highly acute angle. The more buccally placed cristid is the cristid obliqua. It extends to the base of the protoconid and up the anterior face of the hypoconid. A shallow, weakly developed carnassial notch is created between the hypoconid and the protoconid. This notch is similar to the weak notches developed on the lower molars of *Th. potens* and unlike the deep clefts that can be observed in the carnassial notches of the lower molars of *Th. yorkellus* and *Th. cynocephalus*. The lingual cristid that branches from the tubercle on the posterior face of the protoconid is interpreted as a metacristid. It terminates at the base of the protoconid without extending onto the talonid. Its presence strengthens the interpretation of the tubercle as a vestigial metaconid. The moderately large, conical hypoconid comprises the talonid which bears no other cusps. The anterobuccal face of the hypoconid is planed off by an oblique wear facet that faces buccodorsally. The weak cristid obliqua extends directly anteriorly from the apex of the hypoconid. The anterolingual rim of the hypoconid is rounded, lacking a postcristid.

Cladistic Analysis

Th. yorkellus was included in an earlier cladistic analysis of thylacinid relationships (Yates 2014). This analysis already included data from the mandibular specimens of *Th. megiriani* described in this paper. The same characters from the previous were employed with one modification to character 36. Previously this character simply described the absence (0) or presence (1) of carnassial notch in the cristid obliqua of the lower molars. In the present analysis the derived state is divided into two states: a weakly-developed shallow carnassial notch (1) or a deep, strongly-developed carnassial notch (2). The multistate character is treated as ordered. The score for character 34 (metaconid size in m_{2-4}) of *Thylacinus megiriani* was changed from 2 (completely absent) to 1 (present as a minute cuspidule) in the light of the new evidence presented above.

The resulting matrix (Appendix 1) was subjected to a maximum parsimony analysis in PAUP 4.0b (Swofford, 2002) using the following settings: heuristic search; random addition sequence with 500 replicates; and TBR branch-swapping algorithm. The strength of the internal nodes was tested with a bootstrap analysis (1000 bootstrap replicates, heuristic searching with 50 addition sequence replicates).

The search resulted in two equally most parsimonious trees of 93 steps. The topologies of these two trees are completely congruent with the two trees obtained in the earlier analysis (Yates, 2014) with the loss of resolution entirely the result of a variable position of *Maximucinus muirheadae*. If this wildcard taxon is pruned *a posteriori* a fully resolved tree is obtained (fig. 11a). *Th. yorkellus* is found to be the sister species of the modern *Th. cynocephalus*. The *Th. yorkellus* + *Th. cynocephalus* is relatively robust with the second highest bootstrap score of all the internal clades (71 %, fig. 11b). Nevertheless missing data reduces the number of unambiguous apomorphies of this clade to one: the presence of a deep, well-developed carnassial notch and cristid obliqua on each of the lower molars.

270

271 Discussion

272 The recognition of *Th. yorkellus* increases the number of *Thylacinus* species in the Late Miocene – Earliest
 273 Pliocene interval to three: *Th. potens*, *Th. megiriani* and *Th. yorkellus*. A fourth lineage, that of the recent *Th.*
 274 *cynocephalus*, can also be inferred to have arisen in this period (Fig. 12). None of the local fauna that produced
 275 the three known species can be directly dated but they do appear to form a stratigraphic sequence. The
 276 Ongeva Local Fauna occurs in a channel incised into sediments that overlie those that contain the Alcoota Local
 277 Fauna, directly demonstrating that the former is younger than the latter (Megirian, Murray and Wells, 1996).
 278 However the absolute age difference between them is probably not great because many species are shared
 279 between the two deposits including the biostratigraphically important *Kolopsis torus* (Megirian, Murray and
 280 Wells, 1996). The presence of *Zygomaturus gilli* in the Ongeva Local Fauna indicates that it may be correlated
 281 with the Beaumaris Local Fauna from the Black Rock Sandstone of Port Phillip Bay (Megirian, Murray and
 282 Wells, 1996). The Beaumaris Local Fauna straddles the Mio-Pliocene boundary on the basis of local stratigraphic
 283 controls and its included marine invertebrate fauna (Dickinson et al, 2002). The relative difference between the
 284 Ongeva Local Fauna and the Curramulka Local Fauna is difficult to determine. Pledge estimated that the
 285 deposit was late Miocene in age which would make it roughly contemporaneous with, or possibly older than
 286 the Ongeva Local Fauna. However a constrained seriation analysis clustered the Curramulka Local Fauna with
 287 younger Pliocene local faunas that were given the age-name Tirarian while the Ongeva Local Fauna was
 288 clustered with the Beaumaris and Alcoota Local Fauna in the Waitean Age (Megirian et al. 2010). A younger
 289 age for the Curramulka Local Fauna is supported by the presence of a number of macropodid genera that are
 290 not known from the older Waitean fauna, including: *Baringa*, *Troposodon* and *Protemnodon* (Pledge, 1992).
 291 Nevertheless the Curramulka Local Fauna is probably one of the oldest Tirarian assemblages due to its total
 292 lack of rodent remains, despite intensive fine sieving of the silty matrix and presence of numerous other small
 293 vertebrates (Pledge, 1992). Thus an early Pliocene age of 4.5 ma or older would appear likely based on the
 294 timing of the appearance of rodents in other fossil deposits in Australia (Breed and Ford, 2007)

295 These three deposits do seem to form a stratigraphic sequence, and the sequence matches the branching
 296 order of *Thylacinus* species recovered in the cladistic analysis, supporting the hypothesis of an anagenetic
 297 lineage. However, the time difference between them is probably too small for a plausible anagenetic sequence.
 298 It is quite likely that all three local faunas span no more than 2 or 3 ma, from 5 ma to 7 or 8 Ma. If *Th. potens*,
 299 *Th. megiriani* and *Th. yorkellus* did indeed form an anagenetic lineage then the turnover of morphologically
 300 distinct forms would appear to be unrealistically fast, especially given the known range of *Th. cynocephalus* is
 301 nearly four million years (based on the late Pliocene age of the Chinchilla Local Fauna). Furthermore each of
 302 these species can be diagnosed with autapomorphies, suggesting that none is an ancestor of any other

303 Thus it would appear that for a brief period in the latest Miocene through to the earliest Pliocene the genus
 304 *Thylacinus* experienced a modest evolutionary radiation (Fig. 12). However the products of this radiation were
 305 short-lived and by the late Pliocene there is no indication of any surviving thylacinid species other than *Th.*
 306 *cynocephalus* (Dawson 1982). Unfortunately the Pliocene record of *Thylacinus* is sparse and scrappy (Mackness
 307 et al. 2002). Louys and Price (in press) report two specimens in the Queensland Museum that have been
 308 identified as *Th. rostralis* (= *Th. cynocephalus*) and genuinely derive from the Chinchilla Local Fauna. Apart from

309 these specimens, and *Th. yorkellus*, all other Pliocene occurrences of *Thylacinus* are specifically indeterminate
310 (Mackness et al. 2002).

311

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316 Steven Jackson.

317

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Appendix 1. Character-Taxon Matrix

The character list is provided in Yates (2014).

