Early and Middle Pleistocene non-passerine bird fossils from the Thylacoleo Caves, Nullarbor Plain

by

Elen Shute

BA (Hons)
MPhil (Quaternary Science)

Thesis
submitted to Flinders University
for the degree of

Doctor of Philosophy
College of Science and Engineering
7th January 2019

I dedicate this thesis to my parents, Rosalyn and Jason Shute, who would probably stick it on their fridge if they could.

“[N]ot a single bird could be seen coming off the arid coast; not a single appearance of smoke was noticed; all this indicated that this land, whose aspect was frightful, was not inhabited.”

French explorer, Bruni D’Entrecasteaux (1792), making one of the earliest historical references to the Nullarbor Plain (cited in Gillieson *et al*. 1996)

TABLE OF CONTENTS

Chapter 1: Introduction, aims and methods

Chapter 2: Three terrestrial Pleistocene coucals (Centropus: Cuculidae) from southern Australia: biogeographical and ecological significance

Chapter 3: Taxonomic review of the Late Cenozoic megapodes (Galliformes: Megapodiidae) of Australia

Chapter 4: The Early and Middle Pleistocene fossil avifauna of the Thylacoleo Caves: non-passerines

Chapter 5: General Discussion and Conclusions

Abstract

Studying the fossil record of the Pleistocene epoch (2.58 million years ago to 11,700 years ago) is key to understanding how modern ecosystems developed. The dramatic climate fluctuations of the Pleistocene have long been viewed as a major force that shaped the Australian avifauna, driving the evolution of species and sub-species of birds, and creating the distinctive regional bird assemblages seen today. Despite this, very little fossil evidence illuminates either the diversity or distribution of birds across the continent for most of the Pleistocene, and the overall effects of the Pleistocene on the Australian avifauna are difficult to assess.

The research presented here is the first study of a diverse Australian fossil landbird assemblage spanning both the Early and Middle Pleistocene, time intervals that are particularly poorly represented in the Australian fossil record. The fossils examined here come from the Thylacoleo Caves, beneath the Nullarbor Plain, Western Australia – a location of particular interest for understanding the Pleistocene ecology of southern Australia. Today, the Nullarbor is a vast, arid, treeless habitat covered by chenopod shrubs, and is noted for its low bird diversity. It is considered a major arid-habitat barrier that separates and isolates many animal taxa in the moister south-west and south-east of the continent. It has generally been inferred that the Nullarbor Plain lost its tree canopy during the Pleistocene due to increasing aridity, but the timing and processes of this transition are unclear.

Nearly 60 species of non-passerine bird were identified within the Thylacoleo Caves fossil assemblage, more than any other Australian locality of similar age. Up to 14 extinct species were identified, roughly one quarter of the total non-passerine fossil assemblage – more extinct Pleistocene species than have previously been described from the rest of the continent. The Australian avifauna may have been affected by higher rates of extinction during the Pleistocene than previously suspected. Four extinct species from the Thylacoleo Caves are formally described herein. Two of these, ground-dwelling coucals in the genus *Centropus*, are the world's two largest-known cuckoo species. Two extinct megapodes, both larger than their living relatives, are also described, along with fossil megapodes from other Australian localities.

The composition of the fossil avifauna is assessed, and is used to reconstruct the Pleistocene palaeoecology of the Nullarbor Plain. The Early Pleistocene assemblage was found to contain high woodland species diversity, and includes the majority of the extinct taxa. Presence of numerous wetland taxa, including rails, charadriiforms, a duck and a stork, indicate periodic inundation, even if conditions were generally relatively arid. By contrast, the Middle Pleistocene assemblage has low diversity, includes few woodland taxa, and comprises mainly species that prefer open arid habitat similar to that of the Nullarbor Plain today. Few extinct species are present, suggesting that a majority of extinctions may have occurred between the Early and Middle Pleistocene in response to aridity-induced habitat loss.

Declaration

I certify that this thesis:

1) Does not incorporate without acknowledgement any material previously submitted for a degree or diploma in any university; and
2) To the best of my knowledge and belief, does not contain any material previously published or written by another person except where due reference is made in the text.

Acknowledgements

So many people have had a hand in this endeavour it's hard to know where to start. Thanks to Rod Wells and Liz Reed for setting me off on the palaeo path as an undergrad in 2001. The excitement never wore off, and I eventually found my way back to the Flinders Palaeo Lab like a slightly disorientated homing pigeon. To all members of the Palaeo Lab, past and present, students, staff and volunteers – you're a weird and wonderful assortment of characters, and I'm privileged to be a member of such an enthusiastic, skilled, irreverent, cooperative and committed team. I still look forward to coming here every day (apart from every second Friday). Thanks go to Carey Burke and Grant Gully for keeping the labs and field trips running like a well-oiled machine over the last few years.

Special thanks to those who have travelled the PhD path at a similar same time and have shown me how it's done – Matt McDowell, Sam Arman, Aidan Couzens, Rachel Correll, Ben King (who I think lapped everybody), Diana Fusco and Warren Handley. To Diana in particular, thanks for all the sanity-preserving nocturnal hikes and chats and the loan of your dog. Above all, thank you to everyone in the lab for occasionally laughing at my puns. I know it wasn't always easy. It must be a sign of maturity that I have managed not to include any in my thesis, so I guess I finally know my tibiotarsus from my elbow.

To my supervisors Gavin Prideaux and Trevor Worthy, I could hardly be more grateful for all you've done for me. You are both so different, but something I've learnt from both of you is an approach to science that is thoughtful, thorough and modest. Trev, I'm grateful for all you've taught me about the study of bird bones. Few people are as generous with their time and expertise as you are, and you genuinely never seem happier than when a student waltzes into your office and waves a mystery bone under your nose. Gav, you've given me the opportunity of a lifetime by taking me on for this project where others might have told me to take a hike. As if that weren't enough, you've ensured that doing a PhD has been everything it should be and nothing it shouldn't, and you have my gratitude and loyalty always. You deserve an honorary degree in psychology.

Many friendships have helped sustain me through the last few years. To my Belair crew, Claire Binnion, Paul Lewis, Milan Gnezda, Bek Hall and William Driver (none of whom could care less if I was a palaeontologist or not), thank you for all the belly laughs, emotionally intelligent conversations, Spats visits, walks, music, and crap dinner parties. Other friends near and far have also had a hand in supporting, encouraging or distracting me in various ways – Vanesa De Pietri, Aaron Camens, Althea Walker Hallam, Louise Lindon, Christina Adler, Jenny Templeton, Vicky Thomson, Jackie Nguyen, Andy Davice, Shaun Adams, Antonietta Barca, Sara Hurditch, Natalie Warburton, Claudia Grimaldo, Ronald Ranta, Mark Lethbridge and Edo Barbosa. I feel very lucky to have you all in my life.

To my parents Ros and Jason, brother Steff, sister-in-law Bich Anh, niece Ffion and nephew Trystan, thanks to you all for your unfailing support and love in all its forms – up to and including cuddles, conversations, cars, cakes and curtains – before, during and no doubt after this PhD lark is all over. Thanks, Mum, especially, for your patient editorial help, and Dad for the magical self-washing dishes and self-cooking dinners that kept appearing in my freezer while I was writing up my thesis. You've always been my greatest supporters, and I had the great fortune of being born into the kind of family where curiosity was indulged, and learning was something you did for fun. Every kid loves dinosaurs, but not every kid gets taken to the Natural History Museum or on holiday to Lyme Regis. There's a little bit of my childhood in every page of this thesis, and I still want to be a palaeontologist when I grow up.

This research project could not have taken place without more than a decade of patient, uncomfortable and gruelling work by many cave explorers, scientists, students and volunteers, who discovered, explored and mapped the Thylacoleo Caves, and collected the fossils that have been my privilege to study. Without this magnificent collection, which showed up at just the right time in my life, I might never have had the chance to do a PhD at all.

Many museum staff have facilitated my use of the collections that make osteological studies possible. I have thanked many staff and institutions individually in the acknowledgements sections of Chapters 2 and 3, but I particularly want to thank again the collection managers at the South Australian Museum – Philippa Horton and Maya Penck for giving me ready access to the ornithology collection, and Mary-Anne Binnie to the palaeontology collection. Thanks, too, to Helen Ryan of the Western Australian Museum for arranging the loan of all the fossil material from the Thylacoleo Caves that will ultimately make its home in Perth.

My candidature at Flinders University has been supported by a Flinders University Research Scholarship, and a fee offset scholarship under the Federal Government's former Research Training Scheme (RTS). I am also grateful to BirdLife Australia for awarding me a Stewart Leslie Travel Grant that allowed me to attend an overseas conference, and a Student Research Award that contributed towards the research presented here.

List of figures Page

List of tables

Page

Chapter 1: Introduction, aims and methods

1.1 Introduction

The overarching aim of the thesis is to use the fossil assemblage from the Thylacoleo Caves to investigate the diversity and distribution of non-passerine birds on the Nullarbor Plain during the Early and Middle Pleistocene. This chapter provides background information fundamental to the three data chapters that follow. In it I review the literature on the: 1) palaeoecology of the Pleistocene epoch; 2) diversity and distribution of the modern Australian avifauna; 3) Pleistocene fossil record of Australian birds; 4) modern geography and ecology of the Nullarbor Plain; and 5) prior research on the Pleistocene fossil vertebrate assemblage from the Thylacoleo Caves, including birds. Following on from the review is a statement of the specific aims of the thesis, and the general methodological approach used in the collection, curation and identification of the fossil specimens studied in subsequent chapters.

1.2 Background

1.2.1 Historical views on the Australian avifauna during the Pleistocene

It has long been proposed that the climatic perturbations of the Pleistocene played a major role in shaping the diversity and biogeography of the modern Australian avifauna (Gentilli 1949; Keast 1961; Ford 1987), but only since the second half of the 20th Century has the true complexity of the Pleistocene epoch, and the complexity of its impact on faunas, been grasped. As recently as the mid-20th Century, most of the Australian avifauna was considered to be the result of recent colonisation from Asia via Indonesia and New Guinea (Mayr 1944). Moreover, Pleistocene arid phases were believed to have been so severe that they drove all animal life to extinction in the western part of the continent, before being later recolonised from eastern Australia and New Guinea (Gentilli 1949).

However, these ideas were rapidly replaced with an essentially modern view of the evolution, biogeography and antiquity of the Australian avifauna (e.g. Keast 1961), wherein Pleistocene climatic fluctuations were understood to have shaped the continent's existing avifauna by creating aridity barriers and refugia (Ford 1987; Schodde and Mason 1999; Toon *et al.* 2007; Byrne 2008). At the time that Keast was writing in the early 1960s, though, neither the timescales involved nor the complexity of global Pleistocene climatic changes were well understood. The evidence then available was that there were four major Northern Hemisphere glacial cycles that had influenced the Australian climate. Today, more than 100 marine oxygen-isotope stages, representing around 50 global glacial–interglacial cycles, are recognised as having occurred during the Pleistocene (Cohen and Gibbard 2011; Gibbard and Lewin 2016), making the interpretation of the evolutionary and biogeographical history of the Australian avifauna a much more complex affair.

1.2.2 Modern understandings of the origins of the Australian avifauna

Within the last few decades, research has revealed that the Australian bird assemblage is much more ancient than previously envisaged. Fossil and molecular evidence has shown that some of the world's most successful modern lineages of birds, including parrots (Joseph *et al.* 2011; Schweizer *et al.* 2011), pigeons (Pereira *et al.* 2007; Worthy *et al.* 2009; Worthy 2012a;) and passerines (Moyle *et al.* 2016) originated in the Australasian region. Fossils from the late Oligocene to early Miocene (28–11 million years ago) show that even some extant genera have survived in Australia for more than 20 million years (Boles 1995, 2001, 2005; Worthy 2012b; Nguyen *et al.* 2014; Nguyen 2016).

Further, although there has been a degree of bi-directional interchange of fauna between Australia and New Guinea over the last few million years (Joseph *et al.* 2001; Schodde 2006; Joseph and Omland 2009; Marki *et al.* 2017), there is no evidence for the catastrophic loss of species from most of Australia during the Pleistocene, followed by recolonisation from eastern Australia and New Guinea, that Gentilli (1949) imagined: climatic events of the Pleistocene certainly did not play out on an avifaunal *tabula rasa*, but rather in the context of a pre-Pleistocene avian assemblage with ancient roots.

1.2.3 Effects of the Pleistocene on Australian birds

For the last half-century or more, the dominant paradigm has been that the Pleistocene saw an overall trend towards aridity in Australia: overprinted on this trend, arid-habitat barriers arose in more mesic areas during cool, dry intervals of the Pleistocene, driving populations of birds to differentiate by vicariance, thus helping create the patterns of diversity and distribution observed today (Keast 1961; Schodde and Mason 1999; Schodde 2006; Byrne 2008). Schodde (2006) proposed that most extant Australian birds evolved during the Pleistocene, with some having evolved somewhat earlier in the Pliocene. However, a review by Byrne *et al.* (2008) concluded that for most Australian taxa examined, including birds, species diversity was largely established by the Pleistocene, and the climatic fluctuations of the Pleistocene were mostly a driver of range changes and intraspecific variation, rather than speciation.

Recent genetic studies have provided evidence for both speciation *and* sub-specific differentiation during the Pleistocene. For example, certain sub-species of the Variegated Fairy-wren *Malurus lamberti* are inferred to have differentiated during the Middle and Late Pleistocene (McLean *et al.* 2012), while the Chestnut Teal *Anas castanea* and Grey Teal *A. gracilis* seem to have differentiated during the Late Pleistocene (Dhami *et al.* 2013). In some cases the boundaries between what constitutes species and subspecies are blurred (Murphy *et al.* 2011; Toon *et al.* 2012), making it difficult to generalise about the overall effects of Pleistocene climatic fluctuations on bird diversity.

A further complication to understanding the overall impact of Pleistocene climate cycles on bird evolution is that molecular data sometimes conflict with phenotypic evidence for what constitutes a species or subspecies (Joseph *et al.* 2013). For example, genetic-morphological mismatches have been found in the Australian Magpie *Cracticus tibicen*, Pied Butcherbird *Cracticus nigrogularis* and in the entire genus of *Platycercus* parrots (rosellas) (Toon *et al.* 2007; Kearns *et al.* 2010; Shipham *et al.* 2015).

In recognition that the Pleistocene was highly complex and likely affected different taxa in different ways, Dolman and Joseph (2012) used molecular data to test what effects the 'Nullarbor Barrier' had on 10 bird taxa with allopatric distributions in south-western and south-eastern Australia. They found that different taxa had idiosyncratic responses in terms of divergence dates, highlighting the difficulty of making generalisations about the timing of complex vicariance 'events' (see Section 1.6.6). If we are moving towards a coherent narrative of the effects of Pleistocene on the evolution of the Australian avifauna, the current status appears to be an acknowledgement of complexity, rather than the attainment of clear answers and neat generalisations that can be applied across all taxa.

1.2.4 A global view

Australia is not unique in lacking a detailed picture of how events of the Pleistocene affected its avifauna overall. As summarised by Nadachowska-Brzyska *et al.* (2015), there has been a great deal of debate about the overall effects of the Pleistocene on the diversity of birds globally. Some (e.g. Johnson and Cicero 2004; Weir and Schluter, 2004) have argued that there was a net increase in the number of bird taxa during the Pleistocene due to high rates of vicariant speciation. Others (e.g. Zink *et al.* 2004) have argued that there was either a lowered rate of speciation, or that high speciation rates were balanced out by extinctions for no net gain. Which of these scenarios might apply to the Australian avifauna is currently unclear. Did the climatic fluctuations of the Pleistocene result in a net increase in diversity through vicariance, a net decrease in diversity through extinctions, or did these factors balance each other out?

This is too large a question to resolve in this thesis, but the fossil research presented in later chapters provides a rare opportunity to directly survey the diversity of Australian landbirds during the Pleistocene in a way that is spatially and temporally explicit, and that is independent of modern biogeographical distributions, which may mask the events of the past (e.g. Warren *et al.* 2014). Some recent fossil bird studies from other continents have revealed previously cryptic range changes and extinctions during the Pleistocene, in both continental and island contexts, in northern Europe, the Americas and Asia (Meijer and Due 2010; Steadman and Mead, 2010; Oswald and Steadman 2011; Meijer *et al.* 2013; Meijer 2014; Holm and Svenning 2014; Meijer *et al.* 2015; Oswald and Steadman 2015; Steadman *et al.* 2015; Stewart and Jacobi 2015). I hope that the present study will provide a similar new perspective on the Pleistocene history of the Australian avifauna.

1.3 Overview of the Pleistocene epoch

1.3.1 Glacial–interglacial cycles of the Pleistocene

1.3.1.1 Global climate and geography

Following the closing of the Isthmus of Panama during the Pliocene approximately 3 Ma (million years ago), ocean circulation patterns adopted their modern configuration setting the foundation for the modern global climate (Sarnthein *et al.* 2009). Soon after this, periodic fluctuations in the Earth's orbit, known as Milankovitch cycles, interacted with altered ocean circulation patterns, resulting in the repeated glacial–interglacial cycles that characterise and define the Quaternary period, commencing 2.58 Myr ago (Gibbard *et al.* 2010).

When polar ice sheets and glaciers grew during cold intervals, they locked up vast quantities of water. At times, this caused global sea levels to fall more than 100 metres below present levels. Land masses that are currently separated by sea became conjoined as continental shelves were exposed (Lambeck and Chappell 2001): the Bering Strait dried out, Siberia was at times contiguous with North America via a land bridge referred to as Beringia, and the Australian mainland joined with Tasmania and New Guinea to form a single landmass (Yokoyama *et al.* 2001). Warmer phases of the Quaternary, in turn, melted the polar ice sheets and glaciers, raising sea levels once more and cutting off these land-bridge connections.

1.3.1.2 Effects on the biota

Accompanying the profound changes in global climate and geography of the Pleistocene came inevitable changes to regional biotas. As global temperatures, patterns of precipitation, ice cover and land-bridge connections changed, flora and fauna were shuffled from region to region, and this provided conditions for novel ecological assemblages – sometimes called 'non-analogue' or 'no-analogue' communities – to form (Williams and Jackson 2007).

For example, taxa that we currently think of as quintessentially African, such as lions, hippopotamus and hyaena, at times inhabited Europe, including Britain, where they comingled with what we now think of as European and arctic species like red deer and reindeer (Polly and Eronen 2011). In the northern hemisphere, the characteristic Pleistocene 'mammoth steppe' fauna – including mammoth, reindeer, horse and bison – evolved and spread throughout the vast contiguous steppe habitat that spanned Northern Europe, Siberia, Beringia and northern North America (Guthrie 2000).

The extinction of 'ice-age' megafauna such as mammoth, mastodon and woolly rhinoceros from high latitudes in Eurasia and North America late in the Pleistocene is well known, but it is less widely known that over the last few tens of thousands of years of the Late Pleistocene (126,000−11,700 years ago), other continents, including Australia, also lost a majority of their large-bodied animals that had thrived for most of the Pleistocene. South America lost 52 genera of megafauna (Barnosky and Lindsey 2010), while Australia lost 25 genera, including almost all of its large mammals (Prideaux 2007). Thus, modern terrestrial mammalian faunas, of all continents except Africa, are depauperate relative to most of the Quaternary (Barnosky *et al.* 2004).

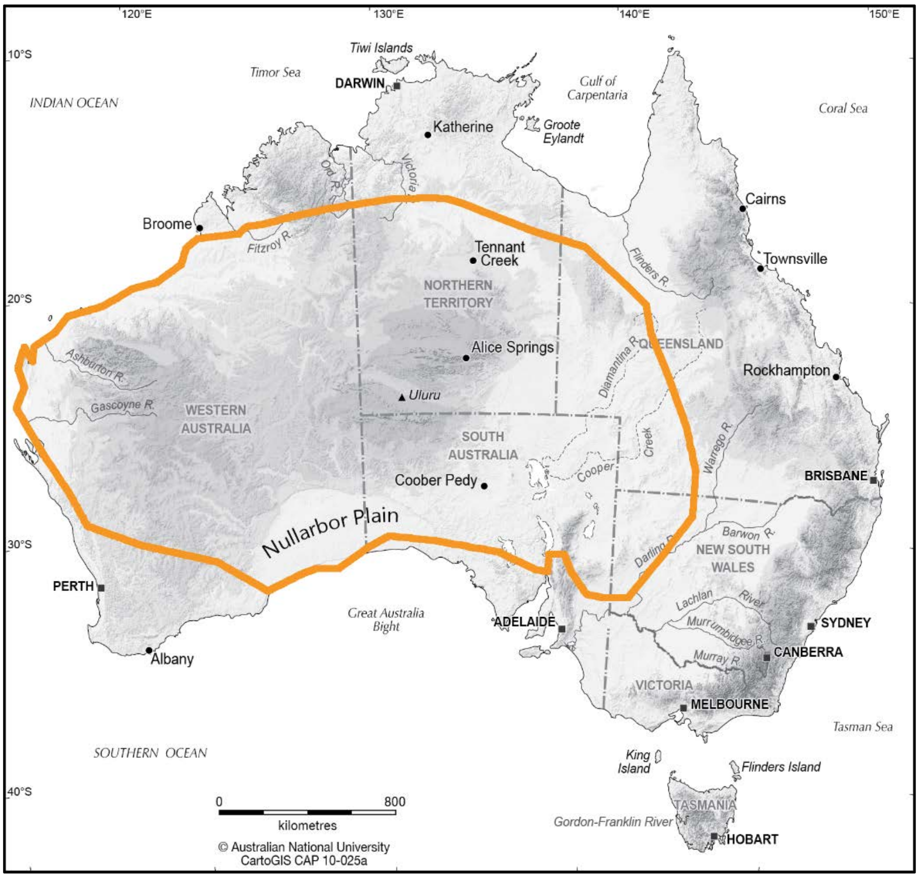
The Pleistocene and Holocene (11,700 years ago to present) also saw the spread of *Homo sapiens* throughout the globe (e.g. Groucutt *et al.* 2015; Stringer, 2016). The relative role of humans and climate change in continent-wide extinctions of megafauna is contentious, and has long been debated (Johnson 2002; Barnosky *et al.* 2004; Miller *et al.* 2005; Guthrie 2006; Dawson 2006; Barnosky and Lindsey 2010; Campos *et al.* 2010; Faith 2011; Field and Wroe 2012; Field *et al.* 2013; Murphy *et al.* 2012; Sandom *et al.* 2014; Jankowski *et al.* 2016; Johnson *et al.* 2016). The causes of Pleistocene extinctions will doubtless continue to be debated, but their scale is undisputed, and vertebrates that are alive in the Holocene must be understood as survivors of the extinction legacy that killed off so many species in the preceding geological epoch.

1.3.2 Australia during the Pleistocene

As on other continents, the Pleistocene was a time of climatic and ecological upheaval in Australia. The following section provides a brief overview of these changes as context for the fossil research presented in later chapters.

1.3.2.1 Aridification

Arid landforms dominate the Australian landscape today: the arid zone, defined by having average annual rainfall of 100–250 mm, covers around 70% of the continent (Byrne *et al.* 2008) (Figure 1.1). The late Pliocene into the Pleistocene saw an overall trend towards very dry conditions. There was an expansion of the arid landforms that dominate today, such as stony and sandy deserts in central Australia (Fujioka *et al.* 2005, 2009; Fujioka and Chappell 2010). Inland mega-lakes in the Eyre and Frome basins in central Australia, and the Murray-Darling basin in south-eastern Australia (McLaren and Wallace 2010; Webb 2010; Cohen *et al.* 2011; McLaren *et al.* 2012) were ultimately lost. This was the culmination of a longer-term trend towards aridification of the continent that began around 15 Ma during the Miocene as the continent drifted northwards (Byrne *et al.* 2008, 2011).



© Australian National University
CartoGIS CAP 10-025a

Figure 1.1: Approximate boundaries of the Australian arid zone (modified from map downloaded from CartoGIS Services, College of Asia & the Pacific, Australian National University, Canberra, 02/11/2017: http://asiapacific.anu.edu.au/mapsonline/base-maps/australia-0)

Unlike continents at higher latitudes, Australian aridity during the Pleistocene was not directly due to glaciation, which was minimal in extent (Barrows *et al.* 2001). Rather, the climate of Australia was affected indirectly by fluctuations in global temperature and atmospheric moisture, via changes in monsoon activity and sea-surface temperature. Although it is often generalised that Australia was more arid during glacial periods and moister during interglacial phases of the Pleistocene (Martin 2006), recent research has revealed spatial heterogeneity in climatic conditions across the continent. For example, the last glacial maximum ~26,000–18,000 years ago saw dry conditions prevail on the Swan Coastal Plain in south-western Australia (Lipar *et al.* 2017) but moist conditions in the Flinders Ranges in the mid-north of South Australia (Treble *et al.* 2017). The periodic filling of mega-lakes in central Australia occurred both during cold glacial and warm interglacial phases, in response to intensification or weakening of monsoonal conditions (Fu *et al.* 2017). Further, although there was an overall trend towards aridity during the Plio-Pleistocene, there were significant moist intervals as well, as detected by, for example, speleothem records (Goede *et al.* 1990; Ayliffe *et al.* 1998; Moriarty *et al.* 2000; Treble *et al.* 2017), lake sediment sequences (Fu *et al.* 2017; Kaal *et al.* 2014) and erosional features (Lipar and Ferk 2015). Many of the complexities of the Pleistocene climate of Australian are only beginning to be dissected.

1.3.2.2 Vertebrate fauna

The fossil record has revealed that during most of the Pleistocene, Australia was home to a suite of now-extinct vertebrates, many of them larger than any living relative. The vast majority of extinct taxa known from this time are marsupials, including iconic megafaunal species such as the 2.5-tonne wombat-like *Diprotodon optatum*, 230-kg short-faced kangaroo *Procoptodon goliah*, and the 100-kg carnivorous marsupial 'lion' *Thylacoleo carnifex* (Wroe *et al.* 1999; Wroe *et al.* 2004; Helgen *et al.* 2006). Extinctions among other vertebrate groups appear to have been more modest, but notable losses of non-marsupial taxa include the giant echidna *Zaglossus hacketti*, weighing 20 kg (Helgen *et al.* 2012), the snake *Wonambi naracoortensis* that reached five metres in length (Scanlon and Lee 2000), large crocodiles (Sobbe *et al.* 2013), and *Varanus priscus*, a giant monitor lizard (Wroe 2002). Only around ten to twelve species of bird are known to have gone extinct, including the two-metre tall galloanseriform bird *Genyornis newtoni*, weighing 275 kg (Murray and Vickers-Rich 2004). Extinct birds are reviewed in more detail below. Most extant vertebrate taxa were alive during the Pleistocene, and lived alongside the suite of extinct taxa.

1.4 The modern Australian avifauna

1.4.1 Scope

As background to the study of fossil birds that follows in later chapters, the following sections comprise a brief overview of the modern continental Australian avifauna. Birds from external territories such as Norfolk Island and the Australian Antarctic Territory are excluded, as are species that are only known as vagrants, and those that have been introduced to Australia since European colonisation. The emphasis is on landbirds, in particular the non-passerine orders, which are the focus of later chapters. Overlap between the avifaunas of New Guinea and Australia is acknowledged (see Schodde, 2006), but the diversity of the New Guinean avifauna is outside the scope of this review.

1.4.2 Taxonomy

This overview is based on the current checklist of Australian birds (Christidis and Boles 2008), which requires updating in light of taxonomic studies that have been published in the last decade, but is still a useful tool in its current form for assessing overall patterns of diversity among Australian birds. Some of the genera and species recognised by Christidis and Boles (2008) differ from those of Dickinson and Remsen (2013) and Dickinson and Christidis (2014), which are used in later chapters. However, the higher-level taxonomy of these authorities is similar, and the list of Christidis and Boles (2008) is convenient due to its geographical scope being limited to Australia.

1.4.3 Diversity

There are 21 orders, 87 families, 307 genera, and 678 species of bird currently resident in Australia (Christidis and Boles, 2008). The number of species within the 21 represented orders is highly uneven, ranging from over 300 species in the Passeriformes (perching birds/songbirds) to two species in the Phaethontiformes (tropicbirds).

The Passeriformes account for nearly half of all species (317 species; 47%). The other 20 orders, collectively referred to as non-passerines, account for the other half (361 species; 53%). Although the passerines and non-passerines contain similar numbers of species, the non-passerines have considerably higher combined diversity at higher taxonomic levels, with 51 families and 191 genera in the non-passerines, and 36 families, 116 genera in the passerines.

Some of the most speciose non-passerine orders (Figure 1.2) include the Anseriformes (ducks, geese, swans) (21 species), Columbiformes (pigeons and doves) (22 species), Ciconiiformes (e.g. pelicans, herons, ibis) (21 species), Accipitriformes (eagles, kites) (18 species), Gruiformes (rails, cranes, crakes) (17 species), and Psittaciformes (parrots and cockatoos) (52 species). The Charadriiformes (waders and shorebirds) are also very diverse, and excluding the two largely marine families in this order – the Stercorariidae (skuas and jaegers) and the Laridae (gulls and terns) – this order comprises some 61 species.

The most speciose family, the Meliphagidae (honeyeaters), comprises more than 70 species, and the Acanthizidae (heathwrens, gerygones, thornbills) contains 40. At the opposite extreme, there are 15 bird families both within the passerines and non-passerines that are represented by a single extant Australian species. In the case of two of these, the Plains-wanderer *Pedionomus torquatus* in the Pedionomidae and the Magpie-goose *Anseranas semipalmata* in the Anseranatidae, the lone species in each family has no close extant relative anywhere in the world.

At the generic level, 166 genera have only one extant species resident in Australia. Of these, more than 70% (118 genera/species) are non-passerines and just under 30% are passerines (48 genera/species). Thus, arguably, the non-passerine orders contain more taxa of unique conservation value.

Many of Australia’s nearly 700 bird species are further divided into sub-species. Excluding introduced taxa and vagrants, but including monotypic species and sub-species, Australia is home to nearly 1,300 bird taxa in total. Around 350 full species are endemic, but when sub-species are also included, more than 900 bird taxa are endemic to Australia (BirdLife Australia 2017). Of these endemics, around a third are non-passerines and around two-thirds are passerines.

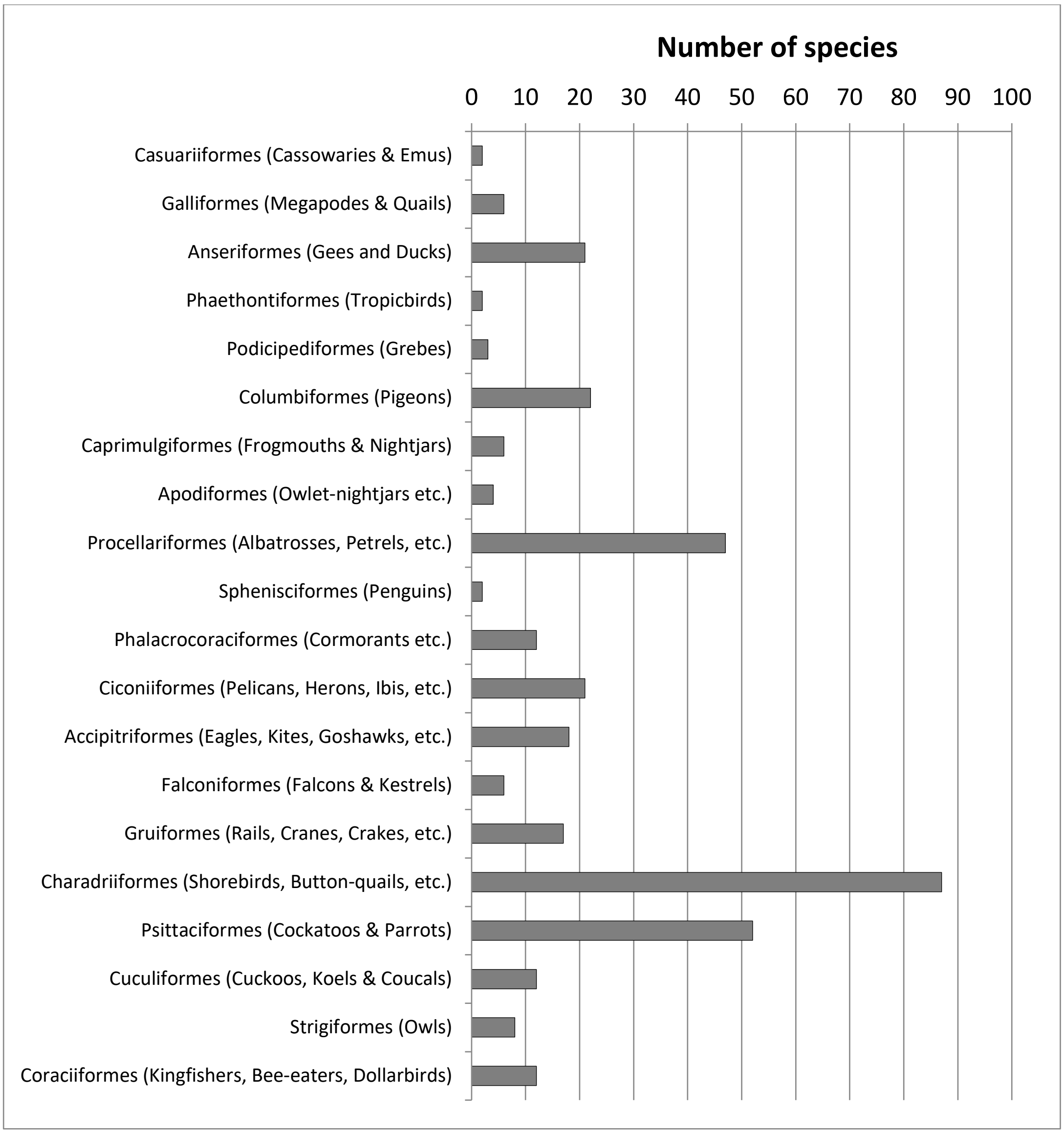


Figure 1.2: Species diversity within non-passerine orders of Australian birds (based on data in Christidis & Boles 2008)

1.4.4 Distribution

The Australian mainland covers an area of ~7.5 million square kilometres and though dominated by the arid zone (Figure 1.1), contains a diverse array of habitat types, from tropical rainforest, to savannah grassland, to alpine regions, to desert, to temperate woodland. Within these diverse biomes are a number of characteristic regional bird species assemblages, termed ‘avifaunulas’ (Schodde 2006). Remnant mesic habitats are confined to the north, east, south-east, and south-west of the continent, comprising a coastal and sub-coastal fringe, with major discontinuities in south-central Australia at the Nullarbor Plain, and along the west coast.

The modern biogeography of birds in Australia is structured mainly by moisture availability, which is closely tied to vegetation type and biomass. One analysis found that evapotranspiration, which captures both moisture and standing biomass, best explains modern patterns of bird diversity and distribution: diversity is concentrated around the more densely vegetated, mesic continental margins, while the arid zone contains approximately half the number of species (Figure 1.3) (Hawkins *et al.* 2005).

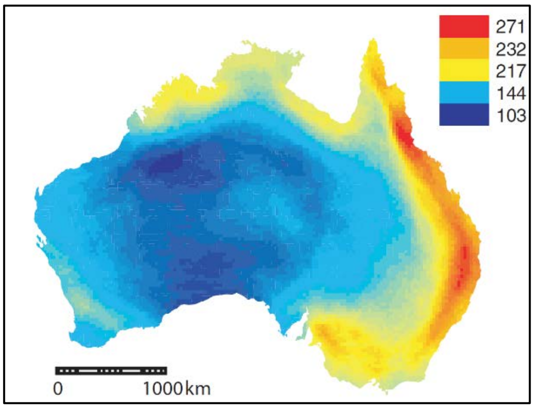


Figure 1.3: Contemporary distribution of bird species diversity on the Australian mainland (adapted from Hawkins et al. 2005). Numbers in the key represent the number of species found at each location.

Gradual drying of the continent since the second half of the Miocene (23–5.3 Myr ago) has concentrated more basal lineages of birds in remnant mesic habitats, while the expansion of the central arid zone has allowed the evolutionary radiation of younger, more derived lineages into the recently-formed arid biome in the middle of the landmass (Figure 1.4) (Hawkins *et al.* 2005; Byrne *et al.* 2008, 2011). Pertinent to the research presented later in this thesis, the south-central region of Australia, in which the Nullarbor Plain and the Thylacoleo Caves are located, contains one of the most highly derived avian assemblages on the continent at the level of family, as represented by orange-red colours in Figure 1.4. This indicates that the Nullarbor region has experienced higher turnover of avian families than most of the continent.

An 'arid' versus 'mesic' framework is useful for a broad understanding of how habitat types and the bird taxa they contain are distributed geographically, but within this are distinct regional assemblages. Schodde (2006) describes five avifaunulas (regional avifaunas) distributed through the Australian mainland, New Guinea, and Tasmania (Figure 1.5). Although they share species in common, each is characterised by certain endemic taxa or distinctive assemblages of species. The largest avifaunula is the Eyrean (Figure 1.5), which covers most of the central portion of the mainland, largely corresponding with the arid zone (Figure 1.1). The other avifaunulas – the Tumbunan, Irian, Torresian and Bassian/Mallee – are far smaller, and are more or less restricted to the higher-rainfall areas. The following sections briefly summarise the character of the five avifaunulas as defined and described by Schodde (2006).

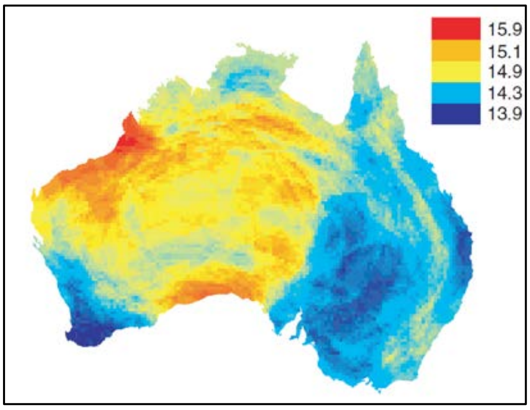


Figure 1.4: Contemporary distribution of basal and derived bird families on the Australian mainland (adapted from Hawkins *et al.* 2005). Relatively more basal families are represented in blue shades, and relatively more derived families in red shades. Numbers in the key represent mean root distance from the base of the bird phylogeny used in the original analysis.

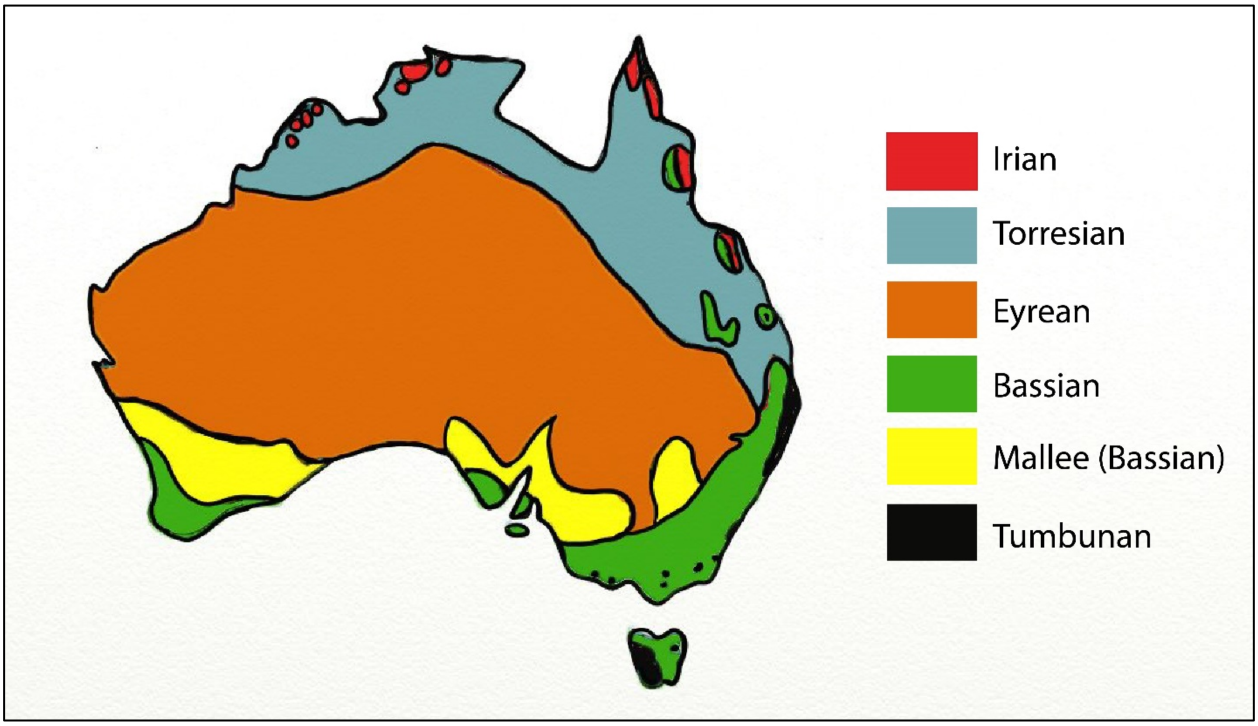


Figure 1.5: The modern avifaunulas of Australia (adapted from Schodde 2006)

The **Tumbunan** avifaunula comprises subtropical and temperate rainforests of Gondwanan origin on the east coast, Tasmania, and montane Papua New Guinea. The Australian area contains an assemblage of just over 50 species, with a high proportion of monospecific genera and ancient lineages, reflecting a history of repeated culling and contraction.

The **Irian** avifaunula, in northern Australia and Papuasia, contains mesophyll rainforest habitat. Its Australian extent comprises only very small isolated pockets of habitat in the Kimberley, Arnhem Land, and eastern Cape York Peninsula. It is the most diverse Australasian avifaunula with over 400 species, but most of these are in Papuasia. The Australian pockets contain 95 species, with low endemism. More non-passerines than passerines are present, with high diversity among pigeons, parrots, kingfishers, raptors, rails, megapodes, swifts and tree-swifts. Passerine diversity is mainly within the honeyeaters, monarchs, fantails, cuckoo-shrikes, and trillers.

The **Torresian** avifaunula comprises monsoonal woodlands with an overstorey of eucalypts and paperbark, spanning the whole of northern Australia as far south as the inland deserts, with outlying pockets in the Pilbara and upper Murray-Darling Basin, as well as New Guinea. Its vegetation is relatively uniform, with an understorey dominated by tall annual grasses, or *Triodia*/*Plechtrachne* hummock grassland on rocky outcrops. Around 90 species of bird inhabit this avifaunula. Passerines are the most diverse group, highest diversity being within the honeyeaters, estrildine finches, butcherbirds and woodswallows. Among non-passerines, most diversity is within the parrots and phabine pigeons. The Torresian avifaunula contains the most diverse guild of granivores in Australia, including the estrildine finches, four platycercine parrots, monospecific *Aprosmictus* (Red-winged Parrot), a number of species of cockatoo, and three species of button-quail. Endemism is high, much of it at the genus level, indicating antiquity of its lineages. Endemic taxa include the Magpie-goose *Anseranas semipalmata*, two raptors, the ground-pigeons, grass parrots in the genus *Psephotellus*, several honeyeaters, a mudnester, a bowerbird, and two grass-finches.

The **Bassian** avifaunula comprises scleromorphic temperate forests and woodlands in south-west Western Australia, south-eastern Australia and Tasmania, with pockets of habitat stretching north through the Great Dividing Range as far as tablelands in north-eastern Queensland. It includes a sub-zone of **Mallee** habitat in southern Australia, which is dominated by low, multi-stemmed *Eucalyptus* trees and sand-plain heath. The assemblage comprises 145 core species, and is rich in nectarivores, ground- and foliage-feeding insectivores, and granivores. Bassian habitats are interrupted by the arid zone along the south-central coast in the region of the Nullarbor Plain. In the south-west corner of Western Australia, the Bassian assemblage holds 65 core species, with high levels of endemism (15 species; 22 sub-species). In South Australia, including the Mount Lofty and Flinders Ranges, the Bassian zone is relatively rich in species (78), and whilst low in endemic species, it hosts 40 endemic sub-species. Tasmania and the Bass Strait islands hold 12 endemic species and 45 endemic sub-species. The south-eastern mainland holds 95 Bassian species with only 10 endemics, but does contain old relictual taxa. Queensland has 48 core Bassian bird species, none of which is endemic, but has 20 endemic sub-species. The Mallee regions intermingle with the Eyrean avifaunula, with 65% of birds in the mallee being of Bassian origin, and 14 being endemic or nearly so.

The **Eyrean** avifaunula covers most of the arid interior. Habitat includes mulga (*Acacia* woodland), spinifex dune deserts and dry stony ranges. Though vast in area, the Eyrean is low in species relative to its size. It has 82 core species, many with Bassian affinities, although some have their origins in the Torresian zone, and many of its species are widespread throughout Australia. Most Australian bird families have representatives in the Eyrean zone. Greatest diversity is seen in the parrots, honeyeaters, acanthizid warblers, and malurid wrens. Its endemics are mostly old, monospecific genera, with 70% of these being represented by a single species.

1.4.5 Conservation status

Thus far, humans appear to have had much less of an adverse impact on the diversity of Australian birds than they have had on mammals during the Quaternary. However, very little is known about what impacts 50,000-plus years of Aboriginal inhabitation had on the continent's birds prior to European arrival. In part this is because the baseline diversity and distribution of Australian birds prior to the arrival of humans in the Late Pleistocene is poorly understood based on the fossil record, making any impacts difficult to detect. At least two extinct species of bird are suspected to have overlapped temporally with humans during the late Pleistocene, and there is circumstantial evidence that humans may have contributed to their decline. Bones of the giant galloanseriform *Genyornis newtoni* have been found in a deposit with stone tools at Cuddie Springs in New South Wales (Fillios *et al.* 2010), but the contemporaneity of the bones and tools at the site has been questioned (Grün *et al.* 2010). Thus, there is only tenuous evidence that humans may have contributed to the decline of this species, and the chronology of its extinction is unknown. Archaeological evidence shows that people consumed the eggs of a large but unidentified species of large megapode prior to its apparent extinction around 47,000 years ago (Grellet-Tinner *et al.* 2017; Grellet-Tinner *et al.* 2016; Miller *et al.* 1999, 2016, 2017) (see Chapter 3 for a discussion of the identity of the species involved).

Around ten other species of bird are known to have gone extinct during the Pleistocene (see Section 1.5.3), but their remains are generally scarce, lack good temporal constraint, and have not been found in archaeological contexts, so there is no evidence for temporal overlap with humans. Future archaeological discoveries may reveal Pleistocene bird extinctions that were caused by humans, but there is currently no evidence, even circumstantial, for a major human-mediated extinction of birds in Australia during the Pleistocene or Holocene. It must be borne in mind that approximately 2.53 million years of the Pleistocene had elapsed before humans entered the continent 50,000-plus years ago.

So far, the number of avian extinctions since European colonisation of the continent has been low. Of the species listed by Christidis and Boles (2008), only one, the Paradise Parrot *Psephotellus* (=*Psephotus*) *pulcherrimus*, is thought to have gone extinct since European colonisation of the continent began in earnest in the late 18th Century, with no verified sightings of the species since 1927 (Garnett *et al.* 2011). Insular dwarf emus were extirpated from Kangaroo Island, Tasmania and King Island, but they were likely conspecific with the extant mainland Emu *D. novaehollandiae* (Heupink *et al.* 2011; Thomson *et al.* 2018). By contrast, around 30 species of Australian land mammal – more than 10% of the pre-European fauna – has been extirpated since the 18th Century (Woinarski *et al.* 2015). Many more bird taxa are now under threat (Garnett *et al.* 2011), but to date they have proven more resilient in the face of habitat clearance and introduced predators than have mammals. This pattern echoes the Pleistocene fossil record, which shows high losses of genera and species occurred among mammals, but with little evidence for similar losses among birds.

1.5 Pleistocene fossil record of Australian birds

1.5.1 Quality of the fossil record

The modern Australian avifauna is well defined in terms of diversity and distribution, but we currently lack a thorough understanding of the timeframe over which the Holocene avifaunulas took on their current structure and composition. The fossil record for most living Australian birds is poor to non-existent, and even though most were presumably extant during the Pleistocene, due to the limitations of the fossil record we do not know where most species lived and when, and with what other taxa they co-existed.

Many sites throughout Australia have yielded Pleistocene bird fossils, but most lack diversity. Baird *et al.* (1991) listed 90 localities and 188 individual sites from which Pleistocene and/or Holocene bird fossils were known: 17 in New South Wales, 11 in Queensland, 28 in South Australia, 11 in Tasmania, 12 in Victoria, and 11 in Western Australia. Mean diversity from these sites is just 3.9 species, with many reported to contain one or two species of bird, often *Genyornis newtoni* or *Dromaius novaehollandiae*. This may be due to a preservation bias against smaller species, or bones of these very large species may simply have been the most obvious, recognisable and identifiable by non-specialists.

Eighteen Quaternary-aged fossil deposits (Figure 1.6) have yielded a more substantial avian component of ten or more species (Table 1.1). All but one of these sites are caves in southern Australia, and most are in the mesic zone. Bird fossils, including those of extinct species, have been collected from various arid-zone sites, particularly in the Lake Eyre Basin, but these localities typically have low taxonomic diversity and represent mainly aquatic taxa (Baird *et al.* 1991). Diverse fossil avifaunal assemblages, and assemblages representing landbirds other than dromornithids or emus, are essentially lacking for the north of the continent and for almost the entire arid zone, severely limiting knowledge about the diversity and distribution of landbirds across the continent during the Pleistocene.

