

CHARACTER Displacement in Pleistocene Kangaroos

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Declaration

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Dr. John Alroy, my supervisor, for help with my methods and editing my drafts.

All other research described in this report is my own original work.



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Abstract.—Palaeontological studies are helpful not only for understanding how communities interacted in the past, but also for testing ecological models in deep time. Macropods have a rich fossil record and there are many living species, making them optimal for palaeoecological studies. Character displacement between closely related coexisting species is a developing ecological topic and testing for it in evolutionary time can enhance our understanding of the processes lying behind it. Using length and width measurements of dentary molars I looked for the presence of displacement in modern and Pleistocene communities of kangaroos using Willams' V-test. Results indicated that there was little to no character displacement and so the hypothesis that this phenomenon enabled kangaroos to coexist was rejected. The Kruskal-Wallis test showed some significant variation for modern and extinct kangaroos but not enough to support displacement. This conclusion brings forward more questions about kangaroo palaeoecology: how do these species coexist? Was competition not as strong as we thought? Did coexisting Pleistocene kangaroos use resource partitioning like modern species do? Further studies of kangaroo ecology, both in modern communities and Pleistocene, will yield greater insights into how species interact with each other and how their evolutionary history has been shaped.

Key words: Palaeoecology, Macropodidae, Australia

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INTRODUCTION

Palaeoecology is the study of past ecological communities and processes using fossil data. These kinds of studies can aid in our comprehension of many ecological theories and of how evolutionary change occurs over time. If past ecosystems have modern analogues, or better yet if fossil species have living descendants, we can use what we know about the current ecosystems to interpret the past.

The Macropodidae (Mammalia: Diprodontia) are an extant group of marsupials that have a rich fossil record spanning millions of years, making them favourable for analysing ecological processes over time (Dawson and Flannery 1985; Fraser and Wells 2006). The abundance of macropods throughout their evolutionary history makes them a great starting point for studying the palaeoecological communities they were part of.

In this thesis I will be addressing the palaeoecology of the kangaroos in the Pleistocene and in modern communities, specifically looking into the presence or absence of character displacement. The first section will be a literature review of character displacement, the Pleistocene, kangaroos and what we already know about their palaeoecology. Following sections will describe the experimental methods and analyses conducted, an interpretation of the results obtained, and the implications for future research. If we can conclude that character displacement has occurred, or is occurring, we can build our understanding of their evolutionary past and of how ecological processes work through time. Concluding that there is no character displacement opens up more questions about kangaroo palaeoecology and about what mechanisms allow them to coexist while maintaining similarity.

1.1 CHARACTER displacement.—Character displacement is a specific ecological model that explains how coexistence can occur in the absence of competitive exclusion (Aguilée et al. 2010). It became a heavily studied idea after Brown and Wilson (1956) presented their work on the theory behind the model and what they interpreted as examples of it in the real world. They defined character displacement as the result of two sympatric species competing for resources and displacing in some character aspect (whether that be morphological, behavioural or social), while maintaining similarity in allopatry. It was emphasised that the competing species must have near identical ecological requirements and therefore compete heavily. Since Brown and Wilson (1956) the idea has been refined

and attempts have been made to specify what conditions must be met to conclude that character displacement is the reason behind competition.

We now describe “ecological character displacement” (ECD) as a character displacement system in which more than two species compete and display predictable variation between species (Dayan and Simberloff 2005). It is important to understand ECD when looking at the effect of competition on sympatric species and it can aid in understanding adaptive evolution and patterns of local extinctions through time (Pfennig and Pfennig 2009).

Character displacement has been studied in a wide variety of organisms, including mammals, fish and extinct groups (Ledevin et al. 2012; Schluter and McPhail 1992). However, the construction of a strict set of criteria has resulted in most supposed examples being rejected. The criteria, best outlined in Schluter and McPhail (1992), are as follows: 1) phenotypic variation has a genetic basis, 2) variation did not occur through chance, 3) patterns result from evolutionary shifting, not sorting, 4) there is a link between phenotypic change and shifts in resource use, 5) compared allopatric and sympatric sites are environmentally similar, and 6) competition occurs between the interested species.

These criteria are useful in making sure that character displacement is not being mistaken for another ecological process, but most points become increasingly difficult to establish the older the material you are looking at. Therefore, applying them to extinct species is near impossible. Furthermore, the more species in your interested ecosystem that are competing, the less likely you need to rely on these points (Dayan and Simberloff 2005). These criteria will be addressed further in the discussion.

Nonetheless, character displacement is supported at a minimal level if variation between closely related, ecologically similar species is equal (Dayan and Simberloff 1998). Hutchinson (1959) proposed a ratio of 1:3 that is needed for species to coexist and reduce competition levels. This idea has since received criticism and is instead used as a rough guide, rather than a rule (Eadie et al. 1987; Simberloff and Boecklen 1981).

1.2 THE Pleistocene.—Covering the period from 2.58Ma to 11.7Ka the Pleistocene is one of the best preserved epochs in the Australian fossil record. Sink holes that fill in rapidly allowed an abundance of fauna to be accumulated in cave systems. Megafauna are

characteristic of the Pleistocene, occurring globally. This term describes any animal, living or from the past, over 40 kg (Field et al. 2008; Martin 1984).

The Australian Pleistocene climate was highly variable, alternating between humid interglacial and dry glacial periods, with an overall move to a drier climate (Morton et al. 2011). Aridity increased heavily during the Last Glacial Maximum (LGM) in the majority of the continent (70%, compared to 40% aridity we have now), with precipitation increasing in the southeast (Field and Wroe 2012; Forbes and Bestland 2007). The movement to a drier Australia is confirmed by the dietary shift of many herbivores to grazing on grassland (C_4 plants), instead of the forested shrubs (C_3 plants) that dominated earlier on (Gröcke 1997; Prideaux and Warburton 2010). Increased prevalence of fire across the continent is likely the result of the loss of Megafauna following the extinction event, or fire usage by humans (Dawson 2006; Rule et al. 2012).

The end of the Pleistocene is characterised by a mass extinction of an estimated 90% of megafauna species in Australia (Prideaux et al. 2007a). The cause of this extinction is heavily debated, with some supporting the idea of climate change and others supporting the idea of a human influence, the Overkill hypothesis (Field and Wroe 2012; Martin 1984; Price and Sobbe 2005; Prideaux et al. 2007a; Prideaux et al. 2009).

Humans arrived in Australia between 45,000-50,000 years ago, which is timed precisely with the megafauna mass extinction and landscape changes (Grün et al. 2010; Miller et al. 1999; Roberts et al. 2001; Rule et al. 2012). If humans were on the continent with the megafauna they would likely hunt the largest animals as they would be the easiest to track down, most of which were browsing macropods (Martin 1984; Owen-Smith 1987). Although there is little direct evidence of human interaction with Megafauna, and even less so for hunting, the timing of arrival is too close to the extinction to refute the idea based on this (Johnson and Prideaux 2004; Martin 1984). Furthermore, a lack of archaeological sites showing megafauna interaction has been used to support a “blitzkrieg” human-induced extinction, where extinction was so rapid that the likelihood of preservation is reduced (Martin 1984).

Reductions in the presence of water bodies, related to shrinking woodlands, towards the end of the Pleistocene have been suggested to have had a significant impact on the megafauna living there (notably the browsers as they were more reliant on regular water bodies than their smaller counterparts) (Cook 2009; Field and Wroe 2012; Horton 1984). This

hypothesis has been used to support the argument that climate change was the overlying cause of the extinction. However, it fails to explain a number of key points, such as why there was heavy selectivity against particular megafauna (Martin 1984). Additionally, there was little to no habitat change prior to the extinction and it is only seen as a result of it (Rule et al. 2012). Fluctuating climatic conditions throughout the Pleistocene are evidence against a climate-caused extinction (Prideaux et al. 2007a). As faunal communities were able to maintain diversity and abundance throughout these fluctuations (such as those in the Naracoorte middle Pleistocene deposits) it is unlikely that similar changes in the late Pleistocene would have caused a mass extinction (Moriarty et al. 2000).

It has been suggested that there was a steady decline of megafauna through the Pleistocene (Wroe et al. 2013). However, additional evidence has shown that despite regular local extinctions, megafauna abundance remained stable until the extinction event (Prideaux et al. 2007a). Findings that Wroe et al. (2013) brought forward to support a gradual extinction caused by climate change have been refuted on the dating methods that were used and the Signor-Lipps effect not being taken into account (Brook et al. 2013).

As a result of the extinction, fire intensity increased due to the build-up of vegetation that was no longer being cleared (Rule et al. 2012). There is strong discussion about the causes of the Australian megafaunal extinction. However, using the evidence we have now it is likely that humans must have played an integral role, like they did across the globe at the same time (Barnosky et al. 2004; Sandom et al. 2014).

Pleistocene fauna from Australia are primarily preserved in cave systems and when dated accurately can reveal important information about past ecological communities and their development over time. The abundance and diversity of kangaroos in Pleistocene deposits around Australia provide a good reference for studying palaeoecology at the species level and understanding evolutionary and ecological concepts. However, ecological reconstructions of Pleistocene communities are handicapped by the nature of preservation in caves. Material is often temporally mixed, and so care must be taken to assure that species did indeed coexist (Forbes and Bestland 2007). This fact highlights the need for using proper and accurate dating methods when investigating ecological interactions of past communities.

1.3 KANGAROOS.—The megafauna in Australia were dominated by marsupials, particularly the Macropodidae (Morton et al. 2011). Of the Macropodidae, the kangaroos are of particular interest due to both their abundance as fossils and diversity. The term kangaroo when describing Pleistocene species refers to the largest species of the genera *Macropus*, *Procoptodon*, *Protemnodon* and *Sthenurus* (including *Simosthenurus*). Technically kangaroos today are only the largest species of *Macropus*: *M. giganteus* (eastern grey), *M. fuliginosus* (western grey), *M. rufus* (red) and the *M. antilopinus* (Antilopine). Subgenera of *M. robustus* are technically assigned to wallaroo, but are commonly grouped with the kangaroos. *Macropus* is the only genus to have survived the megafaunal extinction.

Kangaroos are segregated in the modern day by size and diet. Wallabies, the smallest macropods, are browsers, wallaroos are mixed feeders and the largest macropods, the kangaroos, are grazers (Prideaux et al. 2009). Classifying Pleistocene kangaroos is more difficult. Pleistocene macropod diets are determined through enamel microwear, tooth structure, and carbon isotopes (Prideaux and Warburton 2010; Prideaux et al. 2009). Inferred feeding behaviours were not as we see today. Browsers made up a large proportion of the biggest kangaroos including the *Protemnodon*, *Procoptodon* and *Simosthenurus* whereas mixed feeders and grazers belonged to *Macropus* and *Sthenurus* and covered a variety of sizes (Fraser and Wells 2006; Gröcke 1997; Prideaux et al. 2007b).

