

Earliest known record of a hypercarnivorous dasyurid (Marsupialia), from newly discovered carbonates beyond the Riversleigh World Heritage Area, north Queensland

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Abstract

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Whollydooleya tomnpatricorum gen. et sp. nov. is a new, highly specialised hypercarnivorous dasyuromorphian from a new mid-Cenozoic limestone deposit southwest of the Riversleigh World Heritage Area in northwestern Queensland. Dental dimensions suggest it may have weighed at least twice as much as the living Tasmanian devil (*Sarcophilus harrisi*). Although known only from a lower molar, it exhibits a plethora of carnivorous adaptations including a hypertrophied protoconid, tiny metaconid and a battery of vertical carnassial blades between most of the major cusps, most of which incorporate carnassial notches to immobilise materials being sheared. It is unique among dasyuromorphians in having a massive entoconid that closes the entire lingual side of the talonid. Comparison with previously known thylacinid and dasyurid hypercarnivores suggests its relationships are closer to dasyurids than thylacinids in the main because of the very large entoconid, a cusp that is relatively small to absent in all known thylacinids but commonly small to large in dasyurids. However, the extent of enlargement of the entoconid suggests that it is not closely related to previously known Cenozoic hypercarnivorous dasyurids in the genera *Dasyurus*, *Glaucodon*, *Sarcophilus* or any of the other previously described Cenozoic dasyurids. Although the early late Miocene *Ganbulanyi djadjinguli* is only known from an upper molar, the reduced area of its protocone suggests a correspondingly reduced rather than hypertrophied entoconid in its as-yet-unknown lower molars. Reconsideration of the structure of the talonid in species of *Sarcophilus* even suggests that within that Quaternary lineage, the entoconid may have been entirely lost, with the posteriorly displaced metaconid taking its functional place as an occlusal counterpart for the blades of the protocone. The large size of the new species signals the earliest indication within the dasyurid radiation of a late Cenozoic trend towards gigantism that became evident in many lineages of Australian marsupials. While the age is uncertain, on the basis of associated taxa such as species of *Ekaltadeta*, it is probably either mid or late Miocene in age. Geological features of the deposit suggest it was formed within a pool in a cave environment that periodically underwent desiccation. Some grains suggest an aeolian as well as an alluvial and pluvial origin for the deposit. This may relate to current understanding about environmental change that took place in the region following the mid Miocene climate oscillation.

Keywords

Dasyuridae; Dasyurinae; Thylacinidae; Riversleigh; Miocene; *Whollydooleya*; *Dasyurus*; *Sarcophilus*; *Glaucodon*; *Ganbulanyi*; *Thylacinus*

Introduction

In 2012, M. Archer, P. Creaser and H. Godthelp, with the assistance of the Queensland Parks and Wildlife Service, had the opportunity to explore a Cenozoic terrain approximately 1.2 km southeast of the southwestern border of the Riversleigh World Heritage Area but within the boundaries of Boodjamulla (Lawn Hill) National Park in northwestern Queensland. The purpose was to test an unpublished hypothesis developed by geologist Ned Stephenson. He had concluded (and speculatively mapped) on the basis of satellite data that Cenozoic freshwater limestone deposits similar to those contained within the World Heritage Area might occur within an equally vast region southwest of the known fossil deposits. A similar inference about the fossiliferous potential of the rocks in this same general area had previously been suggested by Rick Arena in 2009 on the basis of Google Earth imagery. One of the first ground-based discoveries that supported this hypothesis, made by P. Creaser, was a fossil deposit named Wholly Dooley Site on an isolated limestone knoll named Wholly Dooley Hill. Small samples of Wholly Dooley matrix were treated with acetic acid in the UNSW laboratory to obtain samples of the vertebrate fauna.

Among the first teeth recovered was a highly distinctive lower molar of a carnivorous marsupial, which is the subject of this paper. In 2013, the National Geographic Society provided research funding to M. Archer and colleagues to continue exploration in this remote region of northwestern Queensland. Additional new sites and faunal assemblages were discovered in 2013 and 2014 in the new area, now named New Riversleigh, but as yet none have produced additional specimens of this new carnivore.

Although several fossil Oligo-Miocene putative dasyurids or dasyurid-like taxa have already been described from the Riversleigh region (i.e., species of *Ganbulanyi*, *Barinya*, *Mayigriphus*, *Malleodectes* and *Joculusium*; Wroe, 1997a, 1998, 1999, 2001; Arena et al., 2011), these are significantly different from *Whollydooleya tomnpatrichorum* gen. et sp. nov. in terms of key structural features (see below in Comparisons). Although the only known specimen of *Ganbulanyi djadjinguli* Wroe, 1998 is a fractured, isolated upper molar with some features suggesting it was a hypercarnivore, in other features it too is clearly distinct as well as significantly smaller than the taxon described herein. Other distinctive Australian carnivorous marsupials previously described as late Oligocene dasyurids (e.g., *Ankotarinja*, *Keeuna*, *Wakamatha* and *Dasyulurinja* [Archer, 1976a, 1982; Archer and Rich, 1979] relegated by Wroe [1996, 1997b] to *Dasyuromorphia incertae sedis* and Godthelp et al. [1999] to *Marsupialia incertae sedis*), are tiny to small insectivores all of which lack the hypercarnivorous specialisations evident in *W. tomnpatrichorum*.

Abbreviations used in this paper include the following: QM F, Queensland Museum palaeontological collections; NMV P, Museum Victoria Palaeontology Collection; prd, protoconid; med, metaconid; hyd, hypoconid; end, entoconid; hyld, hypoconulid; co, cristid obliqua; mcd, metacristid; STB, stylar cusp B; STD, stylar cusp D. Molar morphology follows that used by Archer (1976b) or is self-explanatory or in common use. Thegotic terminology (e.g., alpha-scissorial)

follows that used by Every (1970). Molar serial homology follows that used by Thomas (1888).

Systematics

Dasyuridae Goldfuss, 1820

?Dasyurinae Goldfuss, 1820

Whollydooleya Archer et al., gen. nov.

Generic diagnosis. Species of *Whollydooleya* differ from all other dasyuromorphians in having a massive (rather than blade-like, conical or reduced) entoconid that completely closes the lingual flank of the talonid.

Type species. *Whollydooleya tomnpatrichorum* Archer et al., 2015, sp. nov., by monotypy.

Whollydooleya tomnpatrichorum Archer et al., 2015, sp. nov.

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Specific diagnosis. That of the genus until additional species are known.

Holotype. QM F57892, partial right lower molar, interpreted to be either M_2 or M_3 .

Type locality. Wholly Dooley Site, Wholly Dooley Hill, the New Riversleigh area, southwest and adjacent to the Riversleigh World Heritage Area, northwestern Queensland. Wholly Dooley Site is one of several fossiliferous localities discovered by P. Creaser et al. on Wholly Dooley Hill in 2012. GPS coordinates for this site have been recorded with the Queensland Museum, Brisbane.

Etymology. The generic name refers to Wholly Dooley Site, which was discovered and named in 2012 by P. Creaser following preliminary analyses of satellite data by Ned Stephenson and Google Earth imagery by Rick Arena. The generic name is hereby given masculine gender. The species name honours Tom and Pat Rich for their years of research that included joint work on the mid-Cenozoic deposits of Riversleigh.

Geological context

The Wholly Dooley Site deposit (Fig. 1) shares a number of characteristics with other deposits at Riversleigh that indicate it represents an accumulation formed within a cave whose walls and ceiling have subsequently eroded away (Arena et al., 2014). The host micrite is dominated by calcite, with moderately common broken mollusc shell fragments and detrital quartz grains (Fig. 2A) and uncommon calcite pelloids and calcite rafts (Fig. 2B). The occurrence of calcite cave rafts is indicative of a quiescent pool of carbonate-rich water and suggests that these formed within a karst environment, possibly a small cave pool.