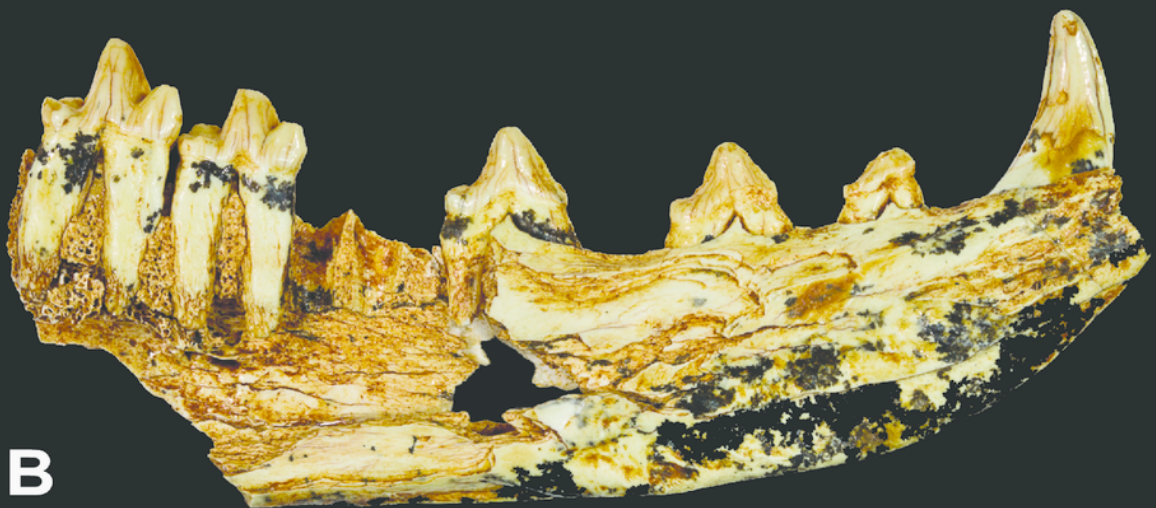
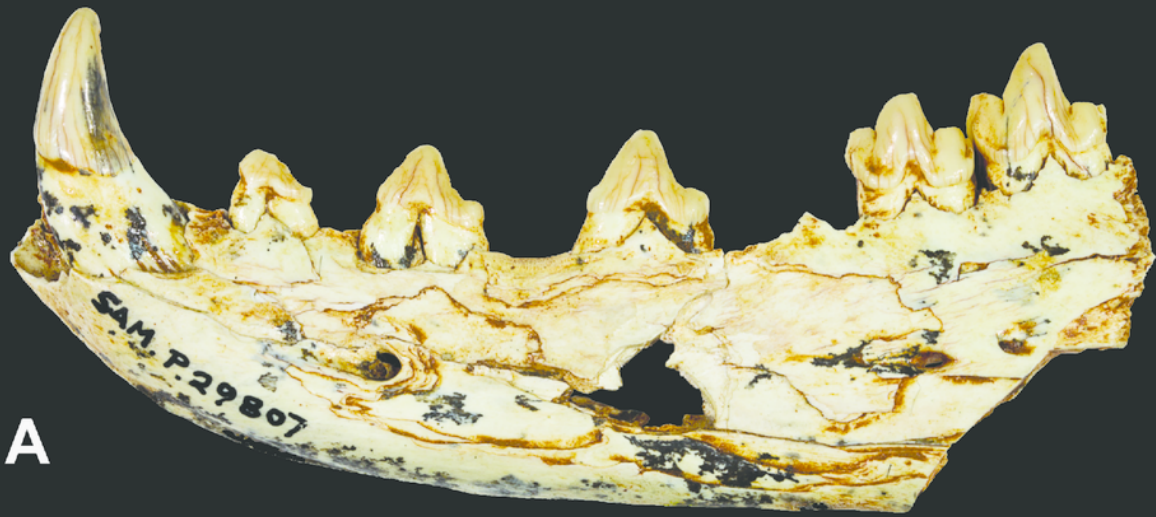
<i>Barinya wangala</i>	0?000001000000000000000010000000000000000000
<i>Antechinus flavipes</i>	000001000000000000000000000000000000000000
<i>Muribacinus gadiyuli</i>	01?????100000000000000000000000000000000000
<i>Badjcinus turnbulli</i>	00?01000?00?0?000000??100000001?2010100010
<i>Mutpuracinus archibaldi</i>	0?0?0000100010000000000010000001??010001000
<i>Nimbacinus dicksoni</i>	0001100010001?000000??010?0001??1010000000
<i>Nimbacinus richi</i>	?00??000100010?0001000010000111?101000?000
<i>Maximucinus muirheadae</i>	????????????10?0200????10????????????????1
<i>Ngamalacinus timmulvaneyi</i>	?1????1001?00??0?00000?000?10????1011100010
<i>Wabulacinus ridei</i>	00??????1?11?021111??10111??01??11001?1?0
<i>Tyarrpecinus rothi</i>	?????011?10010110101??000?00????????1???
<i>Thylacinus macknessi</i>	?????????0?11?02??10??10????01102111010110
<i>Thylacinus potens</i>	??1??0111001?0122210001?100010002221011102

411 *Thylacinus megiriani*
 412 111??001?21?001?221111111001?111?221?1??02
 413 *Thylacinus cynocephalus*
 414 210111000211111222111110121101112221011101
 415 *Thylacinus yorkellus*
 416 ?????????????????????????0111222101?1?1
 417
 418

1

Thylacinus yorkellus, holotype SAM P29807, incomplete left dentary.

Photographs of the specimen. (A) lateral view. (B) medial view. (C) dorsal view. Scale bar = 50 mm.

