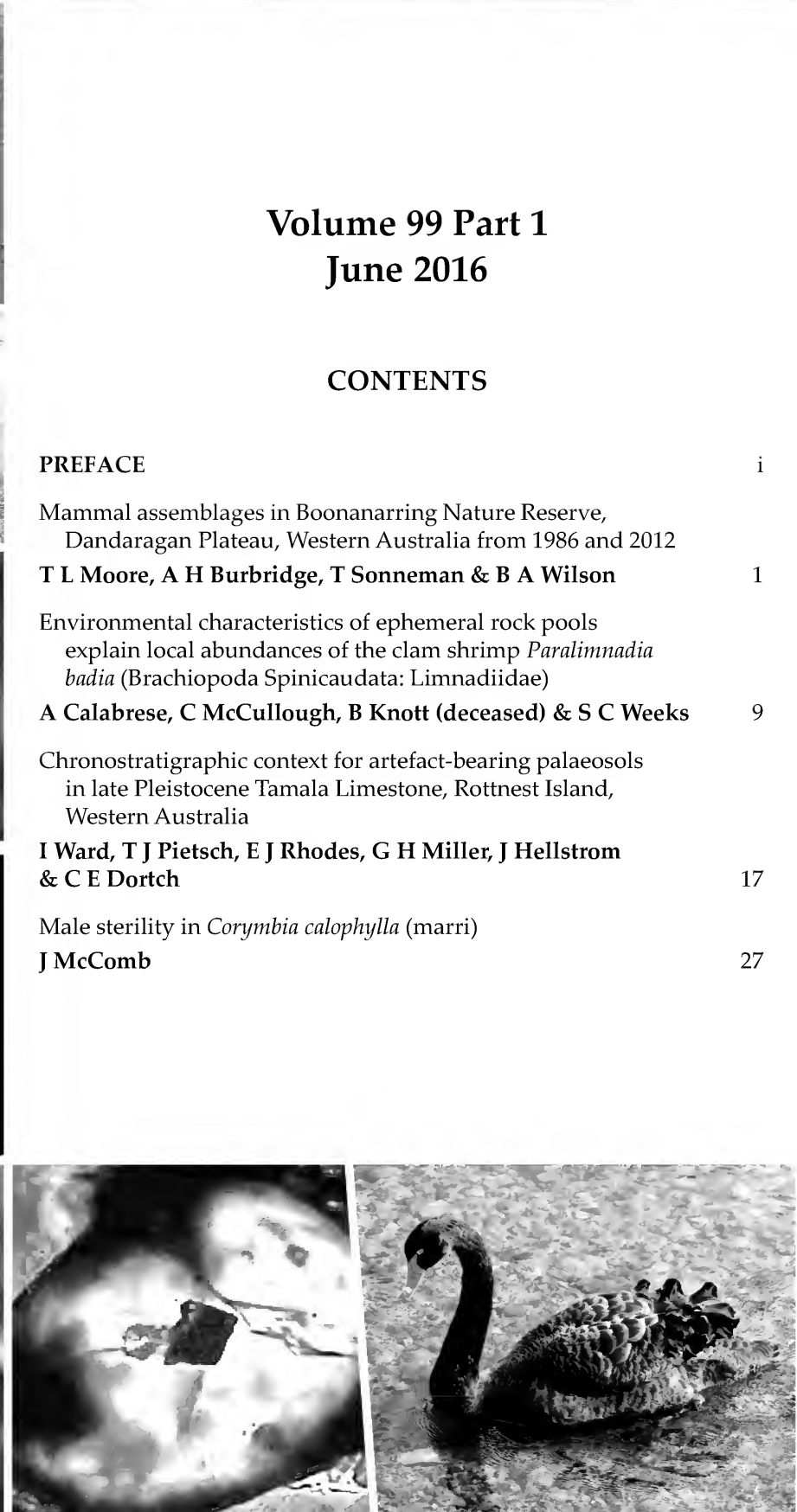




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The Journal of the Royal Society of Western Australia was first published in 1914 and circulates widely within Australia and throughout the world. The journal has a large number of personal subscribers, many of whom are scientists working in Western Australia.

Cover design: The images symbolise the diversity of sciences embraced by the Royal Society of Western Australia. Counter-clockwise from the top they are: Wolfe Creek Meteorite Crater; the world-famous stromatolites at Shark Bay; the numbat (*Myrmecobius fasciatus*), Mangles' kangaroo paw (*Anigozanthos manglesii*) and Gogo fish (*Mcnamaraspis kaprios*), which are the faunal, floral and fossil emblems of Western Australia, respectively; a zircon grain (Western Australian rocks have yielded the oldest zircon dates in the world, up to 4.37 Ga); and the black swan (*Cygnus atratus*) that appears on the logos of the Royal Society and the coat of arms of the Government of Western Australia.

BHL



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PREFACE

The Journal of the Royal Society of Western Australia is proud to include four important papers in issue 99/1, the first issue to be published entirely online.

Ecologists are frequently enjoined to utilise the ecosystem concept for segments of nature of any magnitude, from the entire biosphere down to the tiniest natural entity, and in this issue we see a careful study of clam shrimp populations in relation to their environment in small ephemeral rock pools on granite outcrops in WA's Wheatbelt.

Scientists are also encouraged to take 'a long-term view' and to study the nature of changes in the environment by repeating observations at relatively long intervals. It is thus a pleasure to be able to present a study undertaken on mammal assemblages in a Western Australian Nature Reserve in 1986 and 2012.

Rottnest Island has served the purpose of an 'outdoor laboratory' for Western Australian schools and universities for over a century and this issue includes a significant contribution to the geology of that island. The return of earth science papers to the journal is particularly welcome and serves to emphasise the interdisciplinary nature of the journal.

The marri is often taken as an organism for special study in the field and in the laboratory in the State; the final paper reveals that there is much to be found out about a most familiar organism.

P H Armstrong
Editor-in-Chief

Nedlands
June 2016

Mammal assemblages in Boonanarring Nature Reserve, Dandaragan Plateau, Western Australia from 1986 and 2012

T L MOORE^{1,5*}, A H BURBIDGE³, T SONNEMAN², B A WILSON^{1,4}

¹ Department of Parks and Wildlife, Swan Region, Corner of Hackett and Australia II Drive, Crawley, Western Australia, 6009

² Department of Parks and Wildlife, West Kimberley District, 111 Herbert Street, Broome, 6725

³ Department of Parks and Wildlife, Woodoale Research Centre, Locked Bag 104, Bentley Delivery Centre, Western Australia, 6983

⁴ School of Life and Environmental Sciences, Deakin University, 221 Burwood Highway, Burwood, Victoria, 3125, Australia.

⁵ School of Veterinary and Life Science, Murdoch University, 90 South St, Murdoch, Western Australia, 6150

* Corresponding author: t.moore@murdoch.edu.au

ABSTRACT

Although long term monitoring can provide land managers and researchers with insights into faunal changes there are few such programmes in Australia, and many conservation actions are implemented without assessment of their biodiversity benefits or costs. This study investigated the current status of native small mammals in the Boonanarring Nature Reserve (BNR), Western Australia, aiming to compare the contemporary distribution of mammals to those recorded 26 years ago.

Of particular importance is the evidence that no small mammal species have been lost from the reserve in the last 26 years; *Pseudomys albocinereus*, *Tarsipes rostratus* and *Sminthopsis* (sp)p. were recorded in both years' surveys. Records of *P. albocinereus* in this study are significant as they confirm the persistence of the species on the Dandaragan Plateau, whereas on the adjacent Swan Coastal Plain the species has not been recorded since 1987.

Overall, the persistence of small mammals in this reserve, unlike the nearby reserves on the Swan Coastal Plain (SCP), could be attributed to the mix of vegetation types within the reserve and the larger size of Boonanarring Nature Reserve. However, deficiencies in the monitoring programme were identified. There is a need to improve the long-term monitoring of small mammals within the BNR with long-term, repeat-measures, analysis and reporting.

KEYWORDS: Swan Coastal Plain, *Pseudomys albocinereus*, *Tarsipes rostratus*, *Sminthopsis*, ash grey mouse, monitoring

INTRODUCTION

Long term studies can provide researchers and land managers with insights into faunal changes over time, often in association with abiotic and biotic variables of change. However, biodiversity monitoring in Australia is limited and poorly coordinated (Natural Resource Management Ministerial Council 2010, Lindenmayer & Gibbons 2012, Lindenmayer *et al.* 2012). Managers and researchers who have worked in conservation biology in Australia are often disappointed by the absence of effective biodiversity monitoring that allows evaluation of how well Australia's natural heritage is managed (Garkaklis 2014). There are few long-term programmes, and many conservation actions are implemented without assessment of their biodiversity benefits or costs. Ultimately, a management decision must be made, but a manager needs to feel confident in making management intervention decisions (Varcoe 2012). There is a need to improve this with long-term, repeat-measures data, followed by its analysis and reporting. This is particularly relevant given Australia's significant extinction rate since European settlement (Woinarski *et al.* 2015).

Mammal extinctions and declines have occurred across the continent (McKenzie *et al.* 2007). Australian mammals, including those in the biodiversity hotspot of south-west Western Australia, have seen some of the highest extinction rates and include 50% of the world's extinction events since European settlement (Short & Smith 1994, Woinarski *et al.* 2015). Many factors have been implicated in these declines including climate change and a lack of rainfall, introduced predators, introduced herbivores and habitat modification (Burbidge & McKenzie 1989, McKenzie *et al.* 2007, Wilson *et al.* 2012, Woinarski *et al.* 2015). To conserve mammals, quantifying population trends over time in relation to management practices such as prescribed burning, predator control and abiotic changes such as habitat and climate change factors are pivotal in predicting populations in current and future conditions. This study employed sampling at two time points, 1986 and 2012, in Boonanarring Nature Reserve (BNR) in the south-west of Western Australia to examine changes in the species richness and abundances of mammals over recent decades.

Faunal declines in small isolated reserves are not unexpected (Fahrig 2002, Henle *et al.* 2004, Fischer & Lindenmayer 2006) but fauna populations in larger reserves may also be at risk. Boonanarring Nature

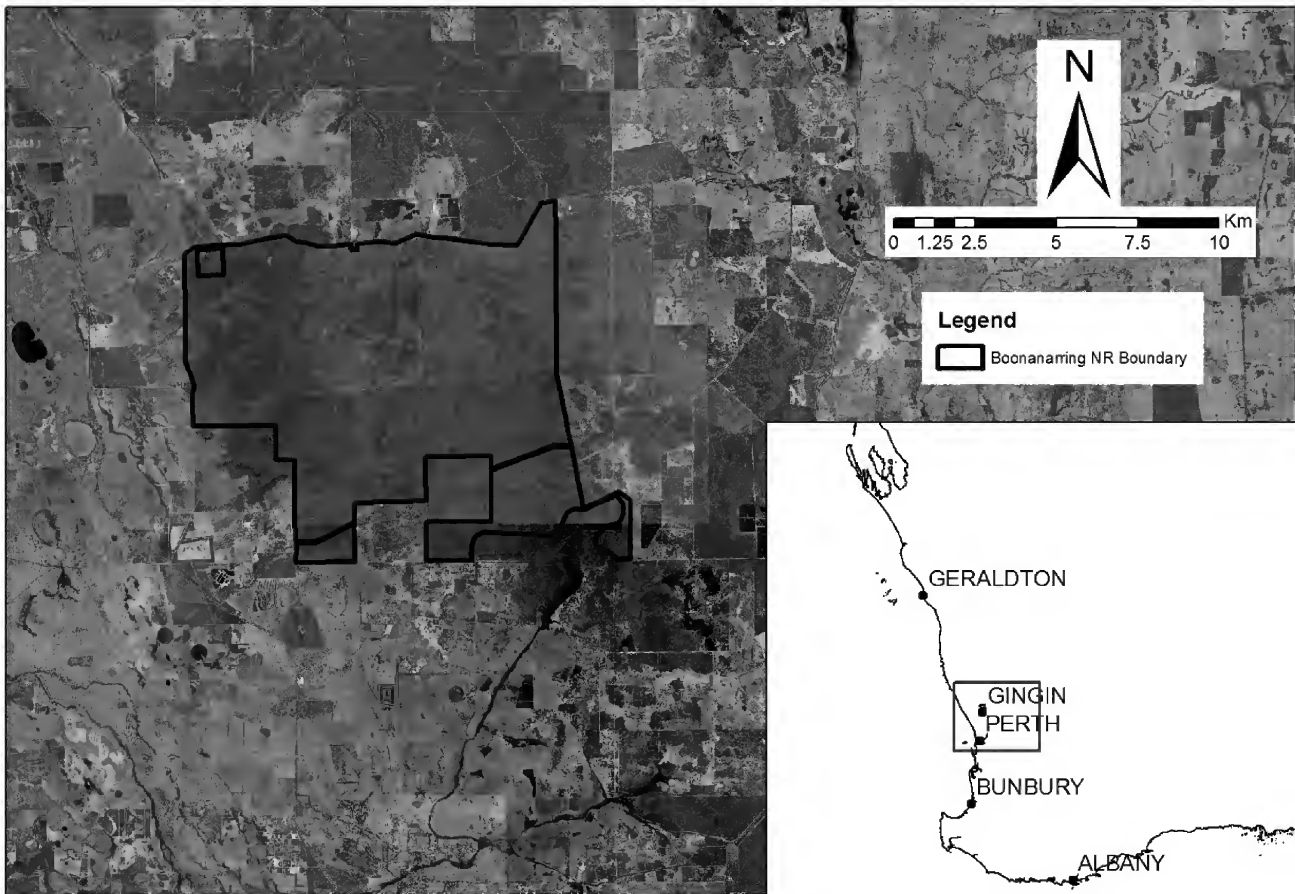


Figure 1. Location of Boonanarring Nature Reserve on the Swan Coastal Plain, Western Australia.

Reserve is located on the Dandaragan Plateau, which borders the Swan Coastal Plain (SCP) and Darling Scarp, near Gingin, Western Australia. Much of the Dandaragan Plateau has been extensively cleared and the dominant land use is dry-land agriculture (92.6%). Only 6.8% is remnant vegetation under conservation management and much of this is present in isolated patches (Department of Conservation and Environment 1983). Despite its isolation BNR has special significance, not only because it is one of the larger nature reserves covering >9000 ha with a level of connectivity to areas of surrounding natural vegetation totalling approximately 10,000 ha. It contains the highest quality and most extensive example of conserved *Banksia* woodlands on Dandaragan soils with unique flora and fauna (Burbidge *et al.* 1996). It was surveyed in 1986 for vegetation and fauna (Burbidge *et al.* 1996) and broad scale vegetation mapping was conducted by Beard (1979) and Heddle *et al.* (1980), but no other biological surveys have been conducted in the reserve. Fauna surveys were thus carried out in 2012 to determine the current status of vertebrate fauna and mammal populations in the reserve.

Burbidge *et al.* (1996) captured three significant native small mammal species (*Pseudomys albocinereus* (ash grey mouse), *Tarsipes rostratus* (honey possum) and *Sminthopsis griseoventer* (grey bellied dunnart) in BNR, and identified fire and introduced predators as likely threats to native mammals. Within conservation lands, fire management by the Department of Parks and Wildlife aims to protect

human life and property, and to a lesser degree biological diversity by reducing fuel loads that could lead to large wild fires. Prescribed burning occurs in BNR but planning for such burns is currently not focused on biological diversity or conservation of native species. Feral predators and weed invasion are other management issues across reserves in south-western Australia but currently no feral predator or weed control occurs in BNR. There are additional, potentially deleterious activities occurring within and surrounding the reserve, including gravel extraction and exploration for oil and gas (Coffey Natural Systems Pty Ltd. 2008; unpublished data).