Morphological similarities among species of Macropodidae make phylogenetic studies difficult. A number of species have in the past been assigned to different Pleistocene kangaroo genera due to this similarity (Dawson and Flannery 1985). The reason is mainly that teeth are used as the diagnostic tool for separating species due to the lack of complete post-cranial skeletons, and it can be difficult to differentiate between them due to dietary and structure similarities. See figure 1 for a current understanding of kangaroo phylogeny.

The earliest known macropod was a tree-dwelling Miocene marsupial (Dawson 2004). The earliest kangaroos, however, are unknown as there is a long gap in preservation (Dawson 2012). The Sthenurinae (*Sthenurus* and *Simosthenurus*) diverged in the Pliocene and *Procoptodon* diverged in the early Pleistocene (Tedford et al. 2006). Browsing macropods radiated during the Pliocene-Pleistocene transition (Prideaux 2004; Tedford et al. 2006). Grazing macropods become prominent towards the end of the Pleistocene likely related to the change in vegetation and niche availability.

Macropods are widespread across the continent, but there are very few species in the extreme southeast relative to other areas (figure 2A) (Dawson and Denny 1969). This is interesting considering the fossil record shows that the majority of species were concentrated in the southeast and southwest of the continent (figure 2B). This may be a relic of the geography of sampling or it could be that there were more species in the forested areas than the arid zone (Horton 1984). The extent of extinct kangaroo ranges can only be determined by looking at where their deposits have been found and so it may not be entirely accurate.

Many animals exhibit sexual dimorphism through body size. Body size is often heavily correlated with tooth size and so the latter can be used as an indicator of dimorphism (Dayan et al. 1992). Sexual dimorphism occurs in all modern kangaroos with the largest, the red kangaroo *M. rufus*, having the highest degree (Field and Wroe 2012; Garvey 2010). Sexual dimorphism can be harder to define in extinct species.. The observation that sexual dimorphism is more common in larger species is called “Rensch’s rule” (Dale et al. 2007; Helgen et al. 2006). Following this rule, it can be suggested that since kangaroos in the Pleistocene were larger than kangaroos today, and that kangaroos today exhibit sexual dimorphism, Pleistocene kangaroos are likely to have also. Although we cannot sex fossil specimens accurately, we can assume sexual dimorphism is occurring if we find two distinct size groups within species in the same area (Bishop 1997). Both *Protemnodon brehus* and *P. gilli* have been suggested to display sexual dimorphism, based on skeletal measurements (Helgen et al. 2006; Horton and Samuel 1978). The presence of sexual dimorphism in coexisting species adds an additional level of competition and so where possible species exhibiting sexual dimorphism should be treated as morphospecies (Simberloff et al. 2000).

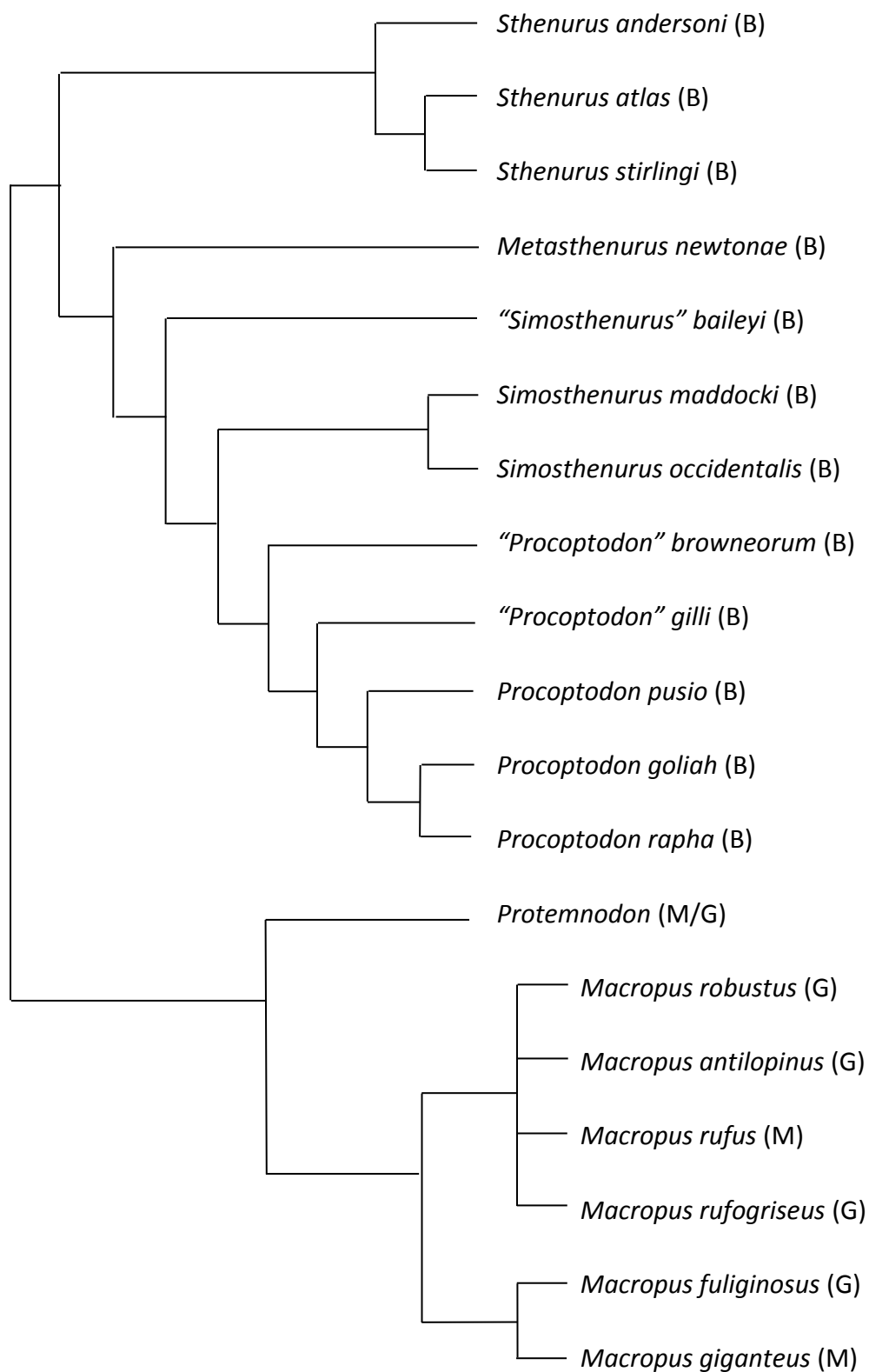


Figure 1 Phylogenetic tree of Macropodidae species included in this study. *Protemnodon* has not been split into species because there is yet to be a conclusive analysis. Length of branches does not represent evolutionary time. (B) indicates browser, (G) indicates grazer and (M) indicates mixed feeders. Adapted from Murray (1991), Gröcke (1997), Prideaux (2000), Milne and O'Higgins (2002), Sears (2005), Fraser and Wells (2006), Helgen et al. (2006), Tedford et al. (2006), Prideaux and Warburton (2010), Butler et al. (2014).

A



B



Figure 2 A) Modern kangaroo abundance across Australia. Darker areas indicate more species are present here. This map shows only the species which were included in this study (Burbidge et al. 2008; Ellis et al. 2008a; Ellis et al. 2008b; Munny et al. 2008; Woinarski et al. 2008). B) Overall distributions of extinct kangaroos included in this study across Australia

1.4 Kangaroo palaeoecology.—Coexistence refers to the cohabitation of species that have overlapping ranges. In any given habitat coexisting species are all linked through food webs, as well as by sharing resources such as space. Coexisting species generally occupy separate niches in order to reduce competition, which should involve character displacement. An alternative is competitive exclusion, in which one or more species go locally extinct as a result of competition (Pfennig and Pfennig 2012).

Macropods today coexist over large areas, and resource partitioning has been suggested for a few cases, enabling them to maintain this coexistence without extinction (Dawson and Denny 1969; Schmidt et al. 2010). It is much harder to determine resource partitioning in Pleistocene communities as we do not have fine scale preservation showing exactly where each species lived in relation to each other. Nonetheless, it can be assumed that species coexisted if they are found in the same area and were deposited at approximately the same time.

Competition occurs when coexisting species share a limiting resource and is more likely to happen the more species you have sharing a resource. It can be difficult to determine definitively if competition was occurring between Pleistocene kangaroos and we rely on circumstantial evidence to suggest it. A combination of high diversity and accumulation of fossils from different species of herbivorous macropods within close proximity implies that competition is likely to have occurred. Limiting resources are a major cause for competition, but is hard to define in the fossil record. The change in vegetation in accordance with the change in feeding behaviour, and the move to aridity in the environment may indicate limiting resources (Miller et al. 1999; Prideaux et al. 2009). Additionally, distinct size variation may be an indicator of competition (Jams et al. 1994).

Kangaroos fill a similar niche to the ungulates in Africa and so ecological studies done on either group can tell us information about the other (Coulson et al. 2006; Fisher et al. 2002; Kleynhans et al. 2011). Not only are kangaroos similar to African ungulates but the Australian Pleistocene environment was similar to the African savannah in the modern day (Kleynhans et al. 2011; Prideaux et al. 2009). In both areas large herbivores are divided into two habitats: woodland and open forest (Horton 1984). Megafauna play an important ecological role, managing vegetation and providing a food source for large predators. It is clear that the Australian megafauna were vital in vegetation management because increases in fire intensity occurred immediately after extinctions occurred (Rule et al. 2012). This fire

intensity was also increased with the arrival of Aboriginals, who proceeded to burn the landscape (Cook 2009; Morton et al. 2011). One difference between the communities of the African savannah and Pleistocene Australia is a severe lack of apex predators in the latter (Freeland 1990; Martin 1984). Diversification of Pleistocene macropods can in part be attributed to a reduced threat of predation. Megafauna in Australia evolved without much of a threat from predation and so they were not adapted for fast escape, which would make it easier for humans to hunt them down (Martin 1984).

Molar progression is an interesting feature kangaroos have evolved to cope with high degrees of wear associated heavily with a grazing lifestyle (Dawson and Flannery 1985; Lentle et al. 2003). Molar progression is the movement of the molars down the jawline, the extent measured against the rim of the eye orbit, to make room for new ones and discard the old worn ones (Lentle et al. 2003). This mechanism is not common but does occur in elephants and manatees (McArthur and Sanson 1988). Molar progression has implications for how kangaroos have evolved and will be addressed in the discussion.