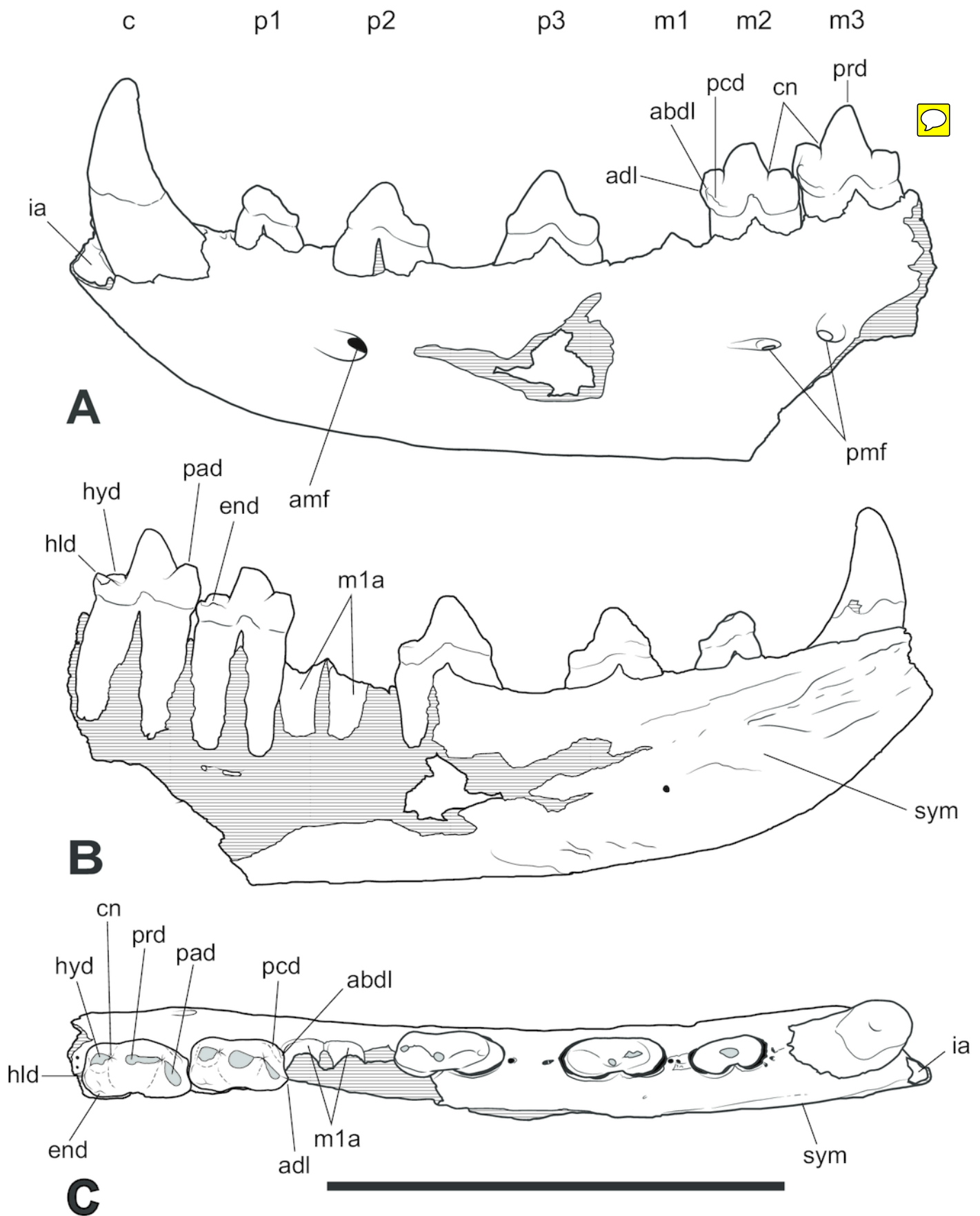


2

Thylacinus yorkellus holotype SAM P29807, incomplete left dentary.

Interpretive drawings of the specimen. (A) lateral view. (B) medial view. (C) dorsal view.

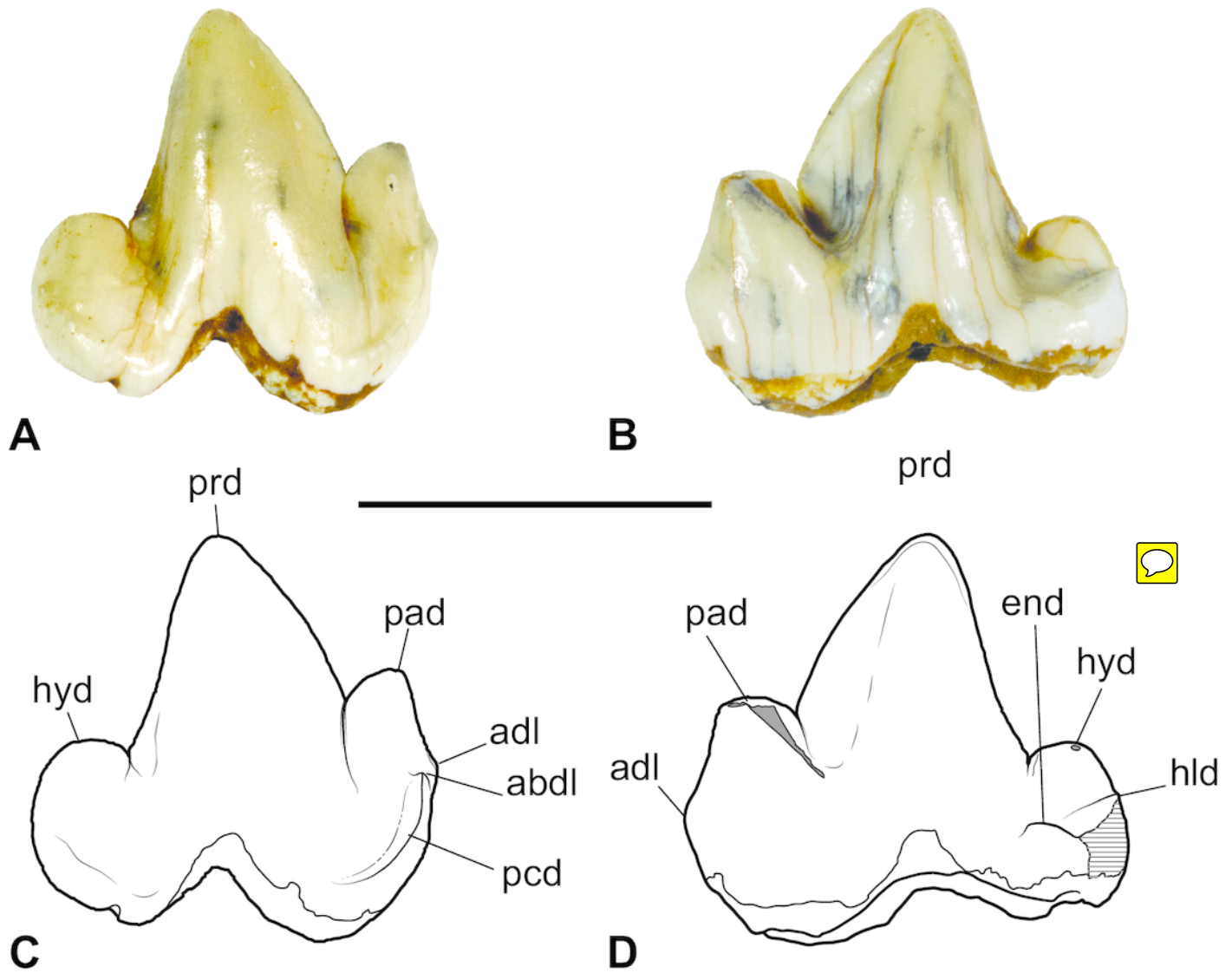
Abbreviations: adl, anterior cuspidule; abdl, anterobuccal cuspidule; amf, anterior mental foramen; c, canine; cn, carnassial notch; end, entoconid; hld, hypoconulid; hyd, hypoconid; ia, incisor alveoli; m1-3, molars 1-3; p1-3, premolars 1-3; pad, paraconid; pcd, precingulid; pmf, posterior mental foramen; prd, protoconid; sym, symphyseal surface. Hatched areas represent broken bone surfaces, grey areas represent wear facets on the teeth. Scale bar = 50 mm.



3

Thylacinus yorkellus, paratype SAM P38799, right m_3 .