There is a clearly defined erosional contact between the host micrite and an overlying layer (layer 2; Fig. 2C). This layer comprises Fe-oxide (various mixtures of hematite and goethite), pelloids (Fig. 2D), detrital quartz grains and abundant late calcite-fill. Quartz in this later fill occurs as equant to prismatic,



Figure 1. Wholly Dooley Site, Wholly Dooley Hill, northwestern Queensland. The grey limestone massifs to the left are unfossiliferous Cambrian limestone and probably represent part of the western and southern walls of the original cave chamber. Fossiliferous Wholly Dooley matrix has been obtained from the excavated depression in the centre. About 7.2 km NE from this point is the approximate centre of the Riversleigh World Heritage Area; about 1.2 km NWN from this point is the southwestern boundary of the RWhA. Photo M. Archer.

subangular to well-rounded grains. Some of the quartz grains are highly fractured and coated in hematite/goethite, suggesting an aeolian origin. The abundance of goethite within this layer as fine colloidal aggregates and growths suggests a change in the environment, with drying-out of the cave system and evaporation of oxygen-rich cave waters, leading to *in situ* Fe-oxide precipitation. This drying-out of the environment is also indicated by the aeolian-derived detrital quartz grains. However, the lack of conspicuous desiccation cracks suggests that the sediment remained damp as it accumulated within the cave environment.

Layer 2 is unconformably overlain (erosional contact) by layer 3. Layer 3 comprises relatively abundant detrital quartz grains, and distinctly rhythmically banded goethite/calcite (Fig. 3A), with calcite also occurring as a void-fill phase (Fig. 3B). The layer also contains rare well-rounded subequant detrital tourmaline grains and cryptocrystalline silica as overgrowths around detrital quartz grains (Fig. 3C). Also

within this layer is possible microbial-mediated goethite (Fig. 3D). The occurrence of rhythmically banded goethite/calcite suggests constantly changing water chemistry, from carbonate-rich waters to oxygen-rich waters, throughout crystallisation of this layer. The microbial-mediated goethite suggests that the system was exposed to at least periodic sunlight, and may indicate unroofing of the cave system.

The proposed paragenesis of Wholly Dooley Site is detrital quartz and tourmaline and fossil bone fragments, followed by calcite (CaCO_3), then rhythmic deposition of goethite ($\text{FeO}(\text{OH})$) and calcite (CaCO_3). However the overall composition is highly variable, ranging from 10 to 30 modal% quartz, 20 to 40 modal% colloidal goethite and 30 to 70 modal% calcite cement. The size and shape of quartz grains are highly variable, ranging from subangular to well-rounded and equant to subprismatic in shape and the quartz grains are poorly sorted. There is also evidence of well-developed undulose extinction within many of

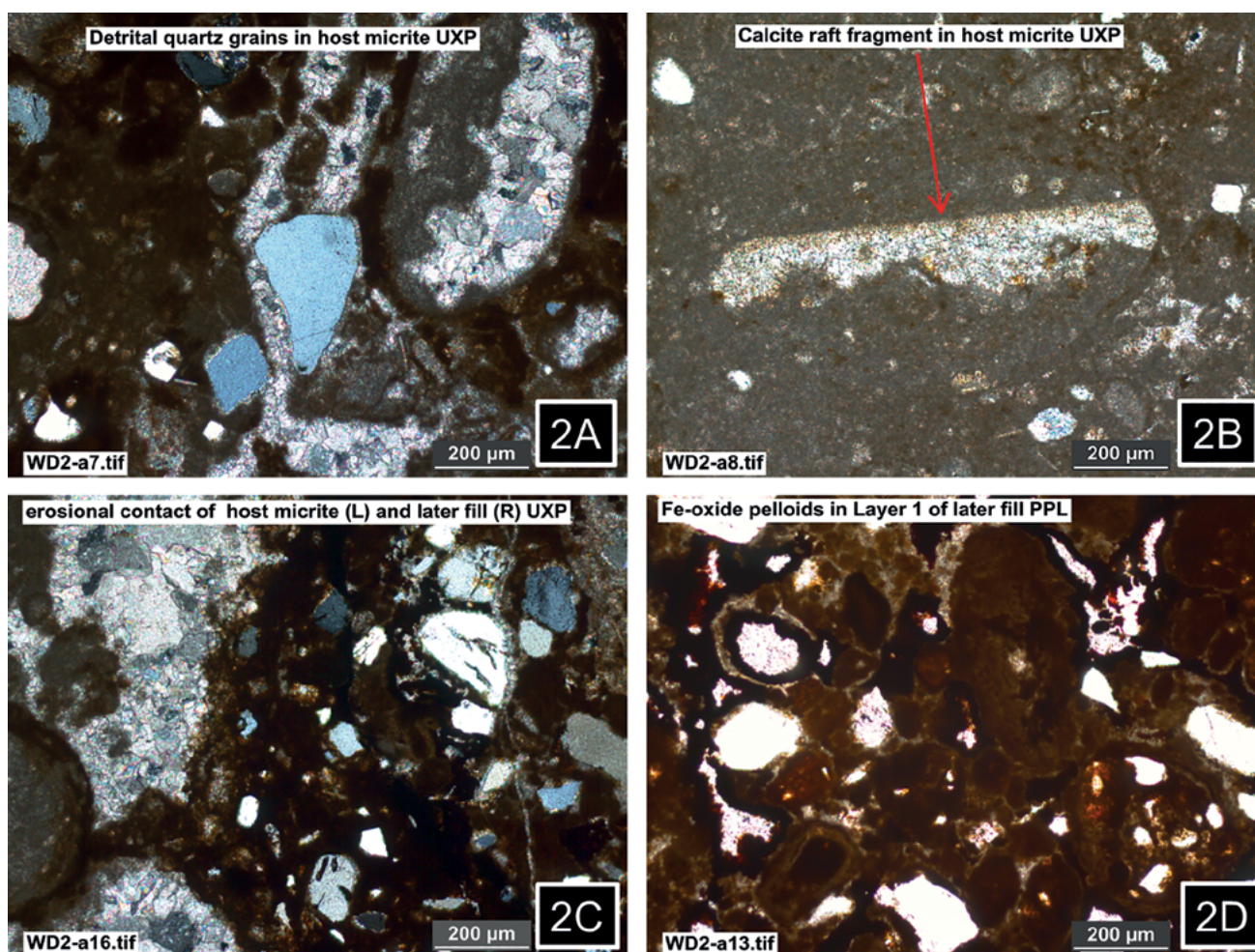


Figure 2. Photomicrographs of geological thin sections from Wholly Dooley Site. A, Detrital quartz grains within the host micrite UXP; B, calcite raft fragment within host micrite UXP; C, erosional contact between host micrite (left) and overlying layer 1 (right) showing abundant aeolian-derived quartz within layer 1 UXP; D, Fe-oxide pelloids and detrital quartz grains within layer 1 PPL. WD2 numbers refer to thin section images produced in the School of Biological, Earth & Environmental Sciences.

the quartz grains, along with uncommon recrystallised quartz grains. These features suggest that the detrital quartz grains are derived from at least three sources, including: 1, a proximal source via eluvial deposition (angular prismatic grains); 2, a more distal source via aeolian deposition (hematite-coated highly fractured equant-shaped well-rounded grains); and 3, a more distal source (subrounded to well-rounded equant to subprismatic grains) introduced via alluvial processes.

On balance, these sedimentological attributes suggest this deposit accumulated under somewhat different circumstances than those involved in accumulation of the previously known Oligo-Miocene fossil deposits from the Riversleigh World Heritage Area. The suggestion of intermittent desiccation may indicate accumulation during a younger, climatically drier period than those involved in triggering Depositional Phases 1–3 in the Riversleigh World Heritage Area (Creaser, 1997; Arena, 2004; Woodhead et al., 2014).

