LATE CENOZOIC EVOLUTION OF THE MACROPODOID DENTITION

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Dedicated to my parents, Pauline and Dennis Couzens, for always supporting my fascination with nature, especially palaeontology.

“Show me your teeth, and I will tell you who you are”

George Cuvier

“In paleontology there is fresh interest in attempting to infer not only the course but also the mechanisms of evolution”

George G. Simpson (1944)

CONTENTS

ABSTRACT

Dietary adaptation has played an important role in the 200 million year diversification of mammals. Changes in the dentition are a critical component of dietary adaptation because teeth influence how efficiently food can be processed. Because mammals have only limited capacity to replace damaged teeth, the ability to build a durable dentition is an important influence on an individual's evolutionary fitness. Herbivores are under especially strong pressure to maintain dental function, because the tougher and more abrasive plant foods they consume require extended dental processing compared with animal protein. Grasses and shrubs growing in open habitats are especially difficult and costly to consume because high concentrations of siliceous plant-cell inclusions (phytoliths) and adhering dust and soil make them highly abrasive. The resultant deterioration of tooth function arising from dental wear can significantly impact an individual's fitness. Open habitats, where herbivores are subject to elevated levels of dental wear, became common during the late Cenozoic as decreasing atmospheric CO_2 concentrations and lower global temperatures prompted the spread of grasses and shrubs. Expansion of these habitats was associated with the diversification of herbivore groups like artiodactyl ungulates, horses, and kangaroos. To deal with higher levels of dental wear many herbivore groups increased dental durability by increasing the size of the tooth crown, continuously replacing chewing teeth , increasing tooth area, increasing enamel thickness, or altering enamel microstructure.

The most diverse marsupial herbivores are the macropodoids (kangaroos and relatives) which are often considered ecological analogues of artiodactyls because they acquired parallel adaptations for grazing and locomotion in open habitats. From at least the late Miocene macropodoids evolved within progressively drier and more open terrestrial ecosystems dominated by shrubs and grasses. During the Miocene–Pliocene transition, macropodine and sthenurine kangaroos diversified to become Australia's dominant terrestrial herbivores. However, unlike ungulate herbivores, macropodoids never evolved very high-crowned prismatic molars, suggesting that they must have acquired a different set of adaptations to increase dental durability.

Thus far no systematic attempt has been made to examine what types of dental adaptations these may have been.

In this study I examine how macropodoids responded to dietary change over the past 25 million years. I show that across extant macropodoids molar crown height variation is positively correlated with increased level of dietary abrasion but not habitat openness. The pattern of fossil and reconstructed molar crown height shows an asymmetric increase in disparity, consistent with either a bounded diffusion model, or a multiple trait optimum model. A phylogenetic comparative analysis reveals that the best-fitting models of crown height evolution are adaptive. A four-peak Ornstein–Uhlenbeck model is favoured over simpler models with fewer optima. Initial increases in molar crown-height during the early Neogene are linked with the evolution of bilophodont molars that were better able to process tough foods like dicot leaves than lower-crowned cusps. Molar crown-height disparity more than doubled across the Miocene–Pliocene transition, primarily in response to the expansion of macropodine kangaroos into grass-dominated Pliocene ecosystems.

However, the increase in molar crown-height amongst Pliocene macropodids remained significantly below levels attained by contemporaneous artiodactyl ungulates and equids. Using high-resolution micro-computed tomography, I tested whether variation in molar enamel thickness allowed macropodoids to diversify despite their low-crowned dentitions. Computation of three-dimensional relative enamel thickness scores reveals that there is an approximately three-fold range of enamel thickness amongst macropodoids. The macropodine genera *Macropus*, *Petrogale* and *Wallabia* are characterised by possessing amongst the thickest molar enamel of any mammal yet examined; comparable to primates with ‘hyper-thick’ enamel like *Australopithecus*, *Paranthropus* and *Homo*. In contrast, the relative molar enamel thickness of the giant sthenurine kangaroos is extremely thin, comparable to hominoids like *Gorilla* which consume large quantities of leaves. Spatial mapping of enamel thickness and linear measurements from seven molar regions suggest that, structurally, bilophodont molars are differentiated from bunodont molars by thick enamel between the buccal and lingual cusps. Linear enamel thickness measurements suggest that Pliocene macropodines co-opted this pattern to build bladed dentitions with thicker molar enamel, better able to resist high levels of wear. Increases in enamel thickness along the blade edge and relief surface are likely adaptive because they help maintain a trenchant lophid, and offset dentine exposure. These results provide strong evidence that thick molar enamel is an adaptive response to high rates of dental wear.

The capacity of dental traits to vary through time is an important determinant of rates and directions of adaptive change. Some functionally and phylogenetically important macropodoid traits show evidence for reevolution after long intervals of absence, but the reasons for this have been unclear. One such trait is the posthypocristid, a longitudinal molar crest bounding a crushing basin on the rear face of basal macropodoid lower molars. Based on a reassessment of the homology of talonid features, and an ancestral state reconstruction analysis, I show that the posthypocristid reevolved separately in the Sthenurinae and Macropodinae, each after more than 15 million years of absence. I examined whether high levels of reversibility in the posthypocristid and other talonid traits were linked to developmental processes regulating tooth proportionality and cusp number. Based on an activation–inhibition model of tooth development, I show that the same statistically significant deviation from the inhibitory cascade leads to posthypocristid reversal in both Sthenurinae and Macropodinae. Based on morphological similarities to mouse dental phenotypes, increased responsiveness of the molar talonid to ectodysplasin dosage may have been an important enabler of posthypocristid reversibility. These results bolster the view that reversals are possible after long periods of absence and show how developmental factors promote homoplasy.

Overall this work shows how major changes in macropodoid dental evolution during the past 25 million years were influenced by both environmental change and developmental factors. In the future, simulations of dental evolution within developmental morphospace will potentially improve our understanding of how natural selection, drift, and constraints, shape transitions between adaptive zones. Significant questions remain about how enamel thickness functions and how its variation at population and macroevolutionary scales is influenced by genetic–developmental processes. The expanded virtual analysis of dental morphology holds great promise for improving our understanding of adaptation and will play an important role in attempts to build a quantitative genotype–phenotype map.

DECLARATION

I certify that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

Aidan Couzens
20 April 2017

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LIST OF PUBLISHED PAPERS AND MANUSCRIPTS

Chapters 2–5 represent published papers or manuscripts in preparation for publication. Chapter 3 has been published in the journal *Evolution* but has been reformatted in line with other chapters and thus differs slightly from the published version.

Chapter 2

Paper 1. Couzens, A. M. C. and G. J. Prideaux. (in preparation). Increased disparity in kangaroo molar crown height across the Miocene–Pliocene transition reflects diversification into grass-dominated ecosystems.

Chapter 3

Paper 2. Couzens, A. M. C., A. R. Evans, M. M. Skinner, and G. J. Prideaux, G. J. 2016. The role of inhibitory dynamics in the loss and reemergence of macropodoid tooth traits. Evolution 70:568–585. doi: 10.1111/evo.12866

Chapter 4

Paper 3. Couzens, A. M. C. and G. J. Prideaux. (in preparation). Molar enamel thickness is functionally linked to dietary abrasion in kangaroos.

Chapter 5

Paper 4. Couzens, A. M. C. and G. J. Prideaux. (in preparation). Kangaroos evolved thick molar enamel as an adaptation to Neogene aridification.

PREFACE

Few attributes are more important to a mammal than its teeth (Polly 2000; Ungar 2010). Teeth mechanically process food before it is chemically digested in the gut and thus play a critical role in the efficient extraction of nutrients and energy (Lucas 2004). When tooth function is compromised by loss or damage, there are significant direct and indirect fitness costs (Logan and Sanson 2002a, b; King et al. 2005; Ozaki et al. 2010), which ensure that a close evolutionary relationship is maintained between tooth form and diet (Evans and Sanson 2003).

The same properties that make teeth excellent tools for food breakdown also facilitate their regular preservation as fossils. Fossil teeth thus provide a uniquely detailed picture of mammalian systematics because the position and relative size of tooth cusps and crests is generally species specific (Jernvall 1995). Thus, even though many fossil taxa are known only from their dentition (Ungar 2010), it has been possible to establish a detailed evolutionary history of mammals based largely on their teeth (Simpson 1944; Beard et al. 1996; Luo et al. 2001; O'Leary et al. 2013).

The role of teeth in food processing places them at the forefront of interactions between an individual and its ecosystem. Indeed, teeth are extremely unusual compared with other organs because their shape is readily altered through direct interaction with the external environment (Lucas 2004). This alteration of tooth shape results from damage to the tooth surface caused by opposing teeth, food, or small hard objects like grit (Fortelius 1985; Lucas et al. 2008). This tooth wear is especially problematic for herbivores because the food they consume requires extended processing and is much more abrasive than other types of food. The close linkage between herbivore tooth morphology and food properties provides an exceptional system within which to study adaptation (Simpson 1944; Jernvall et al. 2006; Ungar 2010; Mihlbachler et al. 2011). As a result, herbivore dietary adaptation has been fundamental in the development of core concepts in modern evolutionary theory such as adaptive zones (e.g., Simpson 1944) and quantitative models of trait evolution (e.g., Lande 1976).

Phases of dietary change and adaptation have emerged as focal points for mammalian diversification (Simpson 1944; Ungar and Sponheimer 2009; Mihlbachler et al. 2011). The Cenozoic Era (last 66 million years) provides the best window into how herbivores responded to climatically-driven changes in diet because it captures the major phase of mammalian diversification (O'Leary et al. 2012), against a backdrop of dynamic global climate change (Zachos et al. 2001). During the late Cenozoic, decreases in global temperatures and atmospheric CO_2 levels promoted the spread of grass-dominated habitats (Cerling et al. 1997). Herbivores feeding in these habitats were subjected to higher rates of dental wear than their counterparts in closed habitats, forcing them to acquire adaptations to increase dental durability. The evolution of higher-crowned or ever-growing molars represents the archetypal herbivore response to increased dental wear, but this view is based almost entirely on studies of ungulates and rodents (e.g., Fortelius et al. 2002; Jernvall and Fortelius 2002; Gomes Rodrigues et al. 2013). A broad group of other herbivores including diprotodont marsupials, proboscideans, sirenians, and some primates also consume abrasive foods, but lack dental traits characteristic of the 'ungulate-model' of dietary adaptation. How did these groups adapt to dietary change during the late Neogene, and can an understanding of their evolutionary responses help to establish a more generalizable model of mammalian dietary adaptation?

Kangaroos and their close relatives (Superfamily Macropodoidea) are the most diverse living marsupial herbivores. Macropodoids are members of the Order Diprotodontia, which includes the vombatoids (wombats and koala), phalangeroids (cuscuses, brushtail possums, and pygmy possums) and petauroids (sugar gliders, ringtail possums, etc.). The dental morphology of macropodoids is broadly similar to other phalangeriform marsupials; they possess one pair of enlarged lower incisors (diprotodonty), a laterally compressed third premolar (ancestrally), and quadritubercular molars (Woodburne 1984a; Aplin and Archer 1987). However, macropodoids are differentiated from other phalangeriforms by the loss of the first upper premolar (P^1), a hypocone on the first upper molar (M^1), possession of a masseteric canal continuous with the dental canal, and an ankle joint specialised for bipedal hopping locomotion (Szalay 1982; Flannery 1987). Macropodoids evolved diverse herbivore diets, including grazing diets reliant upon grasses, separately from mammalian herbivores on northern continents (Arman and Prideaux 2015), but in response to the same large-scale shifts in climate. This makes them an ideal comparative test of the ‘ungulate-model’ of dietary adaptation. The primary aim of this thesis is to examine how environmental change impacted macropodoid dental evolution during the late Cenozoic. Craniodental measurements from extant taxa are used to establish baseline ecomorphological relationships that enable hypotheses about dietary adaptation to be quantitatively tested with the fossil record.

1. INTRODUCTION

The introduction is structured to provide contextual information for analytical chapters 2-5. I begin by reviewing the structure, evolution and function of the mammalian dentition. I then review patterns and process in herbivore evolution with a focus on late Cenozoic herbivore evolution in the Northern Hemisphere.

1.1 Aims

The overarching goal of this study is to examine how macropodoids responded to dietary change during the late Cenozoic. Specifically this study will seek to:

1. Quantify the relationship between molar crown height, diet and habitat variables amongst extant taxa;
2. Use measurements of crown height from fossil and extant taxa to reconstruct morphological diversification during the adaptive radiation of Macropodoidea across the past 25 million years (Myr);
3. Establish patterns of molar enamel thickness variation across extant macropodoids and examine its relationship to tooth function and diet;
4. Reconstruct enamel thickness evolution using fossil and extant macropodoids and test how changes in enamel thickness relate to changes in dental wear and tooth morphology through time;
5. Model molar development to examine how changes in variation arising from development influence the reversibility of dental characters within Macropodoidea.

1.2 Mammal Teeth

1.2.1 Evolutionary Significance of the Mammalian Dentition

There are more than 5000 species of living mammals representing a diverse array of body plans and ecologies (Wilson and Reeder 2005). Many of the defining features of mammals, such as their large complex brains, hair, mammary glands, and middle ear (Nowak 1999; Luo 2007) are directly or indirectly linked with the maintenance of an endothermic physiology (Armstrong 1983). However, endothermy comes at a significant cost: mammals are faced with the constant need to acquire food (Lucas 2004; Ungar 2010). A critical means by which mammals have addressed this problem is by evolving complex teeth with an exceptional capacity to fracture food items (Polly 2015). This makes it possible for food to be substantially preprocessed prior to chemical digestion in the gut (Evans et al. 2007; Luo 2007). Preprocessing dramatically increases the energy and nutrients available for extraction from food, enabling mammals to consume an array of foods, including those of inherently low energetic value (Ungar 2010). Additionally, although other vertebrates like teleost fishes, crocodilians, and squamates also acquired their own complex multicusped teeth (Trapani et al. 2005; O'Connor et al. 2010; Handrigan and Richman 2011), only mammals evolved the ability to use them in the precise mode necessary to 'chew' food (Ungar 2010).

Efficient tooth function depends on optimising the relationship between tooth shape and food properties (Lucas 1982; Evans and Sanson 2003). Teeth are segmented organs formed through the iteration of a basic structural unit or 'module', the tooth cusp. As with other segmented organs, like the vertebral column, functional optimisation in the dentition is achieved by differentiating individual segments for specific tasks. In the case of the mammalian dentition, this is achieved by partitioning the tooth row into discrete tooth types (Figure 1.1) that perform different tasks during feeding. From this perspective, the mammalian dentition is different from most other vertebrate dentitions, which tend to be more homogenous in structure (Polly 2015). The regionalisation of the mammalian dentition follows a deeply-conserved pattern whereby posterior teeth tend to be more complex than anterior teeth (Butler 1939). The increasing structural complexity of the dentition is generally linked with increased processing capacity. Thus the premolars and molars perform the bulk of food processing, whereas the incisors and canines are primarily involved in food acquisition, although they may also perform important roles in social interaction like grooming, fighting, and threat display (Ungar 2010).

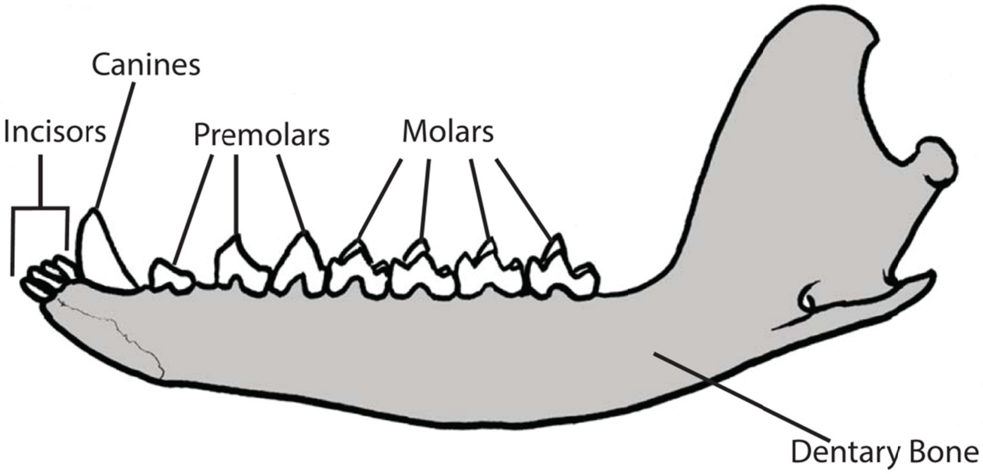

Figure 1.1. Differentiation of the mammalian dentition in the marsupial *Monodelphis*. Modified after Luo (2007).

In addition to reflecting tooth function, tooth shape also provides important information about the evolutionary relationships of mammals (Beard et al. 1996; Luo et al. 2002; Luo et al. 2015). This is because, in most cases, the relative size and position of the tooth cusps and crests is species-specific (Jernvall 1995). Together with the fact that mammalian teeth have a dense fossil record (Alroy 2002), this is an important reason why the mammalian dentition has strongly shaped our picture of mammalian evolution (e.g., McKenna 1982; Beard et al. 1996; Gheerbrant 2009).

1.2.2 Evolutionary Origin of the Mammalian Dentition

The excellent fossil dental record makes it possible to examine the step-by-step acquisition of the mammalian dentition in great detail (Luo 2007; Ungar 2010). Teeth are a vertebrate apomorphy (Rücklin et al. 2012), although aspects of the dentition have been lost in many groups like turtles, frogs, birds and some mammals (e.g., anteaters, baleen whales, echidnas, pangolins) (Meredith et al. 2014). The timing and phylogenetic emergence of the earliest teeth is controversial (Fraser et al. 2010; Rücklin et al. 2012), but both jawed and jawless vertebrates possess tooth-like structures, suggesting that teeth originated before jaws (Rücklin et al. 2011). The earliest teeth were comprised of dentine, bone, and a distinct pulp cavity (Rücklin et al. 2012), with the exterior mineralised layer of enamel acquired later amongst osteichthyans (Qu et al. 2015).

Complex multicusped teeth have originated separately in chondrichthyans, teleost fishes, squamate reptiles, crocodilians, and mammals (Trapani et al. 2005; O'Connor et al. 2010; Handrigan and Richman 2011). However, the developmental capacity for cusp iteration seems to have been present from the outset because the earliest tooth-like structures (i.e., those of 'placoderm' fishes and conodonts) were already multicusped (Jones et al. 2012; Rucklin et al. 2012). Gene expression studies suggest that the different multicusped tooth morphologies were patterned by distinct developmental processes because non-mammalian vertebrates lack the enamel knot signalling centre (Debiais-Thibaud et al. 2015; Polly 2015) responsible for choreographing cusp morphogenesis in mammals (Vaahtokari et al. 1996).

The first evidence for mammal-like tooth differentiation is amongst basal synapsids like the early Permian eupelycosaur *Dimetrodon*, which possessed simple unicuspid teeth regionalised into anterior incisor-like teeth and larger blade-like posterior teeth (Rubridge and Sidor 2001). The first complex multicusped teeth emerge in the cynodonts (Kemp 1983, Luo 2007). Basal cynodonts possessed a postcanine dentition with a single primary cusp that was later elaborated in more derived eucynodonts (e.g., *Thrinaxodon*) to include accessory cusps (Ungar 2010). By the Middle Triassic the cynognathid cynodonts had evolved transversely expanded postcanine teeth (Rubridge and Sidor 2001), indicating increased lateral jaw motion, a key precursor to mammalian chewing. The first 'mammals' (*sensu* Luo et al. 2002) originated during the Late Triassic, and are characterised osteologically by two distinct generations of teeth, precise molar occlusion, and a temporomandibular joint involving contact between the squamosal and dentary bones (Ungar 2010). Alternatively, 'Mammalia' can be restricted to the last common ancestor of crown group taxa, i.e., Monotremata, Marsupialia and Placentalia (Rowe 1988), a definition which excludes many stem groups like the haramyids, morganucodontids and kuehneotherids.

In early stem mammals (*sensu* Luo et al. 2002) like *Morganucodon* and *Sinoconodon*, the molars are laterally compressed tricuspid structures, with a large central cusp and two smaller lateral cusps (Luo et al. 2002). A key innovation associated with the transition from these eucynodonts to crown mammals was buccolingual expansion of the molar to form the tribosphenic upper molar typical of spalachotheroid and dryolestid mammals (Crompton and Jenkins 1968; Crompton 1971). The tribosphenic upper molar is characterised by three cusps, each demarcating a separate apex of a triangle when viewed occlusally (Figure 1.2). The vertex linking the protocone and paracone forms a shearing crest that occludes with the corresponding lower molar crest linking the protoconid and metaconid (Figure 1.2). Traditionally, it was argued that tribospheny evolved uniquely amongst boreosphenidans in the Northern Hemisphere during the Early Cretaceous, but recent evidence suggests that australosphenidans also acquired a form of tribospheny (Luo et al. 2007). Tribospheny may thus have arisen earlier during the Middle Jurassic in the southern continents (Woodburne et al. 2003) or australosphenidans may have acquired it independently (Luo 2007). Subsequent modification of the tribosphenic molar enabled the protocone to occlude within the lower molar talonid basin, adding a crushing capacity to the basic tribosphenic molar (Crompton and Hiiemae 1969). By expanding the range of potential diets, the acquisition of this 'modified' tribosphenic molar was probably an important factor in the subsequent diversification of placental and marsupial mammals (Luo 2007).

Placental and marsupial mammals underwent adaptive radiations during the late Cretaceous or early Paleocene (Meredith et al. 2011; O'Leary et al. 2013); the exact timing is controversial (Foley 2016). Most molecular phylogenies favour a Cretaceous diversification of crown therian mammal orders between 110 and 85 Myr ago (Meredith et al. 2011; Tarver et al. 2016). Fossil evidence and some molecular phylogenies on the other hand favour a later Paleocene radiation (Wible et al. 2007; O'Leary et al. 2013; Mitchell et al. 2014; Phillips 2015). The 'explosive' radiation implied by the latter model suggests that up to 10 mammalian orders originated within as little as 200 thousand years (kyr) after the K–Pg extinction (O'Leary et al. 2013). Given that the ancestral placental mammal is reconstructed as possessing the 'modified' tribosphenic molar (O'Leary et al. 2013), this much more compressed timeline implies a phenomenal rate of dental evolution (Springer et al. 2016). In the case of herbivorous mammals, an especially important event in these basal lineages was the acquisition of a quadritubercular molar by addition of a posterolingual cusp (hypocone) on the upper molar (Hunter and Jernvall 1995). This provided the basic dental template for the subsequent diversification of herbivore molar types over the next 60 Myr.

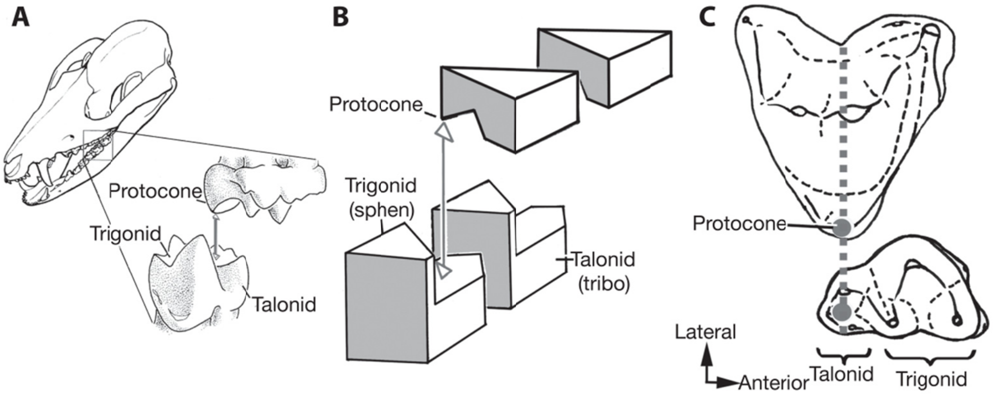

Figure 1.2. A, Skull and dental morphology of a marsupial, the North American opossum *Didelphis virginiana.* B, Schematic model of molar structure and occlusion in the ‘modified’ tribopshenic molar. C, The ‘modified’ tribosphenic molar of therian mammals possessed a protocone involved in crushing food within the talonid basin of the lower molar. After Luo et al. (2007).

1.2.3 Tooth Function and Wear

The fundamental functional unit of mammalian teeth are the cusps (Lucas 1982; Evans and Sanson 2003). Fracturing of food particles by cusps requires an opposing tooth basin to capture and retain the food and is thus functionally analogous to a mortar and pestle (Lucas 2004). Food is fractured when the force at the cusp tip is sufficient to initiate and propagate a fracture through the food particle. Although cusps are effective at fracturing brittle foods, they perform poorly at fracturing ductile objects with high toughness (high fracture strain), such as leaves (Lucas 2004). Mammals have solved this problem by linking cusps together with enamel to form crests that operate as blades. Blades function by contacting two cutting edges at all points during food fracture, ensuring a fracture is propagated through the full thickness of a food item (Lucas 2004). This mode of fracture differs from cusp–basin systems where contact between occluding tools is restricted to a relatively small surface between the cusp apex and the receiving basin (Evans 2005). The different performance of cusps and crests at fracturing foods of different ductility predicts that herbivore tooth types should ‘pivot’ between these alternative strategies when dietary transitions from brittle to more ductile foods occur.

The adaptive relationship between tooth shape and diet is complicated by the fact that tooth surface geometry is continually remodelled by repeated stripping of dental tissue through interactions with opposing teeth, food, and entrained particles (Baker et al. 1959; Lucas 2004; Ungar 2015). The primary agents of dental wear are controversial but are thought to include enamel, either in the guise of opposing tooth surfaces or microscopic enamel chips, and exogenous particles, such as phytoliths and ingested grit (Lucas 2004). There is contradictory evidence on whether phytoliths are sufficiently hard to scratch dental enamel (e.g., Baker et al. 1959; Hlusko 2003; Sanson et al. 2007). Recent experimental work suggests that even though phytoliths may be softer than enamel (Lucas et al. 2013), they can still cause abrasion because they exert sufficient force to cleave or separate the hydroxyapatite prisms from the proteins which bind them together (Xia et al. 2015). The shape of wear surfaces varies depending on the mechanism by which they are generated (Fortelius 1985; Fortelius and Solounias 2000). Attritional tooth wear reflects tooth–tooth contacts leading to formation of planar surfaces called facets, characterised by microscopic parallel scratches (Fortelius 1985). In contrast, abrasive wear arises primarily from tooth–food interactions, and is characterised by rougher, more rounded wear surfaces, with non-parallel scratches (Fortelius 1985; Lucas 2004; Evans 2005). Besides the composition of wear agents, the shape of wear surfaces also reflects the different geometries of wear interactions (Fortelius 1985). Thus, because blade surfaces must remain in contact to propagate a fracture, attritional wear dominates at relief surfaces, whereas abrasion tends to dominate at the rake surface, where lower-angle tooth–food interactions occur (Figure 1.3; Rensberger 1973a; Evans 2005).

Dental wear has important implications for tooth function because it has effects on functional parameters which dictate how teeth fracture food (Ungar and M’Kirera 2003; Evans 2005; King et al. 2005). Perhaps the most predictable impact of dental wear is its tendency to reduce tip and edge sharpness, increasing the force needed to initiate and propagate a fracture (Popowics and Fortelius 1997; Evans and Sanson

1998; Evans 2005). Additionally, formation of a wear land along the relief surface where the blades contact decreases the force needed to push the blades apart, leading to less efficient cutting (Evans 2005). Wear accumulating along the rake edge also increases the force needed to fracture food by decreasing the rake angle (Evans 2005). Finally, because blades are often notched to trap tough foods during the fracture stroke (Anderson and LaBarbera 2008), wear drives a misalignment of opposing notches which promotes point-cutting, where the blades do not maintain contact (Evans 2005).

Predicting the functional changes that result from wear is complicated by the differing composition of dental tissues (Lucas et al. 2008; Benazzi et al. 2013). Continued propagation of dental wear from the occlusal surface toward the crown cervix eventually exposes the softer dentine. This leads to the formation of compensatory cutting edges at the emergent enamel–dentine junction which can intermittently increase cutting efficiency (Fortelius 1985; Logan and Sanson 2002b; King et al. 2005; Pampush et al. 2016). In microchiropterans, more dental wear accumulates on the rake surface compared with the relief surface (i.e., Figure 1.3), which results in a faster rate of dentine exposure on the rake surface compared with the relief surface (Evans 2005). Other features like cusp angularity remain relatively stable as tooth wear proceeds (Ungar and M'Kirera 2003). However, these neutral or intermittently advantageous changes are greatly overwhelmed by functional declines across almost every other parameter. These include reduced tip/edge sharpness, reduced cusp sharpness, diminished cusp occlusion relief, increased wear-land area, reduced volume behind crests, and decreases in rake angle and occlusal complexity (Evans 2005; King et al. 2005). Thus, in the long term, extensive dental wear prompts a decline in tooth performance and herbivore dentitions should thus be functionally optimised to slow or offset its effects.

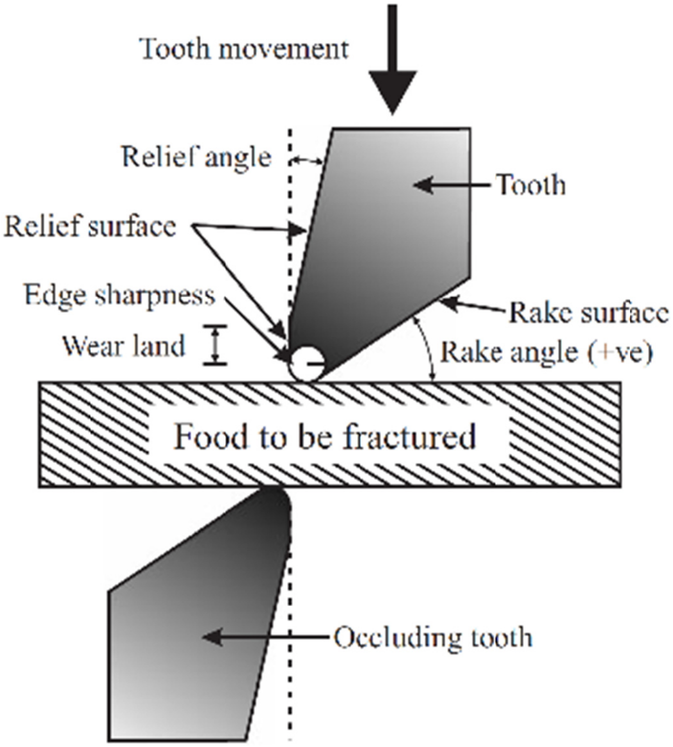

Figure 1.3. Key functional parameters of a dental tool. From Evans and Sanson (2006)

There are both direct and indirect fitness costs resulting from high levels of dental wear (Logan and Sanson 2002a, b, King et al. 2005). For instance, the decreased processing capacity of a worn dentition increases the energetic investment that must be made in chewing force and the number of chewing cycles (Fortelius 1985; Carraway et al. 1996; Verts et al. 1999; Logan and Sanson 2002b; Venkataraman et al. 2014). In sika deer, the correlation between molar durability and longevity suggests that lower dental durability directly reduces an individual's survival prospects (Ozaki et al. 2010). Indirect costs result primarily from decreased investment in reproductive output. An example is the increased infant mortality amongst sifaka lemurs (*Propithecus edwardsi*) during low-rainfall periods when mothers with senescent dentitions have reduced capacity to effectively lactate (King et al. 2005). Likewise, koalas with more worn teeth spend less time socialising due to their increased investment in feeding (Logan and Sanson 2002a). These results strongly suggest that dental wear is likely to be an important selective pressure driving adaptive dental evolution in herbivores.

1.2.4 Mammalian Responses to Tooth Wear

Mammals have evolved a range of adaptive responses to slow or reduce the effects of dental wear (Janis and Fortelius 1988). These span a range of spatial scales, from the orientation of microscopic enamel prisms (e.g., Rensberger 2000) to large-scale changes in the composition and structure of the dentition (e.g., Gomes Rodrigues et al. 2011).

1.2.4.1 Crown Height

Increasing tooth volume by increasing molar crown height (Simpson 1944; van Valen 1960; Damuth and Janis 2011) is perhaps the structurally most straightforward mechanism to increase dental durability (Janis and Fortelius 1988; Tapaltsyan et al. 2015). Crown height is often compared qualitatively between taxa (Figure 1.4) using the terms ‘brachyodont’ (low-crowned), ‘mesodont’ (intermediate) and ‘hypsodont’ (high-crowned). This qualitative approach is problematic because consistent criteria for demarcating thresholds between different crown types have not been applied, and this approach also obscures the more than ten-fold variation in herbivore molar crown height (e.g., Janis 1990). A better approach scores crown height relative to body mass (Van Valen 1960) or to molar width or length, both of which tend to scale isometrically with crown height (Fortelius 1985; Janis and Fortelius 1988). Selection for more rapid crown growth, delayed truncation of growth, or continuous crown growth, provide developmental mechanisms for tinkering with crown height (Tapaltsyan et al. 2015, 2016). By permanently delaying the cessation of crown growth, herbivores like rodents, wombats, and lagomorphs have evolved hypselodont (ever-growing) dentitions (Tapaltsyan et al. 2015). But, this condition is rare compared with increases in vertical tooth size accomplished over a finite developmental period (Janis and Fortelius 1988). For instance, within ungulates alone, high-crowned molars evolved independently at least 17 times (Damuth and Janis 2011). Many other herbivore groups also show tendencies to evolve increasingly high-crowned molars. These include diprotodont marsupials (Janis

1990), multituberculates (Damuth and Janis 2011), gondwanatheres (Gurovich and Beck 2009), taeniodonts (Lucas et al. 1998), notoungulates (Billet et al. 2009; Dunn et al. 2015), rodents (Williams and Kay 2001; Tapaltsyan et al. 2015), lagomorphs (Bair 2007), proboscideans (Sanders et al. 2010; Lister 2013) and sirenians (Domning 1982, 2001). A consistent pattern emerging from studies of herbivore hypsodonty is that bilophodont mammals, such as kangaroos, manatees, tapirs, and cercopithecine primates tend to be lower-crowned than herbivores with prismatic teeth irrespective of diet and metabolic factors (Janis and Fortelius 1988). This has prompted speculation that bilophodont taxa are constrained to relatively low crown heights because of the precise way they occlude (Janis 1990). Proboscideans are perhaps the only ancestrally bilophodont mammals to acquire high-crowned prismatic molars (e.g., Sanders et al. 2010) which suggests that there are indeed limits to the evolvability of bilophodont crown types. In dugongs and xenarthrans the crown was made hypsodont only after completely reducing the enamel cap to establish an ever-growing, entirely dentinous tooth (Domning 1982; Vizcaíno 2009). A more common trajectory amongst bilophodont herbivores is to acquire polylophodont dentitions by either adding tooth crests to a given tooth (Cerling et al. 1999; Jernvall et al. 2000; Lister 2013; Tapaltsyan et al. 2015) or adding extra teeth (see 1.2.4.4).

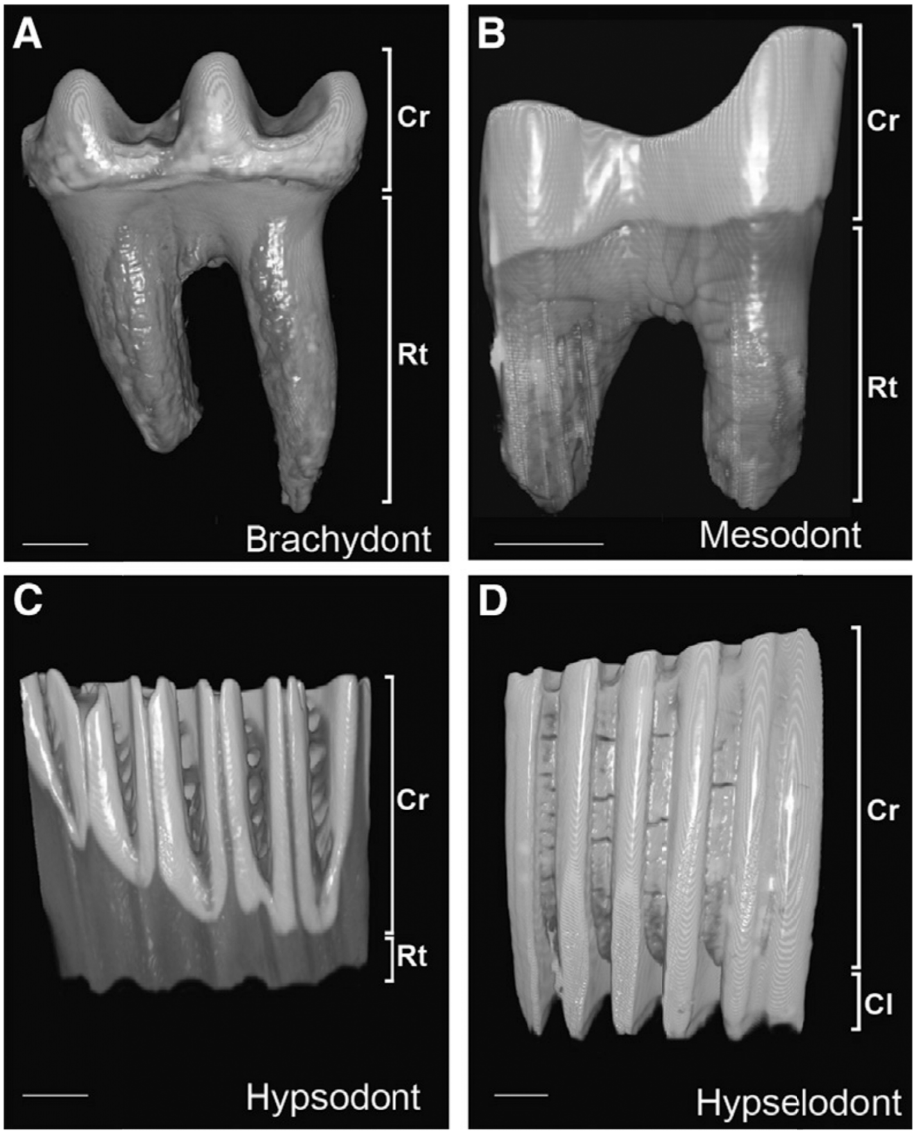

Figure 1.4. Molar crown height variation across Rodentia. A. Low-crowned (brachyodont) molar dentition. B. Mesodont, intermediate molar crown height. C. Hypsodont, high-crowned molar dentition. Abbreviations: Cr, crown, Rt, root, Cl, cervical loop. From Tapaltsyan et al. (2015).

1.2.4.2 Enamel Thickness

A potential alternative to increasing molar crown height is to increase the relative enamel volume of the crown (Lucas et al. 2008; Van Dam et al. 2011; Pampush et al. 2013; Ungar and Hlusko 2016). Due to its much greater hardness, a given volume of enamel will take much longer to abrade away than the same volume of dentine.

The association between zones of thick molar enamel and regions of wear in primate teeth first prompted the hypothesis that thicker enamel may be primarily a mechanism to resist high rates of dietary abrasion (Molnar and Gantt 1977). But, the adaptive significance of thick enamel as a mechanism to resist wear has remained controversial (Lucas et al. 2008; Pampush et al. 2013; Ungar and Hlusko 2016). This is because thick molar enamel could slow the formation of compensatory cutting edges and thus be functionally disadvantageous for a herbivore (Janis and Fortelius 1988), or be an adaptation to resist tooth fracture during hard-object feeding (Kay 1981; Lucas et al. 2008; Pampush et al. 2013).

Many mammals with thick molar enamel, especially primates, consume large quantities of hard foods such as seeds or nuts in addition to leaves (e.g., Iwamoto 1974; Dunbar 1977; Kuroda et al. 1996). This has made it difficult to disentangle adaptive contributions from abrasion and hard-object feeding. However, non-primates unlikely to have been hard-object feeders, such as macropodoids, desmostylids, and elephantids also may have had thick enamel (Janis and Fortelius 1988; Sanders et al. 2010). Interestingly, recent evidence from stable-isotopic and dental-microwear data suggests that the thickest-enamelled hominins like *Paranthropus robustus* were consuming abrasive foods like sedges and tropical grasses, rather than hard foods (Ungar et al. 2008; Ungar and Hlusko 2016; Figure 1.5). This interpretation contrasts sharply with the prevailing "nutcracker-man" hypothesis of *Paranthropus* dietary adaptation (e.g. Kay 1981; Wood and Constantino 2007) and clearly demonstrates the limits to ecomorphological inference. The hypothesis of thickened enamel as a mechanism to resist abrasion is bolstered further by the positive correlation between phytolith load (an index of dietary abrasiveness) and enamel thickness in living cercopithecine primates (Rabenold and Pearson 2011; Pampush et al. 2013). Testing the functional role of enamel thickness amongst mammals and other vertebrates remains hamstrung by a lack of quantitative comparative data. Currently, linear or two-dimensional enamel thickness data are limited to primarily primates and chiropterans (Molnar and Gant 1977; Martin 1985; Dumont 1995; Shellis et al. 1998; Hlusko et al. 2004; Suwa and Kono 2005; Smith et al. 2012; Skinner et al. 2015). Three-dimensional measurements of relative enamel thickness are available for hominoid primates (Kono 2004; Olejniczak 2008a, b; Kono et al. 2014), rodents (Van Dam et al. 2011), and perissodactyl and artiodactyl ungulates (Winkler and Kaiser 2015a, b). Extended taxon sampling is thus required to more robustly test adaptive hypotheses and resolve the ancestral enamel phenotype in different mammalian groups.

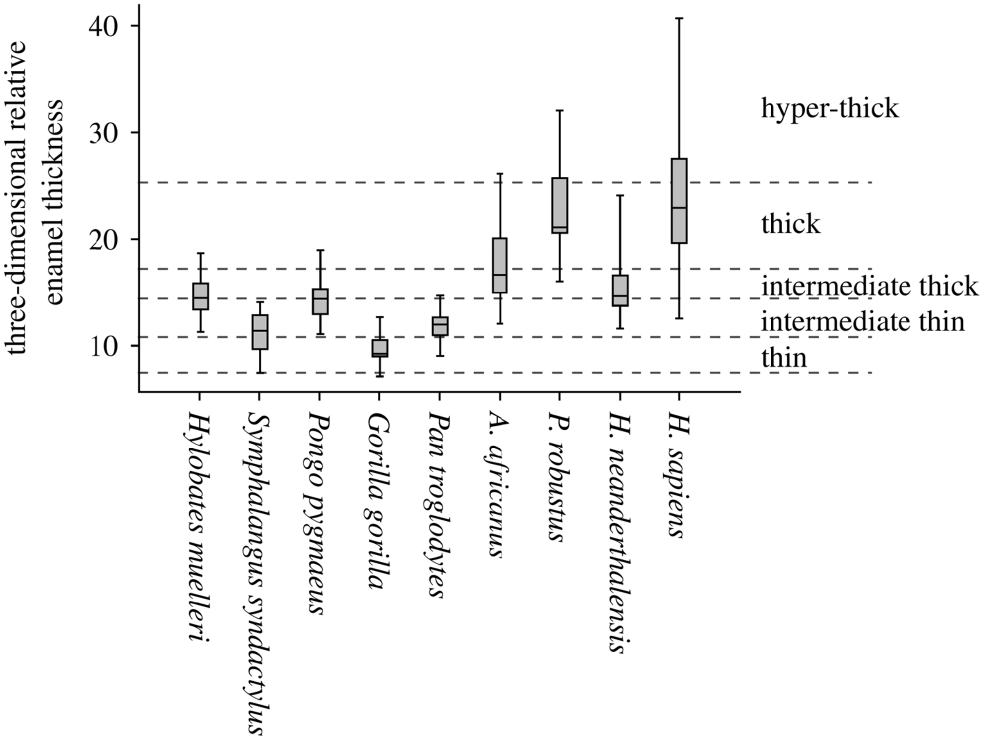

Figure 1.5. Enamel thickness variation amongst extant and fossil hominoids showing the 'hyper-thick' enamel characteristic of *Homo sapiens* and species of *Paranthropus*, e.g., *P. robustus*. From Olejniczak et al (2008a).

1.2.4.3 Occlusal Area

The capability of a tooth to process food is a function of occlusal area, mainly because larger teeth enable more dental tools (i.e., functional structures on the tooth crown such as crests and cusps) to operate per occlusal cycle. Relative increases in occlusal area thus provide a potential mechanism to reduce levels of dental wear by spreading dental wear across a greater number of cutting edges (Lucas 2004). Changes in occlusal area are generally accomplished by increasing the size of postcanine teeth or by increasing occlusal surface convolution (Pilbeam and Gould 1974a; Fortelius 1985). A range of taxa exhibit shifts toward increased postcanine occlusal area, often through the molarisation of premolars or by expanding M1 or

M3 area (Pilbeam and Gould 1974b). Molarisation of premolars has evolved many times in different mammalian groups (e.g., Figure 1.6), including amongst ungulates (Granger 1908; Simpson 1951; Fortelius 1985), primates (Jernvall et al. 2008), rodents and lagomorphs (Rensberger 1973b), sthenurine kangaroos (Prideaux 2004), and multituberculates (Wilson et al. 2012). Other groups like rodents, proboscideans, suids, hippopotamids, and some primates (e.g., basal euprimates), increased postcanine molar area by enlarging posterior molar basins or adding lophs or lamellae to the crown (Jernvall et al. 2000; Beard 2004; Sanders et al. 2010; Lister 2013). Still, how functional factors have interacted with constraints to drive the evolution of postcanine occlusal area along these alternative evolutionary strategies remains an unresolved problem.

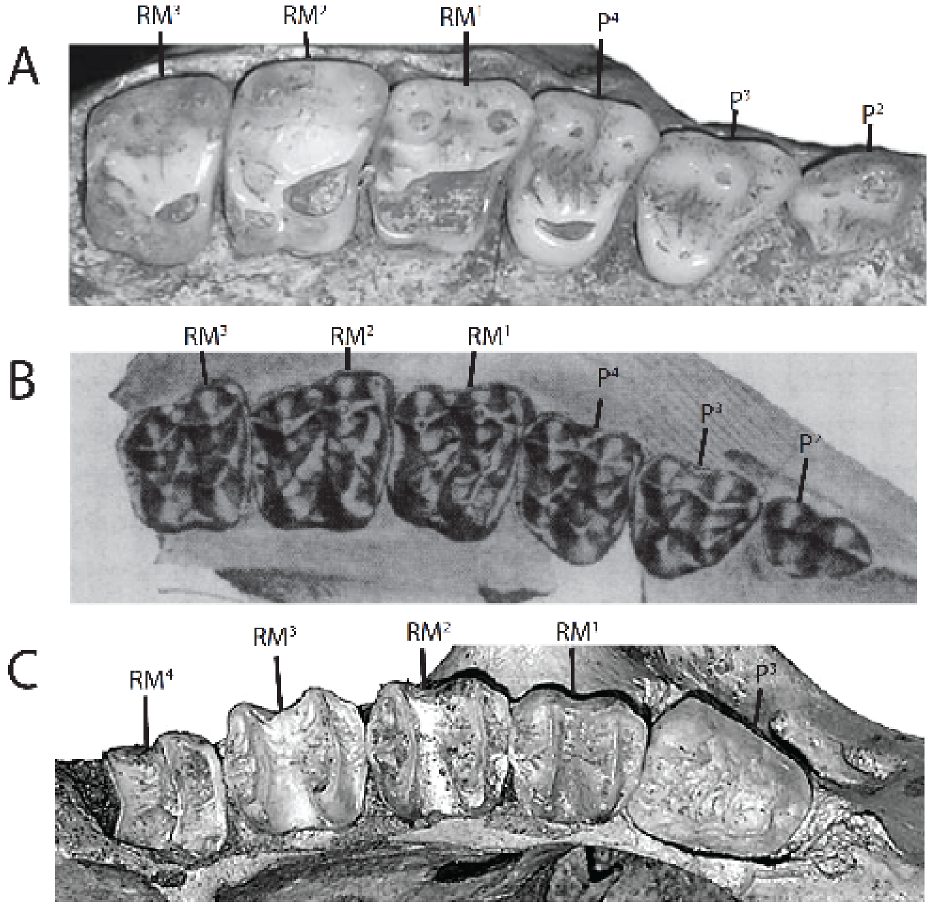

Figure 1.6. Examples of the expansion in premolar area characteristic of herbivores feeding on relatively low-nutrient diets. A. The upper right postcanine dentition of the greater bamboo lemur, *Hapalemur simus*. After Jernvall et al. (2008). B.

Illustrated upper right postcanine dentition of the basal equid, *Orohippus pumilis*. After Granger (1908). C. The upper right postcanine dentition of the sthenurine kangaroo, *Procoptodon browneorum*. After Prideaux (2004).

1.2.4.4 Tooth Replacement

Mammals have evolved a unique form of vertical tooth replacement whereby the juvenile deciduous dentition is replaced by a second permanent set of teeth (Cifelli 2000; Ungar 2010). Some groups such as manatees, rodents, proboscideans, primates, and macropodoids have evolved a significant delay between the eruption of the first and last permanent molar tooth (Sanson 1989; Asher and Lehman 2009; Gomes Rodrigues et al. 2011; Beatty et al. 2012). In addition, in some groups like macropodoids (e.g., larger species of *Macropus*), eruption of the more posterior molars mesially displaces more worn anterior molars until they are ejected from the jaw (Lentle et al. 2003; Gomes Rodrigues et al. 2011). Molar progression is probably advantageous because it postpones dental senescence on the posterior teeth and focuses the masticatory load on the anterior molars (Laursen and Bekoff 1978; Jones 1984; Sanson 1989; Lentle et al. 2003). However, it still remains unclear how, without an actual increase in net dental-tissue volume, molar progression can be an effective response to high rates of dental wear. Additionally, the comparative morphology of molar progression in mammals is not well understood (Lentle et al. 2003; Gomes Rodrigues et al. 2011). In macropodids molar progression is driven by propalinal occlusal pressure between upper and lower dental arcades, suggesting that chewing frequency and duration are important in its operation (Sanson 1989; Lentle et al. 2003). This is supported by observations that unilateral failure of the mandibular dentition to erupt prevents molar progression on the adjacent upper molar arcade (Barber et al. 2008). There is also no evidence for maxillary bone reabsorption, with progression instead resulting from coordinated growth of the maxilla and upper dental arcade (Lentle et al. 2003).

Modern elephants and large-bodied species of grazing kangaroo starve after ejection of the last molar (Laursen and Bekoff 1978), suggesting that there might be selective pressure for continual tooth replacement. However, continuous dental replacement is extremely rare amongst mammals being present in just three extant lineages (Figure

1.7): the silvery mole-rat, *Heliophobius argenteocinereus*, manatees (*Trichechus*), and the nabarlek, or little rock-wallaby, *Petrogale concinna* (Gomes Rodrigues et al. 2011; Beatty et al. 2012). This may indicate that there are significant costs associated with the evolution of this tooth replacement mechanism, which perhaps arise directly from the process of tooth replacement, or indirectly from the developmental costs of maintaining an active stem-cell niche (i.e., cancer). In macropodine kangaroos comminution of food at the anterior-end of the molar row (where molars are ejected) is the first site of oral necrobacillosis, which often progresses to osteological lesions, osteomyelitis, and eventually death (Borland et al. 2012). In one population of the eastern grey kangaroo, *Macropus giganteus*, 54% of individuals had osteological lesions manifesting as bone osteolysis, indicative of long-term oral necrobacillosis (Borland et al. 2012). Since bone necrosis is essentially always observed exclusively at the anterior of the jaw, tooth ejection (rather than eruption) seems to facilitate pathogen invasion. Further work is needed to examine if similar pathologies occur in proboscideans and sirenians with molar progression. Together with developmental insights into how tooth replacement has been reactivated in mammals, this would provide a clearer understanding of why continuous tooth replacement is so rare amongst mammals, and yet widespread amongst other vertebrates (Gomes Rodrigues et al. 2011).

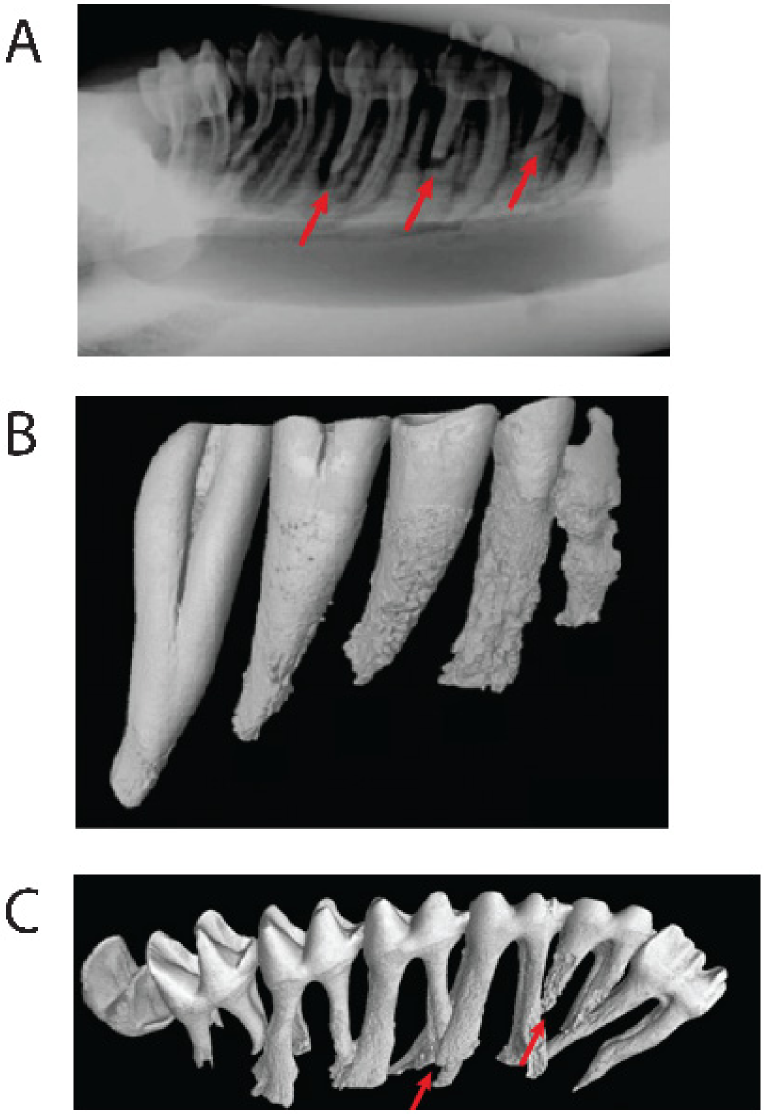

Figure 1.7. Examples of continuous dental replacement in three species of extant mammal. A. Radiographic image of the left lower molar dentition of the extant manatee, *Trichechus manatus*. B. Buccal view of the right lower molar dentition of the silvery mole-rat, *Heliophobius argenteocinereus*. C. Lingual view of the left lower molar dentition in the nabarlek, *Petrogale concinna.* Red arrows denote molar root absorption in preparation for tooth loss. Modified after Gomes Rodrigues et al. (2011).

1.2.4.5 Dental Shape and Complexity

The functional capacity of a tooth is related to occlusal area (Lucas 2004), but only a small portion of tooth area is actually involved with food processing at a given time

(Kullmer et al. 2009). Increasing the number of dental tools could be an important mechanism to disperse wear across a given functional tooth region (i.e., blade edge, cusp area) (Lucas 2004). Occlusal area and complexity are likely to be correlated because adding tools requires more space, and because developmental processes like cell size and cell adhesion dictate how the outer-enamel epithelium deforms during tooth morphogenesis to generate a functional tooth surface (Jernvall 1995; Harjunmaa et al. 2012). The number of dental tools could be increased by either adding cusps or increasing blade length (Evans 2007; Harjunmaa et al. 2012). Several approaches have been developed to measure this 'dental-processing' capacity through the quantification of tooth surface complexity or curvature (e.g., Evans et al. 2007; Bunn et al. 2011; Figure 1.8). A traditional approach to measuring processing capacity is the computation of a shearing ratio, calculated as the summation of shearing-crest length (Figure 1.8D) divided by either body mass, molar length, or molar area (Kay 1975b; Covert 1986; Strait 2001). Recently, dental topographic approaches have been developed which treat the tooth surfaces as topographic information, where tooth basins are analogous to valleys, and cusps to mountains (Ungar and Williamson 2000). These dental topographic approaches are advantageous because they permit analysis of worn teeth, do not require landmarking, increase the spectrum of analysable parameters, increase the speed of analysis, and remove observer bias (Ungar and Williamson 2000; Ungar and M'Kirera 2003; Evans et al. 2007; Bunn et al. 2011; Evans 2013). For instance, occlusal complexity can be measured digitally using orientated patch count which groups surfaces with the same or similar orientation into 'patches', with a higher patch count indicating greater complexity (Evans et al. 2007; Figure 1.8A). A more complex occlusal surface should also be relatively 'curvier' than a less-complex surface with fewer dental tools. The Dirichlet normal surface energy technique quantifies surface curvature by comparing how the path of a point orthogonal to another point changes across the surface (Bunn et al 2011; Figure 1.8). Another method, relief index, computes the ratio of the tooth crown three-dimensional area to the two-dimensional planar area, to express a metric of both the tooth crown height and complexity (Boyer 2008). These dental topographic approaches have been applied to carnivorans and rodents (Evans et al. 2007), chiropterans (Santana et al. 2011), dasyurid marsupials (Evans 2013), perissodactyl ungulates (Evans and Janis 2014), euarchontan mammals (Ungar and Williamson 2000; Ungar and M'Kirera

2003; Boyer 2008; Bunn et al. 2011), and multituberculates (Wilson et al. 2012). Expanding their future application promises tremendous quantitative insights into the relationship between diet, dental adaptation, and the taxonomic diversification of mammals.