Figure 1.6: Pleistocene and Holocene localities that have yielded 10 or more bird taxa

1.5.2 Extant taxa

On the whole, the most diverse fossil avifaunas (Table 1.1) have yielded species assemblages fairly congruent with modern species distributions, but have also provided evidence of range changes for some extant taxa. Significant examples include: a major south-westerly range extension for two genera, *Centropus* (coucals) and *Orthonyx* (logrunners) (Baird 1985); a southern extension for *Atrichornis rufescens* (Rufous Scrub-bird) (Baird 1993); a major south-west range extension for *Pezoporus occidentalis* (Night Parrot) (Baird 1986), and an extension for the Ground Parrot *Pezoporus wallicus* onto Kangaroo Island off the South Australian coast (Hope *et al.* 1977). Evidence from various sites in southern and eastern Australia show that the extant flightless Tasmanian Swamphen *Tribonyx mortierii*, which is now restricted to Tasmania, was widespread on the Australian mainland during the Pleistocene (Baird 1984).

Table 1.1: Diverse Quaternary fossil avifaunas of Australia (listed from west to east). Early and Middle Pleistocene deposits are in bold type. See map in Figure 1.6 for locations.

Site	Locale	Age	No. taxa	Reference
Devil's Lair	Witchcliffe, south-west Western Australia	Late Pleistocene	26	Baird (1991)
Skull Cave	Augusta district, south-west Western Australia	Holocene	10	Baird (1991)
Thylacoleo Caves	**Nullarbor Plain, Western Australia**	**Early, Middle and possibly Late Pleistocene**	**~18**	Prideaux *et al.* (2007)
Madura Cave	Nullarbor region, Western Australia	Late Pleistocene/ Holocene	15	Baird *et al.* (1991); Baird (1986)
Koonalda Cave	Nullarbor region, South Australia	Late Pleistocene	29	Baird, 1986; Baird *et al.*, 1991)
Weekes Cave	Nullarbor region, South Australia	Unknown	10	Baird (1990); van Tets (1974)
Mairs Cave	Flinders Ranges, South Australia	Pleistocene	12	Baird (1991)
Seton Rock Shelter	Kangaroo Island, South Australia	Late Pleistocene/ Holocene	33	Hope *et al.* (1977)
Victoria Fossil Cave	**Naracoorte, South Australia**	**Middle/Late Pleistocene**	**17**	Ayliffe and Veer (1988); Moriarty *et al.*, (2000); van Tets and Smith (1974)
Blanche Cave	Naracoorte, South Australia	Late Pleistocene	19	Laslett (2006), unpub.
Green Waterhole Cave	Tantanoola, south-east South Australia	Possibly Late Pleistocene	16	Baird (1985); Baird (1991)
Amphitheatre Cave	Glenelg River district, south-western Victoria	Holocene	21	Baird (1992)
Curran's Creek Cave	Glenelg River district, south-western Victoria	Unknown, possibly Late Pleistocene and Holocene	16	Baird (1986); Baird *et al.* (1991)
McEachern's Cave	Glenelg River district, south-western Victoria	Late Pleistocene/ Holocene	11	Baird *et al.* (1991)
Pyramids Cave	Buchan district, eastern Victoria	Late Pleistocene	19	Baird (1993); Baird *et al.* (1991)
Clogg's Cave	Buchan district, eastern Victoria	Late Pleistocene/ Holocene	55	Baird (1986); Baird *et al.* (1991)
Mabel Cave	Buchan district, eastern Victoria	Unknown, possibly early Holocene	46	Baird (1986); Baird *et al.* (1991)
Mt Etna	**Rockhampton, Queensland**	**Middle to Late Pleistocene**	**~23**	T. Worthy, *pers. comm.* 11 April 2013; Hocknull *et al.* (2007)

It is noteworthy that two of the species for which range changes have been identified are of conservation concern today: *Atrichornis rufescens* and *Pezoporus occidentalis* are both classed as Endangered (Garnett *et al.* 2011). Furthermore, *Pezoporus wallicus*, which went extinct in South Australia in the 20th Century, was not recorded on Kangaroo Island in historic times. Such examples show the potential value of using the fossil record to indicate the historic ranges of extant bird taxa, including those that are of conservation concern. This information could be used to identify patterns of decline in response to ecological change, and could be used in conservation programs including translocations, as has been suggested for mammalian taxa in similar contexts (McDowell and Medlin 2010).

1.5.3 Extinct species

Over the last 150 years, the Australian fossil record has revealed only around ten to twelve species of extinct bird from the Pleistocene, with the exact number difficult to determine due to taxonomic uncertainty about several of the described species. Those known or suspected to have gone extinct are: the giant galloanseriform *Genyornis newtoni*; either one or two species of megapode in the genus *Progura*, which were larger than any living relative (De Vis 1888; van Tets 1974; Boles 2008; but see Chapter 3); possibly dwarf emus (see above); a flamingo *Phoenicopterus ruber* from central Australia, which is still extant in the Americas, Africa and Europe (Rich *et al.* 1987); a palaelodid *Palaelodus wilsoni* from central Australia (Baird and Vickers-Rich 1998); a giant flightless coucal, *Centropus colossus*, which was larger than any living relative, and is known from one site in south-eastern Australia (Baird 1985); a pilotbird *Pycnoptilus fordi*, which is the smallest extinct Pleistocene species described to date (Baird 1993); a pelican *Pelecanus proavus*, from the Darling Downs in south-eastern Queensland (Rich and van Tets, 1981), which may be conspecific with extant *P. conspicillatus* (Boles 2006); and two species of logrunner, *Orthyonyx hypsilophus* and *O. wakefieldi*, from two different localities in south-eastern Australia (Baird 1985; Baird 1993). A further species, a giant eagle from Green Waterhole Cave, was noted by Baird (1985) but has not yet been formally described. A number of other extinct species of bird from the Pliocene and Pleistocene were described by Charles De Vis in the late 19th and early 20th Centuries, but most have since been synonymised with extant species or are taxonomically suspect (e.g. Olson, 1975, 1977; van Tets and Vickers-Rich, 1980, 1990; Boles, 2006, 2010).

With the exception of the extinct pilotbird *Pycnoptilus fordi* and one of the logrunners (*O. wakefieldi*), all the extinct Pleistocene bird taxa that have been described, plus the undescribed eagle, are relatively large taxa, and several (*G. newtoni*, *Progura* spp., *C. colossus*, *O. hypsilophus* and *P. fordi*) are larger than their closest living relatives. Boles (2006) commented that the large size of extinct Australian bird taxa may have been overemphasised due to preservation bias in favour of large bones, compounded by palaeontologists' preferences for studying large species. It could well be the case that small extinct species have been overlooked to date. Aquatic and weak-flighted ground-dwelling birds are over-represented among the extinct taxa, possibly due to preservation biases towards aquatic taxa and ground-dwelling taxa (Baird 1991; Boles 2006). However, aquatic and ground-dwelling taxa may have been particularly adversely affected by palaeoecological upheavals during the Pleistocene: aquatic taxa by the drying of inland lakes; and ground-dwelling taxa by the disappearance of dense canopy and associated understorey vegetation as mesic vegetation contracted.

Time may tell whether the observed patterns of extinction are truly representative of the bird taxa that were lost from Australia during the Pleistocene. On present evidence, notably few birds appear to have gone extinct during this time, in stark contrast to the catastrophic loss of mammalian taxa during the Pleistocene that has been revealed by the fossil record. However, sites preserving well-studied, diverse Pleistocene avifaunas are few, and are concentrated in the southern mesic margins of the continent (see Figure 1.6). A non-aquatic avian fossil record for the arid interior, and for the north of the continent, is almost entirely lacking.

Individual extinct species are discussed in more detail below, but in terms of the significance of the fossil deposits from which they have been described, it is important to note that some of the high-diversity sites have produced multiple new species of bird: Pyramids Cave in eastern Victoria produced two (Baird *et al.* 1991; Baird 1993) and Green Waterhole Cave in south-eastern South Australia produced three (Baird 1985; Baird *et al.* 1991). Presence of multiple extinct species at these sites may indicate that greater than average avifaunal turnover occurred within these localities, but it is also possible – and perhaps more likely – that Pleistocene avian extinctions occurred elsewhere but have not been detected via the fossil record. In support of this notion, it was only by chance that the two species from Pyramids Cave were discovered, as all bird postcranial fossils from this site were originally earmarked for destructive radiocarbon dating, and only survived because of the untimely death of their collector (Baird 1993).

One cannot help but wonder what other significant bird fossils may have been destroyed, overlooked, or discarded over the course of decades due to their perceived lack of taxonomic value. Historically, birds have received much less attention than mammals in studies of key Australian vertebrate fossil assemblages. Virtually nothing has been published on fossil birds from the Wellington Caves in New South Wales, in contrast to the marsupials (Dawson 1985), and those from caves in the Naracoorte region have only received relatively cursory investigation to date (van Tets and Smith 1974).

This is unfortunate, both in terms of understanding the development of the modern avifauna, and in terms of reconstructing the Pleistocene ecology of Australia more generally. Bird fossils in particular have been noted for their potential for reconstructing Australian Quaternary palaeoenvironments, because a high percentage of their skeletal remains can be identified to genus or species level, and their habitat preferences and tolerances are generally well understood (Baird 1989). Further study of sites with long sediment sequences, such as Cathedral Cave, Wellington, may yet reveal diverse avifaunal assemblages, as may further analysis of relatively neglected fossil avifaunas such as those from Naracoorte.

1.5.4 Temporal representation

A major deficiency in the Pleistocene fossil record of Australian birds is the paucity of deposits from the Early and Middle Pleistocene, which together account for 95% of the duration of the epoch. In part this is probably due to the historical impossibility of direct-dating fossil deposits older than the 50,000-year limit of radiocarbon dating, and the related tendency to label any fossil deposit containing extinct megafaunal marsupials as 'Late Pleistocene' in the absence of dates (Prideaux 2007). Regardless of cause, a lack of fossils from these sub-epochs severely hampers the reconstruction of the recent continental history of the Australian avifauna. Most Quaternary sites that have yielded diverse fossil avifauna are known, or are estimated, to date either to the Late Pleistocene or the Holocene (Table 1.1).

Only three diverse Pleistocene fossil avifaunas are known to pre-date the Late Pleistocene: Victoria Fossil Cave, near Naracoorte in south-eastern South Australia; Mt Etna in central-eastern Queensland; and the Thylacoleo Caves on the Nullarbor Plain (see Table 1.1 and Figure 1.6). One further site, Rackham's Roost, at the Riversleigh locality in northern Queensland, may include the Early Pleistocene, but only eight bird taxa have so far been documented from this site (Nguyen *et al.* 2016).

The fossil-bearing deposit in the main chamber of Victoria Fossil Cave, Naracoorte, was discovered in 1969 (Reed and Bourne 2000). Various chambers of the cave were later dated to the Middle and Late Pleistocene, with the oldest-known parts of the deposit dated in the later part of the Middle Pleistocene, at >213 kyr (Ayliffe and Veer 1988; Moriarty *et al.* 2000). The systematic palaeontology of the avifauna from this cave comprises a brief three-page account of 17 taxa based on 55 specimens (van Tets and Smith 1974). The time-averaged Pleistocene species assemblage was interpreted as representing "savannah woodland, substantial areas of heath, wet and dry grassland and mudflats". Aside from the systematic palaeontology of the assemblage by van Tets and Smith (1974), which has largely been replicated as-is in later publications (e.g. Moriarty *et al.* 2000; Reed and Bourne 2000) the only other substantial account that has been published arising from the Victoria Fossil Cave bird assemblage was the description of a new extinct species of giant megapode, *Progura naracoortensis*, based on fossils from Victoria Fossil Cave and other caves in the Naracoorte area and in eastern Australia (van Tets 1974), and later revision of the taxonomy of this species by Christidis and Boles (2008) (see Chapter 3).

The Mt Etna deposits have yielded over 20 species of bird from more than 300 specimens (T. Worthy, pers. comm. 11 April 2013). However, the systematic palaeontology of the avifauna has not been published to date, and birds were not incorporated into the interpretation of the Middle Pleistocene palaeoecology of the locality by Hocknull *et al.* (2007). A brief summary in Hocknull (2009) lists only four taxa, those being *Coturnix*, *Turnix*, Strigiformes and Passeriformes.

The avifaunal component of the Thylacoleo Caves assemblage, which is the subject of the research presented later in this thesis, has not been extensively studied to date (see Prideaux *et al.* 2007). Composition of the fauna as at 2007 is described below (see Sections 1.7.5 and 1.7.6), but in summary, a minimum of 18 bird taxa were identified, and the Middle Pleistocene assemblage was interpreted as representing an arid- to semi-arid open woodland/shrubland habitat. The assemblage was time-averaged, and has not yet been subject to a temporal analysis. The present research will address the systematics of the birds in the deposit, and will include a temporal analysis of the Leaena's Breath Cave assemblage. In terms of the temporal significance of the deposit, the Thylacoleo Caves fauna, specifically the assemblage from Leaena's Breath Cave, is the first – and so far only – cave deposit in Australia to preserve a fossil avifauna that spans both the Early and Middle Pleistocene. Following further excavation of the caves, the locality thus provides an unprecedented opportunity to investigate the diversity and distribution of landbirds in southern Australia during this severely under-represented window of time.

1.5.5 Previous studies of fossil birds in the Nullarbor region

Twelve Quaternary fossil deposits from the Nullarbor region have previously been documented, primarily by Robert F. Baird in his PhD thesis (Baird 1986) and associated publications. Diversity of fossil birds in these deposits ranged from one to 29 taxa (Table 1.2).

The combined fossil bird record for Baird's Pleistocene and Holocene sites, includes representatives of 13 orders, ≥25 families (≥14 non-passerine families; ≥11 passerine families), ≥35 genera, and ≥39 species. This is similar to the number of bird taxa recorded locally in modern surveys (Burbidge *et al.* 1987). Almost all the identified taxa are present in the region today, with a few exceptions. A species of spoonbill *Platalea* sp., a partial skeleton of which was found in Weekes Cave, was originally interpreted by van Tets (1974) as indicating that moister conditions prevailed in the Nullarbor region in the past, but (Baird 1990) considered it more likely to be an individual that was attracted to flooded claypans after heavy rainfall.

Other fossil bird taxa with no modern record from the Nullarbor region were: Regent Parrot *Polytelis anthopeplus* from the Late Pleistocene deposit in Koonalda Cave, South Australia, a species that today inhabits woodlands in south-western and south-eastern Australia; Night Parrot *Pezoporus occidentalis*, probable remains of which were found in the Late Pleistocene deposit in Madura Cave, Western Australia, an endangered arid-zone species not previously recorded in south-central Australia; and Thick-billed Grasswren *Amytornis textilis* from Koonalda and Madura Caves, which at the time that Baird (1986) was writing was not known to inhabit the Nullarbor, but was observed during surveys shortly thereafter (Burbidge *et al.* 1987).

Notably, no extinct species were recorded from any Late Pleistocene or Holocene site, despite the fact that some of the deposits contained remains of now-extinct marsupial fauna, including *Sarcophilus harrisii* (Tasmanian Devil), *Thylacinus cynocephalus* (Thylacine) and *Thylacoleo carnifex* (Marsupial Lion) (Lundelius and Turnbull 1978). Insofar as the fossil deposits are representative of the regional avifauna, the presence mainly of taxa that are resident today, and the absence of extinct species, seems to indicate that the avifauna of the Nullarbor region has been relatively stable during the Late Pleistocene and Holocene.

1.6 Geological and biological setting of this study

1.6.1 Defining the Nullarbor Plain

The Nullarbor Plain is an arid limestone plain with its southern edge abutting the south-central coast of Australia, straddling the Western Australian/South Australian border. In the literature and in common parlance the name 'Nullarbor' is often applied to the entire onshore portion of the limestone Eucla Basin (Figure 1.7), and the current national conservation framework refers to the entire area as the Nullarbor Bioregion (Commonwealth of Australia 2012).

In the stricter sense, the Nullarbor Plain refers only to the central portion of the Eucla Basin (Figure 1.8), and is characterised by absence of trees and the dominance of low, chenopod shrubland. The other Nullarbor physiographic regions differ in soil and topography (Lowry and Jennings 1974), and are somewhat better vegetated. In this thesis, the term Nullarbor Plain (both words capitalised) is used to refer only to the central, treeless plain (Figure 1.8). The term Nullarbor region is used to refer to the onshore portion of the Eucla Basin more generally, and the term Nullarbor bioregion refers to the area defined in the national conservation framework (Commonwealth of Australia, 2012).

1.6.2 Geology of the Nullarbor region

The onshore portion of the Eucla Basin, a vast limestone plateau covering an area of approximately 240,000 km^2, is the largest areal karst landscape in the world (Miller *et al.* 2012). Most of the plateau consists of a layer of Miocene limestone approximately 20 to 35 metres thick, which was deposited on top of earlier Miocene, Oligocene and Eocene sediments (Doerr *et al.* 2011; Burnett *et al.* 2013). Tectonic uplift and falling sea-levels during the middle Miocene exposed the platform approximately 14–15 Myr ago, and it has remained exposed ever since (O'Connell *et al.* 2011; Miller *et al.* 2012).

Despite its long exposure to weathering processes, the Nullarbor region is regarded as a poorly-developed karst landscape because of its limited array of surface and subterranean features (Webb & James 2006).

Table 1.2: Taxonomic representation of birds in the fossil record of the Nullarbor region (from data in Baird et al. 1991; updated with current nomenclature)

Order	Family	Genus and species	Common name	Madura	Koonalda	Weekes	Abrakurrie	Bildoolja	Horseshoe	Koomooloobuka	New	Old Homestead	Thylacine Hole	Warbla	Weebubbie
Galliformes	Phasianidae	*Coturnix* sp.	Quail, indeterminate species		X										
Anseriformes	Anatidae	Indet.	Duck, indeterminate species		X										
Ciconiiformes	Threskiornithidae	*Platalea* sp.	Spoonbill, indeterminate species			X									
Accipitriformes	Accipitridae	Accipitridae	Eagle/hawk, inditerminate species												X
		Accipiter fasciatus	Brown Goshawk			X									
		Accipiter sp. cf. *fasciatus*	Goshawk, cf. Brown Goshawk		X										
		Accipiter cirrocephalus	Collared Sparrowhawk		X						X				
		Circus sp.	Harrier, indeterminate species		X										
Falconiformes	Falconidae	Indet.	Falcon, indeterminate species											X	
		Falco berigora	Brown Falcon		X								X		
		Falco cenchroides	Nankeen Kestrel		X	X							X		
Columbiformes	Columbidae	*Phaps elegans*	Brush Bronzewing		X										
		Geopelia, cf. *striata*	Peaceful Dove							X					
		Ocyphaps lophotes	Crested Pigeon	X	X										
Caprimulgiformes	Eurostopodidae	*Eurostopodus argus* (=*Caprimulgus guttatus*)	Spotted Nightjar		X										
Apodiformes	Aegothelidae	*Aegotheles cristatus*	Australian Owlet-nightjar	X									X		
Charadriiformes	Charadriidae	Charadriidae indet.	Plover/dotterel/lapwing, indeterminate species	X											
	Scolopacidae	*Calidris* sp.	Sandpiper/stint, indeterminate species	X											

	Turnicidae	*Turnix* sp.	Buttonquail, indeterminate species						X					
		Turnix sp., cf. *velox*	Button-quail, cf. Little Button-quail	X	X	X		X		X				
		Turnix varia	Painted Button-quail	X										
Psittaciformes	Indet.	Indet.	Parrot/cockatoo, indeterminate species				X			X				
	Psittacidae	*Polytelis anthopeplus*	Regent Parrot		X									
		Melopsittacus undulatus	Budgerigar	X	X									
		Northiella haematogaster (=*Psephotus haematogaster*)	Blue Bonnet		X									
		Neophema sp. cf. *splendida*	Neophema parrot, cf. Scarlet-chested Parrot		X									
		Pezoporus occidentalis (=*Geopsittacus occidentalis*)	Night Parrot	X										
		Indet.	Parrot, indeterminate species				X	X						
Cuculiformes	Cuculidae	*Chrysococcyx* sp.	Cuckoo, indeterminate species		X									
		Chalcites basalis	Horsfield's Bronze-cuckoo			X				X				
Strigiformes	Tytonidae	*Tyto "alba"*	Barn owl, indeterminate species		X								X	
		Tyto novaehollandiae	Masked Owl		X	X							X	
Passeriformes	Maluridae	*Amytornis textilis*	Thick-billed Grasswren	X	X									
		Amytornis sp.	Grasswren, indeterminate species					X		X				
	Acanthizidae	*Acanthiza chrysorrhoa*	Yellow-rumped Thornbill	X										
		Acanthizidae indet.	Thornbill or Heathwren species	X										
	Meliphagidae	cf. *Lichenostomus virescens*	Honeyeater, cf. Singing Honeyeater	X	X									
		Indet.	Honeyeater, indeterminate species		X	X								
	Pomatostomidae	*Pomatostomus superciliosus*	White-browed Babbler	X										
	Psophodidae	*Psophodes* sp. (=*Sphenostoma* sp.)	Wedgebill, indeterminate species		X									
		Cinclosoma cf. *alisteri*	(Nullarbor) Quail-thrush	X	X			X		X				
	Pachycephalidae	cf. *Oreoica gutteralis*	Crested Bellbird		X					X				

	Colluricincla sp. cf. *harmonica*	Grey Shrike-thrush	X											
Artamidae	*Artamus cinereus*	Black-faced Woodswallow		X										
	Artamus sp.	Woodswallow, indeterminate species	X		X				X					
Megaluridae	*Cincloramphus cruralis*	Brown Songlark		X										
	cf. *Cincloramphus*	Songlark/grassbird, indeterminate species		X										
Hirundinidae	Indet.	Swallow/martin, indeterminate species		X			X							
Estrildidae	*Taenopygia guttata* (=*Poephila guttata*)	Zebra Finch			X									
Motacillidae	*Anthus novaeseelandiae*	Australasian Pipit		X										
Indet.	Indet.	Unknown song-bird			X			X		X	X			X
		Total no. species	**16**	**29**	**10**	**1**	**4**	**2**	**8**	**2**	**1**	**5**	**1**	**2**

Figure 1.7: Boundaries of the onshore portion of the Eucla Basin (outlined in white) (satellite image downloaded from Google Maps https://www.google.com.au/maps 08/11/2017)

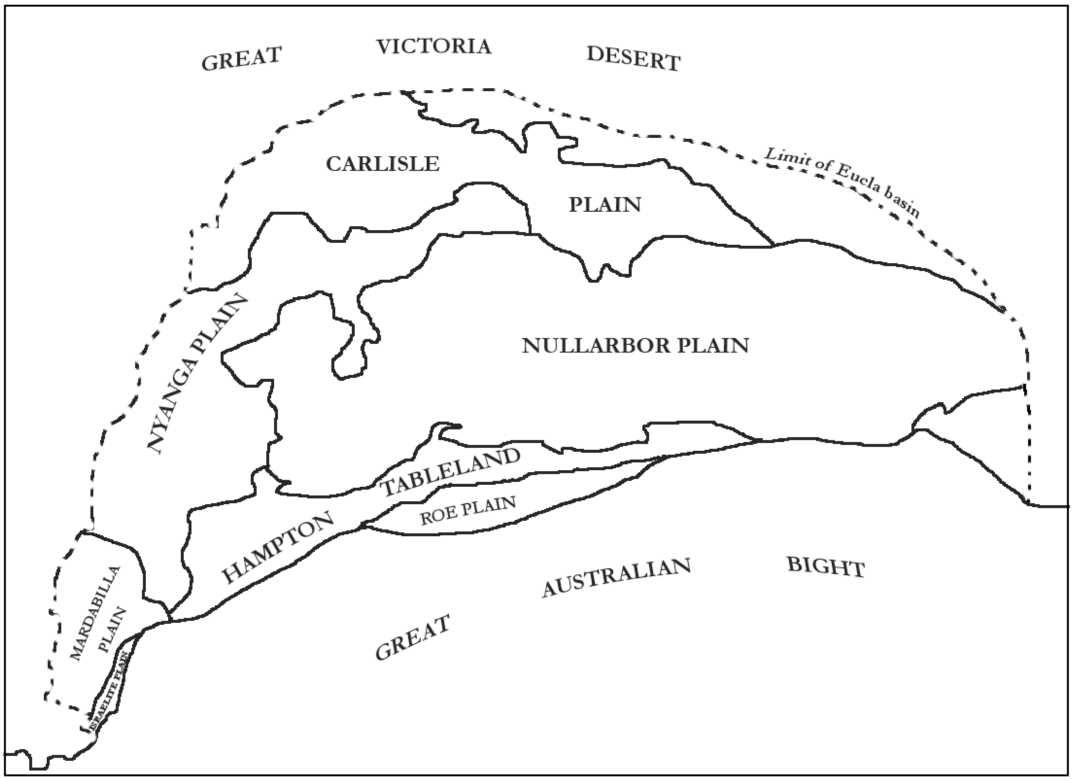


Figure 1.8: Physiographic regions of the Eucla Basin, showing the location of the Nullarbor Plain (modified from Lowry and Jennings, 1974)

The plateau is very flat, with a surface relief of less than 10 m (Gillieson *et al.* 1994). The region as a whole is remarkably evenly weathered, implying that for most of its history it has been relatively dry with a modest vegetation cover and virtual no tectonic activity (Lowry and Jennings 1974).

The landscape has few prominent surface features, and consists mainly of a low, undulating plain, where rocky ridges alternate with shallow, clay-filled depressions or 'dongas' (Miller *et al.* 2012). Much of the limestone surface is hard-capped with calcrete (Lowry and Jennings 1974) overlain by shallow red calcareous soils that average <1 m in depth. The rocky ridges typically have a shallow (<40 cm) gravelly loam soil covering; the sloping transition zone between ridges and depressions have well-drained clay-loams to sandy loam soils with a gravel lag on the surface; and the claypans have deeper (50–100 cm) clay loams and light clays (Gillieson *et al.* 1996). The elongate, clay-lined depressions may be of considerable extent, ranging from a few to several hundred hectares (Gillieson *et al.* 1996). The entire Nullarbor region lacks significant modern watercourses and has no bodies of permanent water (Lowry and Jennings, 1974).

Belowground, the Nullarbor region has thousands of caves (Gillieson *et al.* 1996), some as much as 30 km in length and others up to 150 m deep (Webb and James 2006), but the number of large caves is low relative to the area of the plain, and most caves are relatively small (Burnett *et al.* 2013). Most of the large caves lie close to the coast, with some deep enough to sit below the water table, and so contain underground lakes and extensive flooded passages (Webb and James, 2006). There is virtually no active speleothem formation in Nullarbor caves today due to low available moisture and limited soil organic content. To date, no calcite speleothems from caves in the region have been dated to younger than about 400 kyr (Middle Pleistocene) (Goede *et al.* 1990; Prideaux *et al.* 2007; Sniderman *et al.* 2016). Pertinent to the present study, a speleothem from Leaena's Breath Cave, from which most of the fossils examined in this study were excavated, was found to have formed around 4 Myr ago during the early Pliocene (Woodhead *et al.* 2006).

Though large caves are few, the Nullarbor is pocked with smaller features termed blow-holes, of which tens of thousands are estimated to exist (Doerr *et al.* 2011). These vertical shafts of a few tens of centimetres up to two metres across have strong reversing draughts in response to changes in barometric pressure. An investigation of more than 600 blowholes found that their location is uncorrelated with surface topography, and that they formed by subterranean domes (cupolas) inside caves and passages breaking through to the surface, rather than having formed by surface dissolution from water run-off on the land surface (Doerr *et al.* 2011).

One of the most remarkable characteristics of the region today is its lack of surface water. Following heavy storms, water briefly ponds in surface depressions, and short streams flow into dolines but there are no permanent water bodies (James *et al.* 2012). Mean rainfall grades inland from approximately 200–300 mm a year near to the coast, to around 100–200 mm a year further inland (Bureau of Meteorology data, accessed 13/10/2017 http://www.bom.gov.au/jsp/ncc/climate_averages/rainfall/). Despite the prevailing semi-arid to arid conditions, the lack of surface water and watercourses is not strictly due to a lack of precipitation, since heavy rainfall may occur. Rather, it is explained by high evaporation rates, a low water-table, and porosity of the limestone, which causes the limited precipitation to seep rapidly into the rock (James *et al.* 2012).

Although active watercourses are lacking, the northern Nullarbor has several notable palaeochannels that formerly drained southwards, some of which originated in the Great Victoria Desert (Figure 1.9). The largest palaeochannel, known as ‘The Dip’, is around 130 km long (Lowry and Jennings, 1974). It comprises a series of discontinuous depressions that are up to ~1.5 km wide, and ~11 km long, and lie as much as 6–9 m below the level of the plain (Dunkley 1967). When active, the extinct watercourses terminated inland by draining into the rock, and did not flow as far south as the coast (Lowry and Jennings, 1974). Age of the palaeochannels is unknown, but they may have been active during the Pliocene given other evidence pointing to wetter conditions in the Nullarbor region at that time, including speleothem growth (Blyth *et al.* 2010; Woodhead *et al.* 2006), pollen from mesic plants (Sniderman *et al.* 2016), and the development of erosional features known as pocked valleys near the south-central margin of the plain (Woodhead *et al.* 2006; Lipar and Ferk 2015; Sniderman *et al.* 2016).

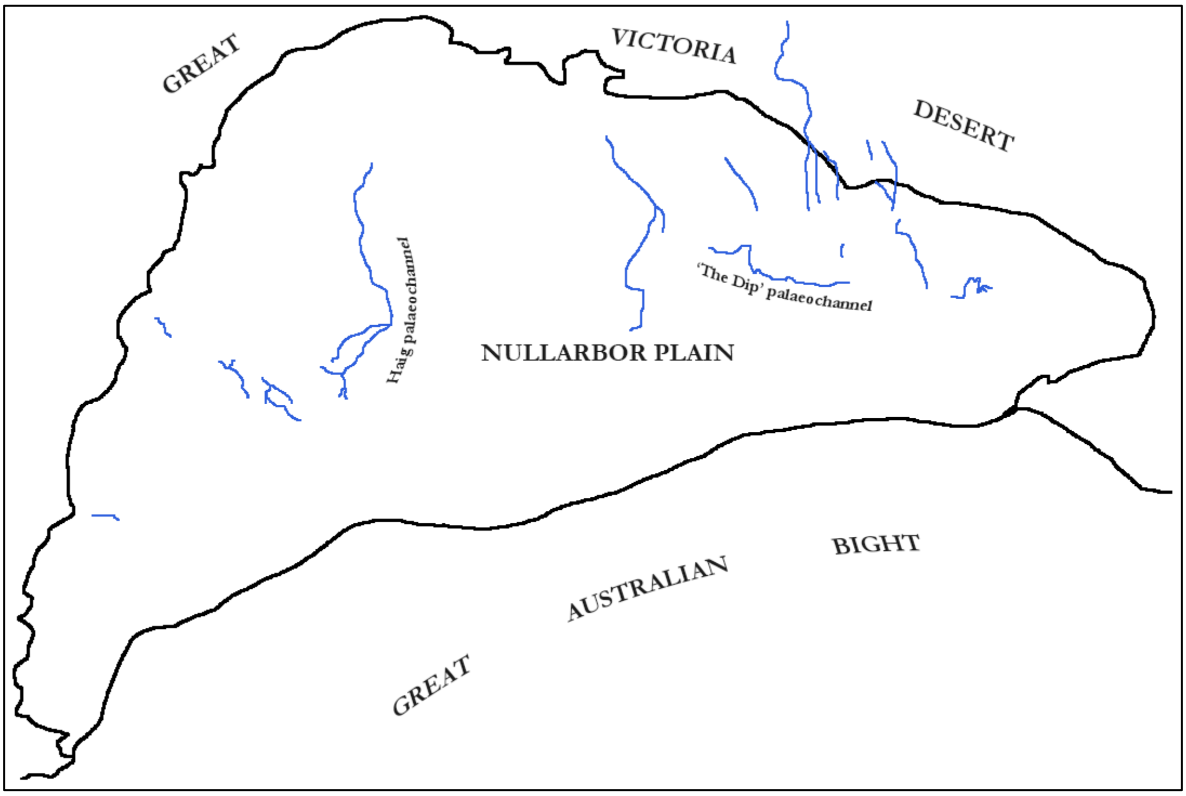


Figure 1.9: Palaeochannels of the Nullarbor region (shown in blue) (adapted from (Lowry and Jennings, 1974)

1.6.3 Vegetation of the Nullarbor region

The Nullarbor Plain is famed for its lack of trees, and with the exception of narrow bands of woodland south of the plain, the entire Nullarbor bioregion is classified as desert and xeric shrubland (Environmental Resources Information Network 2013). Although the 'treeless plain' lacks a tree overstorey, peripheral woodland habitat abuts the plain, mainly in the north and south-west. Vegetation types in the region are strongly delineated into bands that essentially run east/west in parallel with the coast (Gillieson *et al.* 1996). Salt-tolerant chenopods, mostly saltbush (*Atriplex* spp.) and bluebush (*Maireana* spp.), dominate the region. A summary of vegetation types in the Nullarbor region, as described by Beard *et al.* (2013), and mapped in Figure 1.10, is as follows.

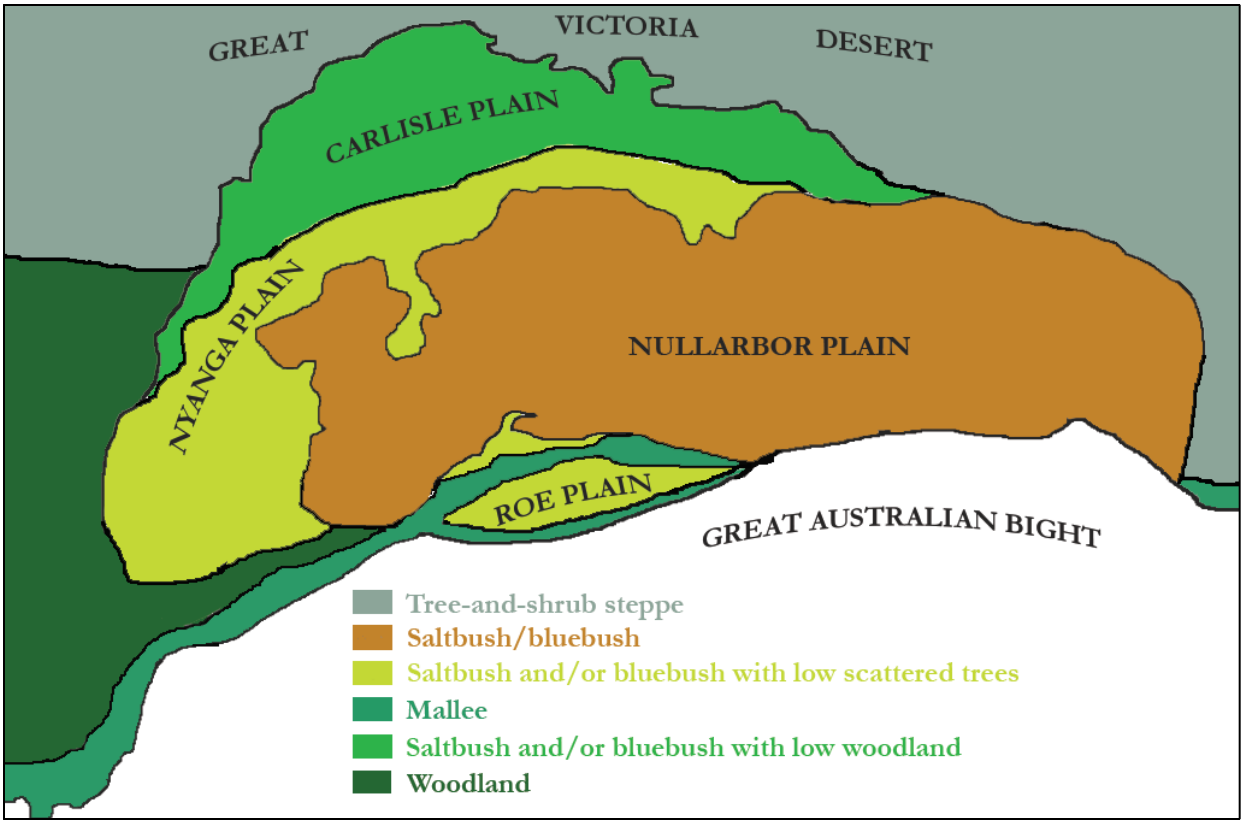


Figure 1.10: Major vegetation types of the Nullarbor region and surrounds (adapted from Beard et al., 2013)

The northernmost band of vegetation, on the Carlisle Plain, is a thickly wooded steppe comprising a bluebush shrub layer with a tree overstorey (10–30% projective foliage cover), mainly of mulga (*Acacia aneura*) with occasional black oak (*Casuarina pauper*) and sugarwood (*Myoporum platycarpum*), and with herbs and grasses in the understorey. Immediately to the south and west of this band, the Nyanga Plain supports a saltbush and/or bluebush association with a thin overstorey of scattered low trees (<10% projective foliage cover), mainly western myall (*Acacia papyrocarpa*), with occasional *Myoporum* *platycarpum*, mallee (*Eucalyptus oleosa*), weeping pittosporum (*Pittosporum angustifolium*), *Acacia aneura*, and *Casuarina pauper*. The Nullarbor Plain itself, covering 7.3 million hectares and dominating the region, supports an association of dwarf saltbush/bluebush with virtually no emergent trees or tall shrubs, with a grass and herb understorey. To the south-west and south-east of the 'treeless plain' a narrow band of mallee vegetation dominated by *Eucalyptus* species lies along the coast, and is interrupted for approximately 250 km by saltbush/bluebush where the treeless plain abuts the coast (Environmental Resources Information Network 2013).

1.6.4 Human impacts on the flora and fauna of the Nullarbor

Prior to and at the time of European colonisation of the Australian continent from the 18th Century onwards, the primary inhabitants of the Nullarbor region were the Mirning Aboriginal people. Archaeological studies indicate that human occupation of the Nullarbor region dates back more than 20,000 years (Martin 1973), and perhaps double that length of time (Roberts *et al.* 1996; Turney *et al.* 2001). This is consistent with archaeological evidence from elsewhere in Australia that the ancestors of today's Aboriginal people spread throughout the arid zone during the Late Pleistocene (Turney *et al.* 2001; Smith *et al.* 2008; Williams *et al.* 2013; Hamm *et al.* 2016). We lack evidence for what impacts the arrival of people in the Nullarbor landscape during the Late Pleistocene had on the local ecology, because we do not know what the regional ecology was like immediately prior to occupation.

Anthropological records compiled by Tindale (1974) state that prior to their dispossession, the Mirning people usually lived close to the coast: one group, the Jirkala-(=Eucla) Mirning, lived mainly on the coastal Roe Plain (Figure 1.8) near Eucla, while the Wonunda-Mirning lived mainly on the more elevated Hampton Scarp. A memoir by a Mirning woman, who recounted visits to the region during her childhood in the 1930s and '40s, emphasised a coastal lifestyle, but also mentioned gathering of bush foods in the northern and southern inland regions (Burgoyne 2000), although she did not specify whether or not this referred to the 'treeless plain'. Tindale (1974) reported that the Mirning would move further inland following heavy rains, but only as far as the southern edge of the treeless plain. However, stone tools of unknown age can be found today lying on the ground in the heart of the plain near the Thylacoleo Caves [pers. obs.], which is much further inland than would be indicated by Tindale's account. This may imply greater use of the inland region in the Late Pleistocene or earlier in the Holocene, or perhaps the Mirning occupied more of the plain in the modern era than was known to Tindale.

Horton's (1996) map of the historical distribution of Indigenous languages of Australia shows the entire Nullarbor region as Mirning land, apart from a narrow band of unoccupied land in the northern Nullarbor Plain. This may suggest that the Mirning inhabited all but the furthest northern parts of the Plain into the late Holocene. The language map shows the far northern Nullarbor Plain as the only region of Australia that was not occupied by Aboriginal people at the time of European contact, which is testament to the harshness of the local environment at least during the late Holocene.

Presumably Aboriginal people managed the Nullarbor region by mosaic burning, as they did elsewhere in Australia. Prideaux *et al.* (2007) speculated that increased frequency of wildfires could have led to the final loss of fire-sensitive woodland vegetation from the Nullarbor Plain and conversion of the local vegetation to the fire-resistant chenopod shrub-steppe present today, the implication being that Aboriginal burning practices from the Late Pleistocene onwards, rather than increased aridity, led to major floral turnover in the region. However, it remains to be established whether the timing of the loss of trees from the Nullarbor Plain coincided with human occupation in the Late Pleistocene and Holocene.

European impacts on the vegetation and wildlife of the Nullarbor region are less equivocal. The vegetation has been heavily grazed by sheep and feral rabbits, and by kangaroos whose numbers have increased due to greater availability of drinking water associated with sheep grazing. This increased grazing pressure has led to a reduction in vegetation cover and increased soil erosion (Gillieson *et al.* 1996). Impacts on faunal diversity have also been severe, with the Nullarbor region having the highest attrition rate among mammalian species of any Australian bioregion since European colonisation (McKenzie *et al.* 2007). The severe loss of small mammals from the region has been suggested as the cause of the decline of the Masked Owl *Tyto novaehollandiae*, which was abundant in the region up to the early 20th Century (White 1919; Richards 1971).

1.6.5 Modern bird diversity of the Nullarbor region

The Nullarbor Plain is characterised by relatively low species diversity, and early European accounts made particular mention of the apparent lack of bird life in the region (Gillieson *et al.* 1996). S.A. White described four birding expeditions to the region, travelling west from Port Augusta, in the certainty that the Nullarbor "must hold many ornithological surprises" (White 1919). However, he noted just 42 species of bird from the eastern Nullarbor Plain and surrounding sand-hill country, and referred to his account as a record of his disappointments. A little over a decade later, McGilp (1932), travelling slightly further west, noted only 38 species.

Cumulative observations of the subsequent century have revealed a somewhat richer regional bird fauna, encompassing the mallee and woodlands that surround the treeless plain, but as with the entire Australian arid zone, many of the birds inhabiting the region are highly mobile and occur irregularly or nomadically (Brooker *et al.* 1979), especially in response to rainfall events (Ryan *et al.* 2012). Diversity is highest near the coast, with 242 species having been recorded in the vicinity of the Eyre Bird Observatory at the western end of the Roe Plain (Figure 1.8). Of these, 89 are waterbirds, shorebirds or seabirds, and the remaining 153 being landbirds (BirdLife Australia, unpublished species list). However, the diversity of landbirds from this well-vegetated, relatively moist coastal location is not representative of diversity further inland.

In a systematic survey, Burbidge *et al.* (1987) identified three distinct assemblages of birds in the Nullarbor region: those inhabiting the myall, mulga, casuarina and eucalypt woodlands of the western, northern and eastern periphery of the plain; those of the southern mallee woodland fringe on coastal dunes and sandplains; and birds of the treeless plain. Species richness was lowest on the treeless plain (mean 6.6 ± 2.8 species per quadrat), while woodlands with an *Acacia* or *Eucalyptus* overstorey supported greatest diversity (mean 17.7 ± 4.8 species per quadrat). Only 18 species were found to be common on the Nullarbor Plain itself (Burbidge *et al.* 1987), of which six were non-passerines and 12 passerines (Table 1.3). This provides a modern baseline against which to measure the diversity of birds the Nullarbor Plain during the Pleistocene, as assessed later in this thesis.

Table 1.3: Common birds of the Nullarbor Plain (from data in Burbidge et al., 1987)

Family	Species	Common name
Non-passerines		
Accipitridae	*Aquila audax*	Wedge-tailed Eagle
Falconidae	*Falco berigora*	Brown Falcon
	Falco cenchroides	Nankeen Kestrel
Otididae	*Ardeotis australis*	Australian Bustard
Charadriidae	*Peltohyas australis*	Inland Dotterel
Turnicidae	*Turnix velox*	Little Button-quail
Passerines		
Maluridae	*Malurus leucopterus*	White-winged Fairy-wren
Acanthizidae	*Pyrrholaemus brunneus*	Redthroat
	Acanthiza iredalei	Slender-billed Thornbill
	Calamanthus sp.	Fieldwren
	Aphelocephala leucopsis	Southern Whiteface
Meliphagidae	*Lichenostomus virescens*	Singing Honeyeater
	Epthianura aurifrons	Orange Chat
Psophodidae	*Cinclosoma cinnamomeum*	Nullarbor Quail-thrush
Artamidae	*Artamus cinereus*	Black-faced Woodswallow
Megaluridae	*Cinclorhamphus cruralis*	Brown Songlark
Hirundinidae	*Hirundo neoxena*	Welcome Swallow
Motacillidae	*Anthus novaeseelandiae*	Australasian (Richard’s) Pipit

As the avifaunal analysis in Chapter 4 focuses on non-passerine taxa, the distribution of non-passerines in the region is summarised here. Burbidge *et al.* (1987) noted that the non-passerine species ubiquitous to all habitat types (woodland, plain, and mallee) were: Nankeen Kestrel *Falco cenchroides*; Brown Falcon *Falco berigora*; Little Buttonquail *Turnix velox*; and Horsfield's Bronze-cuckoo *Chrysococcyx basalis*. Non-passerines characteristic of the peripheral woodlands were: Spotted Harrier *Circus assimilis*; Red-backed Kingfisher *Todiramphus pyrrhopygius*; Galah *Eolophus roseicapilla*; Banded Lapwing *Vanellus tricolor*; Budgerigar *Melopsittacus undulatus*; and Naretha Blue-bonnet parrot *Northiella haematogaster*. Species found in both the peripheral woodlands and/or coastal woodland/mallee were: Mulga Parrot *Psephotellus* (=*Psephotus*) *varius*; Australian Ringneck parrot *Barnardius zonarius*; Owlet Nightjar *Aegotheles cristatus*; Tawny Frogmouth *Podargus strigoides*; Emu *Dromaius novaehollandiae*; and Pallid Cuckoo *Cacomantis pallidus*. Non-passerine species found only in woodlands were the Malleefowl *Leipoa ocellata* and the Boobook owl *Ninox novaeseelandiae*.

Most species of bird in the Nullarbor region are from the Eyrean assemblage, with 47 of the more than 80 autochthonous Eyrean species having been recorded there (Burbidge *et al.* 1987). Some typically Bassian (mallee) species are also present, including Southern Scrub-robin *Drymodes brunneopygia*, Western Yellow Robin *Eopsaltria griseogularis*, Golden Whistler *Pachycephala pectoralis*, Blue-breasted Fairy-wren *Malurus pulcherrimus*, White-browed Scrubwren *Sericornis frontalis*, Red Wattlebird *Anthochaera carunculata*, Purple-gaped Honeyeater *Lichenostomus cratitius*, New Holland Honeyeater *Phylidonyris novaehollandiae*, but only within the coastal mallee fringe, and not on the treeless plain (Burbidge *et al.* 1987). As with the Eyrean avifaunula as a whole, the birdlife of the Nullarbor region comprises mainly species that are widespread throughout the arid zone (Burbidge *et al.* 1987). Passerines dominate the fauna (Burbidge *et al.* 1987; Ryan *et al.* 2012).

The region contains two endemic taxa, both recently elevated from sub-species to species: the Nullarbor Quail-thrush *Cinclosoma alisteri* (see Toon *et al.* 2012); and the Naretha Parrot *Northiella narethae* (see Dolman and Joseph 2015). An additional characteristic taxon, the geographically isolated population of Masked Owl *Tyto novaehollandiae* was also once a notable part of the avifauna, though is possibly now extinct (Debus 1993).

1.6.6 The Nullarbor Plain as a biogeographical barrier

The Nullarbor Plain has long been regarded as one of Australia's major biogeographical barriers (Figure 1.11), due to its aridity, lack of trees, and its 700-km long interruption of the mesic habitats of south-eastern and south-western Australia. The paradigm of the 'Nullarbor Barrier' arose because, as with other putative biogeographical barriers on the Australian mainland, many taxa were observed to have disjunct populations on either side of plain (Schodde and Mason, 1999), and many endemic vertebrate taxa are isolated to the south-west and south-east of the continent (Cracraft, 1991). Around one in five species of Australian bird has a geographical range that is completely or partially divided by the Nullarbor Plain, with nearly 70% of waterbirds so affected (McCracken *et al.* 2002).

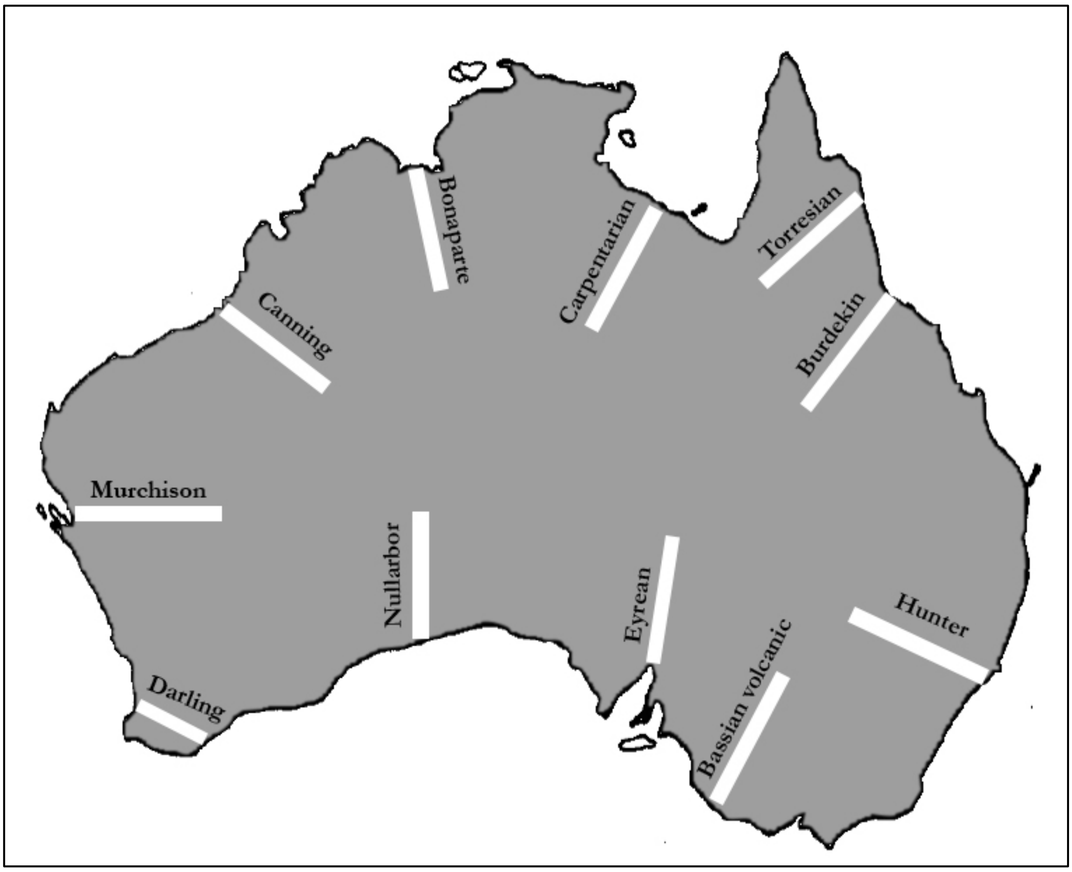


Figure 1.11: Putative biogeographical barriers of Australia (compiled from various sources)

Until relatively recently it was considered unlikely that much interchange occurred between the mesic biotas of south-western and south-eastern Australia after the early Pliocene (Cracraft 1986). However, it has since became widely accepted that the Nullarbor Plain did not grow intensely arid and lose its tree canopy until some three or four million years later, during the Early Pleistocene (Miller *et al.* 2012; Webb and James 2006). Recent genetic, fossil vertebrate and pollen studies have produced somewhat discordant evidence for the timescales on which the Nullarbor Plain may have acted as a biogeographical barrier to gene flow in various plant and animal taxa in southern Australia, and some taxa appear to have been completely unaffected by the putative 'barrier'.