The objectives of this paper were thus to (i) assess the current status of small mammals (abundance and species richness) in BNR, (ii) compare the current status of mammals to that described 26 years ago, and (iii) evaluate any problems associated with long term monitoring.

METHODS

Site description

Boonanarring Nature Reserve is a 'C' class reserve of 9250 ha, 15 km north of Gingin, with connections to 10,000 ha of protected remnant vegetation in Moore River Nature Reserve. It is situated to the southern

Table 1. Fire history and description of each site from the 2012 surveys at Boonanarring Nature Reserve, AB indicates that the site associated with the grid has PVC pit traps. FERA is a fire reference exclusion area. Vegetation data originate from Burbidge *et al.*, (1986).

Site Number	Fire age (years)	Vegetation type
1	14	<i>Corymbia calophylla</i> over heath
2 and AB1	14	Banksia woodland
3 and AB2	14	<i>Eucalyptus wandoo</i> woodland
4	3	<i>Eucalyptus marginata</i> and <i>Corymbia calophylla</i> woodland
5 and AB3	5	Banksia woodland
6	8	<i>Eucalyptus marginata</i> and <i>Corymbia calophylla</i> woodland
7	14 (FERA)	Heathland
8	14 (FERA)	Heathland
9	8	Heathland
10	14	Breakaway- low vegetation
11	14	Unusual tall heath on slope with <i>Eucalyptus</i> sp. woodland

end of the Dandaragan Plateau and is bordered by the SCP to the west and the Darling Scarp to the east (Figure 1). The biological significance of the area was first assessed in 1971 (N. McKenzie pers. comm.) and on the basis of this report it was later recommended that the then unallocated Crown land be combined with smaller reserves and an area of 400 ha of private land along Gingin Brook to form the BNR (Department of Conservation and Environment 1983). The reserve was gazetted as a 'C' class reserve in 1991, and vested in the National Parks and Nature Conservation Authority. Boonanarring Nature Reserve has a range of soil types (mostly lateritic, but also with white, grey or yellow sands) supporting over 570 plant species, 13% of which are recorded as being of special interest. The reserve supports a mix of vegetation types including banksia (*Banksia grandis*, *B. attenuata* and *B. menziesii*), *Corymbia calophylla* (marri), *Eucalyptus marginata* (jarrah), and *E. wandoo* (wandoo) woodlands (Table 1). The reserve is significant as it is rich in flora and vegetation types not present together on any other conservation reserves and being large enough to provide some protection from degradation owing to edge effects. It has a Mediterranean climate of wet winters and dry, hot summers (Burbidge *et al.* 1996, Coffey Natural Systems Pty Ltd. 2008).

At the time of the 2012 survey, the majority of the fauna survey sites had been burnt within the last 14 years (Table 1). The reserve contains a centrally located Fire Exclusion Reference Area (FERA) of 845 hectares for breeding and resting sites of the endangered Carnaby's black-cockatoo (*Calyptorhynchus latirostris*). Prescribed burns are planned for this reserve but a lack of optimal burning conditions had restricted implementation in the previous six years.

Monitoring surveys

1986 survey

Seven (2 ha) sites were trapped from the 17th to the 23rd of March 1986 (Table 2). Pitfall traps (12.5 x 60 cm) were employed at sites one to four and seven, and Elliot traps at sites five and six. Sites one to four had three lines of pitfall traps, sites five and six had three lines of Elliot traps and site seven had two lines of pitfall traps. Trap nights equated to 600 nights (Burbidge *et al.* 1996).

2012 survey

Trapping sites were established in the reserve in autumn and spring 2012. The sites were located in similar positions as those in the 1986 surveys in order to document any changes in mammal faunal assemblages. An additional five sites (7–11) were located in different vegetation types (heathland, breakaway and unusually tall heath) and/or fuel age in spring 2012 in an attempt to survey as many different habitats as possible. The trap efforts for each year are detailed in Table 2.

During two survey periods in 2012, in autumn (15th–23rd April) and spring (15th to the 22nd November), pitfall, Elliott and funnel traps were employed. Autumn surveys monitored six pitfall sites and in spring an additional five sites were surveyed. In autumn each pitfall site had 10 buckets connected by drift fences in a Y formation with two funnel traps at the end of each arm and five Elliott traps distributed within approximately 30m of the pitfall buckets. In spring the same set up was used, except that funnel and Elliot traps were not used. Three additional sites (AB 1, 2 and 3), closely connected to the other trapping locations (details in Table 2), consisting of only pitfall traps (12.5 x 60 cm) were established for the spring survey with a total of six traps per site as it was suspected that *Pseudomys albocinereus* could jump out of the 20L buckets. All pitfall and funnel traps were opened for eight nights and Elliott traps were open for six nights (for capture of mammals, amphibians and reptiles; however we only report on the mammals in this paper). In autumn and spring, trapping was conducted over 948 and 1084 trap nights respectively.

Table 2. Trap nights and survey effort of the 2012 and 1986 surveys in Boonanarring Nature Reserve.

Survey Method	Trap nights in 1986	Trap nights in 2012	
		Autumn	Spring
Pitfall traps (20L buckets)	0	480	880
Funnel traps	0	288	0
PVC pitfall traps	300	0	144
Elliott traps	300	180	60
Total trap nights	600	948	1084

ANALYSIS

As the trapping effort differed between years the mean mammal abundance, species richness and individual mammal species' abundances (as defined by mammal captures) were standardised to ten trap nights using data from all pitfall, Elliot and funnel traps (e.g. mean mammal abundance per ten trap nights at each site). Individual species were only analysed if their captures were above 20 individuals. In 2012 three individuals of *Sminthopsis* were captured but not identified to species. Captures of *Sminthopsis* were added irrespective of the initial species identification, as identification of animals from this genus in the field can be problematic (Kemper *et al.* 2011) and these individuals are herein termed *Sminthopsis* sp(p).

A direct comparison of 1986 and 2012 may be influenced by the season in which the survey was completed. Surveys were conducted in autumn in 1986 and 2012, and in spring 2012. One-way ANOVAs (Inc 2007) were thus performed at the site level to determine: 1) the relationship between mean mammal abundance, mammal species richness and individual mammal species' abundance and the season of trapping (autumn and spring) in 2012, and 2) relationships between mammal abundance, mammal species richness and individual mammal species' abundance and the year (1986 and 2012) and 3) relationships between mammal abundance, mammal species richness and individual mammal species' abundance in 1986 and 2012 using only autumn data.

Capture data were compiled for four species, *T. rostratus*, *M. musculus*, *P. albocinereus* and *Sminthopsis* sp(p). (*Sminthopsis griseoventer* in 1986), including capture numbers, sex ratio and body weights. Weight data for 2012 included mean, standard deviation and range for each species, whereas the weight data for 1986 were less detailed and only included the weight range for each species.

RESULTS

1986 survey

Four mammal species including one introduced species, *Mus musculus*, and three native species,

Pseudomys albocinereus, *Sminthopsis griseoventer* and *Tarsipes rostratus*, were captured in 1986 (Burbidge *et al.* 1996).

2012 survey

Four small mammal species were captured during the 2012 surveys including one introduced species, *M. musculus* and three native species, *P. albocinereus*, *Sminthopsis* sp(p) and *T. rostratus*.

Mus musculus abundance was significantly different between the autumn and spring 2012 surveys with more *M. musculus* captured in autumn than spring (Table 3 and Figure 2). Total mammal abundance, species richness and abundances of the other individual mammals did not differ between the autumn and spring 2012 surveys (Table 3).

Capture data for individual mammal species

Body weights for both sexes and sex ratios between 2012 and 1986 for all species were similar (Table 4; no statistical analysis has been performed). There were some differences in the numbers of *P. albocinereus* of each sex captured. Male *P. albocinereus* captures were higher in spring 2012 (10), than females (5). In autumn 1986 and 2012 similar numbers of each sex were caught (1986: 10 males and 13 females; 2012 one male and female; Table 4).

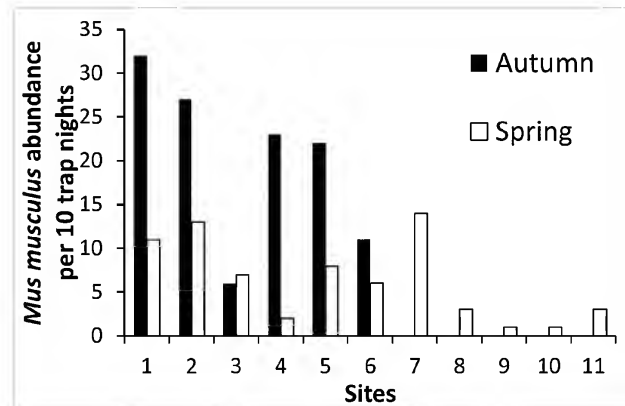


Figure 2. *Mus musculus* abundance in autumn and spring 2012. Only sites one to six were trapped in autumn and all 11 sites were trapped in spring 2012.

Table 3. Relationships between total mammal abundance, mammal species richness and individual mammal species' abundance, and the season of trapping (autumn and spring) in 2012, the year (1986 and 2012) and in autumn only in 1986 and 2012 (excluding the spring 2012 survey data) using a one way ANOVA (*F* and *P* values in bold are significant).

Dependant Variables	Autumn and Spring 2012	1986 and 2012	Autumn only 2012 and 1986
	<i>F</i> and <i>P</i> values	<i>F</i> and <i>P</i> values	<i>F</i> and <i>P</i> values
Total mammal abundance	2.74, 0.11	0.70, 0.41	3.61, 0.08
Mammal species richness	0.436, 0.51	9.733, 0.007	1.103, 0.316
<i>Mus musculus</i> abundance	10.05, 0.006	4.78, 0.04	3.49, 0.08
<i>Pseudomys albocinereus</i> abundance	2.13, 0.16	11.81, 0.003	8.645, 0.01
<i>Sminthopsis</i> sp(p). abundance	1.951, 0.183	0.025, 0.877	0.923, 0.357
<i>Tarsipes rostratus</i> abundance	4.01, 0.06	4.58, 0.04	4.04, 0.06

Comparison of 1986 and 2012

Mammal species richness in 1986 was statistically higher than in 2012 (Table 3; Figure 3a). The abundance of *Mus musculus* was significantly higher in 2012 than 1986 (Table 3; Figure 3b). The abundance of *Pseudomys albocinereus* and *Tarsipes rostratus* were significantly lower in 2012 than 1986 (Table 3; Figure 3c and d). Mammal abundance and *Sminthopsis* sp(p). abundance were unchanged between the two survey years (Table 3).

When examining the differences between the autumn surveys in 1986 and 2012 (excluding spring 2012 surveys to account for the effect of seasonality on trapping results) there was a significant difference between the years for *P. albocinereus* (Table 3). There were less *P. albocinereus* in autumn 2012, similar to the results using both 2012 surveys (autumn and spring; Figure 4). Mean mammal abundance, mammal species richness and *M. musculus*, *Sminthopsis* sp(p). and *T. rostratus* abundances were unchanged between the two surveys (Table 3).

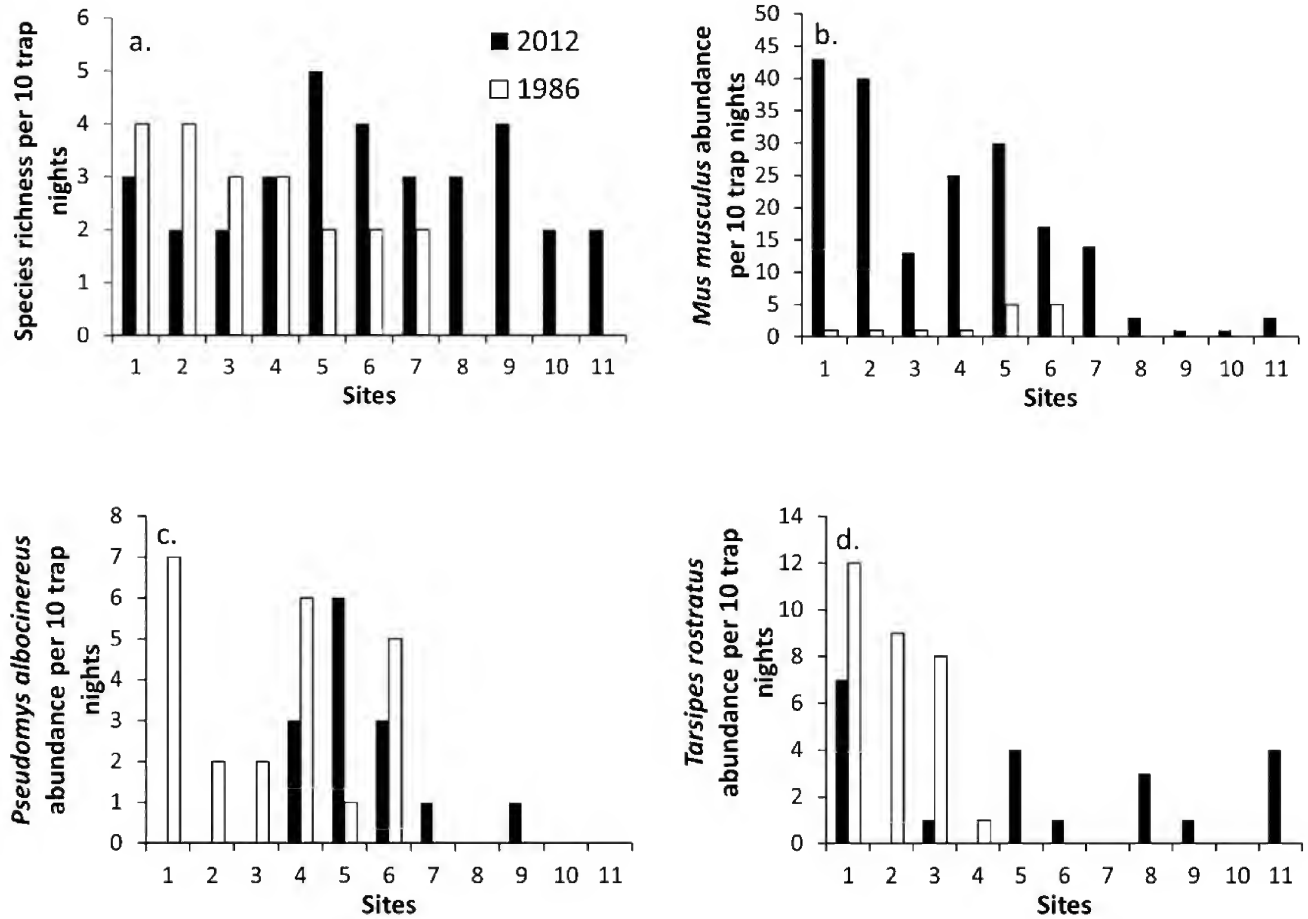


Figure 3. Mammal species richness (a), and the abundances of *Mus musculus* (b), *Pseudomys albocinereus* (c), and *Tarsipes rostratus* (d) at each site in 1986 and 2012.

Table 4. Capture data for *Tarsipes rostratus*, *Mus musculus*, *Pseudomys albocinereus* and *Sminthopsis* sp(p)., including the number of captures, sex ratio and body weights of males and females in 1986 (range) and 2012 (± SD, range); 1986 data taken from Burbidge *et al.* (1996).