Description of the holotype

The holotype (Figs 4A–C, 5, 6, 9A–A'), which is comparable in size to the M_3 of the extant Tasmanian devil (*Sarcophilus harrisi*)¹, retains the entire talonid and broken posterior half of the trigonid. Partially repaired damage to the protoconid, from accidental breakage during preparation, has resulted in retention of a small displaced fracture that extends across the posterior face of the trigonid from the metaconid to the base of the protoconid. Structures missing from this tooth because of natural, taphonomic loss include the protocristid, paraconid and anterior cingulid.

¹ There is uncertainty in the current literature about the nomenclatural relationship of *lanarius* Owen, 1838 and *harrisi* Boitard, 1841. Here we follow Dawson (1982) in using *harrisi* as the appropriate name for the living species on the interpretation that the larger extinct and smaller living Tasmanian Devils are neither clearly synonymous nor chronospecies.

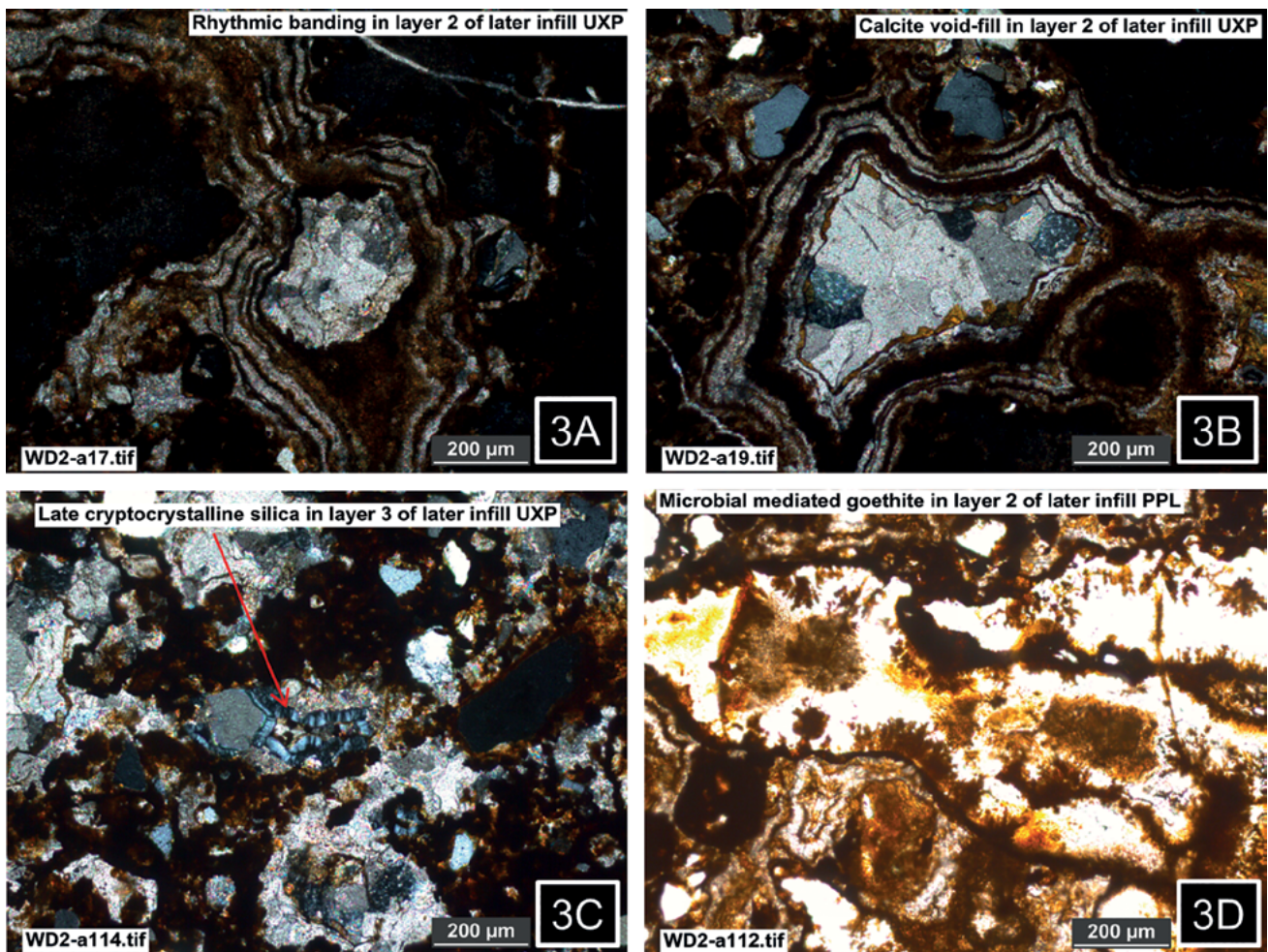


Figure 3. Photomicrographs of geological thin sections from Wholly Dooley Site later infills. A, Rhythmically banded calcite and goethite UXP; B, calcite filling void in layer 2 UXP; C, late cryptocrystalline silica (indicated by red arrow) filling fractures UXP; D, possible microbially mediated goethite precipitation (dendrites) in layer 2 PPL. WD2 numbers represent images of thin sections produced in the University of New South Wales.

The trigonid has a massive, well-developed protoconid and very small metaconid on the posterolingual flank of the protoconid. There is a rudimentary but distinct carnassial notch between the metaconid and metacristid at the point where the metaconid diverges from the posterolingual flank of the trigonid. There is a nearly vertical postmetacristid that descends from the metaconid to form the anterior half of a carnassial notch in a small, very steeply inclined lingual blade composed of the preentocristid and postmetacristid, as occurs in some dasyurids (e.g., species of *Dasyurus*).

The extremely steeply inclined metacristid, which is close to vertical in orientation, has sustained wear resulting from mastication that has breached the enamel on the lingual side of the trigonid with consequent production of a very sharp cutting edge along the shearing edge of this blade. The enamel exposed at the margins of this blade, and elsewhere over the entire crown, is very thin.

The posterior flank of the metacristid has been secondarily (during life) planed off by the preparacrista and preprotocrista of the corresponding upper molar producing a thegotic facette that covers most of the posterior flank of the trigonid trailing the dorsal leading edge of the metacristid blade, as occurs in all other dasyuromorphians. The wear striae on this facette are uniformly shallow, unidirectional and extend the length of the facette, features that are normal attributes of thegotic facettes (Every, 1970). This extensive facette also extends onto the posterobuccal apex of the metaconid after bridging rather than faceting the notch between the metaconid and metacristid. The tip of the protoconid, insofar as it is preserved, exhibits a very small apical wear facette, suggesting that this animal was relatively young at the time of death and that the extremely well-developed facette on the posterior flank of the metacristid is in fact primarily the result of tooth/tooth thegosis rather than mastication involving food. Nevertheless it is possible that the thegotic striations have