In the case of plants, a multi-taxon molecular study by Crisp and Cook (2007) found that divergence dates for sister taxa in the temperate south-west and south-east of Australia, while including both older and younger dates, clustered at around 13–14 Ma. This was an arid interval of the Miocene that immediately followed the most recent marine incursion into the Eucla Basin between around 16–14 Ma. The authors deduced that after the sea retreated from the Eucla Basin and the limestone platform was uplifted, the Plain functioned as an edaphic barrier for some plants that prefer acid siliceous soils, including species of *Banksia*, *Scaevola* (fan flowers), *Allocasuarina* (sheoaks), *Xanthorrhoea* (grass-trees), *Wurmbea* (star-lilies), and various genera of pea, due to the unsuitability of its alkaline substrate for plants that are found to the east and west of the Nullarbor region (Crisp and Cook, 2007).

At first this appears to be a satisfactory explanation for the modern biogeography of certain plants in southern Australia. For example the genus *Banksia* is completely absent from the Nullarbor Plain today, but populations occur in the mesic areas to its west and east (Figure 1.12). However, a recent study of fossil pollen preserved in speleothems from various Nullarbor caves found that abundant eastern Australian-type *Banksia* pollen was present on the Nullarbor Plain between approximately 5 Ma and 3.5 Ma (early to mid-Pliocene) (Sniderman *et al.* 2016), which is at odds with Crisp and Cook's (2007) hypothesis that the Nullarbor Plain was an edaphic barrier for such plants from the middle Miocene onwards. Although individual divergence dates such as those cited by Crisp and Cook (2007) may be correct, the pollen evidence of Sniderman *et al.* (2016) serves as a reminder that genetic divergence between spatially separated sister taxa does not necessarily imply that close relatives have been absent from the intervening geographical area since those sister taxa diverged. Caution should therefore be exercised in using divergence dates between living populations to reconstruct regional palaeoecology. In particular, genetic divergence dates between extant plant taxa in south-western and south-eastern Australia may not accurately re-create the historical taxonomic diversity or structure of the vegetation of the Nullarbor Plain, and may lead to incorrect assumptions about timing and the extent to which the Plain has been a barrier to certain fauna.

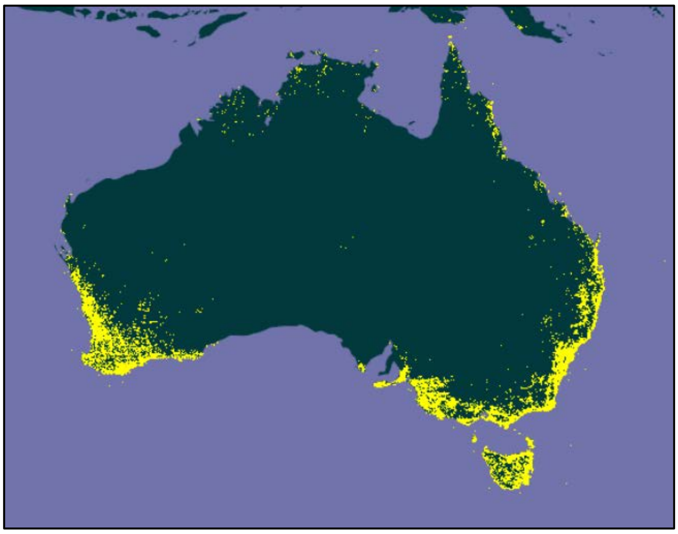


Figure 1.12: Modern distribution of Banksia species in Australia (yellow). Note the mesic distribution of the genus in south-west and eastern Australia, and their complete absence from the Nullarbor region (data downloaded from GBIF https://www.gbif.org/species/8399031, 24/11/2017)

The recent fossil pollen study by Sniderman *et al.* (2016) detected two major floral transitions on the Nullarbor Plain after c. 5.5 Myr ago, although substantial temporal gaps in the speleothem pollen record mean that the number of transitions may be an underestimate. Nevertheless, the study provided the clearest evidence yet for the character of the flora of the Nullarbor Plain over the last 5.5 million years. At the Miocene/Pliocene boundary approximately 5.5–5.0 Myr ago, the pollen signature indicates sparse woodlands or shrublands under semi-arid conditions (approx. 400 mm mean annual rainfall). At around 5 Myr ago, a major floral turnover is evident, with more mesic conditions (mean annual rainfall approx. 1,200 mm) supporting eucalypts, other myrtaceous taxa, and *Banksia*, amongst others. In the middle Pliocene at around 3.5 Myr ago, eucalypts and other myrtaceous taxa and *Banksia* were still present, along with Ericaceae (heaths), Casuarinaceae (sheoaks or relatives), Poaceae (grasses), *Geniostoma*, and other taxa. No pollen was preserved from Early Pleistocene speleothems, therefore the absence of trees during this interval, as suggested by Miller *et al.* (2012), could neither be verified nor disproved.

The Pleistocene pollen record was restricted to a single speleothem approximately 400 kyr old, from one of the Thylacoleo Caves, and indicates that by this interval (Middle Pleistocene) a second major floral turnover had occurred. At this time, the pollen signature is dominated by Chenopodiaceae (saltbush/bluebush; >80%), with minor components of Poaceae (grasses), Myoporaceae (emu-bush/boobiala), Asteraceae (daisies), non-eucalypt Myrtaceae, and Cupressaceae (cypress-pines). The authors interpreted the Middle Pleistocene pollen assemblage as representing a semi-arid chenopod shrubland similar to that of the Nullarbor Plain today, with annual rainfall of approximately 350 mm. This interpretation seems somewhat at odds with the apparently contemporaneous vertebrate fossil record from the Thylacoleo Caves, which showed that arboreal taxa were present in the Middle Pleistocene (Prideaux *et al.* 2007). This paradox is discussed further below (see Section 1.7). It is also hard to explain how the local environment could simultaneously be dry enough to support chenopod shrub-steppe habitat, but also wet enough to cause the speleothem growth that preserved the fossil chenopod pollen.

Faunal studies have produced an increasingly complex picture of the role that the Nullarbor Plain has played as a vicariance barrier during the Plio-Pleistocene. As reviewed by Neaves *et al.* (2012), and summarised in Table 1.4, recent phylogeographic studies of diverse taxa have revealed that the Nullarbor Plain has been a major vicariance barrier for some but by no means all taxa in southern Australia, and that in some cases, genetic structure appears to have been influenced more by other barriers such as the Eyrean barrier (Figure 1.11).

Table 1.4: Population histories & barriers affecting southern Australian species during the Plio-Pleistocene (modified from Neaves et al., 2012)

Taxon	Population history	Original reference
Birds		
Australian Magpie *Gymnorhina tibicen*	Divergence between eastern & western Australia across the Nullarbor arid barrier	(Toon *et al.*, 2007)
Australian Ring-neck Parrot *Barnardius zonarius*	Divergence across the Eyrean arid barrier	(Joseph and Wilke, 2006)
Black-faced Woodswallow *Artamus cinereus*	Expansion, no evidence for presence of barriers	Joseph and Wilke (2006)
Southern emu-wrens (Genus *Stipiturus*)	Divergence between eastern and western Australia across Nullarbor arid barrier	(Donnellan *et al.*, 2009)
Horsfield's Bronze Cuckoo *Chalcites basalis*	Expansion, no evidence for presence of barriers	(Joseph *et al.*, 2002)
Ground Parrot *Pezoporus wallicus*	Divergence between eastern and western Australia across Nullarbor arid barrier	(Murphy *et al.*, 2011))
Musk Duck *Bizura lobata*	Divergence between eastern and western Australia across arid Nullarbor barrier	(Guay *et al.*, 2010)
Pied Butcherbird *Cracticus nigrogularis*	Expansion, no evidence for the presence of barriers (species-specific refugia)	(Kearns *et al.* 2010)
Singing Honeyeater *Lichenostomus virescens*	Expansion, no evidence for presence of barriers	(Joseph and Wilke, 2006)
Spiny-cheeked Honeyeater *Acanthagenys rufogularis*	Expansion, no evidence for presence of barriers	(Joseph and Wilke, 2006)
Splendid Fairy-wren *Malurus splendens*	Expansion and divergence associated with the Nullarbor & Eyrean arid barriers	(Kearns *et al.*, 2009)
Woodswallows *Artamus* spp.	Divergence across the Eyrean arid barrier	(Joseph and Wilke 2006)
Insects		
Morabine Grasshopper *Vandiemenella viatica*	Divergences within South Australia associated Lake Bungunnia (Murray Basin); no evidence of divergence across the Nullarbor	(Kawakami *et al.*, 2009)
Mammals		
Brush-tailed Phascogale *Phascogale tapoatafa*	Divergence between eastern and western Australia across Nullarbor arid barrier	(Spencer *et al.*, 2001)

Fat-tailed Dunnart *Sminthopsis crassicaudata*	Divergence across Murray basin but no evidence of divergence across the Nullarbor arid barrier	(Cooper *et al.*, 2000)
Heath Mouse *Pseudomys shortridgei*	Divergence between eastern and western Australia across Nullarbor arid barrier	(Salinas *et al.*, 2009)
Red Kangaroo *Macropus rufus*	Expansion, no evidence of arid barriers	(Clegg *et al.* 2002)
Western Pygmy Possum *Cercartetus concinnus*	Expansion, no evidence for presence of barriers	(Pestell *et al.*, 2008)
Reptiles		
Bynoe's Prickly Gecko *Heteronotia binoei*	Westward expansion of northern lineages with a major fragmentation in the southern lineages	(Strasburg and Kearney, 2005)
Sand Skink *Egernia multiscutata*	Divergence between Nullarbor and western arid zone clades	Strasburg *et al.* (2007)
Skinks (*Bassiana* spp.)	Divergence between South Australian species (Flinders Ranges region) and between Western and South Australian clades within *B. trillneata*	(Chapple *et al.*, 2004)
Tiger Snake *Notechis scutatus*	Divergence between eastern and western Australia across Nullarbor arid barrier	(Keogh *et al.*, 2005)
Plants		
Blue Gum *Eucalyptus globus* ssp. *bicostata*	Divergence across Flinders Ranges area/Lake Bungunnia (Murray Basin)	(Freeman *et al.*, 2001)
Dry sclerophyll shrub *Correa* spp.	Divergence across Flinders Ranges area/Lake Bungunnia (Murray Basin)	(Othman *et al.*, 2010)

Increasing evidence for varied responses among taxa to presumed climatic changes in the Nullarbor region during the Plio-Pleistocene led Dolman and Joseph (2012) to sample ten species of bird that have populations completely or partially isolated in south-western and south-eastern Australia, on either side of the Nullarbor Plain. Through modelling likely divergence dates of the south-western and south-eastern populations of each species using Bayesian methods, they detected three probable clusters of co-divergence. The youngest cluster fell between 171,085–24,607 yr ago (Middle to Late Pleistocene), the middle cluster between 663,837–67,172 yr ago (Middle to Late Pleistocene), and the oldest between 2,006,355–429,105 yr ago (Early to Middle Pleistocene). As there is overlap between the dates of the clusters there is uncertainty about exactly which taxa diverged in each interval, but two of the mesic taxa, *Petroica boodang* and *Melithreptus lunatus* were confidently assigned to the oldest divergence 'event', while the semi-arid taxa tended towards younger divergence dates. This is consistent with the idea that increased aridity in the Early Pleistocene had greatest effect on mesic taxa.

Although results of the Dolman and Joseph (2012) study show the promise of analysing species assemblages rather than just individual taxa, one obvious problem with the findings is the very wide time intervals represented by the co-divergence 'events'. In reality, it is difficult to regard an interval of 1.5 million years' duration, as in the oldest divergence bracket, as an event, when this timespan encompassed approximately 20 global glacial cycles (Cohen and Gibbard 2011).

A further conundrum that complicates the interpretation of how the Nullarbor Plain functioned as an arid-habitat barrier during the Pleistocene is the apparent decoupling of aridity from the loss of trees during the Middle Pleistocene, as determined from the Thylacoleo Caves vertebrate fossil fauna (Prideaux *et al.* 2007). The finding that arboreal marsupials were present in a low-rainfall regime until a few hundred-thousand years ago put a dent in the long-held theory that increased Pleistocene aridity led directly to the loss of trees from the Plain, and this in turn created a barrier to faunal interchange in southern Australia. The timing and processes by which the Nullarbor Plain lost its trees therefore warrants a thorough re-examination, and may be key to understanding the recent biogeographical history of southern Australia.

1.7 The Thylacoleo Caves – significance, description, and fauna

1.7.1 Significance of the age and location of the caves

The fossils examined for this research project come from the Thylacoleo Caves, beneath the Nullarbor Plain, Western Australia. So far, this is the only known locality in south-central Australia preserving a fossil fauna spanning the Early and Middle Pleistocene (Prideaux *et al.* 2007). Previously-studied fossil deposits in the region are younger (Late Pleistocene to Holocene), and come from the moister, more thickly vegetated band of habitat to the south of the plain. The Thylacoleo Caves, which sit further north in the heart of the 'treeless plain', provide the first direct insight into the Early and Middle Pleistocene vertebrate fauna of the region, and the first fossil record of the zone that today is characterised by aridity and a lack of trees.

Given that increased aridity and the associated loss of trees from the Nullarbor Plain during the Pleistocene has long been hypothesised as a key process that shaped the diversity and distribution of the southern Australian fauna (see *Nullarbor as a barrier*), the Thylacoleo Caves fossil deposits offer an unprecedented opportunity to directly assess the diversity of vertebrates in the region during this crucial window of time. The following sections briefly outline existing knowledge, about the Thylacoleo Caves, the Pleistocene vertebrate fauna they contain, and the palaeoecology of the locality as interpreted from the vertebrate fossil assemblage. Gaps in our understanding of the fossil fauna and its palaeoecology are identified, leading on to the development of the aims and objectives of this study.

1.7.2 Location

Exact locations of the caves has not been publicised due to the risk of fossil looting, but coordinates of the caves are lodged with the Department of Earth and Planetary Sciences, Western Australian Museum, Perth, and are available to *bona fide* researchers. Approximate location of the caves is indicated in Figure 1.13. There are no made roads leading to the caves, and they are only accessible via four-wheel drive vehicles in dry conditions.

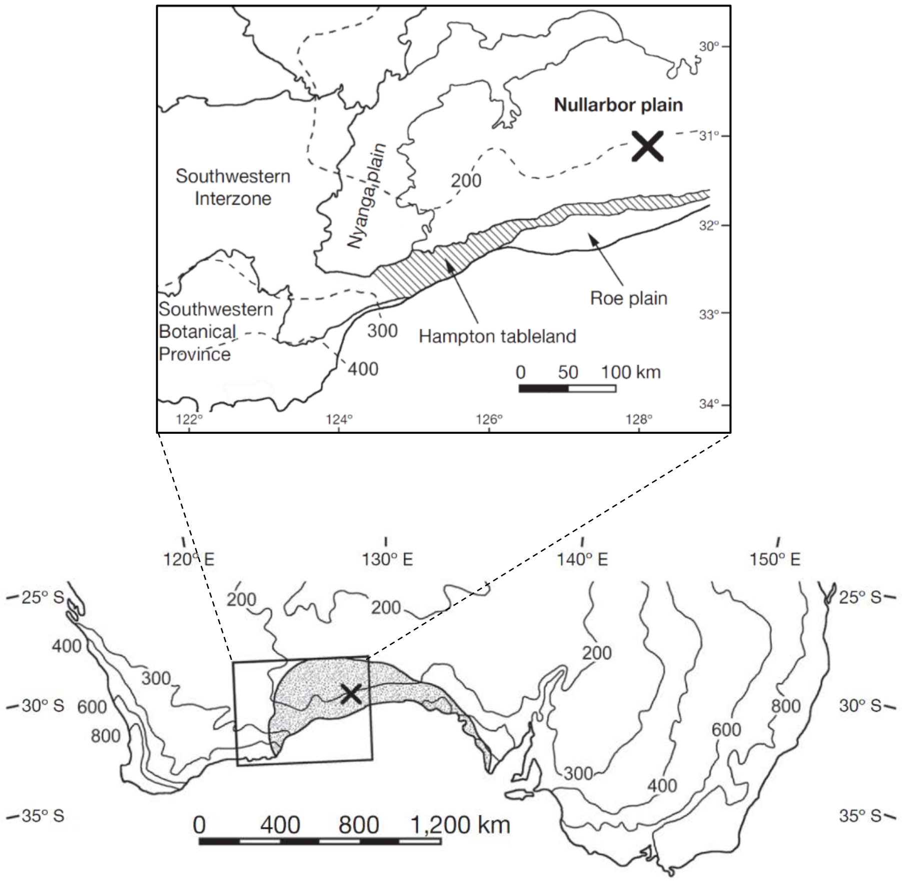


Figure 1.13: Location of the Thylacleo Caves, Nullarbor Plain, Western Australia (marked by black X), showing the Eucla Basin (grey stippled area in lower map), and mean annual rainfall isohyets (mm) (adapted from Prideaux *et al.* 2007)

1.7.3 The caves

Three limestone caves comprise the Thylacoleo Caves fossil locality: Leaena's Breath Cave (hereafter LBC), Flightstar Cave (FSC) and Last Tree Cave (LTC). All contain a similar Pleistocene vertebrate fossil fauna, and were named after the extinct marsupial predator *Thylacoleo carnifex*, complete skeletons of which were found lying on the cave floors (Figure 1.14). The descriptions below are based on information published in Prideaux *et al.* (2007; Supp. Info.) and on personal observations during the 2013 and 2014 field seasons. Maps showing the layout of the caves are included in Chapter 4.

Figure 1.14: A skeleton (WAM 02.7.1) of extinct *Thylacoleo carnifex* (marsupial lion) in Flightstar Cave, 2002. This is the most complete skeleton of the species ever found (photograph courtesy of Clay Bryce, Western Australian Museum)

The locality is roughly 100 km inland from the coast of the Great Australian Bight, on the Western Australian side of the Nullarbor Plain, in the arid, treeless zone. The caves are not immediately adjacent to one another, but are distributed within an approximately 20-km radius. Local vegetation is dominated by saltbush/bluebush, with grasses, herbs and occasional isolated, stunted trees. LBC and FSC are accessed by abseiling approximately 10 m down their vertical solution pipes (Figure 1.15), while LTC is accessed on foot via a collapse entrance.

The solution pipes of LBC and FSC are accessed via a single small (<1 m diameter) entrance at the surface of the plane, and both were hard-capped by calcrete until their recent re-opening. The solution pipes descend through a thick layer of rock before opening into the ceiling of the cavern below. Beneath the solution pipes in both these caves is an area of rockfall comprising a pile of large limestone boulders (e.g. Figure 1.16). Some fossils recovered from these caves were found on or between these boulders.

Figure 1.15: Entrance to Leaena's Breath Cave, 2014 (photograph courtesy of the Flinders University Palaeontology lab)

Figure 1.16: Looking back towards the rockfall area beneath the solution pipe entrance to Leaena's Breath Cave, 2009. Ernie Lundelius for scale (photograph courtesy of the Flinders University Palaeontology lab)

At the foot of the rockpiles in LBC and FSC, the main chambers open out into a relatively flat sediment floor beneath a ceiling bearing stalactites (Figure 1.17). Some fossil specimens used in this study lay on top of the sediment floors, but most were excavated from pits dug down into the silty clay infill sediments of LBC (e.g. Figure 1.17).

Figure 1.17: Sediment floor of Leaena's Breath Cave, 2009, showing the early stages of excavation of Pit A (photograph courtesy of the Flinders University Palaeontology lab)

The structure of LTC differs from the other two caves, in that its entrance is large and sufficiently shallow-angled to walk into, and leads into an entrance chamber with a low ceiling. Beyond the entrance chamber, the cave branches off in two main directions. The main chamber lies directly ahead of the entrance. The ceiling opens into a domed chamber above a steep area of rockfall comprising limestone boulders and at the foot of the rockpile the cavern branches off into smaller side-chambers. Fossils have been collected from the rockpile and from the lower chambers, but unlike LBC and FSC, the main chamber of LTC lacks an expansive sediment floor, with the area of rockfall extending nearly to the far wall of the cavern. To the left of the main entrance of the cave, a convoluted area of rockfall with a low ceiling winds down deep in the cave. Guide ropes are needed to assist climbing down the boulders to reach “The Ossuary”, a small but bone-dense chamber with a low, overhanging ceiling, and a floor of powdery limestone breakdown material (Figure 1.18).

Figure 1.18: "The Ossuary", Last Tree Cave, 2002 (photograph courtesy of the Flinders University Palaeontology lab)

Like other caves and blowholes on the Nullarbor Plain, all three caves ‘breathe’. That is, they are subject to strong reversing draughts, with air moving rapidly in or out of the cave entrance depending on atmospheric pressure. The speed of the draughts can be up to around 100 km/hour, which is strong enough to make entering and leaving the caves challenging. The strength of a reverse draught is illustrated by the photograph in Figure 1.19, in which an inflated air mattress is lifted two metres clear of the entrance of LBC when the cave is breathing out.

Figure 1.19: James Moore demonstrating the speed of a Leaena's Breath Cave reversing draught, 2013 (photograph courtesy of the Flinders University Palaeontology lab)

1.7.4 Age of the sediments and fossil deposits

Several dating techniques were used to build a chronology for the Thylacoleo Caves fossil deposits. Fossils could not be direct-dated via radiocarbon because of their age being >50 kyr, leaving indirect dating of associated sediments as the only way of determining the age of the fossils. Four techniques were applied:

Uranium/Lead (U/Pb) dating of speleothems (Woodhead *et al.* 2006); Uranium/Thorium (U/Th) dating of speleothems; Optically Stimulated Luminescence (OSL) dating of quartz grains within cave fill sediments; and magnetostratigraphy of cave fill sediments (Prideaux *et al.* 2007).

In combination, these techniques have constrained the age of material excavated from pits. However, it should be noted that the age of material recovered from the rockpiles and cave floors is time-averaged, as this comprises a mixture of extinct Pleistocene taxa and material that accumulated recently since the cave entrances re-opened, as evidenced by the presence of mummified animal remains (e.g. Figure 1.20). In addition, minimal dating has been attempted for FSC and LTC to date, with greater emphasis having been placed on LBC because most excavation effort has focused on this cave. Details of dating methods and results are contained in the Supplementary Information to Prideaux *et al.* (2007), and results are summarised briefly below.

Figure 1.20: Mummified remains of a Western Quoll, *Dasyurus geoffroii*, from Flightstar Cave (photograph courtesy of Carey Burke, Flinders University Palaeontology lab)

For FSC and LTC, only OSL dating has been attempted, providing ages for the youngest, near-surface sediments. This provides a minimum age for the accumulation of sediments and buried fossils. For FSC, OSL dating returned ages of approximately 230 kyr (Middle Pleistocene), so material excavated from this cave is probably this age or older, although surface material may be younger. For LTC, OSL dating produced a minimum age of approximately 101 kyr (Late Pleistocene), so excavated material is probably Late Pleistocene or older, although surface material may be younger.

Dating of LBC was more extensive. An *in situ* calcite speleothem was dated via U/Pb to 4.1–3.8 Myr (Pliocene), meaning that the cave itself must have formed before the mid-Pliocene. Dating of surface sediments and fossils have returned various ages. OSL dating of near-surface sediments produced a minimum age of ~195 kyr (Middle Pleistocene). Three coralline calcite speleothems from the cave floor dated via U/Th, the last of which was deposited on top of a fossil bone and therefore gives a minimum date for the age of the fossil, returned dates of 407 ± 17, 394 ± 15, and 392 ± 25 kyr respectively (Middle Pleistocene). The combined results of OSL and U/Th dating thus constrain the age of the youngest sediments and some surface fossils to between ~200–400 kyr (Middle Pleistocene), although modern material, including mummies, are also found on the floor of the cave.

Measurements of palaeomagnetism in the cave fill sediment of LBC detected a reversal of the Earth's magnetic field at approximately 50–70 cm below the level of the sediment floor. This polar reversal was presumed to be the most recent reversal, thus marking the end of the Matuyama Reversed Chron and the beginning of the Brunhes Normal Chron at ~780 kyr, which defines the boundary of the Early and Middle Pleistocene worldwide (Pillans 2003). Sediments deeper than this are thus older than 780 kyr (Early Pleistocene), although their maximum age is unknown, while those approx. 50 cm or shallower are younger than 780 kyr (Middle Pleistocene).

Three sedimentary units were identified within the pit excavations in LBC. The upper unit (Unit 1) spans a depth of 0–35 cm below the surface, Unit 2 spans 35–55 cm, and Unit 3 from 55 cm downwards. Based on the combined evidence of the various dating techniques, Unit 1 sediments and the fossils they contain are therefore of Middle Pleistocene age, Unit 2 Middle to Early Pleistocene, and Unit 3 Early Pleistocene. The sediments lack obvious sub-strata, and it is currently unclear whether the units accumulated gradually and continuously, or with hiatuses and rapid accumulation phases.

1.7.5 Taxonomic diversity of the vertebrate fauna: non-avian taxa

The Thylacoleo Caves vertebrate faunal assemblage is of mixed fortune, including taxa that went extinct during the Pleistocene, others that survived into the Holocene but went extinct since European colonisation, some that are extinct on the Australian mainland but are extant in Tasmania, and some that survive on the mainland today. Extinct Pleistocene taxa are listed in Table 1.5. Extant and recently-extinct taxa are listed in Table 1.6. In the initial analysis of the fossil fauna, Prideaux *et al.* (2007) recorded a minimum of 69 vertebrate species, including mammals, reptiles and birds. Three species of frog were also later identified (Tyler and Prideaux 2016), bringing the total to 72. The diversity of non-avian vertebrates from the deposit is summarised below. The diversity of birds is discussed separately in the next section due to their centrality to the research presented in this thesis.

Body mass of the mammalian species found in the deposits ranges from 10 g to 250 kg (Prideaux *et al.* 2007, Supp. Info). Kangaroos are particularly diverse, numbering 23 species, eight of which were new to science, with two of these, both tree-kangaroos, having been described so far (Prideaux and Warburton 2008, 2009). Nearly one third of marsupials identified from the deposit went extinct during the Pleistocene, of which most were browsers or mixed feeders (Table 1.5). Within the herbivore assemblage, including extinct and extant species, nearly 40% were browsers, nearly 30% grazers, nearly 20% mixed feeders, and the remainder were fungivores or arboreal feeders. The deposit contains marsupials that are extant but no longer found in the Nullarbor region, including Brushtail Possum *Trichosurus vulpecula*, Western Barred Bandicoot *Perameles bougainville*, Tammar Wallaby *Macropus eugenii*, and the recently-extinct Pig-footed Bandicoot *Chaeropus ecaudatus* and Crescent Nail-tail Wallaby *Onychogalea lunata*.

Table 1.5: Extinct non-avian vertebrate taxa from the Thylacoleo Caves (from information in Prideaux et al. 2007, Supp. Info.; Tyler and Prideaux 2016; and Prideaux and Warburton, 2008, 2009); * = new species

Species name	Common name/descriptor	Dietary guild/habitat
AMPHIBIA		
Litoria lundeliusi	Extinct tree-frog*	Arboreal/terrestrial/semi-aquatic
MAMMALIA		
Phascolonus gigas	Giant wombat	Grazer
Thylacoleo carnifex	Marsupial lion	Carnivore
Thylacinus cynocephalus	Thylacine	Carnivore
Baringa sp. 1	Macropodid*	Mixed feeder
Baringa sp. 2	Macropodid*	Mixed feeder
Baringa sp. 3	Macropodid*	Mixed feeder
Bohra nullarbora	Tree-kangaroo*	Arboreal folivore
Bohra illuminata	Tree-kangaroo*	Arboreal folivore
Congruus kitcheneri	Extinct wallaby	Browser
Congruus sp. 1	Extinct wallaby*	Browser
Congruus sp. 2	Extinct wallaby*	Browser
Macropus ferragus	Extinct kangaroo	Grazer
Macropus sp. 1.	Extinct kangaroo*	Grazer
Metasthenurus newtonae	Short-faced kangaroo	Browser
Procoptodon goliah	Short-faced kangaroo	Browser
Procoptodon browneorum	Short-faced kangaroo	Browser
Procoptodon williamsi	Short-faced kangaroo	Browser
Protemnodon brehus	Short-faced kangaroo	Browser
Protemnodon roechus	Short-faced kangaroo	Browser
Sthenurus andersoni	Short-faced kangaroo	Browser
Sthenurus tindalei	Short-faced kangaroo	Mixed feeder

Table 1.6: Extant and recently extinct non-avian vertebrate taxa from the Thylacoleo Caves fossil fauna (from information in Prideaux *et al.* 2007, Supp. Info. and Tyler and Prideaux, 2016)

Taxon name	Common name/descriptor
AMPHIBIA	
Pseudophryne sp. indet.	Myobatrachid ground-frog (indeterminate species)
Neobatrachus sudelli	Sudell's Frog/Painted Burrow Frog
REPTILIA	
Elapidae indet.	Elapid snake (indeterminate species)
Diplodactylus sp. cf. *granariensis*	Western/Giant/Wheat-belt Stone Gecko
Gehyra sp. indet.	Web-tailed gecko/Dtella (indeterminate species)
Underwoodisaurus (=*Nephrurus*) *milii*	Barking/Thick-tailed Gecko
Ctenotus sp. cf. *orientalis*	Eastern Ctenotus Skink
Egernia sp. cf. *kingii*	King's Skink
Egernia sp. cf. *multiscutata*	Southern Sand/Heath/Bull Skink
Tiliqua rugosa	Shingleback Skink
MAMMALIA	
Thylacinus cynocephalus	Tasmanian Tiger
Antechinomys laniger	Kultarr
Dasycercus sp. cf. *blythi*	Brush-tailed Mulgara
Dasyurus geoffroii	Western Quoll
Sarcophilus harrisii	Tasmanian Devil
Chaeropus ecaudatus	Pig-footed Bandicoot
Perameles bougainville	Western Barred Bandicoot
Macrotis lagotis	Bilby
Lasiorhinus sp. cf. *latifrons*	Southern Hairy-nosed Wombat
Trichosurus vulpecula	Brushtail Possum
Bettongia lesueur	Boodie/Burrowing Bettong
Bettongia pusilla	Nullarbor Dwarf Bettong
Macropus eugenii	Tammar Wallaby
Macropus rufus	Red Kangaroo
Onychogalea lunata	Crescent Nail-tail Wallaby
Leporillus conditor	Wopilkara/Greater Stick-nest Rat
Notomys sp. cf. *mitchellii*	Mitchell's Hopping Mouse
Pseudomys australis	Palyoora/Plains Mouse
Pseudomys sp. cf. *bolami*	Bolam's Mouse
Pseudomys desertor	Desert Mouse
Nyctophilus geoffroii	Lesser Long-eared Bat

Predatory marsupials found include: Thylacine *Thylacinus cynocephalus* and Tasmanian Devil *Sarcophilus harrisii,* both of which have been extinct on the Australian mainland for several thousand years; the extinct Pleistocene marsupial 'lion' *Thylacoleo carnifex*; and smaller extant predators such as Western Quoll *Dasyurus geoffroii*, and a mulgara *Dasycercus* sp.

Rodents include: Greater Stick-nest Rat *Leporillus conditor*; a Hopping Mouse *Notomys* sp.; and three species of *Pseudomys* mice. Abundant rodent remains from the more recent pit excavations of LBC await identification and analysis.

Nine reptile species were identified for the original publication on the site, but as with the rodents, material from later excavations awaits identification. Species identified so far are: an Elapid snake; and eight lizard species, including an agamid (dragon) species, three geckos, and four skinks.

Frog taxa include a new extinct species of *Litoria* tree-frog, an unidentified species of *Pseudophryne*, and an extant burrowing species, Sudell's Frog *Neobatrachus sudelli* (Tyler and Prideaux, 2016).

1.7.6 Taxonomic diversity of birds

Bird fossils recovered from the earliest expeditions to the Thylacoleo Caves were the basis of the species list published by Prideaux *et al.* (2007). Some bones were from associated skeletons, and others were disassociated, isolated skeletal elements. Most were recovered from the surface of LBC and LTC, with a small number excavated from a test pit dug in the infill sediment of LBC. Bird fossils from the original excavations were identified by Dr Walter Boles, who found 18 bird taxa from eight orders and ten families (Table 1.7), 13 of which were non-passerine taxa, and five of which were passerines. The number of specimens and the locations from which they were recovered (floor or test pit) were not listed by Prideaux *et al.* (2007), so the bird taxon list as reported was based on a time-averaged assemblage. It could have included specimens from the Early, Middle and Late Pleistocene (see *Age of the fossil deposits* above).

In contrast to the remarkable marsupial assemblage from the locality, with its diversity of known and new extinct Pleistocene taxa, only one extinct species of bird, the 'giant malleefowl' *Progura gallinacea*, was recorded, and no new taxa were noted. *Progura gallinacea* had only previously been recorded from Pleistocene fossil deposits in the eastern half of Australia, thus the locality recorded a significant westerly extension of its known range.

Extant taxa somewhat outside of their known late Holocene range include: the Black-tailed Native-hen *Tribonyx ventralis*, a species of rail that is common through much of Australia but is only found at the southern margins of the Nullarbor region today and is absent from the treeless plain; the Australian Ringneck *Barnardius zonarius*, a parrot common through much of Australia, and which is found in habitats peripheral to the treeless plain; the Torresian Crow *Corvus orru*, which has a core range in the northern two-thirds of Australia but occurs as far south as the Great Victoria Desert, north of the Nullarbor; and the Little Raven *Corvus mellori*, a species of south-eastern Australia whose modern range extends to the Eyre Peninsula immediately to the east of the Nullarbor region, but which does not occur on the Plain. There is thus evidence of modest range extensions in a few species, although all of these occur in the Eyrean avifaunula today (see Section 1.4.4). All bird taxa identified from Thylacoleo Caves were regarded by Prideaux *et al.* (2007) as habitat generalists, and minimal palaeoenvironmental interpretation was therefore attempted based on the cave's avifauna. However, the presence of several species of hollow-nesting parrot was considered indicative of a woodland environment.

Table 1.7: List of bird taxa from the preliminary analysis of the Thylacoleo Caves vertebrate fauna

Order	Family	Genus/species	Common name
Casuariiformes	Casuariidae	*Dromaius novaehollandiae*	Emu
Galliformes	Megapodiidae	*Progura* (as *Leipoa*) *gallinacea*	Extinct 'giant malleefowl'
Accipitriformes	Accipitridae	Accipitridae indet.	Indeterminate bird of prey (small)
		Accipitridae indet.	Indeterminate bird of prey (medium)
Falconiformes	Falconidae	*Falco cenchroides*	Nankeen Kestrel
		Falco sp. indet.	Indeterminate kestrel/falcon
Gruiformes	Rallidae	*Tribonyx* (as *Gallinula*) *ventralis*	Black-tailed Native-hen
Strigiformes	Tytonidae	*Tyto* sp. cf. *T. alba*	Barn Owl
		Tyto sp. indet. 1	Indeterminate tytonid owl 1
		Tyto sp. indet. 2	Indeterminate tytonid owl 2
Psittaciformes	Psittacidae	*Barnardius zonarius*	Australian Ringneck parrot
		cf. *Melopsittacus undulatus*	Budgerigar
		Psittacidae indet.	Indeterminate parrot (medium)
Passeriformes	Corvidae	*Corvus mellori*	Little Raven
		Corvus orru	Torresian Crow
	Indet.	Passeriformes indet. (≥3 spp.)	Indeterminate passerine species

1.7.7 Palaeoecology

Due to the lack of pollen preserved in sediments from the Thylacoleo Caves, interpretation of the Middle Pleistocene flora of the region was based on the vertebrate fauna (Prideaux *et al.* 2007). The species assemblage was interpreted as indicating a mosaic of scleromorphic shrubland and open woodland. Presence of trees was inferred from arboreal taxa such as possums, tree-kangaroos and parrots, as well as small fungivores that would have foraged in woodland. The marsupial fauna includes a mixture of grazing (grass-eating) and browsing (leaf- and stem-eating) species with a large range of body sizes and morphology, indicating that the regional vegetation was diverse. The locality contains a higher proportion of grazing species than Pleistocene sites in mesic south-western and south-eastern Australia, with a composition more similar to Pleistocene faunas of inland Australia. This is considered indicative of a dry, relatively open habitat (Prideaux *et al.* 2007).

Compared to today, it is considered likely that during the Middle Pleistocene the Nullarbor Plain was home to a higher proportion of plants with palatable leaves and fleshy fruits, such as are found today in the peripheral woodlands but not on the plain itself. Examples included mistletoes (Loranthaceae), *Acacia* species (Leguminaceae), *Eremophila* and *Myoporum* (Myoporaceae), *Pittosporum* (Pittosporaceae), quandong and sandalwoods (Santalaceae), and Australian rosewoods (Sapindaceae) (Prideaux *et al.* 2007).

The climatic envelope of the Thylacoleo Caves fauna was investigated via two methods. One used the upper and lower rainfall bounds of extinct taxa found in the deposit, based on modern mean annual rainfall at all known localities where each taxon occurred. The overlap in lowest and highest rainfall values was used to estimate the climatic tolerance of the faunal assemblage, with values found to overlap at 260 mm average annual rainfall.

The second method measured stable carbon and oxygen isotope ratios in the dental enamel of herbivorous marsupials, which records average isotopic values of plants consumed by the animals during their lives. Plant isotopic values is controlled by local climatic conditions (rainfall and evaporation), so the isotopic values of mammal teeth indirectly measures moisture balance in the region an animal inhabited (Hedges *et al.* 2005). Stable carbon isotope values of the fossils, expressed as δ^{13}C ‰, ranged from –13.3 to –7.2‰. This is intermediate between values of modern kangaroos and wombats in the Hampton Tableland at the southern margin of the Nullarbor, which receives 240–270 mm average annual rainfall, and the more arid northern Nullarbor Plain, which receives ~180 mm. Stable oxygen isotope values (δ^{18}O ‰) of the fossils ranged from –0.1 to 7.6‰, overlapping the mid-range of values from the moister Hampton Tableland (–4.4 to 4.2‰) and the mid- to upper range values from the more arid northern Nullarbor Plain (2.0 to 8.4‰).

Overall, combined isotopic evidence and rainfall estimates based on the faunal assemblage indicates that during the Middle Pleistocene, the Nullarbor Plain was a little moister than today, but not dramatically so, with an estimated mean annual rainfall of 230–260 mm (Prideaux *et al.* 2007). A paradox has thus emerged about the palaeoecological history of the region. It has usually been suggested that the Nullarbor Plain lost its trees during the Pleistocene in response to climatic change, specifically increased aridity, yet the Thylacoleo Caves vertebrate assemblage, with its arboreal taxa such as tree-kangaroos and hollow-nesting parrots, indicates that trees were present on the Nullarbor Plain under an arid- to semi-arid climatic regime during the Middle Pleistocene. Therefore, it seems unlikely that there was a straightforward relationship between low annual rainfall and deforestation of the Nullarbor during the Pleistocene, and alternative explanations for vegetation turnover must be sought.

As suggested by Prideaux *et al.* (2007), burning of the vegetation by humans during the Late Pleistocene may have led to the final loss of trees from the Nullarbor Plain and the transition to the modern, fire-resistant chenopod shrubland that characterises the region. However, a chronology for the final loss of trees from the Nullarbor Plain has not yet been established. Arguably, if humans altered the vegetation of the Nullarbor within the last 50,000 years, thereby creating a biogeographical barrier to the dispersal of tree-dependent animal taxa between south-western and south-eastern Australia during the Late Pleistocene, this should be evident from phylogeographic studies. Divergence dates a little younger than this have been indicated for some bird taxa on either side of the Nullarbor region (e.g. 36 kyr for populations of Australian Magpie *Cracticus tibicen* by Toon *et al.* 2007; and a similar date for Musk Duck *Bizura lobata* by Guay *et al.* 2010). Magpies are woodland-dependent and so could potentially have been affected by a loss of trees due to burning at this time. However, Musk Ducks are water-dependent rather than tree-dependent, and aridity would be a better explanation for limited east-west gene flow in this taxon.

1.8 The way forward: knowledge gaps and potential of the Thylacoleo Caves vertebrate fauna

1.8.1 Avifauna

The preliminary analysis of the Thylacoleo Caves vertebrate fauna and the associated palaeoecological reconstruction by Prideaux *et al.* (2007) focused primarily on mammals. Other vertebrate remains, including avian fossils, have been less well studied. Birds were included as a minor component, providing a baseline species list of 18 taxa for the locality, but this was based primarily on fossils that were recovered from surface deposits and were likely time-averaged. As with the vertebrate fauna as a whole, an analysis to assess the diversity of birds through time was therefore not possible, and the assemblage was attributed to the Middle Pleistocene.

However, a test pit dug in LBC indicated that the sediment sequence spanned the Early and Middle Pleistocene (Prideaux *et al.* 2007), revealing the potential for further excavations and analysis. Subsequent fieldwork seasons, in 2009, 2011, 2013 and 2014, led to the recovery of hundreds of additional fossil bird bones from the Thylacoleo Caves, particularly from LBC, with pit excavations extending back through the Middle and Early Pleistocene sediments. The newly collected fossil bird material therefore has potential for investigating the diversity and distribution of birds in south-central Australia during a half-a-million year or more interval of the Pleistocene. This is the first such record for the region and for Australia. It represents the best opportunity to date to directly investigate the diversity and distribution of birds in southern Australia during an interval that is thought to have been key in establishing the Australian avifauna prior to the arrival of humans in the landscape.

Considerable research effort in recent years has been dedicated to attempting to untangle the biogeographical history of birds in southern Australia. Genetic studies in particular have increasingly highlighted idiosyncratic, taxon-specific responses to ecological change in the region. This was foreshadowed by Cracraft (1986), who acknowledged that different bird clades may not have responded with the same patterns to ecological changes in southern Australia during the Plio-Pleistocene, and that there was a need to search for a biogeographical model that could explain variable patterns between different clades. Now, more than thirty years later, it seems as if we may finally be able to begin assessing in earnest how, when and why various taxa did or did not become separated at the Nullarbor Plain during the Pleistocene, by combining molecular perspectives with new palaeontological evidence. This may lead to the development of a new paradigm for understanding the biogeographical history of birds, and other taxa, in southern Australia.

1.8.2 Palaeoecological reconstruction of the Nullarbor Plain

We currently lack a clear picture of how the regional flora and fauna changed – if indeed it did change – from the Early Pleistocene into the Middle Pleistocene. The Thylacoleo Caves fossil deposit spans this crucial time interval, referred to as the mid-Pleistocene transition, or mid-Pleistocene revolution, when changes in the Earth’s orbit led to 41-kyr glacial–interglacial cycles being replaced with 100-kyr cycles (Ford *et al.* 2016). Geological evidence shows that the transition led to climatic changes, notably heightened aridity, in southern Australia (Pillans and Bourman 2001), but its impact on the Nullarbor ecosystem has not been established. The pit excavations of LBC offer a unique opportunity to investigate whether a signature of this transition is recorded in the vertebrate fauna. The research presented in later chapters exploits the utility of birds for palaeoecological reconstruction, given their often very specific and well-established habitat requirements in terms of roosting, nesting, feeding and drinking (see Baird 1989). Ultimately, the data on birds will be combined with data on other vertebrate orders. This will allow a richer interpretation of the Pleistocene ecology of the Nullarbor Plain, and an assessment of whether different vertebrate groups had concordant or discordant responses to ecological change in the region during the mid-Pleistocene transition.

1.9 Aim and objectives of the thesis

The overarching aim of the thesis is to use the fossil assemblage from the Thylacoleo Caves to investigate the diversity and distribution of non-passerine birds on the Nullarbor Plain during the Early and Middle Pleistocene. This aim is addressed via the following objectives:

1) Determine the diversity of non-passerine birds in the Thylacoleo Caves fossil deposit during the Early and Middle Pleistocene using a systematic palaeontological approach
2) Conduct a time-series analysis of the non-passerine fossil assemblage from LBC, to determine whether the Thylacoleo Caves records changes in the composition of the avifauna during the Early and Middle Pleistocene
3) Use the non-passerine fossil assemblage from LBC to reconstruct the palaeoecology of the Nullarbor Plain during the Early and Middle Pleistocene, and determine if this supports the ecological interpretation of Prideaux *et al.* (2007) that the local Pleistocene habitat was a mosaic of a woodland/shrubland in an arid- to semi-arid climatic regime
4) Determine whether the Thylacoleo Caves fossil fauna records range changes for extant species of bird since the Pleistocene, with particular reference to the role of the Nullarbor Plain as a biogeographical barrier to the dispersal of birds in southern Australia
5) Identify and describe new extinct species of non-passerine bird from the Thylacoleo Caves, if applicable
6) Discuss the relevance of the findings for advancing knowledge about the diversity, distribution and evolutionary history of the Australian avifauna.

1.10 Methods

Specific methodologies for individual components of the research project are given in Chapters 2, 3 and 4. The following sections outline the general methodological approach taken in the research project as a whole.

1.10.1 Fieldwork

Fossil material used in this study was collected during various fieldwork seasons at the Thylacoleo Caves between 2002 and 2014. The material is the result of successive excavations by teams of professional palaeontologists, students, volunteers, and caving experts. Early fieldwork seasons were led by John Long, then of the Western Australian Museum, Perth, and Gavin Prideaux, of Flinders University, Adelaide. Later seasons were headed by Gavin Prideaux. My own involvement in fieldwork at the locality comprised two field trips of three weeks each, the first in April/May 2013, during which excavations of Pits A and B in LBC were expanded, the second in April/May 2014, focusing mainly on LTC and FSC.

1.10.2 Excavation and processing of fossils and sediments

Surface specimens were collected from the rockfall areas and cave floors by hand. Details of the pit excavations in LBC are provided in Chapter 4. In the pit excavations, larger fossil specimens were treated *in situ* with a plastic hardener (a polyvinyl, Mowital®) dissolved in ethanol, to allow their intact removal once dry. Smaller bones were not treated individually in the field, and were removed along with the bulk sediment, which was collected in sacks and removed from the cave for processing aboveground.

Aboveground sediment processing techniques were optimised for the field conditions, and were dictated by the remoteness of the location many hours' drive from the nearest habitation, and the limited availability of water during three-week long field seasons. The main constraint was the need to minimise the amount of bulk material to be transported 1,000 km by road back to the laboratory from the field. Due to the scarcity of water, all of which had to be transported to the site by vehicle, sediment was first dry-sieved to remove as much loose material as possible. Wet-sieving only would have been ideal so as to minimise potential abrasion of fossil specimens from dry-sieving, but the need to conserve water meant that this was not feasible. After dry-sieving, the remaining fossiliferous sediment was transferred to wet-sieves where it was soaked and then washed by hand to remove sand, silt and clay. The remaining fraction, comprising bone, teeth and gravel, was then transferred to calico bags and dried for transport. Care was taken at all stages to keep stratigraphic data with the specimens.

1.10.3 Laboratory work

1.10.3.1 Specimen sorting

In the laboratory, bags of sieved material were sorted in trays, and a paintbrush and tweezers were used to remove fossils from remaining sediment. I removed the majority of the bird material myself, but various other workers also assisted.

1.10.3.2 Specimen curation

All bird fossils collected from the Thylacoleo Caves and used in this thesis have been given a WAM (Western Australian Museum) catalogue number. All material will ultimately be deposited at the Museum, in Perth, Western Australia. Some specimens used in the preliminary analysis of the Thylacoleo Caves fauna by Prideaux *et al.* (2007) had previously been given WAM catalogue numbers prior to the commencement of my doctoral research in 2012. I have retained these original numbers where appropriate, for example where a collection of bones registered under a number were from a single associated skeleton, but have given new numbers to some specimens if they were from different taxa and needed to be documented separately.

For specimens collected in field seasons during the 2009–2014 interval, I initially used my own interim cataloguing system which incorporated details of the cave, pit, quadrat, and excavation depth (e.g.

LBC.B3.120.125.001 = Leaena's Breath Cave, Pit B, Quadrat 3, 120–125 cm, specimen 001). Specimens catalogued with this interim system were later given WAM numbers, and these are used throughout the thesis. Details of each specimen were recorded in an Excel spreadsheet, and additional information, such as taxonomic data, was later added as the specimens were identified during the course of this study. This is the basis of the analysis in Chapter 4.