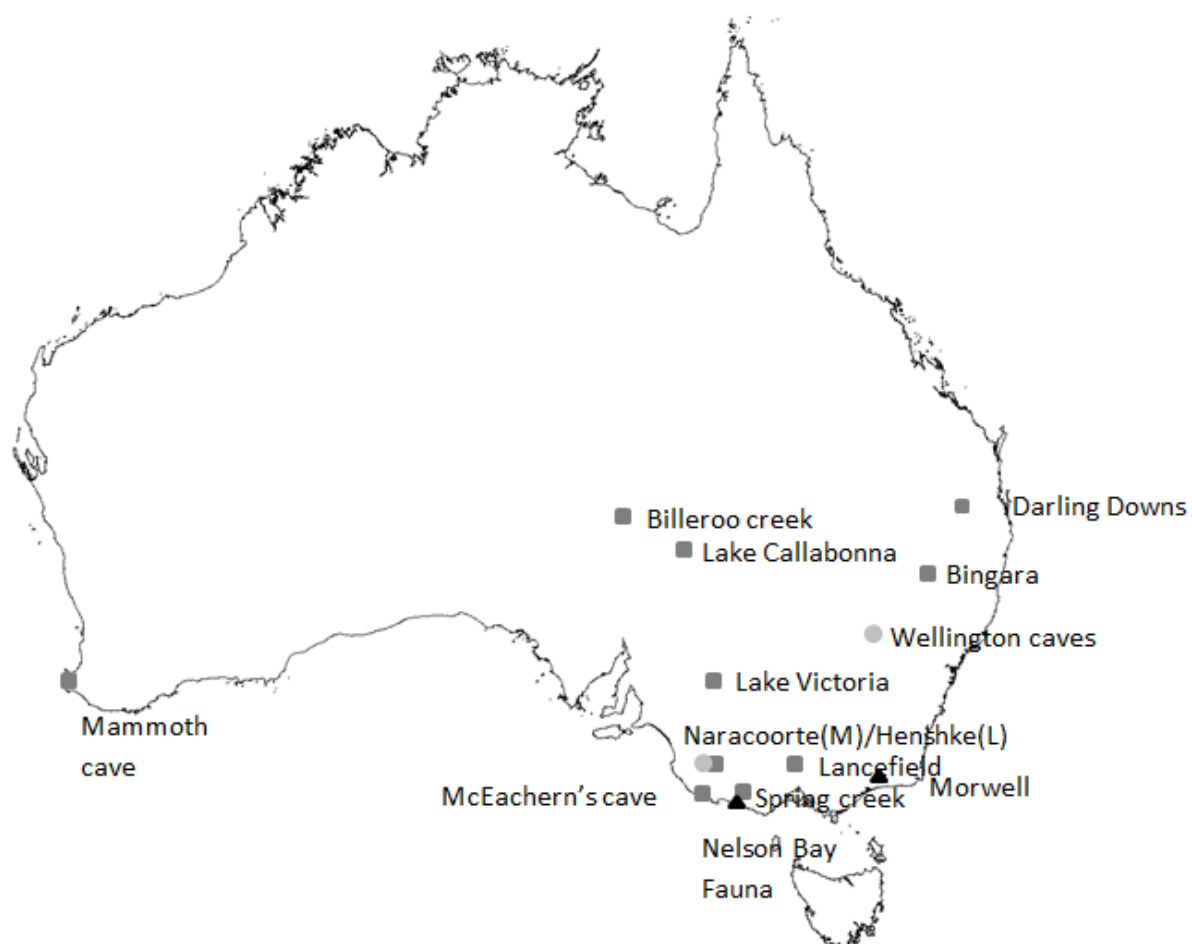
METHODS

Fossil and modern specimens were provided by the Australian Museum, Museum Victoria and the South Australian Museum. Extinct species that were measured were: *M. giganteus*, *M. munjabus*, *M. roechus*, *M. titan*, *Procoptodon goliah*, *P. pusio*, *P. rapha*, *Protemnodon brehus*, *P. anak*, *S. brownei*, *S. gilli*, *S. newtonae*, *S. occidentalis*, *S. andersoni*, *S. atlas*, *S. baileyi*, *S. maddocki* and *S. stirlingi* from the localities: Bingara, Wellington caves, Darling downs, Billeroo creek, Lake Callabonna, Henschke, Victoria fossil cave, Lake Victoria, Lancefield, McEachern's cave, Morwell, Nelson Bay fauna, Spring creek and Mammoth cave (figure 3A). Modern species measured included: *M. antilopinus*, *M. fuliginosus*, *M. giganteus*, *M. rufogriseus*, *M. robustus erubescens*, *M. robustus woodwardi* and *M. rufus* from across Australia (figure 3B). *M. rufogriseus* was omitted from statistical tests because too few specimens were measured.

Pleistocene localities (figure 3A) were selected for analysis based on the availability and abundance of material, the number of species present and the age of the deposits. Ages were determined using a combination of museum records and current dating estimates from the literature. In cave systems with multiple sections of the same age were combined into one single locality, provided there were no known differences in faunal associations (table 1). Pleistocene localities were kept separate if they were singular, well-separated deposit (table 2). Modern localities (figure 3b) were selected based on availability and were also grouped together based on geographical location and habitat variation (table 3).

Only adult specimens were included for analysis in order to reduce to effect of age-based size variation. Adults were identified by full dental eruption and suture closure. Specimens with high wear (due to fossilisation or breakage) were not used because it does not represent the natural dimensions of the teeth. Statistical analyses were carried out using Microsoft Excel 2010 and R (Team 2014).

A



B

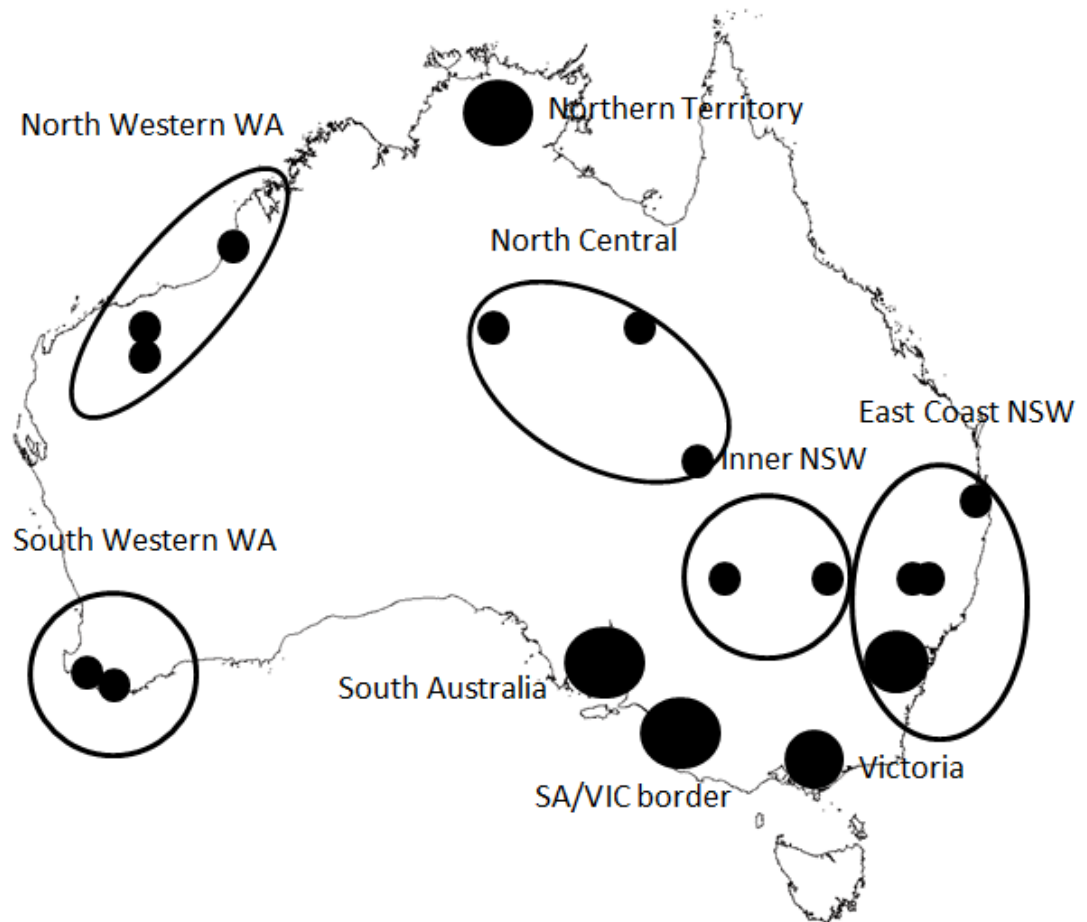


Figure 3 A) Map of Pleistocene localities analysed in here. Black triangles represent the Early subdivision of the Pleistocene, grey circles represent the Middle Pleistocene localities and Dark grey squares represent Late Pleistocene localities B) Map of the modern localities analysed here. The larger black circles indicate that multiple sites made up the locality. Circles around localities show localities that were grouped for the purpose of this study

Table 1 Assignment of individual fossil sites to larger-scale localities. Sites made up of a single deposit are not included here. The number of individuals representing each species in each locality is indicated in brackets “(n)”. “Age” means subdivision of the Pleistocene (Moriarty et al. 2000).

Combined locality	Original localities	Age	Species present	Source(s)
Wellington Caves	Wellington cave, Bone cave, Breccia cave	Middle	<i>M. roechus</i> (3), <i>M. titan</i> (7), <i>M. minor</i> (2), <i>S. andersoni</i> (1), <i>S. atlas</i> (5), <i>S. orientalis</i> (1), <i>Procoptodon rapha</i> (1) <i>Protemnodon anak</i> (1), <i>P.</i> <i>brehus</i> (1)	Dawson (1985)
Darling downs	Darling downs, King’s Creek	Late	<i>M. titan</i> (5), <i>Procoptodon</i> <i>goliah</i> (1), <i>Protemnodon</i> <i>anak</i> (3)	Prideaux (2004)
Henschke	Henschke, Tomato-stick	Late	<i>M. giganteus</i> (4), <i>M. titan</i> (1), <i>Protemnodon roechus</i> (1), <i>S. andersoni</i> (5), <i>S. atlas</i> (2), <i>S. brownei</i> (1), <i>S.</i> <i>maddocki</i> (4), <i>S. gilli</i> (4), <i>S.</i> <i>occidentalis</i> (2)	Gillespie et al. (2006), Pate et al. (2006), Macken et al. (2013)
Victoria fossil cave	Alexandra cave, Haystall cave, Specimen cave, Victoria fossil cave, Fossil cave, Fossil chamber, Upper ossuary, Grant hall	Middle	<i>M. giganteus</i> (4), <i>M. titan</i> (2), <i>S. gilli</i> (19), <i>S. brownie</i> (36), <i>S. occidentalis</i> (7), <i>S.</i> <i>baileyi</i> (5), <i>S. andersoni</i> (5), <i>S. maddocki</i> (3), <i>S. newtonae</i> (4), <i>Protemnodon brehus</i> (1)	Forbes and Bestland (2007), Moriarty et al. (2000), Grün et al. (2001)

Table 2 Extinct localities not consisting of more than one deposit, their respective ages (Pleistocene subdivisions) and the species present in each locality. (*n*) indicates how many specimens represented each species.