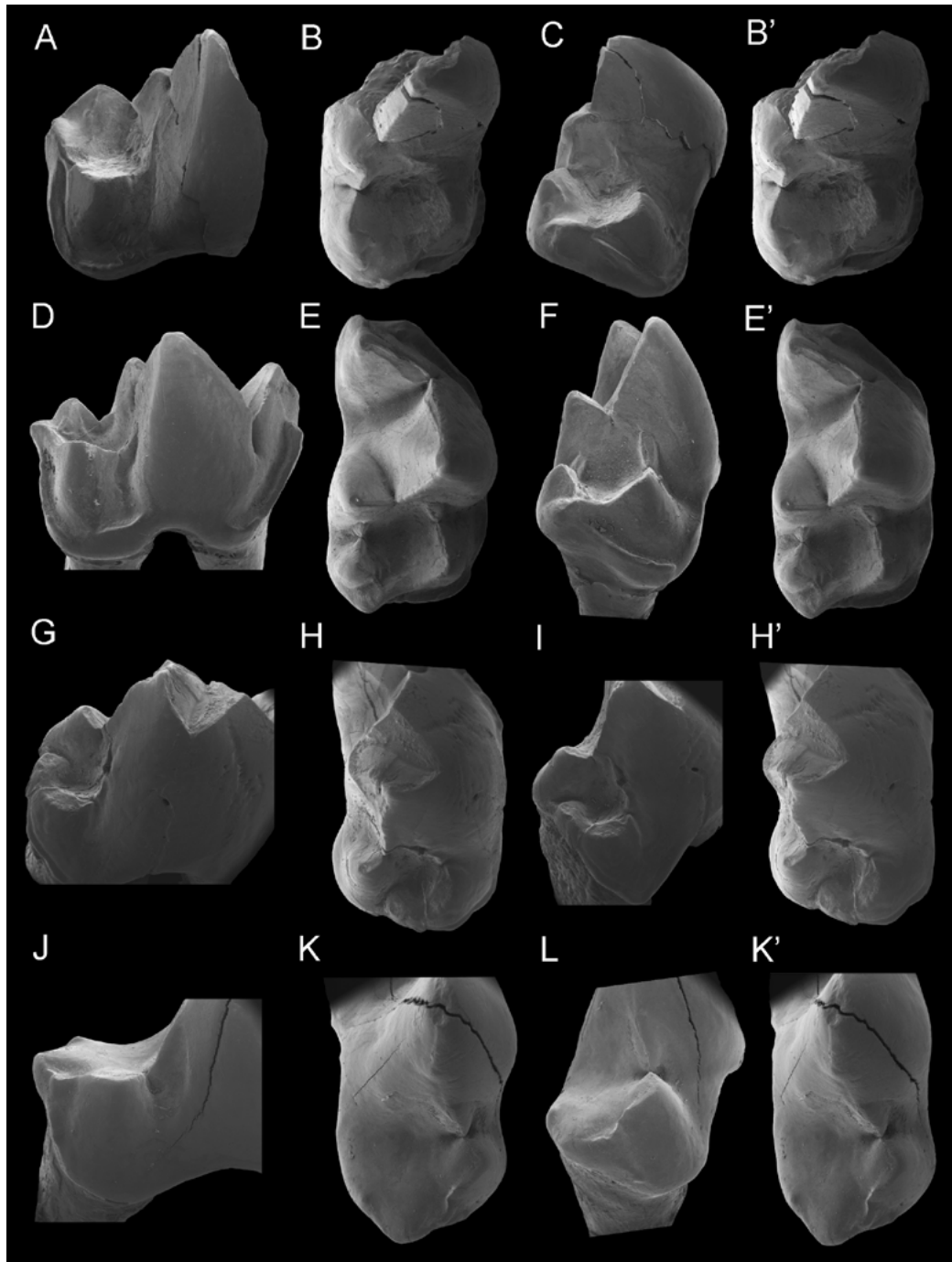


Figure 4. Comparison of the holotype of *Whollydooleya tomnpatrichorum* n. gen. et sp. QM F57892 with other hypercarnivorous dasyuromorphians (not to scale). A–C, *W. tomnpatrichorum*, QM F57892, m2 or m3. A, posterobuccal view; B–B', occlusal stereoview; C, oblique posterobuccal view. D–F, *Dasyurus maculatus*, AR21693, M₃. D, buccal view; E–E', occlusal stereoview; F, oblique posterobuccal view. G–I, *Sarcophilus harrisii*, AR21694, M₃. G, buccal oblique view; H–H', occlusal stereoview; I, oblique posterobuccal view. J–L, *Thylacinus cynocephalus*, AR21695, M₃ talonid (reversed from the LM₃). J, posterobuccal oblique view; K–K', occlusal stereoview; L, oblique posterobuccal view.

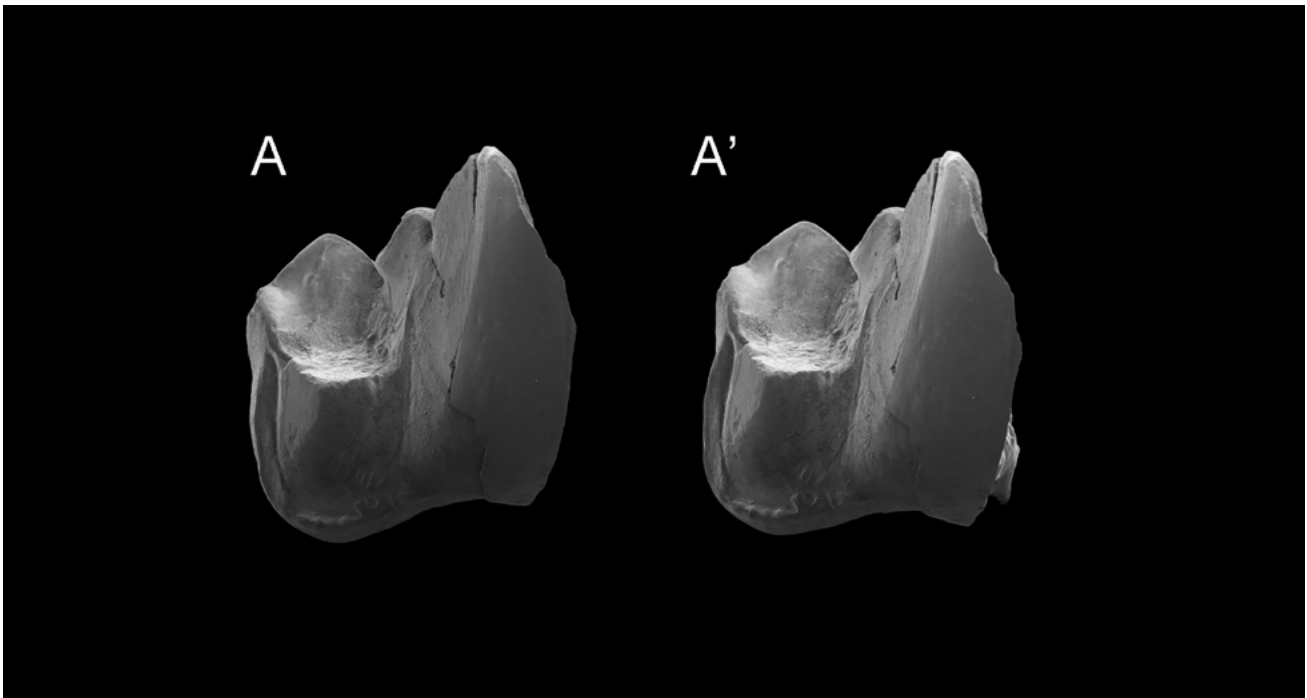


Figure 5. Stereoviews of the holotype of *Whollydooleya tomnpatrichorum* n. gen. et sp. QM F57892 from a buccal oblique view. The margin at the right represents the missing flank of the trigonid.

been overprinted on what may have been more irregular scorings resulting from mastication.

There is no buccal cingulum evident at the base of the protoconid, which is also characteristic of most dasyuromorphians (but not universal; e.g. species of *Dasyuroides* can exhibit better-developed buccal cingulids; Archer 1976b). However, the trigonid is broken, so structures that may have been present anterior to the widest point of the trigonid are unknown.

The talonid is wider than the trigonid and supports three cusps. The hypoconid is robust with a well-developed cristid obliqua and posthypocristid. The cristid obliqua appears to have extended towards the midpoint of the posterior flank of the trigonid, meeting the latter about midway up the height of the trigonid, although it is worn from the lowest point along this blade to the position of its attachment on the trigonid. There is a kink in the cristid obliqua at the low point, suggesting that there may have been a carnassial notch between the posterior descending and anterior ascending sections of the cristid obliqua, as occurs in most dasyuromorphians. On the anterior side of the junction between these two parts of the cristid obliqua, at the low point on the buccal side of the interface between the trigonid and talonid, there also appears to be a remnant of a small neomorphic cuspid. Wear of the cristid obliqua has produced a small carnassial notch that operates obliquely between this cuspid and the prehypocristid.