Species	Captures in 1986	Captures in 2012	Sex ratio (M:F) 1986	Sex ratio (M:F) 2012	Body weight males 1986	Body weight males 2012	Body weight females 1986	Body weight females 2012
<i>Tarsipes rostratus</i>	30	24	14:16	12:10	5.3–7.0	6.78 ± 4.19 (3.1–17.5)	6.0–11.3	7.5 ± 3.92 (2–12)
<i>Mus musculus</i>	14	234	9:5	67:97	8–17.5	11 ± 4.14 (4–32)	8.5–14.5	9.54 ± 2.62 (3–19)
<i>Pseudomys albocinereus</i>	23	17	10:13	11:6	16.2–32	17.93 ± 6.45 (10–28)	15.5–28	20.4 ± 6.78 (10.5–25.5)
<i>Sminthopsis</i> sp(p).	7	29	5:2	14:12 (3 unknown sex)	9.5–11.5	8.25 ± 4.43 (5–19)	9.5–13.5	10.4 ± 4.87 (4.1–18)

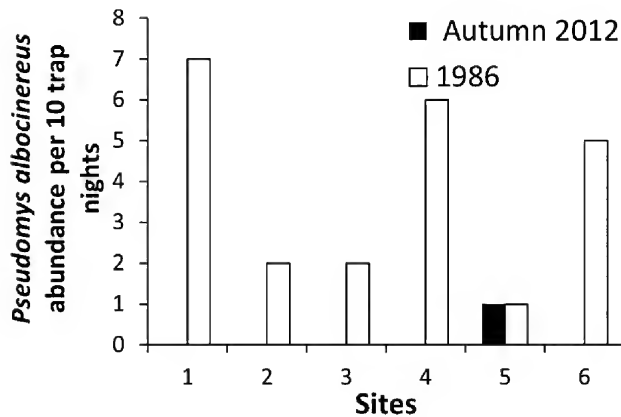


Figure 4. *Pseudomys albocinereus* abundance in 1986 and autumn 2012 at each of the six sites.

DISCUSSION

Current status of small mammals in Boonanarring Nature Reserve

Ecosystems on the Dandaragan Plateau and northern SCP, including BNR, have been severely impacted by clearing, fragmentation, and decreasing rainfall over the last 40 years but there is little knowledge of the significant impacts on mammal fauna and their habitats (Wilson *et al.* 2012, Woinarski *et al.* 2015). This study has contributed important information to the knowledge of the distribution and abundance of native small mammal species in BNR, a significant and large reserve on the southern Dandaragan Plateau (Burbidge *et al.* 1996).

Of particular importance is the information obtained on *P. albocinereus*, for which records have been infrequent over the last few decades. This native rodent has a broad distribution over coastal and inland areas of Western Australia, ranging from Bernier Island in the north-west to Israelite Bay in the south-east (Van Dyck & Strahan 2008). While it was trapped at a range of sites in woodland and heath habitats on the northern SCP by Kitchener *et al.* (1978) it has not been recorded there since 1978. The records in this study are significant as they confirm the presence of the species at least on the Dandaragan plateau, some 26 years after previous studies (Bamford 1986; Burbidge *et al.* 1996).

Pseudomys albocinereus is classified as Least Concern on the IUCN Red List (Morris *et al.* 2008), and not listed under the Western Australian Wildlife Conservation Act 1950 (Department of Parks and Wildlife 2014), even though its former range has been reduced by clearing for agriculture and infrastructure (Bleby *et al.* 2009). Recent work on *P. albocinereus* showed a preference for relatively dense vegetation cover at ground level compared to available microhabitat and suggested that the species may compete with *Mus* in some habitats. Home range size was estimated to be ca. 1.7 ha and most shelters were in burrows or grass trees (*Xanthorrhoea* sp.) (Smith 2015). Up until this study and Smith's (2015) there was a lack of knowledge about the habitat selection and behaviour of *P. albocinereus* (Bamford 1986). However, more data and information are required to develop

a detailed understanding of the relationship of *P. albocinereus* with habitat complexity and fire age, as well as nesting and habitat use behaviour, in order to facilitate informed management. This is particularly important as ongoing habitat fragmentation, decreasing rainfall and inappropriate fire regimes endanger the current range of this species, therefore putting local populations at risk (Bleby *et al.* 2009, Wilson *et al.* 2014, Woinarski *et al.* 2014).

One interesting piece of information on *P. albocinereus*' ecology that was noted, was the slightly higher number of captures of males in spring. In the 2012 trapping, twice as many males were caught as females. In 2014 trapping of the same sites, again more males were captured than females (Smith 2015). Yet in autumn 1986 and 2012 surveys similar numbers of each sex were caught. This suggests that males are more mobile in spring, presumably searching for mates, but during non-breeding seasons (autumn) do not disperse as far. However, more research is required to test this hypothesis.

Captures of *T. rostratus* at eight sites scattered across the reserve in 2012 were indicative of long term persistence of the species in BNR some 26 years after the Burbidge *et al.* (1996) study. *Tarsipes rostratus* is endemic to the south-west of Western Australia. Although the species is not considered to be threatened, it is noteworthy taxonomically as it is the only species in the Family Tarsipedidae. The species is restricted to coastal sandplain heaths and low open woodlands with healthy understorey (Wooller *et al.* 2004, Bradshaw *et al.* 2007). Most studies of the species have been conducted in a cool climate in continuous habitats across the south-coast of Western Australia and may not be representative of much of the range of this species, which is distributed from Shark Bay to the edge of the Nullarbor Plain (Garavanta *et al.* 2000, Wooller *et al.* 2004, Bradshaw *et al.* 2007, Dundas *et al.* 2013). It is also commonly captured in studies on the northern SCP, where the habitat is more open and lacks the connectivity of the south-coast habitat, often being surrounded and fragmented by pine plantations (Clancy 2011, Wilson *et al.* 2012). *Tarsipes rostratus* is evidently an adaptable species found in a range of vegetation types, from those with a dense, flowering understorey to open woodlands, both of which are found in Boonanarring Nature Reserve on the Dandaragan Plateau.

In 1986 *S. griseoventer* was captured at only two sites in BNR, whereas in the 2012 survey, individuals of *Sminthopsis* were captured at all sites except for two. Only one individual (considered likely to have been *S. griseoventer*) has been recorded recently on the SCP in 2007–08 (Wilson *et al.* 2012) indicating that at least one *Sminthopsis* taxon is still extant, albeit in small numbers. The confirmation of the presence of a considerable *Sminthopsis* sp(p) population in BNR is important as there is evidence that other vegetation remnants on the SCP are largely devoid of the species.

Status of mammals in 2012 compared to 26 years previously

Species richness (overall number of species) of small mammals in BNR was maintained between the two survey years (1986 and 2012) with four mammal species recorded: *M. musculus*, *P. albocinereus*, *Sminthopsis* sp(p)

(*S. griseoventer* in 1986) and *T. rostratus*. The significant difference in the mean species richness between autumn 2012 and 1986 surveys is most likely a reflection of differences in captures at the site level. There is therefore no evidence that any small mammal species has been lost from the reserve in the last 26 years.

Overall, the trapping revealed more *M. musculus* captures in 2012 than 1986, with the majority of the 2012 captures being in autumn. The results are consistent with the findings of Bamford's (1986) study at a nearby reserve where *M. musculus* was captured more commonly in autumn than any other time of year. Autumn provides optimal resources for breeding and survival for this introduced rodent (Brown & Singleton 1999). Increased presence of *M. musculus* is particularly concerning as the species may compete with native rodents for nesting and shelter sites as well as food resources (Smith & Quin 1996).

In contrast to *Mus*, the abundance of *P. albocinereus* and *T. rostratus* appeared to be lower in 2012 than 1986. There is a need to confirm if these differences are the result of a declining population trend, by undertaking more repeat measure monitoring. If these differences reflect a decline, they could be a result of many factors including inappropriate fire regimes, changes in water availability, introduced weeds and predators (Torre & Diaz 2004, Bleby *et al.* 2009, Craig *et al.* 2010, Wilson *et al.* 2014). Several studies in the northern SCP and the south-coast of Western Australia demonstrate that higher abundances of *T. rostratus* are found in complex habitat with a fire age of 15–20 years (Bamford 1992, Garavanta *et al.* 2000, Friend & Wayne 2003, Clancy 2011). Future studies should measure habitat complexity (as well as fuel age) to determine the habitat requirements of *T. rostratus* and *P. albocinereus* present in the reserve. Water is required for plants and shrubs to provide food (flowers or seeds) for *T. rostratus* and/or *P. albocinereus* (Wilson *et al.* 2012); with declining rainfall in this area over multiple decades, such factors may be playing a role in the declining abundance of these small mammals. Lastly, although our traps were not appropriate for capturing introduced predators, passive sampling methods did reveal the presence of *Felis catus* and *Vulpes vulpes* in both 1986 and 2012, and *Canis familiaris* in 1986 (Burbidge *et al.* 1996; unpublished data), all of which are predators of small native mammals (Doherty *et al.* 2015). Future work should expand on the knowledge of *T. rostratus* and *P. albocinereus* in BNR and their habitat requirements.

Evaluation of problems associated with long term monitoring in this project

For many long term studies, trap design, location and effort are difficult to replicate. In this study there were minor differences in the 2012 surveys compared to the 1986 surveys. In 2012 it was difficult to determine the exact location of the traps from the 1986 survey using only GPS coordinates, so the traps were located as close as possible. Positions of the trap arrays may have differed by tens of metres between 1986 and autumn 2012, and it is likely that different microhabitats were sampled, and the differences in trap array design (lines vs Y-shapes) would have meant that, for animals with small home ranges, different numbers of home ranges would have been intersected, and different proportions of dispersing

animals might encounter a trap (Friend *et al.* 1989). The number of survey nights also varied, with six nights in autumn 1986 and eight nights each in autumn and spring 2012 (Table 2). The number and types of traps used also differed between the two surveys (Table 2). With these caveats in mind we chose to compare trapping rates as captures/trap nights. Taking these caveats into consideration is also important when assessing any statistical differences identified (Friend *et al.* 1989, Rolfe & McKenzie 2000, Garden *et al.* 2007, Environmental Protection Authority & Department of Environment and Conservation 2010).

CONCLUSION

Boonanarring Nature Reserve to date has provided a sustainable habitat for small native mammals including *P. albocinereus*, *Sminthopsis* sp(p). and *T. rostratus*, most likely due to its large area of remnant vegetation encompassing many habitat types. The continued presence of these species requires active management actions such as appropriate burning regimes and predator control, followed by evaluation of population trends.

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Environmental characteristics of ephemeral rock pools explain local abundances of the clam shrimp, *Paralimnadia badia* (Branchiopoda: Spinicaudata: Limnadiidae)

ALISSA CALABRESE¹, CHERIE MCCULLOUGH², BRENTON KNOTT^{3,4}
& STEPHEN C. WEEKS¹

¹ Program in Integrated Bioscience, Department of Biology, University of Akron, Akron, OH 44325-3908, USA.

² School of Natural Sciences, Edith Cowan University, 270 Joondalup Drive, Joondalup, WA 6027, Australia.

³ School of Animal Biology, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia

ABSTRACT

The conditions of ephemeral freshwater pools are highly variable through time, and their inhabitants must be able to tolerate these changing conditions to survive. Although much research has focused on large branchiopod hatching requirements, there is comparatively little information available on the environmental conditions endured by adult clam shrimp populations. A suite of physical and chemical characteristics, especially pool depth, influence the presence or absence of clam shrimp populations in rock pools on granite outcrops in the Wheatbelt region of Western Australia. Here we examine multiple environmental variables of temporary rock pools and how they may affect adult populations of the clam shrimp, *Paralimnadia badia*.

KEYWORDS: habitat, physiochemical, temporary pool, pool morphology, hydroperiod, environmental variability

INTRODUCTION

Clam shrimp are branchiopod crustaceans (Branchiopoda: Spinicaudata) that are obligate dwellers of temporary waters (Dumont & Negrea 2002). Populations survive dry periods in the form of resting eggs produced by mature females or hermaphrodites. Their eggs lie dormant until appropriate conditions are met for hatching (Brendonck 1996, Brendonck & Riddoch 2000, Brendonck & De Meester 2003). Upon inundation, a fraction of resting eggs hatch, leaving behind a bank of dormant eggs in the sediment (Brendonck 1996, Brendonck & De Meester 2003). Occasionally, eggs will continue to hatch even after the initial inundation, resulting in multiple generations of shrimp in a single pool (Benvenuto *et al.* 2009). Often, rain will fill the pool and eggs will hatch but not reach sexual maturity before the basin dries. In these instances, the egg bank is vital to ensure long-term population persistence (Brendonck & De Meester 2003). In this way shrimp 'hedge their bets' against the unpredictability of their environment which has led to speculation as to which factors might promote this pattern of hatching (Mossin 1986, Brendonck *et al.* 1996, Kuller & Gasith 1996, Simovich & Hathaway 1997, Beladjal *et al.* 2007).

Many physical environmental parameters, including dissolved oxygen, pH, osmotic pressure, light, and temperature, have been individually implicated in

regulating hatching in various large branchiopod species (Bishop 1967, Belk 1977, Scott & Grigarick 1979, Mitchell 1990, Schönbrunner & Eder 2006). However, initial hatching conditions are not sole predictors of clam shrimp presence, as temporary pool environmental conditions change throughout the duration of their inundation and drying regimes (Jocqué *et al.* 2007a). Here we aim to determine environmental factors that are associated with maintenance of adult populations of clam shrimp.

For a hatched population to be sustained, the conditions of the pool must meet survival requirements after initial hatching. Long term maintenance of populations of several species of *Daphnia* have been assessed in relation to habitat characteristics and each species appeared to thrive under different environmental conditions, occupying different pools as a result (Pajunen & Pajunen 2007). Both the size and permanence (length of hydroperiod) of temporary pools have been found to play important roles in predicting species richness (Kiflawi *et al.* 2003). Additionally, since larger pools will resist evaporation for longer periods of time, pool size has been shown as an important factor structuring local communities (Jocqué *et al.* 2007b)

Our study sought to answer how temporary pool environments relate to adult clam shrimp populations. Here we determine which parameters best explain abundances of adult populations of the clam shrimp *Paralimnadia badia* (Wolf 1911; the Australian species *Limnadia* have recently been moved to a new endemic genus *Paralimnadia*, Rogers *et al.* 2012) in a variety of temporary rock pools on granite outcrops in the semi-arid, Wheatbelt region of Western Australia.

⁴Deceased March 2013

METHODS

Study Sites

Although the Wheatbelt region of southwestern, Western Australia is generally flat, occasional large granite outcrops (or 'inselbergs' *sensu stricto*, Withers 2000) can be found in the area (York Main 1997, Withers 2000). The rainy season in this part of Australia lasts approximately from May to October and is the milder time of the year, with mean maximum air temperatures ranging from 20.3°C to 23.7°C (Commonwealth of Australia, Bureau of Meteorology, 26 Sept 2011).

Three outcrops received adequate rainfall for sustained hydration: Holland Rock (Shire of Kent, 33°21.259'S; 118°44.639'E; 13 pools sampled), Dingo Rock (Shire of Lake Grace, 33°0.558'S; 118°36.321'E; 8 pools sampled), and Rockhole Rock (Shire of Bruce Rock, 31°55.970'S; 117°45.209'E; 11 pools sampled). Data from Bruce Rock were collected at a later date than Holland and Dingo (May 2009) and were only used to construct Fig. 3.

Field Sampling

Study pools were selected for a range of sizes and depths, and were sampled for physiochemical parameters and quantities of clam shrimp and other macroinvertebrates in late April to late May 2007. Water quality [temperature, pH, dissolved oxygen (DO), and electrical conductivity (EC)] of each of the three sites was monitored for five consecutive days at four times per day (12:00, 14:00, 16:00, and 18:00) to assess diurnal change, however for most analysis only the average of the mid-afternoon readings (14:00 and 16:00) were used as a result of incomplete sampling across the other two time periods. Pools on Holland and Dingo Rocks were sampled with a YSI 556 multi-probe (YSI, USA). Pools on Rockhole Rock were sampled with a Hydrolab Quanta multi-parameter meter (Hydrolab, USA). Pool dimensions measured included maximum length (l), maximum width (w) and mean depth (d) (each averaged from three measurements). Pool volumes were estimated from these dimensions assuming the shape to be half of an ellipsoid (Formula: $4/3\pi lwd$, Baron *et al.* 1998).