Locality	Age	Species present	Source(s)
Bingara	Late	<i>Procoptodon goliah</i> (5), <i>P. pusio</i> (2)	Stirton and Marcus (1966)
Lake Victoria	Late	<i>P. goliah</i> (3)	Gillespie et al. (2006)
Lancefield	Late	<i>M. giganteus</i> (2), <i>M. titan</i> (32), <i>S. andersoni</i> (2)	van Huet et al. (1998)
McEachern's cave	Late	<i>S. brownei</i> (2), <i>S. gilli</i> (2), <i>S. occidentalis</i> (6)	Gillespie et al. (2006)
Morwell	Early	<i>M. munjabus</i> (4), <i>Protemnodon anak</i> (4)	Kershaw et al. (1991)
Spring creek	Late	<i>M. giganteus</i> (7)	White and Flannery (1995)
Mammoth cave	Late	<i>S. occidentalis</i> (6)	Gillespie et al. (2006)
Billeroo creek	Late	<i>S. stirlingi</i> (2)	Williams (1980)
Lake Callabonna	Late	<i>S. stirlingi</i> (2)	Gillespie et al. (2006)
Nelson Bay Fauna	Early	<i>Protemnodon brehus</i> (2)	Whitelaw (1991), Piper (2007)

Table 3 Original modern localities combined into single large-scale localities. The number of individual specimens measured for each species in each locality is presented in brackets “(n)”.

Combined locality	Original localities	Species present
South Western Australia	Warren river, Southwest WA	<i>M. giganteus</i> (2), <i>M. fuliginosus</i> (2)
North Western Australia	Fortesque river, Woodstock, Fitzroy river	<i>M. robustus erubescens</i> (42), <i>M. robustus woodwardi</i> (2)
Northern Territory	Douglas station, Bella Glen, Mary river, Elsey, Gimbat, Arnhem Bay, Roper river	<i>M. antilopinus</i> (6), <i>M. robustus woodwardi</i> (8), <i>M. rufus</i> (2)
South Australia	Hinck’s reserve, Port Augusta, Port Lincoln, Bunkers, Yunta, Leigh creek, Coonalpyn, Cape Jervis, Mulga, Koala farm	<i>M. fuliginosus</i> (8), <i>M. giganteus</i> (6), <i>M. robustus erubescens</i> (8), <i>M. rufus</i> (16)
Victoria/South Australian border	Flinder’s range, Robe, Bagdad, Geegeela, Sunset	<i>M. fuliginosus</i> (10), <i>M. giganteus</i> (6)
Victoria	Bagshot, Limestone, Glendinning, Mount Edgar, Goulburn river, Koroit, Princes Highway, Yan Yean	<i>M. giganteus</i> (32), <i>M. robustus erubescens</i> (48)
East coast New South Wales	Colong, Narrandera, Boro, Riverina district, Yaven creek, Armidale, Stradbroke	<i>M. giganteus</i> (12), <i>M. rufus</i> (4)
Inner New South Wales	Fowlers Gap, Broken Hill, Bourke, Boggabri	<i>M. giganteus</i> (2), <i>M. rufus</i> (15)
North Central Australia	Banka Banka, Djarra, Kuranda, Diamantina lakes	<i>M. giganteus</i> (4), <i>M. robustus erubescens</i> (2), <i>M. rufus</i> (2)

2.1 MEASUREMENTS. –Length and width of the dentary molars (M1-M4) were measured (figure 4) using digital calipers with 0.01mm precision. Height was measured at the beginning of the data collection process but later omitted due to time constraints, issues with wear associated with age, and the fact that height would not yield information relevant to the ecological aspects of this study. Dentary molars were selected because of their abundance in museum collections, their robust preservation, and the well-documented correlation between their morphology and feeding strategies (Dawson 2006).

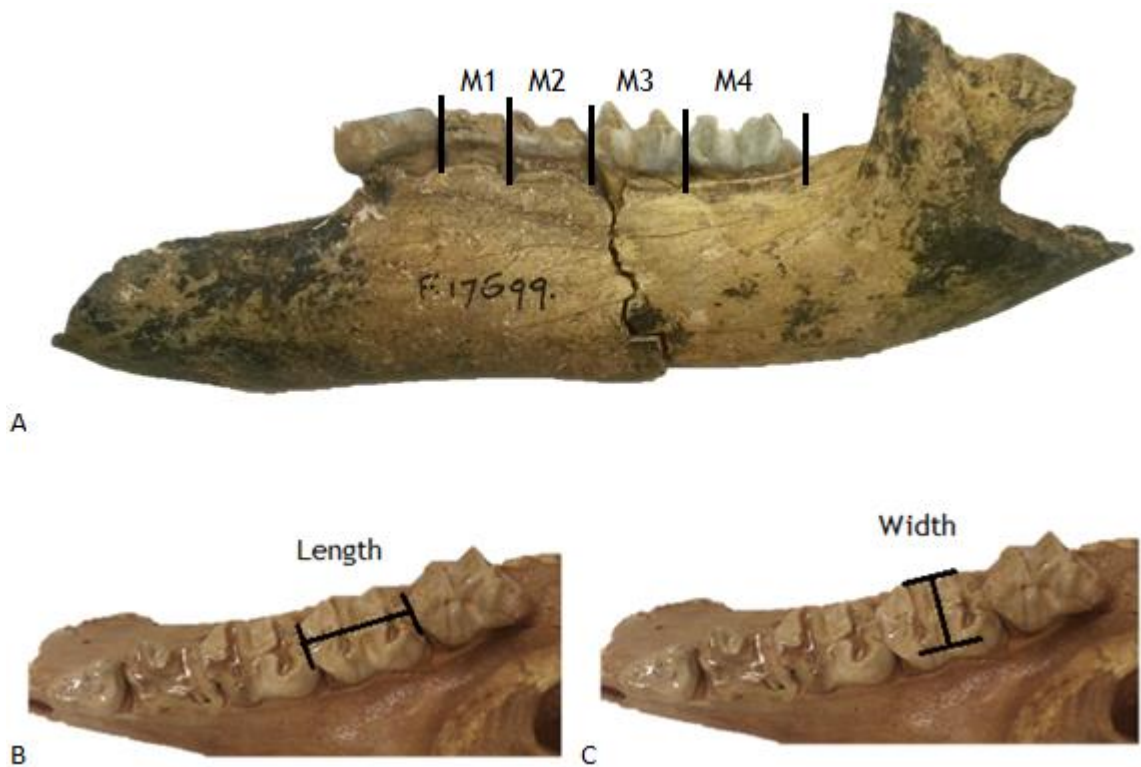


Figure 4 A) Molars M1-M4 on a dentary fragment, B) length measurement of M3, C) width measurement of M3.

2.2 STATISTICAL analyses. –The raw data were log transformed in R and the mean and standard deviations were computed for each species in each locality. T-tests were performed on sexed modern species to determine the presence of sexual dimorphism. Specimens were separated only by species and sex and not by geographical location because I was not interested in looking at geographical variation in dimorphism.

Linear model analyses were performed in R in order to assess the relationships between molar widths and length in each species. This was done for general knowledge

about how related there measurements are, rather than analysing the ecology of the kangaroos. As with the t-tests, specimens were not separated by geographical location but were treated as a single population.

Williams' V-test, a signifier of community-wide character displacement, was employed using the means of the logged data. The goal of the test is to show whether the means are more evenly spaced across the range than one would expect at random. Means for each species (including morphospecies) were combined for each locality for this test. Poole et al. (1979) first presented the formula for V. This statistic calculates variances in "distance" (in this case: size) between species and was formulated as per Williams (1995) (figure 5). Results from this test were then compared to the table of variance and significance that was also provided by Williams (1995) (supplementary information, table 1).

$$V = \frac{SS}{(n - 1)(Range)^2}$$

Figure 5 The V-test as formulated by (Williams 1995). SS is the sum of differences between the means, n is the number of species, range is the difference between the highest and lowest means.

The Kruskal-Wallis test was used to determine whether there was any significant geographical variation within species. It is a non-parametric test of the degree of variation among two or more independent groups, which can have different sample sizes. It was only possible to apply this test to a few extinct species because there are a limited number of localities having a sufficient sample size (i.e., more than two specimens representing a species). The test was carried out on each eligible species sample (including morphospecies) found in locations on each of the 8 measurements.

RESULTS

3.1 T-TESTS.—The results of the t-tests indicate that all extant species display sexual dimorphism in at least one dentary molar dimension (table 4). Sexes were therefore treated as morphospecies for the purpose of further variance tests. T-tests were not able to be conducted on extinct kangaroos because for most species there was too small a sample size to reliably create size groupings and therefore infer sexual dimorphism. It therefore must be kept in mind that fossil samples are likely to obscure significant variation due to dimorphism and that presumably makes the following analyses more conservative.

3.2 LINEAR models.—Linear regression could not be applied to the following morphospecies because there were less than two representatives in each sample: *M. antilopinus* female and *M. robustus woodwardi* female for the modern communities, and *S. orientalis*, *M. minor*, *Procoptodon otuel* and *P. pusio* for the extinct communities.

The results of the linear regression analyses (table 5) show that for modern communities there are strong relationships between dental features, although these differ for each species. The results show that for extinct communities (table 6) there are predictable relationships between dental features, particularly between succeeding widths. These results are expected, as there should be relationships between measurements. Looking at the slopes (tables 5 and 6), most of them for both the modern and Pleistocene species are far below 1.0 and therefore suggest that either variation is allometric or that the ranges of the measurements are too narrow to establish a clear pattern. These results will be further addressed in the discussion.

3.3 WILLIAMS' V-test.—The following sites were omitted from the extinct communities V-test because less than three species were present: Mammoth cave, Spring creek, Lake Victoria, Lake Callabonna, Billeroo creek, Darling downs, Bungendore, Bingara, Nelson Bay fauna and Morwell. The “South Western Australia” site was omitted from the modern V-test because less than three species were present.

For the extinct locality V-tests (table 7) only Victoria Fossil Cave (M2 width and M4 width) and Wellington Caves (M2 width) showed significantly non-random spacing. Similarly,

in the modern locality V-tests (table 8) only South Australia (M3 length) and Victoria (M2 width, M3 width) produced significant results.

3.4 KRUSKAL-Wallis tests.—These tests were applied after splitting localities into three categories: the Middle Pleistocene, Late Pleistocene, and modern. In the Middle Pleistocene tests, only *M. titan* had sufficient sample sizes and numbers of localities to perform this test and M4 length was the only measurement showing significant differences among the sites (table 9).