On the posterior flank of the hypoconid, subtending the posthypocristid blade, there is a distinctive thegotic facette that was produced by the premetacrista of the corresponding upper

molar that parallels the far larger facette produced by the preparacrista of the upper molar on the posterior flank of the trigonid, hence both are the result of the same movement of the mandible. This facette similarly reveals fine, unidirectional oblique striations cut into the enamel. This posthypocristid facette extends ventrally across a small gap to include the buccal half of the ascending posterior cingulid, resulting in breached enamel and a dentine trough within the postcingulid (= the posterior cingulid). This part of the facette developed on the postcingulid was almost certainly caused by thegosis involving the apex of the metacone of the corresponding upper molar. There is also a wear facette on the anterior flank of the hypoconid subtending the prehypocristid that was produced by the postparacrista of the corresponding upper molar, a facette also commonly seen in dasyuromorphians, even in species of *Sarcophilus* that have undergone hypotrophy of the talonid.

The posthypocristid leading edge is notched along its length suggesting that it has been used to segment reasonably hard materials. While these notches could be the result of postmortem damage, given their restriction to the leading edge of this blade, it is more likely that they reflect use during the life of the animal. The posthypocristid terminates lingually before it includes or contacts the hypoconulid.

The hypoconulid is developed as a relatively (compared with the hypoconid and entoconid) small talonid cusp in the form of a short, imprecise, buccolingual vertical blade that is orientated in line with the posthypocristid and in effect extends that blade across a low gap between the two blades emanating from these cusps. Holistically, the hypoconulid-cristid and the

posthypocristid form a combined transverse blade with a carnassial notch in effect developed by the low gap between the two blade segments. The buccal end of the hypoconulidcristid terminates at the junction of the lingual end of the posterior cingulid and the lingual end of the posthypocristid. Unlike the entoconid and hypoconid, there is no distinct high point on the hypoconulid; rather it is a small transverse ridge. It does not extend sufficiently posteriorly to have acted as an effective interlocking device inserted into the anterior cingulid of the succeeding molar. On its posterior flank there is a coarse wear facette indicating interdental abrasion with the anterior edge of the succeeding molar. The overall relationship between the hypoconid and hypoconulid is similar to that seen in some of the largest dasyurine dasyurids (species of *Glaucodon* and *Sarcophilus*) but differs from the condition seen in other

dasyurids and in thylacinids where the hypoconulid of the M_2 is as large as or larger than the entoconid and projects posteriad to interlock within the anterior cingulid of M_3 .

The entoconid has a short preentocristid developed in relation to the postmetacristid, as noted above. Although the posterior as well as anterior flanks of the entoconid are relatively massive, there is no distinct postentocristid as such (although there is a poorly defined ridge descending its posterobuccal flank that is probably a vestigial homologue of this otherwise missing blade); as a result, there was a small open trough between the bases of the entoconid and hypoconulid such as occurs in most dasyuromorphians that have not reduced their talonids. Hence, there was no shearing activity provided by this specific region of the talonid.

The upper part of the buccal face of the entoconid exhibits a wear facette produced by the lingual face of the protocone of the corresponding upper molar. The intra-talonid bases of all talonid cusps facing each other across the talonid basin as well as the central part of the talonid basin itself, appear to be missing enamel. This may have been the result of attrition produced by occlusion with the corresponding protocone of the upper molar, but this seems improbable given the very limited masticatory wear on all cusps of this tooth. It is perhaps more likely that the enamel is missing because of chemical erosion resulting from some taphonomic process such as root-acid dissolution. Hence when cleaning the tooth, we stopped when the surface appeared to represent dentine.

The postcingulid descends from a distinct starting point about three-quarters of the way from the buccal side of the tooth, down around the base of the hypoconid and anteriorly as far as the posterobuccal base of the protoconid. On the buccal side, this cingulid is disrupted by small cuspidis along its length. Seemingly similar cuspidis, unattached to the basal cingulid, occur on the lowest anterobuccal flank of the prehypocristid portion of the cristid obliqua.

Comparisons

Based on overall morphology, there can be little doubt that *W. tomnpatrichorum* represents a dasyuromorphian. While definitive familial identification is uncertain given the lack of basicranial information (Wroe, 1999), the highly derived molar morphology including the plethora of vertical blades with carnassial notches (e.g., metacristid and preentocristid), hypotrophied metaconid and hypertrophied protoconid, strongly suggests that it represents this group. This overall conclusion is also supported by the argument of Voss and Jansa (2009) that while loss of the posterior cingulid (which is conspicuously present in *W. tomnpatrichorum*) is a synapomorphy of Marsupialia, secondary presence of this structure is a synapomorphy of dasyuromorphians.

Of the many different kinds of dasyuromorphians already known (e.g., Archer, 1982; Wroe, 2003), in its very reduced metaconid and hypertrophied protoconid it shares most derived features with dasyurine dasyurids and, to a lesser extent, thylacinids. Comparisons here have been made specifically with all of the largest and most specialised of the dasyurine dasyurids including the living Tiger Quoll (*Dasyurus maculatus*; Figs

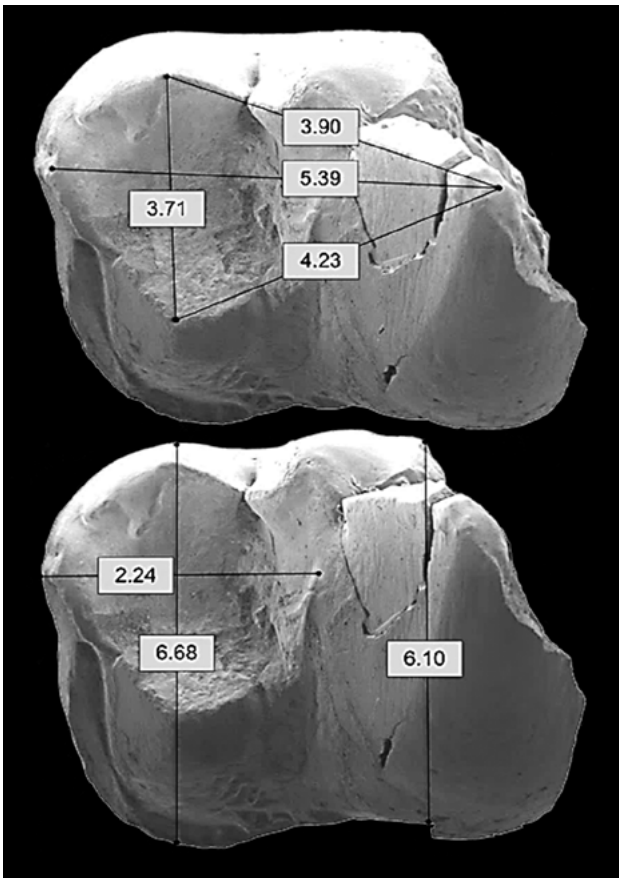


Figure 6. Measurements of the holotype of *Whollydooleya tomnpatrichorum* n. gen. et sp. QM F57892 in occlusal stereoview. In the upper figure, the sides of the triangle link: 1, protoconid to entoconid; 2, protoconid to hypoconid; and 3, entoconid to hypoconid. The longitudinal measure is the distance between the protoconid and the apex of the hypoconulid. In the lower figure, the measures are: talonid width through the entoconid and hypoconid; talonid length from the ascending extremity of the cristid obliqua against the posterior flank of the trigonid to the posterior extremity of the crown through the hypoconulid; and maximum width of the damaged trigonid.



Figure 7. NMV P207018, cast of a right dentary referred to *Glaucodon ballaratensis* by Gerdtz and Archbold (2003) that preserves the RC₁, P₁₋₂ and M₁₋₄. Left upper, buccal view. Left lower, lingual view. Right, occlusal view of the dentition. Scale bar = 1 cm. Photographs by Darren Bellingham.