Each pool was sampled across the entire volume for three, 3-min periods with sweep nets of mesh sizes 2.0 mm and then 0.5 mm. *Paralimnadia badia* abundance approximately halved each sampling event over the three successive rounds of sampling. Consequently, after three rounds in each pool approximately 90% of clam shrimp had been captured. *Paralimnadia badia* were sorted from other macroinvertebrates in white plastic collecting trays, species were identified, counted, and then returned to the pool alive.

Analysis of habitat variables and species distributions

Volume and EC values were \log_{10} transformed to achieve normality. All other variables had normally distributed residuals (using Shapiro-Wilk test for normality). One-way ANOVAs compared the means of environmental variables between pools with and without *P. badia*.

All parametric analyses were made with JMP Pro 10 (SAS Institute Inc. 2012). Ordinations of environmental

data were produced by Principal Components Analysis (PCA) in PRIMER multivariate software (PRIMER-E 2006). Although not suitable for analysis of biotic community structure, the implicit underlying Euclidean Distance matrix of this method makes it suitable for environmental data, with an advantage over nMDS ordination in that ordination axes are interpretable (Clarke & Warwick 2001). Correlations between pairs of environmental variables were then examined with draftsman plots. Combinations of highly correlated variables (Spearman rank higher than 95%) were reduced to a single, representative variable.

The PRIMER BEST procedure (Clarke & Ainsworth 1993) identified the combination of mean water quality and habitat variables for each pool, which best rank-correlated with clam shrimp abundances. These best correlating environmental variables are likely to be those that are most important in defining clam shrimp abundance. Prior to BEST analysis, environmental variables were normalized to the maximum value encountered (Olsgard *et al.* 1997, Clarke & Warwick 2001) and draftsman plots were created to determine which variables were highly correlated with each other (i.e., 95% or greater, Bob Clarke, Plymouth Marine Laboratory UK pers. comm.). Data were then \log_{10} transformed to enhance a linear relationship between variables and finally standardized to account for different variable scales (Clarke & Warwick 2001).

A canonical discriminate analysis (CDA) was then used (JMP Pro 10, SAS Institute Inc.) to determine which environmental variables best described the variation between groups (presence / absence of *P. badia*; see below). Bivariate regressions were then made to describe relationships between *P. badia* abundance, estimated fitness and habitat pH. Fitness was estimated from the size of the carapace, which is directly related to the number of resting eggs per clutch in female clam shrimp (Weeks *et al.* 1997).

RESULTS

Of the 21 pools studied on Holland and Dingo Rocks, 13 contained clam shrimp populations. Pools with and without *P. badia* had different abiotic conditions. Pool depth was related to pool volume and surface area (shown as factor loadings clustering on the loading plot; Fig. 1), which is expected because of the common formula used to derive pool volume. Examined individually, pH was the only abiotic parameter that differed significantly between the two groups (Table 1). Pools containing *P. badia* typically had lower pH than those without clam shrimp. Pools containing *P. badia* had overlapping ranges of all variables with pools lacking *P. badia*. The water temperature of the pools without *P. badia* was also higher, but not significantly so ($p=0.06$). Pool volume, surface area, conductivity, and TDS were higher in the pools that had *P. badia* populations, albeit not significantly.

Mean depth was the most important sole environmental variable explaining clam shrimp abundance according to the BEST analysis (Spearman Rank correlation: $\rho = 0.375$). When pH was added to this model, this water quality variable further helped to explain clam shrimp distribution at $\rho = 0.413$.

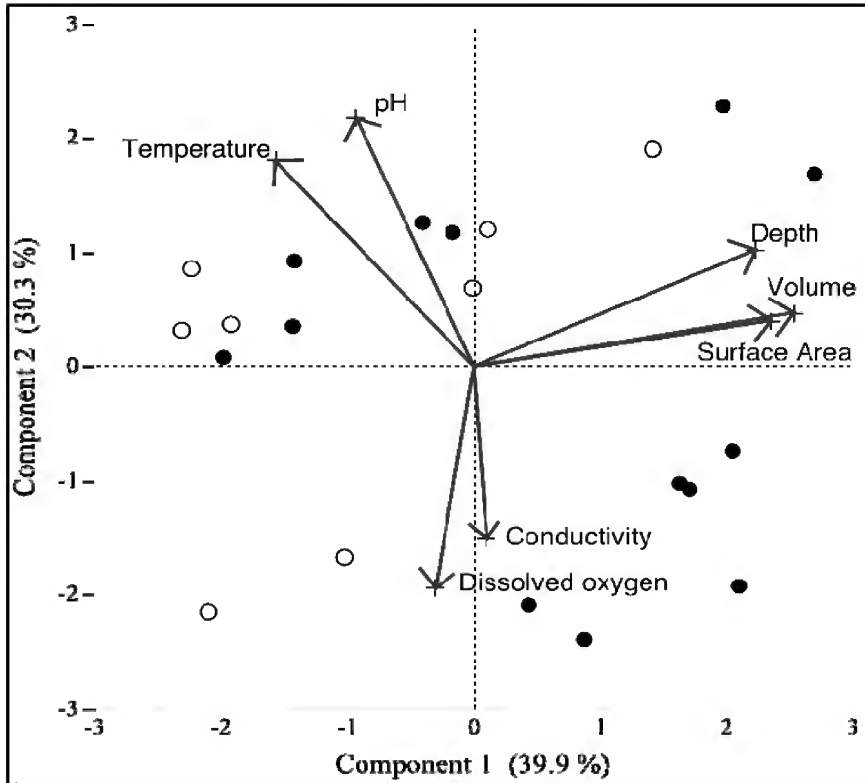


Figure 1. PCA of pool environmental variables. Length of vector indicates strength of correlation between variable and component axes. Asterisks indicate significant correlation of the component with the original variable (* $p < 0.05$). Pools with *P. badia* present are filled circles. Pools without *P. badia* are empty circles.

	Principal Component 1	Principal Component 2
Temperature	-0.35*	0.46*
Dissolved Oxygen	-0.07	-0.49*
pH	-0.21	0.55*
Depth	0.49*	0.26
Surface Area	0.52*	0.10
Conductivity	0.02	-0.38*
Volume	0.56*	0.12

Table 1. Habitat characteristics of 21 total pools with *P. badia* present (n=13) and absent (n=8). Bold type indicates statistically significant difference ($p < 0.05$) between pool environmental variable with and without *P. badia*.

	Pools without <i>P. badia</i>				Pools with <i>P. badia</i>				F-ratio	p-value
	Mean	SE	Max	Min	Mean	SE	Max	Min		
Temperature (°C)	21.2	0.41	26.1	17.3	20.3	0.25	25.8	17.2	3.95	0.061
Conductivity (mS/cm)	0.24	0.03	0.47	0.06	0.27	0.04	0.93	0.04	0.07	0.799
Dissolved oxygen (%)	113	2.75	138	97.3	109	1.60	141	88.9	1.46	0.243
pH	7.09	0.17	9.03	5.91	6.64	0.13	8.57	5.53	4.39	0.049
Depth (mm)	30.7	5.36	70.7	4.33	39.0	2.48	68.3	17.7	2.56	0.126
Volume (L)	136	41.3	420	1.71	276	59.9	930	24.9	2.83	0.109
Surface area (m ²)	7.32	1.41	14.2	0.75	12.2	2.14	28.5	1.98	2.75	0.114

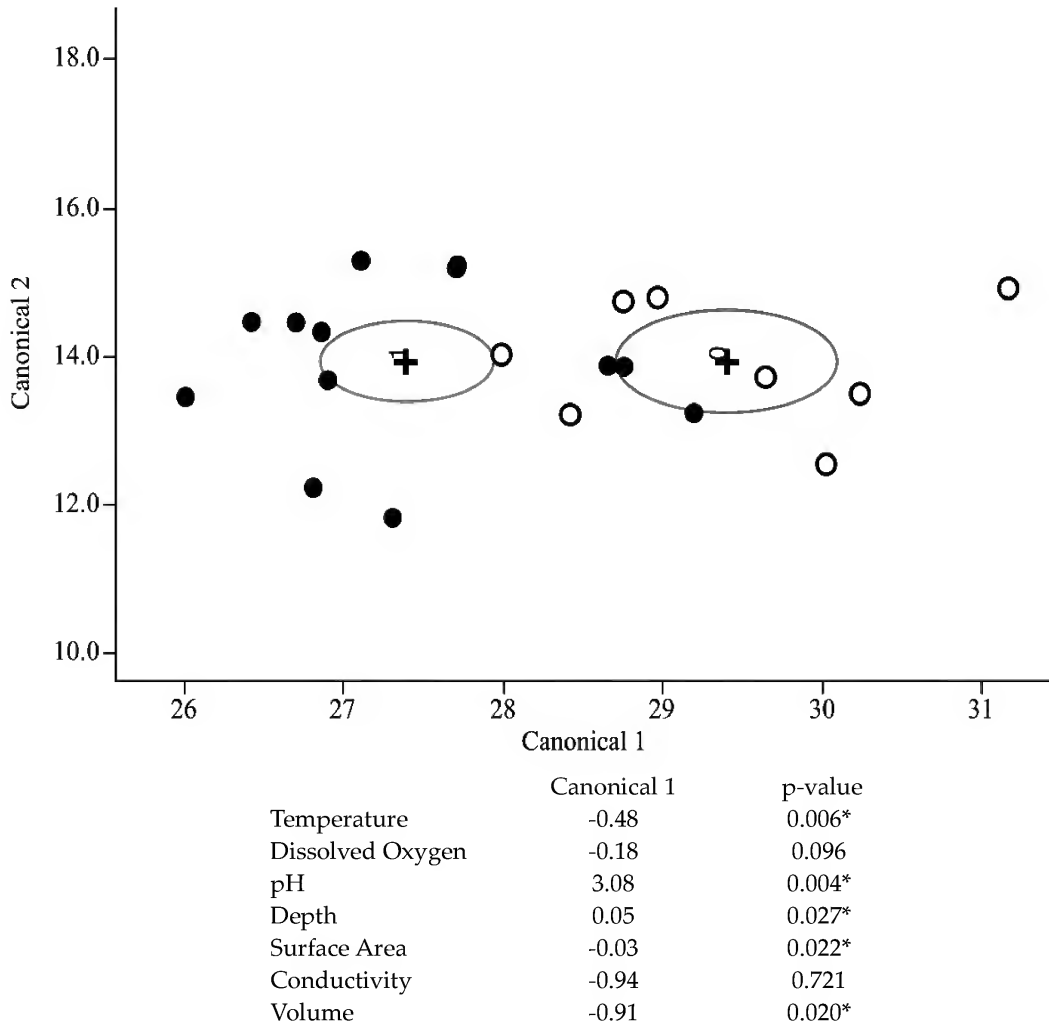


Figure 2. Results of a canonical discriminant analysis (CDA) on all seven dependent variables using data from Holland and Dingo outcrops only. Pools without *P. badia* present are empty circles; pools with *P. badia* present are filled circles. Canonical correlation 1 explains ~100% of the differences between present/absent pools. Ellipses show the means of the centroids of *P. badia*-present pools and *P. badia*-absent pools. Asterisks indicate significant correlations of the canonical scores with each of the original variables (* $p < 0.05$).

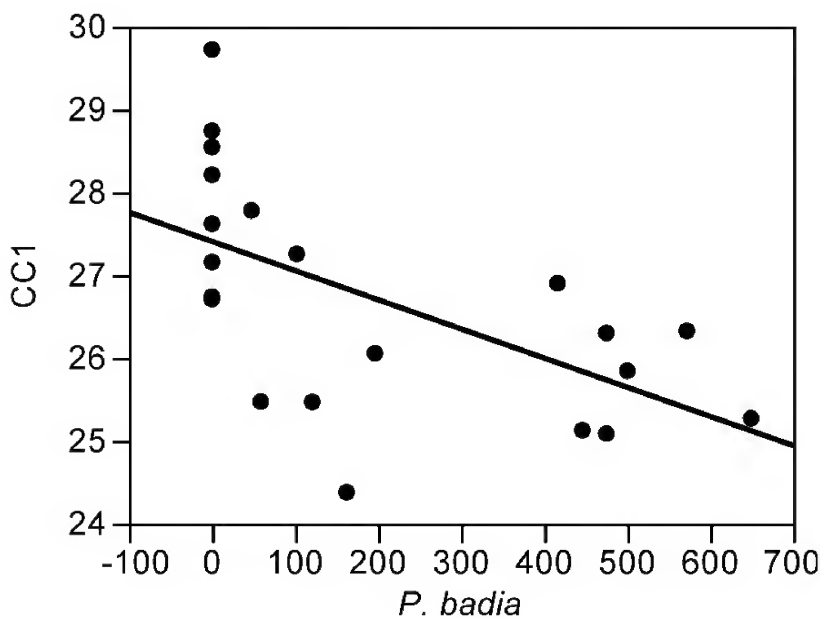


Figure 3. Regression of CC1 on the quantity of *P. badia* present in all pools. Canonical 1 (consisting largely of volume, depth, and surface area) is negatively correlated with the quantity of *P. badia* ($p = 0.0052$).

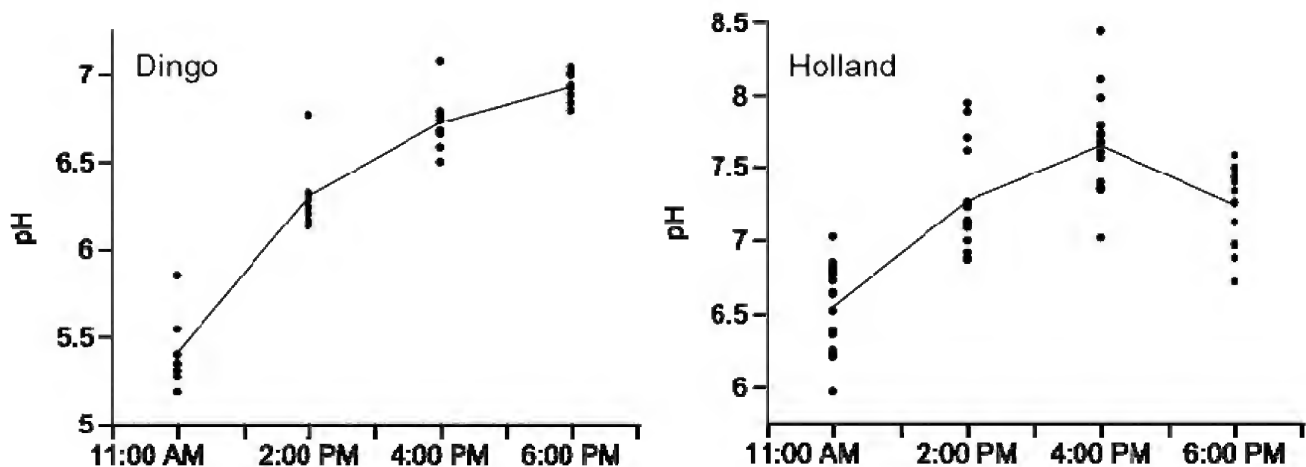


Figure 4. Diurnal variation in pH levels in pools on Dingo and Holland Rocks.

The CDA correctly classified 17 of 21 pools in its assignment of pools into groups that either had *P. badia* or not, or 81% of the total pools in this comparison (Fig. 2). The first canonical correlation (CC1) explained ~100% of the important variation that differed between pools with and without *P. badia*. Five original dependent variables were correlated strongly with CC1: temperature, depth, and surface area were negatively correlated with CC1, while volume and pH were significantly positively correlated with CC1 (Fig. 2). Volume, depth, and surface area are all measures describing pool size. Temperature and pH are variable that are closely associated and influenced by pool size, which suggests that CC1 is mainly describing the size of the pools. This 'pool size' variable is negatively correlated with the quantity of *P. badia* (Fig. 3). Figure 4 displays the diurnal variability of pH in pools on Dingo and Holland rocks.