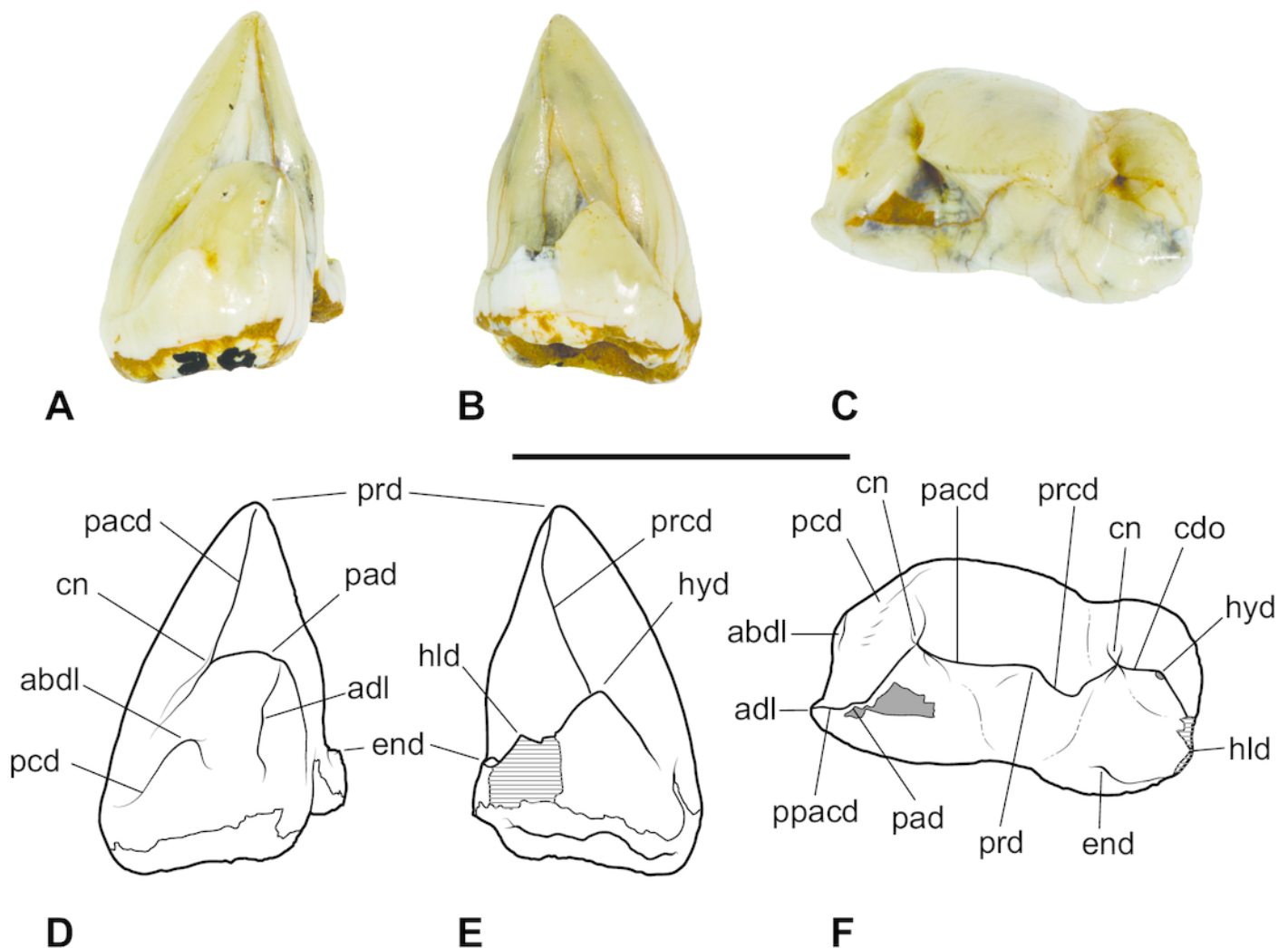
(A) photograph in buccal view. (B) photograph in lingualview. (C) Interpretive drawing of A. (D) Interpretive drawing of B. Abbreviations: adl, anterior cuspidule; abdl, anterobuccal cuspidule; cn, carnassial notch; end, entoconid; hld, hypoconulid; hyd, hypoconid; pad, paraconid; pcd, precingulid; prd, protoconid; Scale bar = 10 mm. [p]



4

Thylacinus yorkellus, paratype SAM P38799, right m_3

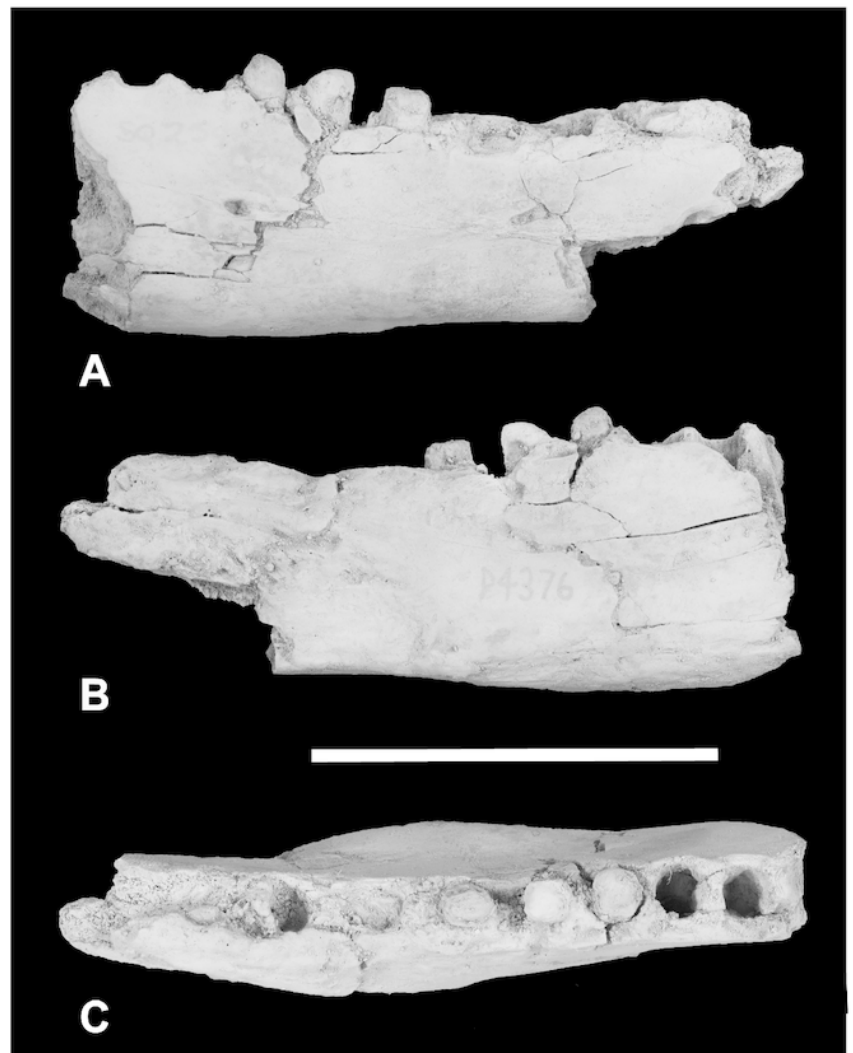
(A) photograph in anterior view. (B) photograph in posterior view. (C) photograph in occlusal view (D) Interpretive drawing of A. (E) Interpretive drawing of B (F) Interpretive drawing of C. Abbreviations: adl, anterior cuspidule; abdl, anterobuccal cuspidule; cdo, cristid obliqua; cn, carnassial notch; end, entoconid; hld, hypoconulid; hyd, hypoconid; pacd, paracristid; pad, paraconid; pcd, precingulid; ppacd, preparacristid; prcd, protocristid; prd, protoconid; Scale bar = 10 mm.



5

Thylacinus megiriani, NTM P4376, fragmentary right dentary.

Monochrome photographs of the specimen after whitening with ammonium chloride. (A) lateral view. (B) medial view. (C) dorsal view. Scale bar = 50 mm.



6

Thylacinus megiriani, NTM P4376, fragmentary right dentary.

Colour photographs of the specimen. (A) lateral view. (B) medial view. (C) dorsal view. Scale bar = 50 mm.