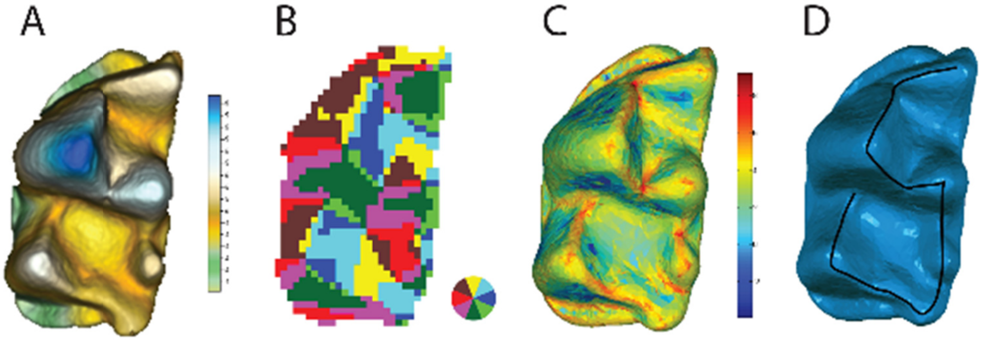

Figure 1.8. Different measures of occlusal shape illustrated on the lower molar of the dasyurid marsupial *Antechinus agilis*. Metrics include: (A) surface relief; (B) orientated patch count; (C) Dirichlet normal energy; and (D) shearing ratio. After Evans (2013).

1.2.4.6 Dental Microstructure

Crown group osteichthyans share teeth covered in hard mineralised enamel (Sansom et al. 1992; Qu et al. 2015) and underpinned by a complex microstructure organised across a range of spatial scales (Maas and Dumont 1999; Sander 2000). At the finest scale enamel is composed of individual enamel crystallites which form columnar modules called prisms (Figure 1.9). The prisms are stacked in bundles to form different enamel types, which may be differentially integrated to form distinct enamel architectures called a schmelzmuster (Koenigswald 2000).

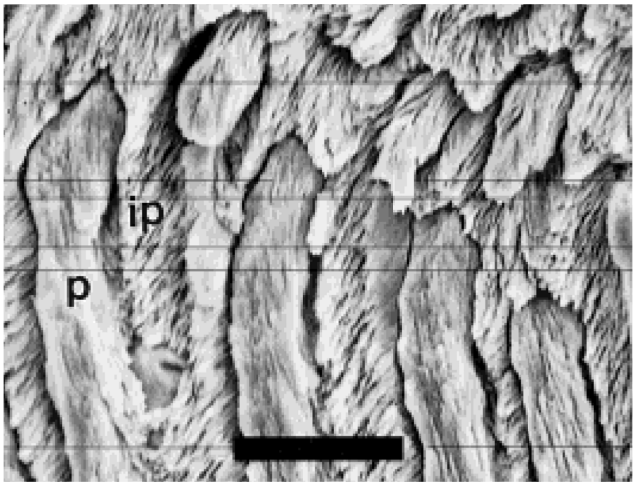

Figure 1.9. Structure of enamel in a longitudinal section through the molar of the red slender loris, *Loris tardigradus*, showing the inter-prismatic enamel and prismatic enamel with crystallites aligned parallel to the prism long-axis. From Maas and Dumont (1999).

Crown mammals have evolved radial enamel (Figure. 1.10), a type of prismatic enamel, distinct from the prismless enamel of reptiles, early mammaliaforms, and toothed birds (Koenigswald 1997; Sander 2000; Maas and Dumont 1999). The radial enamel of placental and marsupial mammals is characterised by prisms orientated parallel to each other as they diverge from the enamel–dentine junction (Koenigswald 1997, 2000; Mass and Dumont 1999). Because most mammals utilise a two-phase occlusal motion, it has been speculated that differences in crystallite orientation could be an adaptation to resist a shifting abrasion direction (Rensberger 2000). Mammals have also acquired a second type of prismatic enamel, called decussating enamel, where the prism orientation changes relative to the enamel–dentine junction (Maas and Dumont 1999). However, at least among placental mammals, radial enamel has been largely replaced by modified variants of radial enamel and decussating enamel (Pfretzschner 1993; Koenigswald 2000), suggesting that microstructural adaptation has been important in the diversification of modern mammalian groups.

Enamel derives its rigidity from its apatite crystal composition (97% by weight; Ungar 2010), but because enamel is composed of discrete crystals its resistance to stress varies depending on prism geometry. By increasing the resistance of enamel to abrasion forces, changes in prism microstructure are a potentially important adaptive response to dental wear (Rensberger 2000). A common feature of marsupial enamel is an abrupt transition zone between enamel types orientated parallel to the enamel–dentine junction, called simultaneous prism decussation (Young 1990; Koenigswald 2000). Decussating enamel, wherein the orientation of the contact surface between prism bundles changes relative to the occlusal surface, provides a mechanism to increase resistance to both fracture and wear forces (Pfretzschner 1993; Mass and Dumont 1999; Rensberger 2000). The three main types of mammalian enamel decussation are Hunter–Schreger bands, irregular enamel, and zipper enamel (Koenigswald 2000). Hunter–Schreger bands are characterised by layers of decussating prisms orientated transversely to the growth axis with abrupt changes in prism orientation occurring at the transition zones (Figure 1.10). Irregular enamel, where decussation occurs amongst prisms in irregular bundles or individual prisms, is taxonomically less common but occurs amongst rodents, lagomorphs, and australidelphian marsupials (Young et al. 1990; Koenigswald 2000). Zipper enamel, characterised by prisms decussating at approximately right angles along the edge of tooth crests, is only known from australidelphian marsupials (Young et al. 1990; Koenigswald 2000). The transition zones between decussating regions of enamel help to resist fracture propagation by increasing the energy needed for fractures to propagate across them (Rensberger 2000; Sander 2000; Yilmaz et al. 2015). The protective properties of decussation can be improved further by warping the decussation plane because this increases resistance to loading in multiple directions (Sander 2000) and is a common feature in high-relief dentitions subject to bending, like the carnassial teeth of carnivorans (Rensberger 1995; Tseng 2011). In herbivore teeth, like those of horses, decussation between the prismatic enamel and inter-prismatic matrix can help to resist the high shear forces which form at the occlusal surface and enamel–dentine junction (Pfretzschner 1993; Benazzi et al. 2013). The synchronous evolution of modified radial enamel and high-crowned dentitions in horses is also interesting because it shows how adaptive changes at one hierarchical level (tooth shape) can cascade ‘down’ to drive compensatory adaptation at a microstructural scale.

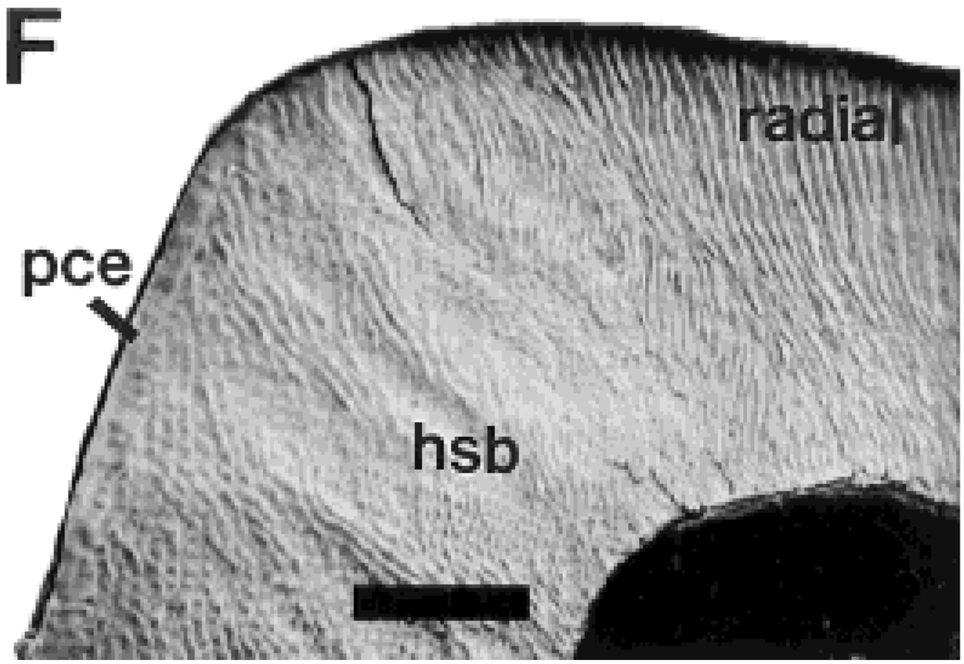

Figure 1.10. Longitudinal section through the buccal margin of a *Lemur catta* (ring-tailed lemur) premolar showing radial enamel (radial), Hunter–Schreger bands (hsb) and prismless enamel (pce). After Maas and Dumont 1999. Scale bar = 100 µm.

1.3 Herbivore Responses to Cenozoic Environmental Change on Northern Continents

Climatically-induced changes in terrestrial ecosystems provide a potentially important driver of morphological adaptation and taxonomic diversification amongst herbivores (Matthew 1915; Simpson 1944; Janis 1993). Climatic changes have been linked to shifts in relative abundance and diversity at relatively short timescales ($\leq$yr 10^4) (Blois and Hadly 2009) but their importance in driving adaptation and diversification at longer, macroevolutionary timescales is much less clear (Prothero and Heaton 1996; Van Dam et al. 2006; Blois and Hadly. 2009). For instance, the divergence of many major mammalian groups is not strongly aligned to major climate events (Alroy et al. 2000). Mammalian species are also often morphologically stable across short-term (Milankovitch-scale) climate oscillations and tend to ‘track’ rather than adapt to favourable habitats (Prideaux et al. 2007b; Raia et al. 2012). This evolutionary ‘insensitivity’ to climatic change contrasts with evidence for rapid adaptation in other traits like body size in response to even short-term (yr 10^4) climate shifts (e.g., Secord et al. 2012). These inconsistencies may indicate that mammalian taxa are only sensitive to specific types of climatic oscillation (Van Dam et al. 2006) and that morphological traits differ widely in their responsiveness to environmental change (Polly et al. 2011). Comparing herbivore responses to global climatic change between different regions, especially the northern continents where the fossil record is well sampled, provides an important means to test how environmental change influences herbivore evolution at a macroevolutionary timescale.

1.3.1 Paleogene

Early Paleogene mammalian communities were dominated by 'archaic' groups not closely related to modern taxa (Janis 1993; Agusti and Anton 2002; Beard 2004; Rose 2006). Paleocene herbivores, such as basal ungulates, possessed relatively undifferentiated low-crowned, bunodont, quadritubercular (four-cusped) molar dentitions (Jernvall et al. 1996; Rose 2006; Mihlbachler et al. 2011). Other groups, such as early proboscideans, had quadritubercular bunodont or bunolophodont molar crown types (Gheerbrant 2009; Sanders et al. 2010; Gheerbrant et al. 2016). Thus, despite the eventual derivation of widely disparate molar morphologies (e.g., Ungar 2010), most herbivore groups diversified from a fundamentally similar quadritubercular molar morphology.

Global climate reached its warmest point in the past 80 Myr during the Early Eocene (Clyde et al. 2001; Figure 1.11). This warm phase has been associated with the emergence and global expansion of many modern herbivore groups, such as the perissodactyls, artiodactyls, lagomorphs and rodents (Agusti and Anton 2002; Rose 1982; Beard 1998). In the Late Eocene, high-latitude cooling due to decreasing global pCO_2 and the thermal isolation of Antarctica (Kennett 1977; DeConto and Pollard 2003; Stickley et al. 2004) increased sensitivity of the global climatic system to orbital variations (Pisias et al. 1985; Zachos et al. 1996, 1997). This phase of climatic cooling was associated with the extinction of many archaic Eocene herbivore groups in North America and Europe (Berggren and Prothero 1992; Agusti and Anton 2002). These groups were replaced by immigrant taxa primarily from Asia, such as tapirs, rhinoceroses, indricotheres, and selenodont artiodactyls (Janis

1993; Beard 1998). At approximately the same time in Asia, global cooling and aridification drove the replacement of the perissodactyl faunas by rodent and lagomorph-dominated communities (Zhang et al. 2012).

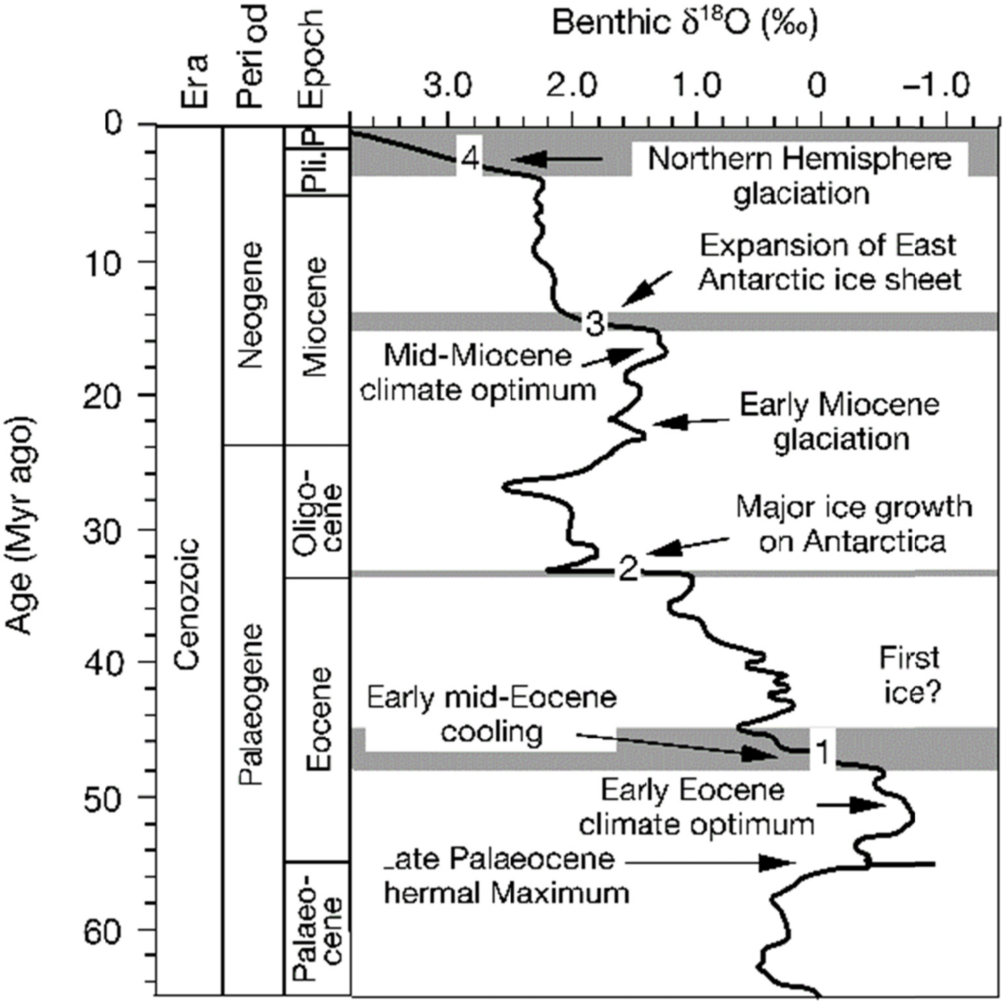

Figure 1.11. Major Cenozoic climatic events and their relationship to the benthic foraminiferal $\delta^{18}O$ record (Pearson and Palmer 2000).

1.3.2 Neogene and Quaternary

The Neogene generally marks a shift in global climate from warm, stable, and wet environments to drier and more variable conditions (Pearson and Palmer 2000; Zachos et al. 2001). During the Neogene, herbivores adapted to consume dicot plant leaves (browsers) were replaced by ungulates, lagomorphs, and murine rodents better adapted to consume grasses (Fortelius et al. 2002; Gomes Rodrigues et al. 2013). However, the climatic transition across the Paleogene–Neogene boundary was not straightforward because from the late Oligocene until the mid-Miocene there was a distinct period of global warmth, culminating in the Middle Miocene Climatic Optimum (Zachos et al. 2001; Figure 1.11). As a result, Early Miocene ungulate faunas in Europe remained compositionally similar to those of the Late Oligocene, consisting primarily of small to medium-sized browsing archaic artiodactyls, moschoid ruminants (musk deer), rhinoceroses, and tapirs (Agusti and Anton 2002). During the late Early Miocene these ungulate groups were joined by African herbivores like equids, anthracotheres, suids, cervids and proboscideans (Agustí et al. 2001).

A key barometer of herbivore response to environmental change during the Neogene is molar crown height (Janis and Fortelius 1988; Fortelius et al. 2002; Mihlbachler et al. 2011; Dunn et al. 2015). In Europe the first groups to become hypsodont were Early Miocene hyotheriine suids and moschoid ruminants (Fortelius et al. 1996). Amongst North American faunas, burrowing mammals like rodents and lagomorphs were the first to acquire high-crowned dentitions, but interestingly millions of years before grasslands became widespread (Jardine et al. 2012). During the early Miocene (~18 Myr) the first high-crowned equids emerged in North America, around 4 Myr after the first palaeobotanical evidence for open, grass-dominated habitats (Strömberg 2006). Because increased dental wear is strongly correlated with the emergence of high-crowned dentitions (Mihlbachler et al. 2011), there seems to have been a behavioural delay in the utilisation of abrasive grasses by equids. In South America, notoungulate molar crown height began to increase much earlier, during the late Eocene, probably in response to increasingly open habitats established with declining rainfall and opening of the Drake Passage (Dunn et al. 2015). After the Early Miocene only hypsodont taxa were able to diversify (Jernvall and Fortelius 2002). Beginning in the Early Miocene, ungulate herbivore dentitions became increasingly complex (Jernvall et al. 1996; Evans and Janis 2014) suggesting that these herbivores were specialising on more fibrous foods. Variations in regional climates and the responsiveness of mammalian groups to selective pressures emerge as the most important factors controlling the emergence of high-crowned dentitions on different continents.

The Middle Miocene Climatic Optimum (14.2–13.8 Myr ago) marked a major reversal of the global cooling trend initiated in the middle Eocene (Zachos et al. 2001; Shevenell et al. 2004; Figure 1.11). Cooling of global climate resumed soon after (Figure 1.12), leading to an expansion of sclerophyllous drought-adapted vegetation and contraction of temperate forests (Utescher et al. 2000). Middle Miocene European and Asian ungulates responded by evolving larger body size, longer distal limb elements, and higher-crowned molar teeth (Agusti and Anton 2002; Fortelius et al. 2002; Damuth and Janis 2011). Competition from derived ungulates may have been important in the replacement of some more archaic ungulate groups like the anchitherine horses. This is because just prior to their extinction the anchitheres show evidence for rapid increases in molar crown height and occlusal complexity, mimicking trends in the Equinae which replaced them (Kaiser 2009; Eronen et al. 2010).

In the late Miocene (8–6 Myr) declining atmospheric CO_2 concentration and lower temperatures (Figure 1.12) prompted the expansion of C_4 plants, such as tropical grasses and shrubs, and the decline of C_3 grasses and trees (Cerling et al. 1997). Across the northern continents this vegetation change and the correlated shift to lower rainfall environments is associated with the ascendancy of higher-crowned artiodactyls, perissodactyls, and rodents. In Europe, high-crowned ungulate herbivores become common from around 8 Myr (Jernvall and Fortelius 2002), whereas in Asia the herbivore fauna remained lower-crowned until the Pliocene (Fortelius et al. 2002). By the late Miocene most North American equids were high-crowned, having largely replaced the lower-crowned anchitheriine horses (Mihlbachler et al. 2011). Although increased molar crown height was a common response to dietary abrasion amongst Miocene herbivores, other mammalian groups integrated increases in crown height with other dental traits. For instance, African proboscideans acquired high-crowned prismatic molars composed of multiple transverse ridges or lamellae, as they shifted toward the consumption of C_4 grasses (Sander et al. 2010; Lister 2013). There is also evidence for analogous 'last throw of the dice' adaptations to those seen amongst anchitheriine horses (e.g., Kaiser 2009;

Eronen et al. 2010) in groups like the gomphothere proboscideans, which evolved additional cusp pairs, lamellae, and increased molar complexity before their replacement by grazing elephantids (Lister 2013). Other afrothere mammals, like the trichechid sirenians, acquired thick molar enamel and continuous molar replacement (Ameghino 1883; Domning 1982; Domning 2001; Beatty et al. 2012). Dugongid sirenians, which were even more reliant on seagrass than the trichechids (Clementz et al. 2009), completely discarded the bilophodonty of ancestral tethytheres, reducing the enamel cap and establishing a continuously-growing molar dentition like some rodents (Domning 1978).

Between 5 and 3 Myr there was another period of global warmth which reversed the cooling trend established since the Middle Miocene Climatic Optimum (Fedorov et al. 2006; Sniderman et al. 2016). The drivers of this event are unclear but this early Pliocene warm ‘reversal’ has been linked to oceanic circulation changes induced by formation of the Panamanian Isthmus (Haug et al. 2001) and Indonesian seaway (Cane and Molnar 2001). During this early Pliocene warm event, groups like cervids, gazelles and spiral-horned antelopes became increasingly dominant in Europe (Agusti and Anton 2002). Perhaps counterintuitively, many archaic herbivore groups which had previously dominated during warm and wet phases, like the hipparion horses, perissodactyls and rhinocerotids, declined in diversity (Janis 1993; Fortelius et al. 2002).

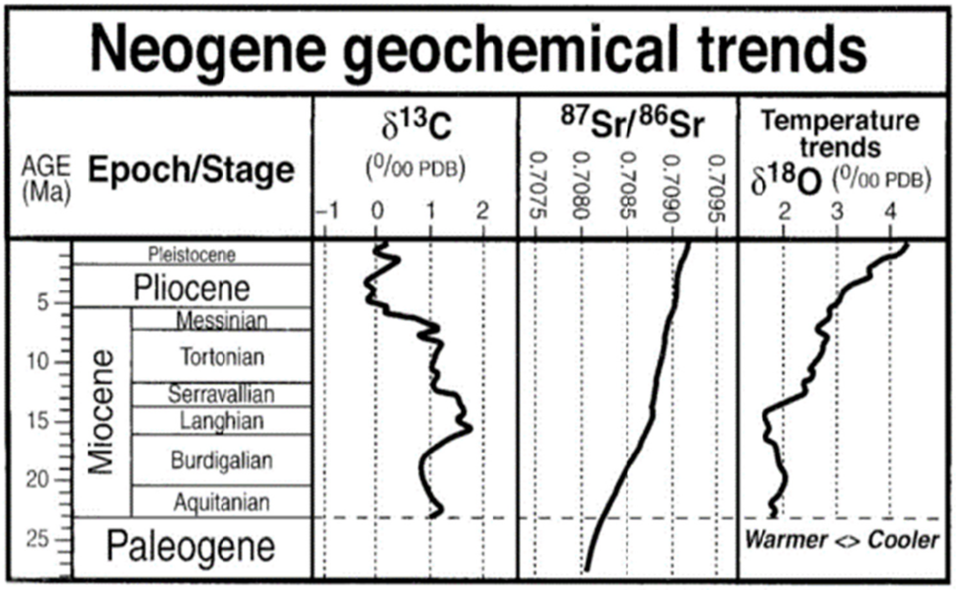

Figure 1.12. Global Neogene geochemical trends (Gibbard and van Kolfschoten 2004). Oxygen isotope ratios become progressively heavier as palaeotemperature decreased over the last 15 Myr of the Cenozoic.

From 3 Myr ago, global marine δ^{18}O curves show a trend toward increasing climatic variability dominated by high-frequency Milankovitch cycles (10^6-yr) (Gibbard and Van Kolfschoten 2004). Between 3 to 0.8 Myr ago, global climate was dominated by a 41-kyr periodicity in insolation maxima, but after 800 kyr ago, the orbital periodicity switched to 100-kyr and 23-kyr frequencies (Figure 1.13; Raymo and Nisancioglu 2003). The combined environmental impacts of eccentricity and obliquity forcing were a key driver of faunal turnover in European rodent communities (Van Dam et al. 2006). A rapid decline in global temperatures from 2.75 Myr ago at high latitudes marked the onset of the Pleistocene glacial cycles as greenhouse gas levels declined (Ravelo et al. 2004). In Europe, crown height values for herbivores through the Pliocene until the early Pleistocene actually decreased relative to the Late Miocene, probably due to an increase in rainfall (Fortelius et al. 2002). During the Late Pleistocene, the Northern Hemisphere herbivore fauna became dominated by taxa adapted to a steppe–tundra habitat, including such iconic animals as the woolly mammoth and woolly rhino, as well as giant cervids, equids, reindeer, and bison. Some of these megaherbivore lineages may have acquired adaptations to cold and dry habitats on the cold Tibetan Plateau during the otherwise warmer Pliocene Epoch (Deng et al. 2011). By the close of the late Pleistocene (ca 12 kyr ago) most of the Northern Hemisphere megaherbivores were extinct, leaving only a few remnant taxa like bison, reindeer, and moose (Koch and Barnosky 2006).

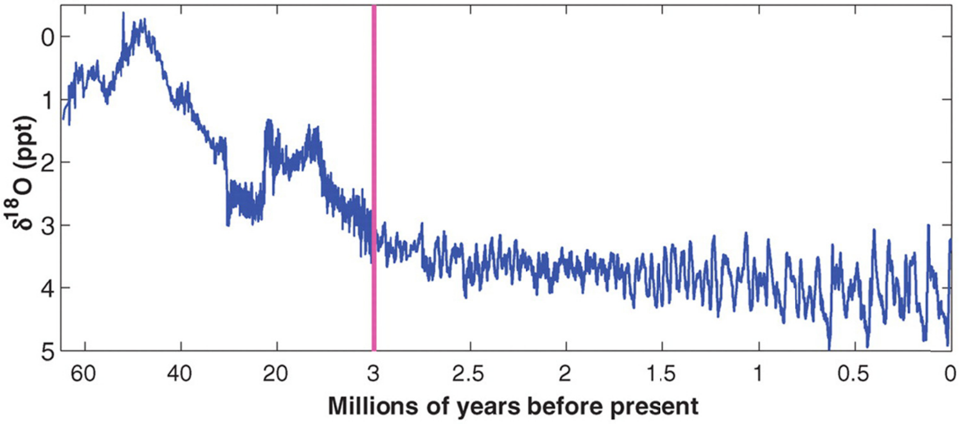

Figure 1.13. $\delta^{18}O$ time series over the Neogene (from Fedorov et al. 2006). Note that ice volume-driven variability in $\delta^{18}O$ increases in amplitude over the last 3 Myr. Between 3 and 0.8 Myr ago the record is dominated by 41-kyr periodicity but after 0.8 Myr ago it shifts to combined 100-kyr and 23-kyr cycles.

1.4 Marsupial Herbivore Evolution in a Changing Australian Environment

Assessing herbivore responses to climatic change in Australia is made challenging because of the comparatively depauperate vertebrate fossil record (Rich 1991). However, intensive taxonomic research over the past four decades has greatly improved our understanding of diversity dynamics and character evolution (Megirian 1994; Black et al. 2012). This has culminated in the establishment of an Australian land mammal age biochronological scheme (i.e., Megirian et al. 2010) which documents the broad patterns of faunal succession over the past 25 Myr. Six land mammal ages are currently recognised, which from oldest to youngest are: Etadunnan (late Oligocene: ~25 Myr); Wipajirian (latest Oligocene–early Miocene: ~25– ~18 Myr); Camfieldian (early to middle Miocene: < 18–?10); Waitean (late Miocene: ?10–~6 Myr); Tirarian (early Pliocene to late Pliocene: ~4.5–3.6 Myr); and

Naracoortean (late Pliocene–recent: ~3–0 Myr). The close correspondence between land mammal age boundaries and Cenozoic epoch boundaries suggests that at least at a first-order scale, global environmental change has been an important driver of Australian mammalian diversity and character evolution.

Terrestrial Paleogene environmental records for Australia are restricted to a few discrete sites due to poor exposure and deep weathering profiles (Alley 1998). The available record suggests that between the late Paleocene and Middle Eocene there was widespread distribution of cool-temperate forests, reflecting high-rainfall, stable temperatures, and limited seasonality (Greenwood et al. 2003). The early Paleogene mammalian record is extremely depauperate, being restricted to just a single early Eocene fossil assemblage (> 55 Myr), the Tingamarra Local Fauna (LF), from southeastern Queensland (Godthelp et al. 1992). Isolated fossils from this site suggest that terrestrial mammalian communities were dominated by small-bodied marsupials with close affinities to Late Paleocene faunas from Peru (Sigé et al. 2009). The Tingamarra LF also documents the earliest Australian evidence for australidelphian marsupials (Beck et al. 2008), the clade which includes all the Australian marsupial herbivores, the Diprotodontia, as well as the carnivorous Dasyuromorphia, Notoryctemorphia, Peremelemorphia, and the South American Microbiotheria (Szalay 1994).

A major gap between the early Eocene and late Oligocene conceals faunal dynamics during most of the Australian late Paleogene (Rich et al. 1991). However, the improved fossil record of the latest Oligocene provides evidence for significant Paleogene taxonomic diversification amongst Australian marsupials (Black et al. 2012), a view consistent with molecular phylogenetic analysis (e.g., Mitchell et al. 2014). Major clades within Diprotodontia were part of this Paleogene radiation, because representatives of the modern groups such as phalangeriforms (possums and kangaroos) and vombatiforms (e.g., wombats, koalas, diprotodontoids) are present in late Oligocene deposits (Aplin and Archer 1987; Long et al. 2002). With the exception of the macropodoids, most phalangeriform marsupials are arboreal and have omnivorous diets, which include insects, fruits, plant leaves, and small vertebrates (van Dyck and Strahan 2008). The vombatiforms on the other hand were a primarily ground-dwelling group (excepting koalas and the diprotodontid

Nimbadon) of large-bodied herbivores (Long et al. 2002). Despite their ecological importance in late Cenozoic ecosystems, the timing and pattern of vombatiform evolution remains poorly understood. The most diverse vombatiform group are the now-extinct Diprotodontoidea, which dominated large herbivore niches during most of the late Cenozoic (Murray and Megirian 1992; Long et al. 2002; Black et al. 2012). The Diprotodontoidea comprised two families, the Diprotodontidae and Palorchestidae (Stirton et al. 1967; Murray et al 2000), for which the sequence and timing of morphological evolution is poorly understood. It is clear however, that diprotodontoids evolved a diverse range of dental morphologies, especially in terms of their incisor and premolar morphology (Murray et al 2000; Long et al. 2002). All dipotodontoids possessed bilophodont molars which they acquired independently of other bilophodont marsupials like the macropodoids.

Phalangeriform and vombatiform marsupials share a quadritubercular molar morphology formed through modification and enlargement of a metaconule to form a hypocone (Tedford and Woodburne 1998). It remains unclear exactly how many times the hypocone evolved amongst diprotodont marsupials (Sánchez-Villagra and Kay 1996). Some groups like the thylacoleonids, pseudocheirids, and phalangerids evidently reverted from a quadritubercular molar to a tricuspid molar morphology, by reducing the hypocone on the posterior molars, or the protocone on M^1 (Aplin and Archer 1987; Murray et al. 1987; Couzens et al. 2016).

The earliest-known marsupial herbivores occur in the Pwerte Marnte Marnte LF, a probable middle or late Oligocene assemblage from central Australia (Murray and Megirian 2006; Megirian et al. 2010). Terrestrial herbivores recognised from this site include macropodoids, diprotodontoids and vombatoids (Murray and Megirian 2006). Evidence regarding Australian vegetation and rainfall is scant for the late Oligocene and early Miocene and Australian palaeontologists have tended to rely heavily on inferences drawn from morphological adaptations and diversity of mammalian herbivores to infer habitat structure (e.g., Archer et al. 1994; Travouillon et al. 2009). This approach is problematic given the potential for circularity in inference.

Wipajirian fossil faunas from the Carl Creek Limestone at Riversleigh in northeastern Australia document a diverse late Oligocene to early Miocene fauna and have been influential in inferring links between marsupial herbivore evolution and climate change (Archer et al. 1994; Black et al. 2012). However, the palaeoenvironmental interpretations from this locality have been controversial (e.g., Megirian 1992; Megirian et al. 2004; Herold et al. 2011; Black et al. 2012; Greenwood et al. 2012). The high mammalian diversity, especially amongst arboreal mammals, and occurrence of many taxa with modern representatives in northern Australia and New Guinea, has been argued to indicate widespread closed, 'rainforest' habitats in the Australian Oligocene and Miocene (Archer et al. 1989). However, continent-scale modelling suggest that a doubling in global atmospheric CO_2 levels above early Miocene estimates would be needed for this to occur (Herold et al. 2011). Furthermore, sedimentological data from the Carl Creek Limestone and other approximately coeval central Australian sites suggests drier and more seasonal conditions (Megirian 1992; Megirian et al. 2004). Plant fossils from the Dunsinane LF at Riversleigh indicate that late Oligocene or early Miocene environments were dominated by Casuarinaceae; more consistent with an open sclerophyll rather than closed-forest habitat (Guerin and Hill 2006). The structure of mammalian body-size distributions also indicates a mix of closed and open forest habitats (Table 3, Travouillon et al. 2009; Greenwood et al. 2012). A consensus view of the proxy evidence thus suggests that the Carl Creek Limestone records seasonal habitats comprising mixed closed and open forest, with 'rainforest' restricted to riparian settings.

In central Australia, silcrete deposition and associated macrofloral records suggest that environments were seasonal, with fluctuating water tables during the latest Oligocene to early Late Miocene (Carpenter et al. 2011). Early Miocene fossil faunas and sedimentological data from the Kangaroo Well LF suggest palaeotemperatures of 14–20ºC and mean annual rainfall <600 mm, likely restricting vegetation to scrub and low forest (Megirian et al. 2004). Further south in the Lake Eyre Basin, stratigraphic, pollen and macrofloral data indicate that significant drainage had concluded by the Late Miocene with only riparian rainforest (Alley et al. 1996; Alley 1998).

Pollen data suggest that, by the late Miocene, a trend to drier and more open, sclerophyll-dominated habitats was underway (Macphail 1997; Sniderman 2016). Late Miocene pollen records indicate sparse shrubland or woodland and a semi-arid climate in southern Australia (Sniderman et al. 2016). Late Miocene–Pliocene palynofloras from south central Australia reveal assemblages dominated by Casuarinaceae rather than rainforest floras (Martin 1990). The best studied and taxonomically richest late Miocene vertebrate fossil assemblage is the Alcoota LF from central Australia. It contains a mammalian herbivore fauna dominated by large-bodied diprotodontoids alongside early sthenurine and macropodine kangaroos (Murray and Megirian 1992). Dental disparity amongst these herbivores is low, with both the macropodids and diprotodontoids possessing low-crowned bilophodont molars. But, it remains unclear whether this 'snapshot' is representative of the broader continental herbivore fauna because the preservation at Alcoota appears skewed toward large-bodied vertebrates. Molecular data suggest that the lagostrophine kangaroos were present (Westerman et al. 2002), and that the macropodine kangaroos were diversifying at this time (Meredith et al. 2009a; Phillips et al. 2013). Neither inference is as yet supported by the sparse fossil record.

Traditionally, the transition from the late Miocene to the early Pliocene was considered to involve intensification of aridity (Tedford et al. 1992; Macphail 1997). However, radiometrically dated pollen records from central Australia suggest that there was actually a distinct shift to warm and wet climates in the early Pliocene (Sniderman et al. 2016). Evidence for such a warm, wet shift is also supported by pollen data from southwestern Australia which shows that vestigial rainforest elements like *Podocarpus* and *Nothofagus* were still present in the middle Pliocene (Bint 1981; Atahan et al. 2004). The fact that this contradicts evidence from other sites for intensification of aridity (e.g., Clark 1994) may reflect the much better chronostratigraphic resolution of more recent studies. The impacts of the Miocene–Pliocene transition on herbivore evolution are not well understood, both because the fossil and palaeoenvironmental record is scrappy, and because the chronostratigraphy of this interval is poorly resolved. The available fossil record suggest that in terms of diversity and abundance, more archaic herbivore groups like the diprotodontoids were largely usurped as the dominant terrestrial herbivores by macropodids during the early Pliocene (Murray and Megirian 1992; Prideaux and Warburton 2010; Black et al. 2012). The early Pliocene vertebrate record also reveals the first evidence for the assembly of a fundamentally modern herbivore fauna and the first clear evidence of faunal provincialism. For instance, the Bluff Downs and Hamilton LF's reveal the first occurrences of the extant macropodid genera *Macropus*, *Dorcopsis*, *Dendrolagus* and *Potorous* (Flannery et al. 1992). Compositionally these two faunas differ sharply from the Palankarinna LF of northern South Australia, which exhibits lower species diversity and is depauperate in taxa with closed forest affinities (Tedford et al. 1992). Declining ecosystem productivity during the Pliocene may also have been important in the evolution of macropodoid gigantism given that first large-bodied macropodine and sthenurine kangaroos appear in sites like the Palankarinna LF, which also contain abundant sedimentological evidence for aridity (Tedford et al. 1992; Prideaux 2004).

Over the past 3.5 Myr declining temperatures and increasing climatic variability prompted major changes in Australian terrestrial ecosystems (Kershaw et al. 2000). From this perspective the late Pliocene is significant because it captures the first evidence for widespread grasslands (Macphail 1997; Martin 2006). Pollen records show that temperate rainforest persisted in southeastern Australia, probably because warm ocean temperatures ameliorated continental aridity (Sniderman et al. 2007). Changes in the terrestrial environment were matched by diversifications amongst marsupial herbivores, especially the macropodine kangaroos, which were the most diverse and abundant herbivores of the late Pliocene (>23 species). Stable carbon-isotopic evidence from herbivore dental enamel in the Late Pliocene Chinchilla LF suggest that this increase in macropodine species richness was coincident with increased consumption of grass and higher levels of dietary partitioning (Montanari et al. 2013; Figure. 1.14). The isotopic data from Chinchilla are also significant in showing that herbivores had yet to specialise on C_4 grass (i.e., grazing), probably because grasslands did not become extensive until the late Pliocene or early Pleistocene (Macphail 1997).

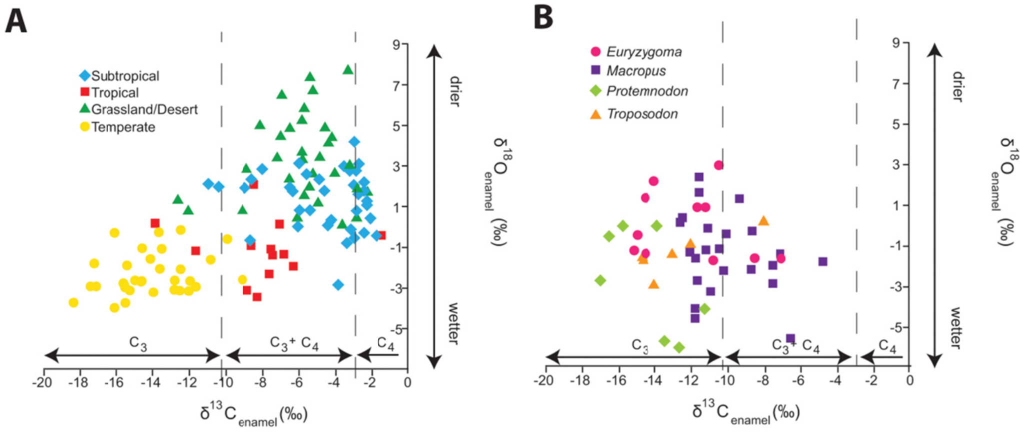

Figure 1.14. Comparison of (A) stable isotopic data for modern marsupial dental enamel and (B) fossil dental enamel from the late Pliocene Chinchilla Local Fauna. Relatively enriched δ^{13}C values provide evidence for C_4 grass consumption, by the macropodine *Macropus* and the diprotodontine *Euryzygoma*. After Montanari et al. (2013).

The terrestrial vertebrate fauna from the early Pleistocene has received relatively little attention, meaning that there is limited understanding of how Australian herbivore evolution was impacted by the onset of glacial cyclicity. The compositional similarity between some late Pliocene and Pleistocene assemblages (i.e., Naracoortean assemblages, Megirian et al. 2010) may indicate a gradual transition rather than ‘turnover’ across this boundary. In northeastern Australia, well-dated cave assemblages suggest that many late Pliocene taxa persisted into the early and middle Pleistocene (Hocknull et al. 2007). Elsewhere it is unclear to what extent taxonomic occurrences straddling the boundary reflect poor chronostratigraphic resolution, because some sites long presumed to be of Pliocene age, like the Rackham’s Roost LF, are now radiometrically dated to the early Pleistocene (Woodhead et al. 2015).

In the early Middle Pleistocene (ca 700 kyr ago), a phase of aridification is recorded in a shift from lacustrine to gypsum-dominated sedimentation in many southern Australian interior basins (Pillans and Bourman 2001; Zheng et al. 2003). Around 500 kyr ago, many iconic marsupial ‘megafauna’ make their first appearance, in cave sediments from the Naracoorte region of southeastern Australia (Prideaux et al.

2007b). Based on morphological convergences, at least some of these Australian marsupials likely filled similar ecological niches to their placental counterparts elsewhere. For instance, the robust mandibles, complex molars, and reduced lower incisors of the giant sthenurine kangaroo *Procoptodon goliah* are similar to Pleistocene elephantids (Prideaux 2004; Prideaux et al. 2009). Middle and late Pleistocene fossil deposits show that sthenurine species richness had approximately doubled relative to the Pliocene, although the exact ecological drivers of this relatively late diversification are unclear (Prideaux 2004). In contrast, macropodine species richness increased only marginally across the Tirarian–Naracoortean transition, perhaps reflecting a saturation of available niche space. The trend towards drier and more variable environments continued during the last 350 kyr, superimposed on glacial–interglacial cyclicity (Kershaw et al. 2003). Fossil assemblages from the Naracoorte region, which span the last 500 kyr, show that although glacial cyclicity prompted fluctuations in herbivore population density, it did not drive extinction (Prideaux et al. 2007b).

During the last glacial maximum there was an intense period of aridity, temperature reduction and vegetation change across the Australian continent (Miller et al. 1997; Kershaw et al. 2003). The most distinctive feature of Australian herbivore evolution over this period was the extinction of virtually all large-bodied (>40 kg) herbivores by 40–50 kyr ago (Roberts et al. 2001; Saltré et al. 2016). The Australian extinction event occurred earlier and was more devastating than ‘megafauna’ extinctions on other continents (Prideaux et al. 2007b), resulting in the loss of at least 34 species of large-bodied herbivore (Roberts et al. 2001; Saltré et al. 2016). Although the debate about Australian megafaunal extinction has been historically polarised between anthropogenic and climatic explanations (e.g., Wroe and Field 2006; Johnson et al. 2016) most recent regional and continent-scale studies find that the pattern and chronology of extinction is most consistent with an anthropogenically-driven process (Roberts et al. 2001; Prideaux et al. 2007a, b; Turney et al. 2008; Prideaux et al. 2009; Prideaux et al. 2010).

1.4.1 Macropodoidea

As the most diverse living marsupial herbivores (Flannery 1989; Prideaux and Warburton 2010), the Macropodoidea potentially provide important insights into how Cenozoic environmental change impacted herbivore evolution. The most basal macropodoid group is the family Hypsiprymnodontidae (Figure 1.15), which includes as its sole extant species, the musky rat-kangaroo, *Hypsiprymnodon moschatus* (Prideaux and Warburton 2010). *H. moschatus* is distinguished from other macropodoids by its relatively simple stomach, retention of a first toe on the hind foot, and quadrupedal bounding gait (Flannery and Archer 1987; Burk et al. 1998; Black et al. 2014). It is unclear if the extinct macropodoid subfamilies Balbarinae and Propleopinae are closely related to Hypsiprymnodontidae or form a sister group to Macropodoidea (Black et al. 2014; Figure 1.15). The family Macropodidae comprise all other kangaroos, wallabies, bettongs and potoroos, representing at least 60 extant species. Four subfamilies are recognised: the extant Potoroinae (bettongs and potoroos), Lagostrophinae (banded-hare wallabies) and Macropodinae ('typical' kangaroos and wallabies), and the extinct Sthenurinae (short-faced kangaroos) (Prideaux and Warburton 2010; Figure 1.15).

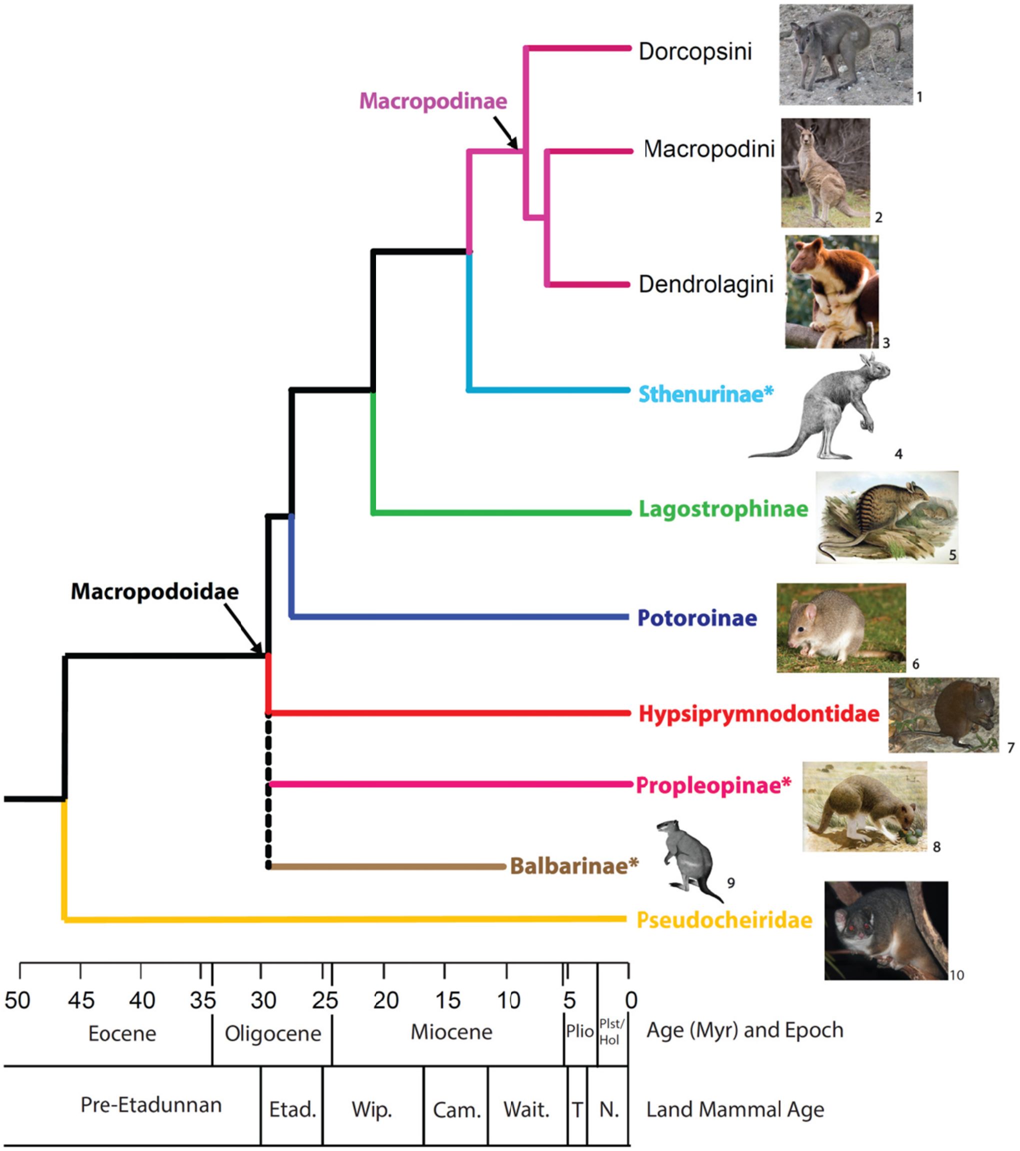

Figure 1.15. Macropodoid relationships based on a consensus topology from morphological and molecular analyses (Meredith et al. 2009a; Mitchell et al. 2014; Prideaux and Warburton 2010; Black et al. 2014). Divergence times derived from Couzens et al. (2016) except for Pseudocheirdiae + Macropodoidea which is derived from Mitchell et al. (2014). *Denotes extinct taxa. Dashed lines denote uncertain branch positions. Abbreviations: Plio, Pliocene; Plst/Hol, Pleistocene and Holocene; Eta., Etadunnan; Wip., Wipajirian; Cam., Camfieldian; Wait., Waitean; T., Tirarian; N., Naracoortean. Land mammal ages follow Megirian et al. (2010). Image credits: **1.** grey dorcopsis, *Dorcopsis luctuosa*, (c) Conrad Savy, retrieved from http://www.inaturalist.org/taxa/42941-Dorcopsis-luctuosa, CC BY-NC-ND 4.0 ; **2.**

eastern grey kangaroo, *Macropus giganteus*, (c) J. J. Harrison, retrieved from https://en.wikipedia.org/wiki/Eastern_grey_kangaroo, CC BY 2.0; **3.** goodfellow's tree kangaroo, *Dendrolagus goodfellowi*, (c) Timmy Toucan, retrieved from https://en.wikipedia.org/wiki/Goodfellow's_tree-kangaroo, CC-BY; **4.** *Procoptodon goliah*, (c) Peter F. Murray, retrieved from Prideaux, G. J. 2004. Systematics and Evolution of the Sthenurine Kangaroos. Univ. Calif. Publ. Geol. Sci. 146:1–623, Plate 110; **5.** munning, *Lagostrophus fasciatus*, (c) John Gould, F. R. S. 1863. Mammals of Australia, Vol. II, Plate 60; **6.** eastern bettong, *Bettongia gaimardi*, (c) J. J. Harrison, retrieved from https://en.wikipedia.org/wiki/Eastern_bettong, CC BY-SA 3.0; **7.** musky rat-kangaroo, *Hypsiprymnodon moschatus*, (c) PanBK, retrieved from https://en.wikipedia.org/wiki/Musky_rat-kangaroo, CC BY-SA 3.0; **8.** *Propleopus oscillans*, (c) Frank Knight, retrieved from P. Vickers-Rich and Gerard F. van Tets, 1990. Kadimakara: extinct vertebrates of Australia, Princeton University Press; **9.** *Balbaroo fangaroo*, (c) Anne Musser, retrieved from Long, J, A., M. A. Archer, T. F. Flannery, and S. Hand. 2002. Prehistoric Mammals of Australia and New Guinea: one hundred million years of evolution, John Hopkins University Press; **10.** Common ringtail possum, *Pseudocheirus peregrinus*, (c) Benjamint444, retrieved from: https://en.wikipedia.org/wiki/Common_ringtail_possum, CC BY-SA 3.0.

The most basal macropodids, the Potoroinae, are primarily small-bodied fungivores, which unlike *Hypsiprymnodon*, primarily hop bipedally and have a more complex, rumen-like forestomach (Burke et al. 1998; Prideaux and Warburton 2010; Arman and Prideaux 2015). Molecular data suggest that potoroines diverged from other macropodids by the late Oligocene (Meredith et al. 2009a; Mitchell et al. 2014), consistent with the occurrence of basal potoroine-like macropodids in latest Oligocene and early Miocene deposits (e.g., Woodburne 1984b; Flannery and Archer 1987). Most potoroines have bunodont, crushing molars with a well-developed shearing premolar, although some like the rufous bettong, *Aepyprymnus rufescens,* have bunolophodont molars, suggesting a more fibrous diet. A diverse range of potoroine-like macropodids (the paraphyletic 'Bulungamayinae', Prideaux and Warburton 2010) are known from early and middle Miocene deposits in central and northern Australia.

Because hypsiprymnodontids, potoroines, and many potoroine-like basal macropodids share bunodont, quadritubercular molars, this crushing-optimised dentition was likely ancestral for Macropodoidea. Basal fossil macropodids, like *Bulungamaya delicata* and *Ganguroo bilamina*, form a structural sequence from bunodont to the fully bilophodont molar dentitions of derived macropodids (Cooke 1992, 1997b). However, because the timing of this transition is not well resolved biochronologically, and due to the occurrence of bilophodonty amongst the extinct balbarines (Cooke 1997a) and extant potoroine, *Aepyprymnus rufescens*, there were probably multiple separate acquisitions of bilophodonty.

Interrelationships of the derived macropodids (kangaroos and wallabies) have received considerable attention over the past three decades (e.g., Flannery 1983, 1989; Meredith et al. 2009a; Prideaux and Warburton 2010). Within these groups, the phylogenetic position of the banded hare-wallaby, or merrnine, *Lagostrophus fasciatus*, has been especially labile, being variously considered a sthenurine (Flannery 1989), a macropodine (Bensley 1903; Raven and Gregory 1946), or a separate lineage (Baverstock et al. 1989). Recent molecular and morphological analyses support the latter view, that *L. fasciatus* is the sole extant member of Lagostrophinae (Westerman et al. 2002; Meredith et al. 2009a; Prideaux and Warburton 2010). Despite recent description of the early Pliocene lagostrophine *Tjukuru* (Prideaux and Tedford 2012), if molecular divergence estimates are correct, most of early lagostrophine evolution remains cryptic from the standpoint of the fossil record.

Revision of the phylogenetic position of *Lagostrophus* prompted a reevaluation of the relationships of the two most diverse macropodid groups, the Macropodinae and Sthenurinae (Prideaux and Warburton 2010). The Sthenurinae is an extinct late Cenozoic clade of primarily large-bodied kangaroos comprising at least 26 species (Prideaux 2004). This subfamily includes the largest kangaroo ever to evolve, the approximately 200-kg *Procoptodon goliah* (Helgen et al. 2006). The Sthenurinae likely originated during the Middle Miocene, before diversifying during the Middle and Late Pleistocene (Prideaux 2004). As a group they show trends toward reduction of the lateral hind-foot digits and larger body mass (Murray 1991; Prideaux 2004; Helgen et al. 2006), akin to other Neogene herbivores such as horses and bovids (e.g.

Janis 1993; MacFadden 1994). Another distinctive feature of the Sthenurinae is extreme shortening of the rostrum, especially amongst Pleistocene sthenurines, a feature which likely increased the crushing force of their lower molars and improved their ability to execute a nipping bite with the incisors (Prideaux 2004). Shortening of the rostrum was linked with enlargement of the jaw musculature, strengthening of the mandibular symphysis, molarisation of the premolar, and increased molar complexity, all traits associated with consumption of tougher, more fibrous plant foods (Prideaux 2004; Prideaux and Warburton 2010). Stable-isotopic and dental microwear data suggest that at least the largest sthenurine, *Procoptodon goliah*, was a specialist browser of C_4 photosynthetic xeromorphic shrubs such as the chenopod genus *Atriplex* (saltbushes) (Prideaux et al. 2009). The middle Miocene diversification of Australian chenopods raises the question of whether plant–herbivore coevolution was an important factor in the parallel diversification of the Sthenurinae. Similarly unclear are the factors responsible for the Middle Pleistocene diversification of sthenurines (Prideaux 2004), a seemingly unique event amongst Neogene browsing herbivores.