DISCUSSION

Our study confirms that temporary rock pools are highly variable environments (Bayly 1982, Williams 2001). To survive this environment, pool inhabitants must cope with extended periods of drought between wet phases as well as the widely variable conditions throughout the inundation phase.

There is a wealth of literature available that quantifies the habitat requirements for large branchiopods to break dormancy (Moore 1963, Belk 1977, Brendonck 1996, Schönbrunner & Eder 2006). The information available regarding the maintenance of populations of clam shrimp mainly suggests that the size of the pools is of key importance (Kiflawi *et al.* 2003 & Jocqué *et al.* 2007b). Frequently, clam shrimp nauplii will hatch from resting eggs, but then the population will crash before they have reached maturity (Jocqué *et al.* 2007b). Much of the available information regarding hatching or sustaining populations is focused on the range of a single parameter (i.e., only temperature or pH; Belk 1977, Scott & Grigarick 1979, Mitchell 1990, Schönbrunner &

Eder 2006). However, by combining all parameters into a multivariate BEST analysis, we showed that pool depth combined with pH best explained *P. badia* abundance in temporary outcrop pool habitats. A canonical discriminant analysis confirmed pool depth and pH as the most vital explanatory variables, while additionally implicating volume, surface area, and temperature as important habitat variables. Temperature was negatively correlated with volume, depth, and surface area, as might be expected: as pool sizes increase, maximum pool water temperatures decrease because larger pools can be more resistant to temperature change. The sampling times used in this analysis were from the warmest parts of the diurnal cycle, and thus the larger volume pools should have been more resistant to warming, explaining the negative correlation.

The environmental variables that described pool morphology were all positively correlated with one another and with CC1. Canonical correlation 1 correctly predicted which pools contained *P. badia* 81% of the time, illustrating that pool morphology was a key habitat characteristic for *P. badia* abundance. This may well be because pools that are on the more ephemeral end of the continuum evaporate before clam shrimp populations have reached sexual maturity.

The apparent association between pH and the presence of *P. badia* (Table 1) is likely an artifact of the sampling regime (i.e., pH values used in this analysis were only from the middle of the day and thus do not take into account the significant diurnal change observed; Fig. 4). It is possible that the variability of pH, like temperature is associated with the size of the pool and this is why it appears significant here. Otherwise it is not obvious why such a subtle difference in mean pH between the two groups (0.45) would have an impact on *P. badia* populations. More information is necessary to determine the significance of this observation.

Clam shrimp species previously reported from these pools were *Eulimnadia dahli* Sars, 1896 and *Paralimnadia badia* (Timms 2006, Weeks *et al.* 2006). Whether these

genera never coexist within the same pool or whether one succeeds the other in the same pools is still unknown. Preliminary evidence suggests that *P. badia* may predominate in pools in the winter (rainy) season, while *E. dahli* may be more common in the summer (Timms 2006).

These data represent the results of an observational and not a manipulative study and so can only suggest a potential relationship between the above variables, not necessarily a direct causal relationship. There may also be other factors beyond pool morphology that could affect the distribution of this species. It is possible that clam shrimp had not yet dispersed to the non-*P. badia* pools, although this scenario is unlikely considering the proximity of the pools to each other on each outcrop. Overflow and wind-mediated propagule dispersal have been shown to be extremely effective in temporary pool metacommunities (Brendonck & Riddoch 1999, Vanschoenwinkel *et al.* 2008a, Vanschoenwinkel *et al.* 2008b). Another possibility is that the presence of a predator excluded *P. badia* from some pools and not others, although this seems unlikely. Some clam shrimp were consumed by predacious water beetle larvae (Dytiscidae) during sampling, but this was a rare occurrence in our observations. Furthermore, in every pool in which these predacious larvae were present, *P. badia* was also present. Additionally, 81% of pools that harboured anuran larvae also had *P. badia*. Our sampling was not exhaustive enough to prove that no predator had an effect on *P. badia* populations, but simply suggests that we did not observe such a phenomenon during our sampling period.

Generally, there is thought to be a continuum of factors structuring communities in habitats ranging from permanent freshwater bodies to temporary freshwater environments (Wellborn *et al.* 1996). Some work has suggested that predation is the dominant structuring force in the most permanent communities while competition is more powerful in structuring pools that are less permanent (Wellborn *et al.* 1996, Wilbur 1987). Indeed, priority effects may play a role in early colonizers monopolizing particular pools (De Meester *et al.* 2002, Jocqué *et al.* 2010).

Another factor that may affect the habitat quality of *P. badia* is dryland salinity. Extensive land clearing in the region has resulted in increased salinities in many aquatic habitats (Anon 1996, National Land and Water Resources Audit 2001). Dust and saline solutes from salt flats around the rock outcrops are likely to be both more alkaline and also more buffered. Some outcrop pools are also showing higher alkalinity through increased bicarbonate concentrations than would be expected from rainfall interaction with acidic granite rock (Pinder *et al.* 2005).

Pool morphology appears to influence the presence of *P. badia* in temporary rock pools. Temperature may also be an influential factor, especially as it is correlated with the size of the pools. Many of these outcrops are already functioning as islands in an ecological desert that is the mono-agricultural Wheatbelt landscape. Consequently, loss of these island habitats to clam shrimp at a local scale may lead to a significant threat to sustained existence for clam shrimp at a more regional scale.

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Chronostratigraphic context for artefact-bearing palaeosols in late Pleistocene Tamala Limestone, Rottnest Island, Western Australia

I WARD^{1*}, T J PIETSCH², E J RHODES³, G H MILLER⁴, J HELLSTROM⁵ & C E DORTCH⁶

¹ School of Social Sciences, University of Western Australia WA 6009, Australia

² Australian Rivers Institute, Griffith University, Qld 4111, Australia

³ Department of Earth, Planetary and Space Sciences, University of California, CA 90095, USA

⁴ INSTAAR and Dept. Geological Sciences, University of Colorado, Boulder, CO 80309 USA

⁵ School of Earth Sciences, University of Melbourne, Vic 3010, Australia

⁶ 24 Howard Street, Fremantle, WA 6160 Australia

* Corresponding author ✉ Ingrid.ward@uwa.edu.au

Abstract

This paper presents absolute dates for artefact-bearing palaeosols intercalated with Tamala Limestone aeolianite successions on Rottnest Island (*Wadjemup*), Western Australia. The absolute chronology for the sub-aerial part of the island's constituent Tamala Limestone is based on 20 optically stimulated luminescence (OSL), two thermoluminescence (TL) age estimates, one U-series assay and three radiocarbon dates. The oldest of these estimates is an OSL age of 140 ± 14 ka at Fairbridge Bluff for the aeolinite beneath the Rottnest Limestone member – a marine member of the Tamala Limestone succession. The palaeosols range in age from 49 to 10 ka. These age estimates provide, for the first time, a chronostratigraphic context for the isolated archaeological finds on the island as well as contributing to the timing and nature of late Quaternary sequences within the Tamala Limestone of the Perth Basin.

KEYWORDS: Rottnest Island, late Quaternary, Tamala Limestone, palaeosols, chronostratigraphy, luminescence dating

INTRODUCTION

Rottnest (or *Wadjemup*) is the largest of a chain of offshore islands and reefs composed of Tamala Limestone, the constituent rock of Quaternary age throughout the Perth Basin (Playford 1983, 1988, 1997) (Figure 1). Separating the sandy beaches around the island are aeolian calcarenite cliffs and headlands that formed when wide areas of the continental shelf was exposed and carbonate productivity was high – this is the Tamala Limestone (Playford 1988, 1997). These aeolianite successions comprise moderately cemented, fine to coarse bioclastic sands and shelly deposits, mainly in large scale cross bedded and planar bedforms (Hearty 2003). Intercalated within the aeolianite successions are moderately cemented calcretes and palaeosols (the “protosols” of Vacher & Hearty 1989), characterised by higher proportions of quartz and clay, calcified roots (rhizoliths), fossil land snails (mainly the gastropod *Austrosuccinea* sp.) and fossil weevil (*Leptopious* sp.) pupal cases (see also Playford 1997; Hesp *et al.* 1999).

It is within these palaeosol units that a number of isolated Eocene fossiliferous chert and calcrete artefacts are recorded at Bathurst Point, Little Armstrong Bay, Charlotte Point, Fish Hook Bay (Figure 1) along with seven other surface finds. Although few in number, the stone artefacts identified *in situ* within Tamala Limestone paleosols on Rottnest Is. (Dortch & Hesp 1994), along with a further nine found on Garden Island (Dortch &

Morse 1984; Dortch 1991; Dortch & Hesp 1994; Dortch & Dortch 2012) indicate human presence on this part of the emergent continental shelf during the late Pleistocene and early Holocene. Minimal ages for these artefacts have been estimated from the time of the island's separation from the mainland around c. 6500 years ago (Churchill 1959; Playford 1997). This paper provides a more complete stratigraphic context and absolute chronology for the artefact-bearing palaeosols.

In situ artefact find sites and previous dating

The Tamala Limestone provides a register of Quaternary sea-level events (Teichert 1950; Fairbridge 1954, 1961; Playford 1988, 1997; Kenrick & Wyrwoll 1991; O'Leary *et al.* 2013; Brooke *et al.* 2014) and is also important from a regional archaeological perspective (see also Dortch & Dortch 2012). During the Last Interglacial (Marine Isotope Stage (MIS) 5), Rottnest Island existed as shallow submerged shoals and reefs overlying Tamala Limestone, as evident from the Rottnest Limestone member at Fairbridge Bluff (Figure 2A). The reef/beach sequence here has been dated between 132 – 121 ka (MIS 5e) (Szabo 1979; Stirling *et al.* 1995, 1998; Price *et al.* 2001). Mean sea level (MSL) was about 3 – 4 m above present for much of this period, increasing to at least 8 m above present around 118 ka (O'Leary *et al.* 2013). This reef/beach sequence is capped by a reddish calcrete and *terra rossa* palaeosol with deep root casts filled with ferruginous, well-rounded, well-sorted quartz-rich dune sands (Figure 2A), indicating sub-areal weathering of the reef towards the end of MIS 5e (or possibly MIS \leq 5d, Hearty 2003; Hearty & O'Leary 2008).

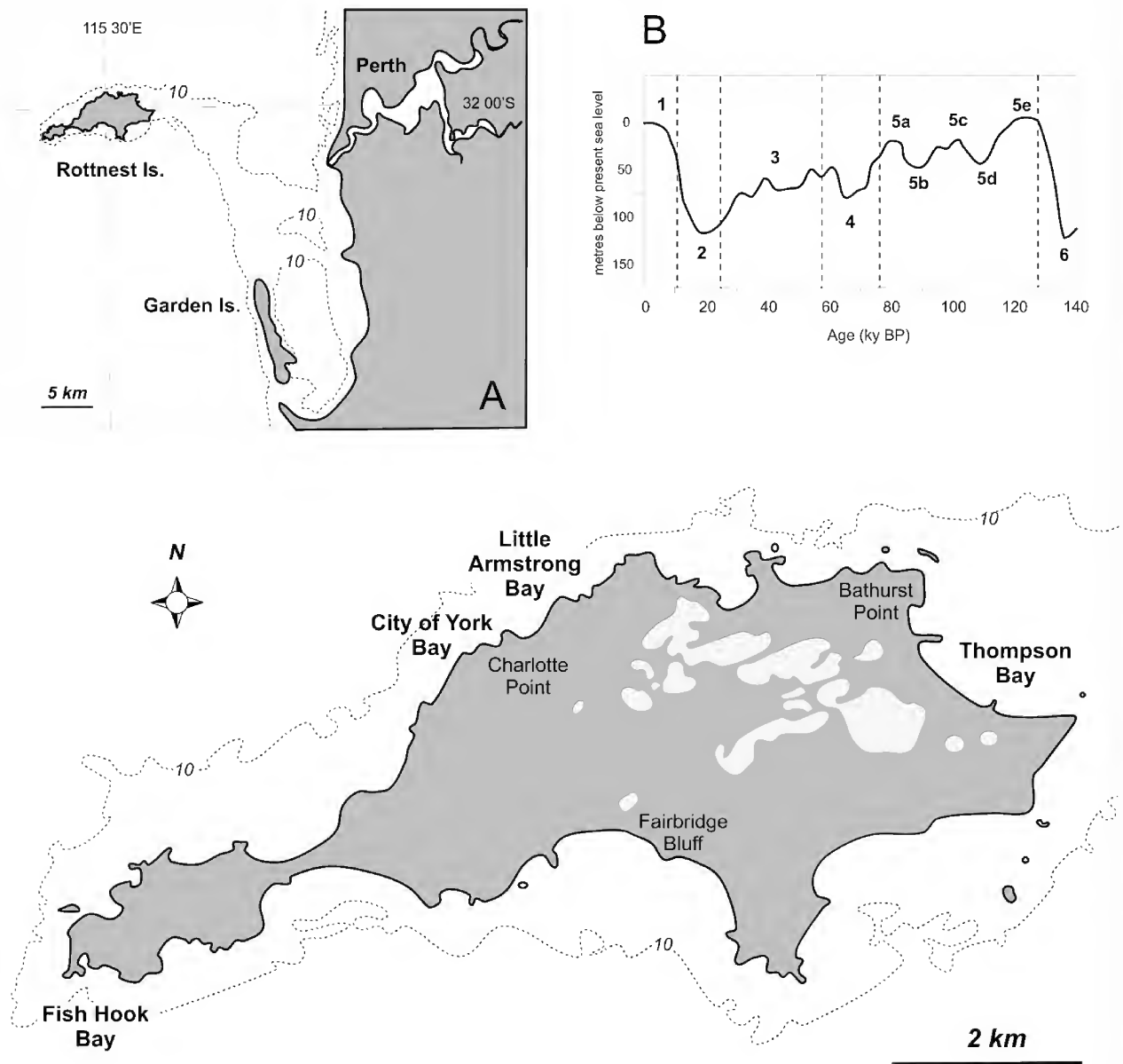


Figure 1. Rottnest Island map showing location of artefact-bearing palaeosols, including Bathurst Point, Little Armstrong Bay, Charlotte Point, City of York Bay and Fish Hook Bay. Inset A shows location of Rottnest Is. in relation to the Perth Metropolitan Region, central Swan Coastal Plain and Swan River/estuary. Inset B shows sea level curve showing major marine isotope stages (sourced from Waelbroeck *et al.* 2002).

Additional absolute ages relate to MIS 4 and are provided from Bathurst Point (Figure 1). Here four prominent stratigraphic units are observed – the first is a basal aeolianite unit 3 – 7 m ASL to below MSL, extending along the c. 500 m cliff length, dated by thermoluminescence (TL) at 67 ± 9 ka (Price *et al.* 2001) and by Optically-Stimulated Luminescence (OSL) dating to 77 ± 12 ka (Playford *et al.* 2013; Brooke *et al.* 2014). This unit is capped (truncated?) by a massive calcrete/breccia calcrete unit (Figure 2B), defined by Hearty (2003) as a well-developed brecciated soil (rendzina) with abundant limestone clasts. Along parts of the eastern side of Bathurst Point, this calcrete/breccia unit can be

seen to be overlain by a dark brown to nearly black silty sand (Figure 3). It is within this brecciated calcrete that a fossiliferous chert core was found (Dortch & Dortch 2012: their Figure 7), cemented and overlain by a thin layer (0.5 – 1 cm) of carbonate cement (see also Hearty 2003).