4D–F, 9B–B’), the early late Miocene *Gadbulanyi djadjinguli* (Wroe, 1998), the Pliocene *Glaucodon ballaratensis* (Figs 7, 9C–C’), the living Tasmanian Devil (*S. harrisi*; Figs 4G–I, 9E–E’), the early Pleistocene devil (*Sarcophilus moornaensis*; Figs 8, 9D–D’), and the Thylacine (*Thylacinus cynocephalus*; Figs 4J–L, 9F–F’). Juxtaposed M₃s of these taxa are presented in Figure 9. No lower molar is known for *G. djadjinguli*. Other mid to late Cenozoic dasyurid-like taxa known on the basis of molars from Riversleigh include species of *Barinya*, *Mayigriphus* and *Joculium* but none of these have hypercarnivorous specialisations of the kind exhibited by *W. tomnpatrichorum*.

Comparisons here primarily involve M₂ and/or M₃ (Fig. 9). While position homology of the holotype of *W. tomnpatrichorum* is uncertain, the large talonid of the Wholly Dooley specimen means that it is highly likely that it is not M₄ given that the talonid of the posterior molar in all dasyuromorphians is much narrower than the trigonid. While it could be an M₁, this seems improbable because the hypoconid is very much lower in height than the

protoconid. In the M₁ of larger dasyuromorphians, particularly the hypercarnivores, the hypoconid on M₁ is commonly almost half to three-quarters the height of the protoconid, while in the M₃ it is rarely more than a quarter the height of the protoconid—which is the condition seen in the holotype of *W. tomnpatrichorum*.

A buccal cingulid surrounding the base of the talonid, which is well-developed in *W. tomnpatrichorum* and all of the larger dasyurines including species of *Sarcophilus* (despite the latter having significantly hypotrophied talonids), is not present in the modern Thylacine (*T. cynocephalus*). It is present, however, in some Miocene thylacinids (e.g., *Badjcinus turnbulli*) and hence its absence in *T. cynocephalus* is almost certainly an autapomorphy.

The most striking feature of the talonid of *W. tomnpatrichorum* is the very large entoconid with well-developed, longitudinal pre-entocristids and poorly-developed postentocristid. These blades virtually enclose the whole of the lingual side of the talonid. This is in distinct contrast to all

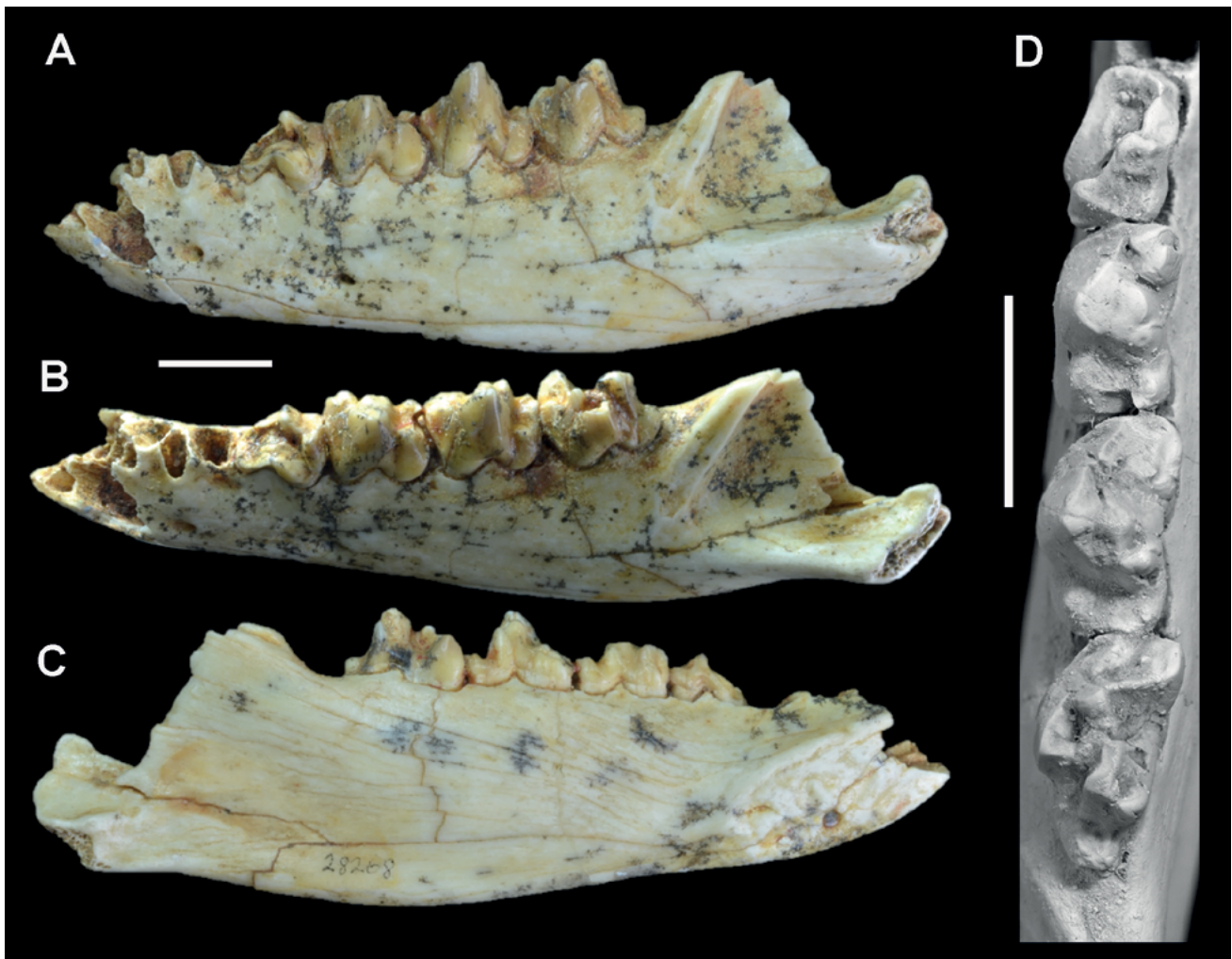


Figure 8. NMV P28684, right dentary of the holotype of *Sarcophilus moornaensis* preserving damaged M_{1-4} . A, Buccal view; B, buccal oblique view; C, lingual view; D, occlusal view of M_{1-4} . Photographs by Erich Fitzgerald.

known thylacinids, which have relatively small to almost absent entoconids that are also conical in shape without hypertrophy of any subtended longitudinal blades.

Considering entoconid development in dasyurines, none exhibit hypertrophy of this cusp remotely to the extent shown in *W. tomnpatrichorum*, although less specialised dasyurines such as species of *Dasyurus* have large (albeit much smaller than those in *W. tomnpatrichorum*) entoconids with distinct pre- and postentocristids. In *D. maculatus* (Figs 4D–F, 9B–B'), there is also a very well-developed carnassial notch, as in *W. tomnpatrichorum*, developed between the preentocristid and postmetacristid. In *D. maculatus*, however, the small, low postentocristid barely contacts the hypoconulid, which results in a failure of the entoconid and associated blades to effectively enclose the lingual side of the talonid; this contrasts with the condition in *W. tomnpatrichorum*, where the entire lingual side of the talonid is enclosed by these structures.