All other kangaroos and wallabies fall within the Macropodinae, the most diverse extant subfamily of marsupials, comprising 13 extant genera (Burk and Springer 2000; Van Dyck and Strahan 2008; Prideaux and Warburton 2010). In addition to being taxonomically diverse, the Macropodinae is the most ecological diverse of marsupial subfamilies, and includes large grazing and mixed feeding kangaroos, small browsing wallabies, rock wallabies and tree kangaroos (Van Dyck and Strahan 2008). Osteologically, macropodines are differentiated from other macropodids by an anterobuccal crest on the third upper incisor (I^3) and contact between the lower incisor (I_1) and the upper palate during molar occlusion (Prideaux and Warburton 2010). The oldest fossil macropodine is the Late Miocene *Dorcopsoides fossilis* from the Alcoota LF (Woodburne 1967) although molecular data imply a somewhat older, middle Miocene origination (Meredith et al. 2009a; Mitchell et al. 2014). The Macropodinae is divisible into three tribes: the New Guinea forest wallabies (Dorcopsini), rock wallabies and tree kangaroos (Dendrolagini), and Macropodini, which includes the remaining taxa (Prideaux and Warburton 2010; Arman and Prideaux 2015). Many members of Macropodini exhibit dental adaptations for consuming grass, such as the enlargement and curvature of the longitudinal molar crests, higher-crowned molars, a reduced premolar, delayed molar eruption, and in larger species of *Macropus*, molar progression (Sanson 1980; 1989; Janis 1990; Lentle et al. 2003; Prideaux and Warbuton 2010). Together with the gelada (*Theropithecus gelada*), the macropodine kangaroos constitute the only extant grazers that utilise a bilophodont molar morphology, otherwise more characteristic of predominantly browsing groups like diprotodontoid marsupials, early elephants, and tapirs. This raises the question: why did macropodines persist with bilophodonty whereas other ancestrally bilophodont groups like dugongs, proboscideans and rodents discarded this strategy in favour of hypselodont or high-crowned prismatic molars? One possibility is that functional constraints imposed by ancestral bilophodonty, or the specialised mode of incisor occlusion characteristic of macropodines, restricted the types of evolutionary modifications that could be made to their molars (Janis and Fortelius 1988; Janis 1990). However, the extent to which such functional constraints are 'unbreakable' is unclear (i.e., Gould 1989), and a better model of dietary adaptation might be one where different phenotypic solutions, of varying accessibility, can have similar fitness characteristics (Evans et al. 2007; Salazar-Ciudad and Marín-Riera 2013). Under this adaptive model, the 'best' solution follows the least convoluted path to the fitness optimum closest to the ancestral state (e.g., Salazar-Ciudad and Marín-Riera 2013). Thus, one explanation for why macropodids did not 'break away' from bilophodonty like proboscideans, dugongs, and rodents, is because the unique interaction of functional constraints and the rapid onset of dietary change soon after bilophodonty was acquired conspired to limit their adaptive options. Up until now, the acquisition of continuous dental replacement in *Petrogale concinna* (Sanson 1989; Gomes Rodrigues et al. 2011), and the unique 'zipper enamel' microstructure of diprotodont marsupials (Young et al. 1990; Koenigswald 2000) have been the strongest indications that macropodoids followed a very different evolutionary path to dental durability compared with that implied by the 'ungulate model' of dietary adaptation (i.e., Fortelius 1985; Janis and Fortelius 1988; Janis 1990). Analysis of macropodoid dental evolution thus has the potential to provide unique insights into how ecology and evolutionary history interact to shape adaptive morphological evolution.

1.5 Summary

The mammalian dentition has provided a powerful context in which to study adaptation (i.e., Simpson 1944; Lande 1976). Teeth function as tools for food breakdown (Evans and Sanson 2003) but physical interactions during chewing alter occlusal shape to produce wear. This wear degrades tooth performance and is especially problematic for herbivores because they rely on extended dental processing, high dental complexity, and precise tooth occlusion to processes tough foods (Fortelius 1985; Janis and Fortelius 1988; Evans et al. 2007). The potentially significant fitness declines associated with high levels of dental wear (e.g., Logan and Sanson 2002a; King et al. 2005) likely make it an important driver of herbivore dental evolution.

Herbivores have evolved a range of dental adaptations to deal with dental wear including increasing the vertical size of the tooth crown (Tapaltyan et al 2015; Janis and Fortelius 1988), increasing occlusal area (Pilbeam and Gould 1974a; Fortelius 1985), increasing dental complexity (Evans et al. 2007; Wilson et al. 2012), evolving supernumerary teeth (Sanson 1989; Gomes Rodrigues et al. 2011), increasing enamel thickness (Molnar and Gantt 1977; Lucas et al. 2008), and modifying enamel microstructure (Rensberger 2000). Increases in molar crown height are a common adaptive response, but it is uncertain whether changes in molar crown height are especially homoplastic (relative to other dental traits), or just more commonly assessed by researchers. Advances in scanning and digital morphometrics provide a means to more effectively test alternative mechanisms like changes in enamel microstructure or thickness.

Changes in global climate are likely to have been a key factor driving adaptation to increase dental durability. All Cenozoic herbivores evolved under a long term transition from a ‘greenhouse’ to an ‘icehouse’ world (Zachos et al. 2001). In the late Miocene, declining atmospheric CO_2 levels prompted the global expansion of drier, more-open environments dominated by grasses and xeric scrub (Cerling et al. 1997). These vegetation changes resulted in a gradual decline in browsing herbivore diversity and an increase in the abundance and diversity of higher-crowned herbivores like ungulates, rodents, and lagomorphs which relied on grasses (Jernvall et al. 1996; Janis et al. 2000; Fortelius et al. 2002; Jernvall and Fortelius 2002; Mihlbachler et al. 2011; Jardine et al. 2012). The first occurrence of high-crowned herbivores varies between continents due to regional differences in climate as well as lineage-specific variations in rates of dietary adaptation. In addition to external environmental factors, competitive interactions between different mammalian groups are likely to have been an important influence on rates of adaptation, diversification, and extinction.

Resolving how climatic change impacted herbivore evolution in Australia has historically been limited by a comparatively poor fossil record (Rich 1991). The current record shows that the Cenozoic Australian mammalian fauna was dominated by australidelphian marsupials (Woodburne et al. 1986; Sigé et al. 2009). The dominant herbivores were diprotodont marsupials, which molecular and fossil data suggest first diversified during the Middle Eocene (Meredith et al. 2009a; Mitchell et al 2014). At the close of the Middle Miocene many relatively archaic diprotodont herbivore groups disappeared to be replaced by more derived marsupial herbivores like the macropodids, pseudocheirid possums, and now extinct diprotodontids (Meredith et al. 2009a, b, Meredith et al. 2010, Prideaux and Warburton 2010; Mitchell et al. 2014).

The macropodoids are of particular interest in understanding how environmental change shaped herbivore evolution in Australia because they are the most diverse and abundant marsupial herbivores. Early macropodoids had low-crowned bunodont or bunolophodont molars, but transitioned during the late Oligocene or early Miocene to bilophodont molars that were more effective at fracturing tough leaves. During the late Neogene macropodids rapidly diversified as Australia became increasingly arid. The two dominant macropodid groups, the Sthenurinae and Macropodinae, likely diversified near the Miocene–Pliocene transition as closed forest declined and open habitats expanded (Macphail 1997; Kadereit et al. 2005; Martin 2006). The differing craniodental morphology of macropodine and sthenurine kangaroos suggests that they occupied distinct adaptive zones (Raven and Gregory 1946; Prideaux 2004), but how these differences emerged and relate to environmental change is poorly understood.

The reliance of many macropodine species on grasses has prompted comparison with ungulate herbivores (Janis 1990; Prideaux and Warburton 2010). However, the bilophodont molars of grazing macropodines are much lower crowned than those of many ungulate herbivores, possibly due to functional constraints (Janis 1990). Another related possibility is that the ‘ungulate model’ of dietary adaptation, which assumes that herbivores subjected to high rates of dental wear will converge on high-crowned teeth, is incorrect. Under this scenario, high rates of dental wear could lead to different dental phenotypes, of broadly similar fitness, depending on the distance and convolution of the path between the ancestral phenotype and the optimal solution (e.g., Salazar-Ciudad and Marin-Riera 2013). Evidence that macropodids followed such an alternative pathway is hinted at by the presence of unique or rare dental traits such as continuous dental replacement and novel enamel microstructure. Macropodoid dentitions seem to share much more in common with afrotheres and cercopithecoid primates than with the ungulate herbivores to which they are often compared (i.e., Janis 1990; Prideaux and Warburton 2010). Probing macropodoid dental evolution further thus has great potential to illuminate the processes and patterns which underpin dietary adaptation.

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2. INCREASED DISPARITY IN KANGAROO MOLAR CROWN HEIGHT ACROSS THE MIOCENE–PLIOCENE TRANSITION REFLECTS DIVERSIFICATION INTO GRASS-DOMINATED ECOSYSTEMS

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Context

The impact of environmental change on taxonomic diversity has been intensively studied amongst mammals, but much less attention has been directed toward understanding how it influences morphological diversity. Due to the comparatively rich dental fossil record and close relationship between tooth shape and diet, mammalian dentitions offer an excellent system to track biotic responses to environmental shifts. In this chapter we use molar crown height, a fundamental metric of tooth shape, to examine how increased aridification and the spread of open habitats impacted macropodoid evolution.

Statement of Authorship

AMCC designed the research, collected data, performed analysis and wrote the manuscript. GJP helped design research, provided guidance and advice, and commented on the draft manuscript.

Key Words: Teeth, marsupial, evolution, diet, adaptation

2.1 Abstract

Environmental change is often considered a key driver of morphological evolution. However, whereas environmental impacts on taxonomic diversity are comparatively well understood, a much poorer understanding exists of how environmental change influences morphological diversity across long time spans. Mammals hold great potential as a model radiation to redress this deficiency. A key way that environmental change is likely to have influenced mammalian evolution is via diet, with herbivores likely to have been especially responsive due to their dependence on particular types of vegetation. Dental morphology in mammals reflects functional adaptations to processing different foods, and mammals have an excellent dental fossil record through the Cenozoic, a dynamic period of global climate. Here we investigate patterns in the evolution of molar crown height (proxy for food abrasiveness) of kangaroos and relatives, the most diverse group of Australian herbivores. We show that initial steady increases in molar crown height through the early to middle Miocene were linked to the advent of bilophodont (parallel-bladed) molars. A dramatic increase in the evolutionary rate and disparity of molar crown-height occurred across the Miocene–Pliocene transition, an interval during which aridification intensified. We link this pattern to selection for greater dental durability associated with an increasing proportion of grass consumption, ultimately correlated with the expansion of more open habitats during the Pliocene.

2.2 Introduction

Many models of macroevolution strongly emphasise the role of environmental change as a driver of diversification (Vrba 1985; Janis 1993; Erwin 2009). However, it is generally not well understood exactly how, and to what extent, environmental change drives diversity across long time spans ($\geq 10^5$ yr) (Prothero and Heaton 1996; Alroy et al. 2000; Van Dam et al. 2006; Erwin 2009). Contributing to this problem is the fact that diversity can be assessed using either trait- or taxon-based approaches (Foote 1997). But, although these metrics are often closely correlated (Foote 1996), they may become decoupled under periods of evolutionary radiation (Briggs et al. 1992; Foote 1992; Jernvall and Fortelius 1996). Mammals have a dense fossil record and radiated across the globe during the climatically-dynamic Cenozoic Era. Thus, they are excellent candidates for resolving how environmental change impacts morphological diversification (Alroy et al. 2000; Blois and Hadly 2009). To date, most studies of mammalian response to environmental change have employed taxonomic or phylogenetic measures of diversity (e.g., Alroy et al. 2000), or assessed impacts over relatively short timescales ($\leq 10^4$ yr) (e.g., Barnosky et al. 2004; Prideaux et al. 2007). The few long-period ($\geq 10^5$ yr) studies suggest that trait-based metrics may more closely track evolutionary responses compared with taxonomic metrics, especially during the early phase of adaptive radiation (Jernvall and Fortelius 1996; Wilson et al. 2012).

Climate-driven changes in prevailing vegetation during the Cenozoic impacted herbivore evolution by prompting morphological specialisation of the craniodental system for different diets (Mihlbachler et al. 2011; Ungar et al. 2011; Lister 2013). One of the most pronounced phases of Late Cenozoic environmental change was the Miocene–Pliocene transition, during which reduced temperatures and declining atmospheric CO_2 levels promoted the spread of grasslands and the decline of forest biomes (Cerling et al. 1997). In Europe and North America these environmental changes triggered the broad-scale decline of browsing herbivores, which consume primarily dicot leaves, and the radiation of grazing and mixed-feeding herbivores, which primarily eat grass (Janis et al. 2000; Fortelius et al. 2002; Jernvall and Fortelius 2002). Herbivores feeding in more open habitats experience higher levels of dental abrasion from grass phytoliths and entrained grit than do browsers in more closed habitats (Mendoza and Palmqvist 2008; Damuth and Janis 2011; Lucas et al. 2013). As a result, selection during the Neogene favoured herbivores with morphological innovations for increased dental durability (Janis and Fortelius 1988), because worn teeth are less efficient at fracturing food particles (Evans 2005).

Increasing the relative vertical relief of the tooth crown, the crown height (Van Valen 1960), is a common evolutionary route to construct more durable molar dentitions (Janis and Fortelius 1988; Fortelius et al. 2002; Jernvall and Fortelius 2002). For example, amongst North American horses, low-crowned anchitheriines were replaced by higher-crowned equines (Mihlbachler et al. 2011). North American rodents show a progressive increase in molar crown height across an almost 50 Myr interval, correlated broadly with climatic cooling (Tapaltsyan et al. 2015). Some members of Afrotheria, such as proboscideans and sirenians, also increased molar crown height during the late Neogene, albeit alongside other traits like increases in occlusal area, delayed dental eruption, hypselodonty, and continuous tooth replacement (Domning 1982; Sanders et al. 2010; Gomes Rodrigues et al. 2011; Lister et al. 2013). Overall, afrotherian mammals and other lophodont herbivores (e.g., cercopithecine primates, diprotodont marsupials) appear to have followed a different adaptive pathway from the many rodent, artiodactyl, and perissodactyl lineages which heavily invested in molar crown height (Janis and Fortelius 1988).

In Australia, the predominant mammalian herbivores for the last 30 million years (Myr) have been diprotodont marsupials (Black et al. 2012). They evolved in response to the same broad patterns of climatic change that influenced herbivore evolution on other continents (Archer et al. 1995; Prideaux and Warburton 2010). The most diverse diprotodont clade is the Macropodoidea, which includes kangaroos, wallabies and their relatives (Prideaux and Warburton 2010). There are two macropodoid families: Hypsiprymnodontidae, represented today only by the musky rat-kangaroo, *Hypsiprymnodon moschatus,* and the Macropodidae, which includes the Potoroinae, Lagostrophinae, Macropodinae, and extinct Sthenurinae (Prideaux and Warburton 2010). Basally-diverging macropodoids, like hypsiprymnodontids and potoroines, have low-crowned bunodont or bunolophodont molars (Prideaux and Warburton 2010; Ungar 2010) that are used to process relatively brittle foods like fungi and fruit (Dennis 2002; Arman and Prideaux 2015). More derived bilophodont macropodids such as lagostrophines and macropodines are folivores, consuming ductile foods like dicot leaves, forbs and grasses (Arman and Prideaux 2015). Extant macropodoid grazers have higher-crowned molars than browsers (Janis 1990), but the adaptive role of molar crown height and the specific role of late Cenozoic environmental change in driving crown height disparity has never been quantitatively explored.

Palaeoenvironmental data suggest that Australian ecosystems underwent significant aridification from the late Miocene (Kershaw et al. 1994; Sniderman et al. 2016). This first drove the diversification and expansion of low-rainfall and salinity-resistant xeric scrub dominated by members of the Chenopodiaceae, and then grasses during the Pliocene (Macphail 1997; Kadereit et al. 2005; Martin 2006). Stable-isotopic data from dental enamel indicate that middle Pliocene herbivores were beginning to partition C_3 and incipient C_4 vegetation resources (Montanari et al. 2013). Morphological, stable-isotopic, and dental microwear data suggest that at least some derived macropodoids, like the giant sthenurine *Procoptodon goliah*, evolved to exploit the burgeoning chenopod resources (Prideaux 2004; Prideaux et al. 2009).

In this paper we use molar crown height as a proxy for tracking dietary adaptation in macropodoids across the Neogene by: (1) examining the correlation between crown height, diet and habitat in living taxa; and (2) examining how changes in crown height relate to major phases of environmental change in Australian terrestrial ecosystems.

2.3 Methods

2.3.1 Approach and Data Collection

Crown height was measured on specimens of modern and/or fossil species in the Australian Museum (Sydney), Australian National Wildlife Collection (Canberra), Flinders University Palaeontology Laboratory (Adelaide), Queensland Museum (Brisbane), South Australian Museum (Adelaide), Museum of Central Australia (Alice Springs), and Western Australian Museum (Perth). Crown height was measured on unworn or minimally-worn molars, where facet development had yet to propagate to the cusp tips. Crown height was measured from the base of the enamel cap (cervix) vertically to the cusp apex of the protoconid and/or hypoconid on lower second and third molars. This measurement was divided by maximum trigonid and maximum talonid buccolingual width for the protoconid and hypoconid, respectively, to calculate the molar crown height. Trigonid and talonid width were chosen as a standardisation for tooth size because they are strong predictors of body size in macropodoids, e.g., condylobasal, or total skull, length (Figure 2.2; Prowse et al. 2015). A major-axis regression was used to correlate these tooth dimensions with total skull length using the `lmodel2` function in `R`.

2.3.2 Comparative Phylogenetic Analysis

A generalised linear model was used to test the effect of diet and feeding habitat, scored as categorical predictors, on mean molar crown height. Dietary categories were based on Arman and Prideaux (2015) and habitat variables were drawn from the literature (Table 2.1). Preferred feeding cover was based on Norbury et al. (1989), but the number of variables was collapsed to avoid over-penalising the linear model (Table 2.1). As species data are not independent (Felsenstein 1985), a phylogenetic generalised least-squares (PGLS) model was used to estimate the effect of diet and habitat on crown height within a phylogenetically-adjusted context. This was achieved by building alternative Pagel's lambda (λ) transformations of the phylogenetic tree and trait data into the linear model (Revell 2010) using the `pgls` function in the `R` package `caper` (Orme et al. 2012). The full linear model, comprising two non-interacting, dependent-variable terms (diet + preferred feeding habitat) was compared with a reduced model where habitat was removed using sample-size-adjusted Akaike information criterion weights (AICc) (Burnham and Anderson 2002). Assumptions of the linear model were validated using various model diagnostics including homogeneity of the residuals and distribution of the response variable. Homogeneity of the residuals (against fitted values) improved visually after the maximum-likelihood value of λ was applied. A correlation test found no significant relationship between fitted values and the phylogenetically-transformed residuals (T_{15}=0.08, p=0.94, r=0.02) supporting inspection of a quantile–quantile plot.

A paired-sample T-test revealed significant differences between molar crown height measured at the M_3 protoconid compared with the hypoconid (T_{110}=−5.63, p=<<0.01). As a result we did not pool these data, but because they were highly correlated, we restricted analysis to the better sampled M_3 hypoconid. Using the `FitContinuous` function in `geiger` (Harmon et al. 2009) mean species molar crown height for the M_2 and M_3 was mapped onto a pruned molecular phylogeny of Macropodoidea (i.e., Mitchell et al. 2014) containing 24 taxa. The more central molar positions of M_2 and M_3 were selected because they tended to be relatively less variable than M_1 and M_4 (Couzens, unpublished data). We fit a single peak Ornstein–

Uhlenbeck model using `FitContinuous` and multiple Ornstein–Uhlenbeck trait optima using the `OUwie` function. Using `OUwie` we modelled between one and four trait optima across the tree by assigning internal nodes to different optima according to the complexity of the relevant model (Figure 2.1).

Ancestral-state reconstruction of lower molar ($M_{2–3}$) hypoconid crown height was performed with the `R` package `ape` using the function `ace`. The time-scaled tree from Couzens et al. (2016) based on the tree topology of Prideaux and Warburton (2010) was utilised. The reconstruction was performed with `type=”continuous”` and `method=”REML”` under a Brownian motion model of trait evolution (`model=”BM”`).

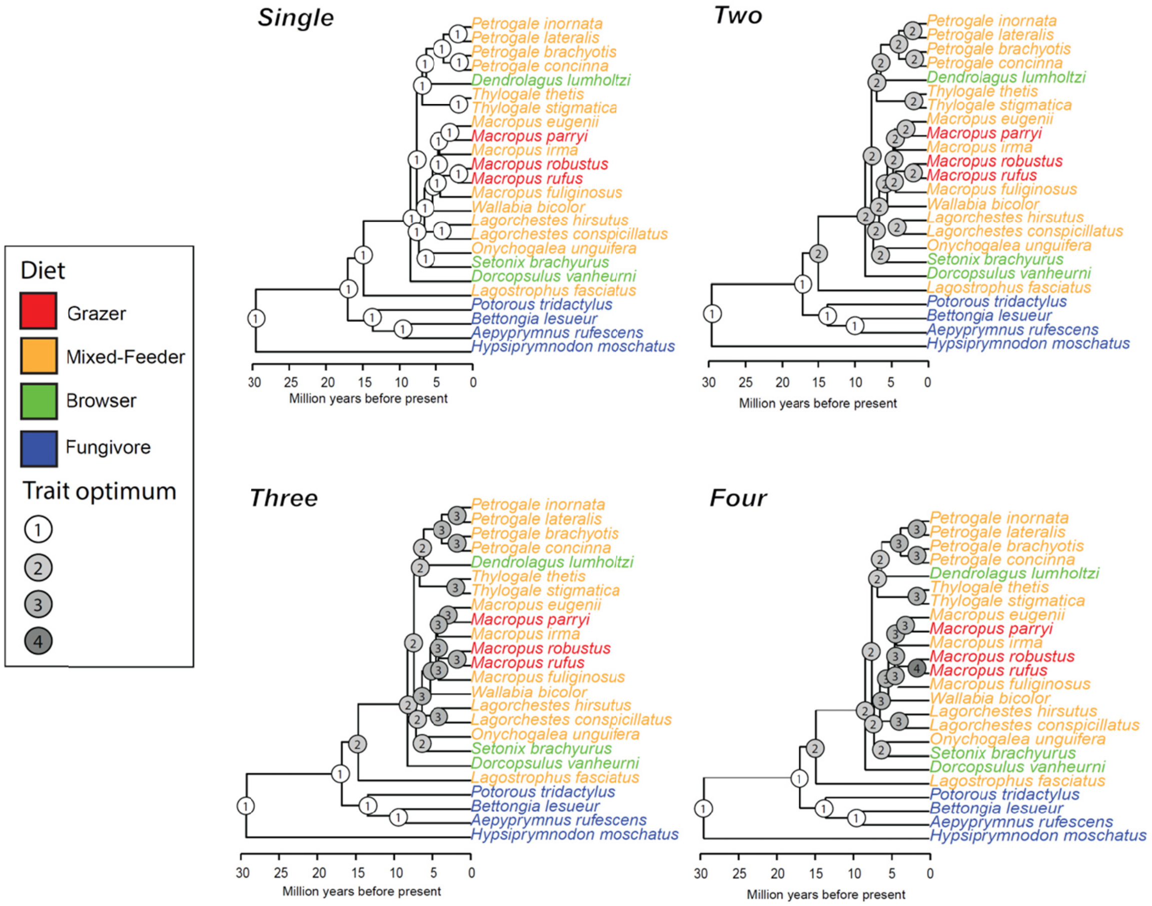

Figure 2.1. Four Ornstein–Uhlenbeck models of trait optima fitted with maximum likelihood to M_{2}-$_{3}$ hypoconid crown height data. Internal nodes are numbered and shaded to demarcate different trait optima. Tip taxa are coloured to demarcate diet categorisations based on Table 2.1.

Table 2.1. Taxa and dietary/habitat classifications used in the PGLS analysis. Where diet variables (after Arman and Prideaux 2015) are coded: F=fungivore, B= browser, MF=mixed feeder, G=grazer. [1.] Unless otherwise specified diet follows Arman and Prideaux (2015). [2.] Preferred feeding cover after Norbury et al. (1989). [3.] Simplified feeding habitat levels used in the linear model: A= open habitat, B= open woodland, C= closed forest/ dense understorey. *Inferred or estimated parameters based on generic level consensus.

Species	**Clade**	**Mean molar crown height ($M_{2/3}$)**	**n**	**Standard error**	**Diet[1]**	**Preferred Feeding Cover[2]**	**Preferred feeding habitat[3]**	**References**
Aepyprymnus rufescens	Potoroinae	1.00	5	0.03	MF*	2*	B	McIlwee and Johnson (1998).
Bettongia penicillata	Potoroinae	0.79	18	0.02	F*	2*	B	Claridge and May (1994); Garkaklis et al. (2004).
Bettongia lesueur	Potoroinae	0.86	15	0.02	MF	1*	B*	Robley et al. (2001); Arman and Prideaux (2015).
Dendrolagus lumholtzi	Macropodinae	0.97	17	0.03	B	4*	C	Martin (2005); Arman and Prideaux (2015).
Dorcopsis luctuosa	Macropodinae	1.07	5	0.02	B*	4	C	Flannery (1990), Vernes (2010), Groves and Flannery (1989)
Dorcopsulus vanheurni	Macropodinae	1.02	12	0.03	B*	4	C	Flannery (1990), Vernes 2010)
Hypsiprymnodon moschatus	Hypsiprymnodontidae	0.87	9	0.03	F	4	C	Dawson (1989), Dennis (2002)
Lagorchestes conspicillatus		1.14	9	0.02	MF	1.5*	A	Johnson and Lyon (1985)

Lagorchestes hirsutus	Macropodinae	1.16	7	0.07	MF	1*	A	Pearson (1989), Short and Turner (1992)
Lagostrophus fasciatus	Lagostrophinae	1.05	18	0.02	MF	5*	C	Short and Turner (1992)
Macropus eugenii	Macropodinae	1.11	20	0.02	MF	4.5*	C	Norbury et al. (1989)
Macropus fuliginosus	Macropodinae	1.32	16	0.03	MF	1	A	Dawson (1989)
Macropus irma	Macropodinae	1.14	10	0.03	MF*	2*	A*	
Macropus robustus	Macropodinae	1.24	8	0.04	G	1	A	Jarman and Phillips (1989)
Macropus rufus	Macropodinae	1.39	14	0.03	G	1*	A*	
Macropus parryi	Macropodinae	1.35	2	0.02	G	1*	A*	
Onychogalea unguifera	Macropodinae	1.27	7	0.02	MF	2*	B	Ingleby (1991)
Petrogale brachyotis	Macropodinae	1.01	1	0.08	MF	3*	B*	
Petrogale concinna	Macropodinae	1.21	2	0.01	MF	3*	B*	
Petrogale penicillata	Macropodinae	1.29	6	0.02	MF	2	B	Short (1989)
Petrogale inornata	Macropodinae	1.12	2	0.01	MF*	3*	B*	
Petrogale lateralis	Macropodinae	1.21	4	0.07	MF*	3*	B*	
Potorous tridactylus	Potoroinae	0.86	18	0.05	F	5	C	Bennett and Baxter (1989), Claridge et al. (1993), Jarman and Phillips (1989)
Setonix	Macropodinae	1.07	22	0.03	B	5*	C	Dawson (1989), Storr

brachyurus								(1964)
Thylogale billardierii	Macropodinae	1.12	13	0.02	MF	2	B	Sprent and McArthur (2002)
Thylogale stigmatica	Macropodinae	1.21	14	0.03	MF	2*	B*	
Thylogale thetis	Macropodinae	1.17	17	0.02	MF	2*	B*	
Wallabia bicolor	Macropodinae	1.10	5	0.04	MF	3.5	A	Jarman and Phillips (1989)

2.4 Results

2.4.1 Molar Width as a Predictor of Body Size

The log of M_3 talonid width was highly correlated (R^2= 0.91) with log total skull length across all macropodoids (Figure 2.2), although clade-specific variation exists; it is weakly correlated in potoroines (*Potorous* R^2=0.61; *Bettongia* and *Aepyprymnus* R^2=0.67). However, sample sizes for the potoroines are low and they are less taxonomically diverse than the clades with higher correlations.

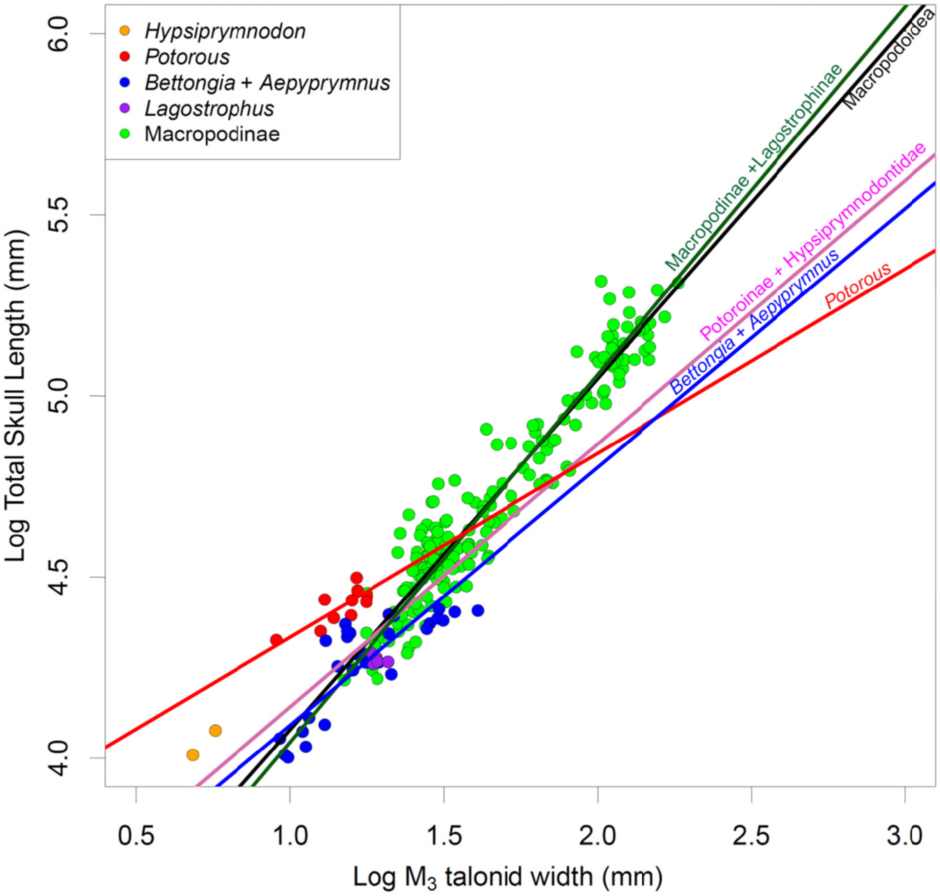

Figure 2.2. Correlation between log M_3 talonid width (mm) and log total skull length (mm) in macropodoids. Major axis regression trend lines are computed for five taxonomic groupings.

2.4.2 Molar Crown Height Variation

In potoroines and hypsiprymnodontids the protoconid is relatively taller than the hypoconid, but this is reversed in *Lagostrophus* and all more derived macropodids (except for M_4). Mean M_3 protoconid-based molar crown height ranged from 0.81 in *Dendrolagus ursinus* to 1.35 in *Macropus rufus*, and mean M_3 hypoconid-based crown height from 0.72 in *Potorous tridactylus* to 1.44 in *M. rufus*. There were significant differences between species for M_3 protoconid-based crown height ($F_{24,60}=9.58$, $p=<<0.01$, $R^2=0.71$), and hypoconid-based crown height ($F_{31,144}=16.16$, $p=<<0.01$, $R^2=0.73$). Crown height was not sexually dimorphic because, when pooled by sex, no significant differences were evident for either protoconid- (Welch two sample, $T_{80,581}=0.77$, $p=0.45$) or hypoconid-based crown height (Welch two sample, $T_{78,965}=-0.11$, $p=0.91$).

2.4.3 Diet and Feeding Habitat as Predictors of Molar Crown Height

When examined with a phylogenetic linear model, diet was found to have a large effect on mean species M_{2-3} molar crown height (hypoconid) based on comparison between AICc values of the full model (diet and habitat) and the reduced model (habitat removed) (Table 2.2). For all Pagel's lambda transformations, the reduced model (habitat removed) outperformed the full model. The best-ranked model based on AICc score included diet with a maximum-likelihood transformation of Pagel's lambda. Estimate terms for this model provide a measure of the effect of each level of the dietary predictor on hypoconid-based molar crown height (Table 2.3). The intercept term in the model is the average value of browsing. Fungivory is linked with a non-significant negative effect on crown height relative to browsing. Mixed feeding and grazing both have significant positive effects on hypoconid-based molar crown height relative to browsing, with grazing having the largest effect.

Table 2.2. Model selection results for $M_{2/3}$ molar crown height. The highest-ranked models all have relatively low phylogenetic correlations and include diet as a predictor.

Rank	**Model**	**AIC**	**AICc**	**n**
1	(Pagel's λ=ML) Diet	−40.11	−38.01	24
2	(Pagel's λ=0) Diet	−38.23	−36.13	24
3	(Pagel's λ=ML) Diet +Habitat	−37.64	−32.70	24
4	(Pagel's λ=0) Diet +Habitat	−35.39	−30.45	24
5	(Pagel's λ=1) Diet	−30.46	−28.35	24
6	(Pagel's λ=1) Diet +Habitat	−27.65	−22.71	24

Table 2.3. Summary table of the best-ranked phylogenetic linear model from Table 2.2. The model is statistically significant based on an F-test ($F_{3, 20}=6.62$, P-value $<<0.01$, Adj. $R^2=0.42$).

Parameter	**Estimate**	**Standard error**	**t-statistic**	**P-value**
Intercept	0.95	0.09	10.75	<<0.01
Grazing	0.30	0.08	3.91	<<0.01
Mixed-feeding	0.13	0.06	2.26	0.04
Fungivory	–0.07	0.10	–0.65	0.52

Table 2.4. Mean and standard error-based confidence intervals for molar crown height across four dietary categories based on (a) no phylogenetic adjustment or (b) the maximum likelihood Pagel's λ transformation.

Model	**Diet**	**Mean**	**Standard error (σ)**	**Lower bound (– σ)**	**Upper Bound (+ σ)**
(a) No phylogenetic adjustment	Fungivore	0.87	0.09	0.77	0.96
	Browsing	1.02	0.06	0.96	1.08
	Mixed-feeding	1.13	0.06	1.07	1.19
	Grazing	1.33	0.08	1.24	1.41
(b) Maximum likelihood transformation Pagel's λ	Fungivore	0.88	0.10	0.77	0.98
	Browsing	0.95	0.09	0.86	1.03
	Mixed-feeding	1.08	0.06	1.02	1.13
	Grazing	1.24	0.08	1.17	1.32

2.4.4 Evolutionary Model Fit

Since species-level crown heights based on the protoconid and hypoconid were highly correlated (R^2=0.84, Pearson T_{28}=8.23, p<<0.01) an evolutionary model fit was performed using the better sampled $M_{2/3}$ hypoconid-based crown height measurements. When tested with `FitContinuous` there was no unambiguous preferred model (Δ AICc <2; Table 2.5) but a single peak Ornstein–Uhlenbeck model had the lowest AICc score. Overall however, an Ornstein–Uhlenbeck model with four adaptive peaks considerably outperformed all simpler Ornstein–Uhlenbeck models and a Brownian-motion model (Table 2.6.).

Table 2.5. Evolutionary model selection results for $M_{2/3}$ hypoconid-based crown height fit with `FitContinuous`. Model abbreviations: Ornstein–Uhlenbeck (O–U). Rank based on AICc scores. K=number of model parameters.

Model	**Rank**	**z0**	**σ^2**	**K**	**lnL**	**AIC**	**AICc**	**Δ AICc**
O–U (1 optima)	2	0.96	0.005	3	12.10	-18.19	-16.93	0.00
Early burst	2	0.96	0.000	3	12.10	-18.19	-16.93	0.70
Brownian motion	3	0.90	0.003	2	10.41	-16.83	-16.23	0.67
Trend	5	0.93	0.000	3	11.41	-16.83	-15.55	2.83
White noise	4	1.09	0.028	2	8.66	-13.32	-12.72	12.72

Table 2.6. Comparison of Ornstein–Uhlenbeck (O–U) models with multiple optima. Rank based on AICc scores.

Model	**Rank**	**α**	**σ^2**	**lnL**	**AIC**	**AICc**	**Δ AICc**
O–U (4 optima)	1	2.12	0.022	26.66	-41.32	-36.38	9.24
O–U (3 optima)	2	9.93	0.196	20.24	-30.47	-27.14	4.53
O–U (2 optima)	3	0.33	0.009	16.36	-24.71	-22.61	5.80
O–U (1 optima)	4	0.08	0.005	12.00	-18.01	-16.81	0.43
Brownian motion	5	NA	0.003	10.47	-16.95	-16.38	NA

2.4.5 Ancestral State Reconstruction

A maximum likelihood-based reconstruction suggests that the most recent common ancestor of all extant macropodoids had low-crowned molars similar to extant *Hypsiprymnodon moschatus* (Figure 2.3). Small increases in molar crown height characterise evolution along the stem leading to the split between Lagostrophinae, Macropodinae, and Sthenurinae (Figure 2.3). Basal members of these clades are all reconstructed as low crowned with intermediate crown heights between extant fungivores and browsers (Figure 2.3). Overall, Sthenurinae, Potoroinae, and Hypsiprymnodontidae show a decreasing trend in crown height whereas Lagostrophinae and Macropodinae increase (Figure 2.3). The disparity of macropodid molar crown height increases substantially after 8 Myr ago, driven largely by macropodine kangaroos (Figure 2.3).

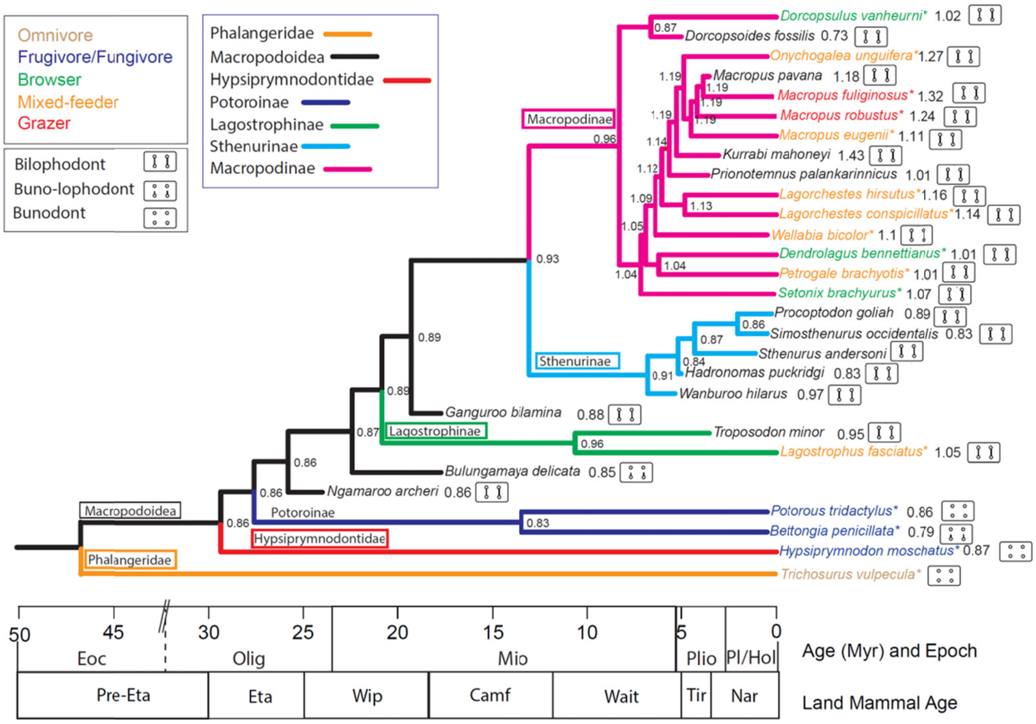

Figure 2.3. Phylogenetic distribution of macropodoid molar crown height (M_{2-3}) and crown type across the late Cenozoic. Phylogenetic tree and divergence estimates after Prideaux and Warburton (2010) and Couzens et al. (2016). Land mammal ages follow Megirian et al. (2010). Land mammal age abbreviations: Nar; Naracoortean,

Tir; Tirarian, Wait; Waitean, Camf; Camfieldian, Wip; Wipajirian; Eta; Etadunnan, Pre-Eta; Pre-Etadunnan.

Table 2.7. Molar crown height ($M_{2–3}$) for 30 fossil macropodoid species. Taxonomic nomenclature following Prideaux and Warburton (2010). First land mammal age occurrence based on Megirian et al. (2010) with italicised ages representing uncertain assignments. Standard error based on bootstrap estimate with 10,000 iterations.

Taxa	**Clade**	**First Land Mammal Age Occurrence**	**Mean relative hypoconid height**	**n**	**Standard error**
Bulungamaya delicata	Macropodidae	Wipajirian	0.85	5	0.03
Balbaroo gregoriensis	Balbarinae	*Wipajirian*	0.83	1	NA
Nambaroo sp.	Balbarinae	Wipajirian	0.75	1	NA
Wururoo dayamayi	Balbarinae	*Wipajirian*	0.96	1	NA
Dorcopsoides fossilis	Macropodinae	Waitean	0.73	32	0.01
Ganguroo bilamina	Macropodidae	*Wipajirian*	0.88	4	0.03
Ganguroo robustiter	Macropodidae	*Wipajirian*	0.83	4	0.03
Hadronomas puckridgi	Sthenurinae	Waitean	0.83	15	0.02
Kurrabi mahoneyi	Macropodinae	Tirarian	1.43	1	NA
Kurrabi merriwaensis	Macropodinae	Tirarian	1.16	1	NA
Macropus dryas	Macropodinae	Tirarian	1.17	5	0.03
Macropus woodsi	Macropodinae	Naracoortean	1.18	1	NA
Macropus dryas	Macropodinae	Tirarian	1.00	3	0.05
Macropus pavana	Macropodinae	Tirarian	1.18	2	0.09
Macropus pearsoni	Macropodinae	Naracoortean	1.51	1	NA
Ngamaroo archeri	Macropodidae	Wipajirian	0.86	2	0.03
Prionotemnus palankarinnicus	Macropodinae	Tirarian	1.01	33	0.02
Procoptodon goliah	Sthenurinae	Naracoortean	0.89	4	0.01
Protemnodon devisi	Macropodinae	Tirarian	0.87	2	0.01
Protemnodon chinchillaensis	Macropodinae	Tirarian	1.05	1	NA
Protemnodon snewini	Macropodinae	Tirarian	1.05	2	0.03
Simosthenurus occidentalis	Sthenurinae	Naracoortean	0.83	14	0.02

Simosthenurus pales	Sthenurinae	Naracoortean	0.85	1	NA
Sthenurus andersoni	Sthenurinae	Tirarian	0.98	4	0.057
Sthenurus atlas	Sthenurinae	Naracoortean	1.11	9	0.027
Sthenurus tindalei	Sthenurinae	Naracoortean	1.13	1	NA
Troposodon bowensis	Lagostrophinae	Tirarian	1.00	13	0.032
Troposodon minor	Lagostrophinae	Tirarian	0.95	6	0.056
Wallabia indra	Macropodinae	Tirarian	0.85	1	NA
Wanburoo hilarus	Macropodinae	Camfieldian	0.97	6	0.045

2.5 Discussion

At the broadest level the skewed pattern of crown height evolution within Macropodoidea (Figure 2.4) conforms to patterns of trait disparity observed in the radiations of many metazoan groups (Gould 1996; McShea 1996; Alroy 1998). Evolutionary model fitting does not support a trend model, and instead the phenotypic distribution is more consistent with a bounded diffusion model (Stanley 1973) or a multiple optima model (Alroy 1998). The drift-based bounded diffusion model, wherein character change is only possible in a unidirectional path away from a lower threshold, provides the simplest explanation for the asymmetric distribution of crown height variance. The stability of minimum macropodoid crown height during the late Cenozoic, wherein it remains relatively invariant and does not deviate strongly toward the mean (Figure 2.4; Bates et al. 2014), fits predictions of this model (McShea 1994). Further crown height data for late Paleogene–early Neogene macropodoids would help to more robustly test this model of crown height diversification. The existence of a minimum molar crown height threshold could reflect developmental or functional limits. Interestingly, minimum molar crown height amongst Neogene proboscideans is similar to that of macropodoids (Figure 2d, 3 and 4 of Lister 2013) which may suggest there is an inherent limit on minimum crown height in mammals. In rodents, buccolingual expansion of the tooth bud and vertical growth of the enamel knots are correlated (Jernvall 1995) and thus a minimum threshold could reflect constraints imposed by coordinated growth of the tooth bud. There may also be important functional limits, because very low-crowned molars may provide insufficient relief to trap food or generate cusps with insufficient sharpness (Evans and Sanson 2005). Recent advances in analytical approaches (i.e., Boucher and Démery 2016) may make it possible to more directly test the importance of a bounded diffusion model for macropodoid dental evolution.

The explanatory simplicity of a passive process like drift is attractive but asymmetric distributions can also be generated by evolution under divergent selective optima (McShea 1994; Alroy 1998). Given the adaptive significance of molar crown height in other mammalian groups (Janis and Fortelius 1988) selection likely played a significant role in macropodoid crown height evolution also. Supporting this is the close correlation between diet and crown height (Table 2.4) and consistent support for an ‘adaptive’ Ornstein–Uhlenbeck model (Table 2.5, 2.6). How might ecological factors like diet have driven diversification in crown height? A simple model invokes niche partitioning as important in ‘pushing’ diverging taxa away from ancestral crown heights, driving the progressive increase in maximum crown height evident in our data (Figure 2.4). This scenario thus implicates intrinsic biotic interactions as important, wherein the difficulty of competitively displacing incumbent taxa drives character displacement (Valentine 1980; Walker and Valentine 1984). However, we also find evidence that extrinsic factors were critical because enrichment of $\delta^{18}O$ from the Middle Miocene Climatic Optimum (Zachos et al. 2001) tracks increasing macropodoid crown height (Figure 2.4). Similar correlations exist amongst Cenozoic rodents and horses (Mihlbachler et al. 2011; Tapaltsyan et al. 2015), but the Australian early Neogene record remains too depauperate and the assemblages too poorly dated to currently investigate this further.

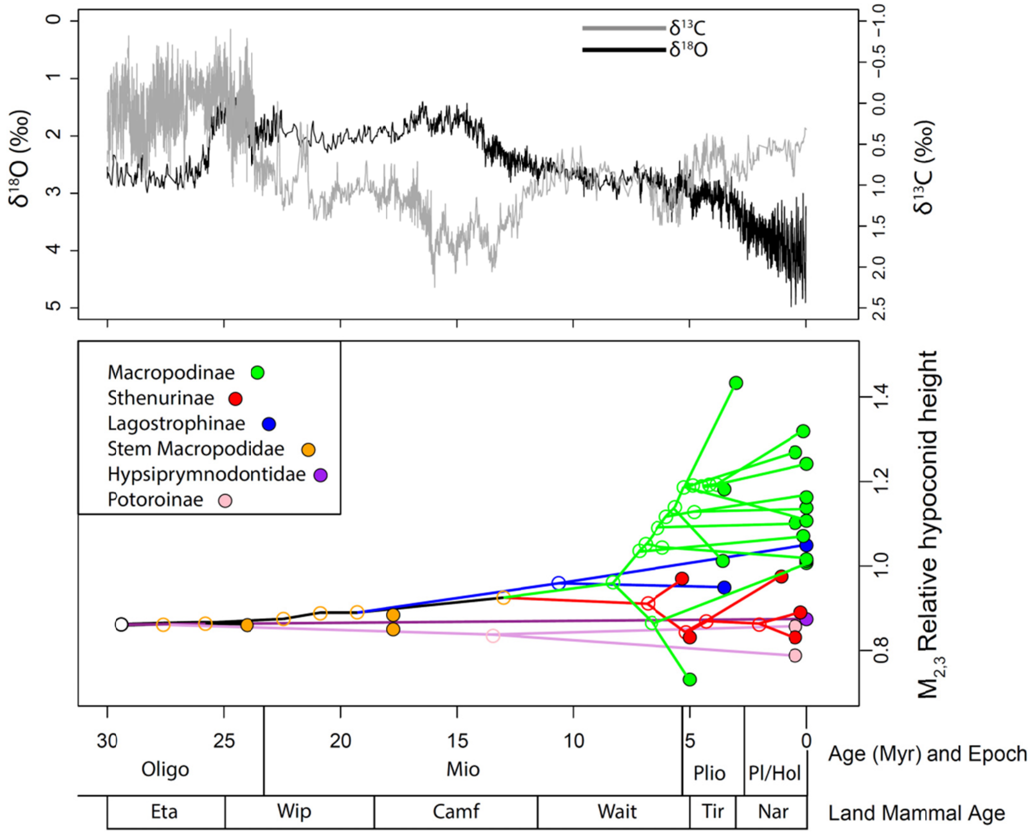

Figure 2.4. Relationship between macropodoid molar crown height ($M_{2/3}$) and global patterns of stable oxygen ($\delta^{18}O$, black) and carbon ($\delta^{13}C$, white) isotopic variation (Zachos et al. 2001; Zhang et al. 2013). Open circles denote ancestral node

reconstructions and closed circles denote measured crown height. Land mammal ages follow Megirian et al. (2010). Land mammal age abbreviations: Nar; Naracoortean, Tir; Tirarian, Wait; Waitean, Camf; Camfieldian, Wip; Wipajirian; Eta; Etadunnan.

Rates of maximum crown height evolution and disparity increase sharply across the Miocene–Pliocene transition suggesting that different evolutionary processes began to regulate dental evolution (Figure 2.4). Slower rates of molar crown height evolution characterise the transition of basal macropodids possessing bunodont or bunolophodont molars toward fully lophodont dentitions (Figure 2.5). This interval is phylogenetically bracketed amongst extant macropodoids by fungivorous and folivorous taxa, suggesting relatively slow crown height evolution corresponded to a diet transition. This adaptive transition during the early Neogene is also favoured by the best fitting Ornstein-Uhlenbeck scenario (Figure 2.1). Decreased levels of selection and high levels of phenotypic drift are likely important in transitions away from adaptive optima (Polly 2008) and such relaxations in selection may be relatively common in dietary evolution (Strömberg 2006; Mihlbachler et al. 2011). Similar molar transformations precede major Neogene radiations in other herbivore groups like proboscideans, wherein late Paleocene bunodont taxa transitioned to the fully bilophodont Eocene taxa ancestral to elephantids (Gheerbrant 2009; Sanders et al. 2010). The bunodont dentitions of the earliest afrotherian and laurasiatherian mammals (Rose 1982; Gheerbrant 2009) also suggests that lineages leading to later pyrothere notoungulates, sirenians, and tapirs underwent similar transitions to bilophodonty as that amongst macropodoids (Domning 1982; Cifelli 1985; Janis 1993). However, together with cercopithecine primates (Benefit 2000; Stevens et al. 2013), macropodoids are unusual in acquiring bilophodonty relatively late, during the late Oligocene or early Miocene (Cooke 1997; Couzens et al. 2016), and retaining this tooth type whereas other ancestrally bilophodont groups (e.g., proboscideans, dugongids) discarded it in favour of higher-crowned prismatic molars. Potentially, the onset of intense environmental change and strong selection during the middle and late Miocene, soon after the acquisition of bilophodonty, prevented macropodoids from ‘experimenting’ with alternative crown types.

By the middle Miocene closed-forest Australian habitats were being replaced by *Eucalyptus*- and *Casuarina*-dominated sclerophyll vegetation resistant to lower rainfall (Kershaw et al. 1994; Macphail 1997; Martin 2006). Fossil and molecular data suggest that sthenurines and macropodines, the major Neogene macropodid groups, originated soon after the Middle Miocene Climatic Optimum (Prideaux 2004; Prideaux and Warburton 2010). Ancestral state reconstruction suggests that the last common ancestor of these sister lineages had low-crowned molars, within the range of extant browsing macropodids like the forest wallabies (*Dorcopsulus*), tree-kangaroos (*Dendrolagus*) and quokka (*Setonix*) (Figures 2.4–2.5). Interestingly all of these lineages have relatively deep divergences within Macropodinae, suggesting they may have retained an ancestral browse diet. However, Pliocene–Pleistocene occurrences of tree-kangaroos of the extinct genus *Bohra* are found across southern Australian arid zones (Prideaux et al. 2007; Prideaux and Warburton 2008, 2009), suggesting a much higher degree of dietary flexibility than has previously been recognised amongst the Dendrolagini (e.g., Mitchell et al. 2014). Early macropodines might also have consumed significant quantities of fungi, because the remarkably low crown height of late Miocene *Dorcopsoides fossilis* falls within the range of extant fungivores (Tables 2.4, 2.7), and its close extant relatives *Dorcopsis* and *Dorcopsulus* consume significant quantities of fungi (Vernes and Lebel 2011).

During the Miocene–Pliocene transition declining atmospheric CO_2 levels, lower temperatures, and reduced rainfall prompted the large-scale replacement of C_3 photosynthesising grasses, trees, and bushes by C_4 grasses and shrubs (Cerling et al. 1997). Speleothem-derived pollen data show that in south-central Australia, aridification intensified during the late Miocene (Sniderman et al. 2016). At this time the first unambiguous lineage-specific trends in crown height evolution become apparent amongst sthenurine and macropodine kangaroos (Figure 2.4). The emergence of these trends is coupled with increased complexity of the selective regime in the best-ranked Ornstein–Uhlenbeck model wherein three dietary optima emerge over the late Neogene compared with just one during the preceding early Neogene (Figure 2.1). The increasing abundance of grasslands during the Pliocene (Macphail 1997; Martin 2006) was likely a key driver of the increase in molar crown height amongst macropodine kangaroos (Figure 2.3, 2.4). Most Tirarian macropodids (e.g., Table 2.7) have mean crown heights within the range of either extant mixed feeders or browsers (Table 2.4) consistent with the view that, although grasslands were not yet widespread, grasses were starting to become an important dietary component for some macropodids (Montanari et al. 2013). Thus, mixed feeding diets most likely emerged during the early Pliocene (Table 2.7) in response to increasing grass availability (Dodson and Macphail 2004; Martin 2006; Sniderman et al. 2007).

A common pattern amongst late Neogene herbivore communities in Europe, North America, and Asia was the gradual decrease in browser diversity (Janis et al. 2000; Fortelius et al. 2002). In Europe, only high-crowned herbivores were able to increase their share of ecological resources after the middle Miocene (Jernvall and Fortelius 2002). However, in Australia, low-crowned browsing sthenurines underwent an expansive radiation comparable to the higher-crowned grazing and mixed-feeding macropodines (Prideaux 2004). High browser diversity in early Miocene North America has been linked to increased primary productivity (Janis et al. 2000). However, sthenurines radiated during a phase of intensifying aridification and declining primary productivity (Sniderman et al. 2016) and many were widely distributed through low-rainfall zones (Prideaux 2004; Prideaux et al. 2007, 2009). Some late Miocene ecosystems in Australia, such as the Nullarbor region, were characterised by only slightly higher rainfall and primary productivity than the same regions today (Macphail et al. 1997; Sniderman et al. 2016). Given the low productivity this implies, especially given current Australian ecosystems have primary productivities around ten times lower than the global mean (Field et al. 1998; Wang and Barrett 2003), an increase in ecosytem productivity (e.g., Janis et al. 2000) is unlikely to account for sthenurine diversification. However, there is evidence that browse became more accessible during the late Neogene in the form of chenopod shrubs (Kadereit et al. 2005), plants resistant to the high salinity and low rainfall typical of many Australia environments (Nix 1981). The arrival and diversification of chenopods in Australia during the middle Miocene is also broadly correlated with the divergence between sthenurine and macropodine kangaroos (Prideaux and Warburton 2010). It is possible that this botanic event played an important role in the Neogene diversification of sthenurines, especially given that at least some, like the giant Late Pleistocene *Procoptodon goliah* were specialist chenopod consumers (Prideaux et al. 2009).

2.6 Conclusions

In this paper we have used molar crown height to track morphological diversification during the Neogene radiation of macropodoids with the aim of testing how environmental change impacts dental disparity. We have shown that molar crown height disparity increased according to a ‘skewed’ distribution common to many other morphological diversifications (Gould 1996; McShea 1996; Alroy 1998). We hypothesise that the difficulty of displacing incumbent taxa was a key mechanism driving early Neogene increases in maximum crown height. Our data provide evidence that extrinsic factors like intensifying aridification became important during the late Neogene, especially by expanding niche space across the Miocene–Pliocene transition, enabling a rapid increase in crown height disparity. The increased rates of crown height evolution across this interval suggest strong selection for more durable molar dentitions better able to resist the higher levels of dietary abrasion associated with the spread of Pliocene grasslands (Macphail 1997; Martin 2006). We have supported this argument by showing that molar crown height is positively correlated with increasing grass consumption amongst extant macropodoids. However, unlike low-crowned herbivores in Europe and North America, which declined in diversity during the Neogene (Janis et al. 2000; Fortelius et al. 2002; Jernvall and Fortelius 2002), in Australia, low-crowned browsing sthenurines underwent a major diversification, perhaps due to their capacity to exploit a diverse C_4 chenopod scrubland (Prideaux 2004; Prideaux et al. 2009). This does not explain however why similar radiations did not occur amongst browsers (e.g., camelids) on other continents where chenopods were already widespread (Kadareit et al. 2005) or why the peak of sthenurine diversification occurred relatively late, during the late Pleistocene. Overall, by quantifying evolutionary responses to environmental change our study provides a platform for predictive models of macropodoid dental evolution which might be relevant to ecometric analyses (e.g., Polly et al. 2016).

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3. THE ROLE OF INHIBITORY DYNAMICS IN THE LOSS AND REEMERGENCE OF MACROPODOID TOOTH TRAITS

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Context

Developmental factors influence the types of variation which can emerge in populations and thus have potential to shape pathways of adaptive evolution. In the case of dental evolution, developmental processes regulating tooth morphogenesis might result in different adaptive potentials for different tooth characters. However, it is not known whether different developmental processes can result in different patterns of evolutionary change. In this chapter I examine how changes in the inhibitory cascade, a developmental rule governing tooth proportionality, is linked with the evolutionary reversibility of functionally and phylogenetically important molar tooth traits in macropodoids.