1.10.3.3 Specimen identification

Identification of fossil bird bones was primarily by comparison with modern and fossil bird skeletons from various museum collections around Australia. Most modern reference skeletons were from the Ornithology collection of the South Australian Museum (SAM), Adelaide, but these were supplemented with material loaned primarily from Museum Victoria (MV) Melbourne, Australian Museum (AM), Sydney, and the Queensland Museum (QM), Brisbane.

Bones were identified with the naked eye and under a low-powered light microscope. Particularly early on in my learning curve, specimen identification was an iterative process where I first identified bones to order or family level by comparisons with a representative taxon from each order represented in the modern Australian avifauna. Identification was also informed by reference to the osteological/palaeontological literature, and I sought expert opinion when required, primarily from Associate Professor Trevor Worthy, who co-supervised this research, but also from Dr Jacqueline Nguyen of the Australian Museum, Sydney, and Dr Vanesa De Pietri of the Canterbury Museum, Christchurch, New Zealand. I reviewed all specimens at least once, making corrections to identifications as my skill-level increased.

Identifications were later refined where possible to genus or species, by comparison with a more comprehensive set of reference skeletons. Identification effort focused upon the most diagnostic elements, mainly limb bones. Less informative elements such as vertebrae and phalanges were generally not considered.

1.10.4 General approach to analysing the avifauna

Due to the need to circumscribe the scope of the research project, two pragmatic decisions were taken. One was to limit the research presented in the thesis to non-passerine birds only, as in many other studies (e.g. Campbell 1979; Olson and James 1991; Steadman and Mead 2010; Meijer *et al.* 2013). Research on the passerine component of the Thylacoleo Caves avifauna will form the basis of a separate research project, and eventually data on passerines and non-passerines will be combined. The second restriction on the scope of the project was to focus the analysis in Chapter 4 on bird fossils from Pit B in LBC, which was the more extensive of the two pits dug in the cave. Surface material, which is of uncertain age, is also documented, but pit material, which is constrained by age, forms the basis of the palaeoecological interpretation of the Pleistocene avifauna. A limited amount of fossil material from Pit A in LBC is also included in the Systematic Palaeontology of the locality (Chapter 4), but most material from this pit is yet been identified, and will be studied at a later date.

1.10.5 Descriptions of new taxa

During the course of the research project, I identified the remains of several birds from the Thylacoleo Caves that are new or are likely to be new extinct taxa. Some of these are formally described in Chapters 2 and 3 (published papers), and as a result it has been necessary to incorporate relevant fossil specimens from other Australian localities into these chapters. The geographic and temporal scope of the thesis, while focusing mainly on the Early and Middle Pleistocene fauna from the Thylacoleo Caves as in the original aims of the research project, therefore extends beyond this in places.

Given their number, it has not been possible to describe all new taxa during the course of this project. Likely new taxa are noted in the Systematic Palaeontology section of Chapter 4, and while some features that distinguish them from extant taxa are reported, these do not constitute formal descriptions. These taxa will be formally described for publication at a later date.

1.11 Summary

The Pleistocene has long been regarded as a key interval that shaped the diversity and distribution of birds in Australia, laying the foundations of the diversity and distribution of the modern continental avifauna. The primary influences believed to have shaped the continental avifauna, including both the distribution of characteristic regional species assemblages (avifaunulas) and the generation of species and sub-species by vicariance, were: 1) cool–arid phases alternating with warm–moist phases driven by global climatic cycles of the Pleistocene, overlain by an increasing trend towards aridity; and 2) the associated cyclical contraction of mesic habitat and expansion of arid habitat, with a trend towards the dominance of the arid zone. These processes are thought to have led to the creation of arid-habitat barriers that effectively confined bird populations to mesic refugia during arid phases of the Pleistocene, thus shaping their evolution.

The Nullarbor Plain has historically been regarded as one of the major arid-habitat barriers in southern Australia because of its lack of trees and surface water, but recent research on extant fauna has been equivocal about the importance of the ‘Nullarbor Barrier’ in controlling gene flow between populations of mesic taxa across southern Australia. A body of recent research into the genetics of various taxa has inferred varied faunal responses to climatic cycles of the Pleistocene: for some taxa, the Nullarbor Plain does not appear to have functioned as a barrier at all; for other taxa, other barriers, particularly the Eyrean Barrier, appear to have exerted more influence; and for taxa that do appear to have been separated by aridity and/or vegetation change in the Nullarbor region, the timing of vicariance appears to have been asynchronous among different species. We currently lack a comprehensive framework for understanding both the nature and the timing of climatic events and habitat transitions that shaped the southern Australian fauna.

Until recently, the vertebrate fossil record has been largely silent on the Pleistocene palaeoecology of the Nullarbor Plain. The discovery of the Thylacoleo Caves fossil deposit in 2002 was a major breakthrough in terms of the potential for understanding the faunal and floral composition of the Nullarbor Plain during the Early and Middle Pleistocene. The preliminary analysis of the fauna indicated that the assemblage represented a mosaic habitat of woodland and shrubland under an arid- to semi-arid climatic regime.

As at 2007, around 18 bird taxa were known from the deposit, including one extinct species, and no new extinct bird taxa. The avifaunal assemblage included several species of hollow-nesting parrot, and contributed to the interpretation that the Middle Pleistocene habitat of the region included trees. However, birds were not the main focus of the study by Prideaux et al. (2007), and their analysis was based on a time-averaged assemblage of mammals. Following further excavations, hundreds of additional bird fossils have now been recovered from the Thylacoleo Caves. This study will document the diversity of the non-passerine fossil avifauna contained within the Thylacoleo Caves fossil deposits, as a way of investigating the diversity and distribution of birds in southern Australia during the Early and Middle Pleistocene. The avian assemblage will be used to help reconstruct the local ecology of the Nullarbor Plain during a crucial phase in the development of the modern avifauna of southern Australia.

1.12 Structure of this thesis

The subsequent chapters of this thesis include a mixture of published and unpublished work. Chapters 2 and 3 are reproductions of peer-reviewed, published journal articles in which I and my co-authors describe extinct taxa from the Thylacoleo Caves and other Pleistocene fossil localities. Chapter 4, which presents the systematic palaeontology of the non-passerine birds from the Thylacoleo Caves and an analysis of the palaeoecology of the Nullarbor Plain during the Early and Middle Pleistocene, has not been submitted for publication. However, for consistency with the journal-article format of Chapters 2 and 3, Chapter 4 is written in the style of a stand-alone manuscript. For this reason, Chapter 4 duplicates some background information included in Chapter 1. Chapter 5 (unpublished) comprises a synthesis of the three data chapters (2, 3 and 4), and a general discussion of how the original work presented in this thesis contributes to the advancement of our knowledge of the Pleistocene avifauna of Australia. It also contains suggested directions for future research.

1.13 References

Ayliffe, L.K., Marianelli P.C., Moriarty K.C., Wells R.T., McCulloch M.T., Mortimer G.E., and Hellstrom J.C. 1998. '500 ka precipitation record from southeastern Australia: evidence for interglacial relative aridity'. *Geology* 26 (2): 147–150.

Ayliffe, L.K., and Veer H.H. 1988. 'Uranium-series dating of speleothems and bones from Victoria Cave, Naracoorte, South Australia'. *Chemical Geology: Isotope Geoscience Section* 72(3): 211–234.

Baird, R.F. 1984. 'The Pleistocene distribution of the Tasmanian Native-Hen *Gallinula mortierii mortierii*'. *Emu* 84(2): 119–123.

Baird, R.F. 1989. 'Fossil bird assemblages from Australian Caves: precise indicators of late Quaternary Environments?' *Palaeogeography, Palaeoclimatology, Palaeoecology* 69: 241–44.

Baird, R.F. 1990. 'The fossil avian assemblage from Weekes Cave (N-15), Nullarbor Plain, South Australia: corrections, additions and reinterpretation'. *South Australian Ornithologist* 31: 29–35.

Baird, R.F. 1993. 'Pleistocene avian fossils from Pyramids Cave (M-89), Eastern Victoria, Australia'. *Alcheringa: An Australasian Journal of Palaeontology* 17(4): 383–404.

Baird, R.F. and Vickers-Rich, P. 1998. '*Palaelodus* (Aves: Palaelodidae) from the Middle to Late Cainozoic of Australia'. *Alcheringa: An Australasian Journal of Palaeontology* 22(2): 135–51.

Baird, R.F. 1985. 'Avian fossils from Quaternary deposits in "Green Waterhole Cave", South-Eastern South Australia'. *Records of the Australian Museum* 37(6): 353–70.

Baird, R.F. 1986. 'The avian portions of the Quaternary cave deposits of southern Australia and their biogeographical and palaeoenvironmental interpretations'. PhD thesis, Monash University, Melbourne.

Baird, R.F. 1991. 'The taphonomy of Late Quaternary cave localities yielding vertebrate remains in Australia'. In *Vertebrate Palaeontology of Australasia*, edited by P. Vickers-Rich, J. Monaghan, R.F. Baird, and T. Rich, 267–301. Pioneer Design Studio, Melbourne.

Baird, R.F., Vickers-Rich P., and van Tets, G. 1991. 'Appendix II: localities yielding avian assemblages of Quaternary age in Australia'. In *Vertebrate Palaeontology of Australasia*, 850–67. Pioneer Design Studio, Melbourne.

Barnosky, A.D, and Lindsey, E.L. 2010. 'Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change'. *Quaternary International* 217 (1–2): 10–29.

Barnosky, A., Koch, P.L., Feranec R.S., Wing, S. and Shabel, A. 2004. 'Assessing the causes of Late Pleistocene extinctions on the continents'. *Science* 306: 70–75.

Barrows, T.T., Stone J.O., Fifield L.K., and Cresswell R.G. 2001. 'Late Pleistocene glaciation of the Kosciuszko Massif, Snowy Mountains, Australia'. *Quaternary Research* 55(2): 179–89.

Beard, J.S., Beeston G.R., Harvey J.M., Hopkins A.J.M., and Shepherd D.P. 2013. 'The vegetation of Western Australia at the 1:3,000,000 Scale. Explanatory Memoir. Second Edition'. *Conservation Science Western Australia* 9(1): 1–152.

BirdLife Australia. 2017. 'The BirdLife Australia working list of Australian Birds, Version 2.1'. BirdLife. Available: http://www.birdlife.org.au/documents/BWL-BirdLife_Australia_Working_List_v2.1.xlsx.

Blyth, A.J., Watson J.S., Woodhead J., and Hellstrom J. 2010. ‘Organic compounds preserved in a 2.9 million year old stalagmite from the Nullarbor Plain, Australia’. *Chemical Geology* 279(3): 101–105.

Boles, W.E. 1995. ‘A preliminary analysis of the Passeriformes from Riversleigh, northwestern Queensland, Australia, with the description of a new species of lyrebird’. *Courier Forschungsinstitut Senckenberg* 181: 163–70.

Boles, W.E. 2001. ‘A swiftlet (Apodidae: Collocaliini) from the Miocene of Riversleigh, Northwestern Queensland’. *Memoirs of the Association of Australasian Palaeontologists* 25: 45–52.

Boles, W.E. 2006. ‘The avian fossil record of Australia: An Overview’. In *Evolution and Biogeography of Australasian Vertebrates*, 387–411. Australian Scientific Publishing, Sydney.

Boles, W.E. 2005. ‘A review of the Australian fossil storks of the genus *Ciconia* (Aves: Ciconiidae), with the description of a new species’. *Records of the Australian Museum* 57(2): 165–178.

Boles, W.E. 2010. ‘A revision of C.W. De Vis’ fossil cormorants (Aves: Phalacrocoracidae). In *Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution*, Ed. W.E. Boles and T.H. Worthy’. *Records of the Australian Museum* 62(1): 145–55.

Brooker, M.G., Ridpath M.G., Estbergs J.A., Bywater J., Hart D.S., and Jones M.S. 1979. ‘Bird observations on the north-western Nullarbor Plain and neighbouring regions, 1967–1978’. *Emu* 79(4): 176–190.

Burbidge, A., Casperson K., and Fuller P. 1987. ‘Birds’. In *A Biological Survey of the Nullarbor Region, South and Western Australia in 1984*, 153–78. Adelaide: South Australian Department of Environment and Planning, Western Australia Department of Conservation and Land Management, Australian National Parks and Wildlife Service.

Burgoyne, I. 2000. *The Mirning - We Are the Whales*. Magabala Books Aboriginal Corporation, Broome, Western Australia.

Burnett, S., Webb J.A., and White S. 2013. ‘Shallow caves and blowholes on the Nullarbor Plain, Australia — flank margin caves on a low gradient limestone platform’. *Geomorphology* 201: 246–53.

Byrne, M. 2008. ‘Evidence for multiple refugia at different time scales during Pleistocene climatic oscillations in southern Australia inferred from phylogeography’. *Quaternary Science Reviews* 27 (27–28): 2576–85.

Byrne, M., Steane D.A., Joseph L., Yeates D.K., Jordan G.J., Crayn D., Aplin K., Cantrill, D., Cook L.G, Crisp, M., Keogh, J.S., Melville, J., Moritz, C., Porch, N., Sniderman, J.M.K., Sunnucks, P., and Weston, P. *et al.* 2011. ‘Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota’. *Journal of Biogeography* 38: 1635–56.

Byrne, M., Yeates D.K., Joseph L., Kearney M., Bowler J., Williams M.A.J., Cooper S., Donnellan, S.C., Keogh, J.S., Leys, R., Melville, J., Murphy, D.J., Porth, N. and Wyrwoll, K-H. 2008. ‘Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota’. *Molecular Ecology* 17(20): 4398–4417.

Campbell, K.E. 1979. *The non-passerine Pleistocene avifauna of the Talara Tar Seeps, Northwestern Peru*. Toronto. *Life Sciences Contribution 118*, Royal Ontario Museum.

Campos, P.F., Sher A., Mead J.I., Tikhonov A., Buckley M., Collins M., Willerslev E., and Gilbert M.T.P. 2010. 'Clarification of the taxonomic relationship of the extant and extinct ovibovids, *Ovibos*, *Praeovibos*, *Euceratherium* and *Bootherium'*. *Quaternary Science Reviews* 29 (17–18): 2123–2130.

Christidis, L., and W. Boles. 2008. *Systematics and Taxonomy of Australian Birds*. CSIRO Publishing, Victoria.

Cohen, K., and Gibbard P. 2011. '2011 global chronostratigraphical correlation table for the last 2.7 million years.' Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy), Cambridge, England.

Cohen, T.J., Nanson G.C., Jansen J.D., Jones B.G., Jacobs Z., Treble P., Price D.M., May, J.H., Smith, A.M., Ayliffe, L.K. 2011. 'Continental aridification and the vanishing of Australia's megalakes'. *Geology* 39(2): 167–170.

Commonwealth of Australia. 2012. 'Interim Biogeographic Regionalisation for Australia, Version 7'. Commonwealth of Australia. http://www.environment.gov.au/parks/nrs/science/bioregion-framework/ibra/maps.html.

Cracraft, J. 1986. 'Origin and evolution of continental biotas - speciation and congruence within the Australian avifauna'. *Evolution* 40(5): 977–96.

Crisp, M., and Cook L. 2007. 'A congruent molecular signature of vicariance across multiple plant lineages'. *Molecular Phylogenetics and Evolution* 43: 1106–17.

Guthrie, D.R. 2006. 'New carbon dates link climatic change with human colonization and Pleistocene extinctions'. *Nature* 441 (7090): 207–9.

Dawson, L. 1985. 'Marsupial fossils from Wellington Caves, New South Wales; the historic and scientific significance of the collections in the Australian Museum, Sydney'. *Records of the Australian Museum* 37(2): 55–69.

Dawson, L. 2006. 'An ecophysiological approach to the extinction of large marsupial herbivores in Middle and Late Pleistocene Australia'. *Alcheringa: An Australasian Journal of Palaeontology* 30 (sup1): 89–114.

Debus, S.J.S. 1993. 'The mainland Masked Owl *Tyto Novaehollandiae*: a review'. *Australian Bird Watcher* 15: 168–91.

Dhami, K.K., Joseph, L., Roshier D.A., Heinsohn R., and Peters J.L.. 2013. 'Multilocus phylogeography of Australian teals (*Anas* spp.): a case study of the relationship between vagility and genetic structure'. *Journal of Avian Biology* 44(2): 169–78.

Dickinson, E.C., and Christidis L., eds. 2014. *The Howard and Moore Complete Checklist of the Birds of the World*. 4th ed. Volume 2: Passerines. 2 vols. Aves Press, Eastbourne.

Dickinson, E.C., and Remsen Jr, J.V., eds. 2013. *The Howard and Moore Complete Checklist of the Birds of the World*. 4th ed. Volume 1: Non-passerines. 2 vols. Aves Press, Eastbourne.

Doerr, S.H., Davies R.R., Lewis A., Pilkington G., Webb J.A., Ackroyd P.J., and Bodger O. 2011. 'Origin and karst geomorphological significance of the enigmatic Australian Nullarbor Plain "blowholes"'. *Earth Surface Processes and Landforms*, October. https://doi.org/10.1002/esp.2233.

Dolman, G., and Joseph L. 2012. ‘A species assemblage approach to comparative phylogeography of birds in southern Australia’. *Ecology and Evolution* 2(2): 354–69.

Dolman, G., and Joseph, L. 2015. ‘Evolutionary history of birds across southern Australia: structure, history and taxonomic implications of mitochondrial DNA diversity in an ecologically diverse suite of species’. *Emu* 115: 35–48.

Dunkley, J.R. 1967. ‘The geographical and historical background’. In *Caves of the Nullarbor - A Review of Speleological Investigations in the Nullarbor Plain, Southern Australia*, 1–12. The Speleological Research Council, Sydney.

Environmental Resources Information Network. 2013. ‘Terrestrial Ecoregions in Australia’. Environmental Resources Information Network, Australian Government Department of the Environment.

Faith, J.T. 2011. ‘Late Pleistocene climate change, nutrient cycling, and the megafaunal extinctions in North America’. *Quaternary Science Reviews*.

Field, J., and Wroe, S. 2012. ‘Aridity, faunal adaptations and Australian Late Pleistocene extinctions’. *World Archaeology* 44(1): 56–74.

Field, J., Wroe, S., Trueman C.N., Garvey J., and Wyatt-Spratt S. 2013. ‘Looking for the archaeological signature in Australian megafaunal extinctions’. *Quaternary International* 285 (February): 76–88.

Fillios, M., Field J., and Charles, B. 2010. ‘Investigating human and megafauna co-occurrence in Australian prehistory: mode and causality in fossil accumulations at Cuddie Springs’. *Quaternary International* 211(1–2): 123–143.

Ford, H.L., Sosdian S.M., Rosenthal Y., and Raymo M.E. 2016. ‘Gradual and abrupt changes during the Mid-Pleistocene Transition’. *Quaternary Science Reviews* 148 (September): 222–33.

Ford, J. 1987. ‘Minor isolates and minor geographical barriers in avian evolution in continental Australia’. *Emu* 87: 90–102.

Fu, X., Cohen T.J., and Arnold L.J. 2017. ‘Extending the record of lacustrine phases beyond the last interglacial for Lake Eyre in Central Australia using luminescence dating’. *Quaternary Science Reviews* 162 (April): 88–110.

Fujioka, T., and Chappell, J. 2010. ‘History of Australian aridity: chronology in the evolution of arid landscapes’. *Geological Society Special Publications* 346: 121–39.

Fujioka, T., Chappell, J., Fifield L.K., and Rhodes E.J. 2009. ‘Australian desert dune fields initiated with Pliocene–Pleistocene global climatic shift’. *Geology* 37(1): 51–54.

Fujioka, T., Chappell, J., Honda M., Yatsevich I., Fifield K., and Fabel D. 2005. ‘global cooling initiated stony deserts in central Australia 2–4 Ma, Dated by Cosmogenic ^{21}Ne-^{10}Be’. *Geology* 33(12): 993–996.

Garnett, S., Szabo J., and Dutson G. 2011. *The Action Plan for Australian Birds 2010*. CSIRO Publishing, Birds Australia, Victoria.

Gentilli, J. 1949. ‘Foundations of Australian bird geography’. *Emu* 49: 85–129.

Gibbard, P.L., Head M.J., Walker M.J.C., and the Subcommission on Quaternary Stratigraphy. 2010. 'Formal ratification of the Quaternary system/period and the Pleistocene series/epoch with a base at 2.58 Ma'. *Journal of Quaternary Science* 25 (2): 96–102.

Gibbard, P.L., and Lewin J. 2016. 'Partitioning the Quaternary'. *Quaternary Science Reviews* 151 (November): 127–39.

Gillieson, D.S., Cochrane J.A., and Murray A. 1994. 'Surface hydrology and soil movement in an arid karst: the Nullarbor Plain, Australia'. *Environmental Geology* 23(2): 125–133.

Gillieson, D., Wallbrink P., and Cochrane A. 1996. 'Vegetation change, erosion risk and land management on the Nullarbor Plain, Australia'. *Environmental Geology* 28(3): 145–153.

Goede, A., Harmon R.S., Atkinson T.C., and Rowe P.J. 1990. 'Pleistocene climatic change in southern Australia and its effect on speleothem deposition in some Nullarbor caves'. *Journal of Quaternary Science* 5(1): 29–38.

Grellet-Tinner, G., Spooner N.A., Handley W.D., and Worthy T.H. 2017. 'The *Genyornis* egg: response to Miller *et al.*'s commentary on Grellet-Tinner *et al.* 2016'. *Quaternary Science Reviews*, February.

Grellet-Tinner, G., Spooner, N.A, and Worthy T.H. 2016. 'Is the "*Genyornis*" egg of a mihirung or another extinct bird from the Australian dreamtime?' *Quaternary Science Reviews* 133 (February): 147–64.

Groucutt, H.S., Petraglia, M.D., Bailey, G., Scerri, E.M.L., Parton, A., Clark-Balzan, L., Jennings, R.P. Lewis, L., Blinkhorn, J., Drake, N.A., Breeze, P.S., Inglis, R.H., Deves, M.H., Meredith-Williams, M., Boivin, N., Thomas, M.G. and Scally, A. 2015. 'Rethinking the dispersal of *Homo sapiens* out of Africa'. *Evolutionary Anthropology: Issues, News, and Reviews* 24 (4): 149–64.

Grün, R., Eggins, S., Aubert, M., Spooner, N., Pike, A.W.G., and Müller, W.. 2010. 'ESR and U-Series analyses of faunal material from Cuddie Springs, NSW, Australia: implications for the timing of the extinction of the Australian megafauna'. *Quaternary Science Reviews* 29(5–6): 596–610.

Guthrie, R.D. 2000. 'Origin and causes of the Mammoth Steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia'. *Quaternary Science Reviews* 20: 549–74.

Hamm, G., Mitchell, P., Arnold, L.J., Prideaux, G.J., Questiaux, D., Spooner, N.A., Levchenko, V.A., Foley, E.C., Worthy, T.H., Stephenson, B., Coulthard, V., Coulthard, C., Wilton, S., and Johnston, D. 2016. 'Cultural innovation and megafauna interaction in the early settlement of arid Australia'. *Nature* 539(7628): 280–83.

Hawkins, B., Diniz-Filho, J., and Soeller, S. 2005. 'Water links the historical and contemporary components of the Australian bird diversity gradient'. *Journal of Biogeography* 32: 1035–42.

Hedges, R., Stevens, R., and Koch, P.L. 2005. 'Isotopes in bones and teeth'. In *Isotopes in Palaeoenvironmental Research*, edited by M.J. Leng, 117–45. Springer, The Netherlands.

Helgen, K.M., Portela Miguez R., Kohen, J. and Helgen, L. 2012. 'Twentieth Century occurrence of the long-beaked echidna *Zaglossus bruijnii* in the Kimberley Region of Australia'. *ZooKeys* 255 (December): 103–32.

Helgen, K.M., Wells, R.T., Kear, B.P. Gerdtz, W.R. and Flannery, T.F. 2006. 'Ecological and evolutionary significance of sizes of giant extinct kangaroos'. *Australian Journal of Zoology* 54(4): 293.

Heupink, T.H., Huynen, L., and Lambert, D.M.. 2011. ‘Ancient DNA suggests dwarf and ‘giant’ emu are conspecific’. *PloS One* 6(4): e18728.

Hocknull, S.A, Zhao, J.X., Feng, Y.X., and Webb, G.E. 2007. ‘Responses of Quaternary rainforest vertebrates to climate change in Australia’. *Earth and Planetary Science Letters* 264: 317–31.

Hocknull, S.A. 2009 (unpub.). *Late Cainozoic Rainforest Vertebrates from Australopapua: Evolution, Biogeography and Extinction.* PhD Thesis, University of New South Wales, Sydney.

Holm, S.R., and Svenning, J.C. 2014. ‘180,000 years of climate change in Europe: avifaunal responses and vegetation implications’. Edited by M. Hofreiter. *PLoS ONE* 9(4): e94021.

Hope, J.H., Lampert, R.J., Edmondson, E., Smith, M.J., and van Tets, G.F. 1977. ‘Late Pleistocene faunal remains from Seton Rock Shelter, Kangaroo Island, South Australia’. *Journal of Biogeography*, 363–385.

Horton, D.R. 1996. ‘The AIATSIS Map of Indigenous Australia’. Australian Institute of Aboriginal and Torres Strait Islander Studies. https://aiatsis.gov.au/explore/articles/aiatsis-map-indigenous-australia.

James, J.M., Contos, A.K. and Barnes, C.M. 2012. ‘Nullarbor Caves, Australia’. *Chemical Geology* 179 (1): 167–186.

Jankowski, N.R., Gully, G.A., Jacobs, Z., Roberts, R.G. and Prideaux, G.J. 2016. ‘A late Quaternary vertebrate deposit in Kudjal Yolgah Cave, south-western Australia: refining regional Late Pleistocene Extinctions’. *Journal of Quaternary Science* 31(5): 538–50.

Johnson, C.N. 2002. ‘Determinants of loss of mammal species during the late Quaternary “megafauna” extinctions: life history and ecology, but not body size’. *Proceedings of the Royal Society B: Biological Sciences* 269(1506): 2221–27.

Johnson, C.N., Alroy, J., Beeton, N.J., Bird, M.I., Brook, B.W., Cooper, A., Gillespie, R., Herrando-Perez, S., Jacobs, Z., Miller, G.H., Prideaux, G.J., Roberts, R.G., Rodriguez-Rey, M., Saltre, F., Turney, C.S.M. and Bradshaw, C.J.A. 2016. ‘What caused extinction of the Pleistocene megafauna of Sahul?’ *Proceedings of the Royal Society B: Biological Sciences* 283(1824): 20152399.

Johnson, N., and Cicero, C. 2004. ‘New mitochondrial DNA data affirm the importance of Pleistocene speciation in North American Birds’. *Evolution* 58(5): 1122–1130.

Joseph, L., and Omland, K.E. 2009. ‘Rowley Review – Phylogeography: its development and impact in Australo-Papuan ornithology with special reference to paraphyly in Australian birds’. *Emu* 109(1): 1–23.

Joseph, L., Toon, A., Schirtzinger, E.E., and Wright, T.F. 2011. ‘Molecular systematics of two enigmatic genera *Psittacella* and *Pezoporus* illuminate the ecological radiation of Australo-Papuan parrots (Aves: Psittaciformes)’. *Molecular Phylogenetics and Evolution* 59(3): 675–684.

Joseph, L., Edwards, S.V., and McLean, A.J. 2013. ‘The Maluridae: inferring avian biology and evolutionary history from DNA sequences’. *Emu* 113 (3): 195–207.

Joseph, L., Slikas, B., Alpers, D. and Schodde, R. 2001. ‘Molecular systematics and phylogeography of New Guinean logrunners (Orthonychidae)’. *Emu* 101(4): 273–280.

Kaal, J., Schellekens, J., Nierop, K.G.J., Martínez Cortizas, A. and Muller, J. 2014. 'Contribution of organic matter molecular proxies to interpretation of the last 55ka of the Lynch's Crater Record (NE Australia)'. *Palaeogeography, Palaeoclimatology, Palaeoecology* 414 (November): 20–31.

Kearns, A.M., Joseph, L. and Cook, L.G. 2010. 'The impact of Pleistocene changes of climate and landscape on Australian birds: a test using the Pied Butcherbird (*Cracticus nigrogularis*)'. *Emu* 110(4): 285–295.

Keast, JA. 1961. 'Bird speciation on the Australian continent', *Bulletin of the Museum of Comparative Zoology* (123): 303–495.

Lambeck, K., and Chappell, J. 2001. 'Sea level change through the last glacial cycle'. *Science* 292: 679–86.

Laslett, T., 2006 (unpub.). *A Palaeoecological Study of a Quaternary Vertebrate Fossil Deposit in Blanche Cave, Naracoorte, South Australia* (Honours Thesis). Flinders University, Adelaide.

Lipar, M., and Ferk, M. 2015. 'Karst pocket valleys and their implications on Pliocene–Quaternary hydrology and climate: examples from the Nullarbor Plain, Southern Australia'. *Earth-Science Reviews* 150 (November): 1–13.

Lipar, M., Webb, J.A., Cupper, M.L., and Wang, N. 2017. 'Aeolianite, calcrete/microbialite and karst in southwestern Australia as Indicators of Middle to Late Quaternary palaeoclimates'. *Palaeogeography, Palaeoclimatology, Palaeoecology* 470 (March): 11–29.

Lowry, D.C, and Jennings, J.N. 1974. 'The Nullarbor karst, Australia'. *Zeitschrift Für Geomorphologie* 18(1): 35–81.

Lundelius, E.L., and Turnbull, W.D. 1978. 'The mammalian fauna of Madura Cave, Western Australia, Part III'. *Fieldiana Geology* 38: 1–120.

Marki, P.Z., Jønsson, K.A., Irestedt, M., Nguyen, J.M.T., Rahbek, C., and Fjeldså, J. 2017. 'Supermatrix phylogeny and biogeography of the Australasian Meliphagides Radiation (Aves: Passeriformes)'. *Molecular Phylogenetics and Evolution* 107 (February): 516–29.

Martin, H. A. 2006. 'Cenozoic Climatic Change and the Development of the Arid Vegetation in Australia'. *Journal of Arid Environments* 66 (3): 533–563.

Martin, H.A. 1973. 'Palynology and historical ecology of some cave excavations in the Australian Nullarbor'. *Australian Journal of Botany* 21(2): 283–316.

Mayr, E. 1944. 'Timor and the colonization of Australia by birds'. *Emu* 44(2): 113–130.

McCracken, K., Fullagar, P., Slater, E., Paton, D.C., and Afton, A.D. 2002. 'Advertising displays of male Musk Ducks indicate population subdivision across the Nullarbor Plain of Australia'. *Wildfowl* 53: 137–54.

McDowell, M.C., and Medlin, G.C. 2010. 'Natural resource management implications of the pre-European non-volant mammal fauna of the southern tip of Eyre Peninsula, South Australia'. *Australian Mammalogy* 32(2): 87.

McGilp, J.N. 1932. 'Birds of the Nullarbor Plain and far west coast of South Australia.' *South Australian Ornithologist* 11(5): 146–151.

McLaren, S., Wallace, M.W., and Reynolds, T. 2012. 'The Late Pleistocene evolution of Palaeo Megalake Bungunnia, southeastern Australia: a sedimentary record of fluctuating lake dynamics, climate change and the formation of the modern Murray River'. *Palaeogeography, Palaeoclimatology, Palaeoecology* 317–318: 114–127.

McLaren, S., and Wallace, M.W. 2010. 'Plio-Pleistocene climate change and the onset of aridity in southeastern Australia'. *Global and Planetary Change* 71(1–2): 55–72.

McLean, A.J., Toon, A., Schmidt, D.J., Joseph, L. and Hughes, J.M. 2012. 'Speciation in Chestnut-Shouldered Fairy-Wrens (*Malurus* spp.) and rapid phenotypic divergence in Variegated Fairy-Wrens (*Malurus lamberti*): a multilocus approach'. *Molecular Phylogenetics and Evolution* 63(3): 668–78.

Meijer, H.J.M., Sutikna, T., Saptomo, E.W., Awe, R.D., Jatmiko, Wasisto, S., James, H.F., Morwood, M.J., and Tocheri, M.W. 2013. 'Late Pleistocene-Holocene non-passerine avifauna of Liang Bua (Flores, Indonesia)'. *Journal of Vertebrate Paleontology* 33(4): 877–94.

Meijer, H.J.M. 2014. 'The avian fossil record in insular southeast Asia and its implications for avian biogeography and palaeoecology'. *PeerJ* 2 (March): e295.

Meijer, H.J.M., and Due, R.A. 2010. 'A new species of giant marabou stork (Aves: Ciconiiformes) from the Pleistocene of Liang Bua, Flores (Indonesia)'. *Zoological Journal of the Linnean Society* 160(4): 707–24.

Meijer, H.J.M., Tocheri, M.W. Due, R.A., Sutikna, T., Saptomo, E.W. and James, H.F. 2015. 'Continental-style avian extinctions on an oceanic island'. *Palaeogeography, Palaeoclimatology, Palaeoecology* 429 (July): 163–70.

Miller, C.R., James, N.P., and Bone, Y. 2012. 'Prolonged carbonate diagenesis under an evolving Late Cenozoic climate; Nullarbor Plain, southern Australia'. *Sedimentary Geology* 261–262 (June): 33–49.

Miller, G., Fogel, M., Magee, J.W., Gagan, M., Clarke, S. and Johnson, B. 2005. 'Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction'. *Science* 309: 287–90.

Miller, G.H., Fogel, M.L., Magee, J.W. and Clarke, S.J. 2017. 'The *Genyornis* egg: a commentary on Grellet-Tinner *et al.* 2016'. *Quaternary Science Reviews*, January.

Miller, G.H., Magee, J.W., Johnson, B.J., Fogel, M.L., Spooner, N.A., McCulloch, M.T. and Ayliffe, L.K. 1999. 'Pleistocene extinction of *Genyornis newtoni*: human impact on Australian megafauna'. *Science* 283(5399): 205–208.

Miller, G., Magee, J., Smith, M., Spooner, N., Baynes, A., Lehman, S., Fogel, M., Johnston, H., Williams, D., Clark, P., Florian, C., Holst, R., DeVogel, S. 2016. 'Human predation contributed to the extinction of the Australian megafaunal bird *Genyornis newtoni* ∼47 Ka'. *Nature Communications* 7 (January): 10496.

Moriarty, K.C., McCulloch, M.T., Wells, R.T., and McDowell, M.C. 2000. 'Mid-Pleistocene cave fills, megafaunal remains and climate change at Naracoorte, South Australia: towards a predictive model using U-Th dating of speleothems'. *Palaeogeography, Palaeoclimatology, Palaeoecology* 159(1–2): 113–143.

Moyle, R.G., Oliveros, C.H., Andersen, M.J., Hosner, P.A., Benz, B.W., Manthey, J.D., Travers, S.L., Brown, R.M. and Faircloth, B.C. 2016. 'Tectonic collision and uplift of wallacea triggered the global songbird radiation'. *Nature Communications* 7 (August): 12709.

Murphy, B.P., Williamson, G.J., and Bowman, D.M.J.S. 2012. 'Did central Australian megafaunal extinction coincide with abrupt ecosystem collapse or gradual climate change?: Megafaunal extinction and climate change'. *Global Ecology and Biogeography* 21(2): 142–51.

Murphy, S.A., Joseph, L., Burbidge, A.H. and Austin, J. 2011. 'A cryptic and critically endangered species revealed by mitochondrial DNA analyses: the Western Ground Parrot'. *Conservation Genetics* 12(2): 595–600.

Murray, P.F., and Vickers-Rich, P. 2004. *Magnificent Mihirungs: The Colossal Flightless Birds of the Australian Dreamtime*. Indiana University Press.

Nadachowska-Brzyska, K., Li, C., Smeds, L., Zhang, G. and Ellegren, H. 2015. 'Temporal dynamics of avian populations during Pleistocene revealed by whole-genome sequences'. *Current Biology* 25(10): 1375–80.

Neaves, L.E., Zenger, K.R., Prince, R.I.T., and Eldridge, M.D.B. 2012. 'Impact of Pleistocene aridity oscillations on the population history of a widespread, vagile Australian mammal, *Macropus fuliginosus*'. *Journal of Biogeography* 39(8): 1545–63.

Nguyen, J., Boles, W., Worthy, T., Hand, S. and Archer, M. 2014. 'New specimens of the Logrunner *Orthonyx kaldowinyeri* (Passeriformes: Orthonychidae) from the Oligo-Miocene of Australia'. *Alcheringa: An Australasian Journal of Palaeontology* 38(2): 245–55.

Nguyen, J.M.T., Hand, S.J., and Archer, M. 2016. 'The Late Cenozoic passerine avifauna from Rackham's Roost Site, Riversleigh, Australia'. *Records of the Australian Museum* 68(5): 201–30.

Nguyen, J.M.T. 2016. 'Australo-Papuan treecreepers (Passeriformes: Climacteridae) and a new species of sittella (Neosittidae: *Daphoenositta*) from the Miocene of Australia'. *Palaeontologia Electronica* 19(1): 1–13.

O'Connell, L.G., James, N.P., and Bone, Y. 2011. 'The Miocene Nullarbor Limestone, Southern Australia; deposition on a vast subtropical epeiric platform'. *Sedimentary Geology* 53: 1–16.

Olson, S.L. 1975. 'The fossil rails of CW De Vis, being mainly an extinct form of *Tribonyx mortierii* from Queensland'. *Emu* 75(2): 49–54.

Olson, S.L. 1977. 'The identity of the fossil ducks described from Australia by CW De Vis'. *Emu* 77(3): 127–131.

Olson, S.L., and James, H.F. 1991. 'Descriptions of Thirty-Two New Species of Birds from the Hawaiian Islands'. *Ornithological Monographs, No.* 45. American Ornithologists' Union, Washington, D.C

Oswald, J.A., and Steadman, D.W. 2011. 'Late Pleistocene passerine birds from Sonora, Mexico'. *Palaeogeography, Palaeoclimatology, Palaeoecology* 301(1–4): 56–63.

Oswald, J.A., and Steadman, D.W. 2015. 'The changing diversity and distribution of dry forest passerine birds in northwestern Peru since the last ice age'. *The Auk* 132(4): 836–62.

Pereira, S.L., Johnson, K.P., Clayton, D.H. and Baker, A.J. 2007. 'Mitochondrial and nuclear DNA sequences support a Cretaceous origin of Columbiformes and a dispersal-driven radiation in the Paleogene'. *Systematic Biology* 56(4): 656–72.

Pillans, B., and Bourman, R. 2001. 'Mid Pleistocene arid shift in southern Australia, dated by magnetostratigraphy'. *Soil Research* 39(1): 89–98.

Pillans, B. 2003. ‘Subdividing the Pleistocene using the Matuyama–Brunhes Boundary (MBB): an Australasian perspective’. *Quaternary Science Reviews* 22(15–17): 1569–77.

Polly, P.D., and Eronen, J.T. 2011. ‘Mammal associations in the Pleistocene of Britain: implications of ecological niche modelling and a method for reconstructing palaeoclimate’. In *The Ancient Human Occupation of Britain*, edited by N. Ashton, S. Lewis, and C. Stringer, 279–304. Developments in Quaternary Science 14. Elsevier, Amsterdam.

Prideaux, G.J., and Warburton, N.M. 2008. ‘A new Pleistocene tree-kangaroo (Diprotodontia: Macropodidae) from the Nullarbor Plain of south-central Australia’. *Journal of Vertebrate Paleontology* 28(2): 463–478.

Prideaux, G.J., and Warburton, N.M. 2009. ‘*Bohra nullarbora* sp. nov., a second tree-kangaroo (Marsupialia: Macropodidae) from the Pleistocene of the Nullarbor Plain, Western Australia’. *Records of the Western Australian Museum* 25: 165–79.

Prideaux, G.J. 2007. ‘Mid-Pleistocene Vertebrate Records’. In *Encyclopedia of Quaternary Science*, edited by S.A. Elias, 1st ed., 1518–37. Elsevier, online edition.

Prideaux, G.J., Long, J.A., Ayliffe, L.K., Hellstrom, J.C., Pillans, B., Boles, W.E., Hutchinson, M.N., Roberts, R.G., Cupper, M.L., Arnold, L.J., Devine, P.D. and Warburton, N.M. 2007. ‘An arid-adapted middle Pleistocene vertebrate fauna from south-central Australia’. *Nature* 445(7126): 422–25.

Reed, E.H., and Bourne, S.J. 2000. ‘Pleistocene fossil vertebrate sites of the south east region of South Australia’. *Transactions of the Royal Society of South Australia*, no. 124: 61–90.

Rich, P.V., van Tets, G.F., Rich, T. and McEvey, A.R. 1987. ‘The Pliocene and Quaternary Flamingoes of Australia’. *Memoirs of the Queensland Museum* 25(1): 207–25.

Richards, A. 1971. ‘An ecological study of the cavernicolous fauna of the Nullarbor Plain southern Australia’. *Journal of Zoology* 164: 1–60.

Roberts, R.G., Spooner, N.A., Jones, R., Cane, S., Olley, J.M., Murray, A.S. and Head, M.J. 1996. ‘Preliminary luminescence dates for archaeological sediments on the Nullarbor Plain, South Australia’. *Australian Archaeology* 42(1): 7–16.

Ryan, K., Page, B., Brandle, R., Jay, J., Ehmann, H. and Armstrong, D. 2012. ‘Trends in the biodiversity of the Nullarbor region: a comparison between 1984 and 2012’. Department of Environment, Water and Natural Resources, Government of South Australia, Adelaide.

Sandom, C., Faurby, S., Sandel, B. and Svenning, J.C. 2014. ‘Global late Quaternary megafauna extinctions linked to humans, not climate change’. *Proceedings of the Royal Society B: Biological Sciences* 281(1787): 20133254–20133254.

Sarnthein, M., Bartoli, G., Prange, M., Schmittner, A., Schneider, B., Weinelt, M., Andersen, N., and Garbe-Schönberg, D. 2009. ‘Mid-Pliocene shifts in ocean overturning circulation and the onset of Quaternary-style climates’.

Scanlon, J.D., and Lee, M. 2000. ‘The Pleistocene serpent *Wonambi* and the early evolution of snakes’. *Nature* 403: 416–20.

Schodde, R., and Mason, I. 1999. *The Directory of Australian Birds: Passerines - A Taxonomic and Zoogeographic Atlas of the Biodiversity of Birds in Australia and Its Territories*. CSIRO Publishing, Canberra.

Schodde, R. 2006. 'Australasia's bird fauna today - origins and evolutionary development'. In *Evolution and Biogeography of Australasian Vertebrates*, edited by J.R. Merrick, M. Archer, G.M. Hickey, and M.S.Y. Lee, 413–58. Auscipub, Sydney.

Schweizer, M., Seehausen, O., and Hertwig, S. 2011. 'Macroevolutionary patterns in the diversification of parrots: effects of climate change, geological events and key innovations'. *Journal of Biogeography* 38: 2176–94.

Shipham, A., Schmidt, D.J., Joseph, L., and Hughes, J.M. 2015. 'Phylogenetic analysis of the Australian rosella parrots (*Platycercus*) reveals discordance among molecules and plumage'. *Molecular Phylogenetics and Evolution* 91 (October): 150–59.

Smith, M.A., Williams, A.N., Turney, C.S.M., and Cupper, M.L. 2008. 'Human—environment Interactions in Australian drylands: exploratory time-series analysis of archaeological records'. *The Holocene* 18 (3): 389–401.

Sniderman, J.M.K., Woodhead, J.D., Hellstrom, J., Jordan, G.J., Drysdale, R.N., Tyler, J.J. and Porch, N. 2016. 'Pliocene reversal of Late Neogene aridification'. *Proceedings of the National Academy of Sciences*, 201520188.

Sobbe, I.H., Price, G. and Knezour, R.A. 2013. 'A ziphodont crocodile from the Late Pleistocene King Creek Catchment, Darling Downs, Queensland'. *Memoirs of the Queensland Museum: Nature* 56(2): 601–6.

Steadman, D.W., and Mead, J.I. 2010. 'A Late Pleistocene bird community at the northern edge of the tropics in Sonora, Mexico'. *The American Midland Naturalist* 163(2): 423–41.

Steadman, D.W., Oswald, J.A. and Rincón, A.D. 2015. 'The diversity and biogeography of Late Pleistocene birds from the lowland neotropics'. *Quaternary Research* 83(03): 555–64.

Stewart, J.R., and Jacobi, R.M. 2015. 'The long term response of birds to climate change: new results from a cold stage avifauna in Northern England'. *PLOS ONE* 10(5): e0122617.

Stringer, C. 2016. 'The origin and evolution of *Homo Sapiens*'. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371(1698): 20150237.

Thomson, V.A., Mitchell, K.J., Eberhard, R., Dortch, J., Austin, J.J. and Cooper, A.. 2018. 'Genetic diversity and drivers of dwarfism in extinct island emu populations'. *Biology Letters* 14(4): 20170617.

Tindale, N.B. 1974. *Aboriginal Tribes of Australia: Their Terrain, Environmental Controls, Distribution, Limits, and Proper Names, with an Appendix on Tasmanian Tribes by Rhys Jones*. Australian National University Press, Canberra.

Toon, A., Mather, P.B., Baker, A.M., Durrant, K.L., and Hughes, J.M. 2007. 'Pleistocene refugia in an arid landscape: analysis of a widely distributed Australian passerine'. *Molecular Ecology* 16(12): 2525–2541.

Toon, A., Austin, J.J., Dolman, G., Pedler, L. and Joseph, L. 2012. 'Evolution of arid zone birds in Australia: leapfrog distribution patterns and mesic-arid connections in quail-thrush (*Cinclosoma*, Cinclosomatidae)'. *Molecular Phylogenetics and Evolution* 62(1): 286–95.

Treble, P.C., Baker, A., Ayliffe, L.K., Cohen, T.J., Hellstrom, J.C., Gagan, M.K., Frisia, S., Drysdale, R.N., Griffiths, A.D., and Borsato, A. 2017. 'Hydroclimate of the Last Glacial Maximum and deglaciation in southern Australia's arid margin interpreted from speleothem records (23–15 Ka)'. *Climate of the Past* 13(6): 667–87.

Turney, C.S.M., Bird, M.I., and Roberts, R.G. 2001. 'Elemental $\delta^{13}C$ at Allen's Cave, Nullarbor Plain, Australia: assessing post-depositional disturbance and reconstructing past environments'. *Journal of Quaternary Science* 16(8): 779–84.

Tyler, M.J., and Prideaux, G.J. 2016. 'Early to middle Pleistocene occurences of *Litoria*, *Neobatrachus* and *Pseudophryne* (Anura) from the Nullarbor Plain, Australia: first frogs from the "frog-free zone"'. *Memoirs of Museum Victoria* 74: 403–8.

van Tets, G. 1974. 'Fossil birds (Aves) from Weekes Cave, Nullarbor Plain, South Australia'. *Transactions of the Royal Society of South Australia* 98(4): 229–30.

van Tets, G., and Smith M. 1974. 'Small fossil vertebrates from Victoria Fossil Cave, Naracoorte, South Australia, III. Birds (Aves)'. *Transactions of the Royal Society of South Australia* 98(4): 225–27.

van Tets, G., and Vickers-Rich, P. 1980. 'A review of the De Vis fossil pigeons of Australia'. *Memoirs of the Queensland Museum* 20(1): 89–93.

van Tets, G., and Vickers-Rich, P. 1990. 'An evaluation of De Vis' fossil birds'. *Memoirs of the Queensland Museum* 28(1): 165–68.

van Tets, G. 1974. 'A revision of the fossil Megapodiidae (Aves), including a description of a new species of *Progura* De Vis'. *Transactions of the Royal Society of South Australia* 98(4): 213–24.

Warren, D.L., Cardillo, M., Rosauer, D.F., and Bolnick, D.I. 2014. 'Mistaking geography for Biology: inferring processes from species distributions'. *Trends in Ecology & Evolution* 29(10): 572–80.

Webb, J.A., and James J.M. 2006. 'Karst evolution of the Nullarbor Plain, Australia'. In *Special Paper 404: Perspectives on Karst Geomorphology, Hydrology, and Geochemistry - A Tribute Volume to Derek C. Ford and William B. White*, 404: 65–78. Geological Society of America.

Webb, S. 2010. 'Palaeotrophic reconstruction and climatic forcing of Mega-Lake Eyre in Late Quaternary central Australia: a review'. *Boreas* 39(2): 312–24.

Weir, J.T., and Schluter, D. 2004. 'Ice sheets promote speciation in boreal birds'. *Proceedings of the Royal Society B: Biological Sciences* 271(1551): 1881–87.

White, S. 1919. 'Four ornithological trips to the Nullarbor Plains'. *Emu* 18: 189–98.

Williams, A.N., Ulm, S., Cook, A.R., Langley, M.C., and Collard, M. 2013. 'Human refugia in Australia during the Last Glacial Maximum and terminal Pleistocene: a geospatial analysis of the 25–12 ka Australian archaeological record'. *Journal of Archaeological Science* 40(12): 4612–25.

Williams, J.W., and Jackson, S.T. 2007. 'Novel climates, no-analog communities, and ecological surprises'. *Frontiers in Ecology and the Environment* 5(9): 475–82.

Woinarski, J.C.Z., Burbidge, A.A., and Harrison, P.L. 2015. ‘Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement’. *Proceedings of the National Academy of Sciences* 112(15): 4531–40.

Woodhead, J., Hellstrom, J., Maas, R., Drysdale, R., Zanchetta, G., Devine, P. and Taylor, E. 2006. ‘U-Pb geochronology of speleothems by MC-ICPMS’. *Quaternary Geochronology* 1: 208–21.

Worthy, T.H. 2012a. ‘A phabine pigeon (Aves : Columbidae) from Oligo-Miocene Australia’. *Emu* 112(1): 23–31.