A



B



C

7

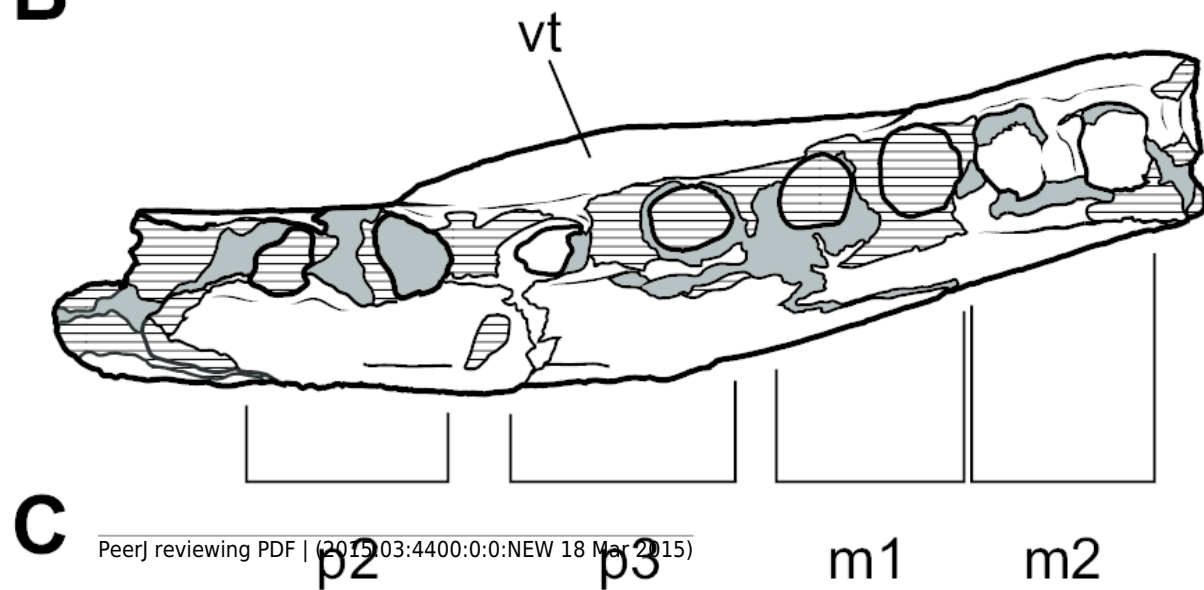
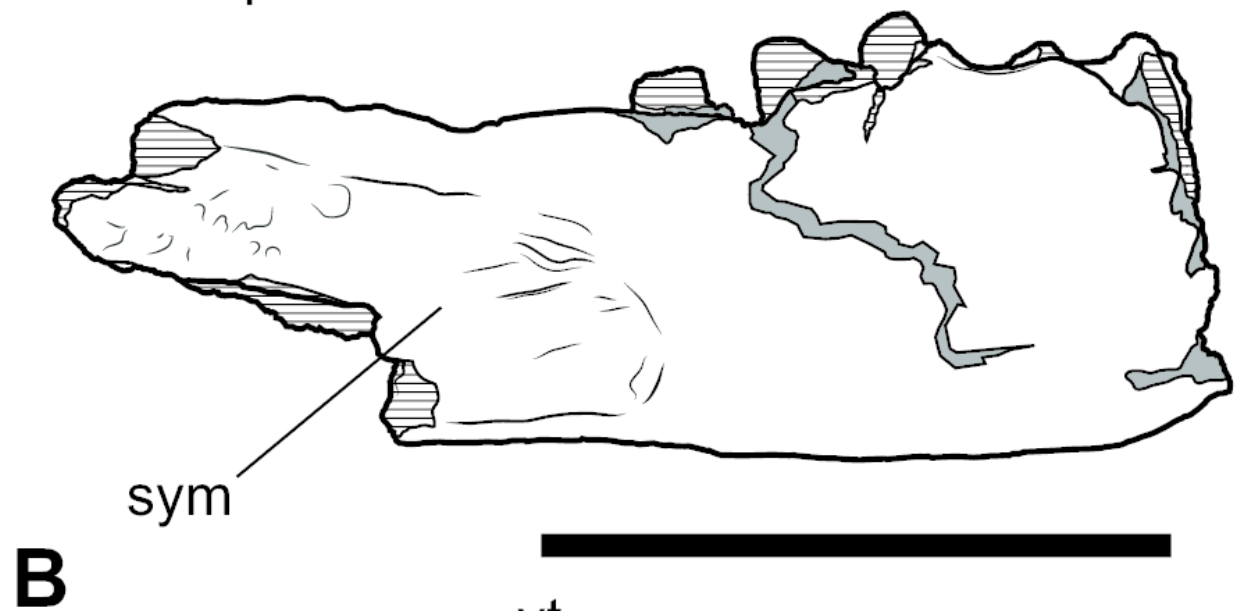
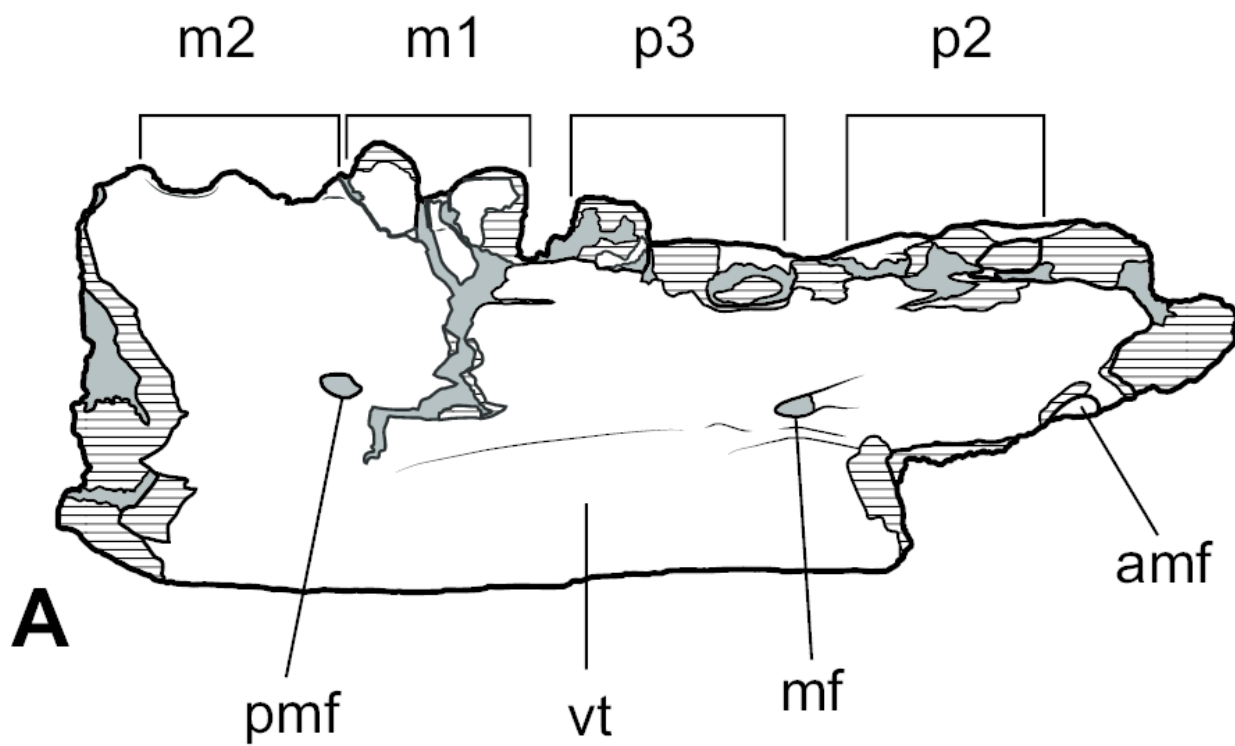
Thylacinus megiriani, NTM P4376, fragmentary right dentary.

Interpretive drawings of the specimen. (A) lateral view. (B) medial view. (C) dorsal view.

Abbreviations: amf, anterior mental foramen; m1-2, molars 1-2; mf, mental foramen; p1-2, premolars 1-2; pmf, posterior mental foramen; sym, symphyseal surface; vt, ventral torus.

Hatched areas represent broken bone surfaces, grey areas represent patches of matrix.

Scale bar = 50 mm.