Statement of Authorship

AMCC designed the research, collected data, performed analysis and wrote the manuscript. ARE, MMS, GJP provided guidance and advice, and commented on the draft manuscript.

Key Words: Dentition, evo-devo, kangaroo, inhibitory cascade, reversal.

3.1 Abstract

The reversibility of phenotypic evolution is likely to be strongly influenced by the ability of underlying developmental systems to generate ancestral traits. However, few studies have quantitatively linked these developmental dynamics to traits that reevolve. In this study, we assess how changes in the inhibitory cascade, a developmental system that regulates relative tooth size in mammals, influenced the loss and reversals of the posthypocristid, a molar tooth crest, in the kangaroo superfamily Macropodoidea. We find that posthypocristid loss is linked with reduced levels of posterior molar inhibition, potentially driven by selection for lophodont, higher-crowned molar teeth. There is strong support for two posthypocristid reversals, each occurring after more than 15 million years of absence, in large-bodied species of *Macropus*, and two giant extinct species of short-faced sthenurine kangaroo (*Procoptodon*). We find that whereas primitive posthypocristid expression is linked to higher levels of posterior molar inhibition, reemergence is tied to a relative increase in third molar size associated with increasing body mass, producing molar phenotypes similar to those in mouse where the ectodysplasin pathway is upregulated. We argue that although shifts in the inhibitory cascade may enable reemergence, dietary ecology may limit the frequency of phylogenetic reversal.

“Numerous characters and trends seem to play genetic “hide-and- seek” in this subfamily” (G.H.H. Tate 1948:254)

3.2 Introduction

The evolutionary reemergence of an ancestral trait is a controversial pattern of evolutionary change (Raff 1996; Kohlsdorf and Wagner 2006; Collin and Miglietta 2008; Goldberg and Igić 2008; Wake et al. 2011). Despite phylogenetic evidence that such reversals may be more common than previously appreciated (Collin and Cipriani 2003; Whiting et al. 2003; Kohlsdorf and Wagner 2006; Wiens 2011) significant uncertainties remain about how development might influence the reversibility of traits (Collin and Miglietta 2008). For instance, it has been argued that trait reversibility may be promoted when there is reutilization of conserved developmental pathways, especially among segmented, terminally developing structures like digits or teeth (Marshall et al. 1994; Raff 1996). But, the reutilization of regulatory pathways and constituent genes is widespread in development (e.g. Lenardo and Baltimore 1989; Logan and Nusse 2004; Sadier et al. 2013; Bier and De Robertis 2015) and ancestral states are recoverable across a diverse spectrum of metazoan structures (e.g., Weatherbee et al. 2006; Kitano et al. 2008; Liubicich et al. 2009; Harjunmaa et al. 2014). Thus, for many traits there is no clear basis by which to predict whether an ancestral state can reemerge. However, this could be addressed if we can quantitatively link "types" of development with the phenotypic variation they can produce (Salazar-Ciudad and Jernvall 2004).

Mammalian teeth offer a powerful system for linking development with patterns of phenotypic variation and evolution (Jernvall and Jung 2000; Polly 2015). The developmental patterning of teeth, like limbs and other organs, involves simultaneous interactions between cell signaling and tissue growth (Salazar-Ciudad et al. 2003) which can result in nonlinear relationships between signaling protein concentration and levels of trait expression (Salazar-Ciudad and Jernvall 2004; Young et al. 2010). In turn, these dynamics provide a mechanism for the reversibility of traits to differ and for asymmetries in rates of character gain and loss (Harjunmaa et al. 2014). Structurally, the most fundamental aspect of mammalian teeth are the cusps, which function to fracture food particles, and whose relative position, size, and number is commonly species-specific (Ungar 2010). The cusp-specific morphology of mammalian teeth is determined by a patterning cascade underpinned by the iterative redeployment of transient gene signaling centers, termed enamel knots (Jernvall and Thesleff 2000). Small changes in the spatial patterning of the earliest enamel knots, cascade through later development to progressively specify the size and position of later forming structures (Jernvall et al. 2000). The spatial arrangement of enamel knots is preserved in fully formed teeth at the enamel–dentine junction (EDJ) as the mineralizing enamel wave front moves cervically, and outwards, from the epithelial–mesenchymal boundary (Butler 1956). As a result, the EDJ topography of fossil and modern teeth can provide insights into patterning processes and character homology (Skinner et al. 2008, 2010; Anemone et al. 2012).

Importantly, the architecture of individual teeth is not autonomous because the inhibitory effect of earlier-initiating, anterior teeth, influences the size of later-developing, more posterior teeth, following an inhibitory cascade (IC) model (Kavanagh et al. 2007). The IC model predicts that the central molar within a three-molar sequence (triplet) will occupy 1/3 of the total triplet area. Changes in the IC have previously been linked to the simplification, reduction, or loss of posterior teeth (Kavanagh et al. 2007; Asahara 2013) which is interesting because reemergent dental traits are often more strongly expressed on posterior molars or terminally developing tooth structures (Kurtén 1964; Scott 2015). One possibility is that inhibitory dynamics may influence the cusp-patterning cascade, perhaps by modulating prepatterning or pattern iteration processes (Jernvall et al. 2000). In therian mammals, lower molar teeth are differentiated into an anterior trigonid and posterior talonid (Figure 3.1). Phylogenetically, the talonid emerges as a single cusp in late Triassic mammaliaforms like *Morganucodon*, and is later expanded in Mesozoic cladotherians (Kielan-Jaworowska et al. 2004). Talonid expansion increases the surface area of the lower molar and was an important innovation in development of a grinding and shearing tribosphenic molar (Crompton 1971). Since herbivory requires complex molar teeth to process tough fibrous foods (Evans et al. 2007), both placental and marsupial herbivores have elaborated the talonid through the addition of cusps, and by linking cusps together with crests to form shearing blades (Ungar 2010). Changes in talonid structure are also often correlated with modifications of the trigonid, reflecting developmental and functional integration of molar tooth features (Kangas et al. 2004; Gómez-Robles and Polly 2012; Harjunmaa et al. 2014).

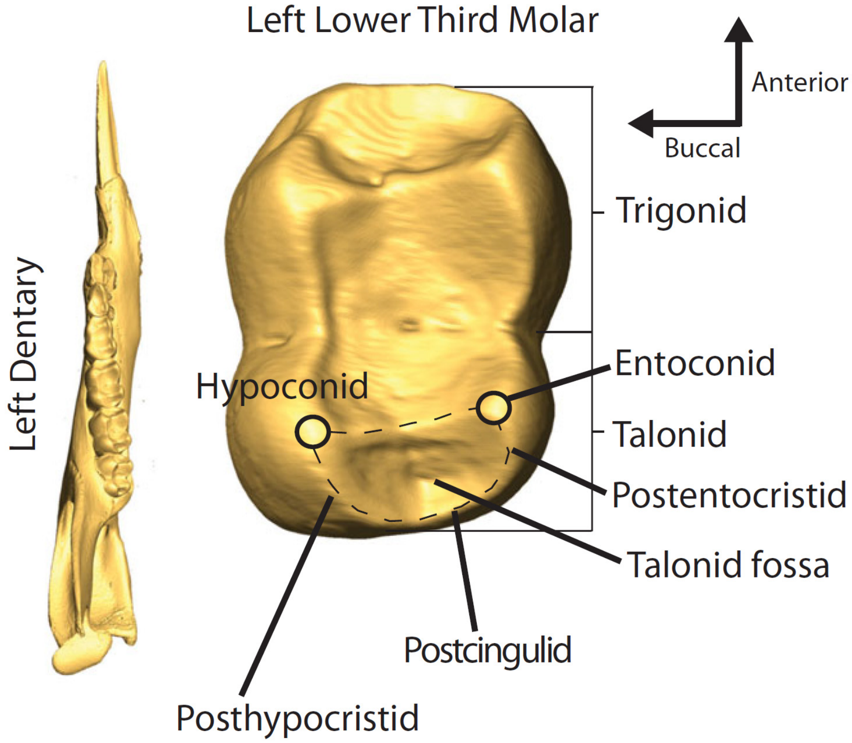


Figure 3. 1. Left lower third molar (M_3) morphology of the potoroine *Potorous tridactylus* including the position of the posthypocristid relative to other talonid structures.

The Macropodoidea (kangaroos and relatives) contains two extant families, Hypsiprymnodontidae, which includes only one extant species, *Hypsiprymnodon moschatus*, and the Macropodidae, which includes all other extant species of kangaroos, wallabies, and bettongs (Prideaux and Warburton 2010). Different talonid configurations are broadly linked to different dietary ecologies across the group. In basal macropodoids like hypsiprymnodontids and potoroines, lower molar teeth have four low cusps, which function in a mortar–pestle configuration with the upper molars to crush fungi, insects, and fruits (Sanson 1989; Arman and Prideaux 2015). Food is trapped and crushed against the posterolingual upper molar cusp (hypocone), within a U-shaped depression positioned on the posterior face of the talonid. This depression, which we call the talonid fossa, is bounded buccally by a distinctive longitudinal crest called the posthypocristid (Figure 3.1). Along with other structures bounding the talonid fossa, like the postcingulid (enamel shelf on the posterior molar margin) and postentocristid (crest directed posteriorly from the entoconid), the posthypocristid is generally absent in derived macropodids that consume more fibrous foods than potoroines (Arman and Prideaux 2015). These derived macropodids emphasize orthal and transverse shearing over the puncture–crush mastication of basal macropodoids (Sanson 1989). However, several large-bodied species of grazing or mixed-feeding kangaroos in the genus *Macropus* and two giant extinct Pleistocene species (*Procoptodon goliah* and *Procoptodon rapha*) of short-faced kangaroo (Sthenurinae) have evolved a talonid crest interpreted as a reemergent posthypocristid (Prideaux 2004; Prideaux and Warburton 2010).

In this article, we use the external and internal morphology of lower molars to examine how inhibitory dynamics influenced the loss and reemergence of the macropodoid posthypocristid. Specifically, we (1) assess phylogenetic support and establish a timescale for posthypocristid reversal and (2) use morphometric data to statistically test if IC changes were linked to posthypocristid loss and reexpression.

3.3 Material and Methods

3.3.1 Institutional Abbreviations

Australian Museum, Sydney (AM); Australian National University, Canberra (ANU); Australian National Wildlife Collection, Canberra (ANWC), Flinders University Palaeontology Laboratory, Adelaide (FU); Northern Territory Museum, Alice Springs (NTM); Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany (MPI-EVA); Queensland Museum, Brisbane (QM); South Australian Museum, Adelaide (SAMA); University of California Museum of Paleontology, Berkeley, USA (UCMP); Western Australian Museum, Perth (WAM).

3.3.2 Dental Imaging

Fossil and modern lower molar specimens representing 17 macropodoid species (Table 3.1) were scanned using X-ray absorption micro–computed tomography (microCT) at: Department of Applied Physics, ANU with a custom industrial microCT scanner; Department of Human Evolution, MPI-EVA with a SkyScan 1172 desktop microCT scanner or an Actis BIR 225 industrial microCT scanner; and Adelaide Microscopy, University of Adelaide, with a SkyScan 1076 desktop microCT scanner. Isometric voxel sizes for scans ranged from 8.6–41 µm. Scanning parameters were optimized based on material properties of each specimen. To reduce noise and increase tissue homogeneity before segmentation, image stacks were filtered using a 2D median filter, followed by either a 2D kuwahara filter (implemented as an Image J 1.46r plugin) or a 2D, shell script programmed, mean of least variance filter (Wollny et al. 2013). Resulting segmentations were assessed manually (slice by slice) against the raw data and adjustments made where necessary. High-resolution dentine and enamel surface files were generated with the "generate surface" module in Avizo 8 and subsequent mesh processing accomplished with MeshLab v1.3.1. Due to lack of contrast, segmentation was not possible for specimens of *Ngamaroo archeri* and *Prionotemnus palankarinnicus* (Table 3.1). Surface files and other supplementary information have been archived in the Dryad digital repository (doi:10.5061/dryad.bt4vj).

3.3.3 Ancestral State Reconstruction

To estimate the interval between loss and reevolution of the posthypocristid we time-scaled a morphological phylogeny of Macropodoidea containing 34 modern and fossil taxa (from Prideaux and Warburton 2010). A matrix of first appearance data based on the fossil record (Table S1) was used to constrain divergence times of tip taxa, based on criteria outlined by Parham et al. (2011; see SI). Before time-scaling, *Thylogale billardierii* was excluded from the tree because it was recovered in a polytomy near the base of Macropodinae (Prideaux and Warburton 2010) and "*Nowidgee matrix*" was replaced by *Bulungamaya delicata*, with which it is purportedly synonymous (Travouillon et al. 2014). Within the `R` statistical environment (3.1.1; R Core Team 2014) the function timePaleoPhy in the package paleotree 2.2 (Bapst 2012) was used to date the phylogeny using the equal method to proportion variance in node age along the stem (Brusatte et al. 2008). Since the earliest fossil representatives of a clade typically underestimate the true clade age (Benton and Donohue 2007) minimum ages for 10 key nodes were con- strained by mean relaxed clock estimates (Table S2; Figure S3.1) derived from a combined nuclear and mitochondrial gene marsupial phylogeny (Mitchell et al. 2014). This was implemented with the node.mins argument in timePaleoPhy. The root age was not allowed to vary (vartime = 0) and all other arguments were kept as default.

Table 1. MicroCT-based reconstructions of the outer enamel surface and enamel–dentine junction for 17 species of fossil and modern macropodoids. ∗Denotes extinct group.

Species	**n**	**Segmentation possible?**	**Specimens**
Aepyprymnus rufescens	2	Y	SAM M18127,SAM M15919
Dendrolagus lumholtzi	1	Y	SAM M1901
*Ganguroo bilamina**	2	Y	QM F19646, QM F24723
*Hadronomas puckridgi**	1	Y	NTM P5327A
Hypsiprymnodon moschatus	1	Y	ANWC CM12696
Lagostrophus fasciatus	1	Y	WAM M5665
Macropus rufus	2	Y	FU 2688, SAM M2217
Macropus robustus	4	Y	SAM M23849, SAM M9057, QM J10746, QM J20843
Macropus sp. indet.*	2	Y	AM F137633A, AM F137633B
*Ngamaroo archeri**	2	N	SAM P31834, SAM P27817
*Prionotemnus palankarinnicus**	1	N	UCMP 44538
*Procoptodon gilli**	1	Y	SAM P47110
*Procoptodon goliah**	3	Y	SAM P47109, SAM P27068, AM F30626A
*Rhizosthenurus flanneryi**	1	Y	QM F23784
*Simosthenurus occidentalis**	5	Y	SAM P47114, SAM P28663, SAM P47115A, SAM P47115B, SAM P28513
Thylogale stigmatica	1	Y	SAM M2599

For ancestral state reconstruction, absence of the posthypocristid was coded as (0) and presence as (1). The `R` function `ace` in the package `ape` (Paradis et al. 2004) was used to compare ancestral state reconstruction models fitted with maximum likelihood. Two models were assessed, an equal rates model where loss and gain were equally likely, and an all rates different model where rates of character loss and gain could vary. The fit of different models was compared using a log-likelihood ratio test. Maximum parsimony analysis was undertaken using the `mpr` function in ape. We determined the interval of loss as the period between the age of the first node where the character was unambiguously reconstructed as missing (> 95% proportional likelihood) and the first node where it was unambiguously present (> 95% proportional likelihood).

We explored two different approaches to excluding fossils to assess how robust ancestral state reconstructions were to the sampling of tip taxa. For the first approach we removed fossil taxa (n = 18) from the timescaled phylogeny resulting in a tree with 16 extant taxa on which the analysis was performed. However, because this greatly reduced the number of tip taxa (especially basal taxa), we also performed analysis on the well-sampled, extant only, MCMC time-calibrated phylogeny of Mitchell et al. (2014). This tree was pruned to include Macropodoidea and three phalangeriform taxa, *Pseudocheirus peregrinus* (Pseudocheiridae), *Trichosurus vulpecula* (Phalangeridae) and *Cercartetus nanus* (Burramyidae) as outgroups.

For ancestral state reconstruction of molar proportions we pruned the time-scaled morphological phylogeny to include taxa for which posterior molar proportion data were available (Figure S3.2). Ancestral states were estimated with ace using the `REML` method, with all other arguments kept as default. Reconstructed node values are reported in Table S3.4.

3.3.4 Tooth Measurements and Data Analysis

Calliper- and microCT-based dental measurements for 34 species of fossil and modern macropodoid were obtained from collections at the AM, ANWC, FU, SAMA, and WAM. Maximum trigonid width, maximum talonid width, and maximum occlusal length were measured for each lower molar tooth (denoted Mx, where x is the positional identity of the tooth). Trigonid and talonid width were averaged and multiplied by occlusal length to compute a crown area. To increase sample size, measurements were included for *Procoptodon browneorum*, *P. gilli*, *P. goliah*, *P. rapha* and *Simosthenurus occidentalis* from Prideaux (2004), and for *Bulungamaya delicata* and *Ganguroo bilamina* from Flannery et al. (1983) and Cooke (1997). For *Procoptodon goliah* we also calculated a "mean" (Figure. S3.4, S3.5) using molar teeth from different specimens, because only one specimen we measured had an undamaged posterior dentition. Because marsupials possess four molar teeth, the dental row was split into anterior ($M_{1–3}$) and posterior ($M_{2–4}$) three-molar sequences (triplets) in order to relate macropodoid dentitions to the IC model of Kavanagh et al. (2007). Molar area ratios for the anterior (Table S3.7) and posterior triplets (Table S3.8) were computed and species means calculated. For anterior (Table S3.5) and posterior (Table S3.6) triplets, species means for central molar area were regressed against the species mean of the corresponding total triplet area. To test the IC model we used the `R` package `lmodel2` to calculate slope estimates and confidence intervals to compare with the predicted slope of 1/3. Following Legendre and Legendre (1998) a major axis regression was used to test the slope. Slope estimates based on standard (reduced) major axis regression, previously used to test the inhibitory cascade (e.g., Kavanagh et al. 2007; Renvoisé et al. 2009) were also calculated, although confidence intervals and slope estimates for this method can be biased when the slope departs from ±1 or n is small (Legendre and Legendre 1998). We used 95% confidence intervals to assess statistical differences. A principle component analysis, implemented with `prcomp` in `R`, was used to test the correlation between the relative strength of activation–inhibition and M_3 hypsodonty (tooth crown height). Hypsodonty was calculated as the shortest vertical distance between the M_3 hypoconid apex and the buccal enamel cervix, divided by the maximum M_3 talonid width. To quantitatively compare relative posthypocristid relief we placed a 2D section (using Avizo 8) midway and perpendicular to the axis of the posthypocristid. We measured the shortest straight line distance (h) from the posthypocristid apex across the talonid fossa, and the vertical distance (v) perpendicular from this line to the floor of the talonid fossa (Figure S3.3). The ratio v/h was used as an index of posthypocristid relief.

3.4 Results

3.4.1 External and Internal Molar Morphology

3.4.1.1 Posthypocristid Morphology in Basal Macropodoids

The posthypocristid in phalangeriform marsupials and basal macropodoids is a crest or ridge directed posteriorly or posterolingually from the hypoconid (Figure 3.2). The talonid fossa of *Hypsiprymnodon moschatus* and most extant potoroines is relatively larger than that of phalangeriform marsupials like *Pseudocheirus peregrinus*, because the posthypocristid is more posteriorly directed in the former compared with the latter (Figure 3.3). Posterolingual redirection of the posthypocristid occurs in basal fossil macropodoids like *Ngamaroo archeri*, *Bulungamaya delicata*, and *Gumardee pascuali* (Figure 3.3, 3.4) where it is associated with reduction of the talonid fossa and increased relief of the talonid wall (Figure 3.4). In potoroines and hypsiprymnodontids a transverse crest or ridge is directed buccally from the entoconid. In *H. moschatus* this ridge has a component directed lingually from the hypoconid, whereas in some basal fossil macropodoids like *Gumardee pascuali* and *Bulungamaya delicata* it is only a buccally directed cristid from the entoconid (Figure 3.4). Compared with the trigonid, the talonid of potoroines and hypsiprymnodontids is relatively more laterally compressed than those of sthenurine, lagostrophine or macropodine kangaroos (Table S3.9). Additionally, in basal macropodoids the talonid becomes progressively more laterally compressed relative to the trigonid moving from anterior to posterior molar positions (Table S3.9). The outer enamel surface (OES) expression of the posthypocristid in basal macropodoids has a strong enamel–dentine junction (EDJ) expression (Figure 3.2).

3.4.1.2 Posthypocristid Expression in Macropodine Kangaroos

In basal macropodines and small-bodied species of *Macropus* (subgenus *Notomacropus*) there is no posthypocristid, and the talonid wall underpins a simple transverse crest, the hypolophid, linking the entoconid and hypoconid. Within *Macropus*, six of 14 extant species recognized by Dawson and Flannery (1985) express the posthypocristid as well as at least seven fossil species (Table S3.10). All species of *Macropus* possessing the posthypocristid are large-bodied species (subgenera *Osphranter* and *Macropus*). Where the posthypocristid is expressed in these subgenera it is generally directed posterolingually from the hypoconid (Figure 3.2). Linkage between the posthypocristid and hypoconid is present at the EDJ but typically obscured at the OES. Posthypocristid relief in *M. fuliginosus*, *M. pan* and *M. robustus* is comparable to or greater than that of many potoroines and hypsiprymnodontids (Table 3.2).

Abnormal macropodine dentitions capture extreme variation in posthypocristid morphology (Figure 3.5). A right $M_{?4}$ of *Macropus rufus* (SAM M2217) possesses a prominent posthypocristid coexpressed with a transverse crest directed buccally from the entoconid, a prominent postcingulid, and a reemergent paraconid on the anterior trigonid margin. The coexpression of a postentocristid, the postcingulid and a posthypocristid in SAM M2217 also occurs in potoroines and hypsiprymnodontids (Figure 3.2). Lateral compression of the talonid relative to the trigonid for this terminal molar is comparable to ratios in basal macropodoids (Table S3.9). In the lower molar teeth of another abnormal specimen, AM F137633A (*Macropus* sp. indet.), the posterior talonid wall is bisected by a medial longitudinal crest paralleling a weakly developed posthypocristid. A small incipient dentine horn is present at the junction of the medial longitudinal crest and the transverse crest linking the entoconid and hypoconid (Figure 3.5).

3.4.1.3 Posthypocristid Expression in Sthenurinae

Basal members of the extinct Sthenurinae like the Miocene *Wanburoo hilarus* and *Hadronomas puckridgi* (Figure 3.2) possess a simple talonid wall which lacks a posthypocristid and is similar to basal macropodines. In the derived Pleistocene sthenurine *Simosthenurus occidentalis*, the posterior face of the talonid wall lacks a posthypocristid, but possesses crenulations of the OES absent at the EDJ (Figure 3.2). In the largest sthenurine *Procoptodon goliah*, the posthypocristid is a longitudinal ridge emerging posteriorly from the hypoconid (Figure 3.2). As with AM F137633A, *P. goliah* molars possesses what we interpret as an incipient dentine horn at the junction of the transverse talonid crest and the medial longitudinal talonid crest. This medial longitudinal talonid crest cannot be the posthypocristid because it does not arise directly from the hypoconid. It is similar to the posthypocristid of primitive macropodoids and *Macropus* because it connects anteriorly with a medial longitudinal “mid-link” crest traversing the talonid basin. In *P. goliah* this crest is almost twice as prominent as the true posthypocristid (Figure 3.2; Table 3.2).

3.4.2 Ancestral State Reconstruction

3.4.2.1 Combining Fossil and Modern Macropodoids

Based on the combined fossil and extant macropodoid phylogeny, maximum likelihood, and parsimony-based inferences (Figure 3.6) robustly support the presence of a posthypocristid as plesiomorphic for Macropodidae (sensu Prideaux and Warburton 2010). The all-rates different and equal rates likelihood models had almost the same log-likelihood values (−15.585 and−15.586 respectively) but a ratio test indicated the more parameterized all rates different model did not perform significantly better ($P = 0.970$). Both models recovered > 95% proportional likelihood that the posthypocristid was present as the root state for Macropodoidea. Using the less parameterized equal rates reconstruction, there was a very high proportional likelihood that the posthypocristid was absent (0.983) by divergence of *Ganguroo bilamina* at 19.3 million years ago (Mya) (Figure 3.6). Parsimony suggests earlier posthypocristid loss, in the last common ancestor of Lagostrophinae, Macropodinae, and Sthenurinae (20.9 Mya), which is also strongly supported by the equal rates reconstruction (proportional likelihood posthypocristid absent = 0.841). However, because likelihood does not unambiguously rule out posthypocristid presence at this node, and because extant *Lagostrophus fasciatus* lacks a posthypocristid, the posthypocristid might have been lost twice, once in the Lagostrophinae, and again in the last common ancestor of *Ganguroo bilamina* and all more derived macropodids.

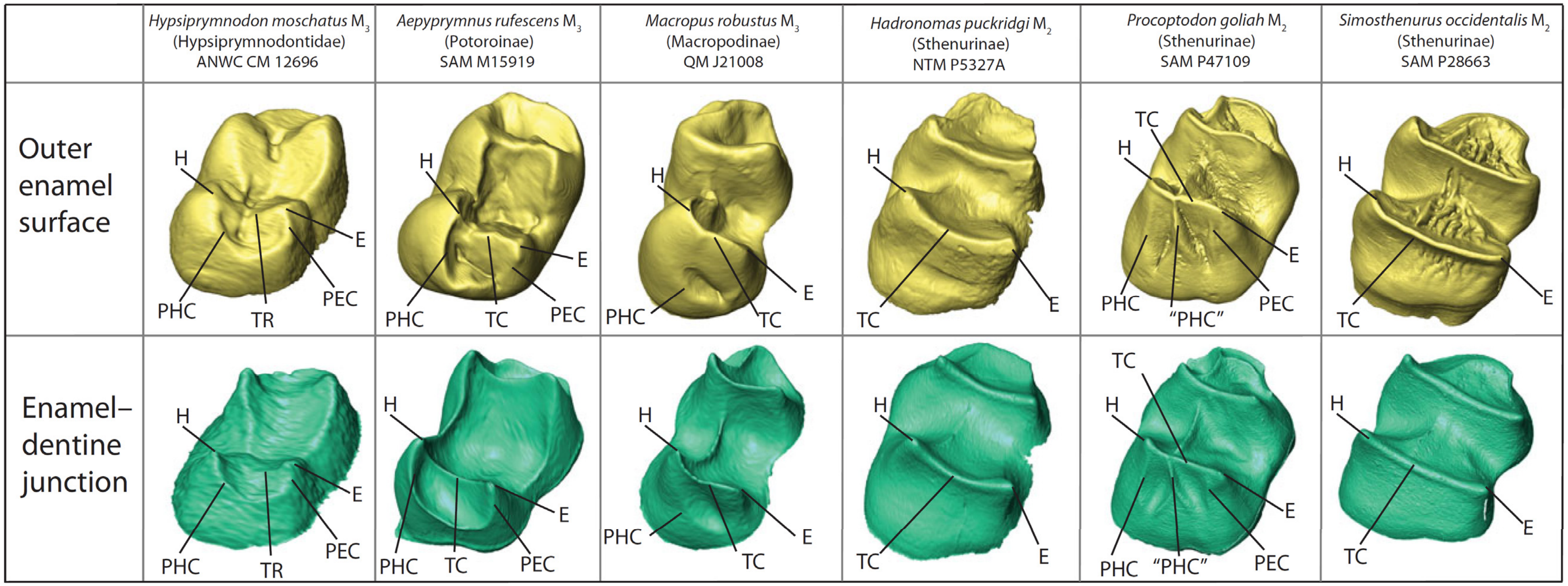


Figure 3.2. Talonid outer enamel surface (OES) and enamel–dentine junction (EDJ) morphology across Macropodoidea. Abbreviations: hypoconid (H), entoconid (E), posthypocristid (PHC), analogous posthypocristid (“PHC”), postentocristid (PEC) and transverse ridge (TR) or transverse crest (TC). Where necessary specimens have been mirrored from right to left side. Teeth are not to scale.

Table 3.2 . MicroCT-based measurements of posthypocristid homolog and analog crests in fossil and modern macropodoids.

Species	**Mean posthypocristid relief**	**n**	**Crest homology**
Aepyprymnus rufescens	0.65	4	Homologue
Bettongia lesueur	0.57	3	Homologue
Hypsiprymnodon moschatus	0.50	4	Homologue
SAM M2217 *Macropus rufus*	0.39	1	Homologue
AM F137633A *Macropus* sp.	0.30	1	Analogue
AM F137633A *Macropus* sp.	0.33	1	Homologue
Macropus fuliginosus	0.73	3	Homologue
Macropus pan	0.78	1	Homologue
Macropus pearsoni	0.51	1	Homologue
Macropus robustus	0.55	11	Homologue
Macropus rufus	0.19	3	Homologue
Ngamaroo archeri	0.42	8	Homologue
Potorous tridactylus	0.31	3	Homologue
Procoptodon goliah	0.37	2	Homologue
Procoptodon goliah	0.59	3	Analogue

At least two examples of posthypocristid reversal occur within Macropodidae; once each within Sthenurinae and Macropodinae. Proportional likelihood reconstruction of internal nodes within *Macropus* suggest posthypocristid reversal by 3.9 Mya, in the last common ancestor of *Macropus fuliginosus* + *Macropus pavana* (proportional likelihood the posthypocristid was present (P_{PHC}) = 0.996). Since the proportional likelihood that the posthypocristid was present at the base of the clade including *Macropus robustus* + (*Macropus fuliginosus* + *Macropus pavana*) is just less than 0.95 (P_{PHC} =0.933) a second reversal within *Macropus* is weakly supported. A single reversal occurred in the sthenurine lineage leading to *Procoptodon goliah* based on likelihood and parsimony. Proportional likelihoods that the posthypocristid was present (>0.95) suggest this occurred within the past 2 million years (Myr), after divergence of Simosthenurus occidentalis. Based on parsimony, the interval between trait loss and reversal for Macropodinae was 16.7 Myr and 20.6 Myr for Sthenurinae. Using an equal rates model the reversal interval is 15.4 Myr in Macropodinae and 19.0 Myr in Sthenurinae.

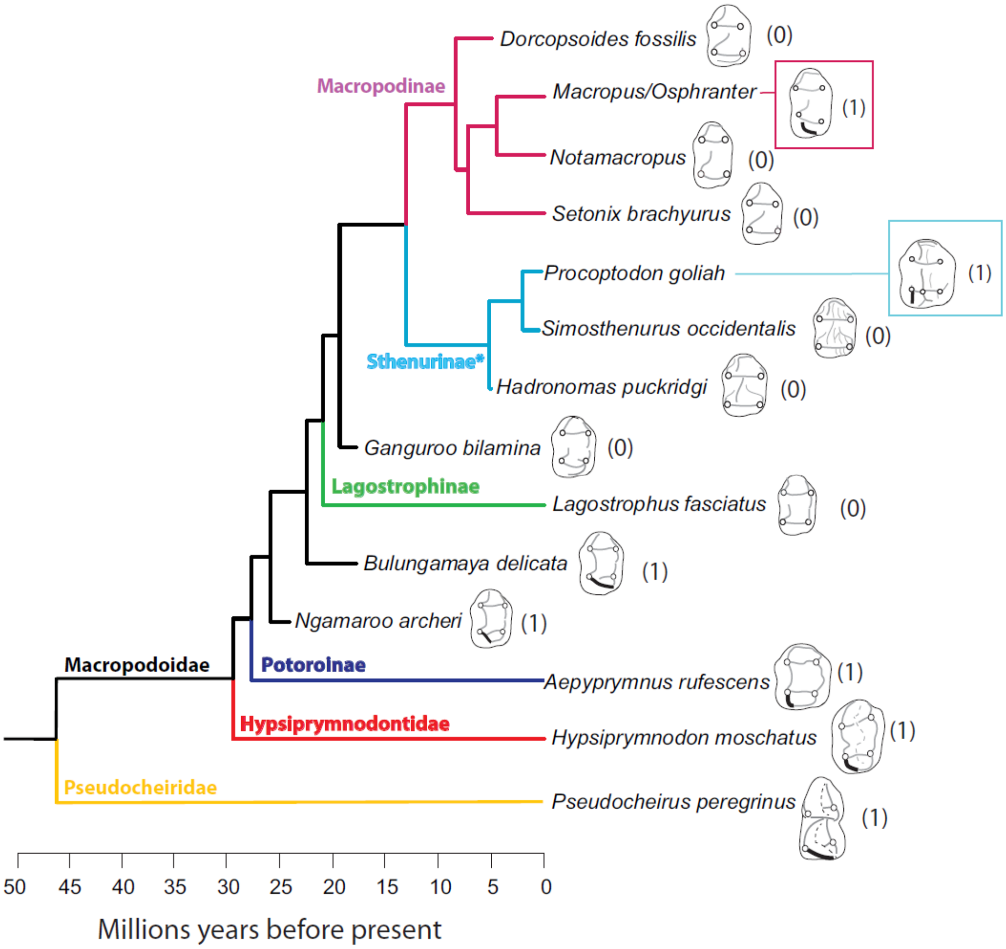


Figure 3.3. Lower third molar (M3) morphology of macropodoid marsupials mapped onto a time-scaled phylogeny with the phalangeriform *Pseudocheirus peregrinus* as an outgroup. Character states are indicated in brackets with “0” corresponding to absence of the posthypocristid and “1” as its presence. The posthypocristid is indicated by bold lines relative to other crests. Boxes emphasize posthypocristid reversals in *Macropus* and *Procoptodon*. Branch termini for extinct taxa correspond to the first appearance datum. Teeth are not to scale.∗Denotes extinct group.

3.4.2.2 Impact of Excluding Fossil Macropodoids

When fossil taxa were removed from the time-scaled morphological phylogeny the less parameterized equal-rates model (log likelihood −7.729) was favoured over the all-rates different model (log likelihood −7.668) (Log-likelihood ratio test; P = 0.728). Based on proportional likelihoods, removing fossil taxa generally increased ambiguity at basal internal nodes, including the root, relative to the inclusive tree. The equal-rates proportional likelihood that the posthypocristid was present at the root decreased from 0.972 when fossil taxa were included, to 0.544 (equal rates) or 0.440 (all rates different) when fossil taxa were removed. Equal-rates support for presence of the posthypocristid in the last common ancestor of Macropodinae and Lagostrophinae increased (0.160 to 0.257) after removing fossil taxa. Node reconstructions closer to branch tips also became more ambiguous, and there was a corresponding increase in support for posthypocristid presence deeper in clades where the combined analysis supported reversal. For instance, when fossil taxa were pruned, support for posthypocristid presence in the last common ancestor of *Onychogalae* + *Macropus* was 0.102, whereas previously there was essentially no support ($P_{\mathrm{PHC}} = 0.003$).

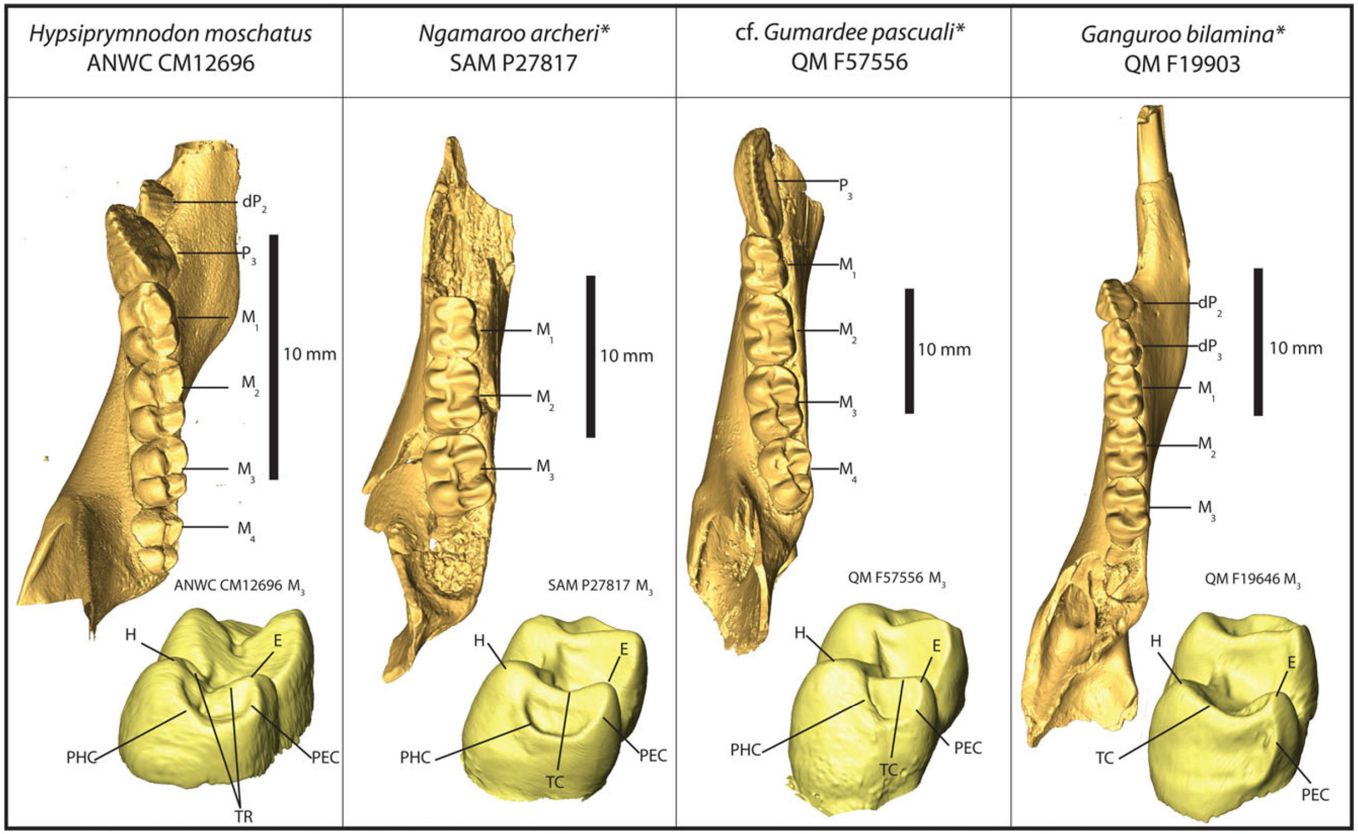


Figure 3.4. Posthypocristid reduction and loss in basal macropodoids. Abbreviations: hypoconid (H), entoconid (E), posthypocristid (PHC), postentocristid (PEC), transverse crest (TC), transverse ridge (TR).Where necessary specimens have been mirrored from right to left side.∗Denotes extinct taxon.

Ancestral state reconstruction using the separate molecular phylogeny of Mitchell et al. (2014), which included overlapping but also different taxa from the pruned morphological tree, revealed that the all rates different model had a higher log likelihood (−11.860) than equal rates (−12.259). However, the all-rates different model did not significantly outperform the equal-rates model (Log-likelihood test; P = 0.372). Proportional likelihoods from the equal rates model strongly support posthypocristid presence as plesiomorphic for the entire tree ($P_{PHC} = 0.981$) and at the macropodoid root ($P_{PHC} = 0.952$). The all-rates different model recovered much lower support for posthypocristid plesiomorphy at the base of the tree ($P_{PHC} = 0.741$) and macropodoid root ($P_{PHC} = 0.649$). Thus the equal rates model recovered ancestral states on the molecular phylogeny that were most similar to those inferred using the combined fossil and modern morphological phylogeny. Because support for posthypocristid plesiomorphy is much weaker using the all-rates different model, only an equal-rates model strongly recovers posthypocristid reversal. However, based on a strict interpretation of likelihoods this equal-rates model supports two reversals in *Macropus*, first at the base of the clade *M. rufus* + (*M. antilopinus* + *M. robustus*) at 1.74 Myr, and then at the base of the sister clade *M. fuliginosus* +*M. giganteus* at 0.64 Myr. Using parsimony the posthypocristid reversal interval for Macropodinae was 10.6 Myr while using equal rates it was 6.6 Myr (*M. rufus* + *M. antilopinus* + *M. robustus*) and 7.7 Myr (*M. fuliginosus* + *M. giganteus*).

3.4.3 The Inhibitory Cascade (IC) in Macropodoids

For the anterior molar triplet, the slope of the full model (including fossil and modern taxa) based on species means was significantly different from the IC predicted slope (n = 31; Table S3.3, Figure S3.4A). Only after all species of *Macropus* possessing the posthypocristid and all sthenurine taxa were removed did the confidence intervals overlap with the predicted slope. Like the anterior triplet, the full model of the posterior triplet did not overlap with the IC slope (n = 31; Table S3.3, Figure S3.4B). Analysis of the posterior triplet did not include data points for SAM M2217 and the "mosaic" *Procoptodon goliah*, although inclusion of these points draws the model further from IC predictions. Slope estimates and confidence intervals for the posterior triplet were further from IC predictions than the anterior triplet. Like the anterior triplet, the posterior triplet only overlapped with the predicted slope after all Sthenurinae, and then *Macropus* species possessing a posthypocristid, were removed. Standard (reduced) major-axis regression produced essentially the same slope estimate and confidence intervals as the major-axis regressions discussed above (Table S3.11). Natural log scaling the data revealed a similar pattern where exclusion of Sthenurinae, and species of Macropus possessing the posthypocristid, improved overlap with IC predictions (Table S3.12; Figure S3.5). However, slope estimates of the full model based on log scaled data were not significantly different from the predicted slope because the predicted slope fell within the 95% confidence interval for the full model. This indicates that when the effects of size are reduced by rescaling the data, all macropodoids broadly conform to IC predictions. There is a strong correlation ($F_{1,17} = 35.63$, $P << 0.01$, adj. $R^2 = 0.658$) between the first principle component of posterior triplet proportions, which explains 95.8% of the total variance, and hypsodonty of the M_3 hypoconid (Table S3.13).

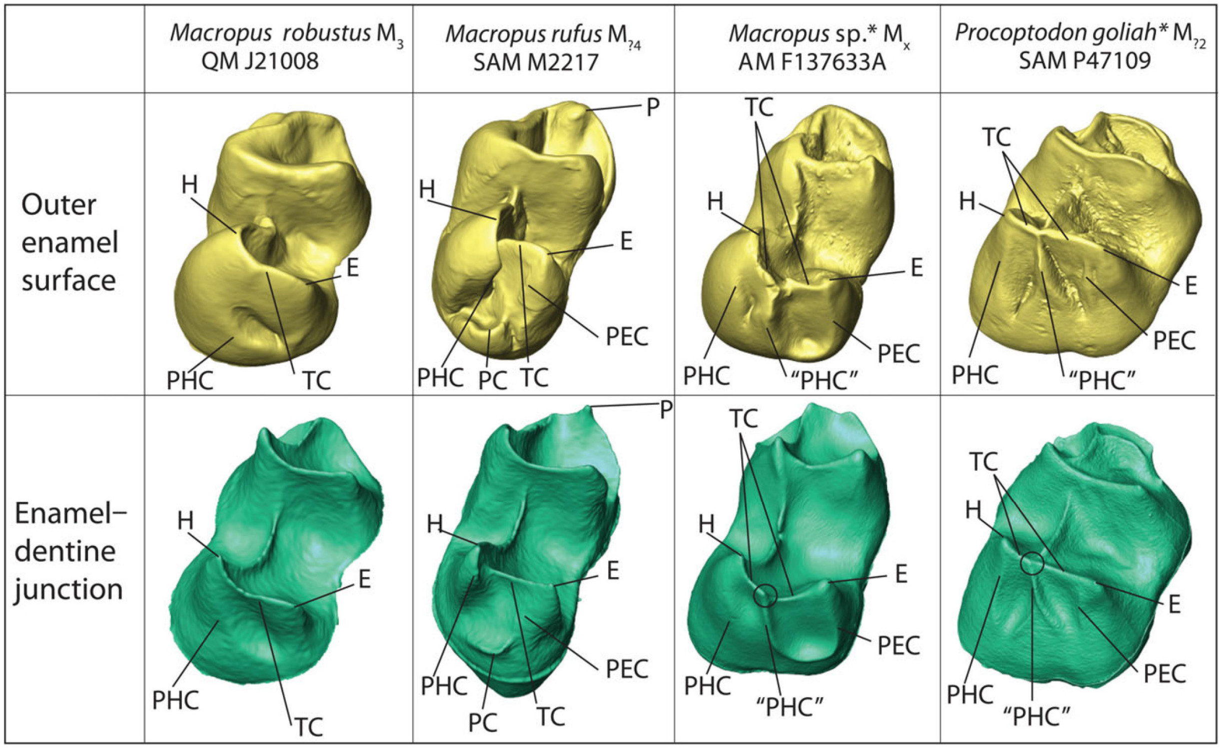
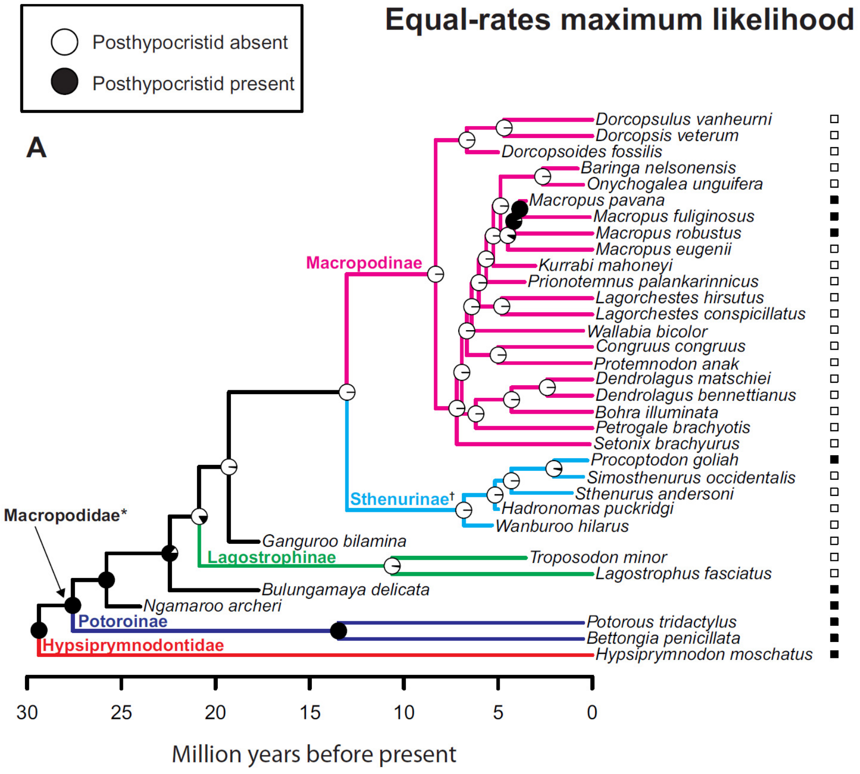


Figure 3.5. Polymorphism in talonid morphology in *Macropus* and comparison with the extinct sthenurine *Procoptodon goliah*. Circles demarcate position of incipient dentine horns. Abbreviations: hypoconid (H), entoconid (E), paraconid (P), postcingulid (PC), postentocristid (PEC), posthypocristid (PHC), analogous posthypocristid ("PHC"), transverse crest (TC). Where necessary specimens have been mirrored from right to left side. Teeth not to scale. ∗Denotes fossil specimen.

Table 3.3. Major-axis (MA) regression for the inhibitory cascade (IC) model. PHC = posthypocristid.

MA regression model							
M_2 v M_1+M_2+M_3	**Intercept**	**Slope**	**R^2**	***n***	***P* (2-tailed)**	**C.I. Min. Slope (2.5%)**	**C.I. Max. Slope (97.5%)**
IC predicted	0	0.333	NA	NA	NA	NA	NA
Full	0.156	0.337	1.000	31	P<<0.01	0.336	0.339
Full − *Macropus* with PHC removed	0.095	0.337	1.000	28	P<<0.01	0.336	0.339
Full − Sthenurinae removed	0.122	0.340	0.998	24	P<<0.01	0.332	0.347
Full − *Macropus* with PHC + all sthenurines removed	0.457	0.334	0.987	21	*P* << 0.01	0.315	0.352
M_3 v M_2+M_3+M_4	**Intercept**	**Slope**	**R^2**	***n***	***P* (2-tailed)**	**C.I. Min. Slope (2.5%)**	**C.I. Max. Slope (97.5%)**
IC predicted	0	0.333	NA	NA	NA	NA	NA
Full	−2.058	0.368	0.998	31	*P* << 0.01	0.362	0.374
Full − *Macropus* with PHC dropped	−1.808	0.369	0.998	28	*P* << 0.01	0.363	0.375
Full − Sthenurinae dropped	0.085	0.348	0.998	25	*P* << 0.01	0.341	0.355
Full − *Macropus* with PHC + all sthenurines dropped)	0.929	0.335	0.986	22	*P* << 0.01	0.316	0.354

Equal-rates maximum likelihood



Maximum parsimony

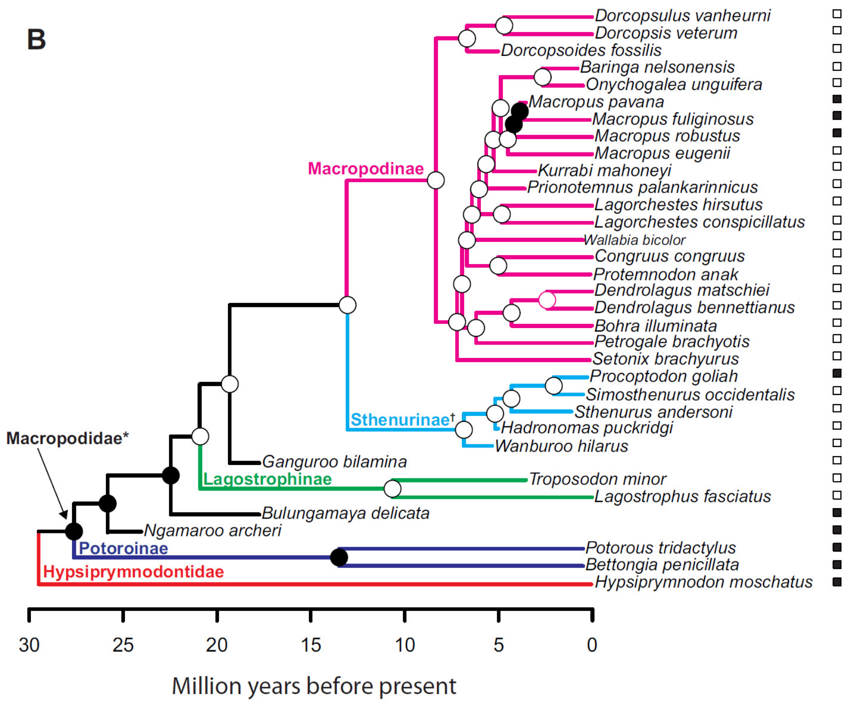


Figure 3.6. Ancestral state reconstruction of the posthypocristid based on (A) equal rates maximum likelihood and (B) maximum parsimony inferred on a combined fossil and modern macropodoid phylogeny (after Prideaux and Warburton 2010). Tip boxes indicate character state coding; white = posthypocristid absent, black = posthypocristid present. Pie charts at nodes define the proportional likelihood of posthypocristid presence or absence. Branch termini for all taxa correspond to first appearance datum.∗sensu Prideaux and Warburton (2010). †Denotes extinct clade.

3.5 Discussion

3.5.1 Homology and Evolutionary Dynamics of the Posthypocristid

Changes in posthypocristid morphology are a key contributor to variation in macropodoid talonid morphology (Figure 3.3). However, establishing posthypocristid homology is challenging be- cause dental traits are often homoplastic (Van Valen 1982; Kraatz et al. 2010; Anemone et al. 2012). Additionally, no unique molecular markers differentiate cusp types (Jernvall and Jung 2000; Jernvall et al. 2000), and relatively small changes in signaling molecule dosage can induce the loss or appearance of new structures (Kangas et al. 2004; Harjunmaa et al. 2014). To address these issues a topological definition of tooth feature identities has been used in place of the traditional "fixed" concept of dental trait homology (Jernvall et al. 2008). Using a topological definition of the posthypocristid, as a crest directed posteriorly or posterolingually from the hypoconid (Figure 3.1), two clear instances of reversal are supported, one among large-bodied species of Macropus, and a second in the sthenurine lineage leading to *Procoptodon goliah* and *P. rapha*. Phylogenetically, this pattern is congruent with previous work (e.g., Prideaux 2004) but differs because we argue that the medial longitudinal talonid crest in *P. goliah* is an analog that parallels the true, more buccally positioned posthypocristid (Figure 3.5, 3.7).

Topological definitions of homology can introduce discontinuities in sequences of descent because the identities of tooth features are not fixed (e.g., Van Valen 1982; Jernvall et al. 2008). For instance, based on Granger's (1908) characterization of premolar molarization in early horses, Van Valen (1982) showed that the cusp topologically identifiable as the third upper premolar (P^3) protocone in the basal horse *Hyracotherium* was displaced posteriorly into a position topologically consistent with a hypocone, by a neomorphic protocone. Likewise, in the Greater Bamboo Lemur (*Hapalemur simus*), Jernvall et al. (2008) suggested that the P^3 paracone was changing identity to a metacone, as a new cusp emerged anteriorly. Loss and reemergence of the posthypocristid may also introduce discontinuities in tooth feature identities (Figure 3.7). With respect to posthypocristid loss, Cooke (1997) proposed that the posthypocristid was coopted into the transverse talonid wall in *Ganguroo bilamina* and all more derived macropodids. Transitional molar morphologies in basal fossil macropodoids such as *Ngamaroo archeri* and *Bulungamaya delicata* suggest that this was accomplished by rotating the posthypocristid into a lingually directed, transverse position, eventually linking the entoconid and hypoconid (Cooke 1997). However, this change in crest topology brings the "posthypocristid" into a position consistent with a distinct transverse crest or ridge present in many basal macropodoids (Figure 3.2, 3.7). A broader problem is that the break in continuity of descent in putative cases of reversal means a "fixed" concept of dental trait homology provides limited criteria to resolve the identity of structures. In the case of the posthypocristid, topological criteria provide a basis for recognizing posthypocristid reversals in *Macropus* and *Procoptodon* because the candidate crest has the "correct" relationship to other talonid structures when compared with the primitive talonid architecture of potoroines and hypsiprymnodontids (Figure 3.7). This interpretation also implies that the crest linking the entoconid and hypoconid in *Ganguroo bilamina* and all more derived macropodoids has lost its "identity" as the posthypocristid by virtue of changed correspondence in relative position (Figure 3.7).

Ancestral state reconstruction based on integrating fossil and modern taxa, and reinterpretation of crest homology, strongly supports plesiomorphy of the posthypocristid in Macropodoidea and at least two subsequent reversals (Figure 3.6). However, posthypocristid plesiomorphy is not as strongly supported when we restrict analysis to extant macropodoids, probably because of the impact of long basal branch lengths on maximum-likelihood inference (Schultz et al. 1996; Cunningham et al.

1998). Specifically, the maximum-likelihood assumption of a homogenous rate of state transitions along basal branches, such as from the root to tip taxa like *Hypsiprymnodon*, may overestimate the likelihood of character change. The similarity in the dentitions of early Miocene and modern species of *Hypsiprymnodon* provides evidence for much lower rates of dental character evolution in these basal branches (Bates et al. 2014). Simulations using ultrametric trees show that accounting for evolutionary rate variability more accurately reconstructs ancestral states than do either equal rates or all rates different models of character evolution (King and Lee 2015). Including fossil taxa in phylogenies provides one means to account for rate variability, by constraining internal node ages and breaking up long branches (Cunningham et al. 1998; Finarelli and Flynn 2006). Thus, the ancestral state reconstruction integrating fossil macropodoid taxa probably resolves the timing and polarity of posthypocristid evolution most robustly. Especially, given the broad consensus between this morphological tree and recent molecular topologies (e.g., Meredith et al. 2009; Mitchell et al. 2014), including ancient DNA approaches which recover the extinct Sthenurinae as sister to Macropodinae (Llamas et al. 2014). As the inclusion of Sthenurinae reveals an additional reversal, incorporating fossil taxa may also increase capacity to detect evolutionary patterns that would otherwise be missed.