The largest of the dasyurines, the species of *Sarcophilus* and *Glaucodon*, have evolved in a different direction with extreme reduction of the entoconid and hypotrophy of the talonid as a whole. In the case of *S. harrisii* (Figs 4G–I, 9E–E'), this correlates with significant reduction of the protocone and other occlusal upper molar counterparts for talonid structures. In *G. ballaratensis* (structure of the M_3 in this species being based on the specimen described by Gerdtz and Archbold, 2003; Figs 7, 9C–C'), the entoconid is clearly present on the foreshortened talonid, but very small. In *S. moornaensis* (Figs 8, 9D–D'), it is even smaller to minuscule, although the talonid is less foreshortened than it is in *G. ballaratensis*. In *S. harrisii* something quite different has occurred (Figs 4G–I, 9E–E'): in conjunction with the far greater hypertrophy of the protoconid and coordinate posterior displacement of the metaconid, the talonid retains only two cusps and has become an 'appendage' at the base of the posterobuccal flank of the metacristid. The buccal-most of these cusps is the hypoconid but the homology

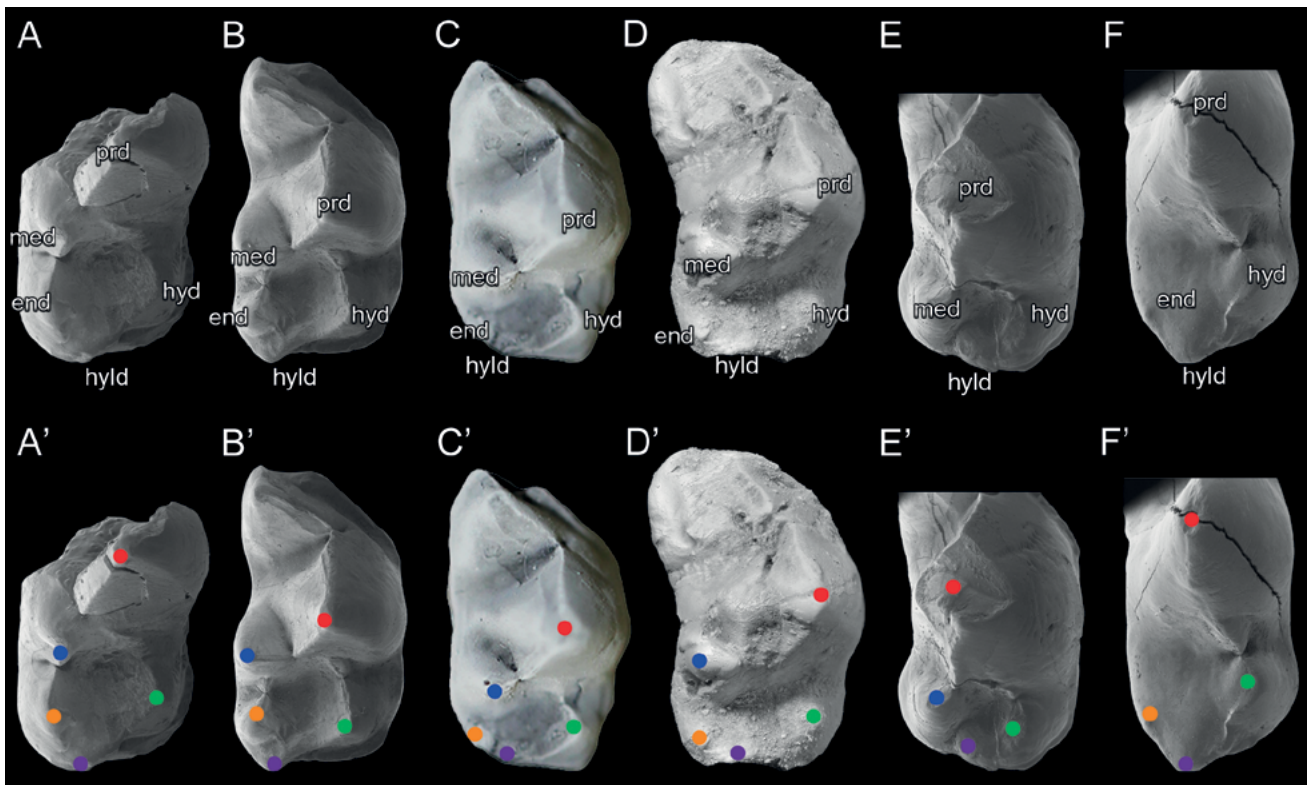


Figure 9. Comparison of the distribution of major cusps (in occlusal view) preserved in the *Whollydooleya tomnpatricorum* holotype (QM F57892) with the RM_3 of representative extinct (†) and recent hypercarnivorous dasyuromorphians. A-A', *Whollydooleya tomnpatricorum* (†); B-B', *Dasyurus maculatus*, AR21693; C-C', *Glaucodon ballaratensis*, P207018 (†); D-D', *Sarcophilus moornaensis*, NMV P28684 (†); E-E', *Sarcophilus harrisii*, AR21694; F-F', *Thylacinus cynocephalus*, AR21695 (image reversed from the LM_3) (†). Abbreviations: end, entoconid (orange dot); hyd, hypoconid (green dot); hyld, hypoconulid (purple dot); med, metaconid (blue dot); prd, protoconid (red dot). Not to scale.

of the other cusp is unclear. If the minuscule size of the entoconid in *S. moornaensis* presages changes leading to the condition seen in *S. harrisii*, then it would seem possible that the entoconid has been lost in *S. harrisii* and the cusp that remains is the hypoconulid. If this is the case, the most interesting consequence is that the posteriorly displaced metaconid may have replaced the function of the entoconid as the occlusal counterpart of the protocone, given that it now occurs directly lingual to the hypoconid and in the topographic position of the entoconid of other dasyurids. An arguably less plausible alternative, given the medial posterior position of the more lingual of the two talonid cusps in *S. harrisii*, would be that this is the entoconid and that the hypoconulid has been lost. Without anecdotal taxa bridging the transition between *Sarcophilus moornaensis* and *S. harrisii*, or perhaps a detailed analysis of occlusal relationships, the evolutionary fate of the entoconid in these large hypercarnivorous dasyurines is unclear. It is interesting to note that a similar argument has been made (Forsiepi et al., 2014) to explain what may have occurred on the other side of the world in relation to evolutionary reduction of the talonid in borhyaenids (Marsupialia, Sparassodonta) leaving uncertainty about the homology of the vestigial cusps in forms that retain talonid structures. There is

even some uncertainty about the fate of the metaconid in more derived hypercarnivorous sparassodontans.

Although the modern Thylacine lacks a metaconid, presence in this Riversleigh taxon of a distinct (albeit reduced) metaconid does not exclude a more distant relationship to thylacinids given that that cusp is present in almost all of the Oligo-Miocene thylacinids. Reduction to loss of the metaconid is likely to be a convergent hypercarnivorous feature relating to hypertrophy of the protoconid and metacristid and longitudinal orientation and hypertrophy of the paracristid as the primary alpha-scissorial carnassial blade (Every, 1970) in derived thylacinids and dasyurids.

The hypoconulid in the M_{1-3} of dasyurids and thylacinids projects further posterior than any other structure on the talonid and locks into the hypoconulid notch of the anterior cingulid of the following molar, thereby restricting differential transverse movement between adjacent teeth. Given the primarily alpha-scissorial function of the molars in these insectivorous/carnivorous marsupials, stability of posture for these molars during vertical shearing is aided by this interlocking system. For this reason, it is curious that the hypoconulid in *W. tomnpatricorum* extends only just beyond the posterior flank of the talonid. This is also the case, however,

in species of *Glaucodon* (very small hypoconulid notch) and *Sarcophilus* (very small in M_2 , absent in posterior molars), and may be a correlate of the larger, wider, potentially more laterally stable molar structure in species of these genera. It is uniquely developed in *W. tomnpatrichorum* more as an oblique transverse ridge (confluent with the posthypocristid, somewhat after the fashion seen in some peramelemorphians) than a discrete, posteriorly directed cuspid.