Of the Middle Pleistocene species (table 10), *M. giganteus* (M4 length), *Procoptodon goliah* (M1 width, M2 width, M3 width, M4 length) and *S. occidentalis* (all except M4 width) showed significant size variation among localities. *S. andersoni*, *S. gilli* and *S. stirlingi* showed no significant variation among populations.

In the modern kangaroo tests (table 11), *M. fuliginosus* female (M2 length, M4 width), *M. giganteus* female (M2 width), male (both M1 and M2 measurements), *M. robustus erubescens* male (both M2 measurements, M3 W and both M4 measurements), *M. robustus woodwardi* male (both M2 measurements), *M. rufus* female (M4 length) and male (M2 width and both M3 measurements) showed significant variance among populations. Both *M. fuliginosus* male and *M. robustus erubescens* female showed no significant variation among populations.

Table 4 Results of the sexual dimorphism t -tests performed on logged extant kangaroo data.
The significance level for the *p*-values is 0.05.

Species	Measurement	t	df	<i>p</i>-value
<i>M. antilopinus</i>	M2 length	-0.6263	1.074	0.6379
	M2 width	-3.1676	1.051	0.185
	M3 length	-0.7675	3.143	0.4963
	M3 width	-16.8676	3.113	0.0003654
	M4 length	-1.729	3.714	0.1644
	M4 width	-6.684	1.77	0.02931
<i>M. fuliginosus</i>	M1 length	-1.2948	5.499	0.2471
	M1 width	-0.9392	4.467	0.3956
	M2 length	-1.119	8.928	0.2924
	M2 width	0.5877	13.732	0.5663
	M3 length	-1.7399	11.892	0.1077
	M3 width	0.1188	6.74	0.9089
	M4 length	-1.3987	8.855	0.1959
	M4 width	1.1306	12.439	0.2795
<i>M. giganteus</i>	M1 length	-2.2991	10.782	0.04255
	M1 width	-0.3698	7.068	0.7224
	M2 length	-1.5767	54.781	0.1206
	M2 width	-0.6389	50.922	0.5257
	M3 length	-3.4292	49.288	0.001232
	M3 width	-1.7605	59.694	0.08344
	M4 length	-4.7559	61.801	1.225e-05
	M4 width	-3.2738	59.773	0.001767
	M1 length	-2.9427	7.987	0.01866
	M1 width	1.8603	5.05	0.1213
<i>M. rufus</i>	M2 length	-3.5105	15.521	0.003015
	M2 width	0.8806	17.091	0.3907
	M3 length	-2.31	21.248	0.03102
	M3 width	0.403	15.665	0.6924
	M4 length	-2.3111	17.565	0.0332

<i>M. robustus erubescens</i>	M4 width	0.5325	25.108	0.599
	M1 length	-0.1179	36.744	0.9068
	M1 width	-1.1825	31.072	0.246
	M2 length	-1.0624	87.958	0.291
	M2 width	-4.1017	89.22	9.037e-05
	M3 length	-0.955	81.741	0.3424
	M3 width	-4.6203	87.862	1.305e-05
	M4 length	-3.6092	95.116	0.0004923
	M4 width	-6.389	85.488	8.396e-09
<i>M. robustus woodwardi</i>	M2 length	0.0621	5.721	0.9526
	M2 width	-0.9524	8.02	0.3687
	M3 length	-2.0406	1.581	0.2107
	M3 width	-0.4938	7.779	0.6351
	M4 length	-2.5967	8	0.03177
	M4 width	-2.8692	8.204	0.02032

Table 5 Linear regression results for extant kangaroos. “-” indicates there were not enough specimens to perform the tests. “L” indicates length, “W” indicates width. R² is adjusted. The significance level for the *p*-values is 0.05.

Species		M1 L ~	M1 L ~	M1 W ~	M2 L ~	M2 L ~	M2 W ~	M3 L ~	M3 L ~	M3 W ~	M4 L ~
		M1 W	M2 L	M2 W	M2 W	M3 L	M3 W	M3 W	M4 L	M4 W	M4 W
<i>M. antilopinus</i> male	Intercept	0.3683	5.539	6.6182	0.001837	1.4868	-0.2308	-5.8720	-0.3525	0.6624	-1.367
	Slope	0.8746	-1.640	-2.4238	1.102907	0.2917	1.0489	3.9227	1.0774	0.6898	1.877
	R ²	0.72	0.3506	0.6225	0.6799	0.6152	0.8064	0.8523	0.8848	0.1532	-0.1439
	<i>p</i> -value	0.09518	0.247	0.1349	0.1131	0.1378	0.06677	0.0505	0.03918	0.3401	0.5127
<i>M. fuliginosus</i> female	Intercept	-	-	-	2.7396	1.93561	-0.3036	11.003	3.9067	2.08120	2.42087
	Slope	-	-	-	-0.1759	0.17970	1.1190	-4.044	-0.5729	0.01612	0.06077
	R ²	-	-	-	-0.00123	0.8165	0.02305	0.1852	-0.1015	-0.09395	-0.00818
	<i>p</i> -value	-	-	-	0.3648	0.003289	0.3219	0.1191	0.6902	0.6465	0.3638
<i>M. fuliginosus</i> male	Intercept	0.3360	0.6696	0.87421	0.5305	-0.7238	0.01701	1.4630	0.8383	0.4139	1.0092
	Slope	0.9809	0.6733	0.55295	0.9262	1.2194	0.95130	0.5191	0.6607	0.8041	0.7556
	R ²	0.3401	0.7905	0.9035	0.6159	0.8357	0.7618	0.3063	0.599	0.8911	0.7889
	<i>p</i> -value	0.1316	0.01118	0.002293	0.1288	0.00248	0.006437	0.1144	0.02519	0.0008706	0.44717
<i>M. giganteus</i> female	Intercept	1.3450	-0.2863	-0.8691	1.3224	1.0267	1.2017	2.2652	1.7285	0.9592	1.8443
	Slope	0.4409	1.0720	1.3819	0.5157	0.5485	0.4096	0.1011	0.2944	0.5514	0.3365
	R ²	0.246	0.4372	0.5811	0.1561	0.06306	0.1766	-0.01139	0.08759	0.1092	0.05139

	<i>p</i> -value	0.1461	0.06323	0.02832	0.0214	0.1052	0.01497	0.4224	0.05848	0.03896	0.116
<i>M. giganteus</i>	Intercept	1.3195	-0.1956	-0.2167	1.2226	0.6321	0.9981	1.9558	0.8731	1.2741	1.6157
male	Slope	0.5042	1.0362	1.0623	0.5776	0.7017	0.5039	0.2725	0.6355	0.4055	0.4701
	R ²	0.08374	0.3467	0.4111	0.08507	0.2649	0.3641	0.007764	0.118	0.1012	0.2402
	<i>p</i> -value	0.1154	0.003731	0.0007778	0.0684	0.002522	0.000195	0.2756	0.03301	0.04532	0.003013
<i>M. robustus</i>	Intercept	2.6052	2.9720	0.8696	1.0445	0.7871	1.3841	2.36717	0.4127	1.4032	1.6347
<i>erubescens</i>	Slope	-0.2677	-0.3785	0.4901	0.6245	0.6016	0.2700	0.03405	0.8103	0.3140	0.4240
female	R ²	-0.03366	0.003287	0.2457	0.3704	0.397	0.03265	-0.02549	0.3542	0.05285	0.1513
	<i>p</i> -value	0.4994	0.3273	0.02489	8.022e-05	3.901e-05	0.1456	0.8619	3.054e-05	0.08272	0.007581
<i>M. robustus</i>	Intercept	0.8916	-0.2750	-0.8489	1.4834	-0.5346	0.8268	2.48797	1.3500	0.5833	1.4992
<i>erubescens</i>	Slope	0.6618	1.0320	1.3242	0.3952	1.1464	0.5612	-0.01706	0.4327	0.7211	0.4958
male	R ²	0.553	0.3476	0.6634	0.07885	0.4623	0.1464	-0.01699	0.1675	0.3624	0.1423
	<i>p</i> -value	4.41e-05	0.002908	1.362e-06	0.02041	4.977e-09	0.001931	0.9044	0.000686	2.176e-07	0.001735
<i>M. robustus</i>	Intercept	0.8779	0.8826	-1.7870	-2.7315	-5.0761	-0.5248	1.1514	1.2964	1.2590	1.1704
<i>woodwardi</i>	Slope	0.6345	0.5136	1.7980	2.4733	2.9093	1.2059	0.6482	0.4710	0.3974	0.6635
male	R ²	0.5671	0.8519	0.73	0.9335	0.5973	0.5666	0.2514	0.334	0.2526	0.4596
	<i>p</i> -value	0.1566	0.05065	0.01894	5.927e-05	0.01498	0.03102	0.143	0.07788	0.1423	0.0387
<i>M. rufus</i>	Intercept	2.14767	-1.1083	0.4077	2.19337	-1.1339	-0.2071	1.5800	0.7753	0.1938	1.9237
female	Slope	-0.05703	1.3948	0.7259	0.02022	1.3379	1.0586	0.4266	0.6655	0.9030	0.3053

	R ²	-0.3283	0.7008	0.4878	-0.1108	0.5587	0.7824	0.1563	0.3418	0.218	-0.04182
	<i>p</i> -value	0.922	0.04859	0.1159	0.9596	0.004949	0.0001839	0.1001	0.02105	0.06121	0.4866
<i>M. rufus</i> male	Intercept	2.180738	-1.0169	0.2310	1.5712	1.1927	0.03739	0.8434	1.1040	1.2596	1.3544
	Slope	-0.004319	1.3445	0.8105	0.4029	0.4652	0.93602	0.8086	0.5488	0.4017	0.6020
	R ²	-0.08333	0.5387	0.5251	0.106	0.1796	0.3783	0.258	0.1391	0.1711	0.3204
	<i>p</i> -value	0.9937	0.000729	0.002033	0.09463	0.03564	0.003912	0.01092	0.04478	0.03545	0.003563

Table 6 Linear regression results for extinct species. “L” is length, “W” is width. R^2 is adjusted. The significance level for the p -values is 0.05.