Worthy, T.H. 2012b. ‘A new species of Oligo-Miocene darter (Aves: Anhingidae) from Australia’. *The Auk* 129(1): 96–104.

Worthy, T.H., Hand, S.J., Worthy, J.P., Tennyson, A.J.D., and Scofield, R.P. 2009. ‘A large fruit pigeon (Columbidae) from the Early Miocene of New Zealand’. *The Auk* 126(3): 649–56.

Wroe, S. 2002. ‘A review of terrestrial mammalian and reptilian carnivore ecology in Australian fossil faunas, and factors influencing their diversity: the myth of reptilian domination and its broader ramifications’. *Australian Journal of Zoology* 50(1): 1–24.

Wroe, S., Crowther, M., Dortch, J., and Chong, J. 2004. ‘The size of the largest marsupial and why it matters’. *Proceedings of the Royal Society B: Biological Sciences* 271(Supp.3): S34–36.

Wroe, S., Myers, T.J., Wells, R.T., and Gillespie, A. 1999. ‘Estimating the weight of the Pleistocene Marsupial Lion, *Thylacoleo carnifex* (Thylacoleonidae: Marsupialia): implications for the ecomorphology of a marsupial super-predator and hypotheses of impoverishment of Australian marsupial carnivore faunas’. *Australian Journal of Zoology* 47(5): 489–98.

Yokoyama, Y., Purcell, A., Lambeck, K. and Johnston, P. 2001. ‘Shore-Line reconstruction around Australia during the Last Glacial Maximum and late glacial stage’. *Quaternary International* 83: 9–18.

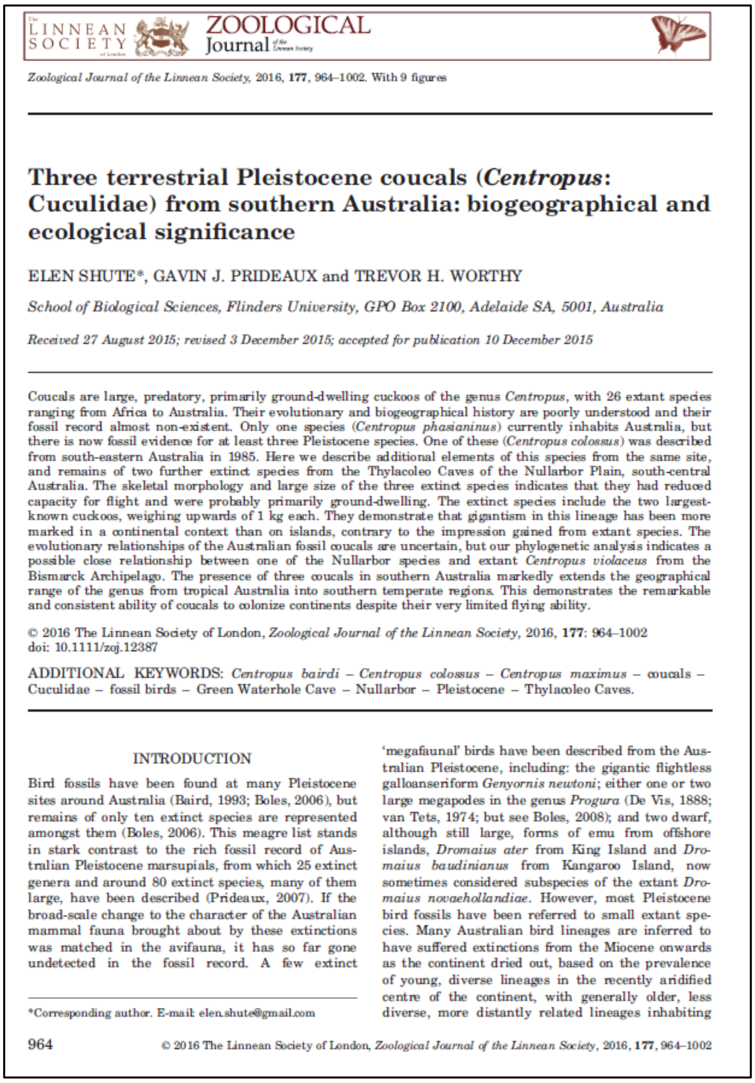
Zink, R.M., Klicka J., and Barber B.R. 2004. ‘The tempo of avian diversification during the Quaternary’. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 359(1442): 215–220.

Chapter 2: Three terrestrial Pleistocene coucals (*Centropus*: Cuculidae) from southern Australia: biogeographical and ecological significance

Manuscript enclosed

The following co-authored manuscript was submitted to the *Zoological Journal of the Linnean Society* for publication on 27th August 2015. Two anonymous peer reviewers requested minor revisions, and the revised version was submitted to the journal on 3rd December 2015. The manuscript was accepted for publication on 10th December 2015, and was published on 13th July 2016.

The published version has been reformatted for inclusion in this thesis, but the content of the text and figures are unaltered.



The LINNEAN SOCIETY of London ZOOLOGICAL Journal of the Linnean Society

Zoological Journal of the Linnean Society, 2016, **177**, 964–1002. With 9 figures

Three terrestrial Pleistocene coucals (*Centropus*: Cuculidae) from southern Australia: biogeographical and ecological significance

ELEN SHUTE*, GAVIN J. PRIDEAUX and TREVOR H. WORTHY

School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide SA, 5001, Australia

Received 27 August 2015; revised 3 December 2015; accepted for publication 10 December 2015

Coucals are large, predatory, primarily ground-dwelling cuckoos of the genus *Centropus*, with 26 extant species ranging from Africa to Australia. Their evolutionary and biogeographical history are poorly understood and their fossil record almost non-existent. Only one species (*Centropus phasianinus*) currently inhabits Australia, but there is now fossil evidence for at least three Pleistocene species. One of these (*Centropus colossus*) was described from south-eastern Australia in 1985. Here we describe additional elements of this species from the same site, and remains of two further extinct species from the Thylacoleo Caves of the Nullarbor Plain, south-central Australia. The skeletal morphology and large size of the three extinct species indicates that they had reduced capacity for flight and were probably primarily ground-dwelling. The extinct species include the two largest-known cuckoos, weighing upwards of 1 kg each. They demonstrate that gigantism in this lineage has been more marked in a continental context than on islands, contrary to the impression gained from extant species. The evolutionary relationships of the Australian fossil coucals are uncertain, but our phylogenetic analysis indicates a possible close relationship between one of the Nullarbor species and extant *Centropus violaceus* from the Bismarck Archipelago. The presence of three coucals in southern Australia markedly extends the geographical range of the genus from tropical Australia into southern temperate regions. This demonstrates the remarkable and consistent ability of coucals to colonize continents despite their very limited flying ability.

doi: 10.1111/zoj.12387

ADDITIONAL KEYWORDS: *Centropus bairdi* – *Centropus colossus* – *Centropus maximus* – coucals – Cuculidae – fossil birds – Green Waterhole Cave – Nullarbor – Pleistocene – Thylacoleo Caves.

INTRODUCTION

Bird fossils have been found at many Pleistocene sites around Australia (Baird, 1993; Boles, 2006), but remains of only ten extinct species are represented amongst them (Boles, 2006). This meagre list stands in stark contrast to the rich fossil record of Australian Pleistocene marsupials, from which 25 extinct genera and around 80 extinct species, many of them large, have been described (Prideaux, 2007). If the broad-scale change to the character of the Australian mammal fauna brought about by these extinctions was matched in the avifauna, it has so far gone undetected in the fossil record. A few extinct 'megafaunal' birds have been described from the Australian Pleistocene, including: the gigantic flightless galloanseriform *Genyornis newtoni*; either one or two large megapodes in the genus *Progura* (De Vis, 1888; van Tets, 1974; but see Boles, 2008); and two dwarf, although still large, forms of emu from offshore islands, *Dromaius ater* from King Island and *Dromaius baudinianus* from Kangaroo Island, now sometimes considered subspecies of the extant *Dromaius novaehollandiae*. However, most Pleistocene bird fossils have been referred to small extant species. Many Australian bird lineages are inferred to have suffered extinctions from the Miocene onwards as the continent dried out, based on the prevalence of young, diverse lineages in the recently aridified centre of the continent, with generally older, less diverse, more distantly related lineages inhabiting

---

*Corresponding author. E-mail: elen.shute@gmail.com

Context

In this chapter are described two new extinct species of coucal in the genus *Centropus* from the Pleistocene deposits of the Thylacoleo Caves. These are the first new extinct Pleistocene bird species that have been described from Australia since 1993. All specimens were excavated from the caves after the publication of the preliminary analysis of the fauna by Prideaux *et al*. (2007), thus these taxa did not appear in the original species list from the locality. One extinct species of *Centropus* has previously been described from another Australian Pleistocene locality, therefore material of that species is also included in the manuscript. Taxonomic relationships between the extinct species and extant members of the genus are analysed. Inferences are made about the Pleistocene ecology of the Nullarbor Plain based on the presence of these extinct species, and the results are also discussed in the broader context of the historical biogeography and evolutionary history of the Australian avifauna.

Statement of authorship

ERS identified the specimens and noted that they represented novel species, wrote the osteological descriptions, coded the post-cranial morphological characters for the phylogenetic analysis, measured the specimens, performed the analyses, photographed the specimens and made the photographic plates, prepared the figures, and wrote the manuscript. GJP headed the excavations during which the specimens were recovered, contributed to the design of the study, provided guidance and advice throughout the research process, and edited the draft manuscript. THW oversaw the design of the study, coded the cranial characters for the phylogenetic analysis, contributed to analyses, edited the draft manuscript, particularly the species descriptions, and provided guidance and advice throughout. Percentage contributions to the manuscript: ES, 80%; GJP and THW, 10% each.

Citation

Shute, E., Prideaux, G.J. and Worthy, T.H. (2016). Three terrestrial Pleistocene coucals (*Centropus*: Cuculidae) from southern Australia: biogeographical and ecological significance. *Zoological Journal of the Linnean Society*, 177: 964–1002.

http://onlinelibrary.wiley.com/doi/10.1111/zoj.12387/full

2.1 Abstract

Coucals are large, predatory, primarily ground-dwelling cuckoos of the genus *Centropus*, with 26 extant species ranging from Africa to Australia. Their evolutionary and biogeographical history are poorly understood and their fossil record almost non-existent. Only one species (*Centropus phasianinus*) currently inhabits Australia, but there is now fossil evidence for at least three Pleistocene species. One of these (*Centropus colossus*) was described from south-eastern Australia in 1985. Here we describe additional elements of this species from the same site, and remains of two further extinct species from the Thylacoleo Caves of the Nullarbor Plain, south-central Australia. The skeletal morphology and large size of the three extinct species indicates that they had reduced capacity for flight and were probably primarily ground-dwelling. The extinct species include the two largest known cuckoos, weighing upwards of 1 kg each. They demonstrate that gigantism in this lineage has been more marked in a continental context than on islands, contrary to the impression gained from extant species. The evolutionary relationships of the Australian fossil coucals are uncertain, but our phylogenetic analysis indicates a possible close relationship between one of the Nullarbor species and extant *Centropus violaceus* from the Bismarck Archipelago. The presence of three coucals in southern Australia markedly extends the geographical range of the genus from tropical Australia into southern temperate regions. This demonstrates the remarkable and consistent ability of coucals to colonize continents despite their very limited flying ability.

2.2 Introduction

Bird fossils have been found at many Pleistocene sites around Australia (Baird, 1993; Boles, 2006), but remains of only ten extinct species are represented amongst them (Boles, 2006). This meagre list stands in stark contrast to the rich fossil record of Australian Pleistocene marsupials, from which 25 extinct genera and around 80 extinct species, many of them large, have been described (Prideaux, 2007). If the broad-scale change to the character of the Australian mammal fauna brought about by these extinctions was matched in the avifauna, it has so far gone undetected in the fossil record. A few extinct ‘megafaunal’ birds have been described from the Australian Pleistocene, including: the gigantic flightless galloanseriform *Genyornis newtoni*; either one or two large megapodes in the genus *Progura* (De Vis, 1888; van Tets, 1974; but see Boles, 2008); and two dwarf, although still large, forms of emu from offshore islands, *Dromaius ater* from King Island and *Dromaius baudinianus* from Kangaroo Island, now sometimes considered subspecies of the *extant Dromaius novaehollandiae*. However, most Pleistocene bird fossils have been referred to small extant species. Many Australian bird lineages are inferred to have suffered extinctions from the Miocene onwards as the continent dried out, based on the prevalence of young, diverse lineages in the recently aridified centre of the continent, with generally older, less the mesic remnant habitats around the continental margins (Hawkins, Diniz-Filho & Soeller, 2005). So far this pattern is poorly reflected in the fossil record. However, in this paper, we present fossil evidence showing that at least one lineage, the coucals, which generally inhabit mesic environments, had a previously unsuspected Australian diversity, and underwent a major geographical contraction since the Pleistocene.

Coucals, members of the genus *Centropus*, are amongst the largest cuckoos. They are predominantly ground-dwelling predators noted for their short, rounded wings and poor flying ability. Coucals are thought to be a relatively basal lineage of the cuculid radiation on the basis of morphological and genetic evidence (Hughes, 2000; Sorenson & Payne, 2005). Unlike more derived cuckoos, they are not brood-parasites but instead build their own nests and raise their own young. Most coucals also exhibit reversed sexual dimorphism and the associated behaviour of males providing most of the parental care, which are characteristics shared by less than 5% of bird species (Maurer, 2008; Maurer et al., 2011). The 26 extant species have a geographical range from Africa, Madagascar, the Indian subcontinent including Sri Lanka, southern and eastern China, the Philippines, South-East Asia including the Malay Peninsula, Borneo, Sumatra, and numerous other islands of the Indonesian archipelago, through to New Guinea, the Solomon Islands, and northern Australia (Dickinson & Remsen, 2013). Australia has only one extant mainland species, the pheasant coucal, *Centropus phasianinus*, one of the largest representatives of the genus. It lives in tropical and subtropical habitats in the north and east of Australia, and is also found in tropical Timor and New Guinea (Fig. 2.1). The eight currently recognized subspecies are: *Centropus phasianinus* mui (Timor; Lesser Sundas); *Centropus phasianinus spilopterus* (Kai Islands; south-east Moluccas); *Centropus phasianinus propinquus* (lowland northern New Guinea); *Centropus phasianinus obscuratus* (lowland northern coast of south-eastern New Guinea); *Centropus phasianinus nigricans* (lowland southern coast of south-eastern New Guinea); *Centropus phasianinus thierfelderi* (lowland subcoastal New Guinea; Torres Strait Islands); *Centropus phasianinus melanurus* (Pilbara and north-western to north-eastern Australia; Melville Island); and *Centropus phasianinus phasianinus* (coastal eastern Australia) (Dickinson & Remsen, 2013). These vary in size and plumage (Mason, McKean & Dudzinski, 1984).

Historically, *Centropus* was considered a late addition to the Australian avifauna. *Centropus phasianinus* is thought to have only crossed the Torres Strait from New Guinea to Australia late in the Pleistocene either via the Sahul Shelf, which connected New Guinea and northern Australia at periods of low sea-level stand during glacial phases of the Pleistocene (Fig. 2.1), or by island-hopping through this region when sea levels were higher (Hindwood, 1954; Mason et al., 1984). This interpretation is supported by three lines of evidence. Southern Asia and Melanesia have the greatest diversity of coucals globally (18 of 26 species; Dickinson & Remsen, 2013), whereas Australia has only *Ce. phasianinus*. This species is not endemic, but is also found in New Guinea and Timor. Furthermore, the Australian range of *Ce.*

phasianinus is limited to the tropical and subtropical north and east grading into the high-rainfall temperate east coast, in close geographical and climatic proximity to New Guinea.

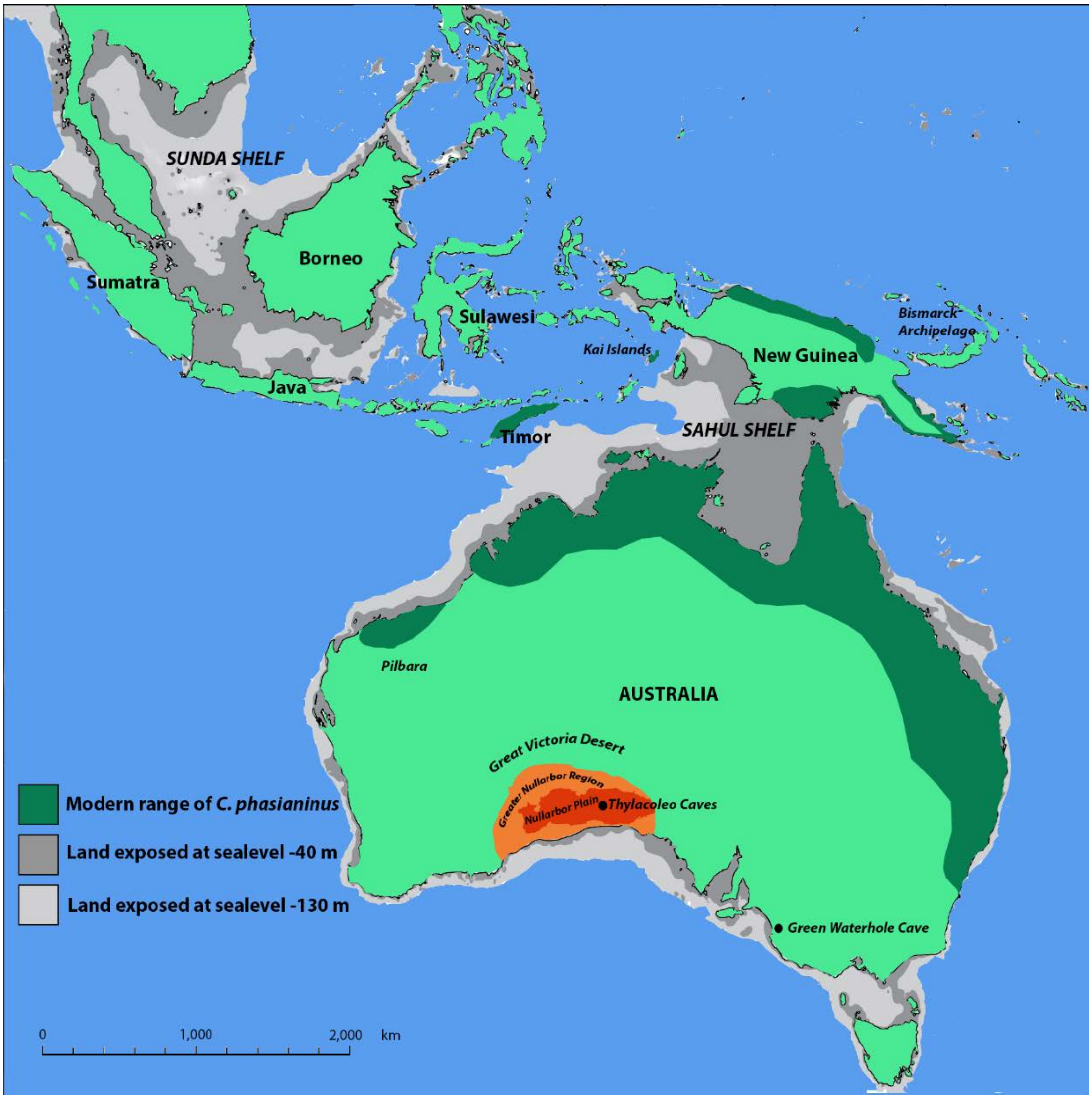


Figure 2.1: Map of key localities mentioned in the text, showing the range of extant *Centropus phasianinus*, and showing landbridge connections between Australia and Melanesia at different Pleistocene sea level low-stands (–40 and –130 m) relative to modern sea level; (modified from Sahul and Sundah Shelf Basemap, CartoGIS CAP, 2013, Map 00-101; downloaded from http://asiapacific.anu.edu.au/mapsonline/base-maps/sunda-and-sahul-shelf, 08-05-2015).

Until skeletal remains of a 'giant' Pleistocene coucal, *Centropus colossus*, were discovered in Green Waterhole Cave in south-eastern Australia (Fig. 2.1; Baird, 1985), there was no reason to suppose that Australia had ever hosted an endemic radiation of coucals. However, this fossil species demonstrated that in the past, the genus had a geographical distribution outside its modern range, and also hinted at greater pre-Holocene diversity. In the nearly three decades that followed, no further coucal fossils were identified from any other Australian locality. Here we provide evidence that this lineage was more diverse and more widely geographically dispersed in Australia during the Pleistocene than hitherto known. We describe a further two species of *Centropus* from the pitfall-trap assemblages of the Thylacoleo Caves on the Nullarbor Plain, Western Australia, describe additional remains of *Ce. colossus* from south-eastern Australia, and calculate bodymass estimates for all three species. We provide palaeoecological interpretations of these species based upon size, morphology, and comparisons with extant coucals, and undertake a phylogenetic analysis to investigate relationships between these extinct taxa and other cuculids. We consider the evolutionary and biogeographical significance of these extinct species in the context of Pleistocene environmental change in Australia.

2.3 Materials & Methods

2.3.1 Abbreviations & definitions

Institutions: AM, Australian Museum, Sydney, Australia; ANU, Australian National University, Canberra, Australia; KU, University of Kansas Natural History Museum, Lawrence, USA; LACM, Los Angeles County Museum, California, USA; MV, Museum Victoria, Melbourne, Australia; NMSF, Senckenberg Natural History Museum, Frankfurt, Germany; QM, Queensland Museum, Brisbane, Australia; SAM, South Australian Museum, Adelaide, Australia; UMMZ, University of Michigan Museum of Zoology, Ann Arbor, USA; WAM, Western Australian Museum, Perth, Australia.

Geological timescale and definitions of key periods discussed herein: Early Pleistocene, 2.58 million to 780,000 years ago; Middle Pleistocene, 780,000 years ago to 126,000 years ago; Late Pleistocene, 126,000 years ago to 11,700 years ago; Holocene, 11 700 years ago to present; Quaternary, 2.58 million years ago to present (Gibbard, Head & Walker, 2010). Other terminology dL, distal left; dR, distal right; DW, distal width; kyr, thousands of years; L, left; Mya, millions of years ago; m., musculus (i.e. muscle, Latin); NISP, number of individual specimens; pL, proximal left; pR, proximal right; PW, proximal width; R, right; SW, shaft width; TL, total length; yr BP, years before present.

Comparative material: Skeletons of modern cuculid taxa were examined as follows – Pheasant coucal, *Centropus phasianinus*: QM O.12529, QM O.12726, QM O.16026, QM O.21036, QM O.28046, QM O.28604, QM O.31395, QM O.31674, QM O.32793; SAM B.32226, SAM B.48695; lesser coucal, *Centropus bengalensis*: KU 41127; violaceous coucal, *Centropus violaceus*: AM O.60593; pied coucal, *Centropus ateralbus*: LACM 91135; channel-billed cuckoo, *Scythrops novaehollandiae*: QM O.21174, QM O.31404, QM O.31959, QM O.31961, MV B.12969, MV B.23619; common koel, *Eudynamys scolopaceus*: QM O.31628, QM O.31672, QM O.32350, QM O.20686, MV B.24066.

Skeletal material of South-East Asian ground-cuckoos in the genus *Carpococcyx* could not be obtained, but three-dimensional computed tomography scans of key elements for coral-billed ground cuckoo

Carpococcyx renauldi (UMMZ 223881; humerus, femur, tibiotarsus, and tarsometatarsus), taken at 300-micron resolution, were provided by the UMMZ. Photographs of the same elements from crested coua *Coua cristata* (NMSF 4489) were also examined. Modern skeletal material of buff-headed coucal *Centropus milo* was not available, but bones that are presumed to be *Ce. milo* from a Holocene archaeological deposit at Vatuluma Posovi (SG-2-1, or Poha Cave) Guadalcanal, Solomon Islands, were examined by T. H. W. from the School of Archaeology and Anthropology collections, ANU, and photographs of its humeri were available.

2.3.2 Measurements

Measurements were taken with digital callipers and rounded to the nearest 0.1 mm. Long-bone circumferences were measured by wrapping a thin strip of paper around the shaft, marking with a pen where the ends overlapped, and then straightening out the paper and measuring the distance between the marks with digital callipers.

2.3.3 Body mass estimates

We estimated body masses for the extinct species using regression equations given in Campbell & Marcus (1992) for bird leg bone circumferences vs. body weight. Although Field et al. (2013) found the best morphometric predictor of body mass in volant birds to be the diameter of the facies articularis humeralis on the coracoid, we did not use this in the present study for two reasons: (1) species of *Centropus* are weak fliers, the larger species particularly so, and the fossil taxa in this study are especially large and their volancy uncertain; and (2) coracoids are lacking for two out of three of the fossil species. Estimates based on leg elements, which could be calculated for all three taxa, were thus preferred. We therefore selected eight equations from Campbell & Marcus (1992) to assess body mass, four based on minimum femoral circumference and four on minimum tibiotarsal circumference. We used their all-species equation because it is based on the largest number of taxa (representatives from 89 avian families), as well as their equations for heavy-bodied birds (from 11 families), long-legged birds (from 13 families), and nonpasserine birds (from 69 families) because the species in this study would fit into any of these groups. We also applied these equations to extant cuculids to determine which produced estimates closest to their known mean body masses.

2.3.4 Simpson log-ratio diagrams

In order to visually compare the body proportions of the species of *Centropus* considered in this study, we used log-ratio diagrams first described by Simpson (1941) and now used widely in palaeontological studies. In this method, a suite of measurements (e.g. limb bone lengths and widths) is made for one or more species, converted to logarithms, and plotted on a graph as differences from the log values of a standard species represented as a straight zero-line on the horizontal axis. In this study we used the channel-billed cuckoo, *S. novaehollandiae*, as the standard, because it is a large Australo-Papuan cuckoo species of similar size to the larger coucals but with markedly different body proportions. The connected values for a species form a line that rises and falls relative to the zero-line, with sharper peaks indicating greater difference in bone proportions from the standard species. If the lines of two species are more parallel to one another, this indicates that they have similar proportions, and if less parallel, the more their proportions differ. The relative size of different species is shown by their height on the y-axis.

2.3.5 Nomenclature

We follow the osteological terminology of Baumel et al. (1993) and the taxonomic nomenclature of Dickinson & Remsen (2013), unless otherwise specified.

2.3.6 Phylogenetic analyses

We undertook a phylogenetic analysis of the extinct species based on the 135-character cuculid osteological data set from Hughes (2000) in which genus-level taxa were used rather than species. In order to calibrate our interpretation of these characters, we independently scored the skeleton of *Ce. phasianinus*, which was one of eight species of *Centropus* upon which the coding of *Centropus* was based by Hughes (2000), the others being *Centropus goliath*, *Centropus viridis*, *Centropus senegalensis*, *Centropus menbeki*, *Centropus toulou*, *Centropus monachus*, and *Centropus superciliosus* (Hughes, 1997). We then scored into the matrix the character states for the three Australian fossil taxa. We also scored two additional large extant Australasian cuculid species, *Ce. violaceus* and *S. novaehollandiae*, which were not included in the original analysis, to test the potential phylogenetic effects of large body size. We did not add any new characters, but added a new state each for Characters 96 and 97 (see Appendix 2 in Hughes, 2000), for a total of 135 characters and 41 taxa. All characters were unweighted, and 24 characters were ordered as in Hughes (2000).

We undertook parsimony analyses in PAUP* 4.0b10 using standard settings (Swofford, 2001), heuristic searches, tree bisection-reconnection branch swapping, and 1000 random addition replicates per search. Support for the consensus tree was assessed by bootstrapping, using heuristic searches and the same options, and 1000 replications. As in the original analysis (Hughes, 2000), trees were rooted using Opisthocomus hoazin (Hoatzin) and Musophagidae (turacos) as the outgroup. As our scoring of extant species revealed hitherto undetected variability amongst species of *Centropus*, we omitted composite scoring of the genus from our final analysis (cf. Hughes, 2000), instead including two extant Australasian taxa, *Ce. phasianinus* and *Ce. violaceus*, separately. Trees were manipulated in FigTree 1.4.2 and labelled in Adobe Illustrator.

2.4 Results

2.4.1 Key locations

The localities discussed in this paper are shown in Figure 2.1.

2.4.2 Systematic palaeontology

CUCULIFORMES WAGLER, 1830

CUCULIDAE LEACH, 1819

CENTROPODINAE HORSFIELD, 1823

CENTROPUS ILLIGER, 1811

Type species: Cuculus aegyptius Gmelin, 1788 [=*Centropus senegalensis* (Linnaeus, 1766)] by subsequent designation, see Gray (1840).

Throughout most of its range, the fossil record of *Centropus* is non-existent. The only extinct species that are recognized are those treated in this paper, which are all from outside the modern range of the genus. Besides these extinct species from southern Australia, the only *Centropus* fossils published in the literature are those of two indeterminate, possibly extant, species from archaeological contexts on the Melanesian islands of New Ireland (Steadman, White & Allen, 1999) and Vanuatu (Worthy et al., 2015), the latter representing a range extension for the genus. The temporal range of the genus is unknown. The oldest fossils, described below, are of Early Pleistocene age, but the genus is likely to be much older than this. The fossils described herein are referred to the Cuculidae, and to *Centropus* in particular, by the following features, based in part on characters noted by Baird (1985) and Hughes (2000), as well as on direct observations of comparative specimens.

Generic diagnosis

Humerus: The fossa pneumo tricipitalis ventralis is shallow with a pneumatic foramen that is small to nearly completely occluded (degree of pneumatization is intraspecifically variable in *Ce. phasianinus*, and may also vary amongst and within other *Centropus* species); the scar for the origin of m. humerotriceps and insertion of m. scapulohumeralis cranialis is large, and is immediately distad of the fossa pneumotricipitalis; the proximal end is tilted caudally in relation to the shaft; the area of bone between the crus ventrale fossae and the intumescentia humeri is craniocaudally compressed in ventral aspect; the shaft is strongly arched dorsally, and round in cross-section proximally; the corpus ventral to the tuberculum dorsale is swollen where it meets the caput humeri, so that the caput does not produce a shelf overhanging the shaft caudally (see Baird, 1985); the crista deltopectoralis is relatively short and low; the fossa m. brachialis does not extend far proximally along the shaft; the impressio m. brachialis is very deep, is placed ventrad of the shaft's midline, and approaches the margo ventralis very closely where it is bounded by only a very thin margin of bone between the ventral and cranial facies; the distal end is strongly expanded ventrally and only weakly expanded dorsally adjacent to the fossa m. brachialis; the processus flexorius is directed ventrally, is finger-like in caudal aspect (narrow in some taxa, e.g. *Ce. phasianinus*, *Ce.* bengalensis, wider dorsoventrally in others, e.g. *Ce. violaceus*), and the tip tapers to a sharp point in cranial aspect; the sulcus scapulotricipitalis is deep, with a prominent ridge of bone separating it from the sulcus humerotricipitalis. The humerus of *Centropus* is distinguished from those of other large cuculids in the Australian/ Melanesian region as follows. The humerus of *Scythrops* has: a relatively stouter and straighter shaft with margo caudalis compressed into a longitudinal ridge that starts immediately dorsal of the crus dorsale fossa and extends as far distally as the crista bicipitalis; a thicker crus dorsale fossae; a wider, more cranially projecting crista deltopectoralis that extends further distally along the shaft, and the impressio m. pectoralis forms a much more elongate scar ventral to the crista deltopectoralis; less ventral expansion of the distal end; and the processus flexorius merges smoothly with the condylus ventralis in cranial aspect rather than forming a distinct distoventral projection. The humerus of *Eudynamys* differs from that of *Centropus* as follows: the shaft is relatively stouter and less cranially arched; the crista deltopectoralis extends further distally and is more dorsocranially flared; the processus supracondylaris dorsalis is more prominent; the sulcus scapulotricipitalis is shallower; and the processus flexorius has a tip that is blunt in cranial aspect rather than sharply pointed as in *Centropus*. The humeri of large, poorly flighted/terrestrial cuculid genera that have ranges overlapping that of the *Centropus* genus outside Australia/Melanesia (*Carpococcyx* in South-East Asia and *Coua* in Madagascar) are distinguished from those of *Centropus* as follows. The humerus of *Carpococcyx* has a shaft that is relatively much stouter, less dorsally arched, and widens more towards either end; the distal part of the crista deltopectoralis joins the shaft at an approximately 45° angle to the longitudinal axis in cranial aspect (closer to 20° in *Centropus*); the area of bone between the crus ventrale fossae and the intumescentia humeri is expanded craniocaudally in ventral aspect (craniocaudally compressed in *Centropus*); the distal end is relatively wider, the sulcus scapulotricipitalis is shallower, and the processus flexorius is more distoventrally extended in cranial aspect, extending further distally than the condylus ventralis; the caudal surface of the corpus is not swollen where it meets the caput humeri, so that the caput overhangs the corpus (Baird, 1985). The humerus of *Coua* is distinguished from that of *Centropus* by having a larger and more pneumatic fossa pneumotricipitalis ventralis and a concomitant narrower crus ventrale fossae; a less pronounced crus dorsale fossae; a more dorsocranially angulated and distally extended crista deltopectoralis; a more prominent processus supracondylaris dorsalis; and a less distinct impressio m. brachialis.

Ulna: The shaft is proportionally short and stout, and dorsoventrally flattened; the olecranon is low and rounded; the processus cotylaris dorsalis is small, and not distally extended; the papillae remigalis caudalis are prominent; the tuberculum carpale is short and does not project far cranially. The ulnae of *Scythrops* and *Eudynamys* are relatively longer and more slender with the shaft rounder in cross-section, rather than being dorsoventrally flattened, they have a larger and more proximally projecting olecranon, and a larger and distally hooked processus cotylaris dorsalis.

Carpometacarpus: This is short and stout, with a rather arched os metacarpale minus such that the spatium intermetacarpale is broadest distally; the trochlea carpalis is craniocaudally narrow and directed somewhat cranially in dorsal aspect; the processus alularis is large and square in dorsal aspect; the fossa infratrochlearis is deep and pit-like; the processus intermetacarpalis is absent; the sulcus tendineus, in the distal third of the dorsal surface of the os metacarpale minus, is deep; and the facies articularis digitalis minor is distally extended compared with the facies articularis digitalis major in dorsal aspect. The carpometacarpus of *Centropus* is distinguished from that of *Scythrops* by having a much larger processus alularis, a more arched os metacarpale minus, a deeper sulcus tendineus, and a much smaller facies articularis digitalis minor (projects strongly distally in *Scythrops* in dorsal aspect). In *Centropus* the carpometacarpus is rather similar in shape to that of *Eudynamys*, but is distinguished by having in dorsal aspect a proximocranially pointing trochlea carpalis (in *Eudynamys* it is directed just proximally), and by greater distal extension of the facies articularis digitalis minor (in *Eudynamys* the facies for the digiti majus et minus have equal distal extent).

Coracoid: The coracoid is elongate with a thin shaft that lacks a foramen nervi supracoracoidei; the processus procoracoideus is long, broad, and flat, and projects ventrally from the shaft; there is a pneumatic pore in the cotyla scapularis; the impressio musculus sternocoracoidei is confined to the sternal end of the shaft; the processus lateralis is relatively small and projects laterally more or less at right angles to the shaft axis. The coracoids of *Scythrops* and *Eudynamys* differ from *Centropus* by having a larger processus lateralis that has an acute, cranially projecting process at its craniolateral extreme (particularly prominent in *Eudynamys*). The coracoid of *Scythrops* is further differentiated from that of *Centropus* by having a relatively stouter shaft, and in having the processus procoracoideus first projecting medially from the shaft before it rotates ventrally and in having a more cranially directed tip, whereas *Eudynamys* has a relatively longer and more slender processus procoracoideus than does *Centropus*.

Scapula: The scapula of *Centropus* is relatively long and slender and does not widen appreciably caudally. The acromion is long, pointed, and projects much further cranially than the facies articularis humeralis. The tuberculum coracoideum is small and not prominent cranially. There is a pneumatic foramen on the cranial extreme of the medial facies. The scapulae of *Scythrops* and *Eudynamys* differ from that of *Centropus* by being relatively broader, widening towards the caudal end (particularly in *Eudynamys*), having an acromion that is much less cranially extended, and lacking a pneumatic foramen on the craniomedial surfa*Ce.*

Sternum: Sternal morphology differs considerably amongst different species of *Centropus*. In *Ce.* bengalensis and *Ce. phasianinus*, the sternum is narrow, the carina sterni is relatively deep, thin, extends the entire length of the sternum, and the apex carinae projects further cranially than the labrum externum of the sulci articularis coracoidei (contra Hughes, 2000), whereas in the near-flightless *Ce. violaceus*, the sternum is broad and dorsoventrally flattened, the carina is shallow and thick and only extends about two-thirds of the way caudally along the sternum, and the apex carinae is placed further caudally than the labrum externum. A spina externa is present in some species (e.g. *Ce.* bengalensis, *Ce. phasianinus*), but entirely absent in others (e.g. *Ce. violaceus*) (see phylogenetic analysis). Similarities amongst species of *Centropus* that differentiate the genus from other large Australian cuculids are: similar cranial and caudal width of sternum (sternum of *Eudynamys* is much narrower cranially than caudally); the processus craniolaterales is long, narrow, and tapered (in *Scythrops* they are proportionally shorter and broader and not projected cranially); the lateral margin has a relatively flat profile in lateral aspect (in *Eudynamys* and *Scythrops* it is strongly curved); the trabecula lateralis is a simple, flat square shape and is directed more or less parallel to the midline of the sternum (in *Eudynamys* the lateral and medial margins flare outward markedly, and in both *Scythrops* and *Eudynamys* they are angled laterally rather than parallel to the midline). The sterna of *Scythrops* and *Eudynamys* differ from that of *Centropus* by having: a proportionally deeper carina that projects further cranially and an acute apex carinae that is cranially recurved. The sternum of *Scythrops* further differs from that of *Centropus* by having a visceral surface that is much more deeply recessed and a cranial margin that is pointed in ventral aspect, whereas in *Centropus* the ventral surface and the cranial margin are flatter.

Pelvis: In dorsal aspect, the pelvis of *Centropus* is relatively long and narrow in the preacetabular part, but has a broad, short postacetabular section on which the cristae dorsolaterales iliae markedly overhang the alae ischiae. At its narrowest point, the preacetabular area is approximately half the width of the postacetabular portion. The cristae iliaca dorsales are conjoined as a very narrow and sharp crest that projects well above the flanks of the alae preacetabulares ilii, which are very deeply concave cranially. At the midline of the cranial-most part of the pelvis in dorsal aspect, a short, narrow process from the crista spinosa synsacri projects cranially beyond the cranial margin of the alae preacetabulares ilii. The cranial margins of the alae preacetabulares ilii are raised in a sharp crest that extend ventrolaterally onto the dorsal surface of the fused rib of the first vertebra in the synsacrum. In some species (*Ce. phasianinus*, *Ce. bengalensis*, and *Ce. ateralbus*), there is an elongate hole at the cranial end of both ilia, but in *Ce. violaceus* the bone is solid here, although it appears thin at the same point. The cranial edge of the ala postacetabularis ilii forms a crest that overhangs the sulcus antitrochantericus, and in lateral aspect the crista dorsolateralis ilii deeply overlaps the alae ischii caudally, overhanging a deep concavitas infracristalis. The foramen ilioischiadicum is nearly as deep as it is long. The tuberculum preacetabulare is a long, acute, cranially projecting process. In ventral aspect, the ilia anteriorly do not project widely from the transverse processes of the synsacrum. The pelves of *Scythrops* and *Eudynamys* differ from that of *Centropus* by having: cristae spinosae synsacri that are exposed and project dorsally, and separated by a deep longitudinal groove on either side from the alae preacetabulares ilii; less concave alae preacetabulares ilii that lack a crest at their cranial margins; little overlap of the cristae dorsolaterales ilii and alae ischii caudally, with concomitant minimal concavitas infracristalis; foramina ilioischiadica that are more elongate; tuberculae preacetabulare that are small and blunt; and in ventral view, ilia that project widely from the transverse processes of the synsacrum. The pelvis of *Scythrops* is further distinguished from that of *Centropus* by having a comparatively wider cranial portion in comparison to the caudal portion of the pelvis, and alae ischii that do not project much further caudally than the alae postacetabulares ilii.

Femur: The shaft is arched cranially in lateral aspect; the proximal end is wide, but the femoral shaft does not thicken substantially where it meets the proximal end; the crista trochanteris does not extend proximad of the facies articularis antitrochanterica and therefore a fossa trochanteris is absent, but the crista projects cranially to overhang the corpus femoris, forming a fossa on the proximocranial surface; the caput femoris is bulbous with a deep fovea ligamentum capitis; the facies articularis antitrochanterica projects caudal of the collum femoris; there are two deep depressions immediately distad of the facies articularis antitrochanterica, interpreted as the impressiones obturatoriae externa (on the lateral facies) and interna (on the adjacent caudal face), separated by a sharp ridge; the sulcus intercondylaris and sulcus patellaris are deep, and almost as wide as the shaft; the cristae lateralis and medialis sulci patellaris are sharply defined, proximally extended, and aligned with the lateral and medial margins of the bone in cranial aspect; the bone at the distal end of the sulcus intercondylaris terminates in a sharp crest in distal aspect; the fovea tendineus m. tibialis cranialis is very deep; the impressio ligamentum collateralis lateralis is deeply recessed on the condylus lateralis; the insertion of m. gastrocnemialis lateralis is circular, and is just proximal and lateral to the trochlea fibularis; the insertion for the ansa m. iliofibularis caudalis is in a shallow fossa distally on the lateral face of the trochlea fibularis immediately distal of the insertion of the m. gastrocnemialis lateralis, and the ansa m. iliofibularis cranialis is distinct and located more proximally on the lateral facies; the condylus medialis projects strongly caudally, forming a deep shelf caudal of the fossa poplitea; the crista tibiofibularis projects strongly, resulting in a deep trochlea fibularis. Besides their size being smaller than for those of any of the Australian species of *Centropus* discussed in this paper, the femora of *Scythrops* and *Eudynamys* differ from that of *Centropus* by having the following features: the shaft is straight in lateral aspect; the collum femoris is short; the sulcus intercondylaris and sulcus patellaris are shorter and shallower; the cristae lateralis et medialis sulci patellaris are lower and more rounded and extend less proximally along the shaft; the distal end is proportionally narrower, with a smaller condylus medialis and condylus lateralis; the condylus medialis and crista tibiofibularis have little caudal projection; the fossa poplitea is shallow; the impressio ligamentum collateralis lateralis is shallow and small. The femur of *Scythrops* is further distinguished from that of *Centropus* by having a deep pneumatic fossa on the caudal surface immediately distal of the facies articularis antitrochanterica and level with the caput femoris. The femur of *Eudynamys* also differs from that of *Centropus* in having a proportionally smaller caput femoris. We did not note any major morphological differences between the femur of *Centropus* and *Coua*, with minor differences being that in *Coua* the caput femoris is proportionally smaller, the cristae lateralis and medialis patellaris do not extend quite as far proximally along the shaft, and the shaft is more tapered from the proximal to the distal end in caudocranial aspect than in *Centropus*. The femur of *Carpococcyx* differs from that of *Centropus* by the following features: the fovea ligamentum capitis occupies a larger area of the caput femoris; the collum femoris is less constricted in cranial aspect, giving the caput femoris a less bulbous appearance than in *Centropus*; the facies articularis antitrochanterica projects further caudally than in *Centropus*; the cranial projection of the crista trochanteris is medially recurved in proximal view, whereas in *Centropus* it is orientated laterally; the impressiones obturatoriae externa and interna and the ridge of bone that separates them are all located on the lateral side of the bone, whereas in *Centropus* the interna is on the caudal surface and the ridge is at the caudolateral junction; and the cristae lateralis et medialis sulci patellaris extend less far proximally, with the medial crista being shorter than the lateral, whereas in *Centropus* the medial is longer.

Tibiotarsus: The shaft is straight in craniocaudal and lateromedial aspects; the crista cnemialis cranialis projects cranially but lacks proximal projection; the crista cnemialis lateralis projects slightly laterally and is hooked distally; the foramen interosseum proximale is large; the crista fibularis projects markedly; the sulcus extensorius is offset laterally of the midline; the incisura intercondylaris is more deeply recessed distally than it is proximally, forming a distinct notch for the articulation of the eminentia intercotylaris of the tarsometatarsus. The tibiotarsi of *Scythrops* and *Eudynamys* differ from that of *Centropus* by having: a proportionally stouter shaft; a foramen interosseum proximale that is barely discernible; a crista fibularis with less lateral projection, but extending relatively further distally; a sulcus extensorius that is placed centrally; distal condyles that are proportionally larger and more rounded in lateral/medial aspect; and a crista cnemialis lateralis with less lateral projection from the shaft of the bone. The tibiotarsus of *Eudynamys* further differs by having an incisura intercondylaris that is uniformly shallow, and *Scythrops* differs by having a shaft that is curved in craniocaudal and lateromedial aspects. The tibiotarsus of *Coua* differs from that of *Centropus* as follows: the crista cnemialis cranialis is more laterally deflected; the foramen interosseum proximale is proportionally longer, having a proximodistally shorter area of contact between the tibiotarsus and the fibula proximally; the shaft is proportionally narrower in its distal half, tapering more distal of the crista fibularis, and not widening as much near the distal end; and in cranial aspect, the condylus medialis and condylus lateralis diverge proximally in cranial aspect (in *Centropus* the condyles are more or less parallel). The tibiotarsus of *Carpococcyx* differs from that of *Centropus* as follows: the crista cnemialis cranialis projects further cranially, and is square in shape in medial aspect, whereas in *Centropus* the crista does not project as far and merges smoothly with the shaft distally; the crista cnemialis cranialis is caudally recurved in proximal aspect, whereas in *Centropus* it is orientated more laterally; the incisura tibialis is deeply recessed, forming a semicircle in proximal aspect (shallower in *Centropus*); the tuberositas popliteus is not distinct, and a thick, low ridge of bone extends distally along the caudal surface of the shaft from this point to about level with the mid-length point of the crista fibularis, whereas this ridge is absent in *Centropus*; the pons supratendineus is wider proximodistally; and the condylus medialis and condylus lateralis project less far from the shaft proximocranially, giving them a rounder shape in medial and lateral aspects, respectively.

Tarsometatarsus: The tarsometatarsus of *Centropus* is elongate, with a length more than six times greater than the proximal width (*Eudynamys* and *Scythrops* have tarsometatarsi with a length ≤5 times greater than proximal width). As in all cuculids, the hypotarsus is bicanaliculate (Mayr, 2015), having two large canals of subequal size (medial slightly larger) that are completely enclosed and are placed side by side; the hypotarsus is offset laterally, sitting almost entirely plantar of the cotyla lateralis and the eminentia intercondylaris; the plantar surface of the hypotarsus is a flattened disc; the eminentia intercotylaris is narrow and very prominent proximally, and projects proximal of the area intercondylaris; the margins of the cotylae lateralis et medialis have a square appearance in proximal aspect, with the cotyla lateralis narrower and more dorsoplantarly elongate than the cotyla medialis; the fossae parahypotarsalis medialis et lateralis are deep, the medial one particularly so, with the excavation continuing distally down most of the plantar surface of the shaft, and the fossae are separated from one another by a ridge that originates from the crista intermedia hypotarsi and extends distally about half way down the plantar surface; the cristae plantares medialis et lateralis are sharp; two foramina vascularia proximalia are present, with their relative proximodistal placement varying amongst species; the sulcus extensorius is deeply excavated; the tuberositas m. tibialis cranialis is placed medially, either on the medial wall of the sulcus extensorius or at the junction of the sulcus and its medial wall, immediately distal of the foramen vasculare proximalis medialis in some species, but with a distinct gap seen in others; the foramen vasculare distale is large; the canalis interosseus distalis is absent, but a deep dorsal groove runs between trochleae metatarsi III and IV merging with the foramen vasculare distale proximally; the fossa metatarsi I is deep and elongate, but does not excavate the medial profile of the shaft in dorsal/ plantar view; trochlea metatarsi II is ball-like and ungrooved, and is less distally extended than trochlea metatarsi III; trochlea metatarsi III is wide with a broad, deep medial groove, and is the most distally projecting trochlea; trochlea metatarsi IV is very short, and has a large trochlea accessoria that is strongly recurved medially and overhangs the fossa supratrochlearis plantaris. The tarsometatarsi of *Scythrops* and *Eudynamys* differ from that of *Centropus* by being relatively shorter, stouter, and more robust; the ridge from the crista intermedia hypotarsi extends relatively less distally along the plantar surface; and the trochlea metatarsi II is narrower and less medially flared. In addition, the hypotarsus of *Scythrops* is less offset laterally from the medial position and the cotylae lateralis and medialis are more equal in size. The tarsometatarsus of *Coua* differs from *Centropus* by the following features: the shaft width tapers more distally, and the distal width is less expanded; the plantar surface lacks a prominent ridge separating the fossae parahypotarsalis medialis and lateralis; the tip of trochlea metatarsi II is more rounded in dorsal aspect, extending further distally, being nearly as long as trochlea metatarsi III, and the trochlea does not flare strongly medially; trochlea metatarsi IV extends further distally, and its trochlea accessoria is directed more plantarly than in *Centropus*, in which it points more medially. The tarsometatarsus of *Carpococcyx* differs from that of *Centropus* as follows: crista lateralis hypotarsi is thicker in proximal aspect; the shaft is proportionally more slender in dorsal aspect with much less lateromedial expansion of the distal end; the medial side of the shaft is dorsoplantarly thick along its entire length (in *Centropus* it is very thin proximally); the plantar surface has a similarly low ridge extending distally from the crista intermedia hypotarsi, but it does not extend far distal of the hypotarsus; distal of this ridge, the sulcus flexorius is excavated along its entire length; fossa metatarsi I is less distinct; and the groove in trochlea metatarsi III is much shallower.