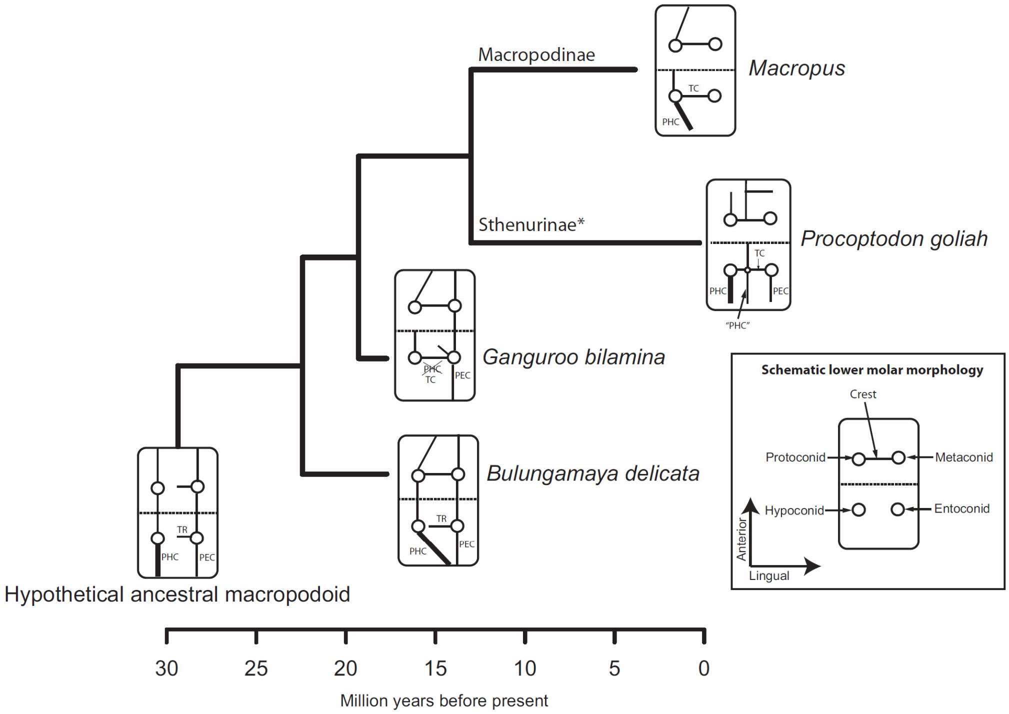


Figure 3.7. Schematic lower molar morphology of macropodoids showing the hypothesized discontinuity in posthypocristid (PHC) identity. Linking of the hypoconid and entoconid by a single crest in *Ganguroo bilamina* and other bilophodont macropodids marks a discontinuity in homology, where the "posthypocristid" shifts identity to a transverse crest or ridge (TC/TR). The posthypocristid reemerges in large-bodied species of *Macropus* and *Procoptodon goliah*. ∗Denotes extinct group. The posthypocristid is highlighted in bold.

3.5.2 Developmental Influence on Posthypocristid Loss and Reversal

The proportions of mammalian teeth are regulated by an IC which reflects a balance between primarily epithelial inhibitors that pro- mote cell proliferation but inhibit differentiation, and primarily mesenchymal activators that promote cell differentiation (Kavanagh et al. 2007). At the ordinal level, most mammalian groups follow IC predictions, although some like canids (Asahara 2013), arvicoline rodents (Renvoisé et al. 2009), and platyrrhine primates (Bernal et al. 2013) exhibit lineage-specific specializations of this core cascade (Polly 2007; Halliday and Goswami 2013). Within developmental morphospace (Figure 3.8A) macropodoids primitively expressing the posthypocristid occupy the lower-left, whereas the large-bodied taxa which reexpress the posthypocristid are situated to the upper right, sometimes far to the right of the predicted IC axis. This suggests that potoroine and hypsiprymnodontid posterior molars are more inhibited, whereas sthenurines, and macropodines that reevolve the posthypocristid have relatively larger M_3 (or smaller M_4) sizes than predicted by the IC model.

Projected ancestral states for the posterior triplet (Figure 3.8B) strongly suggest that the evolution of decreased posterior molar inhibition facilitated reduction and loss of the posthypocristid. As posthypocristid loss bridges an important dietary gap between fungivorous and folivorous macropodoids, loss of this character may have been important in dietary adaptation. In fungivores, like potoroines and *Hypsiprymnodon*, the posthypocristid buccally demarcates a well-developed talonid fossa, which together with the trigonid basin of the adjacent posterior tooth, occludes with the upper molar hypocone (sensu Sánchez-Villagra and Kay 1996) to crush food. Basal fossil macropodoids like *Bulungamaya delicata* and *Ngamaroo archeri*, which have both transitional posthypocristid morphologies and molar proportions (Figure 3.3; Figure 3.8A), also have a reduced talonid fossa suggesting decreased reliance on crushing food. Interestingly, increased hypsodonty in derived macropodids is strongly correlated with both release of the posterior molars from inhibition and reduction of grinding surfaces such as the talonid fossa which are primitively bordered by longitudinal crests like the posthypocristid. As hypsodonty is an important response to high dental wear rates in mammals (Janis and Fortelius 1988) the release from inhibition may have been a key factor enabling macropodids to adapt to more abrasive folivorous diets by coupling reduction in crushing basin size with increased hypsodonty. Associated with the decreased reliance on crushing food, loss of the posthypocristid is also linked with the emergence of transverse crests, or lophs, which enable shearing of tough foliage (Sanson 1989). We thus suggest that interplay between dietary ecology and inhibitory dynamics can help explain why posthypocristid loss was phylogenetically linked with the loss of crushing basins and the appearance of well-developed transverse crests in basal macropodids (e.g., Cooke 1997). Similar interactions between development and selection for consumption of more fibrous foods may have underpinned the evolution of hypsodonty and transverse crests in murine rodents (Rodrigues et al. 2013). Such interplay between dietary ecology and inhibitory dynamics may also prove important in the dietary transitions of other mammalian groups.

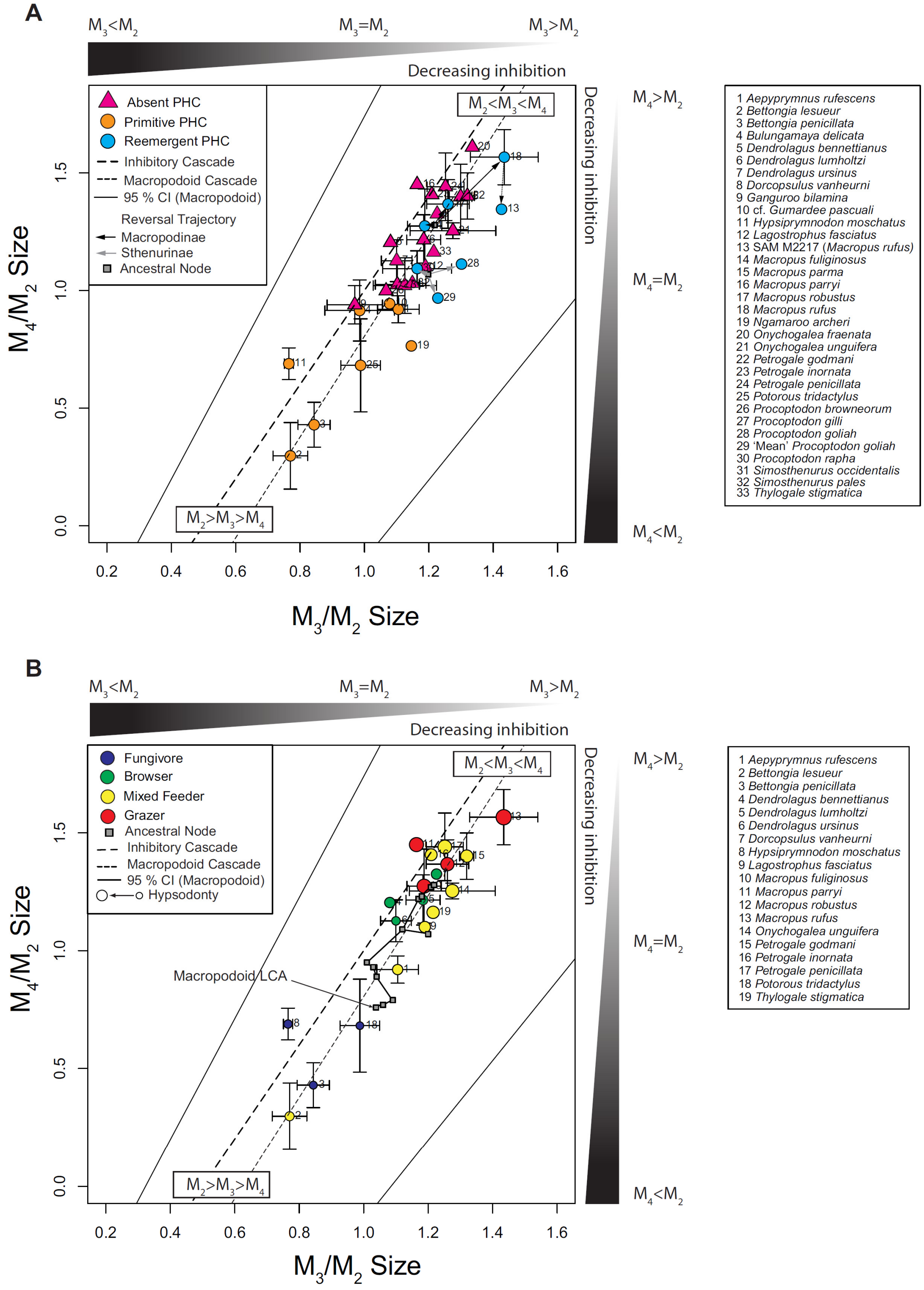


Figure 3.8. Species mean posterior triplet (M2-4) proportions for modern and fossil macropodoid species. Best fit lines are major axis regressions and error bars represent one standard deviation. (A) Primitive and reemergent posthypocristid expression occupy different regions of developmental morphospace: arrowed lines indicate trajectory of reversal in *Macropus* and *Procoptodon*. (B) Posthypocristid loss is associated with the transition from a probable ancestral fungivore diet toward a folivorous diet, along a pathway of decreasing posterior molar inhibition and increasing hypsodonty. Dietary classification and crown height is reported in Table S3.13. Dark branches indicate reconstructed pathway of posthypocristid loss and absence since the macropodoid last common ancestor (LCA). Ancestral states for molar triplet proportions (Table S3.4) were estimated using maximum likelihood on the pruned phylogeny of Prideaux and Warburton (2010) (Figure S3.2).

Most macropodoids conform to IC predictions but we have documented a divergence from these predictions which is closely aligned with posthypocristid reexpression. However, because some taxa that diverge from IC predictions also lack the posthypocristid (Figure S3.4), posthypocristid reexpression may reflect a broader change in talonid patterning influenced by the IC shift. Derived macropodoids with talonid morphologies most divergent from a simple talonid wall are generally furthest from the predicted IC axis (Figure 3.8A), and includes taxa like *P. goliah*, *P. rapha* and *Macropus rufus*, which all reevolve the posthypocristid. Kavanagh et al. (2007) predicted that divergence to the lower right quadrant of the morphospace in Figure 3.8 results from a combination of reduced posterior molar inhibition and early termination of molar development. Thus, posthypocristid reemergence may be linked to a decreased rate of talonid development, which recreates an ancestral architecture. The EDJ topography underpinning posthypocristid expression does suggest that folding of the basement membrane during cusp patterning is important. Jernvall et al. (2000) proposed that two hierarchical patterning processes, an initial prepatterning phase linked with lateral tooth germ expansion, and the subsequent iteration of this pattern associated with anterior–posterior elongation, were responsible for different cusp architectures in mouse and vole teeth. An increase in the relative proportions of posterior molars in derived macropodoids compared with basal potoroines and hypsiprymnodontids (Figure 3.8) is linked with lateral expansion of the talonid relative to the trigonid (Table S3.9). This may suggest that a prepatterning shift which increased lateral growth of the talonid contributed to posthypocristid reduction. However, the talonid of macropodine and sthenurine kangaroos that reevolved the posthypocristid never becomes as relatively compressed as equivalent teeth in potoroines and hypsiprymnodontids (Table S3.9). Potentially, this indicates that the inhibitory influence on pattern iteration, rather than prepatterning, was more important in posthypocristid reversal. The partitioning of primitive and reversed character states within the IC morphospace, and evidence that different patterning processes may underpin similar talonid architectures also supports inferences that different developmental processes can produce similar or homologous phenotypes (Alberch 1980; Wake 1991; True and Haag 2001; Salazar-Ciudad and Jernvall 2002).

Posthypocristid reexpression is often linked to the reexpression of other ancient tooth traits including the postentocristid, postcingulid and trigonid features like the paraconid (Figure 3.2, 3.5). These patterns of dental trait expression are similar to rodent teeth where the ectodysplasin pathway is modulated (Kangas et al. 2004), potentially indicating that the ectodysplasin pathway was involved in posthypocristid loss and reexpression. Experimental evidence indicates that progressive increases in ectodysplasin dosage elicit increasingly modified talonid structures in mice (Harjunmaa et al. 2014). In a similar manner, a progressive increase in responsiveness to or dosage of ectodysplasin pathway molecules along the stem leading to derived macropodids may have been important in posthypocristid reversal. In mouse, transitions from low (*Tabby* mutant) to moderate (wild-type) ectodysplasin protein (EDA) dosages are associated with a transition from bunodont (low rounded cusps) to lophodont teeth (transverse crests linking cusps) (Kangas et al. 2004; Harjunmaa et al. 2014). Some of these changes are similar to the sequence of character change associated with posthypocristid loss and lophid evolution. However, because the lower molars of *Tabby* mutants lack a structure similar to the posthypocristid, the synchronous modulation of other pathways (e.g., Harjunmaaet al. 2014) was probably also important. Increasing EDA dosage above "wild-type" levels (*K14–Eda* mice; Kangas et al. 2004), produces structures reminiscent of those that reevolve or are reexpressed occasionally in derived macropodoids, such as the posthypocristid, postentocristid and postcingulid, as well as new traits like the cristid obliqua, and the paraconid present in some sthenurines. Strikingly, the molars of *K14–Eda* mice possess a well-developed medial longitudinal talonid crest like *Procoptodon goliah* molars. Since the required EDA dosage needed to elicit these features in mouse is small (Harjunmaa et al. 2014) it may not have been developmentally “difficult” to reevolve some talonid traits in macropodoid phylogeny. Increased ectodysplasin signaling has been implicated in the reemergence of pharyngeal teeth in cypriniform fishes (Aigler et al. 2014) and armour plate phenotypes in freshwater sticklebacks (Kitano et al. 2008) suggesting that this pathway may be an important regulator of reversibility in ectodermal organs more broadly.

Posthypocristid reemergence and changes in talonid morphology are linked to a progressive, size-dependent deviation from the predicted IC (Figure S3.4), hinting at a link between absolute size, molar proportionality and tooth morphology. Modest deviations in cusp position and proportionality have been linked to size-related influences on the cusp-patterning cascade in the postcanine teeth of the ringed seal (Jernvall 2000). Wilson et al. (2012) also found evidence that reduced posterior molar inhibition was linked to larger body size in South American ungulates. Alternatively, such similarities could reflect ecophysiological associations with diet (Arman and Prideaux 2015). However, if the absolute size of dental tissues does influence molar proportionality, reversals in sthenurine and macropodine lineages may instead reflect the parallel acquisition of large size and thus be nonindependent. Whether, and exactly how dental tissue scaling might drive IC divergence remains unclear, but changes in signaling molecule diffusion gradients or dosage effects linked to volumetric changes in signaling centres could be important factors.

3.5.3 Implications for Dental Reversal in Mammals

By modulating the cusp-patterning cascade, especially the iteration of cusp patterns, some inhibitory shifts may promote reversals. In particular reducing the slope of the IC axis within the molar proportion morphospace (i.e., Figure 3.8) is often associated with formation of simpler molar architectures in carnivorans and new world primates (Asahara 2013; Bernal et al. 2013; Scott 2015). In the ringed seal, shortening the period of cusp patterning associated with reduction of the posterior teeth produces distal postcanine teeth reminiscent of primitive mammalian molars (Jernvall 2000). One reason these types of inhibitory changes, linked to simplification, may provide an accessible route to reversal is because they potentially require modulation of fewer signalling pathways (Harjunmaa et al. 2012, 2014). For instance, down-regulation of *Fgf3* in mice and human patients results in the progressive reemergence of a plesiomorphic condition where no posterolingual cusp (hypocone) is present on posterior upper molars (Charles et al. 2009). Likewise, *Tabby* mice with a null mutation in ectodysplasin (*Eda*) exhibit a more primitive molar morphology where the talonid is reduced (Kangas et al. 2004). In contrast, adding tooth cusps requires synchronous modulation of multiple pathways including ectodysplasin, activin A and sonic hedgehog (Harjunmaa et al. 2012).

If changes in inhibitory dynamics are more likely to produce simpler (and thus often more primitive) tooth phenotypes (Harjunmaa et al. 2012) we might expect (1) a trend toward dental simplification and (2) frequent reversals associated with character loss. The evolution of the upper molar posterolingual cusp, the hypocone, provides a classic context in which to explore this. The hypocone has convergently evolved more than 20 times in different mammalian groups, in response to a dietary shift toward herbivory (Hunter and Jernvall 1995). The two most common ways to evolve a hypocone are through modification of a metaconule or an enamel shelf called the postprotocingulum (Hunter and Jernvall 1995). However, irrespective of the different lineage-specific derivations of the hypocone (e.g., metaconule vs. postprotocingulum) (Tedford and Woodburne 1998; Anemone et al. 2012) each acquisition represents a separate convergence on a topologically similar cusp pattern (Simpson 1955; Van Valen 1994). Based on a topological definition of the hypocone as the posterolingual upper molar cusp (Van Valen 1994; Hunter and Jernvall 1995; Sánchez-Villagra and Kay 1996) a survey of mammalian lineages possessing a hypocone (Table 1; Hunter and Jernvall 1995) reveals few examples of subsequent loss. Among primates, some tamarins and marmosets (callitrichids) may have reverted to a three cusped molar from a quadritubercular anthropoid ancestor (Kay

1994). In cetaceans, the quadritubercular molar tooth of basal artiodactyls like *Indohyus* was likely simplified to the tricuspid molars of pakicetids by reduction and loss of the hypocone (Gingerich and Russell 1990; Thewissen et al. 2007). Molar simplification also occurred in pinniped evolution (Rybczynski et al. 2009) but it is unclear if basal arctoids proximal to the divergence with pinnipeds possessed a hypocone. Amongst diprotodont marsupials the hypocone may have been lost in derived thylacoleonids (e.g., *Thylacoleo carnifex*). Evidence that the hypocone was present ancestrally in this group is provided by the expanded posterolingual cingulum, and possible vestigial hypocone present on the first upper molar of primitive members like *Wakaleo vanderleuri* (Murray et al. 1987). However, although both the phalangeriform and vombatiform marsupials phylogenetically proximal to thylacoleonids (Murray et al. 1987) possess a hypocone, it is unclear when, and how many times, the hypocone emerged among diprotodont marsupials (Sánchez-Villagra and Kay 1996). Overall, hypocone loss seems to have been much rarer than hypocone gain, perhaps by an order of magnitude or more. Correspondingly, developmental bias towards the generation of simpler tooth phenotypes does not easily explain this marked phylogenetic asymmetry.

Given the potential developmental accessibility of evolutionary pathways that reduce cusp number, why does this asymmetry exist? One possibility is that dietary ecology acts as an evolutionary "road block." Specifically, loss of the hypocone should reemphasize shearing, by enabling occlusal contact between the posterolingual upper molar margin and lower molar anterobuccal margin (Szalay 1969) which would functionally favour a carnivorous or insectivorous diet. However, trophic transitions from herbivore or omnivore to carnivore (or insectivore) are extremely rare among mammals, perhaps because biomass constraints limit niche diversity at higher trophic levels (Price et al. 2012). From this perspective, posthypocristid reevolution in macropodids may have been "allowable" because it did not necessitate a dietary transition away from herbivory.

3.6 Conclusions

We show that the posthypocristid reevolved twice, after an absence of more than 15 Myr, in two separate macropodid lineages. This confirms that reversals are possible even after long intervals of absence (Kurtén 1964, Collin and Cipriani 2003; Prideaux 2004; Wiens 2011). By linking parallel reevolution of the posthypocristid to a shift in the IC which impacts tooth patterning, we provide evidence of how developmental systems can promote homoplasy (Wake et al. 2011). We suggest that an important factor underpinning dental trait reemergence in the macropodoid talonid may have been a progressive increase in responsiveness to or dosage of ectodysplasin pathway factors known to regulate rodent talonid morphology (Kangas et al. 2004; Harjunmaa et al. 2014). Given experimental evidence that changes in talonid traits similar to those in macropodoids are underpinned by relatively small increases in signaling molecule dosage (Harjunmaa et al. 2014), and in view of evidence for repeated reexpression or reevolution of ancient macropodoid tooth traits (Prideaux 2004; this work), we argue that character reversals are not always more "difficult" than character loss. However, although inhibitory dynamics can enable some dental traits to reemerge, we suggest that many phylogenetic reversals do not occur because inhibitory shifts often drive dental evolution towards higher trophic levels where ecological opportunity is more limited. Overall, developmental rules like the IC provide a valuable quantitative framework for understanding why some patterns of trait evolution are more common than others.

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3.9 Supplementary Information

Chronostratigraphic and Molecular Constraints for Branch Length Estimation

The first appearance datum (FAD) for 34 species of fossil and extant macropodoid used to timescale the morphological phylogeny of Prideaux and Warburton (2010) are reported in Table S3.1. We report both the FAD for tip taxa as well as the FAD for the oldest representative of that lineage. Where possible we report the museum prefix number relating to the calibration used which in most cases is the holotype specimen. For some taxa only a very young Pleistocene FAD exists for which museum prefix numbers are often not reported in the corresponding publications. Although not ideal, in these cases it is uncontroversial that such Pleistocene occurrences significantly underestimate the true age of the lineage because molecular divergence estimates or fragmentary fossil material from that lineage, or a sister lineage, indicate a much older origin. For instance although the genus *Potorous* is not unambiguously recognised until the middle Pleistocene (c. 500 ka) the existence of Miocene members of the sister lineage *Bettongia*, such as *Bettongia moyesi* (Flannery and Archer 1987) imply a much older divergence age.

In most cases the FAD represents an incontrovertible minimum age because they are derived from radiometric ages for an overlying stratigraphic unit or where this is not possible the minimum age of the unit within which they are contained. For Riversleigh fossil sites we use point estimates for the age of the deposit rather than chronostratigraphic ages for overlying units or the minimum age of the unit within which they are contained. This is appropriate because susperpositional relationships between fossil sites within the Carl Creek Limestone have not been clearly established (Megirian et al. 2010), but U-Pb radiometric ages of these sites derive from speleothems surrounding, or closely associated with fossil deposits, indicating they approximately date the age of the fossils (Woodhead et al. 2014). Where a magnetostratigraphic age was available for a deposit we report the minimum age for the magnetochron as reported in Gradstein et al. (2004) irrespective of the author's relative assignment of a fossil site within a magnetochron. In instances where the age of a fossil has not been tied to a chronostratigraphic age for the formation or unit, but it has been constrained to an epoch or land mammal age, we have used the upper (younger) boundary of these relative time units to derive a minimum age estimate.

Molecular divergence estimates based on a relaxed molecular clock model from Mitchell et al. (2014) were used to impose minimum estimates for the inception of key clades (Table S3.2). We did not use divergence time estimates from Meredith et al. (2009) because some of the calibrations utilise weakly supported minimum priors. For instance, the fossil calibration for the divergence of Potoroinae and Macropodinae is based on undescribed, fragmentary material from the Bullock Creek LF for which chronostratigraphic constraints are lacking (e.g., Megirian et al. 2010).

Impact of Fossil Calibrations and Molecular Constraints on Branch Lengths

Divergence times recovered for the time-scaled morphological tree are reported in Table S3.3. Divergence ages for key clades imposed by the `molecular mins` argument in the `R` function `timePaleoPhy` generally pull clades deeper in time than strict interpretation of the FAD. However of the ten molecular minimum constraints imposed, three underestimate divergences estimated from the time scaled tree and include the nodes corresponding to (1) Potoroinae + all more derived macropodids; (2) Lagostrophinae + all more derived macropodids and (3) *Dorcopsulus* + *Dorcopsis*. Where divergence estimates based on molecular data underestimate clade minima constrained by the fossil record it may suggest the rate model is misspecified (Phillips 2015). Specifically in the case of Macropodoidea we believe that these incongruences may be primarily linked to sparse utilisation of fossil calibrations and because new radiometric ages (e.g., Woodhead et al. 2014) necessitate revision of previously applied hard minimum priors.

In the case of Potoroinae + all more derived macropodids, the node using the fossil calibrated tree is more than 10 Myr older (16.85 vs. 27.58 Myr). The oldest divergence we recover seems to be driven primarily by inclusion of the late Oligocene macropodoid *Ngamaroo archerii* which is also the oldest taxon included in the phylogeny. Additionally, recent radiometric ages for the Neville's Garden site, which contains both the extinct taxon *Bulungamaya delicata* and *Ganguroo bilamina* also pull ages for this node back beyond the mean molecular estimate from Mitchell et al. (2014).

In our time-scaled phylogeny origination of the Lagostrophinae is approximately 6 Myr older than that inferred by Mitchell et al. (2014) but is very close to some relaxed molecular clock estimates (e.g., Westerman et al. 2002; Meredith et al. 2009). This older divergence appears to be forced by new radiometric dates for the Neville's Garden site (where *Ganguroo bilamina* occurs), and because the topology of the Prideaux and Warburton (2010) tree implies this taxon behaves as a minimum constraint for divergence of Lagostrophinae (Figure S3.1). However, the branching of *G. bilamina* after divergence of Lagostrophinae, and thus its position as a minimum constraint for lagostrophine divergence, is not strongly supported (e.g., Phillips et al. 2015). However, within the analysis of Prideaux and Warburton (2010) boot strap and jacknife support for this topology is approximately as strong as that for the sister relationship of Sthenurinae and Macropodinae recently bolstered by molecular data (Llamas et al. 2014).

Divergence of *Dorcopsulus* from *Dorcopsis* in the recovered time-tree predates molecular estimates for this split from Mitchell et al. (2014) by approximately 1.9 Myr. The older divergence we recover is primarily driven by the Early Pliocene age of the Hamilton LF taxon *Dorcopsis wintercookorum*. We note that there is actually scope for a somewhat older divergence because we use a conservative age of 5 Myr for the next most basally branching species of this clade, *Dorcopsoides fossilis*, from the presumed Late Miocene Alcoota LF (Megirian et al. 2010). The Early Pliocene age of the Hamilton LF seems relatively secure given the stratigraphic association of the dated basalt flow overlying the fossil deposit, and independent chronostratigraphic support from magnetic polarity measurements of the basalt and fossiliferous palaeosol (Piper et al. 2006).

Supplementary Tables

Table S3.1. Stratigraphic first appearance data for 34 species of fossil and extant macropodoid. Abbreviations: Australian land mammal Age (ALMA), local fauna (LF), first appearance datum (FAD). All ages are millions of years before present (Mya) or thousands of years ago (kya). † Denotes extinct taxon.

Tip Taxon	**Tip FAD (Myr)**	**Oldest lineage representative**	**Lineage FAD (Myr)**	**Chronostratigraphic remarks**	**Systematic remarks**	**Reference specimen(s)**
Hypsiprymnodon moschatus	0	*Hypsiprymnodon philcreaseri†*	17.72	*Hypsiprymnodon philcreaseri* and *H. karenblackae* are known from the Wipijirian Camel Sputum and Neville' Garden sites, Riversleigh World Heritage Area, NW Queensland (Bates et al. 2014). Two other species, *H. bartholomaii and H. dennisi* are known from sites whose age is either unknown or poorly constrained biochronologically and radiometrically. Woodhead et al. (2014) date the Neville's Garden site minimally to 17.85±0.13 Myr.	*Hypsiprymnodon philcreaseri* (and *H. karenblackae*) have been recovered in a polytomy with extant *H. moschatus*, other fossil hypsiprymnodontids and extinct balbarine kangaroos (Bates et al. 2014). Hypsiprymnodon is recovered as the sister group to Macropodidae (*sensu* Prideaux and Warburton, 2010) in most molecular and morphological	QMF24148 (Holotype of *H. philcreaseri*; Bates et al. 2014)

					analyses.	
Bettongia penicillata	0.487	*Bettongia moyesi†*	5.332	*Bettongia penicillata* is recognised in Unit 4, Cathedral Cave (Prideaux et al. 2007b), dated to 528±41 kyr. A much older congeneric, *Bettongia moyesi*, is recognised from the Camfeldian ALMA Two Trees and Henk's Hollow sites, Riversleigh World Heritage Area, NW Queensland (Flannery and Archer, 1987). Although biocorrelated to Camfeldian ALMA by Megirian et al. (2010) no unambiguous Camfeldian ALMA sites were dated by Woodhead et al. (2014). In lieu of a clear Miocene age we use the base of the Miocene as a minimum age constraint.	*B. moyesi* has been variously recovered in a polytomy with extant and putative fossil potoroines, and stem macropodids (Bates et al. 2014) or as a weakly supported stem macropodid or potoroine (Black et al. 2014). The monophyly of extant potoroines (e.g. *Bettongia* and *Potorous*), and its sister relationship to the crown clade including Lagostrohinae and Macropodinae, is supported by most recent molecular and morphological analyses.	QMF13007 (*B. moyesi* holotype; Flannery and Archer, 1987)
Potorous tridactylus	0.487	*Potorous tridactylus*	0.487	The oldest well-constrained age for *Potorous tridactylus* from Unit 4, Cathedral Cave (Prideaux et al. 2007b) which is dated to 528 ± 41 kyr. Due to an approximately 230 kyr	Molecular (Meredith et al. 2009; Phillips et al. 2013; Mitchell et al. 2014) and morphological (Prideaux and	NA

				hiatus between Unit 4 and younger Unit 3 we report the minimum age for Unit 4. Pledge (1992) recognised *Potorous* sp. from the Curramulka LF which on biostratigraphic grounds may be older than the Hamilton LF (Victoria) which has a minimum date of 4.46 ± 0.1 Myr (Flannery et al. 1992). However the Curramulka LF is possibly a mixed assemblage with no clear minimum age assignable (pers. comm. G. J. Prideaux).	Warburton, 2010; Kear et al. 2007) analyses consistently recover *Potorous* within a potoroine clade that is sister to other macropodids (sensu Prideaux and Warburton, 2010).	
Ngamaroo archeri†	24.0	*Ngamaroo archeri†*	24.0	*Ngamaroo archeri* is recognised from the late Oligocene Ngama Local Fauna (Kear et al. 2008). We report the age of the stratigraphically younger 'Treasure/Lungfish' LF (Megirian et al. 2010).	*Ngamaroo archeri* is recovered as a basal macropodid with modest statistical support by Prideaux and Warburton, (2010). In this analysis its position along the stem is supported by two unambiguous synapomorphies. Other analyses using different characters recover *N. archeri* in a	SAM P23626 (*N. archeri* holotype; Kear and Pledge, 2007)

					polytomy with Potoroinae and a clade including all other macropodids (Kear and Pledge, 2007).	
Bulungamaya delicata†	17.72	*Bulungamaya delicata†*	17.72	The oldest directly dated site containing *Bulungamaya delicata* is the Neville's Garden site which Woodhead et al. (2014) report a disequilibrium U-Pb age of 17.85 ± 0.13 Myr.	Travouillon et al. (2014) synonymised *Nowidgee matrix* with *B. delicata. Bulungamaya delicata* is generally recovered as a stem macropodid, basal to the divergence of the lagostrophine, sthenurinae and macropodine kangaroos (Prideaux and Warburton, 2010; Kear et al. 2007).	QMF 20011 (*B. delicata* paratype; Travouillon et al. 2014)
Lagostrophus fasciatus	0	*Lagostrophus* sp. cf. *fasciatus*	2.581	The fossil record of *Lagostrophus fasciatus* is poorly constrained. However *Lagostrophus* sp. cf. *fasciatus* is known from the Fisherman's Cliff LF (Marshall, 1973) which probably belongs to the upper part of the Gauss normal polarity (Rich et al. 1991). The base of the Gauss	Originally recovered as the sole living sthenurine by Flannery (1989). Molecular and morphological analyses now support *Lagostrophus fasciatus* as the only extant lagostrophine kangaroo (Westerman et al. 2008; Meredith	(P28891, P28892; referred specimens; Marshall, 1973)

				was subsequently moved to 2.581 Mya (Lourens et al. 2004).	et al. 2009; Prideaux and Warburton, 2010; Mitchell et al. 2014).	
Troposodon minor†	3.53	*Troposodon minor*†	3.53	Oldest well constrained occurrence of *Troposodon minor* is the Bluff Downs LF (Bartholamai 1978; Megirian et al. 2010). Radiometric dating implies a minimum age of 3.60±0.07 Myr (Mackness et al. 2000).	Prideaux and Warburton (2010) found strong statistical support and five unambiguous synapomorphies uniting *Troposodon minor* in a lagostrophine clade with extant *Lagostrophus fasciatus.*	QM F9046, QM F9047, QM 9048, QM 9049, QM 9050, QM 90501, QM 90502, QM 90503 (referred specimens of *Troposodon minor*; Bartholomai, 1978)
Ganguroo bilamina†	17.72	*Ganguroo bilamina*†	17.72	The oldest radiometrically dated site for which *Ganguroo bilamina* is known is the Neville's Garden site which is dated by Woodhead et al. (2014) to 17.85 ± 0.13 Myr.	*Ganguroo bilamina* is recovered as a stem macropodine in most morphological analyses (Prideaux and Warburton, 2010). Philips (2015) considers *G. bilamina* a robust minimum constraint for origin of crown clade Macropodidae to the exclusion of Potoroinae.	QMF24190, QMF19987, QMF23202 (*G. bilamina* paratypes from Neville's Garden site; Travouillon et al. 2014)
Wanburoo	5.332	*Wanburoo*	5.332	The Gag, Encore and Dome	Prideaux and	QM F20525 (*W. hilarus*

hilarus†		*hilarus*†		sites from which type material of *Wanburoo hilarus* are recognised (Cooke, 1999) have not been dated radiometrically. These sites were assigned to the Camfeldian ALMA by Megirian et al. (2010). Both the upper and lower boundary of the Camfeldian lack good goechrononological constraint (Megirian et al. 2010). We use the base of the Miocene as a minimum constraint.	Warburton (2010) recovered *Wanburoo hilarus* as a basal sthenurine underpinned by one unambiguous dental synapomorphy and good statistical support.	holotype; Cooke, 1999)
Hadronomas puckridgi†	5	*Hadronomas puckridgi*†	5	*Hadromoas puckridgi* is known from the late Miocene Alcoota LF (Murray, 1991). Megirian et al. (2010) estimate the Alcoota LF is ca. 6 Myr. Minimum age is constrained by diprotodontoid biocorrelation of the overlying Ongeva LF to the latest Miocene/early Pliocene Beaumaris LF from the Black Rock Sandstone (Murray et al. 1993; Piper et	Flannery (1989) recovered *Hadronomas puckridigii* as a basal macropodine. Subsequent analyses recovered *Hadronomas puckridgii* as a sthenurine (Murray 1991; Prideaux 2004; Kear et al. 2007; Prideaux and Warburton, 2010). Prideaux and	SGM 893 (*H. puckridgi* holotype; Murray, 1991)

				al. 2006).	Warburton (2010) identified three unambiguous synapomorphies and strong statistical support for this placement.	
Sthenurus andersoni†	1.10	*Sthenurus* sp. cf. *tindalei†*	3.596	*Sthenurus andersoni* is known from the ~3 Myr Chinchilla LF and Pleistocene Rackham's Roost Site (Prideaux, 2004). The latter is dated to a min. age of 1.21 ± 0.11 (Woodhead et al. 2014). However, *Sthenurus* sp. cf. *tindalei* is known from the Kanunka and Toolapinna LFs (Prideaux, 2004). Tedford et al (1992) correlate the Tirari Formation (and contained Kanunka and Toolapinna members) to the later part of the early Pliocene Gilbert chron; an estimated minimum age of 3.596 Myr (Lourens, et al. 2004). The minimum radiometric age for Rackham's Roost Site was used as a conservative age for the first appearance of	Prideaux and Warburton (2010) recovered *Sthenurus* (*andersoni*) as basal to a *Simosthenurus*–*Procoptodon* clade based on eight unambiguous synapomorphies, with very strong statistical support. Prideaux (2004) recovered the same broad topology, with *S. tindalei* as a derived member within a *Sthenurus* clade including *S. andersoni* as a basal member.	UCMP56928 (referred specimen of *Sthenurus* sp. cf. *tindalei* ; Tedford et al. 1992; Prideaux, 2004)

				Sthenurus andersoni.		
Simosthenurus occidentalis†	0.487	*Simosthenurus occidentalis†*	0.487	Oldest well dated occurrence of *Simosthenurus occidentalis* is Unit 4, Cathedral Cave (Prideaux et al. 2007b). As for *Potorous tridactylus* we report the minimum age of Unit 4.	*Simosthenurus occidentalis* was recovered with very strong support as a derived sthenurine, sister to a *Procoptodon* clade (Prideaux, 2004; Prideaux and Warburton, 2010). Prideaux (2004) recovered the genus *Simosthenurus* as paraphyletic.	NA
Procoptodon goliah†	0.257	*Procoptodon goliah†*	0.257	*Procoptodon goliah* is recognised in Unit 3, Cathedral Cave (Prideaux et al. 2007b), but we use the mean age of the overlying Unit 2b (257 ±21 kyr).	Multiple unambiguous synapomorphies and very strong statistical support suggest *P. goliah* is a derived sthenurine (Prideaux, 2004; Prideaux and Warburton, 2010).	NA
Setonix brachyurus	0.135	*Setonix brachyurus*	0.135	Oldest well-dated occurrence of *Setonix brachyurus* is Unit B (151 ±7 kyr), Tight Entrance Cave. Formation is capped by a calcite flowstone dated radiometrically to 137 ±2 Kyr (Prideaux et al. 2010).	Prideaux and Warburton (2010) find modest support for *Setonix brachyurus* as a basal macropodine but its branching position relative to other macropodines is poorly	NA

					constrained. Recent molecular studies recover a more derived position as an outgroup to (Meredith et al. 2009), or within (Mitchell et al. 2014), a *Macropus*–*Lagorchestes*–*Onychogalea* clade.	
Petrogale brachyotis	0	*Petrogale penicillata*	0.500	*Petrogale penicillata* is recognised from the QML1284a site, Mt Etna Caves which has a minimum age of 0.5 Myr (Hocknull et al. 2007)	Most recent morphological and molecular analyses recover *Petrogale* as sister to a tree kangaroo clade, within Dendrolagini (e.g., Meredith et al. 2009; Prideaux and Warburton, 2010; Mitchell et al. 2014). Notably the supertree analysis of Cardillo et al. (2004) is an exception which did not recover Dendrolagini.	NA
Bohra illuminata†	0.016	*Bohra wilkinsonorum†*	0.016	*Bohra illuminata* is known from surface sediments in Last Tree Cave, but the	Prideaux and Warburton (2010) recover *Bohra* as sister	WAM 03.5.10 (*Bohra illuminata* holotype)

				minimum age is only 20 ±4 kyr (Prideaux, 2007a; Prideaux and Warburton, 2008). *Bohra wilkinsonorum* is known from the probable late Pliocene Chinchilla LF of southeastern Queensland (Megirian et al. 2010) but age of these deposits is yet to be well constrained.	to *Dendrolagus* with very strong support.	
Dendrolagus bennettianus	0	*Dendrolagus* sp.	0.500	Flannery et al. (1992) referred fragmentary premolar material (NMV P157483; P157481 and P160154) to cf. *Dendrolagus* sp. from the 4.46 ± 0.1 Myr Hamilton LF. A more secure date is *Dendrolagus* sp. from QML1284a site, Mt Etna Caves (Hocknull et al. 2007)	*Dendrolagus* is recovered in most morphological and molecular analyses within Dendrolagini, sister to Macropodini (Phillips et al. 2013). The supertree analysis of Cardillo et al. (2004) did not unite *Dendrolagus* and *Petrogale* in a Dendrolagini clade.	NA
Dendrolagus matschiei	0	*Dendrolagus* sp.	0.500	As for *Dendrolagus bennettianus*.	See comments for *Dendrolagus bennettianus*.	NA
Protemnodon anak†	0.0877	*Protemnodon devisi†*	3.596	*Protemnodon anak* is reported from the Darling Downs (Price and Sobbe, 2005). There is a direct date	Prideaux and Warburton (2010) find *Protemnodon anak* forms a clade with	UCMP 56894 (referred left maxilla of *Protemnodon anak*; Tedford et al. 1992)

				of a *P. anak* tooth from QML1396 to 88.4 ±0.7 kyr (Price et al. 2011). The oldest well-dated occurrence of *Protemnodon* is *P. devisi* from the Kanunka LF (Tedford et al. 1992). See *Sthenurus andersoni* for age justification.	*Congruus congruus* which is sister to the clade including extant members of the Macropododini. This clade has modest to strong support but its position with Macropodinae is not well resolved.	
Congruus congruus†	0.0117	*Congruus kitcheneri†*	0.135	*Congruus congruus* is present in the main fossil chamber of Victoria Fossil Cave, Naracoorte (McNamara, 1994) but its age within this deposit is poorly constrained. Since *C. congruus* is known from Pleistocene deposits we use the age of the Pleistocene–Holocene boundary as a conservative estimate for its first occurrence. However the congeneric *Congruus kitcheneri* is known from unit B Tight Entrance Cave (Ayliffe et al. 2008) which has a minimum age of 137 ±2 kyr (Prideaux et al. 2010).	See comments for *Protemnodon anak*.	SAM P33475 (*Congruus congruus* holotype)

Wallabia bicolor	0.487	*Wallabia bicolor*	0.487	*Wallabia bicolor* is recognised in Unit 4, Cathedral Cave (Prideaux et al. 2007b). As for *Potorous tridactylus* we use the minimum age for this layer.	The position of *Wallabia bicolor* has been phylogenetically labile; molecular studies support a close relationship to *Macropus* while morphological studies recover *W. bicolor* as basal to a *Lagorchestes-Onychogalea-Macropus* clade but without clear synapomorphies (Phillips et al. 2013). Most recent molecular studies recover *Wallabia* as sister (Phillips et al. 2013; Mitchell et al. 2014), or within, the *Macropus* clade (Meredith et al. 2009).	NA
Lagorchestes conspicillatus	0	*Lagorchestes* sp. indet.	3.596	*Lagorchestes conspicillatus* is recognised from Lake Menindee (Tedford, 1967) but the chronostratigraphy of this Pleistocene site is not secure. We used the oldest	Most molecular studies recover *Lagorchestes* as sister to a *Macropus–Wallabia* clade (Meredith et al. 2009; Phillips et al.	UCMP 60809 and UCMP 56922 (referred right ramus and dentary fragment of two *Lagorchestes* sp.; Tedford et al. 1992)

				first occurrence of the genus *Lagorchestes* which is based on two unnamed species recognised by Tedford et al. (1992) from the Kanunka LF.	2013; Mitchell et al. 2014). Prideaux and Warburton (2010) found *Lagorchestes* nested with *Onychogalea* and *Macropus* to the exclusion of *Wallabia*. However, there was <50 % bootstrap and jack knife support for this topology and this clade was defined by homoplastic synapomorphies.	
Lagorchestes hirsutus	0	*Lagorchestes* sp. indet.	3.596	*Lagorchestes hirsutus* is known from a range of Pleistocene sites (see Megirian et al. 2010) for which secure dates are lacking. As for *L. conspicillatus* we use the oldest first occurrence of the genus *Lagorchestes* which is from the Kanunka LF (Tedford et al. 1992).	See remarks for *Lagorchestes conspicillatus*.	UCMP 60809 and UCMP 56922 (referred right ramus and dentary fragment of two *Lagorchestes* sp.; Tedford et al. 1992)
Prionotemnus palankarinnicus†	3.596	*Prionotemnus palankarinnicus†*	3.596	Earliest well constrained occurrence is Lake Palankarinna LF (Tedford et al. 1992; Megirian et al.	Prideaux and Warburton (2010) unite *Prionotemnus* within the	UCMP 44381 (*Prionotemnus palankarinnicus* holotype; Stirton, 1955)

				2010). The age of the Palankarinna LF is not well resolved with respect to the superpositionally overlying Kanunka and Toolapinnna LFs (Tedford et al. 1992) so we report the minimum age of the overlying Tirari Formation.	Macropodini on the basis of two unambiguous dental synapomorphies with poor statistical support.	
Kurrabi mahoneyi†	3.03	*Kurrabi pelchenorum* †	4.36	*Kurrabi mahoneyi* is known from the Bow LF (Flannery and Archer 1984). *Kurrabi pelchenorum* is known from the better chronostratigraphically constrained Hamilton LF (Flannery et al. 1992) which has a minimum radioisotopic age of 4.35 ± 0.1 Myr (Turnbull *et al.* 1965). The age of this site was subsequently recalibrated as 4.46 ± 0.1 Myr by Rich *et al.* (1991). As *Kurrabi mahoneyi* is derived from the Bow LF which is correlated with the Tirarian ALMA the maximum age of the younger Naracoortean ALMA was used to constrain its first	Prideaux and Warburton (2010) recovered *Kurrabi* as a derived member of the Macropodini based on one unambiguous dental synapomorphy with weak statistical support. Flannery (1989) recovered a similar topology except *Kurrabi* was united with *Macropus* (and *Wallabia*) to the exclusion of *Onychogalea*.	NMV P158425(*Kurrabi pelchenorum* holotype; Flannery et al. 1992)

				occurrence (3.03 Myr).		
Macropus eugenii	0	*Macropus* sp. (*Notomacropus*)	0.781	*Macropus eugenii* is present in the Thylacoleo Caves (Prideaux et al. 2007a) but the minimum age is not well defined. However the earliest members of the *Notomacropus* clade to which *M. eugenii* belongs (Dawson and Flannery, 1985; Philips et al. 2013) may be represented by a single molar talonid from the >4.46 ± 0.1 Myr Hamilton LF (Rich et al. 1991). Piper (2007) reports three species of *Notomacropus* from the Nelson Bay LF which corresponds to the upper Matuyama chron (1.77-0.781 Myr; Piper et al. 2006).	See remarks for *Macropus fuliginosus*.	NA
Macropus robustus	0	NA	0	*Macropus robustus* is known from unit 5, Madura Cave, Nullarbor (Lundelius and Turnbull 1989; Megirian et al. 2010). However, assigned radiocarbon ages for this unit may be unreliable (Roberts et al. 2001). The oldest well constrained representatives	See remarks for *Macropus fuliginosus*.	NA

				of the subgenus to which *M. robustus* belongs, *Osphranter* (e.g. *Macropus pavana*), are from the Bluff Downs LF at 3.60±0.07 Myr (Mackness et al. 2000). However, we do not apply these ages because some analyses recover *Osphranter* as polyphyletic (e.g. Prideaux et al. 2010) and relationships of putative fossil *Osphranter* are unknown or poorly supported.		
Macropus fuliginosus	0.135	*Macropus fuliginosus*	0.135	Oldest well dated occurrence of *Macropus fuliginosus* is Unit B, Tight Entrance Cave (Ayliffe et al. 2008) which is older than 137 ±2 kyr (Prideaux et al. 2010)	The branching order of *Macropus* species differs between molecular and morphological studies (Phillips et al. 2013). Amongst extant representatives, most morphological and molecular studies recover the three distinct subgenera (*Macropus*, *Notomacropus* *Osphranter*) proposed by Dawson and	NA

					Flannery (1985) as discrete subclades within a broader *Macropus* clade. Prideaux and Warburton (2010) recovered *Macropus fuliginosus* in a clade with extinct *M. pavana* with modest statistical support, underpinned by one unambiguous dental synapomorphy.	
Macropus pavana†	3.53	*Macropus pavana†*	3.53	Allingham Formation, Bluff Downs LF, northern Queensland (Bartholomai 1978). Minimum age constraint as for *Troposodon minor.*	Dawson and Flannery (1985) considered *Macropus pavana* as member of the subgenus *Osphranter*. Prideaux and Warburton (2010) found *M. pavana* as a sister to *M* (*Macropus*). *fuliginosus* rather than *M*. (*Osphranter*) *robustus* which implies *Osphranter* is polyphyletic.	QM F9108 (*Macropus pavana* holotype)
Onychogalea unguifera	0.487	*Onychogalea unguifera*	0.487	Oldest well dated occurrence is Unit 4, Cathedral Cave (Prideaux et al. 2007b). As for	Prideaux and Warburton (2010) found *Onychogalea*	NA

				P. tridactylus we use the minimum age for this layer.	*unguifera* united in a clade with *Baringa nelsonensis* underpinned by three unambiguous synapomorphies. This clade was in turn sister to *Macropus*.	
Baringa nelsonensis†	0.781	*Baringa nelsonensis*†	0.781	We use the minimum age of *Baringa nelsonensis* from the Nelson Bay LF (Flannery and Hahn, 1984), which correlates with the upper part of the Matuyama chron (1.77-0.781 Myr; Piper et al. 2006).	See above remarks for *Onychogalea unguifera*.	NMV P173608 (*Baringa nelsonensis* holotype)
Dorcopsoides fossilis†	5	*Dorcopsoides fossilis*†	5	Oldest recognised occurrence of *Dorcopsoides fossilis* is the Alcoota LF (Woodburne, 1967). Minimum age inferred as per *Hadronomas puckridgi*.	Prideaux and Warburton (2010) found modest support for *Dorcopsoides fossilis* as sister to *Dorcopsis*–*Dorcopsulus*, including one unambiguous synapomorphy.	CPC 6750 (*D. fossilis* holotype)

Dorcopsis veterum	0	*Dorcopsis wintercookorum*†	4.36	*Dorcopsis veterum* has no fossil record we are aware of. However *Dorcopsis wintercookorum* is known from the Hamilton LF (Flannery et al. 1992). The Hamilton LF has a minimum radioisotopic age of 4.35 ± 0.1 Myr (Turnbull *et al.* 1965), which was subsequently recalibrated to 4.46 ± 0.1 Myr (Rich *et al.* 1991).	Molecular and morphological analyses find *D. vanheurni* and *D. veterum* form a clade within Macropodinae which may be sister to all other macropodines (e.g. Flannery, 1989; Prideaux and Warburton, 2010; Mitchell et al. 2014) or to a *Petrogale–Thylogale–Dendrolagus* clade (e.g., Meredith et al. 2009).	NMV P158453 (*Dorcopsis wintercookorum* holotype)
Dorcopsulus vanheurni	0	*Dorcopsulus vanheurni*	0	*Dorcopsulus vanheurni* has no fossil record as far as we are aware. The genus *Dorcopsulus* also has no clearly recognised Australian fossil record (Megirian et al. 2010).	See phylogenetic remarks for *Dorcopsis veterum*.	NA

Table S3.2. Divergence estimates derived from Mitchell et al. (2014). All ages are millions of years before present (Myr).

Clade	Mean clade age	Node Number
Hypsiprymnodon + all other macropodoids	29.37	1
Lagostrophinae + Macropodinae + Potoroinae	16.85	2
Potorous + *Bettongia*	13.47	3
Lagostrophinae + Macropodinae	14.72	6
Macropodinae	8.32	14
Onychogalea + *Setonix* + *Lagorchestes* + *Macropus* + *Wallabia*	7.19	15
Dendrolagus + *Petrogale*	6.18	17
Lagorchestes + *Macropus* +*Wallabia*	6.40	22
Extant *Macropus*	4.49	28
Dorcopsulus+ *Dorcopsis*	2.78	33

Table S3.3. Estimated divergence dates for key clades based on stratigraphic first appearances datums and molecular constraints (Table S2). All ages are millions of years before present (Myr).

Estimated divergence of key clades	clade age (Myr)
Macropodoidae	29.37
Potoroinae + (Lagostrophinae + (Macropodinae + Sthenurinae))	27.58
Potorous + *Bettongia*	13.47
Ngamaroo + all more derived macropodids	25.79
Bulungamaya + all more derived macropodids	22.43
Lagostrophinae +all more derived macropodids	20.86
Troposodon + *Lagostrophus*	10.63
Ganguroo + (Sthenurinae + Macropodinae)	19.29
Sthenurinae + Macropodinae	13.02
Wanburoo + all more derived sthenurines	6.83
Procoptodon + *Simosthenurus*	2.04
Crown Macropodinae	8.32
Setonix + all more derived Macropodinae	7.19
Petrogale + (*Bohra* + *Dendrolagus*)	6.18
Dendrolagini + all more derived Macropodinae	6.93
Wallabia + (*Lagorchestes* + (*Prionotemnus* + (*Kurrabi* + (*Macropus* + (*Onychogalae* + *Baringa*)))))	6.40
Macropus	4.49
Macropus robustus + (*Macropus fuliginosus* + *Macropus pavana*)	4.17
Macropus fuliginosus + *Macropus pavana*	3.85
Dorcopsoides + (*Dorcopsulus* + *Dorcopsis*)	6.66
Dorcopsulus+ *Dorcopsis*	4.68

Table S3.4. Estimated ancestral states and associated 95 % confidence intervals for posterior molar proportions at 13 internal nodes within Macropodoidea. Node numbers, denoted by integers in brackets, correspond to those labelled on Fig. S1.

Node	M_3/M_2	C.I. Min. (2.5%)	C.I. Max. (97.5%)	M_4/M_2	C.I. Min. (2.5%)	C.I. Max. (97.5%)
Macropodoidea (1)	1.04	0.85	1.23	0.76	0.58	0.94
Macropodidae (2)	1.06	0.91	1.21	0.77	0.63	0.91
Potorous + *Bettongia* (3)	0.96	0.76	1.17	0.62	0.43	0.82
Ngamaroo + all more derived macropodids (4)	1.09	0.98	1.19	0.79	0.69	0.89
Bulungamaya + all more derived macropodids (5)	1.04	0.92	1.16	0.89	0.78	1.00
Lagostrophus + all more derived macropodids (6)	1.03	0.91	1.15	0.93	0.81	1.04
Ganguroo + all more derived macropodids (7)	1.01	0.92	1.11	0.95	0.86	1.05
Macropodinae + Sthenurinae (8)	1.12	0.96	1.28	1.09	0.94	1.25
Procoptodon + *Simosthenurus* (9)	1.20	1.12	1.29	1.07	0.98	1.15
Macropodinni + *Dorcopsulus* (10)	1.17	1.04	1.31	1.22	1.09	1.35
Dendrolagus + *Macropus* + *Onychogalea* (11)	1.18	1.05	1.3	1.23	1.11	1.35
Macropus + *Onychogalea* (12)	1.21	1.11	1.32	1.27	1.16	1.37
Macropus fuliginosus + *Macropus robustus* (13)	1.22	1.11	1.32	1.28	1.18	1.38

Table S3.5. Anterior sequence (M_{1-3}) lower molar area data for 32 species of fossil and living macropodoid. † Denotes extinct taxa. PHC (posthypocristid) state is coded as 1 (present) and 0 absent).

Species	M_1 Area (mm^2)	M_1 sd (mm^2)	M_2 Area (mm^2)	M_2 sd (mm^2)	M_3 Area (mm^2)	M_3 sd (mm^2)	M_1+ M_2+ M_3 Area (mm^2)	M_1+ M_2+ M_3 sd (mm^2)	*n*	PHC state
Aepyprymnus rufescens	21.16	0.43	3	27.48	1.24	3	30.37	2.15	3	1
Bettongia lesueur	11.95	1.16	3	14.6	2.23	3	11.47	2.17	3	1
Bettongia penicillata	15.95	2.06	4	17.83	2.23	4	15.39	2.18	4	1
Bulungamaya delicata†	11.21	0.93	3	12.69	0.51	3	12.05	1.28	3	1
Dendrolagus bennettianus	20.33	NA	1	25.18	NA	1	27.22	NA	1	0
Dendrolagus lumholtzi	21.01	3.36	9	24.21	4.2	9	28.89	4.52	9	0
Dendrolagus ursinus	22.36	1.1	2	28.41	2.93	2	31.33	4.58	2	0
Dorcopsulus vanheurni	9.78	NA	1	11.64	NA	1	14.26	NA	1	0
Ganguroo bilamina†	10.95	0.11	2	11.63	0.44	2	12.35	0.12	2	0
Hypsiprymnodon moschatus	7.33	NA	1	6.93	NA	1	5.23	NA	1	1
Lagostrophus fasciatus	14.06	NA	1	17.19	NA	1	20.1	NA	1	0
Macropus fuliginosus	61.4	10.67	4	89.06	12.62	4	107.97	12.63	4	1
Macropus parma	17.89	0.76	4	25.38	1.45	4	31.26	1.55	4	0
Macropus robustus	56.43	3.06	4	80.57	7.01	4	93.42	14.06	4	1
Macropus rufus	58.32	3.37	4	82.65	9.27	4	110.61	8.84	4	1
Ngamaroo archeri†	13.36	NA	1	18.27	NA	1	20.94	NA	1	1
Onychogalea fraenata	15.09	NA	1	18.22	NA	1	24.33	NA	1	7

Onychogalea unguifera	19.8	1.45	5	29.46	3.58	5	38.58	2.52	5	0
Petrogale godmani	17.78	3.2	3	24.81	4.19	3	32.53	5.66	3	0
Petrogale inornata	16.33	0.19	2	23.97	1.48	2	33.07	2.76	2	0
Petrogale penicillata	18.07	NA	1	27.32	NA	1	32.01	NA	1	0
Potorous tridactylus	12.28	NA	1	15.2	NA	1	14.35	NA	1	1
Procoptodon browneorum†	112.96	18.96	2	134.02	24.92	2	155.49	44.21	2	0
Procoptodon gilli†	84.45	6.1	12	100.21	8.45	12	110.38	8.37	12	0
Procoptodon goliah†	252.88	29.61	4	362.59	48.44	4	454.01	53.79	4	1
Procoptodon rapha†	226.23	6.83	2	306.86	13.23	2	375.41	31.05	2	1
Simosthenurus occidentalis†	128.45	21.9	22	158.83	27.86	22	180.18	33.63	22	0
Simosthenurus pales†	159.84	1.05	2	185.23	9.48	2	212.59	3.12	2	0
Sthenurus andersoni†	69.49	NA	1	85.46	NA	1	102.84	NA	1	0
Thylogale stigmatica	17.29	NA	1	24.18	NA	1	29.38	NA	1	0
Wakiewakie lawsoni†	9.43	1.86	2	11.3	0.97	2	13.84	0.88	2	1

Table S3.6. Posterior lower molar sequence (M_{2-4}) area data for 31 species of fossil and living macropodoid. † Denotes extinct taxa. ‡ Supernumerary molar identities are recoded to conform with typical posterior molar sequence identities (e.g. $M_5 = M_4$, $M_4 = M_3$, $M_3 = M_2$). PHC (posthypocristid) state is coded as 1 (present) and 0 (absent).