Species		M1 L ~	M1 L ~	M1 W ~	M2 L ~	M2 L ~	M2 W ~	M3 L ~	M3 L ~	M3 W ~	M4 L ~
		M1 W	M2 L	M2 W	M2 W	M3 L	M3 W	M3 W	M4 L	M4 W	M4 W
<i>M. giganteus</i>	Intercept	-0.8100	6.821	1.5953	0.3772	0.1304	2.29614	2.76716	0.6627	18.000	0.9470
	Slope	1.5541	-1.705	0.2312	1.0098	0.9234	-0.01601	-0.01510	0.7461	-6.709	0.7920
	R^2	0.9911	-0.3438	-0.3436	0.7969	0.4539	-0.02924	-0.00988	0.6034	0.1839	0.6553
	p -value	0.04259	0.6117	0.6771	5.748e-05	0.009741	0.4516	0.3729	0.0001483	0.04867	5.02e-05
<i>M. titan</i>	Intercept	2.8321	2.468269	-0.1151	1.3874	1.1347	1.0527	1.5053	1.8045	0.57203	1.5511
	Slope	-0.1597	0.003732	1.0063	0.5582	0.5480	0.5223	0.5408	0.3440	0.75658	0.5403
	R^2	-0.1352	-0.3333	0.462	0.1401	0.188	0.3416	0.1865	0.0531	0.6363	0.3368
	p -value	0.5216	0.9933	0.05583	0.04417	0.02225	0.0002117	0.002005	0.07425	1.164e-11	9.201e-06
<i>P. goliah</i>	Intercept	2.4625	1.5975	0.01589	2.4070	2.3374	0.3107	3.29897	3.44627	-0.3880	-2.2494
	Slope	0.1063	0.3863	0.94321	0.1997	0.2066	0.8754	-0.05696	-0.10161	1.1481	1.8421
	R^2	-0.154	0.00755	0.7885	-0.1065	-0.1319	0.7651	-0.1292	0.01922	0.599	0.3693
	p -value	0.8058	0.3443	0.0008583	0.646	0.8021	0.001251	0.7795	0.3178	0.008757	0.04859
<i>P. anak</i>	Intercept	-0.5593	0.5849	0.3287	-0.1829	-1.6550	1.3982	2.2490	-0.08364	0.9624	2.88255
	Slope	1.3533	0.6778	0.7887	1.1692	1.5523	0.3374	0.1418	0.96992	0.5786	-0.05596
	R^2	0.7853	0.5733	0.7216	0.4704	0.2089	-0.1197	-0.1675	0.7973	0.6978	-0.1857
	p -value	0.004923	0.01801	0.009653	0.03621	0.1689	0.6339	0.7245	0.01045	0.01195	0.816

<i>P. brehus</i>	Intercept	-2.529	-2.1135	-0.352	-4.276	1.9520	2.62121	1.8838	3.4627	4.4081	4.7209
	Slope	2.169	1.7181	1.084	2.826	0.2578	-0.06282	0.3737	-0.2304	-0.7396	-0.7128
	R ²	0.0244	0.5247	-0.08281	0.1118	-0.2897	-0.2334	-0.1168	-0.2788	0.6593	0.696
	p-value	0.3713	0.1024	0.4659	0.3076	0.7708	0.6559	0.5277	0.7442	0.05971	0.04981
<i>P. roechus</i>	Intercept	1.464	6.303	-1.4077	2.81957	0.9471	-0.8105	3.1213	2.02544	0.3549	3.9371
	Slope	0.437	-1.410	1.5163	-0.05202	0.6233	1.2814	-0.1263	0.26851	0.8573	-0.4120
	R ²	0.006083	-0.2135	0.8514	-0.3056	-0.03944	0.4538	-0.2296	0.6893	0.5486	-0.2399
	p-value	0.4191	0.5629	0.05083	0.8169	0.425	0.1291	0.6495	0.05156	0.0941	0.667
<i>S. andersoni</i>	Intercept	1.8506	1.1999	0.6063	0.6918	2.9740	0.7515	3.0958	3.3140	0.6119	1.1403
	Slope	0.2189	0.4674	0.6905	0.7421	-0.2129	0.6620	-0.2364	-0.3184	0.7530	0.5692
	R ²	-0.03969	0.1496	0.2588	0.3012	-0.03787	0.6272	-0.03523	0.03641	0.5615	0.4367
	p-value	0.4771	0.1054	0.04366	0.03035	0.4691	0.0007612	0.458	0.2616	0.003039	0.01151
<i>S. atlas</i>	Intercept	1.8495	1.7513	-1.6378	1.5576	0.9728	0.6683	1.9303	0.9928	0.2707	1.6100
	Slope	0.2321	0.2498	1.6414	0.3870	0.5796	0.6929	0.2681	0.6210	0.8935	0.3924
	R ²	0.2175	-0.08658	0.6341	-0.002354	0.1247	0.4122	-0.07491	0.4621	0.838	0.003021
	p-value	0.1633	0.5024	0.01976	0.3663	0.2314	0.07135	0.48	0.05579	0.002393	0.3593
<i>S. baileyi</i>	Intercept	1.69144	2.7792	0.4795	2.8074	1.1388	0.3348	1.5854	0.8819	0.05077	0.9133
	Slope	0.32560	-0.1301	0.7668	-0.1125	0.5353	0.8388	0.4106	0.6577	0.97879	0.6866
	R ²	0.9213	-0.3533	0.9283	-0.2912	-0.07162	0.8957	0.7421	0.4783	0.3734	0.8486

	<i>p</i> -value	0.02657	0.6872	0.02419	0.7748	0.4549	0.009512	0.03845	0.1195	0.1631	0.01683
<i>S. brownei</i>	Intercept	1.6652	0.6653	-0.2248	1.4200	1.5403	0.2028	0.6499	1.7652	1.1552	0.1599
	Slope	0.3466	0.7051	1.0496	0.4720	0.3977	0.9096	0.7985	0.3426	0.5481	0.9823
	R ²	0.2177	0.4372	0.509	0.23	0.2374	0.5694	0.3266	0.1646	0.3695	0.4069
	<i>p</i> -value	0.002423	3.737e-06	6.272e-07	0.001569	0.0009782	6.424e-08	0.0001064	0.009023	6.423e-05	2.254e-05
<i>S. gilli</i>	Intercept	0.7420	0.09765	0.24490	0.34523	0.19088	0.24668	0.41061	-0.04305	-0.34783	0.31789
	Slope	0.6910	0.91752	0.85558	0.88749	0.88671	0.86867	0.87334	1.01901	1.15427	0.91345
	R ²	0.3575	0.6878	0.7966	0.8077	0.8998	0.9512	0.8562	0.7751	0.8752	0.8292
	<i>p</i> -value	0.0005888	9.946e-08	1.236e-09	6.443e-10	1.063e-13	<2.2e-16	8.277e-12	8.602e-10	1.494e-12	6.629e-11
<i>S. maddocki</i>	Intercept	2.26235	2.4455	0.4765	3.2484	1.8637	-0.05107	0.9603	1.2036	0.7178	0.7367
	Slope	0.02939	-0.0501	0.7484	-0.3820	0.2205	0.98915	0.6332	0.5109	0.6917	0.7224
	R ²	-0.1653	-0.1626	0.8371	0.08394	-0.07265	0.5092	0.07937	0.1468	0.4412	0.1763
	<i>p</i> -value	0.9364	0.8895	0.0008988	0.2474	0.4956	0.02825	0.2523	0.2133	0.06199	0.1911
<i>S. newtonae</i>	Intercept	-0.5109	3.5346	2.22759	2.65491	1.9332	0.5796	2.79606	1.3436	-6.8712	6.905
	Slope	1.2644	-0.4218	0.04779	-0.03856	0.2352	0.7446	-0.05241	0.5061	3.8361	-1.751
	R ²	0.6035	-0.3189	-0.3256	-0.297	0.3809	0.7514	-0.3232	0.3419	0.8705	0.01939
	<i>p</i> -value	0.07619	0.8677	0.9031	0.7907	0.1598	0.0363	0.8889	0.1776	0.01324	0.3753
<i>S. occidentalis</i>	Intercept	1.2031	0.63083	0.07223	0.5601	0.4808	0.61490	1.0449	0.6511	0.6243	0.2187
	Slope	0.5306	0.71461	0.92472	0.8065	0.7903	0.74349	0.6326	0.7643	0.7484	0.9432

R^2	0.5068	0.8308	0.753	0.6612	0.895	0.8625	0.427	0.6874	0.3208	0.5038
p -value	8.378e-05	2.256e-09	1.031e-07	2.565e-06	1.849e-11	2.786e-10	0.0004321	6.169e-07	0.002862	8.941e-05

Table 7 V-test results and associated p -values for Pleistocene localities. V statistic values have been rounded off to 4 decimal places. “-” indicates that less than three species were represented for that measurement and so it could not be used. The significance level for p -values is 0.05.

Locality		M1 length	M1 width	M2 length	M2 width	M3 length	M3 width	M4 length	M4 width
McEachern cave	V stat.	0.0740	0.3145	0.0556	0.3828	0.1005	0.2689	0.1543	0.0500
	P -value	0.1-0.9	0.1-0.9	0.1-0.9	0.1-0.9	0.1-0.9	0.1-0.9	0.1-0.9	0.1-0.9
Lancefield	V stat.	-	-	-	-	0.3628	0	-	-
	P -value	-	-	-	-	0.1-0.9	>.9	-	-
Victoria fossil cave	V stat.	0.0200	0.0054	0.0213	0.0043	0.0126	0.0080	0.0054	0.0045
	P -value	0.1-0.9	0.05-0.1	0.1-0.9	0.025-0.05	0.9-0.95	0.1-0.9	0.05-0.1	0.025-0.05
Wellington caves	V stat.	0.0022	0.02	0.0658	0.0028	0.0478	0.0668	0.1026	0.0309
	P -value	0.05-0.1	0.1-0.9	0.1-0.9	0.01-0.025	0.1-0.9	0.1-0.9	0.1-0.9	0.1-0.9
Henschke	V stat.	0.0463	0.0655	0.0606	0.1048	0.0185	0.0234	0.0191	0.0264
	P -value	0.1-0.9	0.1-0.9	0.1-0.9	0.9-0.95	0.1-0.9	0.1-0.9	0.1-0.9	0.1-0.9

Table 8 V-test results and associated *p*-values for modern localities. V statistic values have been rounded off to 4 decimal places. “-” indicates that less than three species were represented for that measurement and so it could not be used. The significance level for *p*-values is 0.05.