Overlying this calcrete/breccia unit is a younger aeolianite succession, exposed mainly on the western side of Bathurst Point, and dated by OSL to 27 ± 4.5 ka (Brooke *et al.* 2014) and 20 ± 2 ka by TL (Price *et al.* 2001) or MIS 2. This aeolianite unit is not present on the east side of Bathurst Point, at the find site of the chert artefact. Here the calcrete/breccia unit is immediately capped by a light brown (7.5 YR 5/3) rhyzolithic-rich palaeosol that

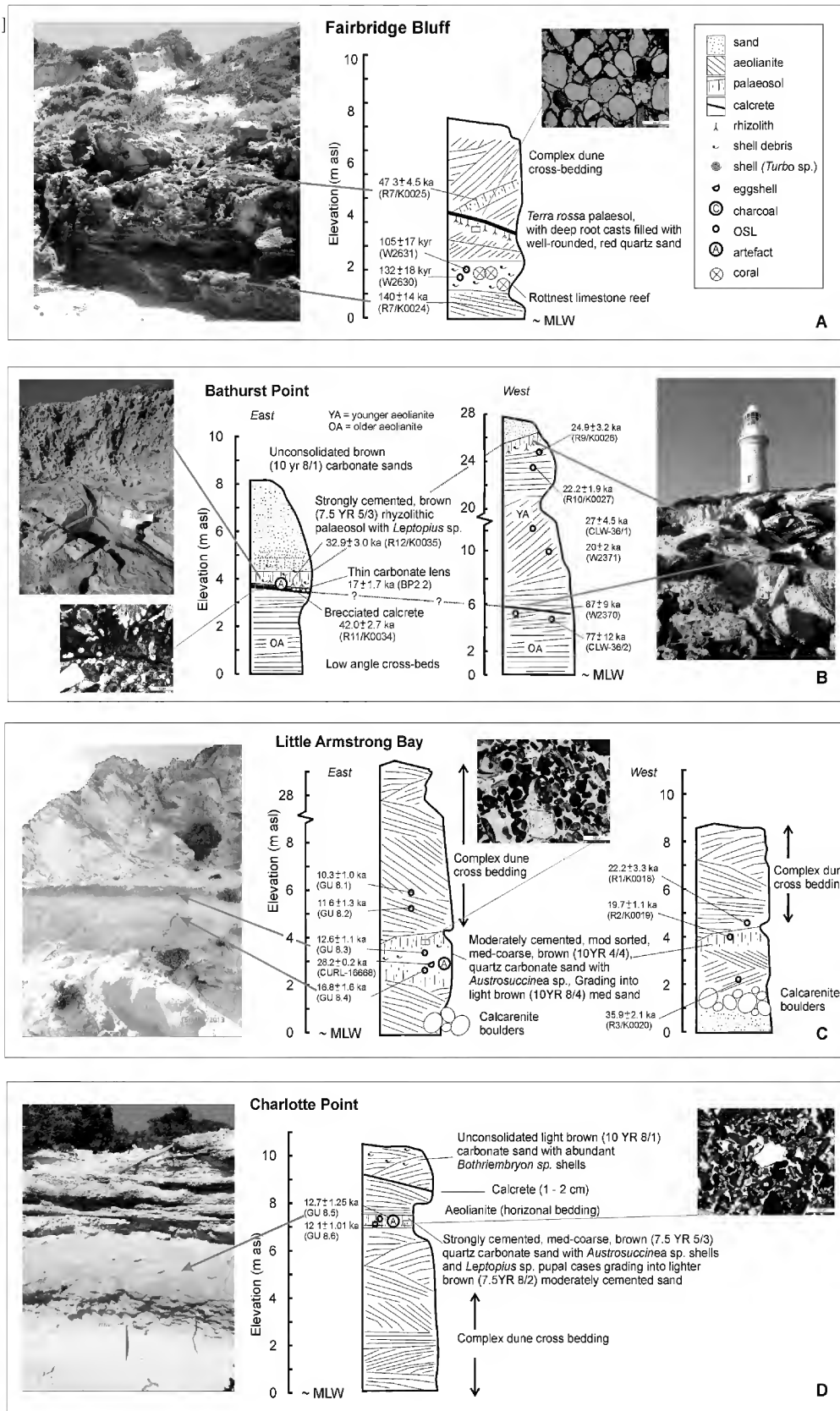


Figure 2. Schematic stratigraphic sections of Rottnest Island Eocene fossiliferous artefact find sites, including A. Fairbridge Bluff, B. Bathurst Point, C. Little Armstrong Bay and D. Charlotte Point. Inset petrographic photos show the quartz-rich (with inherited ferruginous rinds) *terra rossa* palaeosol at Fairbridge Bluff (A), the contrasting carbonate-rich palaeosol (with post-depositional ferruginisation) at Little Armstrong Bay (C) and Charlotte Point (D), and the sharp boundary created by the calcrete overlying the aeolianite unit at Bathurst Point (B) (scale bar is 500 μ m).



Figure 3. Brecciated calcrete unit on the eastern side of Bathurst Point overlain by a dark brown silty sand and capped by a very thin carbonate lens (photo by IW).

can be traced through the largely vegetated dunes across to the western side of Bathurst Point where it overlies the younger aeolianite (Figure 2B). The succession is overlain by unconsolidated to lightly cemented Holocene dune sands containing abundant *Bothriembryon* and introduced land snail taxa (Hearty 2003).

A further two sites, Little Armstrong Bay and Charlotte Point (Figure 1), have each yielded a single *in situ* Eocene fossiliferous chert artefact from a Tamala Limestone palaeosol unit, previously described by Dortch and Hesp (1994). In contrast to the *terra rossa* palaeosol at Fairbridge Bluff, these palaeosols are mainly composed of shelly carbonate, and the minor (5 – 10%) quartz that is present is more angular (Figure 2C and 2D) indicating a less distant source. The artefacts include a stone tool from the foot of sea-cliff on the western side of Little Armstrong Bay (LAB west) and a retouched tool, found half protruding from a prominent palaeosol on the eastern side of the bay (LAB east). The latter was associated with a tiny fragment of emu eggshell (*Dromaius novaehollandiae*) – the sole vertebrate fossil specimen known from the island. An earlier series of Amino Acid Racemisation (AAR) measurements, using the land snail *Austrosuccinea* sp. found *in situ* in palaeosols intercalated within aeolianite successions at three Rottneest Island sites – including Little Armstrong Bay, City of York and Fish Hook Bay – gave a provisional ages of > 50 ka (Hesp *et al.* 1999). However, these dates have been questioned by Brooke *et al.* (2014), and Hesp *et al.* (1999: 11) themselves regard their AAR dates as provisional due to “the paucity of amino acid data concerning the racemisation kinetics in [the genus] *Austrosuccinea*”.

A further two fossiliferous chert artefacts were found eroded from the summit of the cliffs at Fish Hook Bay, on the island’s south-west, and could have been derived from the deflation of the uppermost palaeosol and aeolianite units at the top of the cliff. The following presents new dates for Fish Hook Bay, City of York

Bay and the artefact find sites at Bathurst Point, Little Armstrong Bay and Charlotte Point.

DATING METHODS

OPTICALLY STIMULATED LUMINESCENCE (OSL)

Aeolianite (7) and palaeosol (5) units were sampled (by EJR) in 2003 – 2004 at City of York, Fairbridge Bluff, Bathurst Point and Little Armstrong Bay. A series of small aliquot Optically Stimulated Luminescence (OSL) measurements were undertaken at the Australian National University (ANU), using a conventional SAR approach for small aliquots, and standard Risø equipment as described by Rhodes *et al.* (2010). High OSL sensitivity and favourable luminescence characteristics were observed, although some samples displayed relatively high over-dispersion (statistical scatter) between aliquots (up to 12%), possibly related to spatial variability in beta dose rate within the carbonate and quartz-rich aeolianite (Table 1). Dose rates were determined using NAA-measured radionuclide contents, along with in-field gamma spectrometry for gamma dose rate calculation.

The above ANU dates are complemented by single-grain OSL dating of palaeosols and aeolianites at Little Armstrong Bay and Charlotte Point (Table 1). These OSL measurements, undertaken at Griffith University, augment published OSL dating of samples collected at Bathurst Point by the same laboratory (Table 1; Brooke *et al.* 2014; Playford *et al.* 2013). The modified single aliquot regenerative dose protocol of Olley *et al.* (2004) was used on standard Risø equipment, as described in detail elsewhere (Olley *et al.* 2004; Pietsch *et al.* 2013; Brooke *et al.* 2014). Given over-dispersion values of 18 – 36% (Table 1), burial ages have been calculated using the minimum age model. Radionuclide contents for each GU sample were determined using Neutron Activation

Analysis (NAA - Becquerel Laboratories, Mississauga, Ontario, Canada), with lithogenic dose rates calculated using the conversion factors of Stokes *et al.* (2003); with β -attenuation factors taken from Mejdahl (1979) and cosmic dose rates calculated from Prescott & Hutton (1994) using our best estimate of a time weighted long term burial depth (Table 1) based on examination of the field stratigraphy.

Uranium-series (U-series)

Six small sub-samples of between 20 and 150 mg were cut using a hand-held dental drill from an 8 x 8 cm block of carbonate cement containing the fossiliferous chert core at Bathurst Point. The most indurated available material was targeted, with a preference for the lightest coloured. Analyses of six sub-samples followed the procedure of Hellstrom (2003) and Drysdale *et al.* (2012). Following Hellstrom (2006) an initial $^{230}\text{Th}/^{232}\text{Th}$ ratio of 3.51 ± 0.87 was found to bring the Th-corrected ages of all six analyses into agreement with respect to their uncertainties (i.e. Mean square weighted deviation (MSWD) = 1), meaning it is unlikely that the sample has been affected by uranium mobility since its deposition (Table 1).

Radiocarbon

Radiocarbon (Accelerator Mass Spectrometry (AMS)) radiocarbon dating of the emu eggshell fragment (*Dromaius novaehollandiae*) (CURL-16668) recovered from the palaeosol on the eastern side of Little Armstrong Bay was undertaken at the University of Colorado. In addition *in situ* charcoal fragments (Wk-37948) were collected from a palaeosol 150 m south east of the fossiliferous chert artefact find location and closely adjacent to OSL sample positions at Charlotte Point. The collective fragments were submitted to Waikato Radiocarbon Laboratory for AMS dating.

RESULTS OF THE DATING PROGRAM

FAIRBRIDGE BLUFF/CITY OF YORK

Two new OSL dates, not associated with artefacts, were obtained from Fairbridge Bluff. The oldest date of 140 ± 14 ka for sample R7/K0024 (Table 1, Figure 2A), produced using small aliquot OSL methods, is from an aeolianite sequence immediately overlying and broadly correlating with the Rottne Limestone member (Figure 4). A second, younger age of 47 ± 4.5 ka (R6/K0023; Table 1), also obtained using small aliquot OSL methods, is from the palaeosol unit overlying the aeolianite.

Three other small aliquot OSL dates, not associated with artefacts, were obtained from City of York and include a palaeosol unit sandwiched between two aeolianite sequences (Figure 4). The palaeosol dated at 49 ± 3.3 ka (R5/K0022) and underlying aeolianite giving an equivalent age within uncertainties of 46 ± 2.9 ka (R6/K0023) (Table 1, Figure 4). Together these provide a weighted mean age of 48.1 ± 3.1 ka. The overlying aeolianite yielded an age of 36 ± 2.3 ka (R4/K0021).

Bathurst Point

The massive/breccia calcrete unit immediately underlying a cemented fossiliferous chert artefact is dated by small aliquot OSL to 42.0 ± 2.7 ka (R11/K0034), and gives a maximum age for the artefact. The U-series sample from the carbonate lens overlying and cementing the calcrete/breccia unit yielded a weighted average age of 17.1 ± 1.2 ka (Table 1). A second block sample cut into the top of rhyzolithic palaeosol unit is dated by small aliquot OSL to 32.9 ± 3 ka (R12/K0035) (Figure 2B). This date is discordant with both the U-series age estimate and the c. 20 ka inferred maximum age for the rhyzolithic palaeosol unit near the top of the section 60 m to the west (Figure 2B). Here, the rhyzolithic palaeosol unit rests directly on the underlying younger aeolianite dated by single aliquot



Figure 4. Tamala Limestone stratigraphical succession at City of York Bay (cf. Figure 1; photo by EJR).

Table 1. Age estimates for City of York Bay (COY), Fairbridge Bluff (FB), Charlotte Point (CP), Bathurst Point (BP) and Little Armstrong Bay (LAB) from Single-grain (SG) OSL estimates, single aliquot (SA) OSL age estimates, isotopic (U-series) age estimates (*2 sigma uncertainty) and radiocarbon dating (^{14}C). Water contents were in the range of 3 – 10%. Burial depth calculated as time weighted mean depth, i.e. the time-weighted average distance between the sampling point and the surface, based on our best estimate of the aggradation history at each site. Note, over-dispersion values for small aliquot (SA) OSL is expected to be significantly lower than for single grains (SG), owing to signal averaging effects. D_e is the dose (in Gy) of laboratory b irradiation equivalent to the dose received in the field from all sources (a , b , g , cosmic). s_d is the population overdispersion, it represents the degree of spread in the data beyond that which can be explained by known sources of uncertainty (i.e. measurement uncertainty on each individual single grain or single aliquot D_e). Non-zero s_d values are almost universally found for single grain dose distributions. The greatest component of this is traditionally attributed to partial bleaching (e.g. Olley *et al.* 2004) however there are other important contributors, most notably b -dose heterogeneity (Nathan *et al.* 2003) and variations in instrument uncertainty (Jacobs *et al.* 2006; Pietsch 2009). Radiocarbon dates are reported at 95.4% probability and calibrated using the SHCal13 curve (Hogg *et al.* 2013) in OxCal v.4.2.3 (Ramsey 2013).