Species	M_2 Area (mm^2)	M_2 sd (mm^2)	M_3 Area (mm^2)	M_3 sd (mm^2)	M_4 Area (mm^2)	M_4 sd (mm^2)	M_2+ M_3+ M_4 Area (mm^2)	M_2+ M_3+ M_4 sd (mm^2)	*n*	PHC state
Aepyprymnus rufescens	27.48	1.24	30.37	2.15	25.29	2.35	83.14	4.28	3	1
Bettongia lesueur	13.95	1.09	10.71	0.45	4.09	1.74	28.75	2.1	3	1
Bettongia penicillata	18.57	2.04	15.72	2.55	7.96	1.84	42.24	5.75	3	1
Bulungamaya delicata†	12.32	0.85	12.09	1.05	11.24	1.59	35.65	2.83	4	1
Dendrolagus bennettianus	25.18	NA	27.22	NA	30.32	NA	82.71	NA	1	0
Dendrolagus lumholtzi	24.41	4.78	28.82	5.06	29.36	3.95	82.58	13.41	7	0
Dendrolagus ursinus	28.41	2.93	31.33	4.58	31.88	0.76	91.62	8.27	2	0
Dorcopsulus vanheurni	13.25	NA	16.24	NA	17.55	NA	47.04	NA	1	0
Ganguroo bilamina†	11.19	1.26	10.78	0.57	10.46	0.98	32.44	2.37	6	0
cf. *Gumardee pascuali*†	25.25	NA	27.23	NA	23.84	NA	76.32	NA	1	1
Hypsiprymnodon moschatus	7.49	0.79	5.74	0.71	5.13	0.04	18.36	1.55	2	1
Lagostrophus fasciatus	17.38	NA	20.67	NA	19.12	NA	57.16	NA	1	0
SAM M2217 (*Macropus rufus*)	105.33	NA	150.17	NA	141.65	NA	397.15	NA	1	1
Macropus fuliginosus	92.24	7.05	109.3	6.09	116.77	8.97	318.31	13.66	5	1
Macropus parma	22.05	1.78	28.61	1.53	30.7	0.58	81.37	2.72	2	0

Macropus parryi	35.61	NA	41.44	NA	51.64	NA	128.69	NA	1	0
Macropus robustus	84.44	16.11	106.48	22.05	114.45	18.11	305.37	55.3	6	1
Macropus rufus	72.02	7.36	103.44	14.87	112.68	13.06	288.14	34.19	4	1
Ngamaroo archeri†	18.27	NA	20.94	NA	13.97	NA	53.18	NA	1	1
Onychogalea fraenata	18.22	NA	24.33	NA	29.32	NA	71.87	NA	1	0
Onychogalea unguifera	31.33	3.96	39.68	0.87	39.21	3.91	110.22	8.74	2	0
Petrogale godmani	24.53	3.55	32.43	5.24	34.61	7.46	91.57	16.24	3	0
Petrogale inornata	25.44	NA	30.77	NA	35.8	NA	92.02	NA	1	0
Petrogale penicillata	22.71	1.34	28.46	2.99	32.61	1.32	83.78	3.01	2	0
Potorous tridactylus	13.66	4.63	13.64	5.42	9.77	5.86	37.08	15.91	2	1
Procoptodon browneorum†	116.4	NA	124.23	NA	116.23	NA	356.86	NA	1	0
Procoptodon gilli†	100.23	8.07	110.24	8.37	102.34	7.27	312.8	21.1	11	0
Procoptodon goliah†	303.54	NA	395.05	NA	337.54	NA	1036.13	NA	1	1
‘Mean’ *Procoptodon goliah*†	372.53	NA	457.51	NA	360.44	NA	1190.47	NA	NA	1
Procoptodon rapha†	303.66	10.87	353.96	43.15	332.03	28.42	989.64	79.47	3	1
Simosthenurus occidentalis†	151.38	26.58	170.43	32.63	154.4	30.37	476.21	86.88	18	0
Simosthenurus pales†	185.23	9.48	212.59	3.12	190.78	9.59	588.61	22.19	2	0
Thylogale stigmatica	24.18	NA	29.38	NA	28.11	NA	81.67	NA	1	0

Table S3.7. Anterior sequence molar ratios for 31 species of fossil and extant macropodoids. † Denotes extinct taxa.

Species	*n*	Mean M_2/M_1	Stand. dev.	Mean M_3/M_1	Stand. dev.
Aepyprymnus rufescens	3	1.30	0.06	1.43	0.08
Bettongia lesueur	3	1.22	0.07	0.95	0.10
Bettongia penicillata	4	1.12	0.07	0.97	0.08
Bulungamaya delicata†	3	1.14	0.09	1.07	0.03
Dendrolagus bennettianus	1	1.24	NA	1.34	NA
Dendrolagus lumholtzi	9	1.15	0.07	1.38	0.07
Dendrolagus ursinus	2	1.28	0.19	1.41	0.27
Dorcopsulus vanheurni	1	1.19	NA	1.46	NA
Ganguroo bilamina†	2	1.06	0.03	1.13	0.00
Hypsiprymnodon moschatus	1	0.95	NA	0.71	NA
Lagostrophus fasciatus	1	1.22	NA	1.43	NA
Macropus fuliginosus	4	1.46	0.13	1.77	0.12
Macropus parma	4	1.42	0.05	1.75	0.09
Macropus robustus	4	1.43	0.11	1.66	0.24
Macropus rufus	4	1.41	0.10	1.90	0.15
Ngamaroo archeri†	1	1.37	NA	1.57	NA
Onychogalea fraenata	1	1.21	NA	1.61	NA
Onychogalea unguifera	5	1.49	0.13	1.95	0.06
Petrogale godmani	3	1.40	0.05	1.83	0.05
Petrogale inornata	2	1.47	0.07	2.02	0.15
Petrogale penicillata	1	1.51	NA	1.77	NA
Potorous tridactylus	1	1.24	NA	1.17	NA
Procoptodon browneorum†	2	1.18	0.02	1.36	0.16
Procoptodon gilli†	12	1.19	0.04	1.31	0.05
Procoptodon goliah†	4	1.43	0.06	1.80	0.05
Procoptodon rapha†	2	1.36	0.02	1.66	0.09

Simosthenurus occidentalis†	22	1.24	0.05	1.40	0.10
Simosthenurus pales†	2	1.16	0.05	1.33	0.01
Sthenurus andersoni†	1	1.23	NA	1.48	NA
Thylogale stigmatica	1	1.40	NA	1.70	NA
Wakiewakie lawsoni†	2	1.21	0.14	1.49	0.20

Table S3.8. Posterior sequence molar ratios for fossil and extant macropodoids. † Denotes extinct taxa.

Species	*n*	Mean M_3/M_2	Stand. dev.	Mean M_4/M_2	Stand. dev.
Aepyprymnus rufescens	3	1.11	0.06	0.92	0.06
Bettongia lesueur	3	0.77	0.05	0.30	0.14
Bettongia penicillata	3	0.84	0.05	0.43	0.10
Bulungamaya delicata†	4	0.99	0.11	0.91	0.13
Dendrolagus bennettianus	1	1.08	NA	1.20	NA
Dendrolagus lumholtzi	7	1.18	0.05	1.22	0.11
Dendrolagus ursinus	2	1.10	0.05	1.13	0.09
Dorcopsulus vanheurni	1	1.23	NA	1.33	NA
Ganguroo bilamina†	6	0.97	0.09	0.94	0.08
cf. *Gumardee pascuali*†	1	1.08	NA	0.94	NA
Hypsiprymnodon moschatus	2	0.77	0.01	0.69	0.07
Lagostrophus fasciatus	1	1.19	NA	1.10	NA
SAM M2217 (*Macropus rufus*)	1	1.43	NA	1.34	NA
Macropus fuliginosus	5	1.19	0.05	1.27	0.16
Macropus parma	2	1.30	0.04	1.40	0.14
Macropus parryi	1	1.16	NA	1.45	NA
Macropus robustus	6	1.26	0.07	1.37	0.10
Macropus rufus	4	1.43	0.11	1.57	0.12
Ngamaroo archeri†	1	1.15	NA	0.76	NA
Onychogalea fraenata	1	1.34	NA	1.61	NA
Onychogalea unguifera	2	1.27	0.13	1.25	0.03
Petrogale godmani	3	1.32	0.02	1.40	0.10
Petrogale inornata	1	1.21	NA	1.41	NA
Petrogale penicillata	2	1.25	0.06	1.44	0.14
Potorous tridactylus	2	0.99	0.06	0.68	0.20
Procoptodon browneorum†	1	1.07	NA	1.00	NA

Procoptodon gilli†	11	1.10	0.07	1.02	0.08
Procoptodon goliah†	1	1.30	NA	1.11	NA
‘Mean’ *Procoptodon goliah*†	NA	1.23	NA	0.97	NA
Procoptodon rapha†	3	1.16	0.11	1.09	0.08
Simosthenurus occidentalis†	18	1.13	0.10	1.02	0.12
Simosthenurus pales†	2	1.15	0.04	1.03	0.00
Thylogale stigmatica	1	1.22	NA	1.16	NA

Table S3.9. Trigonid–talonid ratios for fossil and extant macropodoids. † Denotes extinct taxa.

Species	PHC state	mean trigonid/ talonid ratio (M_1	Stand. dev. (M_1)	n (M_1)	mean trigonid/ talonid ratio (M_2)	Stand. dev. (M_2)	n (M_2)	mean trigonid/ talonid ratio (M_3)	Stand. dev. (M_3)	n (M_3)	mean trigonid/ talonid ratio (M_4)	Stand. dev. (M_4)	n (M_4)
Aepyprymnus rufescens	1	0.88	0.03	3	0.96	0.03	3	1.01	0.03	3	1.13	0.05	3
Bettongia lesueur	1	0.87	0.04	4	1.05	0.03	5	1.14	0.09	6	1.46	0.26	4
Bettongia penicillata	1	0.94	0.03	4	1.08	0.07	4	1.17	0.08	4	1.37	0.11	3
Bulungamaya delicata†	1	0.94	0.05	3	1.02	0.06	4	1.04	0.05	4	1.13	0.09	4
Dendrolagus bennettianus	0	1.02	NA	1	0.99	NA	1	1.08	NA	1	1.11	NA	1
Dendrolagus lumholtzi	0	1.05	0.04	9	1.03	0.02	9	1.04	0.03	9	1.10	0.05	7
Dendrolagus ursinus	0	0.97	0.02	2	1.02	0.08	2	0.99	0.03	2	1.04	0.06	2
Dorcopsulus vanheurni	0	1.00	NA	1	1.02	0.02	2	1.06	0.04	2	1.08	NA	1
Ganguroo bilamina†	0	0.96	0.00	2	0.97	0.06	8	1.04	0.05	8	1.08	0.08	6
Gumardee pascuali†	1	NA	NA	NA	0.98	NA	1	1.01	NA	1	1.26	NA	1
Hypsiprymnodon moschatus	1	0.95	NA	1	1.08	0.05	2	1.06	0.01	2	1.15	0.03	2
Lagostrophus fasciatus	0	0.93	NA	1	1.02	0.06	2	1.04	0.01	2	1.13	0.01	2
SAM M2217 (*Macropus rufus*)	1	NA	NA	NA	0.97	NA	1	1.01	NA	1	1.11	NA	1
Macropus	1	0.94	0.03	5	0.99	0.04	9	1.04	0.04	10	1.07	0.03	6

fuliginosus†													
Macropus parma	0	0.91	0.01	4	1.00	0.02	5	1.05	0.02	5	1.13	0.02	2
Macropus parryi	0	NA	NA	NA	0.93	NA	1	0.96	NA	1	0.99	NA	1
Macropus robustus	1	0.93	0.03	4	0.97	0.03	10	1.01	0.06	10	1.05	0.07	6
Macropus rufus	1	0.92	0.02	4	0.93	0.05	7	0.94	0.05	7	0.99	0.05	4
Ngamaroo archeri†	1	0.89	NA	1	0.98	NA	1	1.02	NA	1	1.15	NA	1
Onychogalea fraenata	0	0.90	NA	1	1.01	NA	1	1.01	NA	1	1.03	NA	1
Onychogalea unguifera	0	0.93	0.02	5	0.95	0.04	5	1.01	0.04	5	1.06	0.06	2
Petrogale godmani	0	0.91	0.02	3	0.98	0.03	5	1.02	0.02	5	1.03	0.12	3
Petrogale inornata	0	0.89	0.01	2	0.93	0.03	3	1.04	0.03	3	1.03	NA	1
Petrogale penicillata	0	0.85	NA	1	0.93	0.03	3	0.98	0.06	3	1.01	0.07	2
Potorous tridactylus	1	0.87	0.03	2	0.94	0.04	5	1.06	0.05	5	1.26	0.08	4
Procoptodon browneorum†	0	0.99	0.00	2	1.00	0.01	2	1.00	0.01	2	1.07	NA	1
Procoptodon gilli†	0	1.01	0.02	12	1.03	0.05	13	1.02	0.03	13	1.12	0.03	11
Procoptodon goliah†	1	0.96	0.02	12	1.00	0.04	12	1.04	0.04	8	1.09	0.02	3
Procoptodon rapha†	1	0.96	0.03	3	1.01	0.03	4	1.03	0.02	3	1.04	0.04	4
Simosthenurus occidentalis†	0	0.98	0.02	23	0.99	0.02	26	1.01	0.03	27	1.09	0.04	19
Simosthenurus pales†	0	0.96	0.03	2	0.97	0.03	2	0.98	0.04	2	1.08	0.04	2
Sthenurus	0	0.98	0.02	2	0.99	NA	1	1.05	0.03	2	1.11	NA	1

andersoni†													
Thylogale stigmatica	0	0.99	NA	1	0.95	NA	1	1.02	NA	1	1.06	NA	1
Thylogale thetis	0	0.90	NA	1	0.93	0.04	2	NA	NA	NA	NA	NA	NA
Wakiewakie lawsoni†	1	0.94	0.03	2	0.95	0.06	2	0.98	0.04	2	NA	NA	NA

Table S3.10. Distribution of the posthypocristid in the genus *Macropus*. † Denotes extinct taxa.

	Genus	Subgenus	Species	Status	PHC code
1	Macropus	*Macropus*	*fuliginous*	Extant	1
2	Macropus	*Macropus*	*giganteus*	Extant	1
3	Macropus	*Macropus*	*ferragus*†	Fossil	1
4	Macropus	*Macropus*	*mundjabus*†	Fossil	1
5	Macropus	*Macropus*	*pan*†	Fossil	1
6	Macropus	*Macropus*	*pearsoni*†	Fossil	1
7	Macropus	*Notomacropus*	*agilis*	Extant	0
8	Macropus	*Notomacropus*	*dorsalis*	Extant	0
9	Macropus	*Notomacropus*	*eugenii*	Extant	0
10	Macropus	*Notomacropus*	*greyi*	Extant	0
11	Macropus	*Notomacropus*	*irma*	Extant	0
12	Macropus	*Notomacropus*	*parma*	Extant	0
13	Macropus	*Notomacropus*	*parryi*	Extant	0
14	Macropus	*Notomacropus*	*rufogriseus*	Extant	0
15	Macropus	*Notomacropus*	*thor*†	Fossil	?0
16	Macropus	*Notomacropus*	*wombeyensis*†	Fossil	0
17	Macropus	*Osphranter*	*antilopinus*	Extant	1
18	Macropus	*Osphranter*	*bernardus*	Extant	1
19	Macropus	*Osphranter*	*robustus*	Extant	1
20	Macropus	*Osphranter*	*rufus*	Extant	1
21	Macropus	*Osphranter*	*pavana*†	Fossil	1
22	Macropus	NA	*dryas*†	Fossil	0
23	Macropus	NA	*narada*†	Fossil	?
24	Macropus	NA	*rama*†	Fossil	0
25	Macropus	NA	*titan*†	Fossil	1
26	Macropus	NA	*woodsi*†	Fossil	1

Table S3.11. Standard (reduced) major-axis regression of anterior and posterior molar cascades. PHC=posthypocristid. Based only on species data and does not include the SAM M2217 and ‘mosaic’ *Procoptodon goliah* data point.

SMA Regression Model M_2 v $M_1+M_2+M_3$	Intercept	Slope	R^2	n	P(2-tailed)	C.I. Min. Slope (2.5%)	C.I. Max. Slope (97.5%)
IC predicted	0	0.333	NA	NA	NA	NA	NA
Full	0.151	0.337	0.9998	31	P<<0.01	0.336	0.339
Full − *Macropus* possessing the PHC removed	0.091	0.337	0.9999	28	P<<0.01	0.336	0.339
Full – Sthenurinae removed	0.097	0.34	0.997718	24	P<<0.01	0.333	0.347
Full- *Macropus* (+ PHC) and all Sthenurinae removed	0.356	0.335	0.986933	21	P<<0.01	0.317	0.354
SMA Regression Model M_3 v $M_2+M_3+M_4$	Intercept	Slope	R^2	n	P(2-tailed)	C.I. Min. Slope (2.5%)	C.I. Max. Slope (97.5%)
IC predicted	0	0.333	NA	NA	NA	NA	NA
Full	−2.106	0.368	0.998	31	P<<0.01	0.363	0.374
Full − Macropus possessing the PHC removed	−1.849	0.369	0.998	28	P<<0.01	0.363	0.375
Full – Sthenurinae removed	0.056	0.349	0.998	25	P<<0.01	0.342	0.356
Full- *Macropus* (+ PHC) and all Sthenurinae removed	0.795	0.337	0.986	22	P<<0.01	0.319	0.357

Table S3.12. Standard (reduced) major–axis regression of log-scaled anterior (M_1+M_2+M_3) and posterior (M_2+M_3+M_4) molar triplets. PHC=posthypocristid. Based only on species data and does not include the SAM M2217 and 'mosaic' *Procoptodon goliah* data point.

Log SMA Regression Model M_2 v M_1+M_2+M_3	Intercept	Slope	R^2	n	P(2-tailed)	C.I. Min. Slope (2.5%)	C.I. Max. Slope (97.5%)
IC predicted	−1.099	1.000	NA	NA	NA	NA	NA
Full	−1.038	0.992	0.999	31	P<<0.01	0.978	1.006
Full-*Macropus* with PHC dropped	−1.036	0.991	0.999	28	P<<0.01	0.976	1.006
Full – Sthenurinae dropped	−1.029	0.990	0.995	24	P<<0.01	0.960	1.02
Full- *Macropus* (+ PHC) and all Sthenurinae removed	−0.979	0.977	0.987	21	P<<0.01	0.925	1.031
M_3 v M_2+M_3+M_4	Intercept	Slope	R^2	n	P(2-tailed)	C.I. Min. Slope (2.5%)	C.I. Max. Slope (97.5%)
IC predicted	−1.099	1.000	NA	NA	NA	NA	NA
Full	−1.097	1.011	0.998	31	P<<0.01	0.994	1.028
Full-*Macropus* with PHC dropped	−1.104	1.013	0.998	28	P<<0.01	0.994	1.032
Full – Sthenurinae dropped	−1.060	1.002	0.995	25	P<<0.01	0.971	1.034
Full- *Macropus* (+ PHC) and all Sthenurinae removed	−1.072	1.005	0.988	22	P<<0.01	0.955	1.057

Table S3.13. Mean crown height for 19 extant macropodoids. Standard error is a boot strap estimate based off 10,000 replicates. Hypsodonty values are calculated as M_3 hypoconid height divided by M_3 talonid width. Dietary classification based on consensus categorisation of Arman and Prideaux (2015) except for five species where categorisations (superscript denoted in 'Diet' column) follow: (1) Seebeck et al. 1989; (2, 4, 5, and 6) no data, as for most congenerics; (3) Vernes and Lebel (2011). Dietary abbreviations: B, browser; MF, mixed feeder; G, grazer and F, fungivore.

Species	Diet	Mean M_3 hypoconid hypsodonty	n	Standard error
Aepyprymnus rufescens	MF[1]	0.97	3	0.033
Bettongia lesueur	MF	0.86	7	0.037
Bettongia penicillata	F[6]	0.74	7	0.023
Dendrolagus bennettianus	B	0.98	1	NA
Dendrolagus lumholtzi	B	0.92	11	0.031
Dendrolagus ursinus	B[2]	0.8	4	0.019
Dorcopsulus vanheurni	B[3]	0.98	5	0.037
Hypsiprymnodon moschatus	F	0.79	2	0.003
Lagostrophus fasciatus	MF	1.06	4	0.030
Macropus fuliginosus	G	1.31	6	0.059
Macropus parryi	G	1.33	1	NA
Macropus robustus	G	1.25	5	0.052
Macropus rufus	G	1.44	10	0.037
Onychogalea unguifera	MF	1.24	5	0.018
Petrogale godmani	MF[4]	1.17	4	0.018
Petrogale inornata	MF[5]	1.12	2	0.012
Petrogale penicillata	MF	1.29	4	0.031
Potorous tridactylus	F	0.72	9	0.056
Thylogale stigmatica	MF	1.16	7	0.033

Supplementary Figures

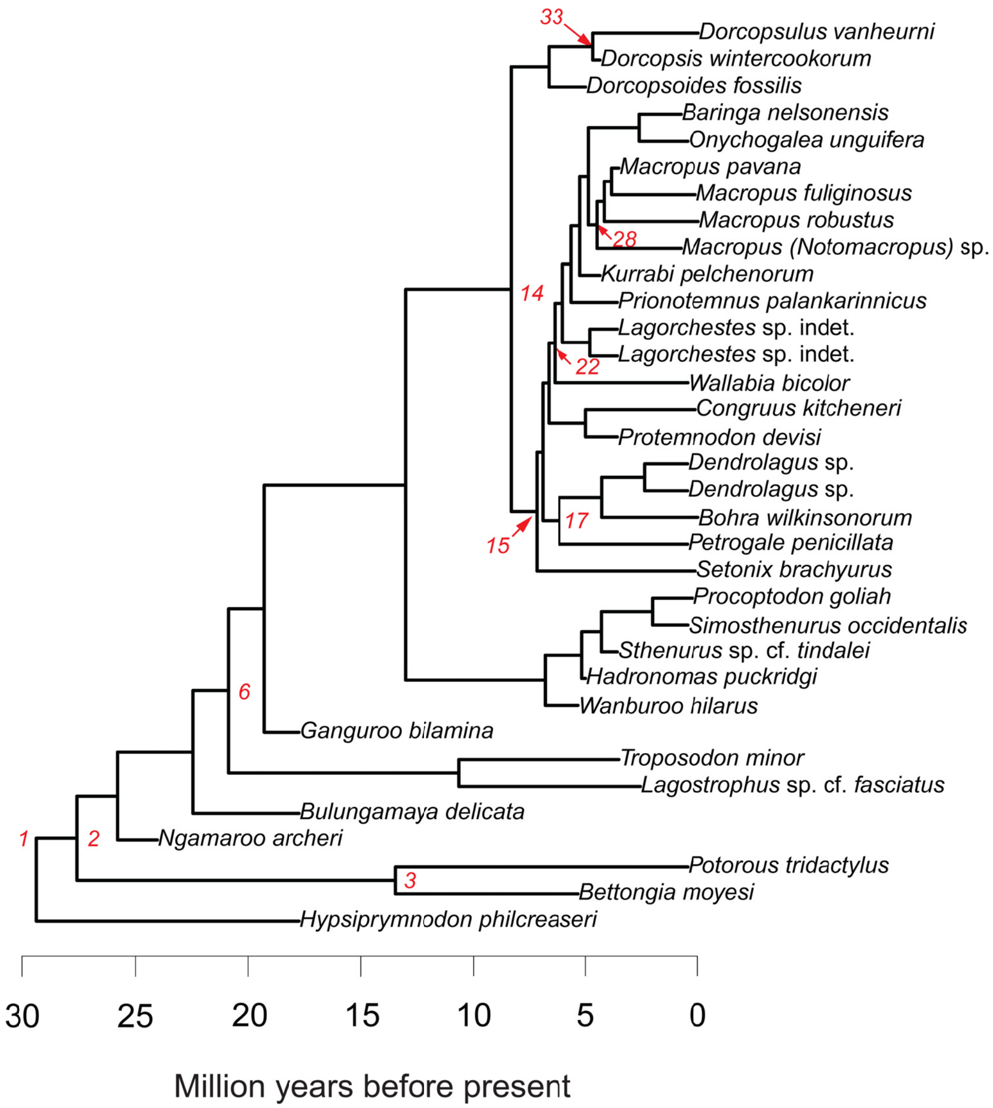

Figure S3.1. Time-scaled morphological phylogeny of Macropodoidea showing nodes (red) constrained with minimum molecular estimates (see Table S2) derived from Mitchell et al. (2014) and first appearance ages and fossil calibrations indicated at branch tips.

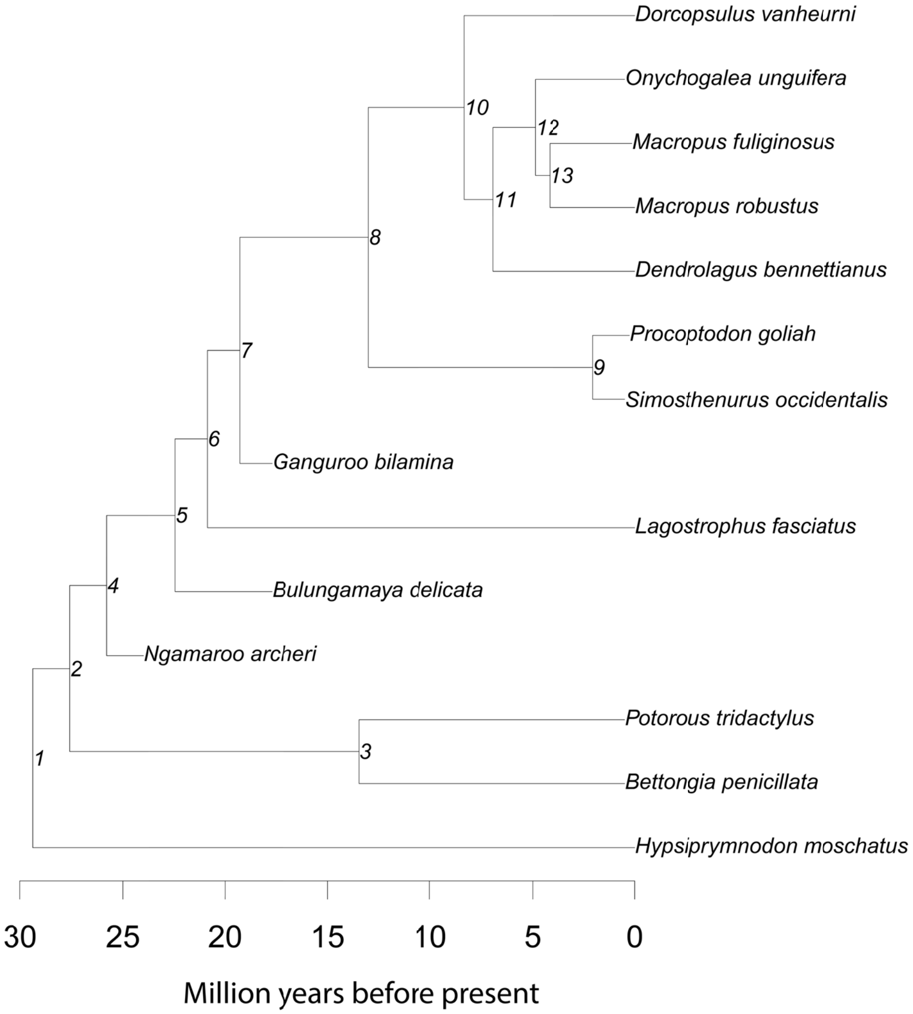

Figure S3.2. Pruned time-scaled morphological phylogeny of Macropodoidea used to reconstruct ancestral states for posterior molar proportions at 13 internal nodes. Node number corresponds to those reported in Table S3.4.

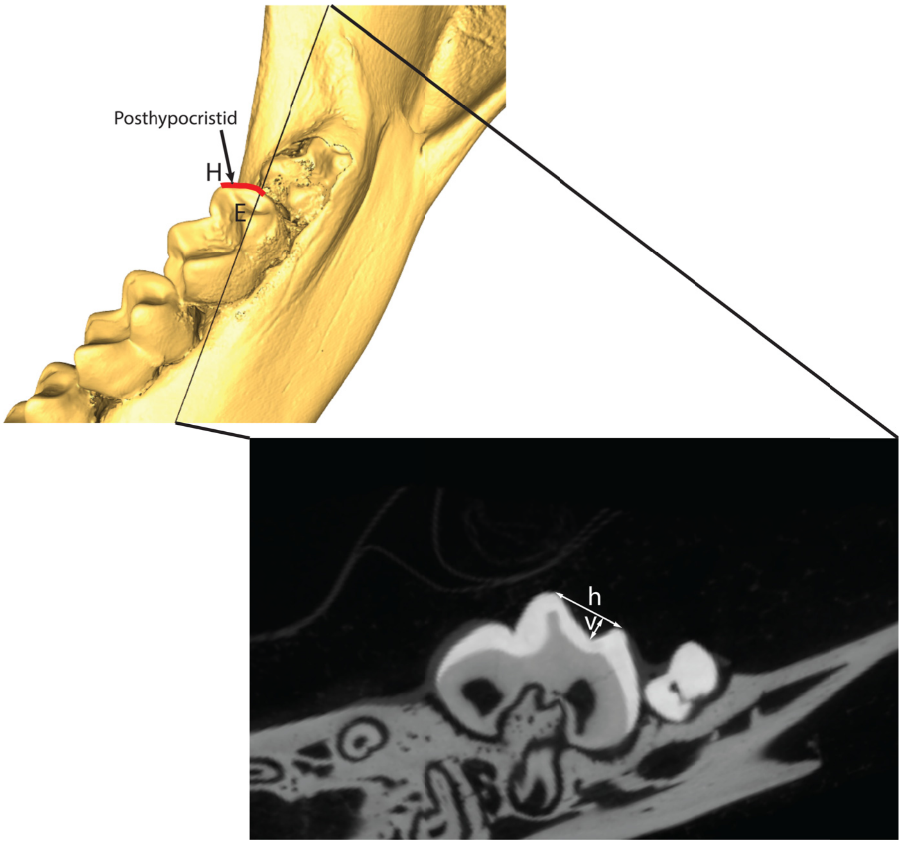

Figure S3.3. Posthypocristid relief measurement. We placed a 2D section perpendicular to the axis of the posthypocristid at the point of maximum relief (normally approximately midway along the crest). From this section we determined the vertical distance (v) from the lowest point (floor of the talonid fossa) to a point orthogonal to a horizontal line traversing the talonid fossa (h). The quotient of v and h provides a relative index of posthypocristid relief. Abbreviations: E, entoconid; H, hypoconid.

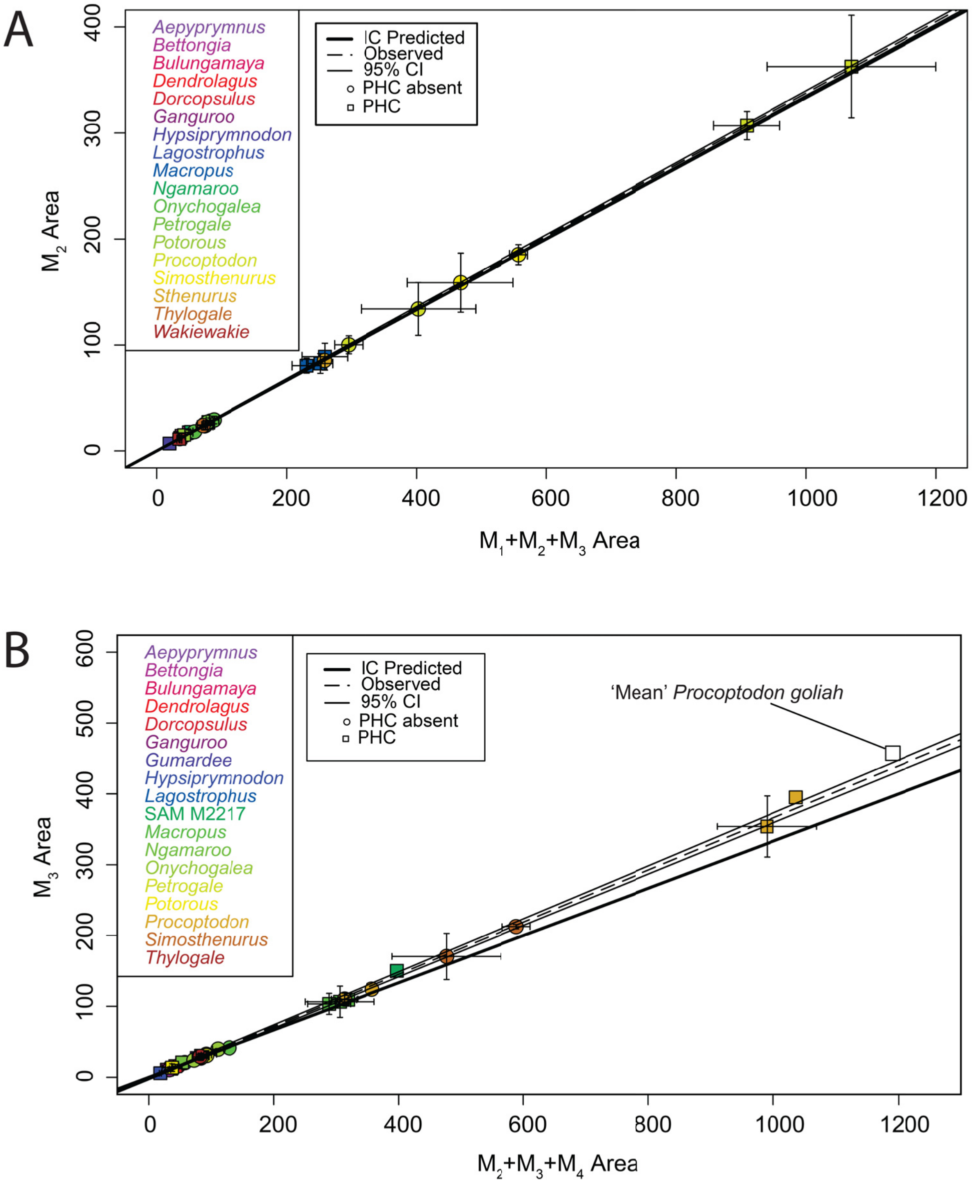

Figure S3.4. Major-axis regression of anterior (A) and posterior (B) molar triplets. The "Mean" *Procoptodon goliah* data point, represents the mean of multiple lower molar specimens. This point and SAM M2217 (*Macropus rufus*) were excluded from calculation of the "Observed" best fit line and confidence intervals. Inclusion of these points drives the best fit line further from inhibitory cascade predictions.

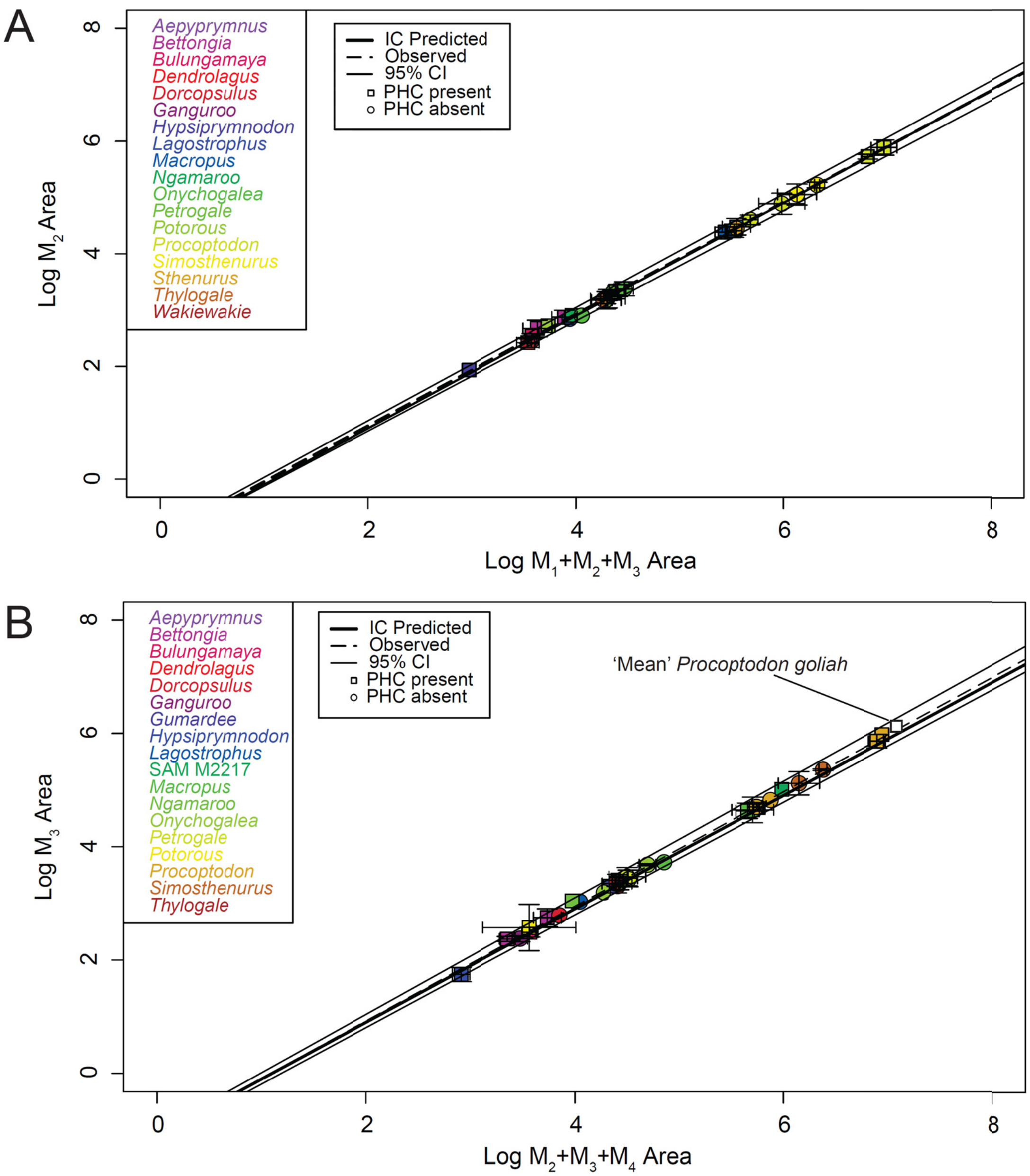

Figure S3.5. Standard (reduced) major-axis regression of log-scaled anterior (A) and posterior (B) molar triplets. Inclusion of the "Mean" *P. goliah* and the abnormal SAM M2217 specimen follows that outlined for Fig. S3.4.

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4. MOLAR ENAMEL THICKNESS IS FUNCTIONALLY LINKED TO DIETARY ABRASION IN KANGAROOS

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Context

This chapter quantitatively describes variation in the molar enamel thickness of extant macropodoids. The role of phylogeny and dietary adaptation in structuring this variation is examined using principle component analysis, multivariate analysis of variance, and phylogenetic modelling. To better understand the evolvability of enamel thickness, comparisons are made with other mammalian groups, especially primates. A model of enamel thickness function under different rates of dental wear is developed.

Statement of Authorship

AMCC designed the research, collected data, performed analysis, and wrote the manuscript. GJP contributed to experimental design, provided guidance and advice, and commented on the draft manuscript.

Key Words: Evolution, tooth, function, diet, mammal, microCT.

4.1 Abstract

Enamel is the hardest mammalian tissue but its functional role in dietary adaptation remains unclear. Thick molar enamel is often linked to hard object feeding, but its potential role as a mechanism to resist dental wear has never been rigorously investigated in herbivores that sustain high rates of dental wear. Using kangaroos and their relatives (Macropodoidea) as a model radiation we show that grazing and mixed feeding taxa have thicker enamel than those consuming less abrasive diets (browsers). Linear and three-dimensional lower molar enamel thickness was measured across 19 extant macropodoid species from high resolution X-ray micro-computed tomography scans. Principal component analysis and multivariate analysis of variance suggest that much of the variation in linear enamel thickness is not strongly linked to diet but instead reflects phylogenetically-conserved processes of amelogenesis. Diet is found to be correlated with enamel thickness at cusp tips, a functionally important enamel phenotype in wear resistance and blade function. Computation of three-dimensional relative enamel thickness scores reveals that multiple macropodine lineages evolved enamel thickness within the range of the thickest-enamelled primate lineages, *Homo* and *Paranthropus*. Overall, grazing and mixed feeding macropodoids tend to have greater whole-crown enamel volume than browsers, primarily because enamel is thicker along the blade edge and relief surface in taxa with more abrasive diets. By demonstrating that molar enamel thickness is positively correlated with levels of dietary abrasion, our work reveals an additional pathway for mammals to acquire dental durability. Given that patterns of enamel thickness variation are virtually unknown for most vertebrate groups, studies of enamel thickness will likely provide an exciting new frontier for analyses of dietary adaptation.

4.2 Introduction

The diversity of living mammals is in no small way attributable to the adaptability of their dentition, which has enabled the exploitation of a highly diverse range of diets (Janis and Fortelius 1988; Hunter and Jernvall 1995; Ungar 2010; Wilson et al. 2012). A fundamental characteristic of most mammalian teeth is the deposition of a hard layer of enamel over a less-mineralised layer of dentine (Lucas et al. 2008). Enamel is composed almost entirely of calcium phosphate prisms, so it is extremely resistant to brittle failure and, thus, ideal as a biomaterial for food reduction (Chai et al. 2009). However, despite these remarkable properties, tooth function can still be compromised by fractures induced by hard objects or changes in surface shape resulting from abrasion by small, hard particles (dental wear). A simple evolutionary response to both these threats is to increase the thickness of the enamel layer because this increases the force needed to induce and propagate a fracture, as well as the amount of wear which the tooth can sustain before function is compromised (Lucas 2004; Lucas et al. 2008). For herbivores with abrasive diets, increasing enamel thickness also probably slows the rate of dental tissue loss (Rabenold and Pearson 2011; Lucas et al. 2013). Enamel thickness is also likely to be an adaptively important trait because it is herritable and highly variable within populations (Hlusko et al. 2004; Suwa and Kono 2005; Ungar and Hlusko 2016).

The importance of thick molar enamel as a morphological character differentiating hominins (with the exception of *Pan*) from thinner-enamelled hominoids (Martin 1985) prompted a concerted focus on variation in primate enamel thickness. Initial assessments were based on histological sections (Molnar and Gantt 1977; Martin 1985; Wall et al. 2006; Boyer et al. 2011), but most recent approaches have employed two and three-dimensional microCT-based analyses (Cerling et al. 1999; Olejniczak et al. 2008a,b). Despite increasing resolution of the taxonomic distribution of enamel thickness within primates, its adaptive significance has remained controversial, largely because it is difficult to distinguish adaptive responses to hard-object feeding from dietary abrasion in living primates (Rabenold and Pearson 2011; Strait et al. 2013). Primates that feed on the ground do not have relatively thicker enamel than canopy feeders which provided evidence that hard-object feeding was a more important factor than dental wear from grit (Kay 1981). However, dietary abrasion from phytoliths could also be an important factor because primates that consume more leaves have thicker enamel (Rabenold and Pearson 2011). The link between enamel thickness and diet is complicated further because average dietary intake may be less important than foods consumed over a short period of stress (Covert 1986; Strait 2001). Thus, thick molar enamel could be an adaptation for foods only eaten during ‘fall-back’ periods when preferred foods are unavailable (Lambert et al. 2004; Constantino et al. 2009). Such dietary flexibility could explain why analyses across primates, chiropterans, and carnivorans have failed to recover a consistent relationship between enamel thickness and diet (Dumont 1995; Constantino et al. 2011).

The geometry of functional tooth features predicts how efficiently food items can be processed (Lucas 1982; Evans and Sanson 2003). Because tooth wear changes tooth geometry in a stereotypical manner (Evans 2005) it is possible to predict specific patterns of enamel-thickness distribution which would optimise tooth performance. For instance, in double-bladed systems, where an upper and lower blade occlude to fracture tough foods like plant leaves, continual contact between the cutting edges produces an adjacent region of no relief that increases friction and makes it easier for the occluding blades to be pushed apart (Evans 2005). Additionally, it is common for blades to be notched to reduce the energetics of food fracture (Anderson and LaBarbera 2008), but dental wear results in misalignment of notches and thus decreases cutting effectiveness (Evans and Sanson 2006). As wear proceeds further, compensatory cutting edges can develop at the junction of emerging dentine islands and the receding enamel which may maintain or increase blade length for many years after wear begins (King et al. 2005). If wear rates are low, deposition of thinner enamel along the blade edge contiguous with the rake surface may be favoured because it will displace the increase in blade length and dental complexity earlier into the functional life of the tooth. However, in high dental-wear regimes, intermittent improvement of processing efficiency may be followed by a rapid and precipitous decline in occlusal performance. Thus, in bladed teeth subject to high rates of dietary abrasion, thicker enamel along the relief surface would help retain blade function by increasing the volume of enamel that must be stripped before the functional cutting edge is obliterated.

Macropodoids (kangaroos, wallabies, and relatives) are the most diverse living marsupial herbivores, comprising at least 70 living species (Van Dyck and Strahan 2008). There are two extant families: Hypsiprymnodontidae represented by a single living species, *Hypsiprymnodon moschatus*, and Macropodidae, comprised of the subfamilies Potoroinae, Lagostrophinae, and Macropodinae. Most macropodoids are generalist folivores that do not consume significant quantities of hard foods like nuts and seeds (Arman and Prideaux 2015). Basal macropodoids, such as *Hypsiprymnodon* and potoroines, are primarily frugivores or fungivores with low-crowned bunodont molars adapted for crushing (Sanson 1989; Janis 1990). In contrast, lagostrophine and macropodine kangaroos have bilophodont molars characterised by two parallel, transverse shearing crests or lophs (Arman and Prideaux 2015).

In this paper we use high-resolution microCT scans from 19 extant macropodoid species to test the functional link between diet and enamel thickness. To do this we use principle components analysis to quantify the relationship between two-dimensional linear enamel thickness (LET) measurements collected from seven tooth regions and diet. Linear enamel thickness data combined with three-dimensional mapping enable us to examine to what extent enamel variation is related to tooth function. We also use three-dimensional relative enamel thickness (RET3D) scores to compare macropodoid and primate molar enamel thickness, providing a basis for exploring the broader significance of enamel thickness in mammalian dietary adaptation.

4.3 Methods

4.3.1 Scan Acquisition

We examined lower molars or dentaries from 19 species of extant macropodoid (Table 3.1) held in the following collections: Australian National Wildlife Collection, Canberra; Flinders University Palaeontology Laboratory, Adelaide; South Australian Museum, Adelaide; Queensland Museum, Brisbane; and Western Australian Museum, Perth. These specimens were scanned using X-ray absorption micro-computed tomography (microCT) scanners at the Department of Applied Physics, Australian National University, Canberra (custom industrial microCT machine), Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany (Actis BIR 225 industrial microCT machine) and Adelaide Microscopy, University of Adelaide (SkyScan 1076 desktop microCT). Isometric voxel-size range was 8.6–41 µm.

Table 4.1. Sampling for linear enamel thickness across 19 species of living macropodoid. Diet follows the 'consensus' categorisation of Arman and Prideaux (2015).

Species	**n**	**Diet**	**Clade**
Aepyprymnus rufescens	4	Mixed feeder	Potoroinae
Bettongia lesueur	6	Mixed feeder	Potoroinae
Dendrolagus lumholtzi	3	Browser	Macropodinae
Hypsiprymnodon moschatus	6	Fungivore	Hypsiprymnodontidae
Lagorchestes conspicillatus	3	Mixed feeder	Macropodinae
Lagostrophus fasciatus	6	Mixed feeder	Lagostrophinae
Macropus fuliginosus	4	Mixed feeder	Macropodinae
Macropus irma	1	Mixed feeder	Macropodinae
Macropus robustus	44	Grazer	Macropodinae
Macropus rufus	7	Grazer	Macropodinae
Onychogalea unguifera	3	Mixed feeder	Macropodinae
Petrogale brachyotis	3	Mixed feeder	Macropodinae
Petrogale concinna	4	Mixed feeder	Macropodinae
Petrogale godmani	2	Mixed feeder	Macropodinae
Potorous tridactylus	3	Fungivore	Potoroinae
Setonix brachyurus	6	Browser	Macropodinae
Thylogale billardierii	5	Mixed feeder	Macropodinae
Thylogale stigmatica	3	Mixed feeder	Macropodinae
Wallabia bicolor	3	Mixed feeder	Macropodinae

4.3.2 Three-Dimensional Relative Enamel Thickness

To calculate three dimensional relative enamel thickness (RET3D) scores we used the following relationship (Olejniczak et al. 2008b):

$$\text{RET3D} = 100 \times (\text{EVOL}/\text{EDJ3DSA}) / \text{DVOL}^{1/3}$$

Where:

EVOL= volume of the enamel cap (mm^3)
DVOL= volume of the coronal dentine including the pulp chamber (mm^3)
EDJ3DSA= three-dimensional surface area of the enamel dentine junction (mm^2)

To measure EVOL the tiff image stack was filtered with a 2D median filter followed by an edge-preserving 2D Kuwahara filter (implemented as an ImageJ 1.46r plugin) or 2D shell script programmed mean of least variance filter (Wollny et al. 2013). Voxels were assigned to labels for enamel, dentine, and air using the *Edit new label field* function in Avizo 8. The resulting segmentations were assessed manually (slice by slice) against the unfiltered image stack and adjustments made if needed. A surface model of the enamel cap was created with the *Generate surface* module using the “unconstrained smoothing” function. The DVOL mesh was created by using the *Select tool* in MeshLab v1.3.1 to remove the outer enamel surface (OES) from the enamel cap, leaving the enamel–dentine junction (EDJ). Surface normals were inverted and holes closed with the *Fill holes* function to obtain a manifold mesh.

To compare macropodoid and hominoid RET3D scores different methods to estimate dentine volume were evaluated. The original approach (i.e., Olejniczak et al. 2008a) defined an average basal plane midway between the most apical plane forming a continuous cervical enamel ring, and the most apical enamel extension (“3D-c” in Table 1 of Benazzi et al. 2014). However, this approach was problematic to apply in macropodoids because the bucco-lingual asymmetry in the cervical enamel boundary leads to large volumetric variation. Alternative approaches which involve fitting a plane to cervical or basal plane points (i.e., Fig.1c, d, of Benazzi et al. 2014) proved similarly problematic. Instead, we used a method which closed the cervical aperture using the ‘trivial’ option in the *Fill holes* function of Meshlab, which approximates a spline fit based on the cervical line, and is essentially equivalent to the “3D-b” method of Benazzi et al. (2014). Using different variants to close the cervical aperture resulted in only small changes in DVOL values.

4.3.3 Spatial Mapping of Enamel Thickness

To spatially ‘map’ enamel thickness the OES and EDJ were separated using the “select” tool in MeshLab v1.3.1 from a surface model of the enamel cap. The *Surface distance* function was used to compute a distance matrix in Avizo 8 by calculating the shortest distance from the OES to EDJ. Finally, the *Surface view* module was used to associate the distance matrix to the OES, enabling the spatial heterogeneity in enamel thickness to be visualised.

4.3.4 Linear Enamel Thickness Measurements

LET measurements were collected by a single observer (AMCC) from seven functionally homologous tooth positions using the *oblique slice* tool in Avizo 8 (Table 4.2; Figure 4.1). We used this functional homology because the large interspecific variability in macropodoid tooth structure (loss and gain of cusps, major changes in cusp topology) meant there were insufficient land marks to set rigidly defined section planes. With the exception of the hypoconid cusp apex (HCA), one of the few measurements which could be rigidly specified by three unambiguous points, triplet measurements were obtained by resetting the section plane three times. The half maximum H method of Spoor et al. (1993) was used to define material boundaries.

4.3.5 Statistical Analysis

Statistical analysis was performed within the `R` statistical environment (version 3.1.1; R Core Team 2014). LET measurements were standardised for tooth size by dividing by the square root of rectangular enamel cervix area calculated as the average of maximum bicervical trigonid width and maximum bicervical talonid width, multiplied by maximum cervical antero-posterior tooth length. Measuring tooth dimensions at the cervix makes dimensions independent of enamel thickness. All LET data was natural log-transformed and then means calculated from the three replicate measurements. A mean was not calculated for HCA because we acquired only a single measurement.

Using the function `prcomp`, variation in the LET data was visualised with a principle component analysis (PCA). Only specimens without missing data were included in the PCA. Multivariate analysis of variance (MANOVA), implemented with `manova` in `R,` was used to statistically test if ‘diet’ and ‘clade’, as categorical variables, were significantly correlated with variation in linear enamel thickness. Prior to analysis, hypoconid apex enamel thickness (HCA) and antero-buccal talonid wall (ABTW) enamel thickness were exponentially transformed (after scaling for tooth size) to satisfy the MANOVA assumption of normally distributed dependent variables.

The `physignal` function in `geomorph` (Adams and Otárola-Castillo 2013) was used to estimate within a multivariate framework the amount of phylogenetic 'signal' in the linear enamel thickness data based on 10000 estimates of the *K* statistic (Bloomberg et al. 2003). Values of the *K* parameter greater than 1 indicate that differences between species are less than expected under Brownian motion, whereas *K* values less than 1 reflect greater differences between species than would be expected under Brownian motion. The pruned MCMC time-calibrated molecular phylogeny from Mitchell et al. (2014) was used as the in-put tree for the `physignal` analysis.

A bootstrap resampling approach was used to estimate the confidence intervals of the RET3D scores at different sample sizes from an intraspecific sample of *Macropus robustus* (n=31). This was done by resampling (with replacement) a sample of size n for all integers between 1 and 30. For each value of n the subsample median was computed 1 000 000 times and the 95% confidence interval for this population of subsample medians compared with the 95% confidence intervals inferred from the total sample (n=31).

Table 4.2. Two dimensional section plane definitions used to measure molar enamel thickness.

Anterior trigonid wall (ATW)	A longitudinal section orientated perpendicular to the OES was positioned midway across the lingual portion of the transverse crest. This section was positioned lingual of the crest midline because enamel thickness becomes variable near the midline and some basal macropodoids lack a well-defined buccal blade component. Measurements collected within the centre of the region of homogenous enamel thickness.
Posterior trigonid wall (PTW)	As for ATW but measurements collected from within the region of homogenous enamel on the *posterior* margin of the transverse crest.
Trigonid basin (TRGB)	A longitudinal section intersecting the lowest point of the trigonid basin. The shortest distance was measured between the lowest OES point of the trigonid basin and the EDJ.
Talonid basin (TALB)	As for TRGB but the section was positioned across the talonid basin, lingual of the mid link crest if present. If the talonid basin was bucco-lingually inclined (e.g. *Macropus*) a transverse plane was used to extract enamel thickness from a region of homogenous enamel thickness within the basin.
Antero-buccal talonid wall (ABTW)	The anterior face of the posterior transverse crest was portioned into lingual and buccal portions based on a clearly defined inflection of crest curvature. Within the buccal portion a section plane (SP1) orientated perpendicular to the local OES and intersecting the tooth surface at the point of maximum curvature. To avoid oblique positioning a second plane (SP2), this time horizontal, was defined using three points from SP1 section: a point at the EDJ, the closest adjacent point at the OES and a third point an arbitrary distance lateral to this point at the OES. If necessary the z-depth of this plane was modulated to extract a measurement within a homogenous enamel zone.
Antero-lingual talonid wall (ALTW)	As for ABTW but within the lingual crest segment. A section plane was positioned midway through the region and measurement collected from upper half of the ALTW. In some taxa like *Dendrolagus* there was no homogenous zone so we measured the minimum enamel thickness.
Hypoconid cusp apex (HCA)	A horizontal plane was defined that intersected the protoconid, metaconid and hypoconid dentine horn tips. This plane was lowered to select points for a second transverse plane defined by the hypoconid dentine horn, entoconid dentine horn and hypoconid cusp tip. The shortest distance between the hypoconid dentine horn and its respective cusp tip was measured. Only a single LET measurement was collected because the HCA section plane could be fit more explicitly than other section planes.