Of all the taxa noted above by way of comparison, the one that is the most enigmatic is the possibly early late Miocene *Ganbulanyi djadjinguli* from Encore Site at Riversleigh. The holotype, an isolated, incomplete, worn upper molar, was originally described by Wroe (1998) as probably conspecific with an isolated massive ovate premolar from the same deposit. Arena et al. (2011), in the course of describing *Malleodectes mirabilis*, suggested that the Encore molar and premolar represented different taxa and named the premolar *Malleodectes moenia*. They argued that both species of *Malleodectes* may have used their massive premolars to crush snail shells. Wroe's (1988) description of the holotype of *G. djadjinguli* suggests that this animal, based on the upper molar, was a hypercarnivore and hence it could possibly be related to *W. tomnpatrichorum*. Direct comparisons between the two teeth are, however, difficult because they are very different in size, exhibit markedly different degrees of wear and represent different tooth positions, the holotype of *W. tomnpatrichorum* being a lower molar while that of *G. djadjinguli* is an upper molar. Nevertheless, one of the key distinctive features of *D. djadjinguli* noted by Wroe (1998) is the relatively small occlusal area represented by the protocone. The very wide talonid and hypertrophied entoconid of *W. tomnpatrichorum* suggests an upper molar morphology that would have been significantly different with an uncharacteristically (for a hypercarnivorous dasyuromorphian) large protocone and associated blades. While tooth size alone clearly indicates that these taxa are not conspecific (the lower molar of *W. tomnpatrichorum* being wider than the upper molar of *G. djadjinguli*), the differences in protocone/talonid morphologies also suggest that the two taxa represent two quite distinct lineages of hypercarnivorous dasyurids. The nature of wear on the two specimens also suggests a significantly different life-style. In the case of the upper molar of *G. djadjinguli*, the wear is heavily apical resulting in conjoined paracone/STB and metacone/STD, wear patterns of a kind commonly seen in the molars of durophagous Tasmanian devils. In the lower molar of *W. tomnpatrichorum*, wear is clearly evident along the leading blade of the metacristid but there is very little apical wear evident on the protoconid and almost none on the hypoconid or entoconid, suggesting that this larger animal was nevertheless not a durophagous hypercarnivore.

Discussion

Whollydooleya tomnpatrichorum exhibits classic features of a marsupial hypercarnivore in being large (evidently larger than a modern Tasmanian Devil), in having a robust molar morphology with a hypertrophied protoconid, highly reduced metaconid and a plethora of vertical shearing blades with carnassial notches on both the trigonid and talonid. The uniformly fine, unidirectional

striations on the posterior flank of the metacristid and posthypocristid indicate thegotic maintenance of the cutting edge of those blades. These features are shared by the larger dasyuromorphians such as species of *Dasyurus*, *Glaucodon*, *Sarcophilus* and some of the more plesiomorphic members of the Thylacinidae. This new species differs, however, from all thylacinids in having a very large entoconid and from the larger, later thylacinids in retaining a distinct metaconid. The massive entoconid distinguishes it additionally from all other dasyurids, including the largest dasyurine dasyurids to which it is otherwise most similar in terms of hypertrophy of the protoconid and reduction of the metaconid.

Until now, the oldest known hypercarnivorous dasyurids have been the dasyurine species of *Dasyurus* (earliest record being middle Pliocene; *Dasyurus dunmali* Bartholomai, 1971; Wroe and Mackness, 1998; Archer, 1982), *Glaucodon* (only known from the Pliocene; *Glaucodon ballaratensis* Stirton, 1957; Gerdz and Archbold, 2003) and *Sarcophilus* (first known from deposits interpreted to be Early Pleistocene in age; *Sarcophilus moornaensis* Crabb, 1982). Although the exact age of *W. tomnpatrichorum* is uncertain, it occurs with a suite of taxa that, at least at the generic level (e.g., *Ekaltadeta*, *Hypsiprymnodon*, cf. *Rhizophascalonus*), are broadly comparable but not identical to Miocene assemblages known from the Riversleigh World Heritage Area (Archer et al., 2006). Differences include, for example, a new species of *Hypsiprymnodon* that is abundantly present in the Wholly Dooley Local Fauna. We have therefore tentatively concluded that this faunal assemblage probably correlates with those from either Faunal Zone C or D in the Riversleigh World Heritage Area, which span approximately 16 to 13 Ma (Woodhead et al., 2014). However, it could be younger than this, possibly early late Miocene in age given the uncertain age of Encore Site, which has been estimated on the basis of biocorrelation to be early late Miocene (Black, 1997a, 1997b; Myers et al., 2001; Brewer et al., 2007; Black et al., 2012; Arena et al., 2014; Arena et al., 2015).

Wroe (2003) and Black et al. (2012) make the point, on the basis of the rich Riversleigh record in particular, that there appears to have been a gradual replacement of cat- and fox-sized thylacinids as the most abundant of the larger mammalian terrestrial carnivores in the late Oligocene to middle Miocene by comparable-sized dasyurids in the later Cenozoic.

Further, until now, few of the albeit rare dasyurids known from the Oligo-Miocene were large enough to qualify as hypercarnivores, *Ganbulanyi djadjinguli* being potentially the only other hypercarnivorous dasyurid. In contrast, *Whollydooleya tomnpatrichorum* was much larger than any of the other dasyurids and most of the thylacinids known to have been present during the Oligo-Miocene. Only late Miocene thylacinids (e.g., *Thylacinus potens* from the Alcoota Local Fauna in the Northern Territory) would have been larger. Using the regression equations for M_3 and M_2 widths published by Myers (2001; table 4; dasyuromorphian dataset), we estimate that a minimum mass for *W. tomnpatrichorum* may have been 20.3 kg if the holotype is an M_3 or 25.5 kg if it is an M_2 . The average mass of living Tasmanian Devil males is 10–11 kg and of females is 7–8 kg (Parks and Wildlife Service

Tasmania). Hence *W. tomnpatrichorum* may well have been at least twice the mass of living Devils, which are, currently, Australia's largest marsupial carnivore. Given Paddle's (2000) mass estimates for average-sized modern Thylacines (*Thylacinus cynocephalus*) of 29.5 kg, it is possible that *W. tomnpatrichorum* may have been as large as some of the smaller individuals of this recently extinct hypercarnivore.

Contemporaneity of other large hypercarnivorous dasyurids (e.g., species of *Dasyurus* and *Sarcophilus*) with a large thylacinid (*T. cynocephalus*) has been the situation in Australia since at least the Pliocene and persisted until Dingoes arrived on the Australian mainland in the mid Holocene and Europeans exterminated the Thylacine from Tasmania.

Whollydooleya tomnpatrichorum, however, seems unlikely, on the basis of the hypertrophied entoconid, to have been on the direct line leading to the species of *Dasyurus*, *Glaucodon* or *Sarcophilus*. It is more likely to represent an independent, probably mid to late Miocene lineage of hypercarnivorous dasyurines that filled the niche occupied later, in the Pliocene to Holocene, by large hypercarnivorous dasyurines such as the living Tiger Quoll and Tasmanian Devil.

Appearance of this large hypercarnivorous dasyurid is the first indication of a trend towards gigantism within this family, which ultimately resulted in the largest known dasyurids of the late Cenozoic. Given that it does not appear to have been a member of the dasyurine lineage that includes *Glaucodon* and *Sarcophilus*, it had to represent a second lineage of dasyurids that underwent gigantism. If this was the case, it is possible that competition between the two could have led to loss of the lineage represented by *W. tomnpatrichorum*. That said, in terms of larger dasyurines, the only known devil remains are in the detail of the Pliocene and Quaternary record.

The presence in the deposit of what appear to be albeit rare aeolian-transported quartz grains and the indications of at least partial desiccation of the accumulating deposit may be a reflection of changing palaeoenvironments within the region. Following the late Oligocene and prior to the mid-Miocene climate oscillation, the faunal assemblages (Faunal Zones B and C) from the Riversleigh World Heritage area appear to suggest closed, biologically-rich forests (Archer et al., 1994, 1997; Travouillon et al., 2009; Black et al., 2012). While very few deposits from the Riversleigh World Heritage Area appear to represent post-Miocene oscillation assemblages, the few that do (e.g., Encore Site) suggest more open, drier forests (Myers et al., 2001; Travouillon et al. 2009). Wholly Dooley Site may have derived from a time when the region's palaeoenvironments were even drier, with potentially some wind-blown components becoming parts of the accumulating fossil deposit. Testing this possibility will involve ongoing research into other components of the Wholly Dooley Local Fauna as well as trying to radiometrically date speleothems that have been obtained from Wholly Dooley Hill.

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