Centropus colossus Baird, 1985

Holotype

SAM P24240 (L humerus with minor damage to the proximal and distal ends).

Referred material

SAM P42065 (L humerus, missing proximal end and with damage to distal end); SAM P42027 (R femur, nearly complete but with some damage to caput femoralis and condyles, and with dendritic etching to the shaft surface). Including the holotype humerus, number of individual specimens = 3, minimum number of individuals = 2.

Locality

All specimens come from the type locality, Green Waterhole Cave (=Fossil Cave, 5L81), near Tantanoola, South Australia (Fig. 2.1). The fossil deposit was below the water table, and the bones were recovered by divers in 1979 along with the remains of numerous other vertebrates (Baird, 1985; Rich, van Tets & Knight, 1985b). *Centropus colossus* was described from a left humerus (Baird, 1985), but we later identified the two additional referred bones, which are from the same site, within the Palaeontology collection of the South Australian Museum.

Age and fauna

The Green Waterhole Cave fossil deposit has not been directly dated, but the species composition of the assemblage suggests a Middle or Late Pleistocene age (Pledge, 1980; Baird, 1985; Prideaux, 2004, 2007). This falls within the Naracoortean land mammal age (Megirian et al., 2010).

Revised diagnosis

A species of *Centropus* distinguished from all extant species of *Centropus* by its much greater size and the following combination of humeral features (Fig. 2.2): a stout, dorsally arched shaft; a caput humeri that is rotated cranioventrally; an incisura capitis that is wide and orientated more proximodistally than dorsoventrally; a tuberculum ventrale that is large and placed quite proximally; a small fossa pneumotricipitalis (the degree of pneumatization is difficult to assess because the fossa of the holotype is filled with putty, and this region is missing in the referred humerus); a crista deltopectoralis that is robust and very short, and in dorsal aspect (Fig. 2.2A) its proximal extreme curves outwards dorsocranially (crista of the holotype is damaged and thus the extent of dorsocranial projection more distally is difficult to assess – see Fig. 2.2K); an impressio m. pectoralis that is reduced to a prominent, proximodistally foreshortened scar ventrad of, and linking to, the distal end of the crista deltopectoralis; a processus supracondylaris dorsalis that is low and rounded; a corpus that is swollen around the fossa m. brachialis; and a processus flexorius that is dorsoventrally wide in caudal aspect. The humerus is very similar in size to that of S. *novaehollandiae*, but differs as noted in the generic diagnosis above. It differs from the humerus of *Ce. phasianinus* by its much larger size, having a relatively stouter shaft that is less arched dorsally, a caput humeri that is offset cranially from the longitudinal axis of the shaft in caudal aspect, a tuberculum ventrale that is placed more proximally relative to the caput humeri, an incisura capitis that is more proximodistally aligned (diagonally traverses the longitudinal aspect of the shaft in *Ce. phasianinus*), a smoothly curved rather than angular profile of the crista deltopectoralis in dorsal aspect, and a dorsoventrally wider processus flexorius. The humerus of *Ce. colossus* is distinguished from those of the two new extinct species of *Centropus* described in this paper as follows. It is much larger than the humerus of *Centropus bairdi* sp. nov. (Fig. 2.2), and is further differentiated from that new species by the following features: the shaft is straighter in dorsal aspect and is proportionally wider (Fig. 2.7); the caput humeri is orientated more cranially in dorsal aspect; the tuberculum ventrale is less caudally projected; the fossa pneumotricipitalis is deeper; the fossa m. brachialis is deeper, and the ventral shaft adjacent to the fossa is swollen (not so in *Ce. bairdi* sp. nov.); the impressio m. brachialis is proportionally much deeper and wider; and the condylus dorsalis is less cranially projected in dorsal aspect. The humerus of *Ce. colossus* approaches the size of that of *Centropus maximus* sp. nov. (Fig. 2.2), but is distinguished from this new species by the following features: the shaft is proportionally wider;

the proximal end is proportionally narrower and not as robust; the caput humeri is more inflated, and extends further proximally than the tuberculum ventrale in ventral aspect; it lacks a prominent scar for the insertion of the m. supracoracoideus between the caput humeri and the crista deltopectoralis (marked in *Ce. maximus* sp. nov.); the intumescentia humeri is less inflated; the impressio coracobrachialis is shallower; the impressio m. pectoralis is less prominent; the shaft adjacent to the fossa m. brachialis is ventrally swollen; the processus supracondylaris is less prominent; the processus flexorius is narrower and less robust; and the condylus ventralis and condylus dorsalis project less far cranially. Description and comparisons Humerus: See revised diagnosis. The second, less complete, humerus (not illustrated) is referred to *Ce. colossus* on the basis of its similar size, robusticity, and morphology compared to the holotype. Measurements: Table 2.1.

Femur: The femur of *Ce. colossus* has not previously been described, but SAM P42027 (Fig. 2.3) is referred to this species for the following reasons: it has the generic features of *Centropus* listed above; comes from the same site as the holotype humerus and is of congruent size; is differentiable from all extant species of *Centropus*, including the only extant Australian species *Ce. phasianinus*, on the basis of its much larger size and robusticity; and is differentiable from the femora of the two new extinct Australian Pleistocene species of *Centropus* described later in this paper. It is around one third longer and has more than double the shaft diameter of the femur of *Ce. phasianinus*, and is further distinguished this species by the following features: the shaft is straighter in cranial aspect, and is proportionally thicker; the caput femoris is proportionally larger; the crista trochanteris and the cranial margin of the facies articularis antitrochanterica merge at approximately a 90° angle to form a continuous, evenly curved crest that is cranially prominent and overhangs the proximocranial surface of the bone (in *Ce. phasianinus* only the crista trochanteris is cranially prominent); the condylus lateralis and condylus medialis are proportionally deeper and wider; the fovea tendineus m. tibialis cranialis is much deeper; the insertion for the m. gastrocnemialis lateralis is proportionally larger, and forms a circular scar proximal to the trochlea fibularis on the caudolateral margin; the impressio ligamentum collateralis lateralis is very large and well marked in a distinct fossa centred laterally on the trochlea fibularis; the impressio ansa m. iliofibularis caudalis distally abuts the insertion for the m. gastrocnemialis lateralis, and the impressio ansa m. iliofibularis cranialis is an elongate scar further proximally on the lateral facies; the fossa poplitea is deeper; and the scar for the origin of the ligamentum cruciati caudalis is large and prominent on the lateral wall of the fossa poplitea, directly proximal to the crista tibiofibularis. The femur of *Ce. colossus* has similar proportions to that of the extinct *Ce. bairdi* sp. nov., which is described later in this paper, but is distinguished by its considerably larger size. The femur of *Ce. colossus* approaches the size of the femur of the extinct *Ce. maximus* sp. nov., which is described later in this paper, but it is more gracile at the proximal and distal ends and has a smaller minimum shaft circumference (see body mass estimates). For further distinguishing features, see the description of *Ce. maximus* sp. nov. below. Measurements (mm): for TL, PW, SW, and DW see Table 2.1; minimum shaft circumference = 25.8.

Remarks

This species was much larger than any extant species of *Centropus*, which as a group are poor flyers. We concur with Baird (1985) that features of the humerus, including the stout, curved shaft, reduced crista deltopectoralis, and small muscle scar for the m. pectoralis are indicative of reduced volancy. To these humeral features, we add a cranially placed caput humeri relative to the longitudinal axis of the shaft in caudal aspect, a more proximodistally aligned incisura capitis, and more proximal placement of the tuberculum ventrale, as well as the large size and robustness of the femur and enhanced development of the crista trochanteris (Rich, McEvey & Baird, 1985a), as indicative of reduced flying ability and greater use of the legs in locomotion.

Table 2.1: Measurements (mm) of *Centropus colossus* holotype and referred material. All skeletal elements are from Green Waterhole Cave, South Australia

Element/Side	Catalogue no.	TL	PW	SW	DW
Holotype					
Humerus, L	SAM P24240	73.5	18.0	7.0	16.0
Referred material					
Humerus, L	SAM P42065	–	–	6.9	16.0*
Femur, R	SAM P42027	88.5	16.1	9.21	19.0

Abbreviations: L, left; R, right; TL, total length; PW, proximal width; SW, mid-shaft width; DW, distal width; *, minimum measurement owing to damage

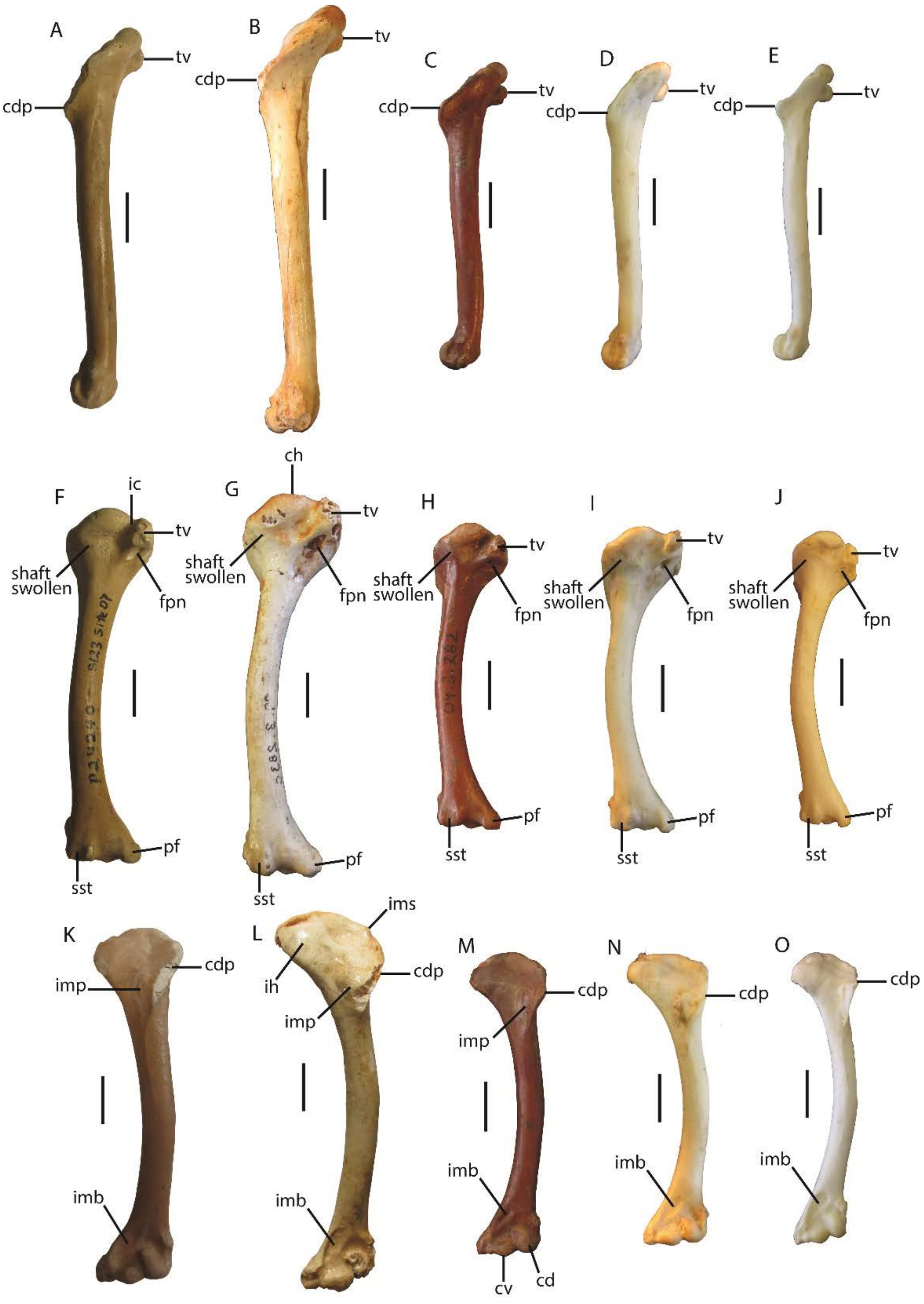


Figure 2.2: Humeri of five extinct and extant Australasian species of *Centropus* in dorsal (A–E), caudal (F–J), and cranial (K–O) aspects. *Centropus colossus*, SAM P24240, left, holotype (A, F, K); ***Centropus maximus* sp. nov**., WAM 09.3.283, right, holotype, image reversed (B, G, L); ***Centropus bairdi* sp. nov**., WAM 09.3.282, left, holotype (C, H, M); ***Centropus violaceus***, left, AM O60593 (D, I, N); and ***Centropus phasianinus***, QM B12969, right, image reversed (E, J, O). Abbreviations: cd, condyles dorsalis; cdp, crista deltopectoralis; ch, caput humeri; cv, condyles ventralis; fpn, fossa

pneumotricipitalis; ic, incisura capitis; ih, intumescentia humeri; imb, impressio m. brachialis; imp, impressio m. pectoralis; ims, insertion of m. supracoracoideus; pf, processus flexorius; sst, sulcus scapulotricipitalis; tv, tuberculum ventrale. Scale bars = 1 cm.

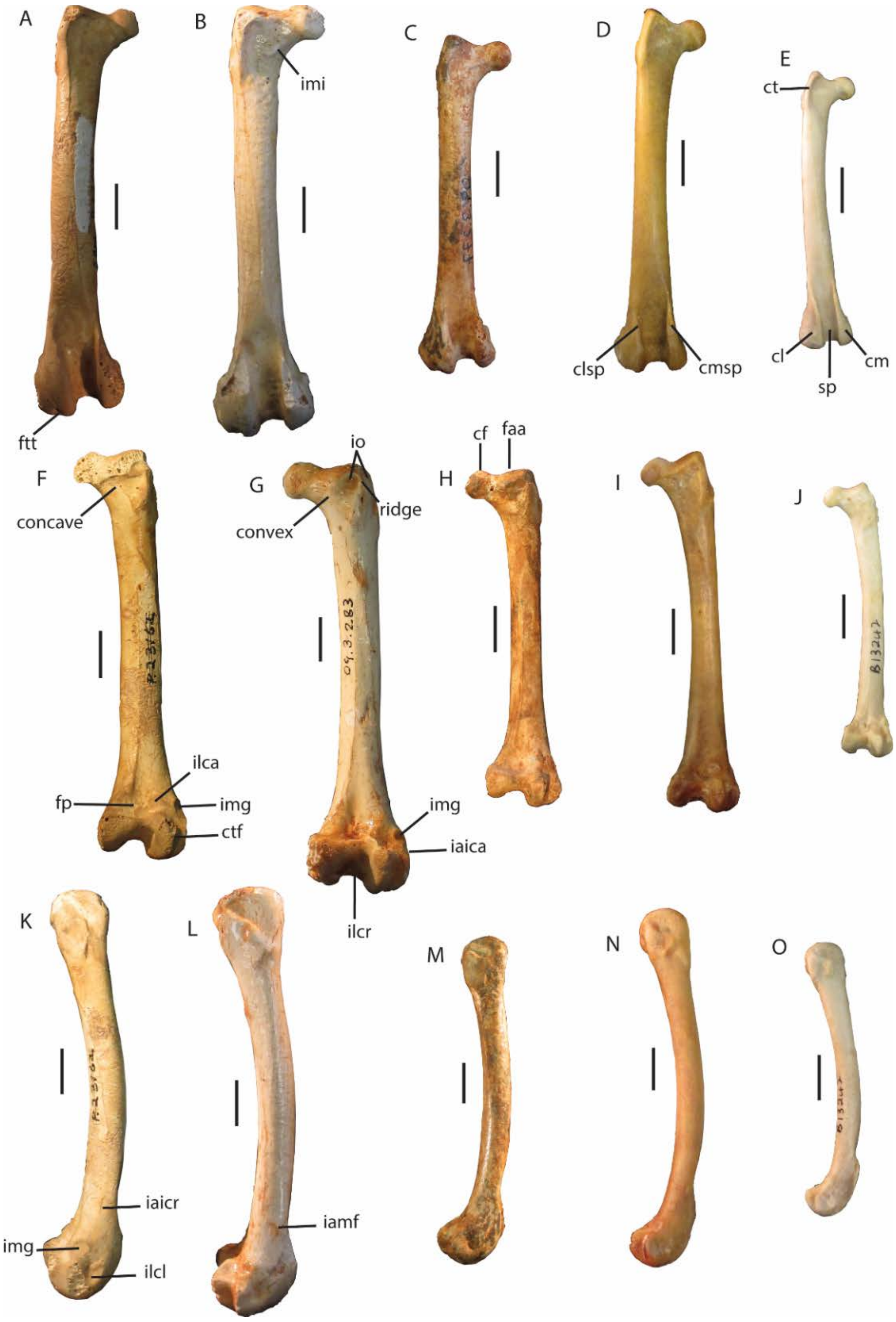


Figure 2.3: Femora of extinct and extant Australasian species of *Centropus* in cranial (A–E), caudal (F–J), and lateral (K–O) aspects. *Centropus colossus*, SAM P42027, right (A, F, K); ***Centropus maximus* sp. nov**., WAM 09.3.283, right, holotype (B, G, L); ***Centropus bairdi* sp. nov**.,

WAM 09.3.277, left, image reversed (C, H, M); ***Centropus violaceus***, AM O.60593, right (D, I, N); and ***Centropus phasianinus***, QM B.13242, right (E, J, O). Abbreviations: cf, caput femoris; cl, condylus lateralis; clsp, crista lateralis sulcus patellaris; cm, condylus medialis; cmsp, crista medialis sulcus patellaris; ct, crista trochanteris; ctf, crista tibiofibularis; faa, facies articularis antitrochanterica; fp, fossa poplitea; ftt, fovea tendinous m. tibialis cranialis; iaica, impressio ansa m. iliofibularis caudalis; iaicr, impressio ansa m. iliofibularis cranialis; ilca, impressio lig. cruciate caudalis; ilcl, impressio lig. collateralis lateralis; ilcr, impressio lig. cruciati cranialis; img, insertion of m. gastrocnemialis lateralis; imi, impressio m. iliofemoralis; io, impressions obturatoriae; sp, sulcus patellaris. Scale bars = 1 cm

Centropus bairdi **sp. nov. (Figures 2.2–2.4)**

urn:lsid:zoobank.org:act:25375F5E-14C5-4AD6-AE12-332F21F5AEA2

Holotype (Fig. 2.2C, H, M)

WAM 09.3.282 (L humerus, complete). Measurements are given in Table 2.2. Referred material WAM 09.3.277 (complete L femur); WAM 09.3.279 (complete R tibiotarsus), and WAM 09.3.278 (R tibiotarsus, shaft with missing proximal and distal ends); WAM 09.3.281 (L tarsometatarsus, missing distal end) and WAM 09.3.280 (L tarsometatarsus, missing distal end). Including the holotype humerus, number of individual specimens = 6, minimum number of individuals = 2. All specimens were excavated from within 3 m of one another and from a similar depth (see Stratigraphy, age, and fauna), but the bones were not articulated or closely associated. All bones are assumed to be from the same species of *Centropus* because of their congruent size and robusticity, and because collectively they are distinct from those of *Ce. phasianinus*, *Ce. colossus*, and *Ce. maximus* sp. nov. described later in this paper (see Diagnosis). Measurements of long bones are given in Table 2.2; additional measurements are given in text where applicable.

Type locality

Leaena’s Breath Cave, Nullarbor Plain, Western Australia. The precise location for the site is registered with the Department of Earth and Planetary Sciences, Western Australian Museum, Perth. Leaena’s Breath Cave is one of the three caves comprising the Thylacoleo Caves (Fig. 2.1). It is formed within the Early Miocene-aged Nullarbor Limestone.

Stratigraphy, age, and fauna

All specimens were excavated from Pit B, Quadrats 1 and 3, Unit 3, in the main chamber of Leaena’s Breath Cave, between 85 and 120 cm below the sediment floor. Leaena’s Breath Cave has a vertical solution pipe entrance approximately 20 m deep, through which the specimens of *Ce. bairdi* are presumed to have accumulated via pitfall trapping. The roof window of the cave is thought to have been open and accumulating fossils at intervals during the Early to Middle Pleistocene, and was then sealed by a calcrete cap until recently. The holotype was excavated by G. J. P. from Pit B, Quadrat 1, at a depth of 115– 120 cm beneath the sediment floor, on Friday 10 May 2013. Fine-grained sediments in Unit 3 are of reversed magnetic polarity, which along with the overall species composition of the assemblage, indicate an Early Pleistocene age > 780 kyr BP (Matuyama Reversed Chron; Prideaux et al., 2007). This falls within the Naracoortean land mammal age (Megirian et al., 2010).

Diagnosis

A species of *Centropus* with a humerus within the length range of that of *Ce. phasianinus*, but with the shaft less strongly arched dorsally and relatively more stout, the corpus thicker where it approaches the caput humeri, the crista deltopectoralis craniocaudally thicker and with a rounder apex, the impressio m. brachialis shallower and much narrower, the ventral margin of the processus flexorius more ventrally extended with associated greater dorsoventral width of the processus in caudal aspect, the condylus ventralis proximodistally shorter and less spherical, a larger expanse of bone dorsad of the condylus dorsalis, the sulcus scapulotricipitalis wider and flatter, and with leg bones considerably longer and more robust.

The holotype humerus (Fig. 2.2C, H, M) differs from those of other large extant and extinct Australian cuculids in both size and morphology: it is very much smaller than the humerus of S. *novaehollandiae*, and the two extinct Pleistocene species *Ce. colossus* (see above) and *Ce. maximus* sp. nov., which is described later in this paper; it is larger and more robust than the humerus of E. *scolopaceus*, with a shorter, more cranially directed crista deltopectoralis (angled more dorsally in E. *scolopaceus*), a thicker crus ventrale fossa, a more proximodistally extended intumescentia humeri, and the processus flexorius directed ventrally rather than distally.

The fossil humerus is longer than that of the medium- sized species *Ce.* ateralbus from the Bismarck Archipelago, but is almost identical in length and shaft width to the humeri of two of the largest extant Melanesian coucal taxa, *Ce.* milo (Solomon Islands) and *Ce. violaceus* (Bismarck Archipelago). *Centropus bairdi* differs from both species by the following features: the proximal and distal widths are smaller; the caput humeri is more prominent proximally; the crista bicipitalis joins the shaft at a sharper angle distally (gradually tapered in *Ce. violaceus* and *Ce.* milo); the crista deltopectoralis is more craniodorsally expanded, with an apex that is more angular (short, robust, and barely projecting in *Ce. violaceus* and *Ce.* milo); the distal end of the bone is more ventrally flared; and the impressio m. brachialis is highly reduced in area. In addition, the fossa pneumotricipitalis of *Ce. bairdi* has almost no pneumatization whereas *Ce.* milo is strongly pneumatic.

Etymology

Named in honour of Dr Robert F. Baird, who described Australia's first extinct species of *Centropus* in 1985, and who worked extensively on the Quaternary bird fossil record of Australia, including fossil cave faunas in the Nullarbor region.

Description and comparisons

All fossil bones of this species are stained dark brown by the clay-rich sediments in which they were buried. Apart from both tarsometatarsi missing their distal ends and one tibiotarsus missing its proximal and distal ends, the bones are in excellent condition, are not significantly eroded, and preserve anatomical detail well. The bone surfaces lack a porous texture and the tarsometatarsi have completely fused epiphyses, indicating that the elements represent adult individuals.

Humerus: In addition to the diagnostic features described above, the humerus of *Ce. bairdi* has the following features: the intumescentia humeri is relatively small, occupying around a third of the proximal width in cranial view; the crus dorsale fossae is relatively thicker than for other species; the impressio m. brachialis is narrow and elongate, hence the area for insertion of this muscle is greatly reduced, and this is accentuated by the fact that the shaft is not swollen ventrally around the fossa m. brachialis, unlike in *Ce. phasianinus*, *Ce. violaceus*, *Ce.* milo, *Ce.* ateralbus, and *Ce. colossus*.

Femur: Single complete specimen (Fig. 2.3C, H, M), with minor erosion of the facies articularis acetabularis on the caput, and of the condylus medialis and condylus lateralis. It is much larger and more robust than the femur of any extant Australian cuculid, including the closest in length, that of *Ce. phasianinus*, but is considerably smaller than the femur of *Ce. colossus* described above, and that of *Ce. maximus* sp. nov. described below (Fig. 2.3). Despite its smaller size, its shape and proportions are similar to that of *Ce. colossus*, being robust and having a straight shaft in cranial aspect (*Ce. phasianinus* has a gracile, laterally bowed shaft – see Fig. 2.3E). The junction between the facies articularis antitrochanterica and the cranial surface of the bone is smoothly rounded as in *Ce. phasianinus*, unlike in *Ce. colossus* where a distinct ridge separates these surfaces. At its caudal edge, the facies articularis antitrochanterica forms a rounded projection that overhangs the caudal facies (does not project in *Ce. phasianinus*, cannot be determined in *Ce. colossus* owing to damage), and distal of this the caudal surface of the shaft is convex (strongly concave in *Ce. phasianinus* and *Ce. colossus*). The fossa poplitea is deeper than in *Ce. phasianinus*, being bounded laterally by a thickened area of shaft proximal of the trochlea fibularis, and medially by a strongly developed crista supracondylaris medialis. The insertion of the m. gastrocnemialis lateralis appears less distinct than in *Ce. phasianinus* or *Ce. colossus*, although it is possible that this region of the femur has been somewhat eroded in this specimen. The femur is shorter but overall more robust than in *Ce. violaceus*, and lacks a proximal projection of the trochanter femoris (present in *Ce. violaceus* – Fig. 2.2F). The impressio ligamentum collateralis lateralis is in a distinct fossa on the lateral facies as in other taxa. The origin of the ligamentum cruciati caudalis is on the lateral wall of the fossa poplitea, directly proximal to the crista tibiofibularis, as in *Ce. colossus* and *Ce. violaceus*, but is less distinct than in those taxa. The groove caudally separating the condylus medialis from the condylus lateralis in which the ligamentum cruciati cranialis runs is shallower and less rectilinear than in *Ce. colossus*. Measurements (mm): for TL, PW, SW, and DW, see Table 2.1; proximal depth: 11.4; minimum shaft circumference = 19.5.

Figure 2.4: Referred material of *Centropus bairdi* sp. nov. from Leaena's Breath Cave, Nullarbor Plain, south-central Australia. Right tibiotarsus WAM 09.3.279 in cranial (A) and caudal (B) aspects; left tarsometatarsus WAM 09.3.280 in dorsal (C), plantar (D) and proximal (E) aspects; left tarsometatarsus of *Centropus phasianinus* MV B.12969 (F) in plantar aspect provided for comparison. Abbreviations: ccl, crista cnemialis lateralis; cf, crista fibularis; cl, condylus lateralis; cm, cotyla medialis; ei, eminentia intercotylaris; fg, facies gastrocnemialis; fdl, canal for tendon of m. flexor digitorum longus; fhl, canal for tendon of m. flexor hallucis longus; fpht, fossa parahypotarsalis medialis; fvp, foramina vascularia proximalia; ii, incisura intercondylaris; ps, pons supratendineus; se, sulcus estensorius; sf, sulcus flexorius; tfb, tuberculum m. fibularis brevis; ttc, tuberositas m. tibialis cranialis. Scale bars = 1 cm.

Tibiotarsus: The tibiotarsus (Fig. 2.4A, B) is large and robust, and is distinguished from those of all extant Australian cuculids by its much larger size. The nearest in size is the tibiotarsus of *Ce. phasianinus*, which is only around 70% of the length of that of *Ce. bairdi* and has a little over half the shaft diameter of the new species. Besides size, there are a few morphological differences from the tibiotarsus of *Ce. phasianinus*: the crista cnemialis cranialis of *Ce. bairdi* does not project as far cranially, and tapers more gradually towards the shaft at its distal extreme; the crista cnemialis lateralis projects less and is less hooked than in *Ce. phasianinus*; and the medial facies of the bone is flattened at its proximal end, from the facies gastrocnemialis to about the mid-length of the shaft, whereas in *Ce. phasianinus* it is more medially convex. The tibiotarsus of the extinct *Ce. colossus* is not known, but the size of its femur (see above) indicates that the tibiotarsus would be significantly larger than that of *Ce. bairdi*. The tibiotarsus of *Ce. bairdi* is very similar in size and morphology to that of *Ce. violaceus*, but the muscular impression caudomedially on the shaft mesad of the crista fibularis is less extensive as revealed by its proximally bounding linea intermuscularis medially being well separated from that on the cranial facies (in *Ce. violaceus*, they are closer together), the shaft is more robust, and the epicondylaris medialis is more pronounced. Measurements (mm): for TL, PW, SW, and DW, see Table 2.1; PW including crista cnemialis lateralis: 14.9; width at distal end of crista fibularis: 11.2; depth of cotyla lateralis: 11.1; depth of cotyla medialis: 12.1; minimum shaft circumference = 19.9.

Tarsometatarsus: The tarsometatarsus of *Ce. bairdi* (Fig. 2.4C–E) is larger than that of any extant Australian cuculid. The more complete of the two specimens (WAM 09.3.280) preserves much of the shaft length (60 mm), but neither the fossa metatarsi I nor the trochleae are preserved. Even without the distal end, the incomplete bone is longer than the tarsometatarsus of *Ce. phasianinus*, and is considerably larger at the proximal end and in the shaft. Besides its greater size, the tarsometatarsus of *Ce. bairdi* is further distinguished from that of *Ce. phasianinus* by the following features: the excavation of the sulcus flexorius on the plantar surface extends into the distal half, whereas in *Ce. phasianinus* the plantar surface of the shaft is flat to convex along its distal half; the cotyla lateralis is proportionally wider, approaching the width of the cotyla medialis, and the tuberculum m. fibularis brevis forms a small shelf of bone that protrudes laterally from its lateroplantar corner (Fig. 2.4E) as in *Ce. violaceus* (in *Ce. phasianinus* the tuberculum has a lateral margin confluent with the condyle and projects plantarly); the eminentia intercotylaris is offset more plantarly from the dorsal margin; and the tuberositas m. tibialis cranialis is larger. The tarsometatarsus of the extinct *Ce. colossus* is not known, but on the basis of the much larger femur of this species, it would be expected to be much wider and longer than that of *Ce. bairdi*. Despite having a more robust femur and tibiotarsus than *Ce. violaceus*, the tarsometatarsus of *Ce. bairdi* is more gracile, and is strongly tapered along the proximal two thirds of the preserved length of the shaft distal of the proximal articular surfa*Ce.* The better-preserved tibiotarsus is contralateral to the two preserved proximal tarsometatarsi, precluding an assessment of the articulation of the tibiotarsus and the tarsometatarsus, but their size is congruent. Measurements (mm): for PW and SW, see Table 2.2; proximal depth including hypotarsus: WAM 09.3.280, 12.33; WAM 09.3.281, 13.5; mid-shaft depth: WAM 09.3.280, 4.3; WAM 09.3.281, not applicable. The more complete specimen, which was excavated from a shallower depth in the excavation (Table 2.2) is a little smaller than the other specimen, but within the range of variation of what would be expected of sexually dimorphic taxa such as coucals.

Remarks

Centropus bairdi was intermediate in size between the extant *Ce. phasianinus* and the extinct *Ce. colossus*, and was larger than any extant species of *Centropus*. The humerus of *Ce. bairdi* is short in comparison to the leg elements (Fig. 2.7), which along with the reduced degree of pneumatization and dramatically reduced area for attachment of the m. brachialis at the distal end of the humerus, suggests that this species was poorly adapted for flying, and perhaps even for gliding. It may have been truly terrestrial.

Table 2.2: Measurements (mm) of holotype and referred material of *Centropus bairdi* sp. nov.; all material is from Leaena's Breath Cave, Nullarbor Plain, Western Australia

Element/Side	Catalogue no.	Pit/Quadrat, Depth (cm)	TL	PW	SW	DW
Holotype						
Humerus, L	WAM 09.3.282	B1, 115–120	61.2	15.1	5.4	12.9
Referred material						
Femur, L	WAM 09.3.277	B3, 110–115	71.4	14.8	6.6	16*
Tibiotarsus, R	WAM 09.3.279	B3, 110–115	121.6	14.0	7.9	12.5
Tibiotarsus, R	WAM 09.3.278	B3, 110–115	-	-	6.5	-
Tarsometatarsus, L	WAM 09.3.280	B1, 85–90	-	12.6	6.1	-
Tarsometatarsus, L	WAM 09.3.281	B3, 115–120	-	13.7	-	-

Abbreviations: L, left; R, right; TL, total length; PW, proximal width; SW, mid-shaft width; DW, distral width; *, minimum measurement owing to damage

Centropus maximus sp. nov. (Figures 2.2, 2.3 and 2.5)

urn:lsid:zoobank.org:act:F2404834-F927-489E-B5E3-9A79A602CB24

Holotype (Figs 2.2, 2.3 and 2.5)

WAM 09.3.283: associated remains of one adult individual comprising: fragments L and R mandibular rami; R pterygoid; nine vertebrae (vert.) assessed against *Ce. violaceus* (cervical vert. 3, 4, and ?6; cervicothoracic vert. 12; thoracic vert. 14, 15, 16, 17, and 18); seven ribs and rib fragments; R, pL, dL humerus; pL, dL ulna; L coracoid; omal fragment L clavicula; pL and part of corpus, mid-portion of R corpus, scapula; cranial portion of sternum, including cranial end of carina; pelvis, missing ala postacetabularis ilii, and most of both pubi and ischii; dL, R femur; fragment of pL tibiotarsus; pL tarsometatarsus; various fragments; NISP = 35. Measurements of long bones are given in Table 2.3; additional measurements are given in text where applicable.

Paratype

WAM 09.3.284: associated remains of one adult individual comprising: cranium, five fragments; L pars caudalis and tip mandible; L missing processus mandibularis, R quadrate; fifteen vertebrae (vert.) (cervical vert. 5-13; thoracic vert. 14-18; one caudal vert.); L, R humeri; R ulna missing olecranon process; R carpometacarpus, missing os metacarpale minus; R phalanx digiti majoris; L coracoid, missing omal portion; pL and part of corpus, scapula; cranial fragment sternum; part furcula; pR, pL, dL femora; L, R tibiotarsi; R fibula; L, dR tarsometatarsi; five L pedal phalanges, (I.1; III.1; III.2; ungual ?III.3; IV.1); NISP = 47. Measurements of long bones are given in Table 2.3; additional measurements are given in text where applicable.

Type locality

Flightstar Cave, Nullarbor Plain, Western Australia (Fig. 2.1). The precise location for the site is registered with the Department of Earth and Planetary Sciences, Western Australian Museum, Perth. Flightstar Cave is one of three caves comprising the Thylacoleo Caves. It is formed within the Early Miocene-aged Nullarbor limestone and preserves a vertebrate fossil assemblage that is of Early to Middle Pleistocene age (Prideaux et al., 2007).

Stratigraphy, age, and fauna

The holotype and paratype were shallowly buried in powdery limestone breakdown material between boulders in the rockpile beneath the solution-pipe entrance, through which the specimens of *Ce. maximus* are presumed to have accumulated via pitfall trapping. The femur (09.3.283a) of the holotype was collected on 30 April 2014 by Lindsay Hatcher and Michael Simpson, and the remainder of the holotype and all bones of the paratype were collected by them the following day (1 May). Upper infill sediments elsewhere in the cave, upon which other extinct megafauna were found, have a minimum age of 230 ± 27 kyr (Prideaux et al., 2007). The holotype and paratype of *Ce. maximus* are presumed to belong to the same fossil fauna, and thus are probably of Early or Middle Pleistocene age. The holotype and paratype skeletons were found adjacent to one another and have similar preservation, and are likely to have died at the same time.

Diagnosis

The largest known extinct or extant species of *Centropus*, with a humerus slightly longer than that of *Ce. colossus*, but with a proportionally more slender shaft, a wider and more robust proximal end, a less inflated caput humeri that does not extend further proximally than the tuberculum ventrale in ventral aspect, a strongly marked scar for the insertion of the m. supracoracoideus between the caput humeri and the crista deltopectoralis orientated proximodorsally, a more inflated intumescentia humeri, a deeper impressio coracobrachialis, a more prominent impressio m. pectoralis, a crista bicipitalis that is very robust and craniocaudally thick distally, a shaft that is not ventrally inflated around the fossa m. brachialis, a more prominent processus supracondylaris dorsalis, a more robust processus flexorius that is as deep as it is long distad of the tuberositas supercondylare ventrale, and with larger, more robust leg bones.

The humerus of *Ce. maximus* is considerably larger than those of any extant species of *Centropus*, including the large Melanesian taxa *Ce.* milo and *Ce. violaceus*, indicating that this species was of much greater size than any living coucal. It is also much larger than the humerus of the extinct Australian Pleistocene species *Ce. bairdi* sp. nov. described above. Based on published tarsus lengths of cuculids (Erritzøe et al., 2012), the tarsometatarsus of *Ce. maximus* (measured without the eminentia intercondylaris as it would be measured in live birds and preserved skins) is, at 112.9 mm, also nearly 25 mm longer than that of the next largest cuculid (*Carpococcyx* renauldi = 89 mm; Erritzøe et al., 2012).

Etymology

Maximus = 'largest' (Latin, masculine), to acknowledge the very large size of this species, which was greater than that of any known member of the genus, and indeed greater than any known cuckoo species.

Description and comparisons

The bones of the holotype and paratype are off-white in colour, stained slightly in places by orange/brown sediment. They are very fragile and some are damaged, with breaks (e.g. shaft breakages of long bones) having occurred to some bones during collection. Where possible, breaks have been repaired. Although damaged in places, the bones are not significantly eroded, and preserve anatomical detail very well. The bone surfaces lack a porous texture and the epiphyses of the tarsometatarsi of both individuals are completely fused; therefore, both are fully grown adult birds, the paratype being a slightly larger individual. Cranial bones: The mandibular fragments show that in comparison with *Ce. violaceus*, the symphyseal area is proportionally shorter and shallower, and is not drawn out into a deep, narrow, elongate, downcurved tip: the shape is more like that of *Ce. phasianinus*. The caudal dentary fragments of WAM 09.3.283 (L and R) preserve the area transitioning from covered to uncovered in rhamphotheca in modern specimens. At 12.2 mm high at the caudal end of the dentary, the bill was some 20% bigger than that of *Ce. violaceus*. The pars caudalis of the mandible lacks the processus medialis but the preserved parts are very similar to those of the species of *Centropus* examined, and overall the pars caudalis is 30% larger than that of *Ce. violaceus*. The pterygoid is 19.3 mm long and essentially the same shape as in *Ce. violaceus*. The R quadrate is well preserved, and at 22 mm high, some 22% taller than that of *Ce. violaceus* (18 mm). It is larger overall than that of *Ce. violaceus* and differs from it only by the presence of a large foramen pneumaticum caudomediale sensu Elzanowski & Stidham (2010), by lacking a foramen pneumaticum rostromediale (a small hole in this facies is interpreted as damage), and by having a pars quadratojugalis and fovea quadratojugalis that are less prominent than in *Ce. violaceus*, much less so than in *Ce. phasianinus*.

Humerus: As well as the generic characters described above, the humerus of *Ce. maximus* has the following features: a thin crus dorsale fossa; a large and deep impressio coracobrachialis occupying nearly half of proximal width; the contour of the crista bicipitalis is reduced distoventrally; the impressio m. pectoralis is about 10 mm long and noticeably elevated off the adjacent facies distally; a thick crista deltopectoralis; and a low caput humeri as in *Ce. violaceus*.

Ulna: WAM 09.3.284 is nearly complete, with a little damage at the proximal and distal ends. The olecranon is damaged, so the total length of the bone is probably about 1 mm more than measured if shaped like in *Ce. violaceus*. The ulna is distinguished from those of all extant Australian cuculids, except for S. *novaehollandiae*, by its considerably greater length and broader shaft (S. *novaehollandiae* has an ulna around 15% longer). The ulna is distinguished from that of S. *novaehollandiae* by having: a strongly dorsoventrally flattened shaft, rather than being round in crosssection; a very reduced and poorly marked impressio brachialis; a less distally extended processus cotylaris dorsalis; a smaller, less projecting tuberculum carpale; and extremely large and protuberant papillae remigalis caudalis. The ulna of *Ce. maximus*, although larger, is similar in shape to those of *Ce. phasianinus*, *Ce.* bengalensis, and *Ce. violaceus*. Proportionally it is most similar to that of the near-flightless *Ce. violaceus* than to those of the more volant species, having a robust, especially flattened shaft that widens considerably as it approaches the proximal end and a similarly weakly marked impressio brachialis. However, it is distinguished from the ulna of *Ce. violaceus* by its larger size, its much larger papillae remigalis caudalis, and a cotyla ventralis that is proportionally wider dorsoventrally. The ulna of *Ce. colossus* is not known, but based on humeral/femoral proportions may be of similar size to that of *Ce. maximus*. The ulna of *Ce. bairdi* sp. nov. is also unknown, but is presumed to be considerably smaller than that of *Ce. maximus*.

Carpometacarpus: WAM 09.3.284-k (L) preserves the entire length but lacks the os metacarpale minus, the proximoventral portion of the bone is damaged, and the processus pisiformis and surrounding area are missing. Morphologically it is very similar to, but about 25% longer, and more robust, than those of the extant *Ce. phasianinus* and *Ce. violaceus*, and is much bigger than that of *Ce.* bengalensis. It is further distinguished from the carpometacarpus of *Ce. violaceus* by having subequal distal extension of the facies articularis digitalis major and the facies articularis digiti minoris, whereas in *Ce. violaceus* the facies articularis digiti minoris projects rather more distally. The sulcus tendineus is deeper and the shaft in cranial view is straighter (proximally it is tilted ventrally in *Ce. violaceus*).

Coracoid: WAM 09.3.283 (L) is near complete, missing only the tip of the processus procoracoideus and the lateral margin of the processus lateralis. It is distinguished from the coracoid of all large extant Australian cuculids and that of the Melanesian *Ce. violaceus* by its much greater size and its proportionally stouter shaft. The omal width is proportionally wide and the facies articularis clavicularis is large as in *Ce. phasianinus* and *Ce.* bengalensis, whereas *Ce. violaceus* is narrower here and has a reduced facies articularis clavicularis. The processus procoracoideus is slightly damaged at the tip, but is proportionally narrower than that of other *Centropus* species. The lateral extent of the processus lateralis cannot be determined. The acrocoracoid is not penetrated by pneumatic foramina from the sulcus supracoracoideus beside the facies articularis clavicularis, as in *Ce. violaceus* but unlike in *Ce. phasianinus*, which is pneumatic. Also in ventral view, the sternal margin of the sulcus supracoracoideus/acrocoracoid is only slightly cranial to the sternal margin of the facies articularis humeralis.

Scapula: WAM 09.3.283 (L) is the most complete specimen, preserving the cranial end but lacking the caudal extremity, whereas 09.3.283 (R) lacks its cranial end and caudal extremity but preserves most of the shaft. The scapula is distinguished from those of all extant Australian cuculids and that of the Melanesian *Ce. violaceus* by the greater size of the articular surfaces and the width of the corpus. Although neither scapula from the holotype preserves the entire length, when both are aligned side by side, the estimated total length of the scapula of this individual is > 64 mm. It has pneumatic foramina medially caudal to the tuberculum coracoideum, which is only a small medial prominen*Ce.* The acromion is robust with a prominent laterally directed facies articularis clavicularis.

Sternum: WAM 09.3.283 (holotype) has the most complete specimen, preserving around 1.5 cm of the length of the cranial portion of the sternum, including the sulci articularis coracoidei, L and R processus craniolaterales, and the full anterior depth, although not the length, of the carina. Amongst the sterna of the species of *Centropus* that were available to us, it bears closest resemblance to *Ce. violaceus* in both size and morphology, being somewhat larger and more robust, and sharing its lack of a spina externa (see phylogenetics results), and having a very shallow, thick keel that lacks a cranially projecting apex carinae (carina relatively deeper, thinner, and with a cranially projecting apex carinae in *Ce.* bengalensis and *Ce. phasianinus*). Besides its greater size and robusticity, the sternum of *Ce. maximus* is distinguished from that of *Ce. violaceus* by the following features: the profile is less dorsoventrally flattened in cranial aspect so that the sternal basin is relatively deeper; the carina is somewhat proportionally deeper; the labrum externa of the sulcus articularis coracoideus projects further cranially either side of the midline (more or less flat in *Ce. violaceus*); and there is a distinct gap between the left and right sulci articularis coracoidei (they form a continuous groove in *Ce. violaceus*). The overall size of the cranial portion of the sternum is similar to that of S. *novaehollandiae*, but *Ce. maximus* is distinguished from this species by being much more robust with thicker bone, having a much shorter and thicker carina that does not project as far cranially as the labrum externa of the sulcus articularis coracoideus, and lacking a spina externa (thin and prominent in S. *novaehollandiae*). This specimen preserves four processus costales and the processus craniolaterales are cranially directed as in other species of *Centropus*. The carina of this species is reduced relative to that of *Ce. phasianinus* (approx. 17% of femur length in *Ce. maximus* vs. 23% in *Ce. phasianinus*), but less reduced than in *Ce. violaceus* (approx. 12%), suggesting that the extinct taxon may have been more volant than *Ce. violaceus*. Measurements (mm) (WAM 09.3.283): cranial width, > 42.9; depth of carina, 18.0; maximum width of carina, 5.5.

Pelvis: WAM 09.3.283 (holotype) preserves the only known pelvis. It reveals the complete length of the synsacrum, but neither left nor right ala postacetabularis ilii, ala ischii, nor pubii survives. The pelvis is distinguished from that of all large extant Australian cuculids and that of *Ce. violaceus* by its much greater size and robusticity. Compared to pelves of all other species of *Centropus* examined, including *Ce. violaceus*, the cranial end is absolutely and proportionally much deeper dorsoventrally, and the foramen acetabuli is absolutely and proportionally much larger. The ala preacetabularis ilii is very deeply concave, creating a large fossa iliaca dorsalis. Owing to damage to the bone surface, it is not possible to determine if the ala preacetabularis ilii is perforated as in *Ce.* bengalensis, *Ce. phasianinus*, and *Ce.* ateralbus, or solid as in *Ce. violaceus*, but two holes are present in the relevant place and at least attest to the ilium being very thin at this point, even if it were not perforated before death. If the cranially projecting process at the cranial extreme of the dorsal surface was present as in other species of *Centropus*, it is not preserved in this specimen, but, as preserved, the left side indicates that *Ce. maximus* had a less acute proximal extension to the fossa iliaca dorsalis. Measurements (mm) (WAM 09.3.283): length of synsacrum, 85.9; maximum width (measured between the caudal rims of the left and right antitrochanters), 60.9; minimum width (measured at the narrowest part of the alae preacetabulares ilii), 23.8; cranial depth, 29.9.

Femur: WAM 09.3.283 (R) is the most informative specimen, and is complete with some damage to the facies articularis acetabularis on the caput, as well as to the condylus medialis and the cristae lateralis and medialis sulci patellaris. It is very large and robust, and is far larger than the femur of any extant Australian cuculid, including *Ce. phasianinus*, and is also considerably larger than the femur of the extinct *Ce. bairdi* sp. nov. described above, and that of the Melanesian taxon *Ce. violaceus*. It is similar in length and shaft width to the femur of *Ce. colossus* described above, but is slightly longer and is more robust at its proximal and distal ends. It is distinguished from the femur of *Ce. colossus* by the following features: the collum femoris is craniocaudally thicker; the facies articularis antitrochanterica projects caudally, and the caudal facies distal of this projection is convex, as in *Ce. bairdi* sp. nov., rather than concave as in *Ce. colossus* (Fig. 2.3); on the craniomedial facies between the trochanter and the collum femoris there is a marked insertion for the m. iliofemoralis internus, which has about half the area of that in *Ce. colossus*; the impressiones obturatoriae interna and externa are larger and deeper; the shaft is craniocaudally thicker where it meets the proximal end of the bone, and the trochanter femoris is wider in lateral aspect; the distal end has wider and deeper condyles; the trochlea fibularis is deeper and wider, and is separated from the fossa poplitea by a zone containing a shallow fossa, and a proximocranial extension of the crista tibiofibularis; the impressio ligamentum cruciati cranialis is larger and deeper; the fovea tendineus m. tibialis cranialis is larger and deeper; and the origin of the ligamentum cruciati caudalis is smaller, less prominent, and is more medially located on the lateral wall of the fossa poplitea. Measurements (mm): for TL, PW, SW, and DW see Table 2.3; minimum shaft circumference = 26.2.

Figure 2.5: Skeletal elements of *Centropus maximus* sp. nov. from Flightstar Cave, Nullarbor Plain, south-central Australia. Tibiotarsus (WAM 09.3.284, L, paratype) in cranial (A) and caudal (B) aspects; fibula (WAM 09.3.284, R) (C); pelvis (09.3.283, holotype) in dorsal (D), ventral (E), lateral (F) and cranial (G) aspects; clavicula (09.3.283, L, omal fragment) (H), and (09.3.284, sternal fragment) (I); scapula (09.3.283, L) in lateral aspect (J); coracoid (09.3.283, L) in ventral (K) and dorsal (L) aspects; tarsometatarsus (09.3.284, L) in dorsal (M), plantar (N), and proximal (O) aspects, and distal tarsometatarsus (09.3.284, R) in dorsal (P) and plantar (Q) aspects; sternum (09.3.283, cranial portion) in cranial (R) aspect; ulna (09.3.284, R) in dorsal (S) and ventral (T) aspects, and ulna (09.3.283, L) in cranial (U) aspect; carpometacarpus (09.3.284, R) in dorsal (V) and ventral (W) aspects; mandible (09.3.283, L ramus, fragment) (X) and mandible (09.3.284, tip) in ventral aspect (Y). Abbreviations: ac, acromion; apc, apex carinae; api, ala preacetabularis ilii; cf, crista fibularis; cid, crista iliaca dorsalis; cm, cotyla medialis; cv, cotyla ventralis; fa, foramen acetabuli; fah, facies articularis humeralis; fas, facies articularis sternalis; fhl, canal for tendon of m. flexor hallucis longus; fg, facies gastrocnemialis; fi, foramen ischiopubica; fip, foramen interosseum proximale; fmI, fossa metatarsi I; fph, fossae parahypotarsales; fvp, foramina vascularia proximalia; ol, olecranon; pcd, processus cotylaris dorsalis; pa, processus acrocoracoideus; pl, processus lateralis; pp, processus procoracoideus; prc, papillae remigalis caudalis; ps, pons supratendineus; re, tuberositas retinaculum extensorium medialis; sac, sulcus articularis coracoideus; sc, sulcus tendineus; sf, sulcus flexorius; tfb, tuberculum m. fibularis brevis; ttc, tuberositas m. tibialis cranialis. Scale bars = 1 cm.