Site	Lab code	Unit	Method	Depth (m)	D_e (Gy)	s_d	U (ppm)	Th (ppm)	K (%)	Dose rate (mGya $^{-1}$)	Age (ka)
COY	R4/K0021	Upper aeolianite	SA OSL	4.0	8.82±0.24	4.2	0.740±0.002	0.440±0.022	0.081±0.001	0.28±0.02	36.3±2.3
COY	R5/K0022	Palaeosol	SA OSL	5.5	28.07±1.13	12	0.560±0.003	1.840±0.092	0.463±0.002	0.66±0.03	49.1±3.3
COY	R6/K0023	Lower aeolianite	SA OSL	7.5	23.72±0.84	9.6	0.610±0.003	1.420±0.071	0.410±0.002	0.60±0.03	46.2±2.9
FB	R8/K0025	Palaeosol	SA OSL	0.3	42.97±1.39	8.2	0.460±0.025	3.430±0.172	0.571±0.029	1.048±0.09	47.3±4.5
FB	R7/K0024	Aeolianite	SA OSL	1.0	65.31±2.39	9.9	0.520±0.026	1.330±0.067	0.219±0.011	0.506±0.05	140.0±14.0
CP	GU8.5	Palaeosol	SG OSL	3.0	8.28±0.46	18	0.8±0.04	2.1±0.11	0.164±0.082	0.63±0.06	12.7±1.25
CP	GU8.6	Palaeosol	SG OSL	3.5	8.72±0.16	19	1.0±0.05	1.8±0.09	0.199±0.099	0.68±0.06	12.1±1.01
CP	Wk 37948	Palaeosol	AMS ^{14}C	2.0							10.3±0.06
BP (West)	R9/K0026	Aeolianite	SA OSL	3.0	6.31±0.152	4.2	0.700 ± 0.001	0.450 ± 0.023	0.072 ± 0.001	0.294 ± 0.037	24.9 ± 3.2
BP (West)	R10/K0027	Aeolianite	SA OSL	4.5	6.2 ± 0.157	4.4	0.640 ± 0.001	0.380 ± 0.019	0.115 ± 0.001	0.324 ± 0.027	22.2 ± 1.9
BP (East)	R12/K0035	Palaeosol	SA OSL	3.5	7.71 ± 0.256	7.7	0.320 ± 0.016	0.690 ± 0.035	0.058 ± 0.003	0.270 ± 0.027	32.9 ± 3.0
BP (East)	R11/K0034	Palaeosol	SA OSL	4.0	11.36±0.271	2.9	0.420 ± 0.021	0.770 ± 0.039	0.066 ± 0.003	0.321 ± 0.037	42.0 ± 2.7
BP (East)	BP2.2	Calcrete	U-series	3.9							17.1 ± 1.7*
LAB (East)	GU8.1	Aeolianite	SG OSL	24.0	4.02±0.07	19	1.1±0.06	0.5±0.03	0.069±0.003	0.39±0.04	10.3±1.04
LAB (East)	GU8.2	Aeolianite	SG OSL	24.0	3.49±0.12	24	0.8±0.04	0.5±0.03	0.050±0.003	0.30±0.03	11.6±1.27
LAB (East)	GU8.3	Palaeosol	SG OSL	26.5	7.58±0.19	29	1.1±0.06	2.0±0.10	0.211±0.011	0.60±0.05	12.6±1.10
LAB (East)	GU8.4	Palaeosol	SG OSL	27.5	8.07±0.33	36	0.9±0.05	1.0±0.05	0.178±0.009	0.48±0.04	16.8±1.59
LAB (East)	CURL-16668	Palaeosol	AMS ^{14}C	27.5							28.2±0.18
LAB (West)	R1/K0018	Upper aeolianite	SA OSL	4.0	5.02±0.159	8.3	0.730±0.001	0.570±0.029	0.050±0.050	0.267±0.04	22.2±3.3
LAB (West)	R2/K0019	Palaeosol	SA OSL	4.5	8.08±0.221	1.4	0.850±0.003	1.630±0.082	0.194±0.001	0.475±0.02	19.7±1.1
LAB (West)	R3/K0020	Lower aeolianite	SA OSL	6.5	9.51±0.337	11.6	0.640±0.001	0.550±0.028	0.133±0.001	0.308±0.01	35.9±2.1

OSL to between 25 – 22 ka (Table 1). This age discrepancy may be explained by the presence, within the upper surface of the rhyzolithic palaeosol unit at Bathurst Point east (i.e. artefact find site), of large clasts of what may be older calcarenite. Hence the true age of the rhyzolithic palaeosol unit is considered to be < 20 ka.

Little Armstrong Bay

At Little Armstrong Bay (LAB) east, two single-grain OSL dates 12.6 ± 1.1 ka (GU8.3) and 16.8 ± 1.6 ka (GU8.4) pertain to samples taken just above, and at the same depth in this palaeosol, as the Eocene fossiliferous chert artefact and the emu eggshell fragment (Table 1). Significantly older than these age estimates is the calibrated radiocarbon date for the eggshell fragment at 28.2 ± 0.18 ka (CURL-16668). The discrepancy between it and the younger OSL dates from the same position in this palaeosol indicates that the eggshell fragment is probably re-worked from an older deposit – or recrystallised.

Two single-grain OSL dates of 10.3 ± 1.0 ka (GU8.1) and 11.6 ± 1.3 ka (GU8.2) were obtained from the aeolianite immediately overlying the fossiliferous chert artefact and emu eggshell-bearing palaeosol at LAB east (Figure 2C). These age estimates are much younger, but in chronological sequence, with the single-grain OSL date of 16.8 ± 1.6 ka for the palaeosol itself at LAB east and the single aliquot date of 19.7 ± 1.1 ka from the same palaeosol at LAB west (Table 1). The single aliquot OSL age estimate of 22.2 ± 3.3 ka, for the aeolianite overlying the palaeosol at LAB west (Table 1), is out of chronological sequence, indicating possible mixing of older grains in this sample. The single aliquot OSL age estimate of 35.9 ± 2.1 ka (R3/K0020) from the aeolianite below the palaeosol at LAB west provides a likely age for the corresponding aeolianite underlying the artefact-bearing palaeosol at LAB east (Figure 2C).

Charlotte Point

Two single-grain OSL dates (GU 8.5 and GU 8.6) from the artefact-bearing palaeosol at Charlotte Point give an absolute age of 12.7 – 12.1 ka (Table 1, Figure 2D). The palaeosol unit comprises a strongly cemented, brown (7.5 YR 5/3) medium-coarse grained quartz carbonate sand grading into a lighter brown (7.5 YR 8/2) and more loosely cemented quartz carbonate sand with *Austrosuccinea* sp. shells (Figure 2D). Charcoal from a pedogenically similar palaeosol 150 m south-east of the chert artefact find location, has yielded a slightly younger radiocarbon age of 10.3 ka (Wk 37948, Table 1). This date is however fully acceptable; together with the two OSL dates, it records the period through which the original sediments were deposited and developed into a soil.

DISCUSSION

DATED TAMALA LIMESTONE HISTORY FOR ROTTNEST ISLAND

A summary of the dated aeolianite sequences on Rottnest Is. is given in Figure 5. Eighteen previously unpublished OSL dates (Table 1) augment the absolute chronology for Rottnest Island's Tamala Limestone succession given

by Price *et al.* (2001); Playford *et al.* (2013) and Brooke *et al.* (2014). The latter two papers note *three* major phases of dune deposition in the Tamala Limestone of Rottnest Island. A possible *fourth* or earlier phase of dune deposition is dated by single aliquot OSL to 140 ± 14 ka (MIS 6/5e), confirming Playford's (1997:725) suggestion that 'part of the Tamala Limestone near Fairbridge Bluff underlies the [Rottnest Limestone] reef, and must have formed a little earlier perhaps at about 135 – 140 ka'. Hence the major shoaling of Rottnest began during, or just after 125,000 yr ago (see also Hearty 2003).

A second major phase of dune deposition dates from around 77 ka (MIS 4) (Playford *et al.* 2013; Brooke *et al.* 2014). A third phase of dune deposition is dated to 49 – 36 ka (MIS 3) at Bathurst Point find site, City of York (Figure 4) and Little Armstrong Bay (Figure 2C). The final phase of aeolianite deposition represented at Bathurst Point and Fish Hook Bay broadly correlates with MIS 2 (27 – 23 ka), approximately the initial stages of the LGM (Andrews 2013; Clark *et al.* 2009). Thus the main periods of carbonate aeolianite deposition show a general younging seaward trend, dating to MIS 5e (~140 ka), MIS 5a (~80 ka), MIS 3 (~46 – 36 ka) and MIS 2 (~25 ka) on Rottnest Island and MIS 5e (~115 ka) and later on the mainland (Figure 5). Hearty (2003) adds a further two aeolianite stages on Rottnest Is. at MIS 5c (~100 ka) and MIS 1 (~15 ka). However, these latter dates are based on contestable amino acid racemisation (AAR) ages of 'whole-rock' biogenic samples, that likely date reworked calcareous marine invertebrates rather than the depositional age of the dunes (Dortch & Hesp 1994; Brooke *et al.* 2014). We would concur. Alongside Brooke *et al.* (2014), our OSL chronology indicate that coastal carbonate barriers and dune fields form very rapidly and under a wide range of climatic conditions and sea levels (*c.f.* Hearty 2003). Given the high potential for reworking of this shelf and coastal sediment prior to its final deposition and cementation, the data also show that OSL, especially single-grain OSL, is an effective and reliable method for dating these deposits (see also Playford *et al.* 2013).

Dated palaeosol history for Rottnest Island

According to Semeniuk (1986), fossil soils and calcretes in this region mark periods of local interruption in dune building during more humid periods of the Pleistocene, albeit with variable rates of lithification. Like the aeolianite sequences, the sometimes very thick (~1 – 2 m) palaeosol sequences on Rottnest Is. are laterally discontinuous and, from the chronology, appear to have formed in relative quick succession within the aeolianites but under a wide range of climatic conditions. The latter may well result in quite different palaeosol characteristics, as implied by the very preliminary analyses undertaken in this study.

A summary of the dated palaeosol sequences on Rottnest Is. is given in Figure 5, which indicate palaeosol units corresponding to MIS 3 (~49 – 33 ka) and MIS 2 (~17 – 10 ka) on Rottnest Island. The earliest of these date to 49 ± 3.3 ka and 47.3 ± 4.5 ka (MIS 3) at City of York Bay and Fairbridge Bluff respectively. Alongside the palaeosol units at Little Armstrong Bay and Charlotte Point, these two palaeosol units also contain significantly higher proportions of carbonate material than the older (MIS 5e/5d), almost pure quartz *terra rossa* palaeosol recorded

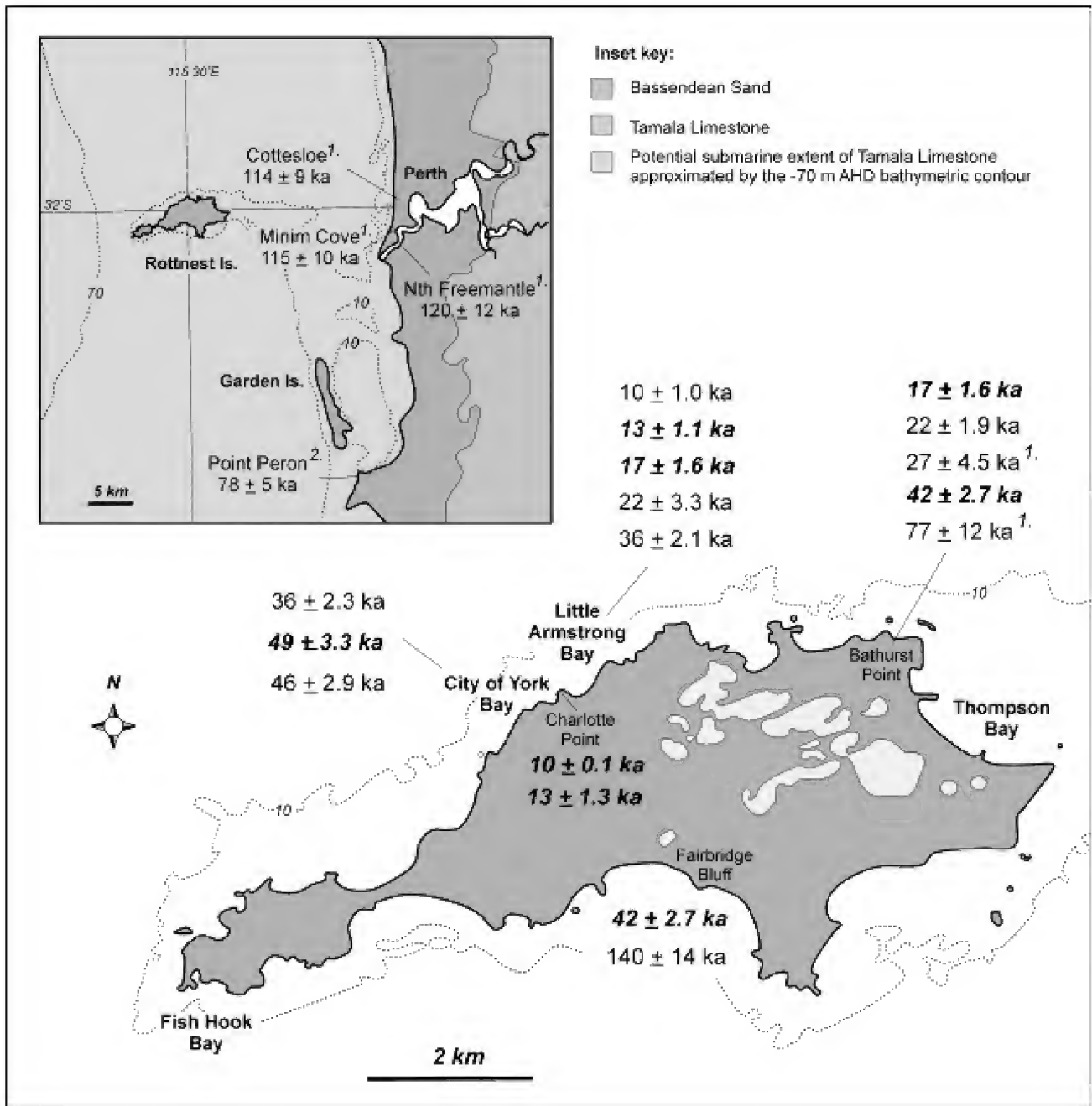


Figure 5. Summary of TL/OSL age estimates for aeolianite and palaeosol (in bold italics) sequences on Rottnest Is. and the adjacent mainland (inset figure), including previously published dates of 1. Brooke *et al.* (2014) and 2. Price *et al.* (2001). Inset figure also shows potential offshore extent of Tamala Limestone (after Smith *et al.* 2011).

at Fairbridge Bluff (Figure 2A), and also at Minim Cove and Cottesloe (Brooke *et al.* 2014). These contrasting carbonate-rich and quartz-rich palaeosols likely reflect the variable movement of mainland (westward) and exposed shelf (eastward) sediments across the shelf in association with changing sea level (Hearty & O’Leary 2008, 2010).

Other palaeosols, such as those at Charlotte Bay and Fish Hook Bay (Dortch and Hesp 1994), also contain variable amounts of charcoal (and fossil plant material)

but this does not appear to be age-related. Likewise, although the palaeosols at the City of York Bay and Little Armstrong Bay and pedogenetically very similar, and their stratigraphic positions and heights above sea level are also much the same (Dortch and Hesp 1994: 26), nevertheless they yield different depositional ages (Figure 5). In contrast, the exposed palaeosol units on the east and west side of Little Armstrong Bay do show a similar age and pedogenic characteristics and hence likely belong to a single depositional unit. The palaeosol

horizon at Charlotte Point also share similar sediment characteristics (albeit with inclusion of charcoal) and age to the Little Armstrong Bay. However, as indicated by Dotch and Hesp (1994), the palaeosols often cannot be traced laterally very far and caution should be taken before assuming any correlation between these.

The artefact-bearing palaeosols mainly date to the late (17 – 10 ka) stages of MIS 2 and possibly to MIS 3 if the oldest date of 42 ka for Bathurst Point is assumed. This brecciated calcrete/palaeosol unit forms partly as a result of mechanical fracturing by roots (see Arakel 1982), which are clearly evident in the overlying rhyzolithic palaeosol dated to around 17 ka (Figure 2B). Dissolution and recementation are common in such calcretes, as evident from the thin calcrete unit that caps the brecciated calcrete (Figure 3) and also in thin section (Figure 2B). Subsequent erosion of the rhyzolithic palaeosol, possibly as sea-level encroached Rottnest Is., may have resulted in exposure of the embedded artefact (see also Ward *et al.* 2016). Indurated palaeosols and duricrusts intercalated within Tamala Limestone aeolianite successions occur along many parts of the West Australian coastline (Playford *et al.* 2013, p.102) hence the possibility of other embedded artefacts being similarly exposed.

Palaeosols, occasionally featuring rhizotubules and *Leptopious* sp. pupal cases are revealed in many places along the littoral zone. At Little Armstrong Bay a massive, brown sandy palaeosol unit continues c. 200 m within the intertidal zone. Playford (1997) also describes root pipes in the Tamala Limestone extending below sea level at many localities around the coast (e.g. at Fairbridge Bluff). The luminescence dating of the ‘older aeolianite’ at Bathurst Point (Figure 2B) implies that some, perhaps even all of the palaeosol units exposed in the littoral are older than c. 77 – 66 ka (MIS 4). Correspondingly Smith *et al.* (2011) indicate the Tamala Limestone (and by implication intercalated palaeosol units) may extend as far as the -70 m bathymetric contour (Figure 5). However, no artefacts have been identified in any of these older or partially submerged palaeosol units exposed on Rottnest Island.