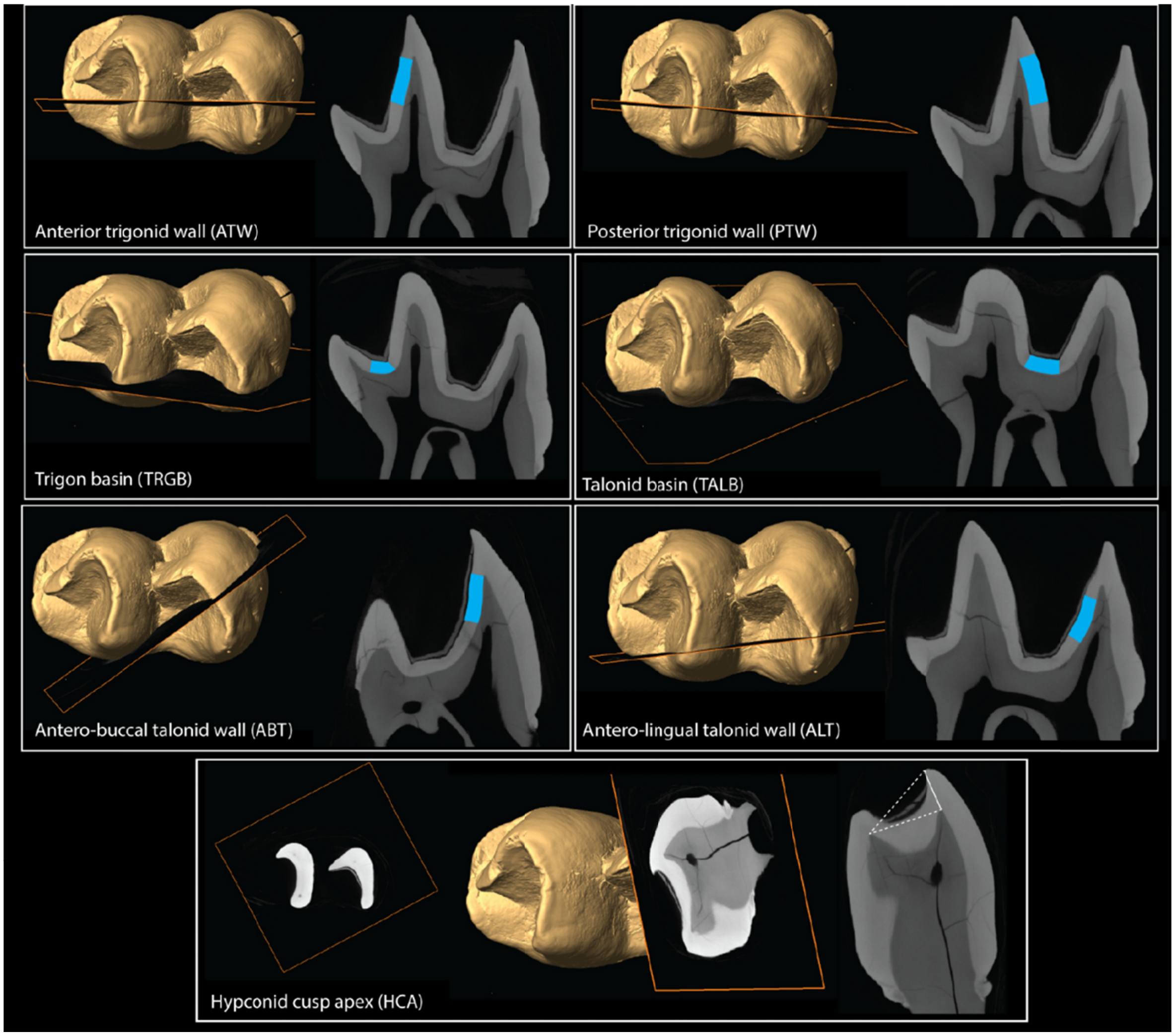

Figure 4.1. Example two dimensional section plane orientation and position in a right third lower molar of *Macropus rufus* (FU2003.9.12-12).

4.4 Results

4.4.1 Three-Dimensional Enamel Mapping

Across Macropodoidea the thickest enamel was deposited between the dentine horn tips in the middle of the loph, with the thinnest enamel deposited in the talonid and trigonid basins (Figure 4.2). Different patterns of enamel-thickness distribution occur in the molar teeth of bunodont macropodoids compared with bilophodont taxa, with the former characterised by relatively more homogenous enamel thickness (Figure

4.2). A distinguishing feature of hypsiprymnodontid and potoroine lower molars relative to other macropodoids is the possession of thick enamel along the buccal and lingual tooth margins. *Hypsiprymnodon* and *Potorous* also have relatively thicker basin enamel than other macropodoids. Enamel thickness across the posterior talonid and trigonid wall forms a relatively homogenous zone in *Lagostrophus* and the Macropodinae. *Lagostrophus* is distinctive in possessing thicker enamel on the posterior trigonid and talonid wall than in macropodine molars (Figure 4.2). Mixed feeding and grazing macropodids, especially species of *Macropus*, have more thickly-enamelled cusp apices than browsing macropodids (Figure 4.2).

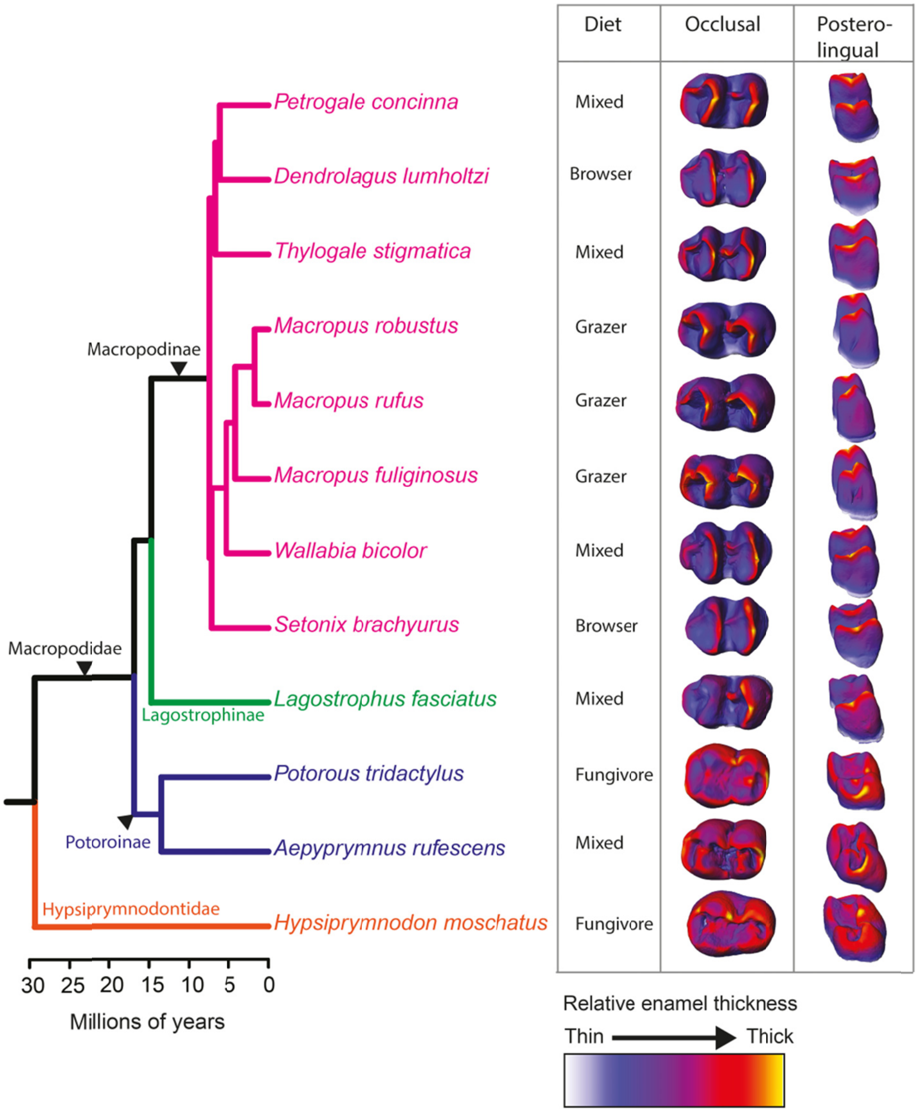

Figure 4.2. Spatial distribution of enamel thickness in minimally-worn lower molars of 12 extant macropodoid species. Phylogenetic relationships and branch lengths based on Mitchell et al. (2014).

4.4.2 Intraspecific Variation in Three-Dimensional Enamel Thickness

Analysis of enamel thickness variability in *Macropus robustus* (n=31) reveals a range of RET3D scores (15.92–26.84). Resampling from within this population where n ≥ 2 produced 95% confidence intervals that fell within the 95% confidence intervals for the entire population (Figure 4.3). Sampling n ≥ 8 estimated the mean from the parent population to within one standard deviation (1σ). A Shapiro–Wilk test indicates that both the population from Greymare in southeastern Queensland (n=16) and individuals from other sites (n=14) are approximately normally distributed, and this remains when both populations were pooled (W=0.97, p=0.45). However, a two sample T-test assuming equal variances found that the Greymare population did have significantly greater RET3D scores than *M. robustus* individuals from elsewhere (23.40 vs 19.91; $T_{28}=3.84$, $p<<0.01$). When the pooled data was partitioned by sex, a Shapiro–Wilk test confirmed the data was normally distributed and a T-test assuming equal variances found no significant differences between the sex-partitioned RET3D populations ($T_{20}=—1.39$, P=0.18). However, females had significantly greater RET3D scores compared with males when analysis was restricted to the Greymare population ($T_{14}=—4.06$, $p<<0.01$) although samples were small (n<10).

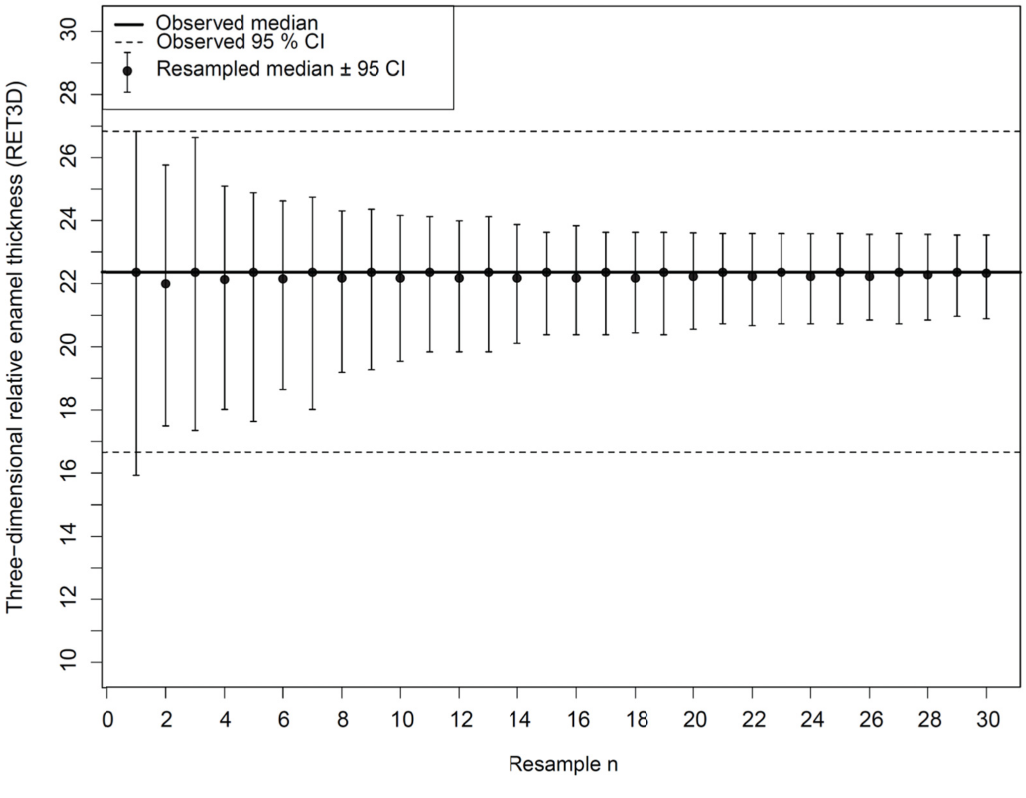

Figure 4.3. Confidence intervals (95%) based on 10^7 bootstrap estimates of the pooled median RET3D score at different values of n. Observed confidence intervals based on a sample (n= 31) of *Macropus robustus* lower third molars.

4.4.3 Two-Dimensional Enamel Thickness

The first five principle components account for more than 95% of the total variance based on linear thickness measurements from seven tooth regions (Figure 4.4). PC1 loadings (eigenvectors) for each tooth region were more even than along PC2 (Table 4.3). However, for both PC1 and PC2 enamel thickness from the hypoconid had the largest loadings. The *K* statistic was lower than 1 (0.76), which suggests that species are more different from each other than would be expected under a Brownian motion model of continuous trait evolution. However, the *K* estimate was not statistically significant (p=0.073) and, with less than 20 taxa included (n=13), the analysis was likely underpowered (i.e., Bloomberg et al. 2003).

There was considerable overlap between folivores within the PC1 and PC2 morphospace, although fungivores form a distinct group (Figure 4.5). Removing the large sample of *Macropus robustus* from the PCA did not significantly alter this relationship between diet categories. MANOVA revealed that diet was significantly correlated with linear enamel thickness variation (Wilks test, Approx $F_{3,38}$=2.86, p<<0.01). This result did not change if the large sample of *Macropus robustus* was included in the analysis. However, the correlation was not significant when the LET data was averaged at a species level (Wilks test, Approx. $F_{3,11}$=1.91, p=0.57), probably because the decreased ratio of observations in the dependent variable (i.e. the number of species) relative to the number of dependent variables reduced power to detect differences. The correlation between taxonomic group (i.e., 'clade') and linear enamel thickness was stronger than the correlation with diet (Wilks test, Approx. $F_{3,39}$=3.37, p<<0.01).

The variance structure changed when the PCA was restricted to the three tooth regions with the highest taxonomic coverage: the trigonid basin, talonid basin, and hypoconid cusp apex (Figure 4.6). There was also a stronger correlation between diet and linear enamel thickness (Wilks test, Approx. $F_{3,46}$=4.78, p<<0.01) and a corresponding increase in the strength of correlation between taxonomic affiliation and linear enamel thickness (Wilks test, Approx. $F_{3,46}$=5.13, p<<0.01).

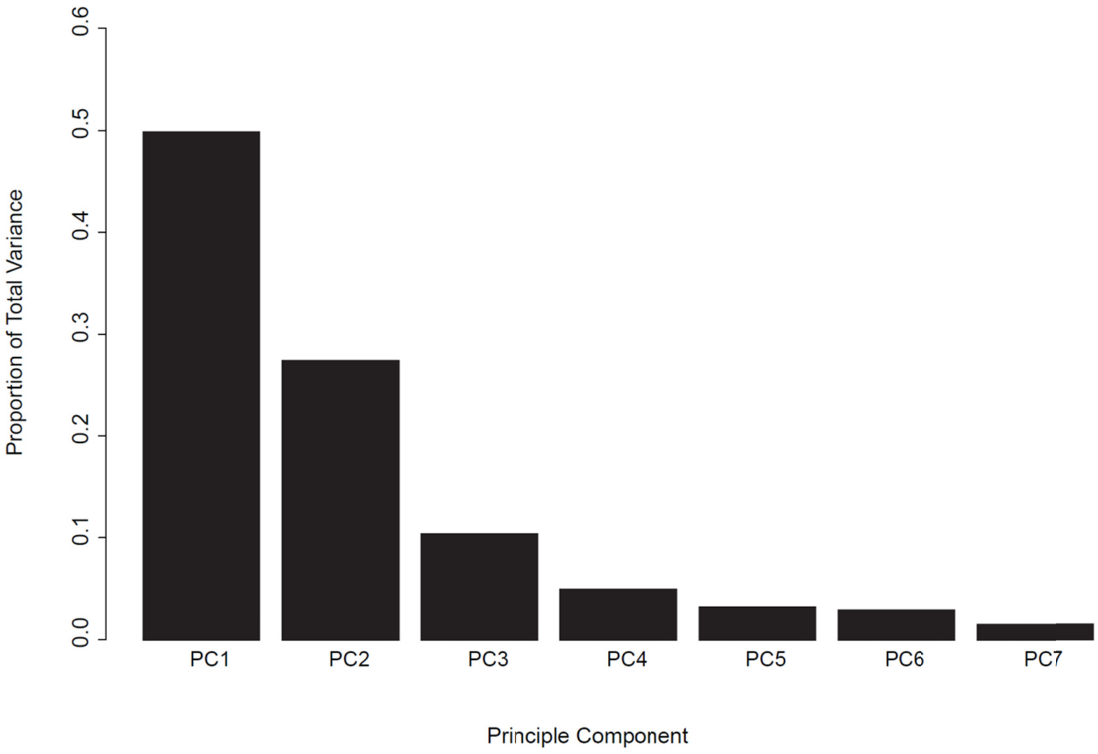

Figure 4.4. Proportion of variance explained by principle component analysis of linear enamel thickness data for seven molar tooth regions. The first five principle components account for more than 95% of the total variance.

Table 4.3. Eigenvector scores for different linear enamel thickness parameters included in the principle component analysis.

Linear enamel thickness parameter	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
ABTW	-0.426	0.153	-0.009	0.465	-0.587	0.449	-0.179
HCA	-0.564	-0.739	0.329	-0.064	0.148	-0.030	-0.034
TALB	-0.187	0.513	0.764	-0.334	-0.017	-0.038	-0.064
ALTW	-0.408	0.215	-0.416	-0.480	0.350	0.508	0.056
TRGB	-0.382	0.329	-0.05	0.579	0.524	-0.321	0.174
ATW	-0.312	0.111	-0.343	-0.255	-0.234	-0.599	-0.542
PTW	-0.235	0.032	-0.12	-0.192	-0.425	-0.277	0.797

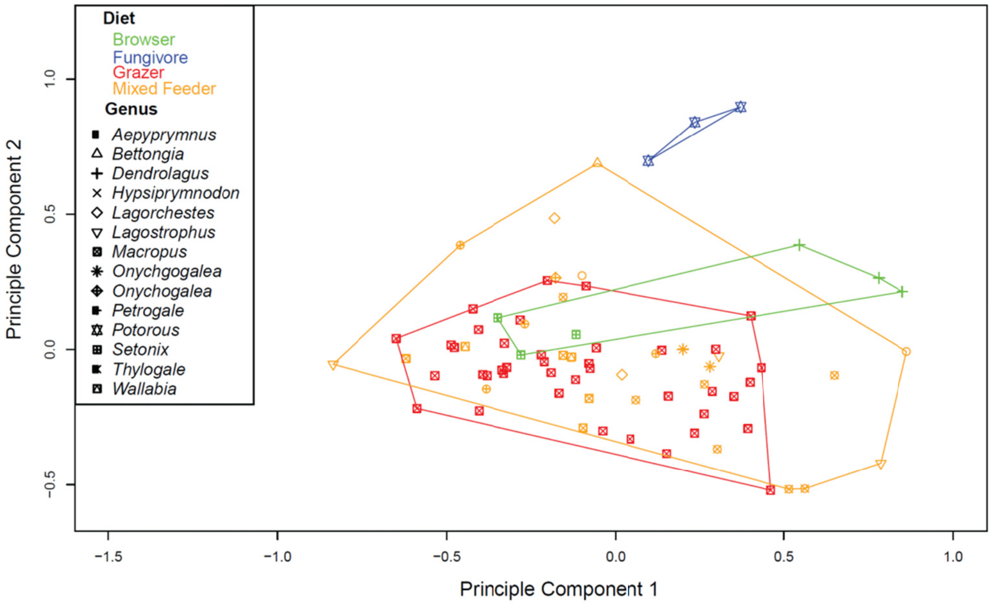

Figure 4.5. Bivariate plot of principle components 1 and 2 based on analysis of the full linear enamel thickness dataset. *Aepyprymnus rufescens* (n=2), *Bettongia lesueur* (n=1), *Dendrolagus lumholtzi* (n=3), *Lagorchestes conspicillatus* (n=2), *Lagostrophus fasciatus* (n=3), *Macropus fuliginosus* (n=4), *Macropus robustus* (n=36), *Macropus rufus* (n=5), *Onychogalea unguifera* (n=3), *Petrogale concinna* (n=3), *Petrogale godmani* (n=1), *Potorous tridactylus* (n=3), *Setonix brachyurus* (n=3), *Thylogale billardieri* (n=4), *Thylogale stigmatica* (n=3), *Wallabia bicolor* (n=2).

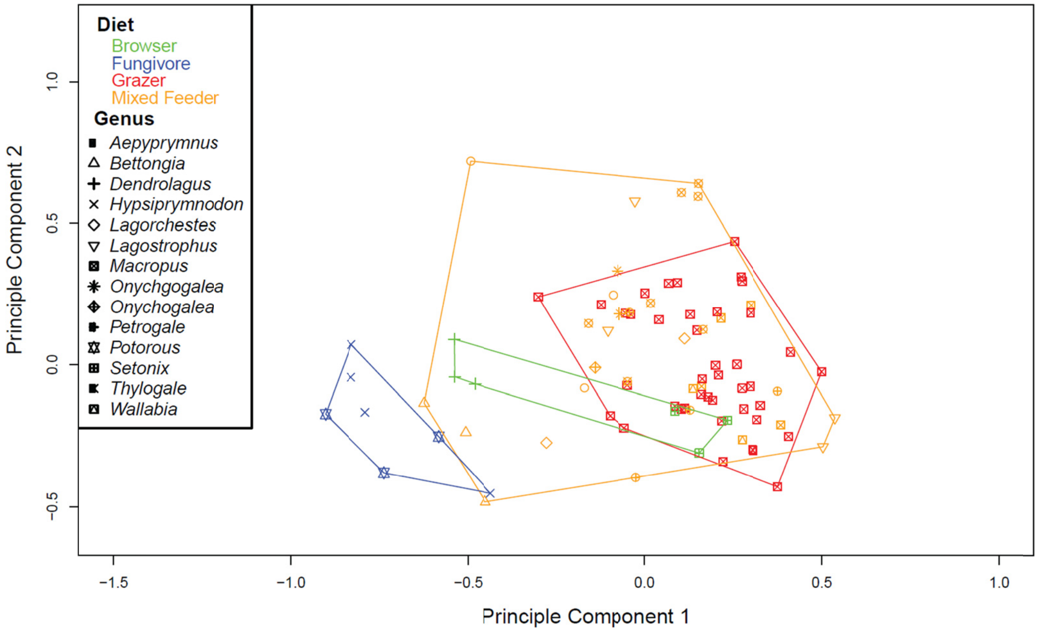

Figure 4.6. Bivariate plot of principle components 1 and 2 based on analysis of enamel thickness measurements from the trigonid basin, talonid basin and hypoconid cusp apex. Sample sizes for taxa: *Aepyprymnus rufescens* (n=3), *Bettongia lesueur* (n=3), *Dendrolagus lumholtzi* (n=3), *Hypsiprymnodon moschatus* (n=4), *Lagorchestes conspicillatus* (n=2), *Lagostrophus fasciatus* (n=4), *Macropus fuliginosus* (n=4), *Macropus robustus* (n=37), *Macropus rufus* (n=5), *Onychogalea unguifera* (n=3), *Petrogale concinna* (n=3), *Petrogale godmani* (n=1), *Potorous tridactylus* (n=3), *Setonix brachyurus* (n=3), *Thylogale billardieri* (n=4), *Thylogale stigmatica* (n=3), *Wallabia bicolor* (n=2).

4.4.4 Three-Dimensional Relative Enamel Thickness (RET3D)

There was considerable variation in median RET3D scores between macropodoid species (Table 3.4). RET3D scores were generally higher in mixed-feeding and grazing macropodoids than amongst fungivores and browsers (Figure 3.7). However, the range of RET3D scores within *Macropus robustus* almost encompasses the full range of other macropodoid consumers. The most variable RET3D scores were associated with grazers whereas browsers had the least variability. Using the complete RET3D dataset, a non-parametric Kruskal–Wallis rank sum test did not reveal significant differences between RET3D scores and diet (X^2_3=7.04, p=0.07).

However, excluding RET3D scores from the M_4 of *Hypsiprymnodon moschatus* prompted a significant correlation (Kruskal–Wallis X^2_3=8.33, p=0.04), suggesting that tooth identity is important for RET3D analysis when there are strong anterior–posterior gradients in tooth size.

Table 4.4.Variation in M_2/M_3 RET3D scores across 11 extant macropodoid species.

Species	**Median RET3D**	**Diet**	**Minimum**	**Maximum**	**n**
Aepyprymnus rufescens	20.86	Mixed	18.62	23.10	2
Dendrolagus lumholtzi	15.64	Browser	15.20	16.09	2
Hypsiprymnodon moschatus	19.98	Fungivore	19.98	19.98	1
Macropus fuliginosus	21.85	Grazer	21.15	22.56	2
Macropus robustus	22.36	Grazer	15.92	26.84	31
Macropus rufus	20.44	Grazer	18.74	22.13	2
Petrogale concinna	24.65	Mixed	17.72	24.78	3
Potorous tridactylus	19.26	Fungivore	18.65	19.87	2
Setonix brachyurus	19.76	Browser	19.75	19.77	2
Thylogale stigmatica	21.96	Mixed	21.43	22.50	2
Wallabia bicolor	25.41	Mixed	25.41	25.41	1

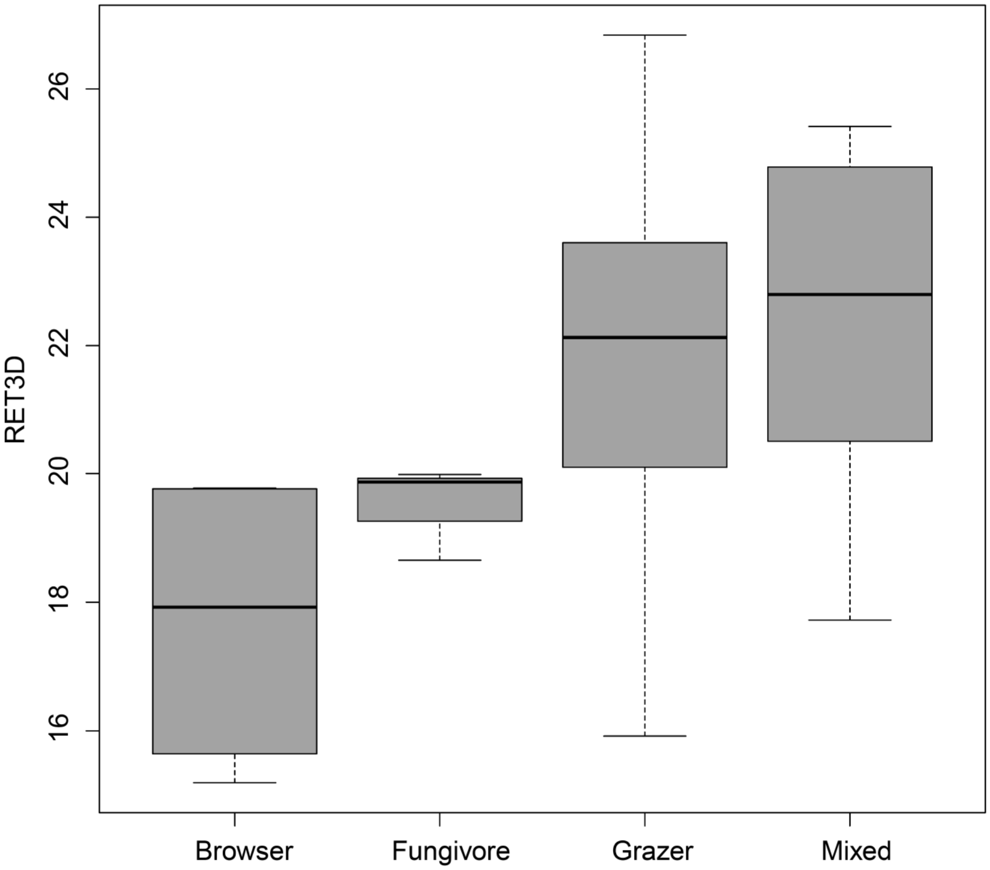

Figure 4.7. Box and whisker plot showing the relationships between RET3D and diet for 11 living macropodoid species. Bold horizontal line is the median, lower and upper box margins are first and third interquartile ranges respectively, and whiskers reflect maximum and minimum data points.

4.4.5 Linear Predictors of Molar Enamel Volume

Two-dimensional linear measurements of enamel thickness are generally highly correlated with whole crown enamel volume. Calculations of the coefficient of determination (R^2) based on ordinary least-squares regression and major axis regression produce similar results (Table 4.5). The most highly correlated linear predictor of enamel volume is the enamel thickness of the posterior trigonid wall (PTW; major axis, R^2=0.98), although ABTW and HCA also have coefficients exceeding 0.90 (Table 4.5). Enamel thickness measurements from tooth basins generally have much lower correlations with whole-crown volume than predictors from other tooth regions. The linear relationship between HCA and EVOL had a much lower slope than other linear predictors (Figure 4.8), which is cusp-apex enamel is relatively thicker for a given enamel volume.

Table 4.5. Linear and major axis regressions of species mean two-dimensional enamel thickness against whole-crown enamel volume. Abbreviations: ABTW; anterobuccal talonid wall, HCA; hypoconid cusp apex, TALB; talonid basin, ALTW; anterolingual talonid wall, TRGB; trigonid basin, ATW; anterior trigonid wall, PTW; posterior trigonid wall.

Linear parameter	**ABTW**	**HCA**	**TALB**	**ALTW**	**TRGB**	**ATW**	**PTW**
Linear model adj. R^2	0.95	0.93	0.81	0.81	0.76	0.87	0.98
Linear model P statistic	<<0.01	<<0.01	<<0.01	<<0.01	<<0.01	<<0.01	<<0.01
n	8	6	8	9	8	9	9
Major axis R^2	0.96	0.95	0.84	0.83	0.80	0.88	0.98
Major axis P statistic	<<0.01	<<0.01	<<0.01	<<0.01	<<0.01	<<0.01	<<0.01

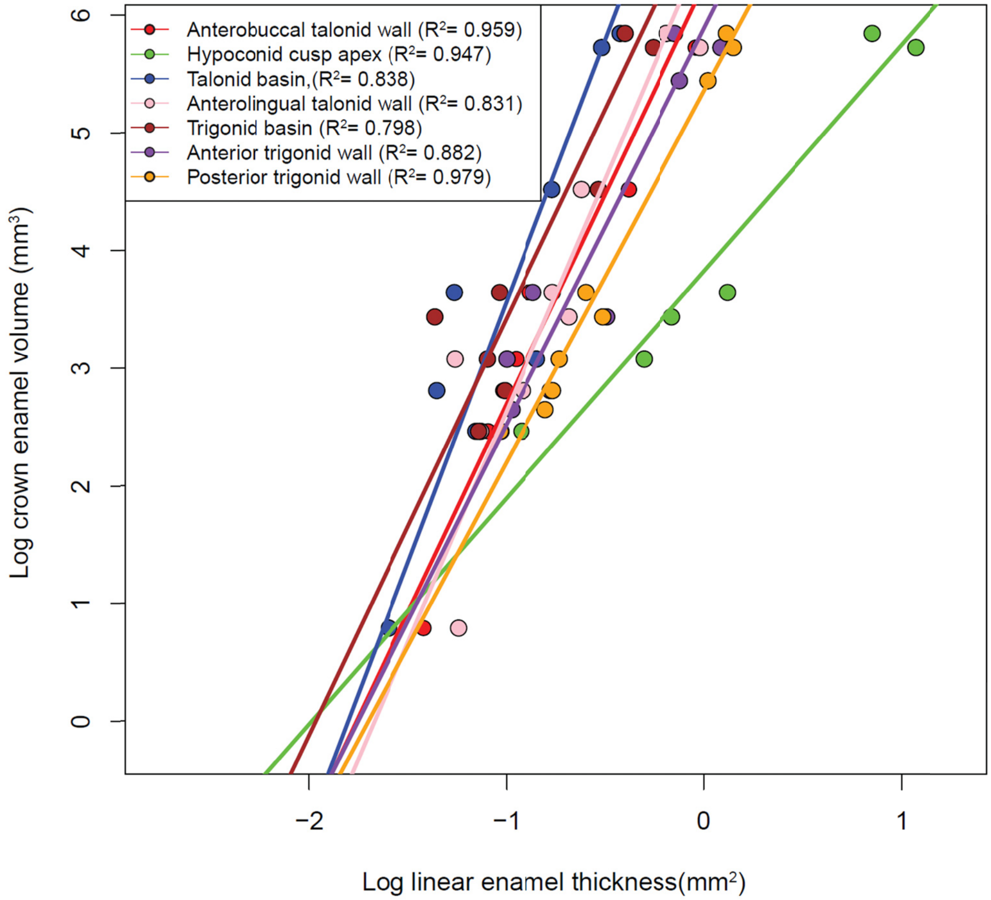

Figure 4.8. Major axis regression of log transformed species mean linear enamel thickness and molar-crown enamel volume. The relationship between hypoconid cusp apex enamel and whole-crown enamel volume is very different from other tooth regions. Based on the coefficient of correlation, enamel thickness of the posterior trigonid wall is the best linear predictor of whole-crown enamel volume.

4.5 Discussion

This study provides the first detailed examination of enamel thickness variation in a non-primate group. Whilst there is considerable variation across macropodoid species in terms of whole-crown enamel thickness (Table 4.4), our bootstrapping approach suggests that at a population-level, even relatively small sample sizes ($n \geq 2$) provide a precise estimate of the 'population' median (within 95% confidence intervals). Furthermore, the intraspecific variability within *Macropus robustus* suggests that samples sizes greater than 7 estimate mean RET3D to within one standard deviation (1σ). These results suggest that even comparatively small samples of fossil teeth could provide a relatively accurate picture of species-level enamel thickness in Macropodoidea. Our results also show that linear measurements of enamel thickness from the anterobuccal talonid wall, posterior trigonid wall, and hypoconid cusp apex provide relatively accurate estimates of whole-crown enamel volume, with coefficients of determination equal or exceeding 0.95 (Figure 4.8). This observation suggests that whole-crown enamel volume should be accurately inferable from damaged fossil specimens, or those where heavy mineralisation reduces tissue contrast on microCT scans.

Variation in molar enamel thickness is commonly linked to functional factors like diet (Lucas et al. 2008). However, the analysis presented here bolsters the view that there is no simple 'threshold' relationship between enamel thickness and diet (Dumont 1995). Instead, we find evidence for clade-specific constraints that 'trap' lineages in local adaptive optima. For instance, the relatively thick molar enamel of the browsing macropodine *Setonix brachyurus* is more similar to mixed feeding and grazing macropodines than other browsers like *Dendrolagus* (Figure 4.5; Figure 4.6). These incongruencies between diet and relative enamel thickness might reflect the broad nature of diet categorisations used and the seasonally variable diets of most macropodoids (Arman and Prideaux 2015). However, Dumont (1995) also found limited evidence for convergence between frugivorous chiropterans and primates. Ecologically the only primate comparable to grazing kangaroos like *Macropus*, based on year-round reliance upon grasses, is the cercopithecine *Theropithecus gelada* (Iwamoto 1974; Dunbar 1977). Three-dimensional relative enamel thickness scores are unavailable for *T. gelada* but two-dimensional relative enamel thickness values for this taxon (e.g. Shellis et al. 1998; McGraw et al. 2012; Pampush et al. 2013) fall *below* the RET3D range of grazing macropodoids (Table 4.4; Figure 4.7). This is despite both *Macropus* and *Theropithecus* evolving within the last 4 million years (Cerling et al. 2013; Phillips et al. 2013). This might be further evidence of constraints on the enamel phenotype especially given that RET2D underestimates RET3D scores in most primates (Olejniczak et al. 2008a). At the opposite end of the dietary spectrum, several species of cercopithecine and hominoid primate consume large quantities of leaves (i.e., Bunn and Ungar 2009) like browsing macropodines such as *Dendrolagus* (Arman and Prideaux 2015). However, whilst hominoids like *Gorilla* seasonally consume large quantities of fibrous foods (Nishihara 1995; Kuroda et al. 1996) in addition to feeding preferentially on fruit (Doran et al. 2002), they have much thinner enamel than browsing macropodines. This raises the question: where are the very thin-enamelled macropodoids equivalent to primates like *Gorilla*, *Pan* and *Symphalangus*? We suspect that this thin-enamelled region of morphospace was actually occupied by extinct sthenurinae and balbarine kangaroos.

Our results thus suggest that while enamel thickness may have the potential to be responsive to selection across short time-scales (Hlusko et al. 2004; Ungar and Hlusko 2016), at larger time-scales phylogenetic constraints influence enamel thickness variation. Traits may become ‘trapped’ in local optima when the relationship between the genotype–phenotype map results in discontinuities in morphospace (unrealisable phenotypes), or when the link between a phenotype and the optimum fitness is very complex (Salazar-Ciudad and Marin-Riera 2013; Marshall 2014). When the phenotype–fitness landscape is relatively complex, even small movements from an ancestral state risk migration into a local optimum, far from the global optimum (Salazar-Ciudad and Marin-Riera 2013). Some traits such as occlusal complexity are more likely to reach the global optimum because they have high ‘degeneracy’ whereby very different morphologies can have similar fitness values (Salazar-Ciudad and Marin-Riera 2013). For instance, despite starkly different cusp morphologies the occlusal complexity of postcanine dentitions in carnivorous rodents and carnivorans is broadly equivalent (Evans et al. 2007). Relative enamel thickness should theoretically also have high degeneracy because different crown types could converge on the same relative enamel volume. For instance, our analysis shows that overlapping relative enamel volumes evolved amongst macropodine kangaroos like *Macropus* and hominins including *Paranthropus robustus* and *Homo sapiens* (Table 4.4, Olejniczak et al. 2008a). High degeneracy of enamel phenotypes could be advantageous if lifetime investment in enamel was selectively favoured to improve dental durability.

Our analysis uncovered significant variation in enamel thickness across the occlusal surface. The drivers of this variation are unclear because the primary axis of enamel-thickness variation is not straightforwardly related to either diet or phylogeny. We hypothesise that the primary axis of enamel thickness variation (PC1) may reflect a developmental 'signature' associated with enamel formation (amelogenesis). Supporting this, PC1 loadings between tooth regions are very even as would be expected if variance between tooth regions was globally coordinated by a developmental factor. The lack of phylogenetic covariation implies a deeply-conserved developmental signature, encompassing all Macropodoidea.

Diet was an important determinant of variation across functional tooth structures like the cusp tips and tooth basin floor (Table 3.3) because separation between diet groups increased when analysis was restricted to these 'core' functional regions. Eigenvector scores suggest that enamel thickness at the cusp apex (hypoconid; HCA) has a disproportionately large influence on variance compared with other tooth regions (Table 4.3). Interestingly, the sign of the HCA eigenvector was opposite that of other tooth regions (Table 4.3) suggesting that cusp-apex enamel plays a unique functional role. Functional variation in enamel thickness is partitioned along a gradient defined by fungivores and browsers, typified by relatively thin cusp-apex and talonid-basin enamel, through to mixed-feeding and grazing kangaroos with thickly-enamelled cusp apices and tooth basins. We hypothesise that this partitioning by diet reflects (1) differences in the occlusal interactions of bunodont, compared with bilophodont teeth, and (2) the importance of enamel thickness in optimising blade function when rates of dental wear are high. Macropodoids that crush food items with cusps (e.g., potoroines, hypsiprymnodontids) have relatively little contact between the cusp tip and opposing tooth basin, as indicated by the absence of planar occlusion facets. In these macropodoids, food properties are likely the most important functional determinant of cusp and basin enamel thickness. The relatively thin enamel of potoroines and hypsiprymnodontids are consistent with their reliance upon soft, brittle foods like fungi (Arman and Prideaux 2015).

Bilophodont macropodids utilise a double-bladed dental system where food is fractured between opposing crests (Sanson 1989). Because blades are more efficient at fracturing thin, ductile foods like leaves than cusps (Lucas 2004) the transition between bunodont and bilophodont teeth likely reflects a diet switch to tougher foods. The different dynamics of food fracture in cusp- compared with bladed-occlusal systems was likely an important influence on enamel thickness evolution. In bladed systems, precise contact is needed between the opposing relief surfaces of the upper and lower blades for efficient cutting (Evans 2005; Anderson and LaBarbera 2008). Three-dimensional mapping shows that the localisation of thick enamel along the relief surface distinguishes browsers from fungivorous macropodoids (Figure 4.2) and thus thick enamel may help to maintain blade contact. Within the folivorous macropodoids the PC2 axis can be differentiated into browsers with relatively thinly-enamelled cusps, and mixed feeders and grazers with more thickly-enamelled cusp tips. As the hypoconid is integrated into the transverse crest on the talonid (the hypolophid), the cusp apex enamel thickness provides a proxy for blade-edge enamel thickness. The thinner enamel deposited over the blade tip in browsers (Figure 4.2) is probably advantageous because it leads to more rapid exposure of the enamel–dentine junction and faster formation of a secondary occlusal morphology. In contrast, the thicker enamel along the crest edge and posterior blade margin in grazers and mixed feeders (Figure 4.2) slows exposure of the dentine and increases the enamel volume which must be stripped by abrasion before the cutting edge is obliterated (Figure 4.9). Thicker enamel may thus provide a mechanism to maintain blade function in the face of high wear rates. All folivorous macropodoids likely benefit from the increased cutting efficiency associated with dentine exposure (e.g., Fortelius 1985; King et al. 2005). However, grazing and mixed feeding kangaroos must balance the intermittent improvement in fracture efficiency afforded by dentine exposure with the acceleration of loph collapse it promotes (Koenigswald. 2014). This may indicate that an important functional ‘pivot-point’ lies along the browser–grazer spectrum, whereby taxa must preference either preservation of blade integrity or establishment of a secondary occlusal morphology.

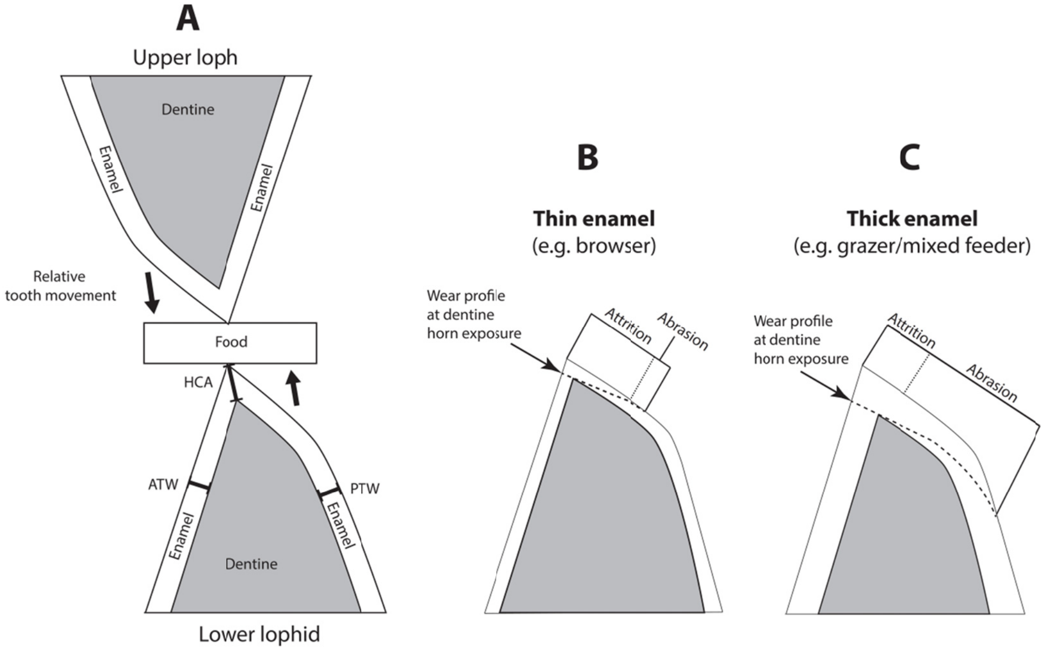

Figure 4.9. Schematic lateral view of (A) blade function associated with the trigonid wall (protolophid) and changes in blade morphology with (B) thin molar enamel typical of a browser and (C) thick molar enamel typical of mixed feeding and grazing kangaroos. Only wear-induced changes associated with food fracture during the initial phase of occlusion are described. Abbreviations: ATW, anterior trigonid wall; PTW, posterior trigonid wall; HCA, cusp-apex enamel. Attrition abrasion boundary denoted by finely dashed line.

Functional factors should drive partitioning of variances between different tooth regions, because each operates as a distinct tool during food breakdown (Evans and Sanson 2003). However, the similar magnitude and sign of the PC1 eigenvector for enamel thickness across different tooth regions, as well as the lack of a clear functional signal along this axis, suggests that covariation between tooth regions has been an important evolutionary constraint. Given that just three enamel matrix protein coding genes, *Amelx*, *Ambn* and *Enam*, are responsible for more than 97% of enamel protein secretion in mouse (Fincham et al. 2000, Wright et al. 2011) , covariation between the enamel thickness of different tooth regions could reflect pleiotropic effects. Enamel formation is a two-stage process involving an initial secretory step, where ameloblasts secrete enamel proteins into the extracellular matrix, and a second maturation step, when the organic matrix is almost completely replaced by inorganic hydroxyapatite crystallites (Fincham et al. 2000). Mutations in *Amelx* and two different mutations in *Enam* are linked with thin enamel phenotypes in mouse (Wright et al. 2009), and knockout of *Amelx* produced a ten-fold decrease in incisor enamel thickness (Wright et al. 2009). Proteases such as enamelysin (*Mmp-20*) and kallikrein-4 (*Klk4*), responsible for remodelling protein structure following secretion of the enamel matrix proteins (Kim et al. 2005), also have the potential to considerably alter enamel thickness (Wright et al. 2009, 2011). It is currently not possible to interpret both the linear and volumetric variation in primates or macropodoids in terms of genetic factors without comparable phenotypic data for knockout or knockdown experiments in mouse. A key future aim should be to examine the influence of enamel formation genes in mammals beyond mouse, and to more accurately quantify variation in enamel thickness in existing and future animal models with microCT.

It is interesting that most of the functional variation in enamel thickness is localised to the cusp tips, especially given that the dentine horns, which structurally underpin cusp shape, are remnants of gene signalling centres that coordinate cusp patterning (Jernvall and Thesleff 2000). In hominin primates, transcription factor binding sites (e.g., SOX9, OCT1, DLX5) are situated upstream from promoters for enamel secretion and maturation genes, and there is evidence that at least some of these regulatory regions have been subject to selection (Horvath et al. 2014). The evidence for a molecular link between signalling proteins secreted during tooth patterning and mineralisation genes raises the prospect that patterning of the tooth crown may strongly influence enamel thickness variation. Consistent with this, enamel mineralisation typically initiates first at the apex of the dentine horn in unerupted kangaroo molars (Couzens, unpublished data). It may thus be difficult for enamel thickness variation across other parts of the tooth crown to become decoupled from variation at sites proximal to the enamel knots, like the cusp tips, and these sites may thus play an important role in coordinating enamel thickness variation across the crown.

4.6 Conclusions

In this paper we have quantitatively examined variation in two- and three-dimensional enamel thickness in macropodoids and tested the relationship between this variation and functional and developmental factors. We find that several macropodine species independently acquired molar enamel comparatively as thick as that amongst hominins such as *Homo* and *Paranthropus* (Olejniczak et al. 2008a, b; Benazzi et al. 2014). Interestingly, the largest component of enamel variation is not strongly correlated to diet or phylogeny and instead may reflect processes associated with amelogenesis. Computation of three-dimensional relative enamel thickness reveals that extant macropodoids exhibit lower levels of disparity than primates, consistent with their narrower dietary diversity. We find that most of the functional variation in enamel thickness is localised to the edge of the crests and cusps where it likely modulates fracture efficiency. The thin-enamelled crests of browsing kangaroos promote formation of a sharp cutting edge, whereas the thick-enamelled crest edge and relief surface of mixed feeding and grazing taxa may act to slow obliteration of the blade edge. Thus, while previous work has linked enamel thickness to food hardness (Kay 1981; Martin 1985) our anlysis shows that thick enamel can also be an adaptation to high dental wear rates. Our work thus demonstrates the plausibility of dental wear as a selective driver of thick molar enamel in hominin lineages (Molnar and Gantt 1977; Rabenold and Pearson 2011). We predict that enamel thickness will prove to be an important factor underpinning mammalian dietary adaptation more broadly.

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5. KANGAROOS EVOLVED THICK MOLAR ENAMEL AS AN ADAPTATION TO NEOGENE ARIDIFICATION

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Context

This chapter examines how patterns of enamel thickness evolution were linked to aridification and vegetation change during the late Neogene. Using high resolution X-ray micro-computed tomography I quantified two- and three-dimensional molar enamel thickness in fossil macropodoids spanning the past 25 million years. The coevolutionary relationship between molar enamel thickness and crown height is examined and an alternative model of herbivore dietary adaptation is proposed.

Statement of Authorship

AMCC designed the research, collected data, performed analysis and wrote the manuscript. GJP contributed to experimental design, provided guidance and advice, and commented on the draft manuscript.

Key words: Macropodoid, microCT, Australia, diet, teeth.

5.1 Abstract

Changes in diet characterize critical periods in the evolution of major mammalian groups. The aridification of terrestrial ecosystems during the Neogene resulted in some herbivores shifting from diets reliant on dicotyledonous browse, toward increasing reliance on abrasive grasses and shrubs. A common mechanism by which herbivores increase dental durability to consume these foods was by increasing tooth crown height. However, there is a greater than ten-fold variation in mammalian crown height and some groups which consume grasses retained a low-crowned dentition. Macropodoids are the most diverse marsupial herbivores, but despite most species consuming grass, they lack the very high-crowned prismatic molars typical of grass-consuming ungulates and rodents. We hypothesised that macropodoids instead invested in thick molar enamel as a mechanism to adapt to increased levels of dietary abrasion during the Pliocene. To test this we examined changes in macropodoid molar dental wear, crown height, and enamel thickness over a 25 million year interval. During the early Neogene dental wear levels were low but there is a marked increased during the Pliocene, especially amongst macropodine kangaroos. The increase in Pliocene dental wear amongst macropodine kangaroos is associated with an approximate doubling of molar enamel thickness. In contrast, from at least the late Miocene sthenurine kangaroos evolved a thin-enamelled molar phenotype. Dental wear data suggest that sthenurine kangaroos further specialised into a low-abrasion diet during the middle and late Pleistocene, around the time that their species richness and abundance peak. We predict that variation in enamel thickness is likely to be an important adaptive alternative to evolving very high-crowned dentitions, especially amongst mammals with bladed dentitions like diprotodont marsupials, proboscideans, trichechid sirenians, and cercopithecine primates. Our results thus support a ‘many-to-one’ model of trait adaptation where contingency strongly shapes the optimum phenotypic solution for a given fitness landscape.

5.2 Introduction

Periods of dietary change are linked to important intervals of diversification in different mammalian groups (Mihlbachler et al. 2011; Ungar and Sponheimer 2011; Wilson et al. 2012). Herbivores are especially sensitive to dietary change because the composition of vegetation resources they rely on fluctuate in response to climatic variables (Cramer et al. 2001). Climate has varied markedly over the Cenozoic (past 65 million years) (Zachos et al. 2001), during which the bulk of modern mammalian diversity emerged (O'leary et al. 2013). During the late Cenozoic there was pronounced global cooling, associated with declining atmospheric CO_2 levels, and intensification of circum-Antarctic ocean circulation (Pearson and Palmer 2000; Zachos et al. 2001). The Miocene–Pliocene transition is an especially important phase in this cooling trajectory because it marks the point at which atmospheric CO_2 levels fell sufficiently low to promote diversification of open, primarily C_4 photosynthesing plant ecosystems, dominated by grasses and xeric scrub (Cerling et al. 1997). Herbivores feeding in these ecosystems are subject to high levels of dietary abrasion arising from increased ingestion of grit, tooth enamel fragments, and siliceous plant cell inclusions (phytoliths) (Baker et al. 1959; Mendoza and Palmqvist 2008; Lucas et al. 2013; Xia et al. 2015). Herbivores have evolved a suite of dental adaptations to combat dental wear (Janis and Fortelius 1988). These include increasing tooth crown size (Fortelius 1985; Damuth and Janis 2011; Tapaltsyan et al. 2015), replacing worn tooth crowns (Gomes Rodrigues et al. 2011; Beatty et al. 2012), increasing blade length (Lucas 2004), increasing enamel thickness (Lucas et al. 2008; Raebenold and Pearson 2011; Van Dam et al. 2011; Pampush et al. 2013; Ungar and Hlusko 2016), or modifying enamel microstructure (Rensberger 2000).

Although a range of adaptive pathways exist, many lineages increase the vertical size of the tooth crown (Janis and Fortelius 1988). Increases in crown height are likely to be homoplastic because developmental and ecological factors promote the 'evolvability' of this trait (Tapaltsyan et al. 2015). However, crown height varies more than 10-fold across mammalian herbivores, and many herbivores consuming abrasive foods (e.g. diprotodont marsupials, trichechids sirenians, cercopithecine primates) lack very high-crowned dentitions (e.g. Janis 1990; Lister 2013). Potentially, these herbivores followed a different adaptive pathway from that epitomised by artiodactyl ungulates (e.g. Fortelius 1985; Janis and Fortelius 1988), perhaps because they were forced to optimise functionally non-ideal dental morphologies (Ungar and Hlusko 2016). This model of herbivore dietary adaptation thus emphasises a 'many-to-one' concept, where different phenotypes can have similar fitness optima (Salazar-Ciudad and Marin-Riera 2013).

Modulating enamel thickness provides a potentially important mechanism to improve dental durability because thicker enamel should slow the destruction of functional tooth features like cusps and crests (Lucas et al. 2008; Ungar and Hlusko 2016). Consistent with this, molar enamel is relatively thicker in primates which ingest a greater phytolith load (Rabenold and Pearson 2011; Pampush et al. 2013). Additionally, isotopic and microwear data suggest that the thickest-enamelled hominins were primarily consuming abrasive grasses or sedges (Ungar et al. 2008; Cerling et al. 2011). Qualitative appraisals also indicate that many late Cenozoic herbivore groups like the proboscideans and sirenians evolved thick molar enamel (Domning 1982; Sanders et al. 2010). However, the adaptive role of thick enamel remains controversial (Constantino et al. 2009; Rabenold and Pearson 2011; Strait et al. 2013; Ungar and Hlusko 2016) because many thick-enamelled primates also consume significant quantities of hard foods for which thick enamel might help resist tooth fracture (Kay 1981; Lucas et al. 2008). Comparative data on enamel thickness from non-hard-object feeding herbivores is needed to test whether thick enamel was an important adaptive response to increased levels of dietary abrasion.

Kangaroos, wallabies, and their close relatives (Superfamily Macropodoidea) are a diverse radiation (~extant 70 species) of primarily folivorous herbivores (Prideaux and Warburton 2010; Arman and Prideaux 2015). Although molecular data suggest that macropodoids diverged from other phalangeriform marsupials in the middle Eocene, the most diverse extant kangaroo groups like the Macropodinae and extinct Sthenurinae only emerged relatively recently during the late Neogene (Prideaux 2004; Meredith et al. 2009; Prideaux and Warburton 2010; Phillips et al. 2013). Macropodoid evolution across the Miocene–Pliocene transition is associated with a doubling in molar crown height disparity, probably reflecting macropodine diversification into grass-dominated Pliocene ecosystems (Chapter 2). But this still leaves macropodoids with substantially lower-crowned dentitions than other grass consuming herbivores (Janis 1990). Accordingly, it remains unclear what types of dental adaptations macropodoids may have acquired to deal with high-levels of dental wear.

Here we test whether macropodoids evolved thick molar enamel as a mechanism to deal with high levels of late Neogene dental wear. To do this we integrate high resolution X-ray microCT-based measurements of enamel thickness with dental wear and molar crown height data to track dietary adaptation over a 25 million year interval.

5.3 Methods

5.3.1 Dental Imaging

Teeth (n > 300) from fossil and living macropodoids, phalangerid, and diprotodontoid marsupials were scanned with high resolution X-ray microCT at voxel sizes between 9 and 42 µm. Fossil specimens were sourced from collections at the Australian Museum, Flinders University Palaeontology Laboratory, South Australian Museum Adelaide, Queensland Museum, University of California Museum of Paleontology, and Western Australian Museum. Specimens were imaged with X-ray absorption micro-computed tomography (microCT) scanners at: Department of Applied Physics, Australian National University (custom industrial microCT machine), Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology (Actis BIR 225 industrial microCT machine), and Adelaide Microscopy (SkyScan 1076 desktop microCT).