Locality		M1 length	M1 width	M2 length	M2 width	M3 length	M3 width	M4 length	M4 width
North Western Australia	V stat.	0.3472	0.0661	0.1582	0.2551	0.1250	0	0	0.2551
	<i>P</i> -value	.1-.9	.1-.9	.1-.9	.1-.9	.1-.9	>.9	>.9	.1-.9
Northern Territory	V stat.	-	-	0.0448	0.0832	0.0357	0.0724	0.0960	0.0340
	<i>P</i> -value	-	-	.1-.9	.1-.9	.1-.9	.1-.9	.1-.9	.1-.9
South Australia	V stat.	0.0082	0.0444	0.0117	0.0443	0.0044	0.0188	0.0245	0.0235
	<i>P</i> -value	.05-.1	.1-.9	.1-.9	.9-.95	.01-.025	.1-.9	.1-.9	.1-.9
VIC/SA border	V stat.	0.3528	0.1250	0.3580	0.3200	0.1800	0.5000	0.0139	0.5000
	<i>P</i> -value	.1-.9	.1-.9	.1-.9	.1-.9	.1-.9	>.999	.1-.9	>.999
Victoria	V stat.	0.1537	0.0825	0.2271	0.0031	0.0918	0.0503	0.0332	0.0486
	<i>P</i> -value	.1-.9	.1-.9	.95-.975	.01-.025	.05-.1	.025-.05	.1-.9	.1-.9
East coast New South Wales	V stat.	0.5000	0	0.1250	0.0556	0.0062	0.6250	0.0556	0.0372
	<i>P</i> -value	.1-.9	>.9	.1-.9	.1-.9	.1-.9	>.999	.1-.9	.1-.9
Inner New South Wales	V stat.	-	-	0.2813	0.3400	0.0022	0.2551	0.3025	0.5
	<i>P</i> -value	-	-	.1-.9	.1-.9	.05-.1	.1-.9	.1-.9	>.999
North Central Australia	V stat.	0	0	0.0533	0.0230	0.0325	0.0601	0.0186	0.0550
	<i>P</i> -value	>.9	>.9	.1-.9	.1-.9	.1-.9	.1-.9	.1-.9	.1-.9

Table 9 Kruskal-Wallis tests for geographic species variation in the Middle Pleistocene. The significance level for the p -values is 0.05.

Species		M1 length	M1 width	M2 length	M2 width	M3 length	M3 width	M4 length	M4 width
<i>M. titan</i>	chi-squared	1.5	0	2.7778	0.7714	3.0857	0.0216	4.2	2.1609
	df	1	1	1	1	1	1	1	1
	p -value	0.2207	1	0.09558	0.3798	0.07898	0.8831	0.04042	0.1416

Table 10 Kruskal-Wallis tests for geographic species variation in the Late Pleistocene. The significance level for the p -values is 0.05.

Species		M1 length	M1 width	M2 length	M2 width	M3 length	M3 width	M4 length	M4 width
<i>M. giganteus</i>	chi-squared	0	0.2	2.4667	1.7033	3.1736	2.2347	7.0714	4.8179
	df	1	1	2	2	2	2	2	2
	p -value	1	0.6547	0.2913	0.4267	0.2046	0.3271	0.02914	0.8991
<i>P. goliah</i>	chi-squared	0.5	5	2.6889	5	0.2	5	5	1.8
	df	1	1	1	1	1	1	1	1
	p -value	0.4795	0.02535	0.1011	0.02535	0.6547	0.02535	0.02535	0.1797
<i>S. andersoni</i>	chi-squared	0.2143	3.5294	0.2143	0.0551	0	0.8571	2	0.5
	df	1	1	1	1	1	1	1	1
	p -value	0.6434	0.06029	0.6434	0.8143	1	0.3545	0.1573	0.4795
<i>S. gilli</i>	chi-squared	1.8027	1.8333	1.125	0.6071	1.8133	4.0545	5.7771	2.0741
	df	2	2	2	2	2	2	2	2
	p -value	0.406	0.3998	0.5698	0.7382	0.4039	0.1317	0.05566	0.3545
<i>S. occidentalis</i>	chi-squared	11.4833	10.2	10.0571	9.781	11.5583	10.425	7.8667	4.1333
	df	3	3	3	3	3	3	3	3
	p -value	0.00938	0.01694	0.01809	0.02052	0.00906	0.01528	0.04885	0.2474
<i>S. stirlingi</i>	chi-squared	0	1.5	2.4	2.4	0	0.6	0.6	2.4
	df	1	1	1	1	1	1	1	1

<i>p</i> -value	1	0.2207	0.1213	0.1213	1	0.4386	0.4386	0.1213
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Table 11 Kruskal-Wallis tests for geographic species variation in modern kangaroos. The significance level for the p -values is 0.05.

Species	Sex		M1 length	M1 width	M2 length	M2 width	M3 length	M3 width	M4 length	M4 width
<i>M. fuliginosus</i>	Female	chi-squared	-	-	4.5	0.3333	1.6364	0.4091	2.2273	5.5
		df	-	-	1	1	1	1	1	1
		p -value	-	-	0.03389	0.5637	0.2008	0.5224	0.1356	0.01902
	Male	chi-squared	2.1429	0.0857	1.7992	0	1.35	0.15	0.6	0.15
		df	1	1	1	1	1	1	1	1
		p -value	0.1432	0.7697	0.1798	1	0.2453	0.6985	0.4386	0.6985
<i>M. giganteus</i>	Female	chi-squared	4.4643	3.6071	8.6392	12.0335	10.6811	3.3919	4.7819	6.2025
		df	2	2	5	5	5	5	5	5
		p -value	0.1073	0.1647	0.1244	0.03433	0.05808	0.6398	0.4431	0.287
	Male	chi-squared	11.9013	12.8284	12.4706	13.0359	8.3775	7.8258	5.3067	4.5352
		df	4	4	4	4	4	4	4	4
		p -value	0.0181	0.01215	0.01417	0.0111	0.07869	0.09817	0.2572	0.3384
<i>M. robustus erubescens</i>	Female	chi-squared	1.6135	0.4667	0.1326	0.0037	0.1449	0.0266	0.0416	0
		df	1	1	1	1	1	1	1	1
		p -value	0.204	0.4945	0.7157	0.9515	0.7035	0.8704	0.8384	1
	Male	chi-squared	1.6595	5.7486	11.8663	13.8097	7.2232	10.4686	10.1654	19.5335
		df	3	3	3	3	3	3	3	3

		<i>p</i> -value	0.646	0.1245	0.007856	0.003176	0.06511	0.01498	0.01721	0.000212
<i>M. robustus</i>	Male	chi-squared	2.4	3.4286	4	4	0.4444	3.75	1	0.444
<i>woodwardi</i>		df	1	1	1	1	1	1	1	1
		<i>p</i> -value	0.1213	0.06408	0.0455	0.0455	0.505	0.05281	0.3171	0.505
<i>M. rufus</i>	Female	chi-squared	1.3333	0	1.2	0.8333	1.05	0.1929	7.75	0.3429
		df	1	1	1	1	1	1	1	1
		<i>p</i> -value	0.2482	1	0.2733	0.3613	0.3055	0.6605	0.00535	0.5582
	Male	chi-squared	4.7849	7.2929	8.1095	9.614	14.6696	11.5789	3.0703	1.7065
		df	3	3	4	4	4	4	4	4
		<i>p</i> -value	0.1882	0.06313	0.08765	0.04746	0.005438	0.02077	0.5461	0.7895

DISCUSSION

The results of the V-tests indicate that there was very little character displacement in both fossil and modern kangaroo species. There was no suggestion of character displacement in the Pleistocene localities McEachern Cave, Lancefield or Henschke Cave, nor was there for the modern localities North Western Australia, Northern Territory, Victoria/South Australia border, East coast NSW, Inner NSW and North Central Australia. Displacement was supported in the extinct localities Victoria Fossil Cave and Wellington Cave and in the modern localities of South Australia and Victoria. These two significant results, however, are likely a random outcome due to the large number of tests performed. This can be supported or refuted by performing the same tests with a greater sample size, which will increase the accuracy of any results. Alternatively, these two results may be initial indicators that an ecological mechanism like displacement is occurring and thus further study is required.

The results of the Kruskal-Wallis tests demonstrate that some features show significant variation between different populations, but the same amount -if not more -show no significant variation. This leaves us in the same place as with the V-test: despite there being evidence for variation, it is not enough to say there are large geographic differences, with perhaps the exception of the modern *M. robustus erubescens* male where 5 of 8 measurements showed significant variation between populations. We expect to see geographic variation when species overlapping at one locality displace each other. The lack of variation shown by the Kruskal-Wallis tests therefore argues against character displacement.

If we compare which measurements gave us significance in both tests this can help determine the likelihood of character displacement. In the measurements of extinct communities, there was significance in both the V-tests and Kruskal-Wallis test only for M2 width. In the measurements of modern communities there was significance in both the V-tests and Kruskal-Wallis tests for M2 width, M3 length and M3 width. The small number of nominally significant results relative to the number of tests that were performed supports the finding that character displacement was not occurring at any substantial level in either Pleistocene or modern kangaroo communities, as indicated by dentary molars.

Slopes indicated by the linear regressions fell well below 1.0 and so variation is allometric, however since there was high variation in the measurements taken it is difficult

to determine whether the pattern revealed is real or a result of random variation. Although the linear regressions show some relationship between dentary features of extinct and modern kangaroos, it should be kept in mind that modern kangaroos undergo molar progression, meaning that their molars move further down their jaws as they get older to make room for newer molars (Butler et al. 2014). Progression may have an effect on the results obtained here because of the association with wear. As the teeth progress down the jaw they reduce in size until they are completely lost. Therefore, the approximate age of the kangaroo would be important to determine when looking at tooth sizes, not only whether they are adult or juvenile. All of the above points lead to the conclusion that the data is noisy and so more measurements are needed for all species in all localities, to perform the same methods on. Further refining of approximate dates of specimens will also assist in future studies.

Whether or not molar progression occurred in extinct kangaroos is still not known. There is no evidence to suggest that molar progression occurred in Miocene kangaroos which may be because they are believed to have been browsers and are therefore less likely to have displayed progression (Dawson and Flannery 1985). As diet in the Pleistocene moved towards grazing, the likelihood for molar progression would have increased. In fact, figure 6 shows what may be evidence of molar progression in a Pleistocene kangaroo. In this figure we can easily see molars 2-4 but where the first molar should sit there is no surface left, which is similar to what we see in modern kangaroos which exhibit molar progression (figure 7). Nevertheless, more research is needed to determine whether molar progression was occurring in extinct kangaroos to help us understand how it developed evolutionarily.



Figure 6. Possible molar progression of extinct Middle Pleistocene kangaroo *M. titan* from Wellington Caves, specimen provided by the Australian Museum. Molars 2-4 are visible. Bar indicates 1cm scale.



Figure 7. Molar progression in the modern red kangaroo (*M. rufus*) from NSW, specimen provided by the Australian Museum. Molars 2-4 are visible. Bar indicates 1cm scale.

We can conclude from these tests that despite there being some evidence for character displacement and geographical variation, there is no discernable pattern in Pleistocene or modern species of kangaroo communities. This result has implications for palaeoecological studies. If what I found here is true, and character displacement has not acted on extinct or modern kangaroo communities, how have they been able to maintain coexistence and similarity?

4.1 CHARACTER displacement criteria.—It was mentioned in the introduction that a set of 6 criteria were brought forward to help improve character displacement studies. Addressing these criteria in terms of the species analyses here will help to reinforce the results. Again it must be noted that the more species you look at for character displacement, the less you need to rely on these points (Dayan and Simberloff 2005).