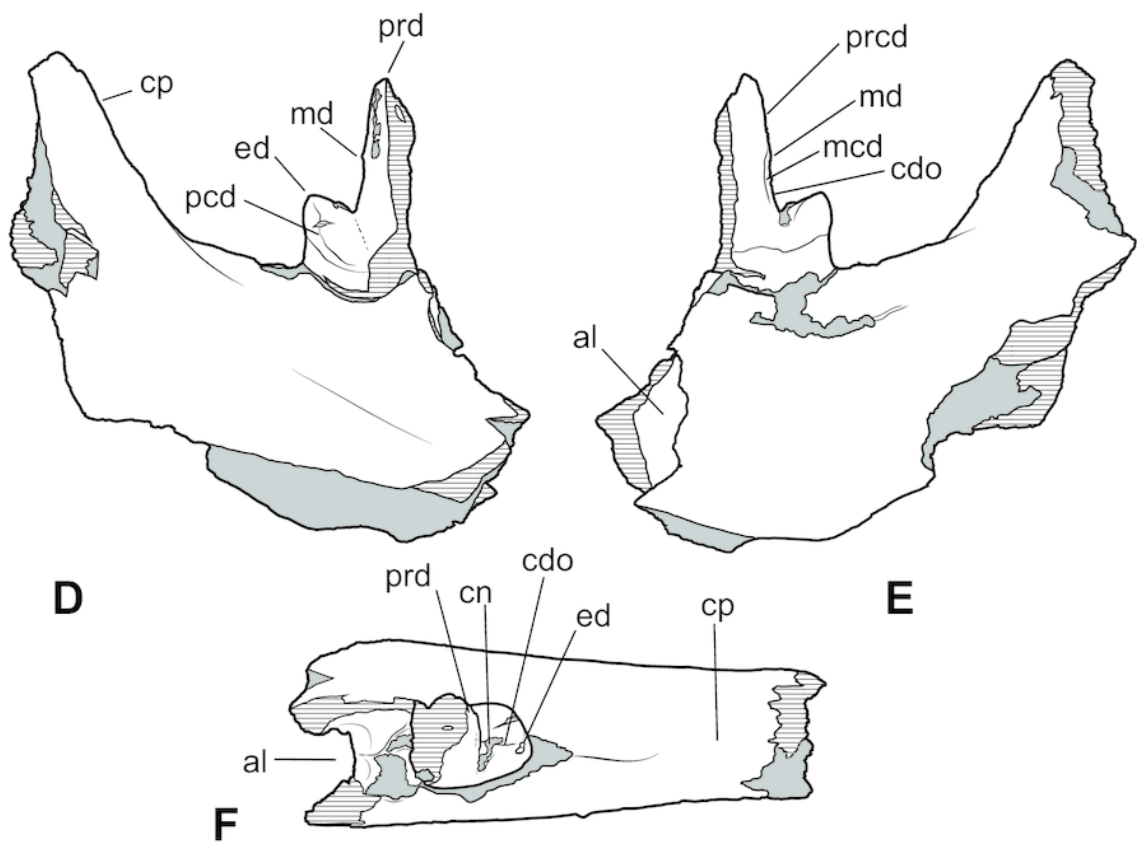
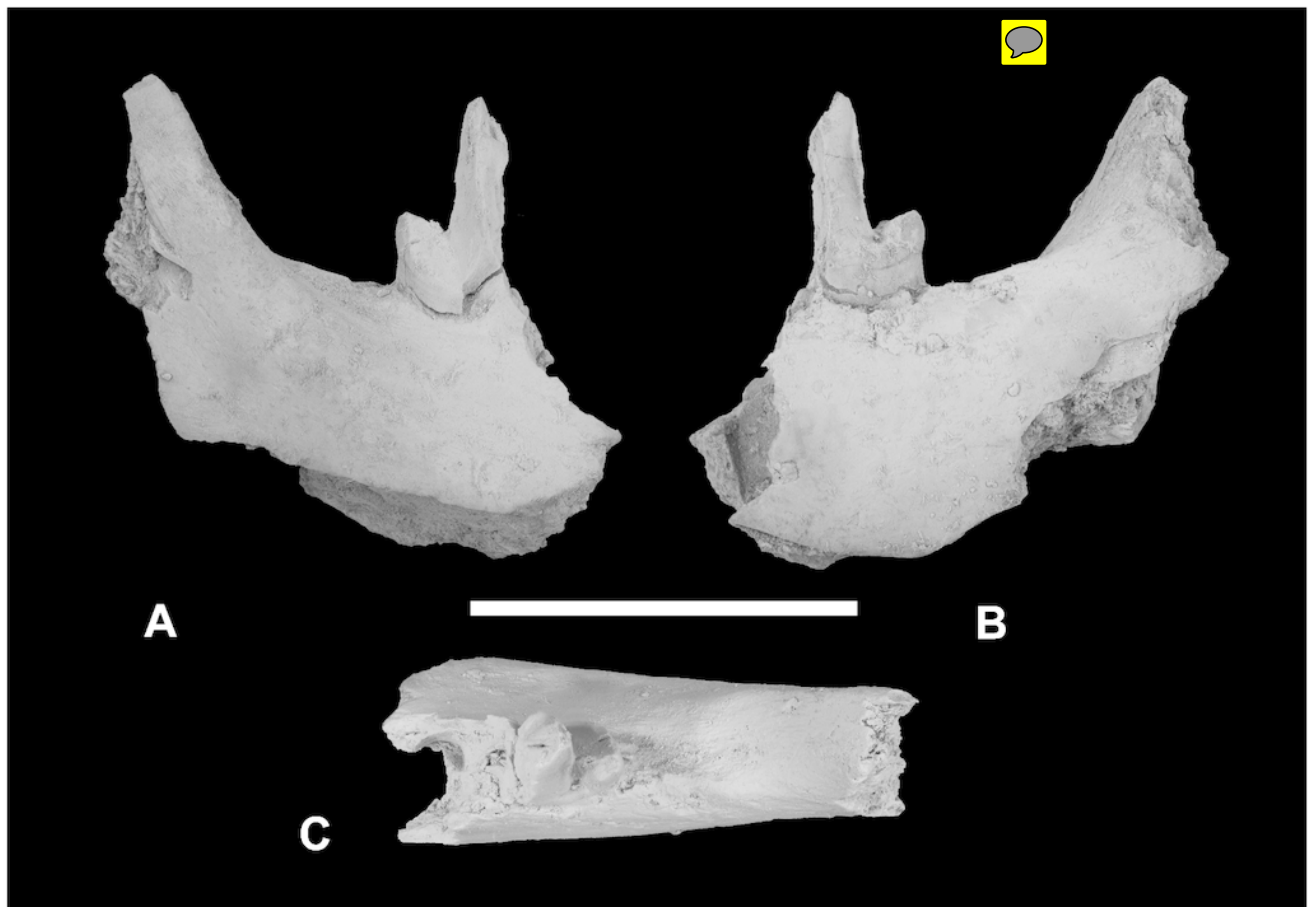
8

Thylacinus megiriani, NTMP4377, fragment of right dentary including partial right m4.

(A-C) monochrome photographs of the specimen after whitening with ammonium chloride.

(D-F) interpretive drawings of A-C. (A, D) lateral view. (B, E) medial view. (C, F) dorsal view.

Abbreviations: al, alveolus for anterior root of m4; cdo, cristid obliqua; cn, carnassial notch; cp, base of coronoid process; ed, entoconid; mcd, metacristid; md, metaconid; pcd, postcristid; prcd, protocristid; prd, protoconid. Grey areas represent patches of matrix, hatched areas represent broken bone or tooth surfaces. Scale bar = 30 mm.



9

Thylacinus megiriani, NTMP4377, fragment of right dentary including partial right m4.