A
fg
cf
09.3.284d
re
ps
B
fip
C
D
api
cid
E
09.3.283k
F
cid
api
fa
fi
G
H
I
09.3.284m
J
ac
fac
K
pp
09.3.283f
fas
L
pa
pl
fas
M
fvp
ttc
N
fph
sf
O
shl
cm
R
sac
cv
S
prc
09.3.284j
T
U
ol
pcd
cv
V
st
W
P
tmII
tmIII
tmIV
Q
fmI
X
Y

Tibiotarsus: WAM 09.3.284 (L and R) show that the tibiotarsus of this species is remarkably large and robust, roughly double the length of the tibiotarsus of its extant Australian congener, *Ce. phasianinus*. The tibiotarsus of *Ce. colossus* is not known, but given that its distal femur is less robust than that of *Ce. maximus* (see above), its tibiotarsus would also be expected to be slightly more gracile. The tibiotarsus of *Ce. maximus* is markedly larger (nearly 30% longer) than that of the extant *Ce. violaceus* and the extinct *Ce. bairdi* sp. nov. described above. Apart from its larger size, the tibiotarsus is further distinguished from those of *Ce. bairdi* and *Ce. violaceus* by the following features: the facies gastrocnemialis is even more flattened than in *Ce. bairdi*, but the flattened surface of the shaft distal of the facies only extends about one-fifth of the length along the medial facies of the shaft, rather than half way; there is a deep depression at the proximocaudal part of the facies gastrocnemialis; the foramen interosseum proximale is very deep and crescent-shaped, and is readily apparent even in the absence of an articulated fibula; the pons supratendineus is about twice as wide as it is proximodistally long, and proportionally shorter proximodistally than in *Ce. bairdi*; the tuberositas retinaculi extensori for the insertions of the transverse ligament are very distinct (less pronounced in *Ce. bairdi* and even less so in *Ce. violaceus*), and the proximal tuberosity is relatively more distally located (proximal distance from pons equivalent to only half the shaft width at the pons) than in *Ce. bairdi* and even more so than in *Ce. violaceus* (proximally, distance from the pons is equivalent to shaft width at the pons); the sulcus extensorius is more laterally located than in *Ce. bairdi*, and especially so relative to *Ce. violaceus*; the incisura intercondylaris is wider than in *Ce. violaceus* and the condyles diverge widely cranially (parallel in *Ce. violaceus*), more so than in *Ce. bairdi*; and the condylus medialis is markedly deeper than it is proximodistally long (round in *Ce. violaceus*, off round in *Ce. bairdi*). Measurements (mm): for TL, PW, SW, and DW see Table 2.3. WAM 09.3.284d: width at crista fibularis, > 16.1; depth lateral cotyla, 15.0; depth medial cotyla, 15.7; minimum shaft circumference = 23.6.

Tarsometatarsus: WAM 09.3.284-f is the most informative specimen, preserving the entire length of the bone but with damage to the hypotarsus and trochleae metatarsi II and IV, whereas WAM 09.3.284-g preserves trochlea metatarsi II. The tarsometatarsus of *Ce. maximus* is much larger than that of any extant cuculid species, and is also considerably larger than that of the extinct *Ce. bairdi* described above. The tarsometatarsus of *Ce. colossus* is not known, but was probably slightly smaller than that of *Ce. maximus*, given its slightly smaller and more gracile femur. In addition to the features mentioned in the generic diagnosis for *Centropus* above, the tarsometatarsus of *Ce. maximus* has the following features: the tuberculum m. fibularis brevis is small and projects laterally at the lateroplantar corner of the lateral cotyla, as in *Ce. bairdi*; the impressiones retinaculi extensorii are low and small; the foramen vascularis medialis is placed more proximally than the foramen vascularis lateralis, but both are of similar size; the tuberositas musculus tibialis cranialis is very large, is placed on the medial wall of the sulcus extensorius, and there is a distinct gap between it and the foramen vascularis medialis (see phylogenetics results);

the sulcus flexorius is deeply excavated from the fossae parahypotarsales to almost as far distal as fossa metatarsi I; fossa metatarsi I is very deep, but does not excavate the medial shaft margin; trochlea metatarsi III is wider than it is dorsoplantarly deep, and its dorsal and plantar widths are the same (i.e. the planes of the trochlea are parallel, and do not converge plantarly as in *Ce. violaceus*) and it has a broad, deep medial groove; and the medial surface of the shaft is thick as in *Ce. bairdi*, unlike the dorsoplantarly compressed margin seen in *Ce. violaceus*. Measurements (mm): for TL, PW, SW, and DW, see Table 2.3. Proximal depth incl. hypotarsus: WAM 09.3.284 (L), 19.0; midshaft depth: WAM 09.3.284 (L), 7.0.

Phalanges: The paratype WAM 09.3.284 preserves five phalanges from the left foot (I.1, III.1, III.2, ungual ?III.3, and IV.1) and os metatarsal I. The metatarsal (hallux) is about 20% longer than that of *Ce. violaceus* and proportionally similar. Phalanges 1 and 2 of digit III and phalanx 1 of digit IV are almost identical in length to those of *Ce. violaceus* and therefore much shorter relative to body size, but they are much wider and deeper and thus more robust. In the phalanges of digit III, the dorsal surface projects strongly proximally (in III.1 this projection articulates with the wide, deep groove in trochlea metatarsi III of the tarsometatarsus; in III.2 it articulates with a groove in the distal end of III.1) providing lateral stability in the toe. The ungual is markedly curved, and of similar length to that of *Ce. violaceus* and thus is shorter relative to body size (the unguals of the available *Ce. violaceus* specimen are covered with the keratin sheath, making comparisons difficult). Overall, the phalanges of *Ce. maximus* appear to have been proportionally shorter than in *Ce. violaceus*, with a smaller foot span relative to body size presumed to correlate with more terrestrial habits in the extinct species. The more robust phalanges of *Ce. maximus* are consistent with the toes supporting the weight of a larger, heavier animal.

Table 2.3: Measurements (mm) of the long bones of the holotype and paratype of *Centropus maximus* sp. nov.; all material is from Flightstar Cave, Nullabor Plain, Western Australia; alphabetical subnumbers are given fo reach element from the associated skeletons

Element/Side	Catalogue no.	TL	PW	SW	DW
Holotype					
Femur, R	09.3.283a	93.4	18.2	9.0	21.9
Femur, dL	09.3.283b	–	–	9.0	21.9
Tarsometatarsus, pL	09.3.283g	–	–	10.1	–
Humerus, R	09.3.283c	80.2	20.5	6.9	16.9
Humerus, pL	09.3.283d	–	20.6	–	–
Humerus, dL	09.3.283e	–	–	–	16.6
Ulna, pL and dL	09.3.283 h and n	–	10.9	6.5	8.6
Coracoid, L	09.3.283f	53.8[†]	11.1[†]	5.0	16.7[†]
Scapula, pL	09.3.283i	–	15.7[§]	5.1	–
Scapula, dR	09.3.283z	–	–	5.2	–
Paratype					
Femur, pR	09.3.284a	–	20.6	–	–
Femur, pL	09.3.284b	–	–	9.4	–
Femur, dL	09.3.284c	–	–	–	22.7[*]
Tibiotarsus, L	09.3.284d	166.1	24.0[*]	9.2	17.4
Tibiotarsus, R	09.3.284e	–	–	9.2	–
Tarsometatarsus, L	09.3.284f	116.6	18.5	8.0	–
Tarsometatarsus, dR	09.3.284g	–	–	7.9	18.6[*]
Humerus, L	09.3.284h	81.5	–	6.9	–
Humerus, R	09.3.284i	–	20.0[*]	7.0	17.9
Ulna, R	09.3.284j	67.0[*]	9.0	6.8	8.6
Carpometacarpus, R	09.3.284k	37.7	11.7	–	9.6
Phalanx digiti majoris, L	09.3.284p	17.2	–	–	–
Coracoid, L	09.3.284o	–	–	–	17.1[†]
Scapula, pL	09.3.284l	–	–	5.1	–

Abbreviations: L, left; R, right; TL, total length; PW, proximal width; SW, shaft width; DW, distal width; *, minimum measurement due to damage; †, measurements of coracoid are as follows: TL is measured medially, PW is the width of the omal end, DW is the width of the sternal end; §, proximal width of scapula is measured from the acromion to the ventrodistal margin of the facies articularis humeralis.

Remarks

This species was the largest known cuculid from anywhere in the world, with measurements of the humerus and femur indicating that it outsized the previously known largest species, *Ce. colossus*, also from the Pleistocene of southern Australia. *Centropus maximus* had a tarsus length much greater than that of any extant member of the cuckoo family, including terrestrial species such as the Geococcyx roadrunners and Neomorphus ground-cuckoos of the Americas and the *Carpococcyx* ground-cuckoos of South-East Asia, and its long tarsometatarsus was matched by a very long and robust femur and tibiotarsus. The humeral morphology (curved, relatively slender shaft, much reduced caput humeri, and ventrally extended distal end) indicates that this species was poorly adapted to flight, and the very large and robust leg elements coupled with small feet suggest that this taxon was probably adapted to terrestrial locomotion, rather than to climbing.

2.4.3 Body mass and proportions

Body mass estimates: The eight selected regression equations of Campbell & Marcus (1992) produced a range of estimates for each of the three fossil species, with considerable variation within and amongst species (Table 2.4): estimates for *Ce. colossus* ranged from 2.2–2.3 kg; *Ce. bairdi* from 1.1–2.1 kg; and *Ce. maximus* from 2.3–3.1 kg. To assess which equation produced the most reliable estimates for large cuculids, we applied the same calculations to specimens of extant species. The resulting estimates are graphed as a proportion of published mean body mass for each species (Gilliard & LeCroy, 1967; Dunning, 2008; Erritzøe et al., 2012; Fig. 2.6). The equation based on nonpasserine tibiotarsus data consistently overestimated the body mass of extant cuculids whether they are highly volant (e.g. *Scythrops*, *Eudynamys*) or minimally so (*Ce. phasianinus*, *Ce.* bengalensis, *Ce. violaceus*) (Fig. 2.6). Thus we regard the maximum estimates for the two fossil species to which we could apply this equation as implausibly high (2.1 kg for *Ce. bairdi*; 3.1 kg for *Ce. maximus*). The long-legged bird tibiotarsus equation produced the best estimates for extant *Ce.* bengalensis and *Ce. phasianinus* (1.1 and 1.2 times known mean body mass, respectively). This equation also produced a highly accurate estimate for the individual S. *novaehollandiae* specimen we measured, which despite not being a long-legged taxon, had an estimated mass within 10 g of the actual weight recorded on its museum label. However, although it worked well for the smaller species, the long-legged bird tibiotarsus equation appeared to significantly overestimate the body mass of the largest extant species included in our comparison, *Ce. violaceus*, as did all other equations, signalling that they may also have produced overestimates for the very large extinct species.

Table 2.4: Body mass estimates for extinct and extant cuculids (g), using equations for different groups of birds from Campbell & Marcus (1992). Minimum and maximum body mass estimates for each species are highlighted in bold. Equations are as follows: All taxa – Femur, $\log_{10}M = 2.411*\log_{10}LC_F – 0.065$; Tibiotarsus, $\log_{10}M = 2.424*\log_{10}LC_T + 0.076$; Heavy-bodied birds – Femur, $\log_{10}M = 2.293*\log_{10}LC_F – 0.110$; Tibiotarsus, $\log_{10}M = 2.416*\log_{10}LC_T + 0.140$; Long-legged birds – Femur, $\log_{10}M = 2.529*\log_{10}LC_F – 0.216$; Tibiotarsus, $\log_{10}M = 2.794*\log_{10}LC_T – 0.418$; Non-passerines – Femur, $\log_{10}M = 2.412*\log_{10}LC_F + 0.002$; Tibiotarsus, $\log_{10}M = 2.419*\log_{10}LC_T + 0.170$. In each equation, M = mass (g), LC_F = least circumference of the femur (mm), and LC_T = least circumference of the tibiotarsus (mm). Mean body masses of extant species from Dunning (2008) and Erritzøe *et al*. 2012.

	Species							
Equation	*Centropus colossus*	*Centropus bairdi*	*Centropus maximus*	*Centropus bengalensis*	*Centropus phasianinus*	*Centropus violaceus*	*Scythrops novaehollandiae*	*Eudynamys scolopaceus*
All-species, femur	**2185**	**1113**	**2260**	196	578	**1083**	571	279
All-species, tibiotarsus	–	1682	2532	219	564	1315	643	348
Heavy-bodied birds, femur	2228	1173	2300	225	628	1142	**521**	314
Heavy-bodied birds, tibiotarsus	–	1903	2860	249	640	1488	730	396
Long-legged birds, femur	2266	1117	2346	181	561	**1084**	554	**262**
Long-legged birds, tibiotarsus	–	1632	2614	**156**	**464**	1228	538	**265**
Non-passerine, femur	**2558**	1303	2645	229	676	1266	668	326
Non-passerine, tibiotarsus	–	**2058**	**3094**	**269**	**691**	**1609**	**788**	**427**
Mean, femur equations	2309.3	1176.5	2387.8	207.8	610.8	1143.5	578.5	295.3
Mean, tibiotarsus equations	–	1818.8	2775	297.7	589.8	1410	674.8	359
Mean, all equations	2309.3	1497.6	2581.4	215.5	600.3	1276.9	626.6	327.1
Actual mean body mass of species	N/A	N/A	N/A	148	390	500†	648	233

† = Based on two individuals, both weighing 500 g.

However, the mean and range of body mass for *Ce. violaceus* are unknown. Its recorded weight (500 g) is based on only two individuals, the specimen reported in Gilliard & LeCroy (1967) (cited by Dunning, 2008 and Erritzøe et al., 2012) and the Australian Museum specimen used in our study (unpublished collection data). The skeleton of *Ce. violaceus* is far larger and more robust than that of *Ce. phasianinus*, for which individuals of >600 g are known (Dunning, 2008; Erritzøe et al., 2012), and so a body mass of rather more than 500 g for at least some *Ce. violaceus* individuals seems intuitive. However, this species may be lighter than expected owing to reduced musculature of the pectoral girdle, which may also be true of the three extinct species (see Systematic palaeontology). For smaller cuculids we regard the long-legged bird tibiotarsus equation as the one most suitable for estimating body mass. If this equation were also accurate for large species, then our best estimate for *Ce. bairdi* would be 1.6 kg, and for *Ce. maximus* 2.6 kg. This equation could not be applied to *Ce. colossus*, but three of the four femoral equations produced estimates of 2.2–2.3 kg for this species. Given the uncertainty about the suitability of any of these equations for very large coucals, the actual body masses of the extinct species may have been rather lower than those estimated. If 500 g is accepted for *Ce. violaceus*, then the long-legged bird tibiotarsus equation overestimated its mass by 2.46 times. Assuming that the same overestimate is true of *Ce. bairdi* and *Ce. maximus*, their revised estimates would be 664 g and 1 kg, respectively. Applying a similar correction to *Ce. colossus*, based on a 2.17-times overestimation of the mass of *Ce. violaceus* using the all-species femur equation, its revised mass would also be around 1 kg.

Simpson log-ratio diagram: The postcranial body proportions of extant and extinct species of *Centropus* are shown in Figure 2.7, where they are graphed relative to the comparator species, the highly volant channel-billed cuckoo S. *novaehollandiae*. Differences amongst the species of *Centropus* are minor and their proportions are similar: all have shorter proximal (humerus) and distal (ulna and carpometacarpus) wing elements than S. *novaehollandiae*, a shallower keel on the sternum, elongate coracoids, wide femoral midshafts, and very elongate tarsometatarsi. The proportions of the extant taxa *Ce.* bengalensis and *Ce. phasianinus* appear especially similar to one another, as do the proportions of the extant *Ce. violaceus* and extinct *Ce. maximus*. The limited skeletal remains for *Ce. bairdi* and *Ce. colossus* indicate that they shared similar humeral proportions, but had dissimilar femoral proportions.

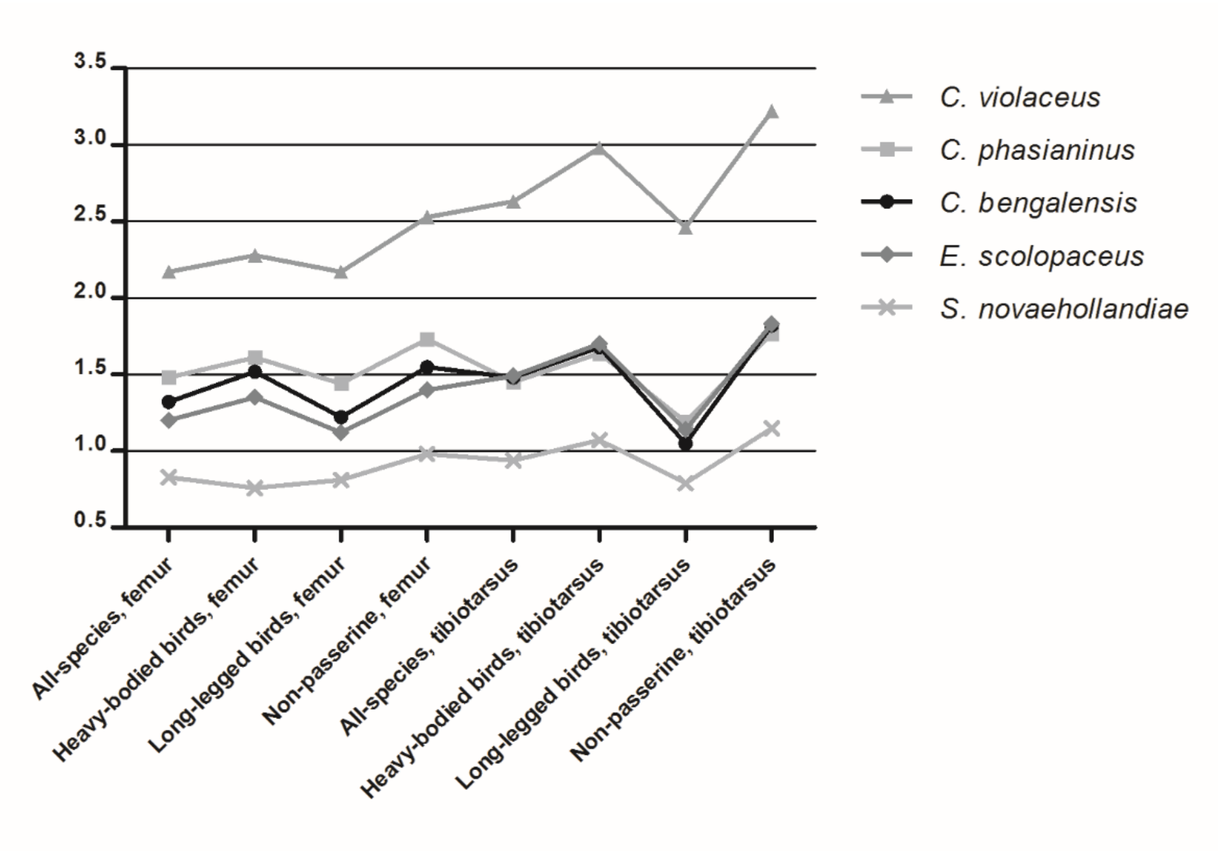


Figure 2.6: Body mass estimates for extant cuculids, using eight regression equations derived from Campbell & Marcus (1992); estimates are expressed as a proportion of published mean body mass for each species (Dunning, 2008); Erritzøe *et al.*, 2012) (e.g. a value of 2 on the *y*-axis indicates that the estimated body mass is double the average for that species). Abbreviations: *C.*, *Centropus*; *E.*, *Eudynamys*; *S*, *Scythrops*.

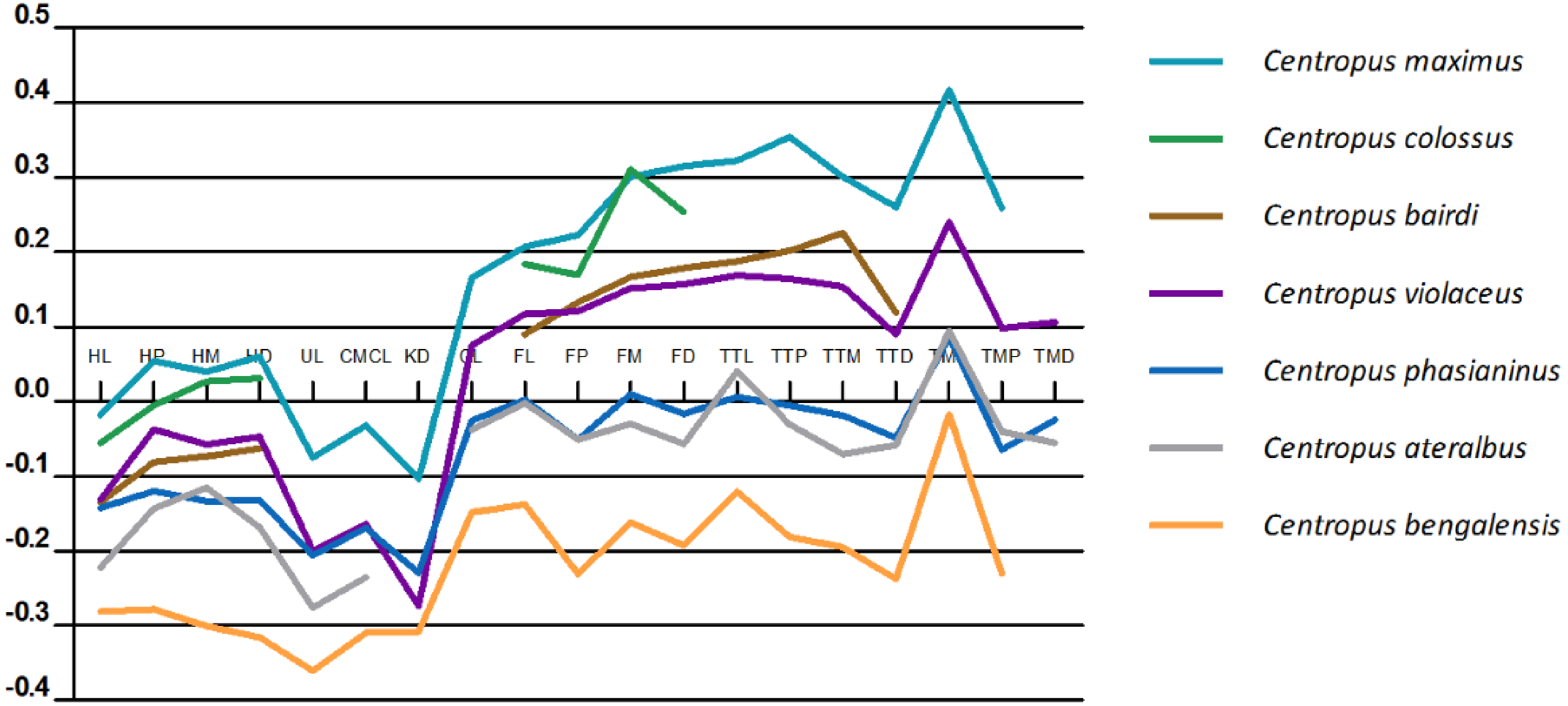


Figure 2.7: Simpson log ratio diagram of extinct and extant *Centropus* bones; zero line represents the standard species Channel-billed Cuckoo *Scythrops novaehollandiae* against which all values are calculated. Abbreviations: HL, humerus length; HP, humerus proximal width; HM, humerus midshaft width; HD, humerus distal width; UL, ulna length; CMCL, carpometacarpus length; KD, keel depth; CL, coracoid medial length; FL, femur length; FP, femur proximal width; FM, femur midshaft width; FD, femur distal width; TTL, tibiotarsus length; TTP, tibiotarsus proximal width; TTM, tibiotarsus midshaft width; TTD, tibiotarsus depth; TML, tarsometatarsus length; TMP, tarsometatarsus proximal width; TMD, tarsometatarsus distal width. Gaps in lines reflect absent data due to incomplete specimens.

2.4.4 Phylogenetic Analysis

Executing Hughes's (2000) original data matrix in PAUP* with the same settings and without any additional species recovered the original tree topology, so we were confident that the reconstructed data matrix was error-free. Since the publication of the original study, it has been established that the outgroup used by Hughes (2000) – Opisthocomus (Hoatzin) and the Musophagidae (turacos) – is not monophyletic (e.g. Jarvis et al., 2014). However, setting the outroot as paraphyletic or as a polytomy did not alter the topology of the original tree, indicating that the outgroup remains appropriate for polarizing the included characters. Adding all the extant and fossil taxa into the original matrix produced a poorly resolved consensus of > 8000 shortest trees, but it placed *Scythrops* close to *Eudynamys*/Urodynamis as expected. *Centropus phasianinus*, *Ce. violaceus*, and the three Australian fossils were the only taxa besides *Coua* that did not join a clade within the polytomy (tree not shown). To determine the causes of poor tree resolution, we trialled adding different species combinations to the original data set. Using only extant cuculids without any fossils, the best resolution at the basal end of the tree was found when *Ce. violaceus* was included and *Ce. phasianinus* excluded, and thus *Ce. phasianinus* was temporarily excluded in order to further investigate the effects of the fossils upon tree topology.

Simultaneously adding all three fossil species produced a polytomy, as did adding *Ce. bairdi* and *Ce. colossus* individually. However, adding *Ce. maximus* alone produced a resolved consensus of only four shortest trees, in all of which *Ce. violaceus* and *Ce. maximus* formed a clade between *Carpococcyx* and *Coua*. It is likely that the poor resolution seen with the inclusion of *Ce. bairdi* or *Ce. colossus* is because of the limited number of skeletal elements that we have for each (~5% of scored characters for *Ce. colossus*; 18% for *Ce. bairdi*). The more complete remains of *Ce. maximus*, by contrast, allowed scoring of 40% of all characters, and 57% of postcranial characters. We therefore excluded *Ce. bairdi* and *Ce. colossus* from further analysis in order to examine the affinities of *Ce. maximus*. With *Ce. bairdi* and *Ce. colossus* thus excluded and *Ce. phasianinus* reincluded, the resultant consensus of 16 shortest trees (Fig. 2.8) was less well resolved than when *Ce. phasianinus* was excluded. It nevertheless retained similar topology to the tree of Hughes (2000), with the bootstrap analysis confirming monophyly of the Cuculidae with 100% support. *Scythrops novaehollandiae*, which was not included in the original phylogenetic study, joined the clade that Hughes designated as the 'Cuculinae', albeit with dramatically lowered bootstrap support for that clade compared with the earlier study (52 vs. 98%). The 'Phaenicophaeinae' of Hughes was slightly less well supported (52 vs. 54%) with Rhinortha no longer falling within the clade. The 'Crotophaginae' retained 100% support, as did the 'Neomorphinae'. The 'Centropodinae', within which Hughes included *Centropus* and *Coua*, collapsed into a polytomy, but within this there was strong (90%) support for a clade formed by the extant *Ce. violaceus* from Melanesia and extinct *Ce. maximus* from the Nullarbor Plain. *Centropus phasianinus* did not join this clade, and

Carpococcyx continued to form its own clade separate from *Coua* and *Centropus* with 100% bootstrap support.

Variations in the arrangement of the branches for *Carpococcyx*, *Coua*, *Ce. phasianinus*, *Ce. violaceus*, and *Ce. maximus* within the 16 shortest trees from which the consensus tree is derived are summarized in Figure 2.9, with the branch orders shown at A, B, C, and D having been recovered four times each. The position of *Carpococcyx* remained stable in all trees, whereas the remaining four ingroup taxa were arranged four different ways. *Coua* and *Ce. phasianinus* were each other's nearest neighbours in all trees, forming a clade in a quarter of trees (Fig. 2.9C). The extinct *Ce. maximus* and extant *Ce. violaceus* formed a clade in all trees, although the position of this clade varied in relation to *Coua* and *Ce. phasianinus*: in 50% of trees, *Ce. phasianinus* was the nearest neighbour to the *Ce. violaceus*/ *Ce. maximus* clade (Fig. 2.9A, D); and in 75% of trees *Ce. phasianinus* was equally close or closer to the *Ce. violaceus*/*Ce. maximus* clade than was *Coua* (Fig. 2.9A, C, D).

In the bootstrap consensus tree (Fig. 2.8), the *Ce. violaceus*/*Ce. maximus* clade was supported by 13 apomorphies, of which only three were unambiguous: Character 69 [tarsometatarsus, position of tuberositas m. tibialis cranialis: distinct gap between the tuberositas and foramina vascularia proximalia, consistency index (CI) = 0.250, 0 ==> 1]; Character 96 (sternum, form and fusion of rostrum sterni: spina interna and spina externa absent, CI = 0.833, 0 ==> 5); and Character 97 (sternum, size of spina externa: absent, CI = 1.000, 0 ==> 2).

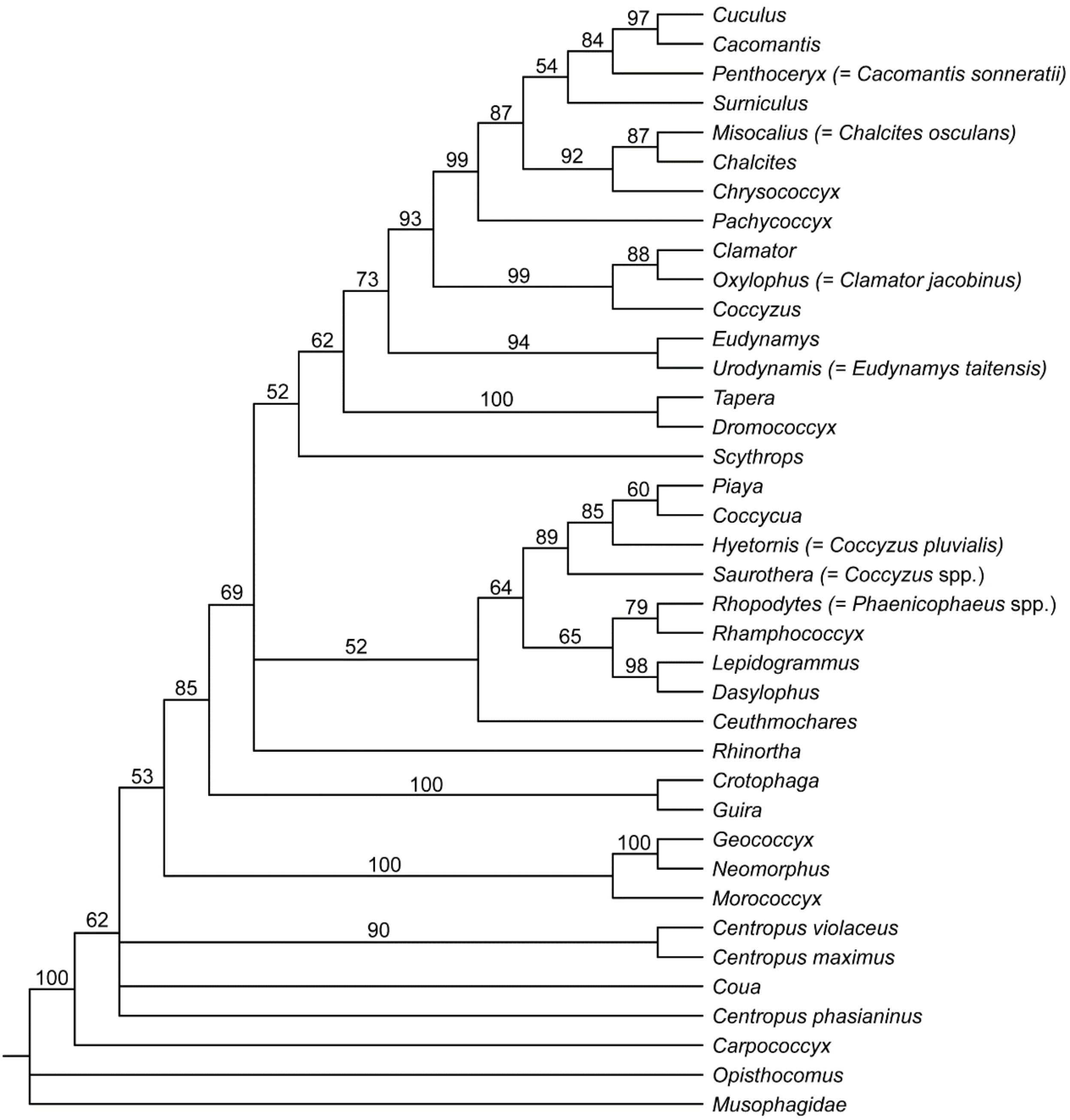


Figure 2.8: Phylogeny of cuculids, including the extinct Australian species, *Centropus maximus* sp. nov., based upon the 135-character osteological phylogeny of Hughes (2000); bootstrap consensus of 16 shortest trees (tree length = 308, consistency index = 0.59, retention index = 0.87); numbers above branches/nodes are bootstrap support values, expressed as percentages; taxon names in parentheses reflect current synonyms of taxa included in Hughes' (2000) original analysis.

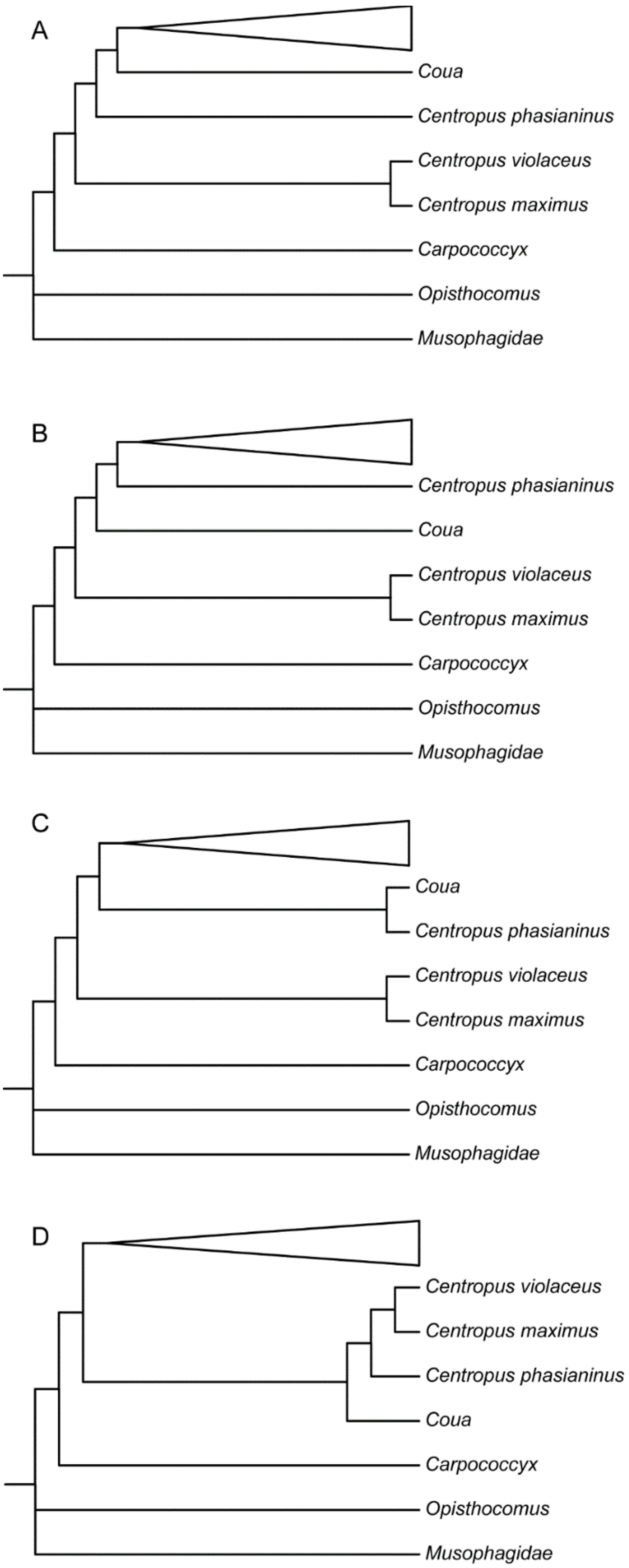


Figure 2.9: Subtrees of the phylogeny shown in Figure 2.8, showing differences in topology amongst the 16 shortest trees on which the consensus tree is based (topologies shown at A, B, C and D were each recovered four times). Changes in the position of *Coua*, *Centropus phasianinus*, *Centropus violaceus*, and *Centropus maximus* sp. nov. show that there was conflict in the relationships of the *Centropus* and *Coua* taxa.

2.5 Discussion

2.5.1 Evolutionary relationships

Our phylogenetic analysis consistently differentiated the extinct species from Australia's other large cuckoo genera, *Scythrops* and *Eudynamys*. It also differentiated them from *Carpococcyx*, supporting our osteological observations that the extinct Australian taxa are not geographical outliers of that exclusively South-East Asian genus of terrestrial cuckoos. Differentiation from the Madagascan *Coua* was more problematic, however, as we discuss below. A further limitation was that the sparse remains of *Ce. bairdi* and *Ce. colossus* precluded the production of a wellresolved tree in which the affinities of all three extinct taxa could be determined. Therefore, most of our discussion centres around how to better characterize *Centropus* and *Coua*, and the affinities of *Ce. maximus*.

The bootstrap consensus tree from Hughes (2000) was fully resolved with no polytomies, and was based on composite scorings of 33 cuckoo genera. The scoring for *Coua* was based on examination of five members of that genus, and for *Centropus* eight. Only a few variable characters distinguished these two genera from one another, but this was enough to resolve the tree with 80% support for the *Centropus*/*Coua* branch. When we independently scored an additional extant species of *Centropus* (*Ce. violaceus*), which had features that Hughes (2000) did not observe in eight other *Centropus* species, the character set no longer adequately separated *Centropus* from *Coua*, even with the fossils excluded. Given the lack of clear apomorphies distinguishing these two genera in the original study, it is unsurprising that additional species destabilized the original tree topology, even though we were careful to calibrate our interpretation of the characters. With extinct *Ce. maximus* included, extant coucal taxa that are closely genetically related (*Ce. phasianinus* and *Ce. violaceus*) failed to form a clade, with 75% of shortest trees actually showing a closer relationship between *Ce. phasianinus* and *Coua* than between *Ce. phasianinus* and *Ce. violaceus* (Fig. 2.9). This erroneous indication of paraphyly within *Centropus* alerts us that this character set needs revising to better distinguish between *Centropus* and *Coua*, and we do not therefore believe the conflict in this part of the tree to be evidence of a close relationship between the fossil taxa and *Coua*.

Centropus and *Coua* are speciose genera (26 and ten extant species, respectively), and it could be fruitful to evaluate the skeletal morphology of more of these along with *Carpococcyx* in any future osteological phylogeny of the Cuculidae. This could help to identify the affinities of fossil relatives such as those we have described, but might also help to clarify the evolutionary relationships of *Coua*, *Centropus*, and *Carpococcyx* themselves, about which there is disagreement (e.g. Hughes, 2000; Dickinson & Remsen, 2013; Johnson, Goodman & Lanyon, 2000; Posso & Donatelli, 2006; Sorenson & Payne, 2005). As per our generic diagnosis for *Centropus*, there are discrete characters and proportional differences that seem to distinguish it from *Coua*. For example, we observed variation in humeral features (crista deltopectoralis, crus dorsale fossa and crus ventrale fossae, processus supracondylaris dorsalis, impressio m. brachialis) that were not captured by the Hughes (2000) character set and could be revisited. We also identified a further feature separating humeri of *Centropus* from *Carpococcyx* (craniocaudal compression of the bone between the crus ventrale fossae and the intumescentia humeri in *Centropus*), which could also be assessed in *Coua* species. Similarly, differences that we noted between the tibiotarsus (deflection of the crista cnemialis cranialis, extent of contact between fibula and tibiotarsus, divergence or not of condylus medialis and lateralis) and tarsometatarsus (presence/ absence of a ridge separating the fossae parahypotarsalis medialis and lateralis, shape and relative distal extent of trochleae) of *Centropus* and *Coua* could also be re-evaluated across more members of these genera. Other skeletal elements should also be re-examined.

Despite the limitations discussed above, the relatively complete skeletons of *Ce. maximus* allowed us to assess the phylogenetic placement of this species from the Nullarbor Plain. Our bootstrap consensus tree, and all 16 of the shortest trees from which it was derived, placed it in a clade with the extant violaceous coucal, *Ce. violaceus*, from Melanesia (Figs 8 and 9; 90% bootstrap support). This is in accord with our observation that the skeletal proportions of these two taxa are remarkably similar (Fig. 2.7). The *Ce. violaceus*/*Ce. maximus* clade may indicate a genuine close evolutionary relationship between these Australasian taxa, which seems plausible given that they are found in proximate regions, but it is also possible that the three unambiguous apomorphies that join these two taxa could relate to large body size and/or similar biomechanics and locomotion, rather than shared ancestry.

One such apomorphy is a distinct gap between the tuberositas m. tibialis cranialis and the foramina vascularia proximalia of the tarsometatarsus. The tuberosity is the attachment for the primary muscle responsible for the forward swing of the leg (Rubenson & Marsh, 2009), with proximodistal placement varying between avian taxa. More distal placement is associated with climbing and clinging habits (Zeffer & Norberg, 2003), but also with slow forward legswing during walking in large, heavy taxa (Zeffer, Johansson & Marmebro, 2003). In *Ce. violaceus* this character state therefore matches its known climbing behaviour based on limited field observations: Orenstein (1976) reported this species to live in the lower forest canopy, and Gilliard & LeCroy (1967) observed it hopping vigorously up trees and sidling up vines for many metres. Diamond (2002) reported similar behaviour in the buff-headed coucal *Ce.* milo, but we did not have access to tarsometatarsi of this species to assess placement of the tuberositas. In a species as large as *Ce. maximus*, however, distal placement could relate to slow leg swing during walking (see Functional morphology) and so does not necessarily indicate shared ancestry with *Ce. violaceus*.

The other two unambiguous apomorphies defining the *Ce. maximus*/*Ce. violaceus* clade relate to the sternum, in particular the total absence of the spina externa, which is a character state not shared by any other cuculid taxon included by Hughes (2000), and for which we had to add two new character states in the present study (see Material and Methods). This absence of the spina externa indicates adaptation away from flight (see Functional morphology), which could be a shared evolutionary feature, but could equally have evolved separately in response to increased body size and reduced volancy in *Ce. violaceus* and *Ce. maximus*, and may not therefore reflect a true phylogenetic signal. Regardless of which is true, we note that the data set includes three characters – Characters 96, 97, and 98 – that essentially relate to the same region of the skeleton – the rostrum of the sternum. Given that these characters accounted for two of the three unambiguous apomorphies that define the *Ce. violaceus*/ *Ce. maximus* clade, this double-counting could be artificially enhancing the apparent phylogenetic signal. These characters, along with various others included in the Hughes (2000) phylogeny, should probably be concatenated in any future re-evaluation of the Cuculidae. Despite these possible weaknesses in the *Ce. violaceus*/*Ce. maximus* clade, a close relationship between them cannot be ruled out.

When electing to use Hughes' (2000) data set as the basis for our analysis, we noted that there were differences in the relationships between cuckoo subfamilies that she designated and those in Sorenson & Payne's (2005) molecular phylogeny, the latter of which was the foundation for Dickinson & Remsen's (2013) classification of the cuckoos. Although there are differences in the relationships between subfamily groupings in the molecular vs. the morphological trees, the identity of the clades themselves are in broad agreement. We note that the osteological phylogeny (Fig. 2.8) shows apparent paraphyly within the genus Coccyzus based on current nomenclature as compared to that used by Hughes (2000). This could be taken to indicate error in the osteological characters, but in a separate study, Hughes (2006) also identified molecular evidence of paraphyly within Coccyzus and has argued for resurrection of older genus names to accommodate this. This increases our confidence in the ability of the osteological phylogeny to differentiate amongst major clades, despite the limitations mentioned above.

2.5.2 Functional morphology and palaeoecology

2.5.2.1 Centropus body plan

The Simpson log-ratio diagram (Fig. 2.7) shows that relative to the highly volant comparator species, S. *novaehollandiae*, the extant species of *Centropus* that we examined (*Ce.* bengalensis, *Ce. violaceus*, *Ce. phasianinus*, *Ce.* ateralbus) share very similar skeletal proportions consistent with their notably reduced capacity for flight and increased walking/running ability, including short wing elements, shallow keel on the sternum, slender, elongate coracoids, and elongate leg elements, especially the tarsometatarsus. We observed little allometric variation despite the varied body sizes of these extant species. Insofar as the fossil taxa are preserved, they closely follow the body plan observed in extant species of *Centropus* species, with the larger epiphyses (Doube et al., 2012) and greater shaft diameters (e.g. Campbell & Marcus, 1992) in the larger taxa likely to correlate with greater body mass.

2.5.2.2 Large size and body mass

At present, the body masses of the three extinct coucals can only be considered as ranges. Given the uncertainty about the body mass range for *Ce. violaceus* and thus the suitability of the equations for estimating the mass of these very large coucals, it is most parsimonious to assume that the body masses of the extinct coucals fell somewhere between our downward adjusted estimates and the estimates produced using the equations that worked best for the smaller cuculids (see Results). Thus we consider that *Ce. colossus* had a mass somewhere between 1 and 2.3 kg, and *Ce. bairdi* between 664 g and 1.6 kg. The mass of *Ce. maximus* was probably between 1 and 2.6 kg, thus being similar to *Ce. colossus*. However, the femur and humerus of *Ce. maximus* are longer than in *Ce. colossus*, and they also have larger proximal and distal ends, indicating a larger animal overall. The pectoral girdle of *Ce. maximus* is also less reduced than in *Ce. violaceus* (e.g. proportionally deeper keel on the sternum), and so the lowest corrected estimate for *Ce. maximus* (1 kg) is perhaps too small. Overall, these are unsatisfyingly large ranges, but further data are needed on extant large, weakly flying coucal species to better assess the relationship between skeletal measurements and body mass.

We also note that coucals are sexually dimorphic, with females on average being considerably larger than males. For example, in *Ce.* p. *phasianinus* in Australia, mean male body mass is 302 g and for females 445 g (Erritzøe et al., 2012). Thus our body mass estimates for the extinct coucals, which are based on individual specimens, may fall within a considerable but unknown range within their species. Furthermore, the body mass estimates for *Ce. maximus* were based on circumference measurements on the most complete specimens, with the femur coming from the slightly smaller (holotype) individual, whereas the estimates based on the tibiotarsus came from the slightly larger paratype skeleton. The femur and tibiotarsus of *Ce. bairdi* may also have come from different individuals. This introduces a further element of variation into the estimates. Nevertheless, the extinct coucals would have been amongst the larger predatory land bird species in Pleistocene Australia, and *Ce. colossus* and *Ce. maximus* are the two largest known coucal species. Even if the lowest estimates of around 1 kg for these two extinct species are accepted, this would make them nearly 25% heavier than the heaviest extant coucal, *Ce.* milo, which has a reported mean mass of ~770 g (Erritzøe et al., 2012). Today, only four predatory bird species in Australia that hunt on dry land have a mean mass exceeding 1 kg: the wedge-tailed eagle, Aquila audax (males, 3.1 kg; females 3.8 kg); the black-breasted buzzard, Hamirostra melanosternon (1.2 kg); the white-bellied sea-eagle, Haliaeetus leucogaster (males, 2.4 kg; females 3.3 kg); and the powerful owl, Ninox strenua (males, 1.4 kg; females, 1.3 kg) (Dunning, 2008). An undescribed extinct Pleistocene accipitrid from Green Waterhole Cave (Baird, 1985) was also reportedly larger than A. audax.

Today, the largest species of *Centropus* live in Australia and Melanesia. The heaviest taxa are found in both basal and derived positions in the molecular phylogeny; thus, large size seems to have evolved repeatedly within the genus (Sorenson & Payne, 2005). The very large size of the extinct Australian species does not therefore necessarily indicate that they are particularly closely related to one another. Nor does it indicate to which extant taxa they are most closely related, nor whether they are basal or derived. Why such large species should have evolved on the Australian mainland is a mystery. Sorenson & Payne (2005) commented that the large body size of several species and subspecies of *Centropus* on Melanesian islands, as well the large size of Coccyzus lizard-cuckoos in the West Indies, reflects a general evolutionary pattern of increased body size in island bird populations. However, the extinct Australian coucal species demonstrate that gigantism within a bird lineage, and within the cuckoos in particular, has in the past been even more exaggerated in a continental rather than an island context.

The ecological correlates of large body size in these coucals are unknown, but our study does provide more evidence that Pleistocene (and probably pre- Pleistocene) Australia provided a conducive environment for the evolution of large-bodied, predominantly ground-dwelling birds. Boles (2006) remarked that the large size of Australia's extinct Pleistocene birds has perhaps been overemphasized, being the result of bias in research interest towards big species. Smaller extinct species may indeed have been overlooked thus far because they are not immediately remarkable, but regardless there is growing evidence for a suite of large, predominantly ground-dwelling birds inhabiting Australia during this epoch. In addition to the three coucals, there were 'giant' megapodes in the genus Progura, the truly gigantic dromornithid Genyornis newtoni, which is estimated to have weighed 292 kg (Murray & Vickers-Rich, 2004), and one species of large logrunner (Orthonyx hypsilophus) (Baird, 1985). The extant flightless Tasmanian swamphen, Gallinula mortierii, also inhabited the Australian mainland during the Pleistocene (Baird, 1984, 1986). All of these species would have coexisted with marsupial carnivores (e.g. the extinct 'marsupial lion' Thylacoleo carnifex and thylacine, Thylacinus cynocephalus, locally extinct Tasmanian devil, Sarcophilus harrisii, and extant quolls Dasyurus spp.); thus, absence of predators cannot be readily invoked as a reason for the evolution of these large, poorly flying and/or ground-dwelling birds, as it often can be for birds with a similar habitus in island contexts.