(1) Phenotypic variation has a genetic basis: establishing the genetic basis of phenotypic variation in fossils is not possible. However, because we can see a relationship between tooth structure and feeding strategy over evolutionary time, as well as a modern division of species by this feeding strategy, we can assume that there has to be a genetic basis. Additionally, there appears to be genetic variation between island and mainland phenotypes of tooth structure in modern grey kangaroos (Kirsch and Poole 1972). Alternatively, competition may not be the main factor acting on these populations of kangaroos. Further study is therefore needed here.

(2) Variation did not occur through chance: the Kruskal-Wallis test and particularly the V-test results show that variation indeed could have been random. Therefore variation may have occurred by chance, which supports the conclusion here that the results are not consistent with the character displacement model. Further studies using greater sample sizes may yield more robust Kruskal-Wallis test results.

(3) Patterns result from evolutionary shifting, not sorting: A deeper look into kangaroo habitation prior to the Pleistocene would help to show whether any species evolved in sympatry instead of allopatry. However, this may not be feasible because exceptional sampling, dating and species identification is needed.

(4) There is a link between phenotypic change and shifts in resource use: Although there is a relationship between the vegetation shift at the end of the Pleistocene and a move to large macropod grazing, this would only apply to character displacement studies performed on kangaroos post-extinction. Further study is needed in earlier kangaroo deposits (such as the Nelson Bay Fauna, Morwell and early Darling Downs) in order to determine whether or not this was occurring prior to the communities studied here.

(5) Compared allopatric and sympatric sites are environmentally similar: Although the Pleistocene had oscillated between dry and wet, the areas of interest

had overall similar climates for each separate time frame (Morton et al. 2011). Therefore, compared allopatric and sympatric sites were environmentally similar. Only comparing sites occurring at the same time omits the problem of climates oscillating through time.

(6) Competition occurs between the interested species: this point was addressed earlier, and the fact remains that competition between Pleistocene kangaroos is supported only by circumstantial evidence. In systems where there is a high number of ecologically similar species there is normally some degree of competition. Furthermore, habitat segregation in modern macropods suggests that there was competition between these species in the past. It is highly likely, therefore, that competition was occurring in Pleistocene kangaroos.

Points 5 and 6 support the need to test for character displacement in extinct kangaroo communities, and the first point can be used as weak support. Criteria 2, 3 and 4 do not support analysing character displacement in extinct kangaroos. Investigating these criteria, where possible using fossil data, can shed light on the likelihood of displacement. The fact that there is some weak support for displacement in extinct kangaroo's advocates further investigation.

4.2 CHARACTER displacement has not developed in kangaroos.—In this section I will discuss the implications for palaeoecology on the assumption that this study is correct in determining that character displacement did not occur.

Firstly, it can be suggested that pairwise competition was not as strong as one might have assumed it was in the Pleistocene. The continued sympatry of kangaroos through to the modern day does not necessarily suggest that competition was not occurring. Instead, diffuse competition is likely to have occurred. Diffuse competition was first coined by MacArthur (1972) and describes the situation where a great number of species are competing against each other in a single system. Even if competition is not strong between individual species pairs, the accumulation of weak competition can have a significant effect on all species involved.

It is possible that in order to move through competition, whether it is caused by heavy interspecies competition or diffuse competition, Pleistocene kangaroos may have used

resource partitioning. Modern kangaroos are been found to display very fine scale habitat segregation where species coexist, which can include variation in feeding time or inhabiting slightly different areas within a single location (Dawson and Denny 1969; Milne and O'Higgins 2002). An example of modern kangaroo habitat segregation is between the eastern and western greys (*M. giganteus* and *M. fuliginosus*, respectively) and swamp wallabies (*Wallabia bicolor*) in Eastern Australia (Schmidt et al. 2010). It is possible therefore, that kangaroos in the Pleistocene used behavioural resource partitioning instead of morphological.

Microhabitat segregation would be immensely difficult to establish in Pleistocene communities as the preservation scale is not fine enough to show this. Most specimens come from mass deposits in caves. These cave deposits preserve specimens that fall into sink holes, which may not show in situ compositions of species. That is, the species found there don't need to have necessarily lived in close association with the other species, but may have fallen in while passing through.

In both the Australian Pleistocene and modern African savanna there is a substantial abundance of animals which share ecological requirements (Western et al. 2009). This is interesting considering that animals which overlap in dietary requirements should, in theory, outcompete each other. Further study into both the herbivores of the African savanna and Pleistocene Australia can reveal the ecological mechanisms allowing an abundance of similar species to coexist, if character displacement is rejected.

Phylogenetic inertia may be one explanation for why we did not find character displacement. Phylogenetic inertia means that character traits do not change as quickly as we would expect in response to adaptive forces (Hansen and Orzack 2005). If this was occurring in kangaroos it would be difficult to assign phenotypic change to environment, despite the heavy correlation between the two, using fossil data.

4.3 CHARACTER displacement has developed in kangaroos. –Character displacement still may have been present in Pleistocene, or modern, kangaroo communities, but was not detected in this study. There are a number of explanations, all of which could form the basis for future research. Here I will address a number of points to explain why it was not detected.

Firstly, the dataset might not be large enough, in terms of the number of species, species sample sizes, or localities. Sample size is a continuing issue in palaeontology, particularly in vertebrates. Including more localities such as the Nullabor Plain and measuring more specimens from the localities in this study would give the dataset greater statistical power.

Secondly, although teeth are intimately related to feeding mechanisms and therefore should be good indicators of character displacement, it would be worth redoing this study using the maxillary molars, which were not included here because of time constraints and the greater availability of dentary specimens. Doing so may give more support for the character displacement hypothesis. Skull length is another measurement not employed in this study which may give insight into morphological variation in coexisting kangaroos (Milne and O'Higgins 2002). Skull length has been used in the past to describe character displacement in mammals (Dayan et al. 1989, 1992; Simberloff et al. 2000). Investigating skull length in kangaroos might be just as important, if not more, than analysing tooth size. Furthermore, the distinction between the two groups of kangaroos in the Pleistocene, short and long faced, may be crucial in how much this variation played a role in coexistence. The biggest issue in doing this is finding Pleistocene specimens where skull length can be measured, as many specimens are fragments.

Thirdly, including a greater range of macropods for both fossil and modern communities would be beneficial for this study. Smaller macropods were not included here due to time restrictions, but would add a great deal more variation for analysis. We know that macropods today are divided according to size and feeding habit, but what is the scale of difference between them? Within feeding habits is there much variation between species? Including smaller macropods into a palaeoecological study and analysing relationships between size, feeding behaviours, and ecological interactions with others would improve our understanding of Pleistocene communities.

4.4 IMPLICATIONS for character displacement and palaeoecology.—The results of this study suggest that character displacement did not occur between sympatric Pleistocene kangaroos. These results have implications for a number of palaeoecological evolutionary questions.

A lack of character displacement suggests that competing species should have undergone competitive exclusion. However, the fact that sympatry was maintained refutes this hypothesis. There is therefore some other ecological process occurring on Pleistocene kangaroos. Competition between kangaroos and other herbivores should be taken into account for further palaeoecological studies as should modern competition with other herbivores and particularly with introduced species.

The idea that there were differences in the loss of browsers compared to grazers was refuted by Johnson and Prideaux (2004) but further statistical tests supported the original idea that there were differences (Bowman et al. 2010). The fact that the largest of megafauna species were browsers, and had a greater chance of extinction compared to the grazers, supports the idea of human hunting as a cause of extinction. This is because, as mentioned earlier, humans are more likely to have targeted larger animals (Owen-Smith 1987).

Climate change is unlikely to have caused the extinction because it was not different to any previous fluctuations, which the kangaroos were able to survive. Although debate is still continuing about the causes of the extinction, the dating methods used by Grün et al. (2010) and Rule et al. (2012) are reliable for dating human arrival and suggest that they were the primary cause for Australian extinctions, as they were globally (Sandom et al. 2014).

This study is a preliminary investigation of kangaroo palaeoecology using methods that had not been applied before, but it leaves much open for further study. There is an opportunity to look further into the evolutionary history of kangaroos, which can reveal changes over a longer period of time and give us a better understanding of how and when they have occurred. If these changes can be correlated to vegetation shifts, local extinctions or species compositions it will help to develop our understanding of kangaroo palaeoecology.

CONCLUSION

The results of the V-tests do not support character displacement in dentary molar size as a mechanism for continued coexistence between kangaroos from the Pleistocene or in modern Australia. The Kruskal-Wallis test showed support for some geographical variation between dentary molars, but not enough to support displacement. It is likely that instead of

developing character displacement to create slight variations in resource use, kangaroos survived using resource partitioning. This is supported by resource partitioning seen in modern coexisting macropods. Kangaroos are ecologically similar to ungulates in the African savanna and so comparisons between each group's ecology can reveal important information about how they have survived in such abundance. Similarity between herbivorous assemblages of the modern African savanna and Pleistocene kangaroos allow comparisons to be made between these two groups.

Increasing the dataset to include more specimens would reduce the noise of the data and may give more accurate results pertaining to character displacement. Investigating the presence of displacement using other features such as maxillary molar size and skull length are possible future studies, which may reveal more about kangaroo palaeoecology. More research is needed to get a clearer understanding of kangaroo palaeoecology and to show which mammalian communities exhibit character displacement. This study continues the investigation into kangaroo palaeoecology and raises more questions about how they have maintained the abundance they have, while living in sympatry, throughout their evolutionary history.

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SUPPLEMENTARY INFORMATION

Table 1 V test values (top row) and their associated p -values. 0^n indicates n leading zeroes, e.g., $0.0^6500 = 0.000000500$. Adapted from Williams (1995). The significance level for the p -values is 0.05.

Number of species	.001	.0025	.005	.01	.025	.05	.10	.90	.975	.99	.995	.9975	.999
3	.0 ⁶ 500	.0 ⁵ 312	.0 ⁴ 125	.0 ⁴ 500	.0 ³ 312	.00125	.00500	.405	.451	.475	.490	.495	.498
4	.0 ³ 137	.0 ³ 347	.0 ³ 688	.00139	.00345	.00689	.0138	.179	.218	.249	.279	.294	.305
5	.0 ³ 601	.00113	.00179	.00286	.00528	.00839	.0130	.0985	.123	.145	.169	.185	.197
6	.00116	.00179	.00247	.00345	.00540	.00767	.0109	.0625	.0772	.0922	.110	.122	.135
7	.00137	.00196	.00259	.00342	.00494	.00654	.00868	.0432	.0530	.0631	.0762	.0853	0.0939
8	.00148	.00201	.00254	.00320	.00426	.00551	.00707	.0316	.0386	.0457	.0553	.0625	.0692
9	.00149	.00194	.00238	.00289	.00378	.00466	.00586	.0241	.0292	.0346	.0419	.0474	.0530
10	.00147	.00184	.00219	.00259	.00330	.00399	.00493	.0189	.0228	.0270	.0325	.0368	.0412