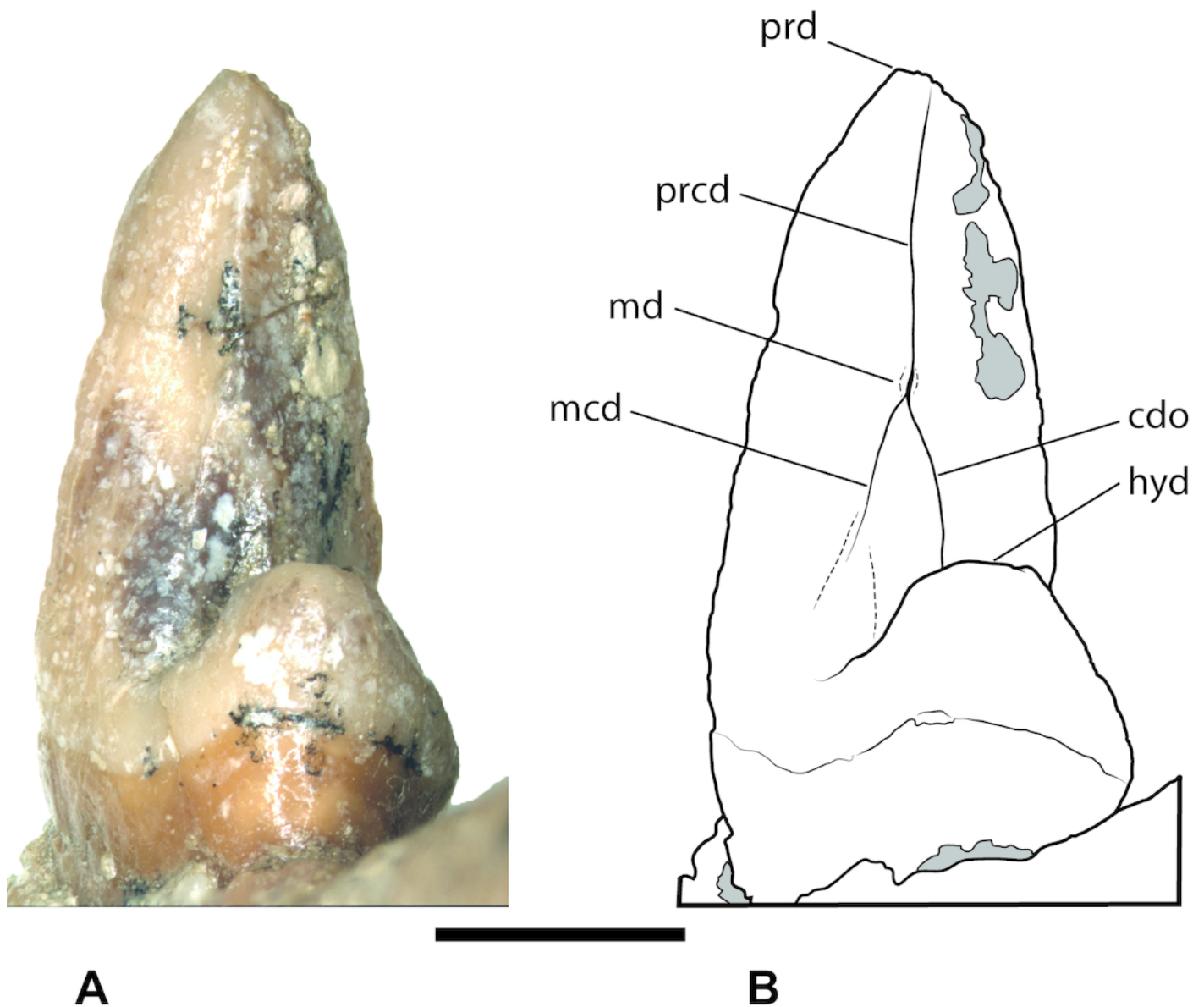
Colour photographs of the specimen. (A) lateral view. (B) medial view. Scale bar = 30 mm.



10

Thylacinus megiriani, NTM P4377, right m_4 in posterolingual view.

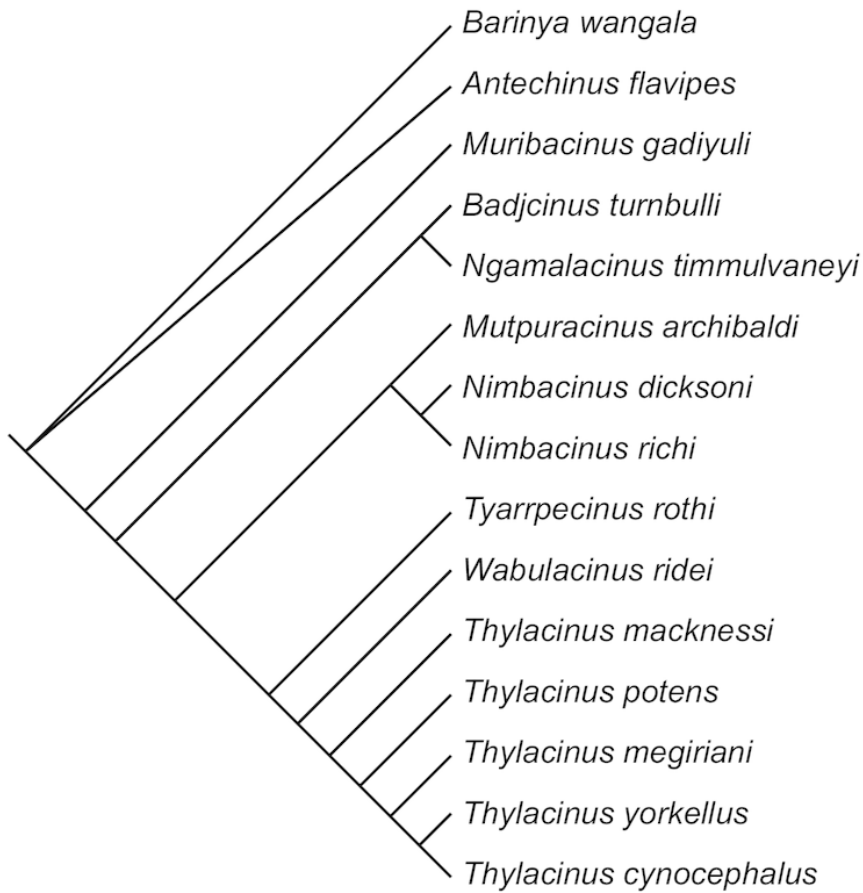
(A) photograph. (B) interpretive drawing. Abbreviations: cdo, cristid obliqua; hyd, hypoconid; mcd, metacristid; md, metaconid; prcd, protocristid; prd, protoconid. Grey areas represent patches of adherent matrix. Scale bar = 5 mm.