CONCLUSION

With an absolute chronology spanning MIS 6 to MIS 2 (~140 ka – 10 ka), Rottnest Island is today one of Australia’s best dated Late Quaternary localities and one of Western Australia’s most iconic geoheritage sites (Ward 2013). This secure chronology, particularly of the palaeosol units, is of great importance to further investigation of prehistoric archaeological sites as well as to other Quaternary field studies on the island. The artefact-bearing palaeosol units mainly date to MIS 2 (17 – 10 ka). However, further dating and pedogenic characterisation of palaeosol units around the island is needed before considering the possibility of a widespread distribution of one or more archaeologically significant palaeosol units (see Dortch and Hesp 1994). Similarly more detailed chronological studies – such as this one – are needed to further define dune-building and calcrete-forming episodes in the Tamala Limestone (Playford 1997). With continued evaluation of the Rottnest Island absolute chronology, the island will become an increasingly valuable site for Quaternary investigations.

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Male sterility in *Corymbia calophylla* (marri)

JEN MCCOMB

School of Veterinary and Life Sciences, Murdoch University, Perth, Western Australia 6150

✉ jmccomb@murdoch.edu.au

Most *Corymbia calophylla* trees have inflorescences of hermaphrodite flowers with a variable number of male flowers. Some trees have been identified that have either only female flowers, or a seasonally variable production of female flowers at the beginning of the flowering season, changing to production of hermaphrodite flowers after the first 2–3 weeks of flowering. In the flowers of the female trees, the anthers develop normally until the stage of meiosis when premature disintegration of the tapetum is followed by degeneration of the pollen mother cells. Female trees appear to be rare but widespread.

KEYWORDS: Female flower; Pollen sterility.

INTRODUCTION

Early illustrations of buds and flowers of marri (*Eucalyptus calophylla* (Lindl.) KD Hill & LAS Johnson) such as those by Baker and Smith (1920, Fig. 2 in Carr et al. 1971) showed flower buds of two shapes – some pear-shaped and others more spherical or top-shaped. This remained unremarked by botanists until Carr et al. (1971) reported that the pear-shaped buds were hermaphrodite, while the spherical ones were male, i.e. female sterile. Earlier observers may have thought the degenerated ovary contents in spherical buds were a result of fungal or insect damage, but this is not the case with most corymbs having some male flowers amongst the hermaphrodite ones. The proportion of male flowers varies and some trees have only male flowers (Carr et al. 1971). The variety *maideniana* Hochr. from the Darling Range, was shown to be based on a type specimen with only male flowers (Carr & Carr 1972).

A further variation of floral structure is reported here. During collection of pollen for hand pollinations, some marri trees were identified that had only female flowers.

METHODS

An attempt to collect pollen from newly opened buds of marri in the Kalamunda hills and foothills resulted in the identification of a number of trees that produced no pollen. Anther development was examined to determine the cause of the male sterility. Hermaphrodite and male sterile buds at different stages of development were collected (Table 1), fixed in formalin acetic alcohol, processed for sectioning in paraffin wax, cut at 8 µm and stained in 0.5% toluidine blue. Buds were fixed over the period 14th December 2013 to 4th April 2014.

Observations were made over several years to determine the consistency of expression of male sterility.

Herbarium specimens were examined at the Perth herbarium and for those without pollen obvious on

the anthers, anthers of flowers or unopened buds were crushed in aceto-orcein and examined for the presence of pollen.

RESULTS

In a number of Kalamunda trees initially only female flowers (i.e. male sterile flowers), were present but after one to two weeks the trees produced hermaphrodite ones. The initial occurrence of female flowers varied with season. Four trees were identified that produced only female flowers over the entire flowering season, at least to the height of 5 m. This was consistently the case for two of the trees that were observed over the flowering periods of 2013 to 2016 which included years of abundant flowering as well as sparse years. A third female tree did not flower in 2015, and the fourth tree was burned in 2015 and did not flower in 2016. The female trees set the usual crop of capsules and seeds. Trees with female flowers also had some female sterile flowers in their corymbs making these flowers totally sterile.

The female flowers on living trees and herbarium specimens were generally smaller than the hermaphrodite ones (Figure 1) and this size difference is the best indication that a tree may be female. Anthers of female flowers after anthesis, in living specimens and herbarium specimens are pale and small, but otherwise similar to those of male or hermaphrodite flowers from which the pollen had been shed and collected by insects. Thus to identify a female flower it is necessary to examine the anthers of mature unopened buds. It is possible that the herbarium collections referred to as 'female' could be from trees that later in the season produce hermaphrodite flowers, but the flower size would suggest they are from female trees.

The anthers from hermaphrodite buds had darkly stained premeiotic pollen mother cells with a well defined tapetum. During meiosis (Figure 2A) and through to the stage of tetrads (Figure 2B) and uninucleate pollen, the tapetum was still in place although becoming vacuolated. The mature anthers showed the normal development of the fibrous layer and

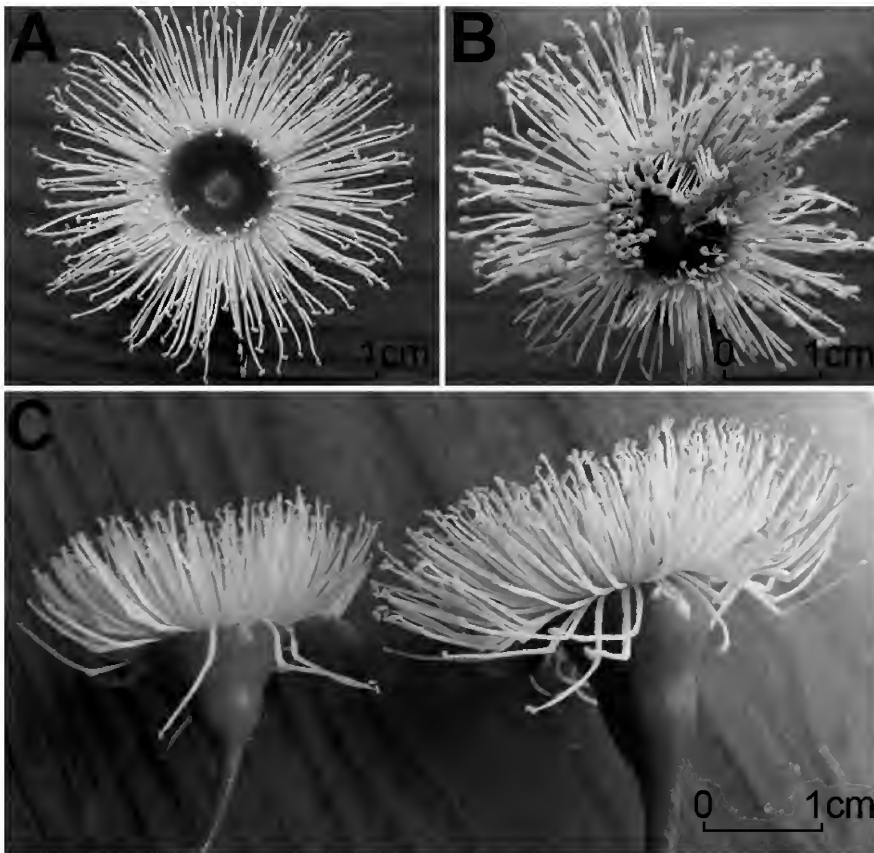


Figure 1. *Corymbia calophylla* trees from Kalamunda. A. Female flower, B. Hermaphrodite flower. C. Left female, Right Hermaphrodite flowers.

Table 1. *Corymbia calophylla* trees: locations and flower fertility

Location/herbarium number	Sex of flowers	Histology
Remnant tree on road verge at No 20 James Rd. Kalamunda.	Hermaphrodite and male, 2013–16	Sections of hermaphrodite flowers
Remnant tree on road verge of 29 Betti Rd (between James and Grace corners) Kalamunda	Hermaphrodite and male 2013–2016. Initially female in first weeks of flowering, 2013, 2016.	Sections of hermaphrodite flowers
Remnant tree on road verge SW corner of Robbins Rd and Grace Rd. Kalamunda.	Female, 2013–14, 16	Sections of female flowers
Remnant tree on road verge at No 5 Betti Rd. Kalamunda. (PERTH 08733619)	Female 2013–16	Sections of female flowers
Remnant tree on road verge at No 18 James Rd Kalamunda (PERTH 08733627)	Female 2015, 16.	
Tree in a remnant patch of trees at corner of Crystal Brook Road and Welshpool Road, Wattle Grove	Female 2015.	
Herbarium specimen Between Dunsborough and Cape Naturaliste (PERTH 01319256)	Female 1982	
Herbarium specimen Marangup Reserve off Toodyay Rd (PERTH 08029164)	Female 2007	

tricolpate pollen with dark stained deposits at each pore (Figure 2C).

In the anthers of the two female, (male sterile) trees sectioned, there were no major differences from male fertile anthers until the onset of meiosis. At meiosis in the female trees, the pollen mother cells rounded up and the tapetal cells were very faintly stained and more vacuolated than in the hermaphrodite trees. The most

advanced meiotic stages were pachytene or diplotene (Figure 2D). Degeneration of the sporogenous tissues followed quickly (Figure 2E) with pollen mother cells becoming vacuolated then cell contents of each locule degenerating into a small deeply stained area. This reduced the size of the anther and distorted its shape, but the subepidermal fibrous layer developed normally with the empty locules splitting open at anther maturity

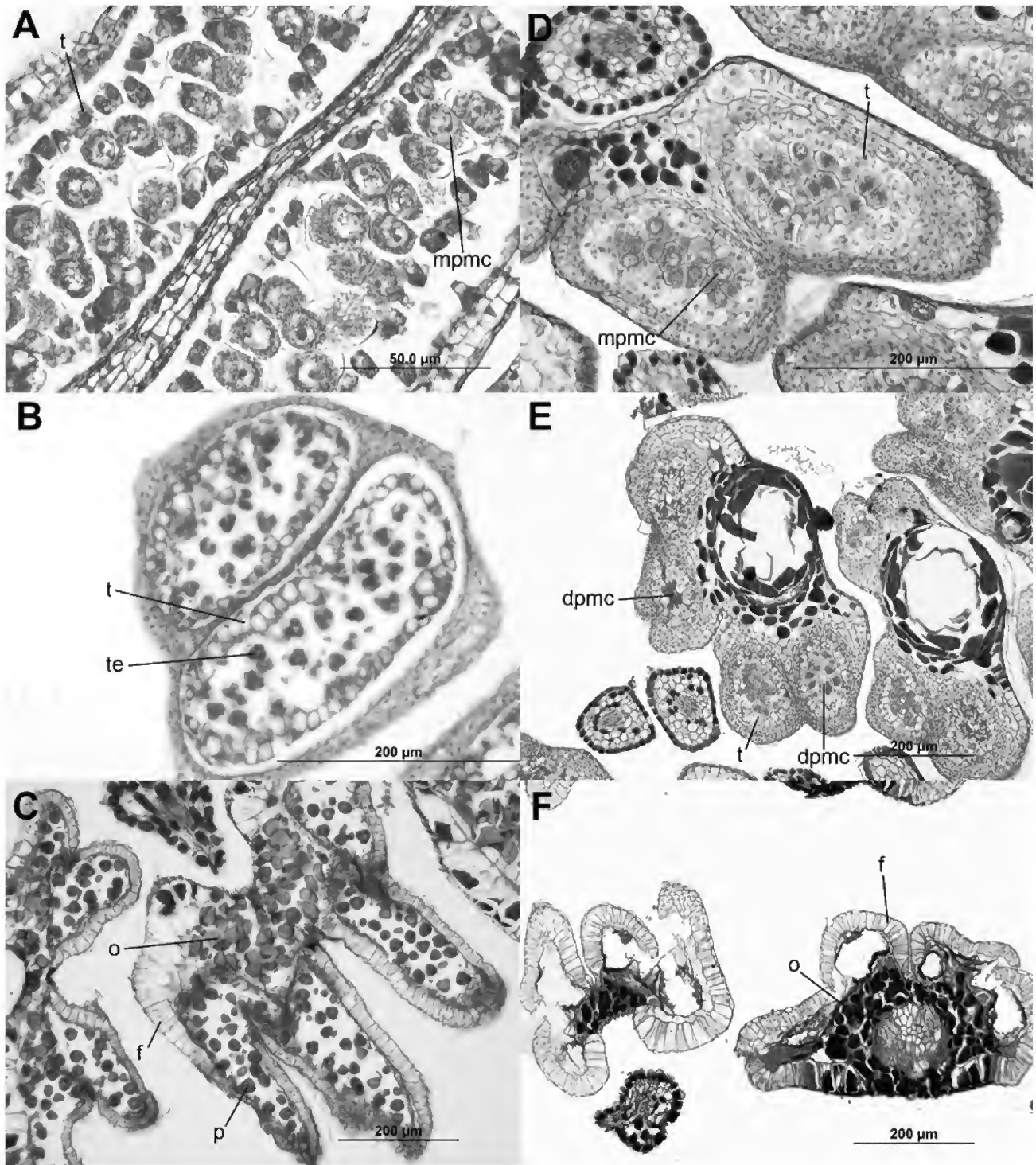


Figure 2. *Corymbia calophylla* anther development. Trees from Kalamunda A-C. Fertile anthers from hermaphrodite flowers. A, anthers at early prophase of meiosis, B, tetrad stage, C. Pollen in mature anthers. D-F. Sterile anthers from female flowers. D. anthers at early prophase, note vacuolate tapetum, E. degeneration of pollen mother cells. F. anthers with empty locules but mature walls with fibrous layer developed. t, tapetum, mpmc meiotic pollen mother cells, te tetrads, dpmc degenerating pollen mother cells, f fibrous layer, o oil cells, p pollen.

(Figure 2F). The development of the oil cells in the filament was similar to the fertile anthers.

The female trees set crops of capsules comparable to those on nearby hermaphrodite trees.

The two herbarium specimens observed to have only female flowers had short pale anthers and although there

were a few small pollen grains on the surface of open flowers of the Dunsborough specimen, an unopened bud showed no pollen in the anthers and this tree is considered a putative female (Figure 3). Similarly no pollen was present in anthers from unopened flowers of the Toodyay specimen.

DISCUSSION

Flowers of marri are usually hermaphrodite or male, but female flowers and completely sterile flowers also occur. The production of female flowers may be transient at the beginning of the flowering season or a tree may produce only female flowers. In the female flowers the pollen mother cells and tapetum degenerate at the onset of meiosis, but the anther wall matures as in the fertile anthers. Tapetal abnormalities are frequently related to male sterility though mostly reported in herbaceous plants (Kaul 2012).

If the first flowers that open on a tree are female they must be outcrossed to set fruit, while in female trees all flowers will be outcrossed. Hermaphrodite flowers may be geitonogamously pollinated or outcrossed. Eucalypts, as with other forest trees, show inbreeding depression associated with self pollination (Sedgley and Griffin 1989).

The mix of male flowers, or sterile flowers in the corymb probably adds to its attraction for insects without being a sink for resources following seed set. The stigma of the hermaphrodite flowers does not become receptive until 7–9 days after anthesis (J. McComb data not shown) and this long period means that each corymb has a long lasting display of flowers.

Pryor (1976) reported that some trees of *E. pulverulenta* Sims had pollen with no protoplasmic content, and a detailed study by Peters *et al.* (1990) showed a wide range of pollen sterility in both a natural and cultivated population, with number of trees in the cultivated stand having no fertile pollen. Pryor (1976) also reported an unusual type of male sterility from *E. grandis*. In this case the pollen grain wall released no protein on to a stigma or a sucrose or agar gel and the grains failed to germinate.

While male flowers have previously been reported from *C. calophylla* and closely related species, as well as from other genera of Myrtaceae (Bentham, 1869), there are few reports of female flowers. *Melaleuca cornucopia* Byrnes is recorded as having female flowers and can be monoecious or gynodioecious (Byrnes 1985).

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