Two-dimensional linear enamel thickness (LET) measurements were collected from seven tooth regions using the *oblique slice* tool in Avizo 8.1 as described in Chapter 4. Three-dimensional relative enamel thickness (RET3D) scores were computed for 14 fossil macropodiforms, one phalangerid, and two diprotodontoid species following methods outlined in Chapter 4. Fractured teeth were reconstructed by filling cracks with 'enamel' enabling straightforward segmentation and production of a manifold dentine surface. After extraction of the enamel–dentine junction surface the coronal aperture was closed with the 'trivial' method in the *Fill holes* function in MeshLab v1.3.1.

5.3.2 Dentine Exposure

Dentine exposure was scored using a modified version of the McArthur–Sanson wear index (McArthur and Sanson 1988; Figure 5.1). Six additional wear patterns (Figure 5.2) were included to capture wear patterns not observed in extant macropodine kangaroos. Teeth were scored in occlusal view within one of eight dentine exposure categories ranging from unworn (0) to heavily worn (7). Teeth with intermediate wear stages were assigned to the lower dental wear stage except for slightly worn teeth ("0.5") which were assigned to wear state "1". Teeth categorised for wear were randomly sampled from collections. Only lower second and third molars ($M_{2, 3}$) were included in the analysis because the different morphology of the M_1 and M_4 resulted in different dentine exposure patterns. To increase sample size, isolated fossil teeth likely to be M_2 or M_3 were also included. Teeth were assigned to eight taxonomic groups and binned in Australian land mammal ages (i.e., Megirian et al. 2010).

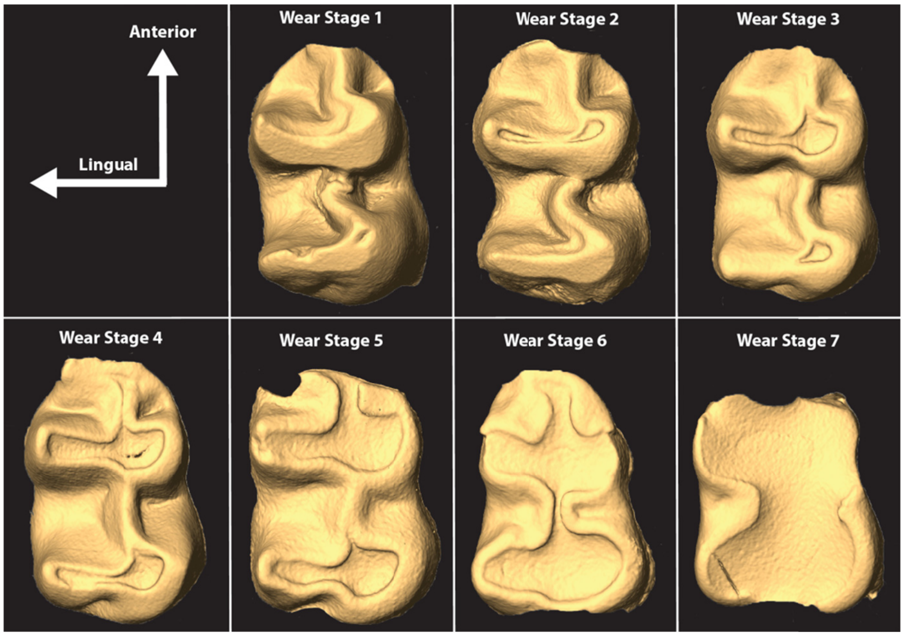

Figure 5.1. Dentine exposure levels based on the McArthur–Sanson wear index (McArthur and Sanson 1988). Example levels are based on specimens of *Macropus robustus*.

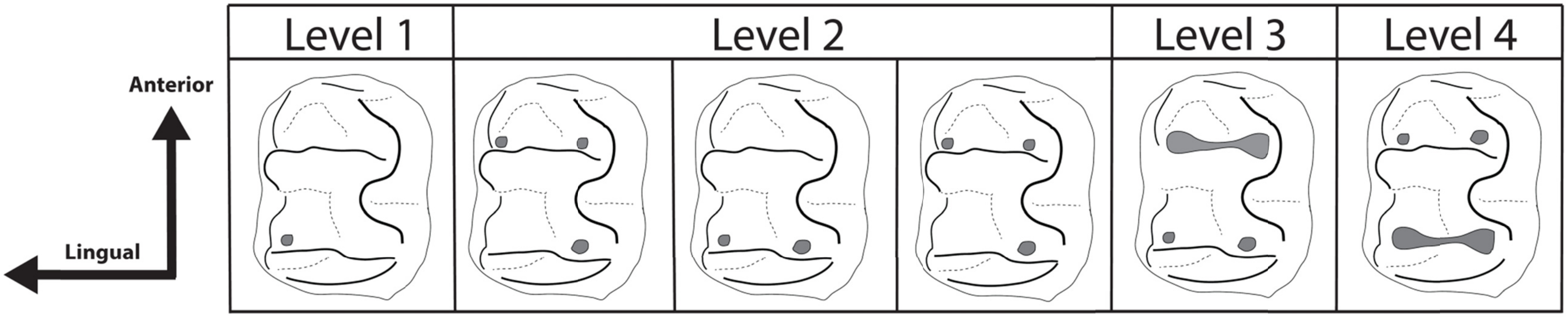

Figure 5.2. Alternative dentine exposure levels recognised in macropodoids.

5.3.3 Statistical Analysis

Linear enamel thickness (LET) data were standardised for size by dividing linear enamel thickness measurements from each of the seven tooth regions by the square root of rectangular bicervical area, calculated as the mean of maximum trigonid and talonid bicervical width, multiplied by maximum anteroposterior bicervical length. Variation was visualised with a principle component analysis implemented with `prcomp` in `R` (version 3.1.1; R Core Team 2014). Major axis regression was implemented with `lmodel2`. Ancestral state reconstruction of relative enamel thickness and molar cusp height was performed using a Brownian motion model with the `ace` function in `ape` (Paradis et al. 2004) and the `REML` method. A previously published timescaled morphological phylogeny was used for this analysis (Prideaux and Warburton 2010; Couzens et al. 2016).

5.4 Results

5.4.1 Dentine Exposure

Considerable variation exists in dentine exposure levels both between taxonomic groups and across Australian land mammal ages (ALMA) (Table 5.1). There is an increase in median dentine exposure levels in younger land mammal ages. Median dentine exposure levels are similar in the Wipajirian, Camfieldian, and Waitean but increase in the Tirarian for both macropodine and sthenurine kangaroos. Tirarian lagostrophines display low median levels of wear (1.5) but the range of dentine exposure scores is comparable to Tirarian macropodines. For all macropodoids, except sthenurines, Naracoortean wear levels are higher than preceding land mammal ages. Modern macropodine dentine exposure is lower than for the Naracoortean but this likely reflects undersampling of browsing macropodines like *Dendrolagus* and *Dorcopsis* which are uncommon in Naracoortean assemblages.

Table 5.1. Summary statistics for dentine exposure levels (1–7) across seven major macropodoid groups binned by Australian land mammal age (i.e., Megirian et al. 2010).

Taxonomic group		**Wipajirian**	**Camfieldian**	**Waitean**	**Tirarian**	**Naracoortean**	**Modern**
Balbarinae	**Median**	1	1	–	–	–	–
	Range	4	3	–	–	–	–
	n	34	9	0	0	0	0
Hypsiprymnodontidae	**Median**	1.5	–	–	–	–	1
	Range	1	–	–	–	–	0
	n	2	0	0	0	0	1
Lagostrophinae	**Median**	–	–	–	1.5	2.5	–
	Range	–	–	–	5	3	–
	n	0	0	0	20	2	0
Macropodidae	**Median**	1	1	–	–	–	–
	Range	5	3	–	–	–	–
	n	77	13	0	0	0	0
Macropodinae	**Median**	–	–	1.5	3	4.5	3
	Range	–	–	4	6	6	6
	n	0	0	38	45	6	211
Potoroinae	**Median**	–	–	–	–	–	1
	Range						
	n	0	0	0	0	0	16
Sthenurinae	**Median**	–	2	1	2.5	1	–
	Range	–	5	3	1	3	–
	n	0	4	10	2	14	0

5.4.2 Two-Dimensional Measurements of Enamel Thickness

Based on PCA of the full linear data matrix, principle components (PC) 1–5 cumulatively account for 96.3% of total variance. The first three principle components, which together account for 88.6% of total variance, partition the potoroines *Bettongia* and *Potorous* from the bilophodont macropodoids (Figure 5.3). Restricting analysis to the first two principle components (83.4% cumulative variance) reveals a strong phylogenetic component to the data wherein taxa cluster with more closely related members (Figure 5.3). The most basal fossil macropodoids, like *Ngamaroo* and *Gumardee*, fall within the centre of the morphospace, with *Ngamaroo* proximal to macropodine mixed feeders, and *Gumardee* close to browsing *Dendrolagus* (Figure 5.3). No fossil macropodoids fall proximal to the living fungivores *Bettongia* and *Potorous*.

Relative to other macropodoid clades the Lagostrophinae fall closest to the Macropodinae. The most basal macropodine kangaroos included in the analysis such as *Prionotemnus* and *Dorcopsoides* are proximal to, but outside, the extant mixed feeding convex hull. *Protemnodon* is distant from other macropodines, falling within the sthenurine hull. The extinct lagostrophine *Troposodon* falls closest to extant mixed feeding *Lagostrophus*. The Sthenurinae overlap with convex hulls for the balbarine and macropodine kangaroos, but there is no overlap with extant members of these two clades. Basal sthenurines like *Rhizosthenurus* and *Wanburoo* fall closest to browsing *Dendrolagus*, but derived sthenurines like *Procoptodon*, *Sthenurus*, and *Simosthenurus* are not closely aligned with any living kangaroos.

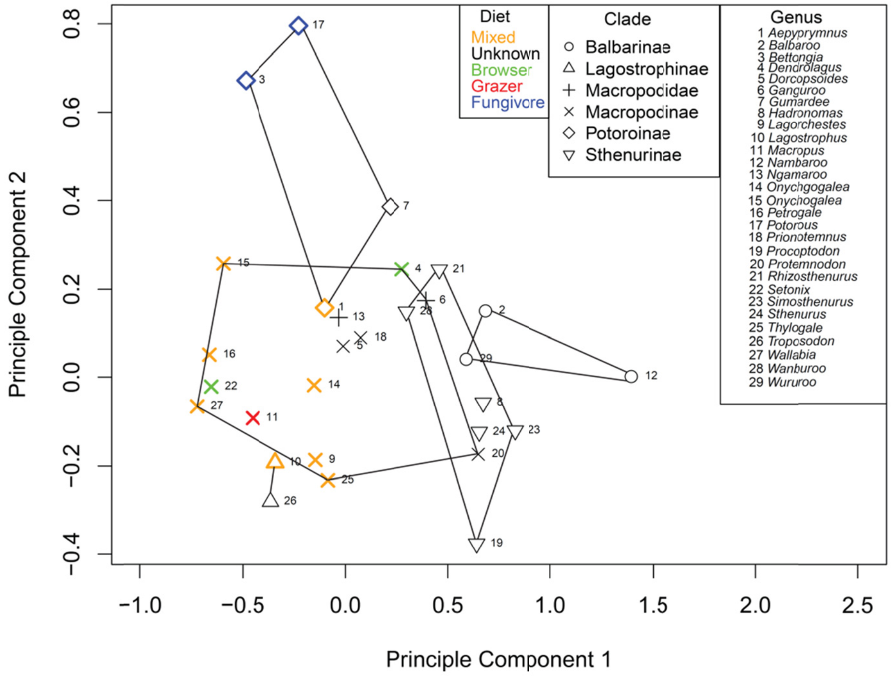

Figure 5.3. Bivariate plot of principle components 1 and 2 for linear enamel thickness data across 29 extant and fossil macropodoid genera. The 13 extant genera are colour coded by diet following Arman and Prideaux (2015). Different symbols reflect subfamily affiliation with morphospace occupation for each defined by convex hulls.

5.4.3 Three-Dimensional Relative Enamel Thickness (RET3D)

Marsupial RET3D scores ranged from 6.43 in the diprotodontid *Zygomaturus trilobus* to 26.90 in the macropodine, *Macropus robustus*. Amongst macropodoids the sthenurines and balbarines have the lowest RET3D scores and are most similar to the pseudocheirid *Trichosurus vulpecula*. Thus, comparatively high RET3D scores seem to differentiate crown group macropodoids from balbarines, pseudocheirids and diprotodontids. Within Macropodoidea there is approximately a three-fold range in RET3D scores, with the sthenurines having the thinnest, and macropodines the thickest molar enamel (Figure 5.4). Ancestral state reconstruction (Figure 5.6) suggests that the different clade specific trajectories in RET3D amongst macropodine and sthenurine kangaroos evolved soon after their middle Miocene divergence. This view is bolstered by the relatively low RET3D scores of basal sthenurines like *Rhizosthenurus* and *Hadronomas* compared with basal macropodines like

Dorcopsoides (Figure 5.5). Given the relatively thick molar enamel inferred for the ancestral crown group macropodoids, the thin molar enamel of balbarine and sthenurine macropodoids may reflect convergence.

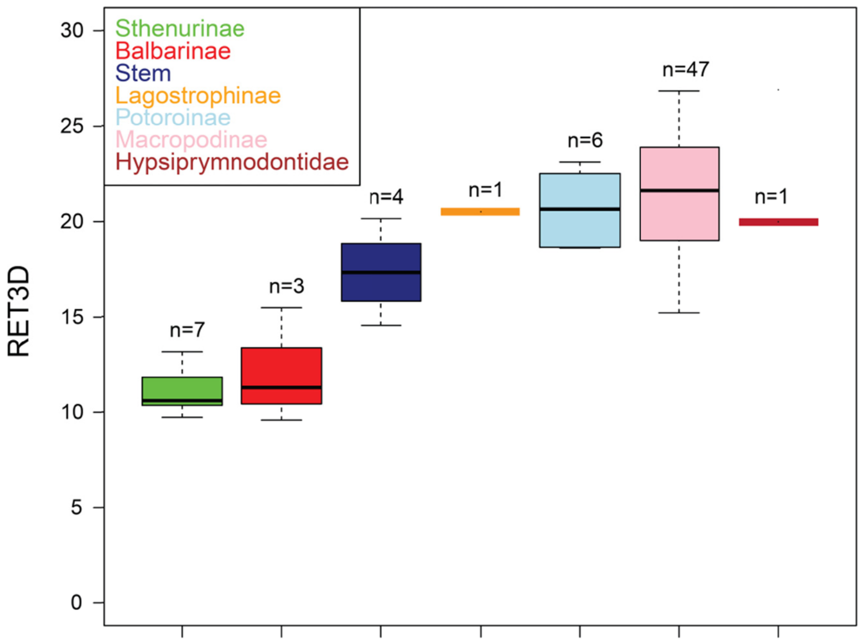

Figure 5.4. Boxplot of three dimensional relative enamel thickness (RET3D) across seven macropodoid groups.

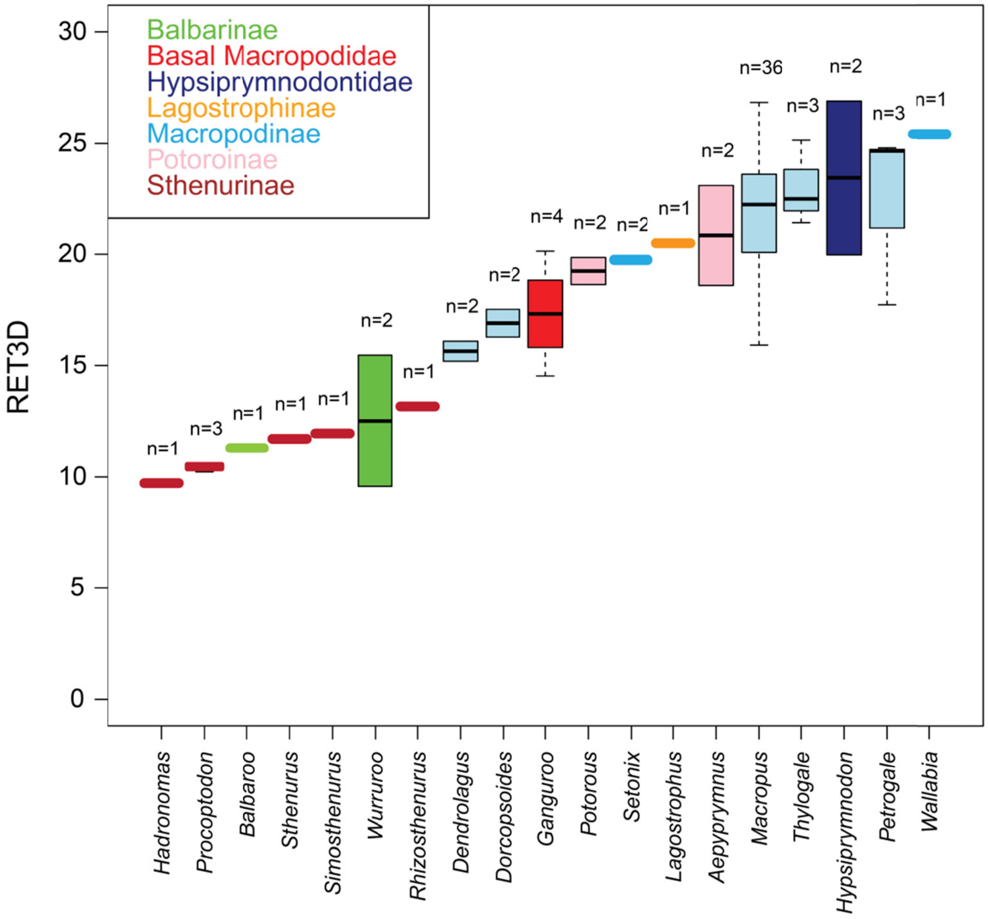

Figure 5.5. Boxplot of three dimensional relative enamel thickness (RET3D) for 19 fossil and modern macropodoid genera. Horizontal bars represent the median, the box defines the interquartile range, and the error bars represent the range. Relevant sample size (n) is indicated above each box.

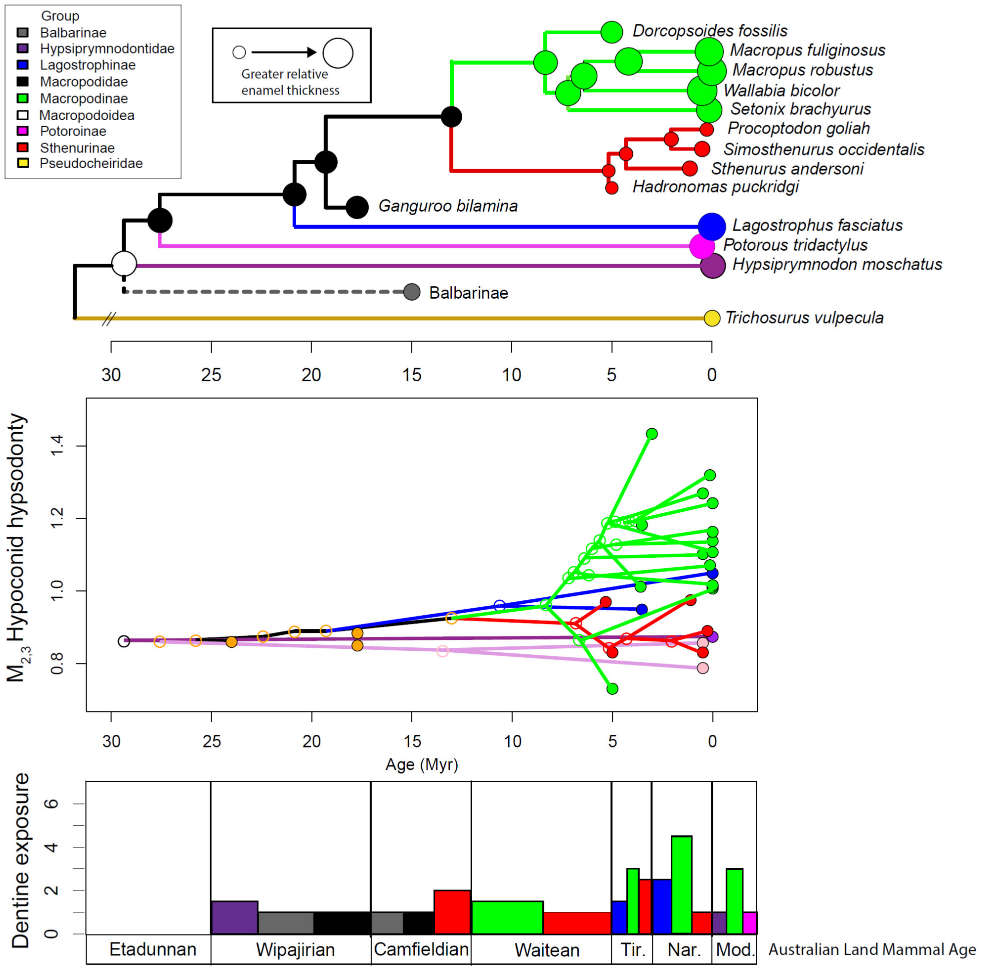

Figure 5.6. Patterns of molar crown height and enamel thickness evolution over the past 30 million years and correspondence with dentine exposure levels. Abbreviations: Tir., Tirarian; Nar., Naracoortean; Mod., Modern.

5.5 Discussion

Our data show that fossil and modern macropodoids exhibit similar RET3D disparity to extant primates (Olejniczak et al. 2008b), the only other well-sampled mammalian group. Interestingly, much of the increase in disparity relative to extant macropodoids (Chapter 4) is driven by the thin-enamelled extinct Balbarinae and Sthenurinae. These extinct groups fill a gap in extant macropodoid enamel thickness morphospace which amongst primates is occupied by thin-enamelled leaf consumers like *Gorilla* (Chapter 4). The presence of thin-enamelled balbarines and possums like *Trichosurus* close to the base of Macropodoidea suggests that thin enamel may have been the primitive state for ancestral macropodoids. However, with the exception of Sthenurinae, all crown group macropodoids possess thicker enamel than the Balbarinae or *Trichosurus*. This implies that either there were at least four separate origins of a thick enamel phenotype, or more parsimoniously, the ancestor of crown group macropodoids had thick-enamelled molars (Figure 5.6.). The starkly different RET3D scores of modern hypsiprymnodontids and extinct balbarines also weakens support for their monophyly (e.g., Black et al. 2014). Amongst bilophodont macropodids, RET3D scores for *Ganguroo* suggest that stem macropodids may have already possessed comparatively thick molar enamel by the middle Miocene, and thus that the thick molar enamel of derived macropodines like *Macropus* and *Petrogale* reflects the continuation of a trend in enamel evolution. In contrast, sthenurines likely reverted to a thin enamel phenotype after divergence from the macropodid stem as evinced by low RET3D scores in Miocene *Rhizosthenurus puckridgi* and *Hadronomas puckridgi*. Interestingly, browsing macropodines like *Setonix* and *Dendrolagus* (Arman and Prideaux 2015) have enamel approximately twice as thick as the sthenurine *Procoptodon goliah*, which dental morphology, stable isotopic, and microwear data suggest was also a browser (Prideaux et al. 2009). Overall, the pattern of enamel thickness evolution within Macropodoidea does not support the view that this trait has been highly evolvable (i.e., Ungar and Hlusko 2016) and instead suggests that phylogenetic 'constraints' have been important in shaping its evolution.

For the early Neogene, dental wear data suggest that macropodoids were subject to low levels of dietary abrasion. Median dentine exposure levels before the Pliocene did not compromise the shearing capacity of the tooth because the lophs remained intact (i.e., levels 1–2; Figure 5.1). The low levels of dentine exposure may also indicate that early macropodoids were subject to low levels of selection for dental durability. The proximity within the two-dimensional enamel thickness morphospace of *Ngamaroo archerii* and *Ganguroo bilamina* to extant browsing macropodids, rather than extant fungivores (Figure 5.3), suggests that basal macropodids were already acquiring a spatial distribution of enamel better suited to folivory. Low levels of dental disparity (Figure 5.6), both in terms of enamel thickness, dental wear and crown height, raise the possibility that basal macropodids shared similar diets and were not yet under pressure to partition food resources. Low levels of dietary abrasion also characterised the transition from bunodont to higher-crowned prismatic molars in North American equids (Mihlbachler et al. 2011). Since these basal macropodids possessed transitional dental morphologies (Cooke 1997), adaptive dietary transitions may be more likely during periods of relaxed stabilising selection (Simpson 1944).

High-resolution U–Pb dating of speleothem-derived pollen from southern central Australia suggests that aridification intensified during the late Miocene (Sniderman et al. 2016). However, the dental wear data suggests that macropodids did not shift to more abrasive diets until the Tirarian (Figure 5.6). Similar delays between environmental change and diet shifts occurred amongst North American equids (Stromberg 2006; Mihlbachler et al. 2011). Amongst east African proboscideans dietary change tracked environmental change across the Miocene–Pliocene transition but there was more than three-million years of adaptive lag in dental morphology (Lister 2013). In the case of macropodoids the increase in dietary abrasion during the Tirarian is correlated with a dramatic increase in molar crown height disparity associated with the spread of Pliocene grasslands (Chapter 2). However, divergence in enamel thickness between macropodine and sthenurine kangaroos was underway earlier, by at least the late Miocene, before the increase in Tirarian dietary abrasion levels (Figure 5.6). We hypothesise that by the late Miocene sthenurines had started to reduce enamel thickness in order to improve cutting efficiency of the lophids, whereas macropodines retained the comparatively thick-enamelled phenotype of basal macropodids like *Ganguroo*. The middle Miocene origination of Sthenurinae is approximately coeval with the last occurrence of thin-enamelled balbarine kangaroos, which might indicate that sthenurines evolved to fill the thin enamel morphospace vacated by the balbarines (Figure 5.6). The balbarines might also have been competitively displaced by the sthenurines as occurred amongst some proboscidean and equid lineages (Eronen et al. 2010; Lister 2013).

Unlike terrestrial ecosystems on other continents (i.e., Cerling et al. 1997) there is no evidence for widespread grasslands in Australian ecosystems before the late Pliocene (Macphail 1997; Sniderman et al. 2016). Instead, terminal Miocene and early

Pliocene habitats in Australia were likely dominated by open woodland and scrub (Murray and Megirian 1992; Macphail 1997; Kadereit et al. 2005). Isotopic analysis of fossil molar enamel from the middle Pliocene Chinchilla LF indicates that *Macropus* and *Protemnodon* were not yet reliant upon C_4 grasses or shrubs (Montanari et al. 2013). However, early Pliocene macropodines like *Prionotmenus*, although relatively low-crowned, were beginning to acquire a spatial pattern of enamel thickness more similar to extant mixed feeding macropodids than browsers (Figure 5.3). With increasing levels of dietary abrasion, low-crowned Pliocene macropodines were likely forced to increase enamel thickness to maintain blade function. Enamel thickness mapping shows that the transverse crests of bilophodont macropodoids are largely formed from deposition of thick enamel between the buccal and lingual dentine horns (Figure 4.2). Plio-Pleistocene macropodine kangaroos may have extended this ancestral pattern of enamel deposition used to establish bilophodont molars, to construct more thickly-enamelled transverse crests.

By the close of the Miocene many late Neogene equids and artiodactyls had evolved high crowned molars (>1.5, crown height/width ratio) (Fortelius et al. 2002; Jernvall and Fortelius 2002; Mihlbachler et al. 2011) but this crown height threshold was not breached by any macropodoid in our data set (Figure 5.6). This might be due to functional constraints associated with the precise fitting of the lower incisors within the upper incisor arcade (Prideaux and Warburton 2010) or the precise molar occlusion associated with bilophodonty (Janis 1990). Precise occlusion is important in bladed dentitions because misalignment promotes ‘point’ cutting (Evans 2005; Anderson and LaBarbera 2008). However, both proboscideans and rodents successfully coopted ancestrally bilophodont or polylophodont molars into high-crowned prismatic teeth (Sanders et al. 2010; Gomes Rodrigues et al. 2013; Lister 2013; Tapaltysan et al. 2015) suggesting that there are not explicit limits on the evolvability of bilophodont dentitions.

Amongst crown group placental herbivores, very high-crowned or hypselodont molar dentitions (>3, crown height/width ratio) characterise Glires (e.g., lagomorphs, heteromyid rodents; Jardine et al. 2012; Tapaltsyan et al. 2015), artiodactyl ungulates (e.g. bovids, cervids) and perissodactyls (e.g., equids). Still, the vast bulk of large herbivores in Neogene ecosystems had molar crown heights similar to grazing kangaroos (e.g. Fortelius et al. 2002; Jernvall and Fortelius 2002). For instance, only three North American artiodactyl families (Antilocapridae, Camelidae, and Merycoidodontidae) and two perissodactyl families (Equidae and Rhinocerotidae) acquired hypsodont or very hypsodont dentitions (Jardine et al. 2012). Thus, even amongst many ungulate groups the acquisition of very high-crowned dentitions (>3 HI) was far from a ubiquitous pattern.

Instead, we hypothesise that there may be at least two adaptive strategies herbivores have followed in response to high rates of dental wear: (1) acquisition of very high-crowned prismatic molars and; (2) low/ intermediately-crowned lophodont dentitions with thick enamel. Macropodine kangaroos provide an example of a herbivore group subjected to high rates of dental wear which invested heavily in thick molar enamel rather than molar crown height. Like macropodine kangaroos, Neogene rodents also coupled increases in molar crown height (Tapaltsyan et al. 2015) with thicker molar enamel (Van Dam et al. 2011). Increased enamel thickness is also a feature of sirenian (Domning 1982, 2001) and proboscidean evolution (Sanders et al. 2010; Lister 2013). Many Neogene proboscideans retained low or intermediate molar crown heights similar to grass-consuming macropodids (e.g., Figure 2, Lister 2013). Other features suggest that proboscideans, trichechid sirenians, and derived macropodids might occupy a similar dietary adaptive zone. For instance, whilst no macropodoids evolved polylophodont molars, as did some rodents and proboscideans (Jernvall et al. 2000; Lister 2013), they did acquire, at least once, the analogous feature of continuous tooth replacement, a character shared with manatees (Sanson 1989; Gomes Rodrigues et al. 2011; Beatty et al. 2012). Further quantitative enamel thickness data is needed for afrotherian and laurasiatherian herbivores to better understand how their respective investment in enamel thickness compares with that of macropodids and primates.

5.6 Conclusions

In this paper we have investigated how the evolution of enamel thickness was related to shifts in dental wear driven by Neogene environmental change. Dental wear data indicate that during the early Neogene, when basal macropodoids were transitioning from a bunodont to a bilophodont molar dentition, they were subject to low-levels of dietary abrasion. Increased dietary abrasion first becomes evident in the Pliocene, but this lags behind pollen and sedimentological evidence for intensified aridity in central and southern Australia (Macphail 1997; Sniderman et al. 2016) suggesting that the principle source of dietary abrasion was the expansion of Pliocene grasslands (Macphail 1997). By the late Miocene sthenurines had already specialised as thin-enamelled browsers, whereas macropodines likely acquired thick molar enamel in response to the late Pliocene emergence of grasslands (Macphail 1997). Intriguingly, our results suggest that macropodine kangaroos acquired their thick molar enamel in parallel to Plio-Pleistocene hominin lineages (Martin 1985; Olejniczak et al. 2008a, b; Skinner et al. 2015). However, despite the great adaptive emphasis placed on thick molar enamel (e.g., Martin 1985; Lucas et al. 2008; Horvath et al. 2014) the adaptive radiation of thin-enamelled sthenurine kangaroos indicates that enamel can be a flexible trait in dietary adaptation. Thick-enamelled macropodine kangaroos share many dental similarities with other comparatively low-crowned herbivore groups such as proboscideans, sirenians, and primates, suggesting they may occupy a common adaptive zone. Enamel thickness will likely prove to be an important trait for increasing dental durability in these and other mammalian groups.

5.7 Acknowledgements

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6. DISCUSSION

Context

The Discussion synthesises outcomes presented in chapters 2–5, but it is focused toward defining emerging questions, and considering approaches and data that may help resolve them. Four general areas are examined:

1) Limitations in our current understanding of macropodoid dietary evolution, and the role of the fossil record in testing hypotheses presented using novel approaches and existing datasets;
2) The potential adaptive importance of enamel thickness in herbivore evolution;
3) Using enamel thickness to better understand how genetic–developmental processes influence trait evolution;
4) The role of the inhibitory cascade as a quantitative model for predicting the evolution of serially-homologous structures;

The Discussion concludes with an overview of the central outcomes of this work and their broader implications for mammalian dietary adaptation.

6.1 Probing Macropodoid Dietary Adaptation Further with the Fossil Record

Two adaptive phases are recognised as having been especially important in macropodoid dietary evolution: an early transition from a bunodont to a bilophodont molar morphology, and a second late Neogene phase during which the folivorous macropodoids adaptively radiated. However, whilst many studies of adaptive radiation focus on the diversification phase when new ecospace is occupied (e.g., Losos et al. 1998), this largely ignores the importance of the 'stem' phase during which many critical innovations are acquired (e.g. the mammalian hypocone, Hunter and Jernvall 1995; the mammalian middle ear, Luo 2007). In the case of macropodoids, dental evolution along the stem connecting the last common ancestor of all macropodoids with the ancestor of Sthenurinae and Macropodinae is important because it involves the acquisition of bilophodonty, a trait which underpins the late Neogene radiations of macropodids (Chapter 2). Species diverging along this stem (e.g., *Ganguroo*, *Bulungamaya*, *Ngamaroo*) are successive dental intermediates between bunodont and bilophodont molar types (Cooke 1997; Couzens et al. 2016). Methodological techniques like stable isotopic and dental microwear analyses have the potential to test whether this important morphological transition tracked or lagged behind dietary change. For instance, were bunolophodont macropodoids, like *Bulungamaya delicata*, already consuming tough leaves before the acquisition of full bilophodonty? Resolving the biochronology of these early macropodoids with the help of a new U–Pb chronometer (i.e., Woodhead et al. 2014) will also help to determine whether the bunodont–bilophodont transition was a protracted, or relatively rapid event (<5 Myr), as it may have been in paenungulate mammals (Gheerbrant et al. 2016).

In many ways the early history of the major crown macropodid groups is just as cryptic as the early history of Macropodoidea. Major gaps exist between molecular estimates for clade origination and the earliest fossil representatives. For instance, Sthenurinae and Macropodinae are estimated to have diverged near the Middle Miocene Climatic Optimum, but the earliest known fossil macropodine is *Dorcopsoides fossilis* from the late Miocene of central Australia. This suggests that at least the first 6 Myr of macropodine evolution remains concealed. Likewise, molecular divergence ages for Lagostrophinae (i.e., Westerman et al. 2002; Meredith et al. 2009a; Mitchell et al. 2014) suggest that more than 10 Myr of lagostrophine evolution is currently undocumented. Further excavation of Camfieldian and Waitean (middle and late Miocene) age fossil sites such as Bullock Creek, Alcoota, Encore Site (Riversleigh), and the Sunlands LF (lower Murray Region of South Australia) will be crucial for reconstructing the early history of the major macropodid groups. In particular, it will help establish how lineages were able to transition between adaptive zones, and later partition and fill new ecospace.

In Chapter 2 I hypothesise that a simple bounded diffusion model might account for much of the early dynamics of crown-height evolution. Unlike many interpretations of marsupial evolution (i.e., Black et al. 2012) this model posits that intrinsic factors like ecological incumbency, rather than environmental change exclusively, were important in morphological diversification. What then is the role for environmental change in morphological diversification? Specifically, does environmental change need to be a pervasive pressure to drive morphological evolution, or can it be influential over short spans? The data presented in Chapter 2 suggest that over a comparatively brief window of time, spanning from the late Miocene until perhaps the late Pliocene, aridification drove a rapid increase in the rate and disparity of crown height evolution, primarily by creating new dietary niche space. In particular, environmental change appears to have influenced crown-height evolution through the influence of adaptive optima. Taxa close to adaptive optima should display correlates of adaptive success like higher relative abundance, longer stratigraphic durations, and larger geographic ranges (Jernvall and Fortelius 2002; Carotenuto et al. 2010; Raia et al. 2011). Further testing of the adaptive optima hypothesised in Chapter 2 is thus possible through the analysis of existing taxon occurrence databases (e.g., Megirian et al. 2010), or using phylogenetic approaches which enable shifts in evolutionary rate and trait disparity to be directly linked with origination and extinction rates (e.g., Raia et al. 2011; Lloyd 2016). Environmental change could also drive morphological diversification through the extinction and replacement of herbivore groups (Vrba 1993; Janis 1993). The extinction of thin-enamelled balbarines and subsequent emergence of the similarly thin-enamelled sthenurines in the middle Miocene may be an example of this. However, it is unclear if early sthenurines competitively displaced balbarines or were mere passive beneficiaries of the balbarine demise. The latter would undermine the importance of the incumbency process I have proposed (Chapter 1), or indicate that environmental pressures modulate its operation. Additionally, although turnover events may be important processes in Cenozoic ecosystems (Janis 1993; Vrba 1993), they will not necessarily increase trait disparity if lineages diversify within previously explored morphospace (Polly 2008).

6.2 Enamel Thickness as an Adaptation to Resist Dental Wear

In Chapter 3 enamel thickness is shown to be an important adaptive response to high rates of dietary abrasion amongst macropodoids. What then, might be the adaptive role of enamel thickness in other mammalian groups? Our ability to effectively address this question is limited by the sparse comparative dataset; largely restricted to fossil and modern primates (Olejniczak et al. 2008a,b; Skinner et al. 2015). An important future aim should be to acquire high-resolution microCT data from other mammalian groups, or leverage publically-accessible microCT scan datasets. A key task should be to establish the ancestral enamel thickness phenotype amongst basal mammaliaforms. Based on their tooth morphology many of these basal mammaliaforms, such as morganucodontids, were likely insectivores (Kielan-Jaworowska et al. 2004) with relatively thin molar enamel. However, other mammaliaforms, e.g., multituberculates, which possess high dental complexity and other indicators of herbivory (Evans et al. 2007; Wilson et al. 2012), are good candidates for the early acquisition of thicker molar enamel. Establishing enamel thickness amongst stem and basal therians would provide a platform from which to test the adaptive role of enamel in Cenozoic placental and marsupial herbivores.

Despite the comparative evidence presented in chapters 4 and 5 that variation in enamel thickness is linked to levels of dental wear, the exact mechanism by which thick molar enamel resists abrasion, and how enamel function alters during the life of a tooth, remains unclear. These questions reflect broader uncertainties about exactly how different tooth types function (Lucas 2004) and how wear impacts tooth function (Ungar and M'Kirera 2003; Evans 2005). These problems are inextricably linked because all dental tools experience wear (Ungar 2015). Current insights into how wear impacts tooth function is based largely on qualitative assessments of just a few tooth types; quantitative studies are rare (e.g. Evans 2005; King et al. 2005; Ungar and M'Kirera 2003). Three-dimensional surface files and microCT scan data generated in the course of this and other projects provide an opportunity to redress this deficiency via high-throughput measurement of surface morphology (e.g., relief index, Boyer 2008; Dirichlet normal energy, Bunn et al. 2011; occlusal patch count, Evans et al. 2007).

The difficulty in developing a generalisable model of enamel function is made more challenging because wear could have highly specific impacts on different tooth types. For instance, wear may actually improve grinding capacity in selenodont teeth by forming a rugose occlusal morphology (Fortelius 1985; Janis and Fortelius 1988), whereas in lophodont teeth, like those of kangaroos or some primates, it probably only transiently improves fracture efficiency (King et al. 2005; Koenigswald 2014). One way to overcome this would be to focus on the functional structures common to all teeth: cusps, crests, and basins. Simulation approaches could be useful to determine how spatial changes in enamel thickness influence fracture performance (e.g., Evans and Sanson 2003; Anderson and Rayfield 2012), and this could then be compared with natural variation in enamel thickness. Many existing models of tooth function include enamel only as a 'static' parameter, without considering how differences in enamel density or changes in thickness (arising through wear) modulate fracture efficiency during the life of the tooth (Lucas et al. 2008).

One example of how wear influences tooth function is the interaction between facet geometry and enamel thickness. As bilophodont teeth wear the facet geometry becomes progressively shallower (Koenigswald 2014) which alters the effective enamel thickness exposed at the wear land (i.e., Evans 2005). In effect, there is a discrepancy between the 'shortest-path' linear measurement of enamel thickness derived from a section plane, and the 'functional' enamel thickness determined by the facet plane geometry. When the facet angle is steep early in tooth function, the effective functional enamel thickness may be much greater than the shortest linear path from the enamel–dentine junction to the outer enamel surface. The discrepancy between measured and functional enamel thickness decreases with decline of the facet angle, as the tooth transitions to a crushing modality. Ideally, it is this 'functional' enamel thickness which should be captured, but this requires a very precise knowledge of the changing facet geometry; effectively, a simulated abrasion of the tooth crown. It is thus ironic that, whilst many studies of enamel thickness have gone to great efforts to collect 'true', shortest-path, linear enamel thickness measurements (e.g., Martin 1985; Suwa and Kono 2005), oblique section planes almost certainly more closely approximate the 'functional' enamel thickness at the cusp apex, crest edge, and crest margins. From an evolutionary perspective, the steep facet angles early in the bilophodont tooth lifespan mean that even small increases in enamel thickness along the crest (loph) edge will pay bigger functional dividends than increases in enamel across occlusal surfaces where the facet angle is lower (e.g., tooth basins). It would be interesting to understand more about how the discrepancy between the 'linear' and 'functional' enamel thickness changes over the tooth surface in other crown types.

In Chapter 4, I hypothesise that the thicker enamel along the crest edge in macropodoids subject to high levels of dietary abrasion functions to help retain a trenchant loph, and slows exposure of the enamel–dentine junction. Exposure of the dentine is significant in bilophodont dentitions because it marks the point at which blade-like function of the tooth is compromised by collapse of the transverse crests (King et al. 2005; Koenigswald 2014). In browsing macropodoids subject to lower rates of dietary abrasion the enamel is still thick along the crest edge, but the average enamel thickness is approximately three-times thinner than in grazers (Chapter 4). Wear rates are probably sufficiently low in browsers that collapse of the lophs is not an important problem, although it still occurs in taxa like *Dendrolagus* (Koenigswald 2014). Limited exposure of the dentine along the loph axis is likely beneficial because of the increase in secondary occlusal complexity (King et al. 2005). In this sense, thin enamel ín browsers may be just as adaptive as the thick enamel of mixed feeders and grazers. Enamel thickness likely has a more generalisable importance for blade function, beyond just the adaptive attributes of thick enamel. Because cutting blades are a ubiquitous vertebrate solution to fracturing tough foods (Lucas 2004; Anderson and LaBarbera 2008), it would be interesting to know in what ways enamel thickness varies across blades on different tooth types. For instance, are there similarities in the way that enamel thickness varies across the lingual and buccal walls of longitudinal crests in selenodont dentitions compared with the anterior and posterior walls of the transverse crests in bilophodont teeth? These kind of broad comparative insights are crucial for the establishment of general models of enamel function.

The examination of enamel function in Chapter 4 focuses primarily on the role of enamel thickness early in the tooth lifespan, when the molar functions primarily as a blade (Koenigswald 2014). This focus is appropriate because principle component analysis and spatial mapping show that most enamel-thickness variation is localised in early abrading structures like the crest edge and cusp tips, and because all bilophodont dentitions transition through this blade-like phase. However, dentine-exposure data (Chapter 5) reveal that, from the Pliocene, macropodine and lagostrophine dentitions were subject to much more extensive abrasion, wherein teeth spent more time operating as crushing tools rather than blades. The role of enamel thickness during this senescent phase is less clear and probably complex, because the spatial distribution of enamel is highly altered from its unworn state. The role of enamel in tooth function is also probably transitory because once the basinal enamel is abraded away there is only a dentine depression bordered by an enamel margin. The morphology of worn macropodid molars exhibit similarities with highly senescent bunodont or bunolophodont dentitions in some hominins and lemuroid primates, e.g., *Hadropithecus* (King et al. 2005; Godfrey et al. 2015; Ungar and Hlusko 2016). Examining how enamel may function in such teeth could thus yield general insights into whether any functionality is maintained at this advanced state of dental senescence.

6.3 The Evolvability of Enamel Thickness

Variation in enamel thickness in unworn teeth arises from genetic–developmental regulation of amelogenesis (Fincham et al. 1999). By modulating the types of variation that emerge in populations, genetic–developmental processes can influence patterns of trait evolution (Jernvall and Jung 2000). In Chapter 3 I argue that developmental ‘constraints’ on the way enamel thickness is patterned may explain the large proportion of enamel thickness variation that is not straightforwardly linked to diet. Developmental factors might also help explain why diet related variation in macropodoid enamel thickness is largely restricted to the cusp tips, even though other tooth regions define functionally important parameters (e.g., Evans and Sanson 2003). Just four genes are required to produce more than 97% of the enamel matrix protein present in tooth enamel (Fincham et al. 1999; Qu et al. 2015), a remarkably small genetic repertoire given more than 300 genes regulate tooth morphogenesis (Salazar-Ciudad and Jernvall 2002). Gene knockout or knockdown experiments show that mutations in these genes can be associated with huge variation in enamel-thickness (e.g., Wright et al. 2009; Sheng et al. 2010; Gibson et al. 2011). However, despite many of these studies utilising microCT, few, if any, map or systematically quantify enamel thickness variation, making it difficult to link evolutionary diversity with specific genetic variants. Spatially mapping or quantifying enamel thickness variation could thus provide great insight into the underlying genetic–developmental regulation of enamel thickness patterning. For instance, the spatial mapping of macropodoid enamel thickness shows that enamel is consistently thickest at cusp apices and crest edges. Is this pattern observed also in previous enamel gene knockout or knockdown experiments in animal models? Is it possible for enamel to be thicker in tooth basins than at the crest or cusp apex? Probing these kinds of questions could help establish morphogenetic rules for enamel patterning like those developed for cusp patterning and tooth proportionality (e.g., Jernvall 2000; Kavanagh et al. 2007).

The small number of enamel genes potentially implies high levels of pleiotropy and thus relatively restricted patterns of phenotypic variation (Carroll 2008). This could potentially explain why there is a relatively conserved pattern of enamel-thickness variation, at least amongst macropodoids and hominids (e.g., Kono 2004; Kono et al. 2014). It might also explain why phylogeny constrains patterns of enamel thickness variation in macropodoids (chapters 4 and 5). For instance, despite having perhaps as much as 10 Myr to specialise, browsing macropodines have enamel much more similar to mixed feeding and grazing macropodines, and approximately twice as thick as extinct browsing sthenurines. These observations do not support the view that enamel is especially 'evolvable' (cf. Hlusko et al. 2004; Pampush et al. 2013; Ungar and Hlusko 2016) and instead indicate there are lineage specific constraints on the pace (and possibly direction) of adaptive enamel evolution, as hinted at by earlier studies (e.g., Dumont 1995). Further analysis of enamel thickness variation amongst other mammals and vertebrate groups is clearly warranted. This is because transcriptional and post-transcriptional mechanisms of gene regulation provide potential avenues to diversify gene function, minimise pleiotropy, and increase trait variability (e.g., Filipowicz et al. 2008; Keren et al. 2010). A common transcriptional mechanism to regulate gene expression is through the addition of upstream (*cis*–) protein binding sites (Carroll 2008) and thus an increase in the number of these binding regions might enable more complex spatial patterns of enamel deposition to evolve. Recent evidence suggests that strong selection in the upstream regions of the enamel genes *Amelx*, *Ambn*, *Enam* and *Mmp20* has occurred amongst hominoid primates (Horvath et al. 2014). Furthermore, binding sites for the homeobox transcription factor DLX5 and the neural crest marker SOX9 suggest a molecular link between tooth patterning and later amelogenesis. One possibility is that the expression of signalling molecules like DLX5 in the mesenchyme during enamel-knot induction or maintenance (Zhao et al 2000) is important in 'priming' the subsequent processes of amelogenesis. Such a putative link between molecular signalling during cusp patterning and enamel mineralisation might also explain why most of the variation in enamel thickness (Chapter 3) is localised to the cusp apices and crest edges. An interesting next step would be to examine experimentally how levels of *Dlx5* expression are related temporally and spatially to sites of enamel mineralisation using either an *in-situ* hybridisation or a real-time transcriptional assay approach.

6.4 The Inhibitory Cascade as a Regulator of Evolvability

In Chapter 3, I have shown how changes in the inhibitory cascade are linked with the reversibility of a tooth crest features. Decreases in the slope of the inhibitory cascade were postulated to promote reversibility of tooth characters by differentially activating or inhibiting the cusp patterning programme. Inhibitory cascade-like rules have also been shown to account for variation in limb, phalangeal, and somite proportionality (e.g., Kavanagh et al. 2013; Young et al. 2015). Marshall et al. (1994) argued that meristic traits like teeth and digits may be highly reversible because only small changes to a patterning program are theoretically needed to change the number and size of these elements. However, the potential unification of disparate organs like teeth, limbs, digits, and somites within an inhibitory cascade framework also suggest that the specific molecular regulators are less important in determining reversibility than the way they interact (Young et al. 2015). Consistent with this, there is much evidence that the genetic constituents of a developmental pathway are not static, such that orthologous genes can acquire completely different functions (True and Haag 2001). But, this ‘developmental systems drift’ does not change the homologies of traits (Bolker and Raff 1996). Thus, it seems questionable whether focusing on the loss and gain of individual genes (i.e., Marshall et al. 1994) can provide much insight into either the likelihood or timescale for reversals in complex traits.

A better approach may be to ask whether particular patterns in the way that molecular regulators interact promote reversibility. For instance, do similar shifts in the inhibitory cascade illicit analogous evolutionary changes in disparate morphological contexts? Vertebrate digit patterning offers a potential test case to examine this question. The loss and gain of digits has occurred in many different vertebrate groups such as squamates, archosaurs, cetartiodactyls, and marsupials, often accompanied by changes in limb proportionality (Wiens and Slingluff 2001; Larsson et al. 2002; Cooper et al. 2014). However, strong evidence for phylogenetic reversal is generally lacking, with the possible exception of the skink genus *Bachia* (Kohlsdorf and Wagner 2006). Accordingly, *Bachia* might be a profitable context within which to explore the 'deep homology' of reversibility in segmented organs. If a common regulatory logic controls reversibility in segmented structures, then based on analogy with the macropodoid posthypocristid (Chapter 5), increases in central segment proportion greater than one-third should accompany reversals. Given the similar role fibroblast growth factor, bone morphogenetic protein, and sonic hedgehog signalling play in limb and cusp patterning (Jernvall 1995) a tentative case for analogy can be made between digit and tooth cusp/crest patterning. Additionally, both digits and teeth are terminally differentiating structures associated with an otherwise complex morphogenetic process (Marshall et al. 1994). A reasonable hypothesis might thus be that the re-evolution of digits in *Bachia* was associated with a disproportionate enlargement of the central limb segment (zeugopod). Although this hypothesis is very speculative, especially given our limited understanding of inhibitory cascade-like rules (Young et al. 2015), it does illustrate how a mechanistic understanding of development could yield a predictive approach to trait evolution.

Perhaps the most powerful aspect of morphogenetic rules like the inhibitory cascade is their capacity to predict how segments vary (Kavanagh et al. 2007; Young et al. 2015). This capacity lends itself to modelling, but thus far evolutionary simulations within the inhibitory cascade 'space' have not been explored. Simulating evolution within a developmental morphospace like the inhibitory cascade has advantages over approaches based on 'unbounded' morphospaces (e.g., Lande 1978; Polly 2004; Harmon et al. 2010). This is because, by explicitly accounting for how development influences trait variation, it is theoretically possible to model discontinuities in trait variation, constraints, and the loss and gain of characters (Salazar-Ciudad and Jernvall 2002; Polly 2008). In Chapter 3 evidence is presented that activation–inhibition levels are correlated with molar crown-height variation in Macropodoidea, suggesting that a decrease in levels of posterior molar inhibition would be a molecular mechanism to evolve higher-crowned molars. Consistent with this, an increase in molar crown height occurs along the stem connecting the last common ancestor of all macropodoids with the last common ancestor of the Sthenurinae and Macropodinae (Figure 8 in Couzens et al. 2016). This evolutionary trajectory occurs along a pathway of decreasing molecular inhibition and reflects a transition between adaptive optima (Chapter 2). What kinds of evolutionary processes controlled this transition? Simpson's (1944) concept of 'quantum evolution' assumed that transitions between adaptive zones were rapid and enabled primarily by phenotypic drift. This notion of rapid transitions between adaptive peaks, and its correlation with 'early bursts' of phenotypic evolution, has only been tested using conventional quantitative phenotypic approaches (e.g., Harmon et al. 2010). How would the influence of inhibitory dynamics on macropodoid crown-height variation mediate the transition between adaptive optima? Potentially this could be examined by determining how many generations of crown-height evolution are needed to bridge the phenotypic gap in the inhibitory cascade space under Brownian motion and Ornstein–Uhlenbeck processes. An effective test would then be to compare the simulated transition intervals with the 'known' transition interval determined from molecular clock analyses (i.e., Meredith et al. 2009; Mitchell et al. 2014). This kind of approach also has the potential to address other macroevolutionary transitions given that inhibitory dynamics may regulate the proportionality of limbs, digits, and somites (Kavanagh et al. 2013; Young et al. 2015).

6.5 Conclusions

In this thesis I have examined how dental evolution within Macropodoidea was shaped by environmental and developmental factors. During the late Cenozoic, macropodoids diversified their dental morphology as environments became drier and more variable. Molar crown height data spanning the past 25 Myr suggests an asymmetric increase in disparity since the late Oligocene, which may reflect evolution within a constrained morphospace or between distinct adaptive optima. Initial increases in molar crown height during the early Neogene are closely linked with the formation of bilophodont molars better able to fracture tough leaves than the bunodont molars of ancestral macropodoids. Evolutionary model-fitting suggests that molar crown height variation has been shaped by at least four distinct adaptive optima. These optima likely reflect selection driven by diet, because trait optima approximate mean molar crown height associated with the four diet groupings recognised within Macropodoidea (Arman and Prideaux 2015). A rapid increase in molar crown height disparity occurred during the Pliocene wherein maximum molar crown height reached levels characteristic of extant mixed feeding kangaroos. The jump in molar crown height disparity across the Miocene–Pliocene transition seems to have been linked to the expansion in niche space driven by the Pliocene emergence of grasslands (Macphail 1997; Sniderman et al. 2016).

The maximum crown height attained by macropodoids during the late Neogene is much lower than grass consuming ungulates (Janis 1990; Chapter 2), but comparable to lower-crowned artiodactyls, perissodactyls, and proboscideans. Instead of evolving very high-crowned teeth, macropodoids modified enamel thickness to deal with diets of varying abrasion. Two divergent trajectories in macropodid enamel evolution are evident wherein: (1) sthenurines reduced enamel thickness to increase cutting efficiency of the lophid on relatively soft browse; and (2) macropodines and lagostrophines acquired thick molar enamel to deal with increasing levels of grass consumption. Spatial measurements and three-dimensional mapping suggest that thick enamel at the crest edge was an adaptation to retain a functional blade edge when wear levels were high. The molar enamel thickness of several macropodine species falls within the range of the thickest-enamelled primates like *Paranthropus boisei* and *Homo sapiens*, indicating that thick molar enamel is homoplastic in therian mammals. Because thick-enamelled macropodids are exclusively folivores, our data strongly suggest that thick molar enamel was an evolutionary response to high levels of dietary abrasion (Chapter 4). This in turn demonstrates the plausibility of models of hominin enamel function which emphasise food abrasiveness rather than hardness (Molnar and Gantt 1977; Ungar and Hlusko 2016). Potentially, thick molar enamel was also an important dental adaptation in other low-crowned herbivores like proboscideans, sirenians, cercopithecine primates, and other diprotodont marsupials.

The capacity of dental traits to evolve is likely to be strongly influenced by the way development influences trait variation (Jernvall and Jung 2000). Dental traits with high levels of evolvability are likely to be important reservoirs of adaptive variation. A special case of this ‘evolvability’ problem is the question of why some traits are able to reevolve after long periods of absence. Amongst macropodoids, I found strong maximum-likelihood and parsimony support for parallel reversals of a functionally, and phylogenetically important tooth crest, the posthypocristid, after more than 15 million years of absence (Couzens et al. 2016). I also found that dental traits on the molar talonid, like the postentocristid, postcingulid, and posthypocristid, are comparatively more reversible than other dental characters, which is consistent with the responsiveness of similar traits to ectodysplasin protein dosage in rodents (Harjunmaa et al. 2014). Reversibility of talonid structures amongst macropodids is linked to changes in inhibitory dynamics suggesting that tooth proportionality and the cusp-specific architecture of molars are developmentally and evolutionarily linked. Overall, these results support the notion that reversals are not necessarily uncommon evolutionary phenomena (Kurtén 1964; Collin and Cipriani 2003; Prideaux 2004). Due to the deeply-conserved nature of signalling pathways and the capacity for different genes to regulate homologous structures (Bolker and Raff 1996; True and Haag 2001), it also seems unlikely that there is a strict timeline for trait reversibility. Overall, this thesis shows how quantitative comparative analyses based on digital techniques like microCT can advance our understanding of the patterns and processes underlying dental evolution. However, it also underlines how little we know about tooth function, comparative dental morphology, processes of dietary adaptation, and the evolutionary developmental biology of the mammalian dentition.

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