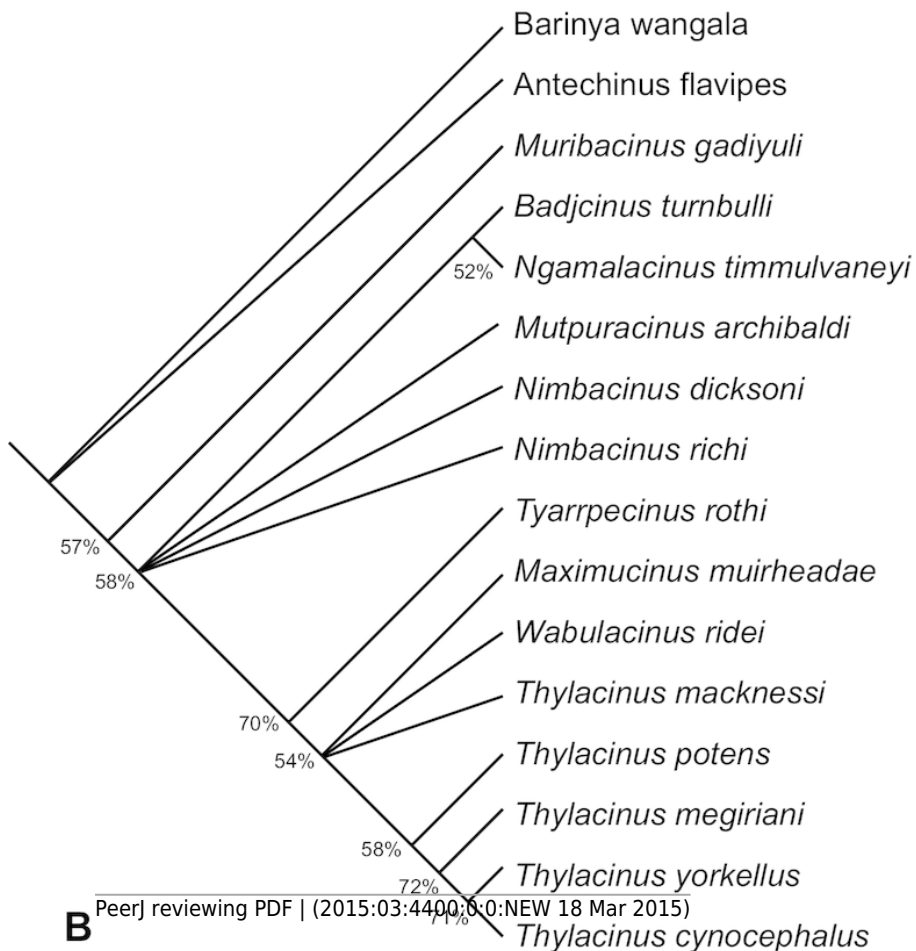
11

Results of the cladistic analysis of thylacinid interrelationships.

A) reduced cladistic consensus tree of two most parsimonious trees (tree length = 93 steps) obtained after a posteriori pruning of *Maximucinus muirheadae*. (B) strict consensus with bootstrap support values for clades with values > 50 %.



A



B

12

A phylogenetic tree of *Thylacinus*, calibrated to the geological timescale.

Note that the dates of *Th. potens*, *Th. megiriani* and *Th. yorkellus* are not tightly constrained and the ages given here are approximations with the grey bars indicating a range of plausible ages. Numbers represent ages in ma. Dates of boundaries taken from Cohen et al. (2013).

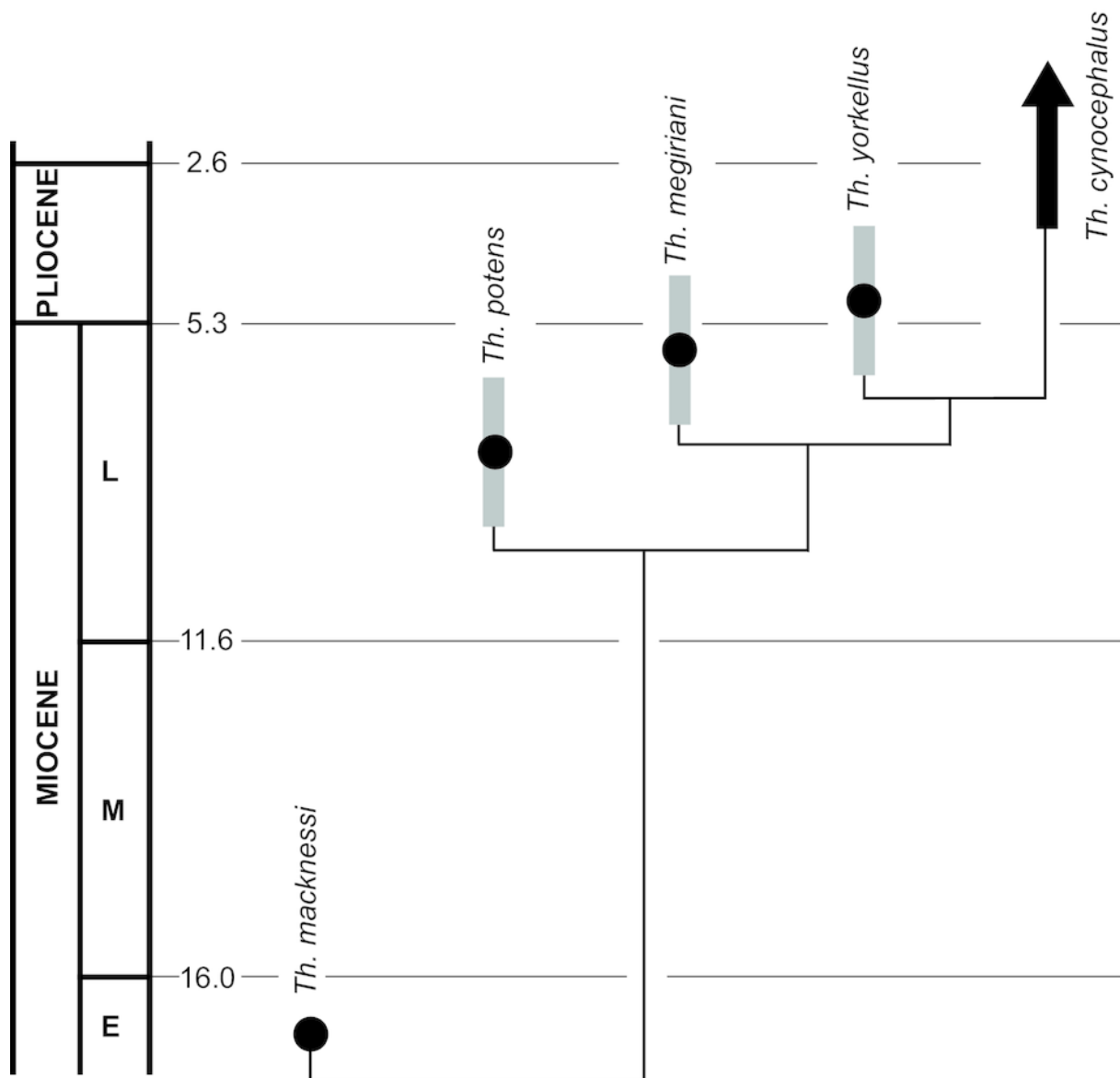


Table 1 (on next page)

Canine measurements of *Thylacinus yorkellus*.

Holotype SAM P29807.

Height (mm)	Basal Length (mm)	Basal Width (mm)
15.2	8.7	6.5

2

Table 2 (on next page)

Dental measurements of *Thylacinus yorkellus*.

Abbreviations: L, anteroposterior length of the crown; W, maximum buccolingual width of the crown; trigW, buccolingual width of the trigonid; talW, buccolingual width of the talonid.

Measurements are in mm. Note that M1L of SAM P29807 is an approximation based on the measurement taken from the empty alveolus.

	P ₁ L	P ₁ W	P ₂ L	P ₂ W	P ₃ L	P ₃ W	M ₁ L	M ₂ L	M ₂ trigW	M ₂ talW	M ₃ L	M ₃ trigW	M ₃ talW
SAM P29807	7.2	3.1	9.8	4.0	10.4	4.4	~8.7	11.0	5.5	5.8	12.0	6.5	5.7
SAM P38799	-	-	-	-	-	-	-	-	-	-	11.3	6.0	6.0

2

Table 3(on next page)

Approximate basal lengths of the teeth in *Thylacinus megiriani*.

Referred specimen, NTM P4376. Measurements taken from alveoli.

P_2 (mm)	P_3 (mm)	M_1 (mm)	M_2 (mm)
15.6	18.0	14.3	13.4

2

Table 4(on next page)

Dental measurements of *Thylacinus megiriani*.

Referred specimen, NTM P4377. Abbreviations: H, height of crown, from crown-root junction to tip of protoconid; trigW, buccolingual width of trigonid; talW, buccolingual width of talonid. Note that trigonid width is measured as preserved and that due to incompleteness this represents a minimum value and that the true value may have been greater.

M₄H (mm)	M₄trigW (mm)	M₄talW (mm)
16.9	(7.3)	6.5

2