2.5.2.3 Functional morphology of the extinct species

Various features of the skeleton of *Ce. bairdi*, along with its large body size, suggest that it was probably an exceptionally poor flyer even for a coucal. The humerus was of similar length to those of several smaller congeners (*Ce. phasianinus*, *Ce. violaceus*, and *Ce.* milo), but it is narrower at its proximal and distal ends than those of the latter two, and has a notably reduced area for attachment of the m. brachialis compared with all other species of *Centropus* examined, including two of the weakest flying ones, *Ce. violaceus* and *Ce. milo*, which hop and climb up vegetation, glide between trees with occasional wing flaps to control descent, and appear incapable of sustained flight (Gilliard & LeCroy, 1967; Diamond, 2002; Erritzøe et al., 2012). The humerus of *Ce. bairdi* is also barely pneumatic. Its leg bones, by contrast, are long compared with the humerus, and the femur and tibiotarsus are robust, which is all consistent with increased emphasis on the legs in locomotion. With reduced wing musculature even relative to extant species that are barely volant, *Ce. bairdi* may have lacked sufficient wing power even to glide and therefore have been truly terrestrial.

Centropus maximus was slightly larger than *Ce. colossus* based on measurements of the humerus and femur, but given their similar body sizes, they may have occupied different ecological niches or have had allopatric ranges as the current known distribution could suggest. The very limited remains of *Ce. colossus* make functional morphological inferences difficult, but we consider it likely that it had compromised flying ability. Coucals as a genus are noted for their weak, laboured flight, and the high body mass of this species, coupled with a suite of features of its humerus (e.g. reduced crista deltopectoralis, small scar for m. pectoralis, cranial placement of the caput humeri, proximal placement of tuberculum ventrale), indicate adaptation away from flight. Without additional skeletal elements, however, we cannot infer if it was truly flightless, whether it could glide or if it was capable of flapping flight, or if it could climb.

By contrast, most postcranial elements of *Ce. maximus* are known, allowing a better assessment of its functional morphology. Its relatively slender humeri and large, robust leg elements indicate increased emphasis on the hind limbs for locomotion. The depth of the keel on its sternum is reduced relative to extant *Ce. phasianinus* and *Ce.* bengalensis (Fig. 2.7) and so it is presumed to be less volant than these species, which themselves fly poorly, but the keel is less reduced than in *Ce. violaceus*, which only glides. Another sternal feature shared by *Ce. maximus* and *Ce. violaceus* is the total absence of the spina externa (see Phylogenetic analysis, and Fig. 2.5R), which when present serves as an attachment for the membrana sternocoracoclavicularis (Baumel et al., 1993), thus stabilizing the pectoral girdle for flight. Its absence is consistent with adaptation away from flapping flight. By contrast, the papillae remigalis caudalis on the ulna of *Ce. maximus* are highly exaggerated (Fig. 2.5S), indicating strong articulation of the secondary flight feathers. These may therefore have supported the great mass of this bird during gliding or weak flight, especially if it first made its way up vegetation in the manner of *Ce. violaceus* and *Ce.* milo (Gilliard & LeCroy, 1967; Diamond, 2002; Erritzøe et al., 2012). However, we interpret the proportionally smaller feet of *Ce. maximus* compared with the climbing *Ce. violaceus* to mean that it was better adapted to walking than to climbing, and that it was therefore probably primarily a terrestrial species. The limited mandibular remains for *Ce. maximus* suggest that its bill may have had a wedge-shaped profile more similar to that of *Ce. phasianinus* than to the long, hooked bill of *Ce. violaceus*, but it is unknown if this shape relates to climbing, or to catching/processing prey.

2.5.2.4 Pleistocene ecology of southern Australia

Current fossil evidence suggests that as with *Ce. phasianinus* today, the three extinct species inhabited areas relatively close to Australia's moister continental margins, although inland fossil sites that preserve Quaternary land-bird assemblages are essentially lacking. Unlike *Ce. phasianinus*, however, the extinct species lived at similar latitudes to Africa's southernmost coucal populations, and far outside of the Australian tropical/subtropical climate and vegetation zone with which the genus is today associated. Throughout their global range, the 26 extant species of *Centropus* are overwhelmingly associated with moist, well-vegetated habitat. They are notably absent from truly arid, sparsely vegetated areas within their current range, such as the Sahara and most of the Arabian Peninsula, as well as Iran and Afghanistan, despite inhabiting wetter adjacent areas, including sub-Saharan Africa, the Nile Delta, and the Indian subcontinent. Today, *Ce. phasianinus* is heavily associated with water – indeed one of its alternative common names is the swamp pheasant (Fraser & Gray, 2013). In more inland areas of Australia the species is restricted to riparian habitat (Higgins, 1999), and the population in the monsoonal Pilbara region of north-western Australia (Fig. 2.1) is effectively separated from more easterly populations by the arid Great Sandy Desert/Canning Barrier (Mason et al., 1984; Schodde, 2006). Given the overwhelming preference of species of *Centropus* for moist, well-vegetated habitats around the world, it seems reasonable to assume that Australia's three extinct species also relied upon at least seasonally moist conditions.

Although the hydrological regime that sustained the extinct Australian coucals seems unlikely to have been truly arid, until recently there was little to suggest that Pleistocene conditions around the Thylacoleo Caves were moister than today. Prideaux et al. (2007) found no isotopic evidence for significantly wetter conditions on the Nullarbor Plain during the Middle Pleistocene compared with today. The Nullarbor Plain is currently arid to semi-arid, and has apparently lacked organized surface drainage and active water-bodies since before the Pleistocene (Lowry & Jennings, 1974; Webb & James, 2006). The age of the *Ce. maximus* fossils from Flightstar Cave is uncertain, but all *Ce. bairdi* fossils were found in Unit 3 of Leaena's Breath Cave, which dates to the Early Pleistocene (> 780 000 years ago), and are thus older than the predominantly Middle Pleistocene fossil material analysed by Prideaux et al. (2007). The Early Pleistocene faunal assemblage from Unit 3 is yet to be characterized in relation to vegetation and rainfall, but it perhaps represents a moister phase on the Nullarbor Plain that previously went undetected. This is corroborated by the recent discovery from Unit 3 of the remains of three frog species, two of which probably required ephemeral pools for breeding, which would indicate at least seasonally moist conditions (Tyler & Prideaux, in press). Only the arid-adapted Neobatrachus sudelli is represented in the younger Middle Pleistocene units of Leaena's Breath Cave and frogs are unknown on the Nullarbor Plain today (Tyler & Prideaux, in press). Interestingly, *Ce. phasianinus* in northern Australia is known to rely heavily upon tree-frogs as prey during the breeding season (Taplin & Beurteaux, 1992). *Centropus violaceus* has also been recorded taking tree-frogs (Gilliard & LeCroy, 1967), and various other coucal species from Asia and Africa also eat frogs (Erritzøe et al., 2012). Frogs may therefore have played an important role in the diets of the two Nullarbor species as well.

Some vertebrate taxa within the Thylacoleo Caves assemblages (e.g. tree-kangaroos, browsing marsupials, hollow-nesting parrots) indicate that a diversity of trees persisted in the region well into the Pleistocene, that the regional vegetation structure during the Middle Pleistocene was more complex than the low saltbush/bluebush shrub-steppe of today, and was probably a mosaic of woodland and grassland (Prideaux et al., 2007). Coucals inhabit both forest and savannah habitats throughout their wide range across three continents, and so the presence of *Ce. bairdi* on the Nullarbor Plain during the Early Pleistocene does not indicate whether woodland/ grassland was also present during this earlier phase, or whether a different vegetation community prevailed. However, it seems almost certain that all three extinct coucal species, which we interpret as being entirely or largely ground-dwelling, required areas of dense understorey for cover. Baird (1985) also interpreted the vegetation around Green Waterhole Cave as having dense understorey, with particular reference to the presumed low-light conditions required for foraging in the logrunner Orthonyx hypsilophus. Our study therefore highlights the likely loss of dense understorey from the Nullarbor region at some stage between the Early Pleistocene and today, which probably had profound effects on the fauna of the region. Historically, when considering the role that the Nullarbor region has played as a biogeographical barrier for the fauna of southern Australia during the Pleistocene, it has generally been the loss of trees that has been emphasized. Recent studies have begun to consider species assemblages and specific dietary/habitat niches of individual taxa that are now missing from this region, to better understand the ecological dynamics of southern Australia (e.g. Dolman & Joseph, 2012, 2015). Our study raises the possibility that the loss of dense understorey may have had a more profound impact on some taxa than the loss of trees per se. We hope that further analysis of the Thylacoleo Caves fauna will elucidate in finer detail the nature of the local vegetation and hydrology during different portions of the Pleistocene.

2.5.2.5 Extinction

The discovery of hitherto-unsuspected diversity amongst coucals in Australia provides evidence of another bird lineage that has suffered species loss and major geographical contraction in the geologically recent past. Although the causes and timing of extinction of *Ce. bairdi*, *Ce. colossus*, and *Ce. maximus* may never be determined, it is tempting to count them amongst Australia's Pleistocene megafaunal extinctions. The loss of large-bodied animals, mainly marsupials, from Australia during the Pleistocene has been extensively documented, with the relative roles of human impact and climatic change still hotly debated. Pertinent to the extinction of *Ce. bairdi* and *Ce. maximus*, Prideaux et al. (2007) speculated that burning of vegetation by humans during the Late Pleistocene (~40 kyr BP) may have fundamentally altered the Nullarbor's habitat, establishing the fireresistant chenopod shrub-steppe seen today, and leading to loss of the more complex habitat structure that supported the previously diverse faunal assemblage. However, there is currently no evidence for the timing of the emergence of the chenopod shrub-steppe, and climatic change remains another possible cause of vegetation change on the Nullarbor Plain and for the extinction of *Ce. bairdi* and *Ce. maximus*.

In relatively close proximity to the type locality of *Ce. colossus*, recent evidence has come to light of a significant regional mass extinction of plants in south-eastern Australia sometime after the Early Pleistocene, but here the vegetation lost was pyrophilic, and extinction is thought to have been brought about by temperature and rainfall fluctuations caused by global glacial/interglacial cycles (Sniderman, Jordan & Cowling, 2013). This does not prove that climate- related vegetation change/loss caused the demise of *Ce. colossus*, but it does alert us to the fact that dramatic vegetation change in south-eastern Australia had previously gone undetected. Although very localized, Sniderman et al.'s (2013) study highlighted that on a continental scale there is much yet to learn about Pleistocene vegetation change. If, however, humans were somehow agents of extinction for any of the three extinct coucals, indirect impacts seem more likely than overhunting, as coucals and some other cuckoos have a reputation for being highly unpalatable: for this reason huntergatherers release *Carpococcyx* spp. from traps (Erritzøe et al., 2012); greater black coucal, *Ce.* menbeki, turns nauseatingly rancid almost immediately after death and is similarly avoided (Diamond, 1994); and Cowles (1959) reported that Zulu hunters who would eat almost any animal would not eat 'rain coucals' (probably *Ce.* superciliosus), although this he reported to be because of superstition. Nestlings of various coucal species are also reported to be well defended against predators, in part because they emit foul-smelling excreta when attacked.

2.5.3 Biogeography

2.5.3.1 Historical biogeography of Australia

The pheasant coucal is regarded as a characteristic species of the Torresian fauna, which corresponds with the high-rainfall areas of tropical/subtropical northern and north-eastern Australia and New Guinea (Schodde, 2006). By contrast, the three extinct species discussed in this paper had their ranges in what are now different faunal and climatic zones (Schodde, 2006) – the temperate Bassian zone in the case of *Ce. colossus*, and the arid Eyrean zone in the case of *Ce. bairdi* and *Ce. maximus*. Although unexpected, the discovery of a species of *Centropus* by Baird (1985) in the moist south-east of Australia, relatively near the eastern range of *Ce. phasianinus* and within the same band of mesic habitat, was less surprising than finding two more species of *Centropus* in the now arid south-central Nullarbor region. As discussed above, the reasons for the loss of these species are unclear, as is the nature of hydrological change on the Nullarbor Plain during the Pleistocene. If increased aridity caused their demise, then their extinction could be a previously invisible example of contraction within a lineage in response to trends towards aridification and associated reduction of plant biomass, which has been documented amongst many of Australia's flora and fauna (e.g. Hawkins et al., 2005; Byrne et al., 2011). The contraction of the range of this genus also hints that the faunal zones recognized in Australia today may only have stabilized relatively recently during the Middle to Late Pleistocene. As with the fossil tree-kangaroos described from the Thylacoleo Caves fossil assemblage, the unexpected discovery of coucals from south-central Australia highlights how incomplete our understanding is of Australia's recent zoogeography. They also demonstrate the value that even comparatively recent fossils can have for identifying previously invisible faunal turnover in Australia. In Europe, bird fossils have provided considerable perspective on the persistence and turnover of bird species and genera from the Early into the Middle and Late Pleistocene (Finlayson et al., 2011). Australia will never have such a good avian fossil record as Europe for reasons of preservation, but high-quality sites that do exist, such as the Thylacoleo Caves deposits, should be maximally exploited for the data they can provide on the evolution of the continent's fauna and habitat.

In the case of both the tree-dwelling kangaroos and the poorly flying, cover-dependent coucals, dispersal across the continent must have happened via contiguous, or sequentially contiguous, vegetation corridors. The assumption of historical connectivity is strengthened by the presence on the Nullarbor Plain of not one but two species each of coucal and tree-kangaroo, the implication being that favourable habitat allowed multiple taxa, or their ancestors, to reach the same area independently. Fossil tree-kangaroos in the genus Bohra are known from the Thylacoleo Caves and various sites in eastern, southeastern, and central Australia, and these date from possibly the late Miocene, and certainly through the Pliocene and Pleistocene (Prideaux & Warburton, 2008, 2009). They are unknown from the northern third and north-western half of the continent, but this may reflect the general geographical bias in exploration for Quaternary-aged fossil sites (Prideaux, 2007). Thus, former linkages and dispersal routes remain unknown.

As a result of this study and that of Baird (1985), we now know that from the Early Pleistocene (> 780 kyr BP) to the present day, Australia has been home to at least four species of *Centropus*. We do not know how long this genus has been represented in Australia, the extent of temporal overlap amongst any of the species, nor indeed how late any of the three extinct species survived. Nevertheless, there is now ample evidence of an endemic Australian radiation of this lineage, with species in northern, eastern, and southern Australia. However, in the absence of a sound understanding of the geographical origin of the genus, and without a more comprehensive fossil record and a dated molecular phylogeny to constrain the timing of its radiation, it remains unknown how the Australian coucals fit into the global radiation.

Given that diversity of *Centropus* is maximal in South-East Asia/Melanesia (18 of 26 species), and is high through to southern Africa, an origin outside of Australia is most likely. If so, it is hypothetically possible that coucals were part of the faunal interchange that occurred between Australia and New Guinea at various intervals during the Miocene from 10 Mya onwards (Heinsohn & Hope, 2006). In contrast with extant mammal genera, which generally evolved in the Plio-Pleistocene, there is evidence that many extant bird genera evolved upwards of 5 Mya during the latest Miocene and have persisted to the present day (e.g. Olson & Rasmussen, 2001; Worthy, 2012; Nguyen et al., 2014). Longer-lived genera are rarer, but species of extant genera, e.g. Collocalia (Boles, 2001), Ciconia (Boles, 2005), Menura (Boles, 1995), and Orthonyx (Boles, 1993; Nguyen et al., 2014) are known from the Late Oligocene–Early Miocene of Riversleigh, north-western Queensland, Australia. Thus, although the time of entry of *Centropus* into Australia is unknown, it could plausibly long precede 5 Mya.

There has also been abundant opportunity for faunal exchange between New Guinea and Australia much more recently than the Miocene (e.g. Voris, 2000). To date, no remains of *Centropus* species have been found in any Australian Miocene or Pliocene site despite decades of work, which could be taken to indicate their Early Pleistocene arrival. Curiously however, neither have they been found in the many Pleistocene cave deposits at Naracoorte in south-eastern South Australia, despite close geographical proximity (< 100 km) to Green Waterhole Cave where *Ce. colossus* was discovered, and despite the temporal overlap of these fossil localities. It seems unlikely that *Centropus* would have been absent from the Naracoorte region given their presence around Green Waterhole Cave, so the reason for a lack of their bones in the Naracoorte fossil record is a mystery. This is especially puzzling given that these were large, probably predominantly ground-dwelling birds that should have been eminently susceptible to pitfall trapping. It is possible that their remains have been overlooked amongst the fossil bird remains from the various Naracoorte caves, which have so far been the subject of surprisingly little research. Absence from the poorly known Australian Pliocene and Miocene record does not therefore rule out their presence on the continent during these times.

2.5.3.2 Global biogeography of Centropus

Taking a wider geographical perspective, coucals have an unusually broad geographical distribution for a clade of birds with such notably poor volant ability. They seem simultaneously to be a genus of immense dispersal capability on the one hand, having even found their way to Madagascar, yet on the other hand they also evidently speciate readily: there are 63 distinct extant taxa of *Centropus* comprising 26 species, 12 of which are monotypic, and 14 of which are polytypic and account for 51 subspecies between them (Dickinson & Remsen, 2013). Many of these taxa are endemic to Asian/Melanesian islands, presumably because populations have evolved in isolation because of their weak flight. Despite this, the addition of at least three extinct species from southern Australia demonstrates that, similarly to Africa, which has seven extant species of *Centropus*, speciation within this genus has not been restricted to insular habitats. Few highly terrestrial bird genera have a similar global geographical distribution to *Centropus*, one exception being the buttonquails Turnix spp. These small, ground-dwelling birds are also diverse (15 species, eight of which are monotypic, seven polytypic, accounting for 48 subspecies, and thus 56 taxa in total; Dickinson & Remsen, 2013), and like coucals, they are found in Africa, Madagascar, the Indian subcontinent, Asia, Melanesia, and Australia. The only real differences in distribution compared with *Centropus* are a slight extension north of Africa into southern Spain, and a notable absence from Borneo. Both genera also share the characteristic of reversed sexual dimorphism, the females outsizing the males. Could these two genera have originated in the same geographical region at a similar time, and then dispersed simultaneously via similar routes and habitat corridors in response to similar life-history traits, or is their shared range coincidental? A joint study of these genera could be a tool to investigate patterns in historical biogeography, as well as to shed light on the evolutionary biology of terrestrial birds more generally.

2.6 Conclusion

There is now compelling fossil evidence that Australia hosted an endemic radiation of coucals during the Pleistocene, and that the current limitation of the genus to northern/eastern Australia is relictual or the result of recent recolonization. Lack of local diversity in this genus must now therefore be explained in terms of extinction processes, but this requires a better understanding of the geographical and temporal distribution of the three Pleistocene species. Our data show that Pleistocene species loss in Australia's birds has been underestimated. We hope that future fossil finds will clarify whether the exceptionally large species discussed here were part of localized biodiversity 'hotspots', or whether the species turnover long observed in Australia's Pleistocene marsupial megafauna is matched in the avifauna on a continental scale.

2.7 Addendum

While in press, we found an additional right femur of *Centropus colossus* from Green Waterhole Cave within the Flinders University Palaeontology collection, slightly smaller than SAM P42027, which will be registered with the South Australian Museum.

2.8 Acknowledgements

Thanks to the many individuals and institutions that have had a hand in supporting this project. Members of the Flinders University Palaeo Lab, the Western Australian Museum, and many students and volunteers have given their time to excavate the Thylacoleo Caves over the last decade, and have painstakingly removed thousands of fossil bones from tonnes of dirt. Lindsay Hatcher and Michael Simpson collected the *Ce. maximus* specimens from Flightstar Cave in uncomfortable circumstances (from between the rocks, at arm's length, with the collector unable to see their own hands and having to be guided by the other!). Special thanks to Carey Burke who prepared the fossils, Grant Gully who provided logistical/technical support, and Ben King who gave advice on phylogenetic analysis. Thanks to the following people for facilitating access to museum collections, and for providing loans, photographs, scans, and collection data: Mary-Anne Binnie and Philippa Horton (South Australian Museum); Heather

Janetzki (Queensland Museum); Gerald Mayr (Senkenberg Museum); Mark Robbins (University of Kansas Natural History Museum); Karen Roberts (Museum Victoria); Ross Sadlier, Jaynia Sladek, Walter Boles and Jackie Nguyen (Australian Museum); Helen Ryan (Western Australian Museum); and Janet Hinshaw (University of Michigan Museum of Zoology). Michelle Lynch (MicroCT Core, School of Dentistry) and Adam Rountrey (Paleontology Museum) (University of Michigan) scanned the *Carpococcyx* skeletal elements, extracted the surface data, and compiled the scans. Thanks also to Jan Hughes for providing information about her phylogenetic work on cuckoos, and to Bob Baird and Leo Joseph for discussions about coucals. Two anonymous reviewers provided very helpful comments on the manuscript. This work was conducted as part of E.S.'s PhD project on the Thylacoleo Caves fossil avifauna, in which she is supported by a Flinders University Research Scholarship and a scholarship from the Flinders University Faculty of Science and Engineering. BirdLife Australia provided research funding to E.S. via the Stewart Leslie Bird Research Award, for which grateful thanks. This research is also part of Australian Research Council Discovery Early Career Researcher Award project DE13 0101133 (T. H. W.), and Australian Research Council Future Fellowship Grant FT130101728 (G. J. P.). Additional funding for fieldwork was provided by a National Geographic grant, Sixty Minutes (Channel 9), the Western Australian Museum, Geological Survey of Western Australia, and Flinders University.

2.9 References

Baird, R.F. 1984. The Pleistocene distribution of the Tasmanian Native-hen *Gallinula mortierii mortierii*. *Emu* 84: 119–123.

Baird, R.F. 1985. Avian fossils from Quaternary deposits in 'Green Waterhole Cave', south-eastern South Australia. *Records of the Australian Museum* 37: 353–370.

Baird, R.F. 1986. Tasmanian Native-hen *Gallinula mortierii*: the first Late Pleistocene record from Queensland. *Emu* 86: 121–122.

Baird, R.F. 1993. Pleistocene avian fossils from Pyramids Cave (M-89), eastern Victoria, Australia. *Alcheringa: An Australasian Journal of Palaeontology* 17: 383–404.

Baumel, J.J., King, A.S., Breazile, J.E., Evans, H.E., Vanden Berge, J.C. 1993. Handbook of avian anatomy: nomina anatomica avium, 2nd edn. Cambridge, Massachusetts: *Publications of the Nuttall Ornithological Club* 23.

Boles, W.E. 1993. A logrunner *Orthonyx* (Passeriformes, Orthonychidae) from the Miocene of Riversleigh, north-western Queensland. *Emu* 93: 44–49.

Boles, W.E. 1995. A preliminary analysis of the Passeriformes from Riversleigh, northwestern Queensland, Australia, with the description of a new species of lyrebird. *Courier Forschungsinstitut Senckenberg* 181: 163–170.

Boles, W.E. 2001. A swiftlet (Apodidae: Collocaliini) from the Miocene of Riversleigh, northwestern Queensland. *Memoirs of the Association of Australasian Palaeontologists* 25: 45– 52.

Boles, W.E. 2005. A review of the Australian fossil storks of the genus *Ciconia* (Aves: Ciconiidae), with the description of a new species. *Records of the Australian Museum* 57: 165–178.

Boles, W.E. 2006. The avian fossil record of Australia: an overview. In: Merrick, J.R., Archer, M., Hickey, G.M., Lee, M.S.Y., eds. *Evolution and biogeography of Australasian vertebrates*. New South Wales, Australia: Auscipub, 387– 411.

Boles, W.E. 2008. Systematics of the fossil Australian giant megapodes *Progura* (Aves: Megapodiidae). *Oryctos* 7: 191– 211.

Byrne, M., Steane, D.A., Joseph, L., Yeates, D.K., Jordan, G.J., Crayn, D., Aplin, K., Cantrill, D., Cook, L.G., Crisp, M., Keogh, J.S., Melville, J., Moritz, C., Porch, N., Sniderman, J.M.K., Sunnucks, P., Weston, P. 2011. Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. *Journal of Biogeography* 38: 1635–1656.

Campbell, K.E., Marcus, L. 1992. The relationship of hindlimb bone dimensions to body weight in birds. In: K. Campbell, ed. *Papers in avian palaeontology honouring Pierce Brodkorb*. Natural History Museum of Los Angeles County, Science Series, 395–412.

Cowles, R.B. 1959. *Zulu Journal: Field Notes of a Naturalist in South Africa*. Los Angeles, California: University of California Press.

de Vis, C. 1888. Australian ancestry of the crowned pigeon of New Guinea. *Proceedings of the Royal Society of Queensland* 5: 127–131.

Diamond, J. 1994. Stinking birds and burning books. *Natural History* 103: 4–12.

Diamond, J. 2002. Dispersal, mimicry, and geographic variations in northern Melanesian birds. *Pacific Science* 56: 1– 22.

Dickinson, E.C., Remsen, J.V. Jr, eds. 2013. *The Howard and Moore complete checklist of the birds of the world*, Vol. 1: Non-passerines, 4th edn. Eastbourne: Aves Press.

Dolman, G., Joseph, L. 2012. A species assemblage approach to comparative phylogeography of birds in southern Australia. *Ecology and Evolution* 2: 354–369.

Dolman, G., Joseph, L. 2015. Evolutionary history of birds across southern Australia: structure, history and taxonomic implications of mitochondrial DNA diversity in an ecologically diverse suite of species. *Emu* 115: 35–48.

Doube, M., Yen, S.C.W., Klosowski, M.M., Farke, A.A., Hutchinson, J.R., Shefelbine, S.J. 2012. Whole-bone scaling of the avian pelvic limb. *Journal of Anatomy* 221: 21–29.

Dunning, J.B. 2008. *CRC handbook of avian body masses*, 2nd edn. Boca Raton, Florida: CRC Press.

Elzanowski, A., Stidham, T.A. 2010. Morphology of the quadrate in the Eocene anseriform Presbyornis and extant galloanserine birds. *Journal of Morphology* 271: 305–323.

Erritzøe, J., Mann, C.F., Brammer, F.P., Fuller, R.A. 2012. *Cuckoos of the world*. Helm identification guides. London: Christopher Helm.

Field, D.J., Lynner, C., Brown, C., Darroch, S.A.F. 2013. Skeletal correlates for body mass estimation in modern and fossil flying birds. *PLoS ONE* 8: e82000.

Finlayson, C., Monclova, A., Carrion, J.S., Fa., D.A., Finlayson, G., Rodriguez-Vidal, J., Fierro, E., Fernandez, S., Bernal-Gomez, M., Giles-Pacheco, F.. 2011. Ecological transitions – but for whom? A perspective from the Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 329: 1–9.

Fraser, I., Gray, J. 2013. *Australian bird names – a complete guide*. Victoria, Australia: CSIRO Publishing.

Gibbard, P.L., Head, M.J., Walker, M.J.C., The Subcommission on Quaternary Stratigraphy. 2010. Formal ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 Ma. *Journal of Quaternary Science* 25: 96–102.

Gilliard, E.T., LeCroy M,. 1967. Results of the 1958-1959 Gilliard New Britain expedition: 4. Annotated list of birds of the Whiteman Mountains, New Britain. *Bulletin of the American Museum of Natural History* 135: 173–216.

Gmelin, J.F. 1788. Caroli a Linne, *Systema Naturae per Regna Tria Naturae: Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis*. Leipzig: Georg Emanuel Beer.

Gray, G.R. 1840. *A list of the genera of birds with an indication of the typical species of each genus compiled from various sources*. London: Richard and John Taylor.

Hawkins, B.A., Diniz-Filho, J.A.F., Soeller, S.A. 2005. Water links the historical and contemporary components of the Australian bird diversity gradient. *Journal of Biogeography* 32: 1035–1042.

Heinsohn, T., Hope, G. 2006. The Torresian connections: zoogeography of New Guinea. In: Merrick, J.R., Archer, M., Hickey, G.M., Lee, M.S.Y., eds. *Vertebrate zoogeography and evolution in Australasia*. New South Wales, Australia: Auscipub, 71–93.

Higgins, P., ed. 1999. *Centropus phasianinus*, Pheasant Coucal. In: Parrots to Dollarbird. *Handbook of Australian New Zealand and Antarctic birds*. Vol. 4, Melbourne, Australia: Oxford University Press, 793–806.

Hindwood, K.A. 1954. The distribution of the Coucal (*Centropus phasianinus*) in Australia. Emu 54: 1–6.

Horsfield, T. 1823. *Zoological researches in Java and the neighbouring islands*, Vol. 6. London: Kingsbury, Parbury & Allen.

Hughes, J.M. 1997. *Systematics of new world cuckoos (Aves, Cuculidae) and the evolution of brood parasitism*. PhD thesis, Ontario, Canada: University of Toronto.

Hughes, J.M. 2000. Monophyly and phylogeny of cuckoos (Aves, Cuculidae) inferred from osteological characters. *Zoological Journal of the Linnean Society* 130: 263–307.

Hughes, J.M. 2006. Phylogeny of the cuckoo genus Coccyzus (Aves: Cuculidae): a test of monophyly. *Systematics and Biodiversity* 4: 483–488.

Illiger, J.K.W. 1811. *Prodromus Systematis Mammalium et Avium: Additis Terminis Zoographicis Utriusque Classis*, Eorumque Versione Germanica. Berlin: Sumptibus C. Salfeld.

Jarvis, E.D., Mirarab, S., Aberer, A.J., Li, B., Houde, P., Li, C., Ho, S.Y.W., Faircloth, B.C., Nabholz, B., Howard, J.T., Suh, A., Weber, C.C., da Fonseca, R.R., Li, J., Zhang, F., Li, H., Zhou, L., Narula, N., Liu, L., Ganapathy, G., Boussau, B., Shamsuzzoha, Bayzid, M., Zavidovych, V., Subramanian, S., Gabaldon, T., Capella-Gutierrez, S., Huerta-Cepas, J., Rekepalli, B., Munch, K., Schierup, M., Lindow, B., Warren, W.C., Ray, D., Green, R.E., Bruford, M.W., Zhan, X., Dixon, A., Li, S., Li, N., Huang, Y., Derryberry, E.P., Frost Bertelsen, M., Sheldon, F.H., Brumfield, R.T., Mello, C.V., Lovell, P.V., Wirthlin, M., Cruz Schneider, M.P., Prosdocimi, F., Samaniego, J.A., Vargas Velazquez, A.M., Alfaro-Nunez, A., Campos, P.F., Petersen, B., Sicheritz-Ponten, T., Pas, A.N., Bailey, T., Scofield, P., Bunce, M., Lambert, D.M., Zhou, Q., Perelman, P., Driskell, A.C., Shapiro, B., Xiong, Z., Zeng, Y., Liu, S., Li, Z., Liu, B., Wu, K., Xiao, J., Yinqi, X., Zheng, Q., Zhang, Y., Yang, H., Wang, J., Smeds, L., Rheindt, F.E., Braun, M., Fjeldsa, J., Orlando, L., Barker, F.K., Jønsson, K.A., Johnson, W., Koepfli, K.P., O'Brien, S., Haussler, D., Ryder, O.A., Rahbek, C., Willerslev, E., Graves, G.R., Glenn, T.C., McCormack, J., Burt, D., Ellegren, H., Alstrom, P., Edwards, S.V., Stamatakis, A., Mindell, D.P., Cracraft, J., Braun, E.L., Warnow, T., Jun, W., Gilbert, M.T.P., Zhang, G. 2014. Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* 346: 1320–1331.

Johnson, K.P., Goodman, S.M., Lanyon, S.M.. 2000. A phylogenetic study of the Malagasy *Coua*s with insights into cuckoo relationships. *Molecular Phylogenetics and Evolution* 14: 436–444.

Leach, W.E. 1819. Eleventh room, upper floor. In: Anonymous, ed. *Synopsis of the contents of the British Museum*, 15th edn. London: British Museum, 63–67.

Lowry, D.C., and Jennings J.N. 1974. The Nullarbor Karst Australia. *Zeitschrift Für Geomorphologie* 18: 35–81.

Mason, I.J., McKean, J.L., Dudzinski, M.L. 1984. Geographical variation in the Pheasant Coucal *Centropus phasianinus* (Latham) and a description of a new subspecies from Timor. *Emu* 84: 1–15.

Maurer, G. 2008. Who cares? Males provide most parental care in a monogamous nesting cuckoo. *Ethology* 114: 540– 547.

Maurer, G., Double, M.C., Milenkaya, O., Süsser, M., Magrath, R.D. 2011. Breaking the rules: sex roles and genetic mating system of the Pheasant Coucal. *Oecologia* 167: 413–425.

Mayr, G. 2015. Variations in the hypotarsus morphology of birds and their evolutionary significance. *Acta Zoologica*. doi:10.1111/azo.12117. [Epub ahead of print].

Megirian, D., Prideaux, G.J., Murray, P.F., Smit, N. 2010. An Australian land mammal age biochronological scheme. *Paleobiology* 36: 658–671.

Murray, P.F., Vickers-Rich, P. 2004. *Magnificent mihirungs: the colossal flightless birds of the Australian dreamtime*. Bloomington, Indiana: Indiana University Press.

Nguyen, J.M.T., Boles, W.E., Worthy, T.H., Hand, S.J., Archer, M. 2014. New specimens of the logrunner *Orthonyx kaldowinyeri* (Passeriformes: Orthonychidae) from the Oligo-Miocene of Australia. *Alcheringa: An Australasian Journal of Palaeontology* 38: 245–255.

Olson, S.L., Rasmussen, P.C. 2001. Miocene and Pliocene birds from the Lee Creek Mine, North Carolina. In: Ray C, Bohaska D, eds. Geology and paleontology of the Lee Creek Mine, North Carolina, III. Vol. 90: *Smithsonian Contributions to Paleobiology*. Washington, D.C.: Smithsonian Institution Press, 233–365.

Orenstein, R.I. 1976. Birds of the Plesyumi area, central New Britain. *Condor* 78: 370–374.

Pledge, N.S. 1980. Macropodid skeletons, including *Simosthenurus* Tedford, from an unusual 'drowned cave' deposit in the south east of South Australia. *Records of the South Australian Museum* 18: 131–141.

Posso, S.R., Donatelli, R.J. 2006. Análise filogenética e implicações sistemáticas e evolutivas nos Cuculiformes (Aves) com base na osteologia, comportamento e ecologia. Revista Brasileira de Zoologia 23: 608–629.

Prideaux, G.J. 2004. Systematics and evolution of the Sthenurine kangaroos. Vol. 146: *Geological Sciences*. Berkley, California: University of California Publications.

Prideaux, G.J. 2007. Mid-pleistocene vertebrate records. In: Elias SA, ed. *Encyclopedia of Quaternary Science*, 1st edn, Amsterdam, Netherlands: Elsevier, 1518–1537. Online Edition.

Prideaux, G.J., Warburton, N.M. 2008. A new Pleistocene tree-kangaroo (Diprotodontia: Macropodidae) from the Nullarbor Plain of south-central Australia. *Journal of Vertebrate Paleontology* 28: 463–478.

Prideaux, G.J., Warburton, N.M. 2009. *Bohra nullarbora* sp. nov., a second tree-kangaroo (Marsuplialia: Macropodidae) fromthe Pleistocene of the Nullarbor Plain, Western Australia. *Records of the Western Australian Museum* 25: 165–179.

Prideaux, G.J., Long, J.A., Ayliffe, L.K., Hellstrom, J.C., Pillans, B., Boles, W.E., Hutchinson, M.N., Roberts, R.G., Cupper, M.L., Arnold, L.J., Devine, P.D., Warburton, N.M. 2007. An arid-adapted Middle Pleistocene vertebrate fauna from south-central Australia. *Nature* 445: 422–425.

Rich, P.V., McEvey, A.R., Baird, R.F. 1985a. Osteological comparison of the scrub-birds, *Atrichornis*, and lyrebirds, *Menura* (Passeriformes: Atrichornithidae and Menuridae). *Records of the Australian Museum* 37: 165–191.

Rich, P.V., van Tets G.F., Knight, F. 1985b. *Kadimakara: extinct vertebrates of Australia*. Lilydale, Victoria: Pioneer Design Studio.

Rubenson, J., Marsh, R.L. 2009. Mechanical efficiency of limb swing during walking and running in Guinea Fowl (*Numida meleagris*). *Journal of Applied Physiology* 106: 1618–1630.

Schodde, R. 2006. Australasia's bird fauna today – origins and evolutionary development. In: Merrick, J.R., Archer, M., Hickey, G.M., Lee, M.S.Y., eds. *Evolution and biogeography of Australasian vertebrates*. Sydney, Australia: Auscipub, 413–458.

Simpson, G.G. 1941. Large Pleistocene felines of North America. *The American Museum Novitates* 1131: 1–27.

Sniderman, J.M.K., Jordan, G.J., Cowling, R.M. 2013. Fossil evidence for a hyperdiverse sclerophyll flora under a non- Mediterranean-type climate. *Proceedings of the National Academy of Sciences*, USA 110: 3423–3428.

Sorenson, M.D., Payne, R.B. 2005. A molecular genetic analysis of cuckoo phylogeny. In: Payne RB, ed. *The cuckoos*. New York, New York: Oxford University Press, 68–94.

Steadman, D.W., White, J.P., Allen, J. 1999. Prehistoric birds from New Ireland, Papua New Guinea: extinctions on a large Melanesian island. *Proceedings of the National Academy of Sciences*, USA 96: 2563–2568.

Swofford, D. 2001. PAUP*: phylogenetic analysis using parsimony (* and other methods) (version 4.0b10). Sunderland, Massachusetts: Sinauer Associates.

Taplin, A., Beurteaux, Y. 1992. Aspects of the breeding biology of the Pheasant Coucal *Centropus phasianinus*. *Emu* 92: 141–146.

van Tets, G. 1974. A revision of the fossil Megapodiidae (Aves), including a description of a new species of *Progura* De Vis. *Transactions of the Royal Society of South Australia* 98: 213–224.

Tyler, M.J., Prideaux, G.J. (in press). Early to middle Pleistocene occurrences of *Litoria*, *Neobatrachus* and *Pseudophryne* (Anura) from the Nullarbor Plain, Australia: first frogs from the "frog-free zone". *Memoirs of Museum Victoria*.

Voris, H.K. 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* 27: 1153–1167.

Wagler, J.G. 1830. *Natürliches System der Amphibien: mit vorangehender Classification der Säugethiere und Vögel: Ein Beitrag Zur Vergleichenden Zoologie*. Munich: J. G. Cotta.

Webb, J.A., James, J.M. 2006. Karst evolution of the Nullarbor Plain, Australia. In: Special paper 404: Perspectives on karst geomorphology, hydrology, and geochemistry – a tribute volume to Derek C. Ford and William B. White, Vol. 404: *Geological Society of America*, 65–78.

Worthy, T.H. 2012. A new species of Oligo-Miocene darter (Aves: Anhingidae) from Australia. *The Auk* 129: 96–104.

Worthy, T.H., Hawkins, S., Bedford, S., Spriggs, M. 2015. Avifauna from the Teouma Lapita Site, Efate Island, Vanuatu, including a new genus and species of megapode. *Pacific Science* 69: 205–252.

Zeffer, A., Norberg, U.M.L. 2003. Leg morphology and locomotion in birds: requirements for force and speed during ankle flexion. *The Journal of Experimental Biology* 206: 1085– 1097.

Zeffer, A., Johansson, L.C., Marmebro, A. 2003. Functional correlation between habitat use and leg morphology in birds (Aves). *Biological Journal of the Linnean Society* 79: 461–484.

Chapter 3: Taxonomic review of the Late Cenozoic megapodes (Galliformes: Megapodiidae) of Australia

---

Manuscript enclosed

The following manuscript was submitted to the journal *Royal Society Open Science* on 10th March 2017. Amendments were made based on comments from two open peer reviewers (Dr Gerald Mayr and Dr David Steadman), and the revised manuscript was submitted on 11th May. It was accepted for publication on 17th May, and was published on 14th June 2017.

It has been reformatted for this thesis document, including conversion of the referencing from Vancouver style (numbered references) to Harvard style (author-date in-text references). This has in places necessitated very minor re-wording of the text, but the content is essentially unaltered, and no information has been added or removed.

Context

During the course of my PhD research, I identified that remains of three species of megapode of different sizes were present in the Pleistocene fossil deposits of the Thylacoleo Caves. Referal of these taxa to genus and species was impossible due to confusion over the taxonomic status of fossil megapodes previously described from elsewhere in Australia. This prompted a comprehensive review of fossil megapodes from the Australian Plio-Pleistocene. The following chapter is the result of that process, and includes the description of two new extinct genera, re-description of two previously described extinct species, the description of three newly-discovered species, two of which are from the Thylacoleo Caves, and a phylogenetic analysis examining their relationships to each other and to extant megapodes. At the time that Prideaux *et al.* (2007) published a preliminary analysis of the vertebrate fauna from the Thylacoleo Caves, one large extinct species of megapode, then believed to be *Leipoa* (=*Progura*) *gallinacea* was identified as being present in the deposits. Research present in the following chapter shows that this referral was incorrect, and the remains previously attributed to *'Leipoa' gallinacea* from the Thylacoleo Caves belong instead to a new species in the genus *Progura*. The study has revealed that a major, and previously unknown, contraction of the megapode lineage occurred in Australia since the Pleistocene. The results are discussed in the context of the evolution and extinction history of the Australian avifauna.

Statement of authorship

ERS identified the Thylacoleo Caves specimens and identified the presence of two new species, participated in the design of the study, made the skeletal comparisons for the systematic palaeontology, collected and analysed the skeletal measurements, conducted the phylogenetic analysis, prepared the photographic plates and drafted the manuscript. GJP directed excavations of the Thylacoleo Caves and excavated much of the included material, provided direction and advice on the study design, edited the draft manuscript and directed the broader research project on the fossil fauna of the Thylacoleo Caves of which this study forms a part. THW provided direction and advice on the study design, developed the character set for the phylogeny on which this phylogenetic analysis is based, scored cranial material of the extinct Australian taxa for the phylogenetic analysis, oversaw the systematic palaeontology and data analysis and edited the draft manuscript. Percentage contribution of the authors is as follows: ES, 75%; GJP, 10%; THW, 15%.

Citation

Shute, E., Prideaux, G.J. and Worthy, T.H. (2017). Taxonomic review of the Late Cenozoic megapodes (Galliformes: Megapodiidae) of Australia, *Royal Society Open Science,* **4**: 170233. DOI: http://dx.doi.org/10.1098/rsos.170233

http://rsos.royalsocietypublishing.org/content/4/6/170233

ROYAL SOCIETY
OPEN SCIENCE

rsos.royalsocietypublishing.org

Research

Taxonomic review of the late Cenozoic megapodes (Galliformes: Megapodiidae) of Australia

Elen Shute, Gavin J. Prideaux and Trevor H. Worthy

School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide,
South Australia 5001, Australia

ES, 0000-0002-2714-2688; THW, 0000-0001-7047-4680

Megapodes are unusual galliform birds that use passive heat sources to incubate their eggs. Evolutionary relationships of extant megapode taxa have become clearer with the advent of molecular analyses, but the systematics of large, extinct forms (*Progura gallinacea*, *Progura naracoortensis*) from the late Cenozoic of Australia has been a source of confusion. It was recently suggested that the two species of *Progura* were synonymous, and that this taxon dwarfed into the extant malleefowl *Leipoa ocellata* in the Late Pleistocene. Here, we review previously described fossils along with newly discovered material from several localities, and present a substantial taxonomic revision. We show that *P. gallinacea* and *P. naracoortensis* are generically distinct, describe two new species of megapode from the Thylacoleo Caves of south-central Australia, and a new genus from Curramulka Quarry in southern Australia. We also show that *L. ocellata* was contemporaneous with larger species. Our phylogenetic analysis places four extinct taxa in a derived clade with the extant Australo-Papuan brush-turkeys *Talegalla fuscirostris*, *L. ocellata*, *Alectura lathami* and *Aepypodius bruijnii*. Therefore, diversity of brush-turkeys halved during the Quaternary, matching extinction rates of scrubfowl in the Pacific. Unlike extant brush-turkeys, all the extinct taxa appear to have been burrow-nesters.

1. Introduction

Megapodes (Megapodiidae) are a family of galliform birds endemic to Oceania. Uniquely among birds, they do not use body-heat to incubate their eggs [1]. Rather, most species bury their eggs in large nest mounds of soil and leaf litter, which they rake together using their very large feet: heat generated by decomposition of the vegetation incubates the

Cite this article: Shute E, Prideaux GJ, Worthy TH. 2017 Taxonomic review of the late Cenozoic megapodes (Galliformes: Megapodiidae) of Australia. *R. Soc. open sci.* **4**: 170233.
http://dx.doi.org/10.1098/rsos.170233

Received: 10 March 2017
Accepted: 17 May 2017

Subject Category:
Biology (whole organism)

Subject Areas:
evolution/palaeontology/taxonomy and systematics

Keywords:
megapodes, taxonomy, nomenclature, fossil birds, Pleistocene extinctions

Author for correspondence:
Elen Shute
e-mail: elen.shute@gmail.com

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.3792301.

THE ROYAL SOCIETY
PUBLISHING

3.1 Abstract

Megapodes are unusual galliform birds that use passive heat sources to incubate their eggs. Evolutionary relationships of extant megapode taxa have become clearer with the advent of molecular analyses, but the systematics of large, extinct forms (*Progura gallinacea, P. naracoortensis*) from the late Cenozoic of Australia, has been a source of confusion. It was recently suggested that the two species of *Progura* were synonymous, and that this taxon dwarfed into the extant Malleefowl *Leipoa ocellata* in the Late Pleistocene. Here we review previously described fossils along with newly discovered material from several localities, and present a substantial taxonomic revision. We show that *P. gallinacea* and *P. naracoortensis* are generically distinct, describe two new species of megapode from the Thylacoleo Caves of south-central Australia, and a new genus from Curramulka Quarry in southern Australia. We also show that *L. ocellata* was contemporaneous with larger species. Our phylogenetic analysis places four extinct taxa in a derived clade with the extant Australo-Papuan brush-turkeys *Talegalla fuscirostris*, *Leipoa ocellata*, *Alectura lathami* and *Aepypodius bruijnii*. Therefore diversity of brush-turkeys halved during the Quaternary, matching extinction rates of scrubfowl in the Pacific. Unlike extant brush-turkeys, all the extinct taxa appear to have been burrow-nesters.

3.2 Introduction

Megapodes (Megapodiidae) are a family of galliform birds endemic to Oceania. Uniquely among birds, they do not use body-heat to incubate their eggs (Dekker 2007). Rather, most species bury their eggs in large nest mounds of soil and leaf litter, which they rake together using their very large feet: heat generated by decomposition of the vegetation incubates the eggs (Jones, Dekker, and Roselaar 1995). A few species do not build mounds, and simply bury their eggs in warm sand, using either geothermal heat from volcanoes or the heat of the sun for incubation (Jones and Göth 2008), while some species in the genus *Megapodius* are flexible in their nesting strategies depending on environmental circumstances (Harris, Birks, and Leaché 2014).

There are seven extant genera of megapodes, containing 22 species: *Megapodius* (13 species), *Talegalla* (three species), *Aepypodius* (two species), and one species each in *Alectura*, *Leipoa*, *Macrocephalon*, and *Eulipoa* (Dickinson and Remsen 2013). However, it has been estimated that at least half of megapode species, mostly those on Pacific islands, have gone extinct since human colonisation during the Holocene (Steadman 1999).

A recent molecular phylogenetic analysis of extant megapodes identified two well-supported clades: a 'brush-turkey' clade containing the genera *Talegalla*, *Leipoa*, *Alectura* and *Aepypodius*; and a 'scrubfowl' clade of *Macrocephalon*, *Eulipoa* and *Megapodius* (Harris, Birks, and Leaché 2014) (Figure 3.1). In that study, which was based on 14 nuclear and two mitochondrial loci, only the position of *Macrocephalon* differed from an earlier phylogeny that used fewer loci (Birks and Edwards 2002), so it seems a consensus on relationships has been reached. In the more recent study, biogeographical modelling determined that the 'brush-turkey' clade probably had its origins in Australia–New Guinea, while the 'scrubfowl' clade probably evolved in Wallacea and thence dispersed widely through Oceania.

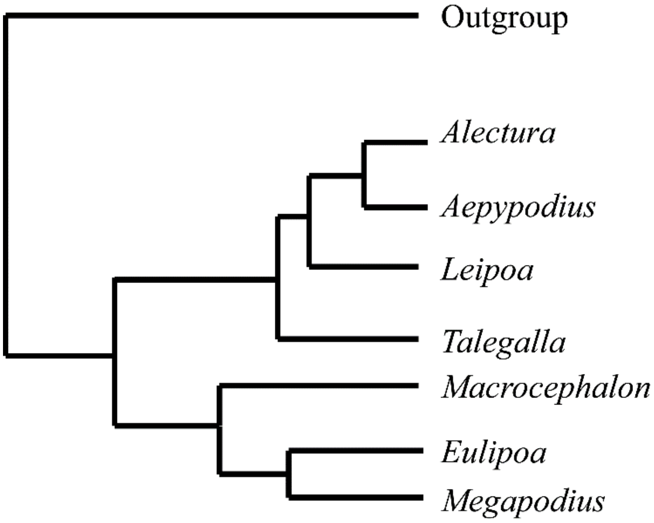


Figure 3.1: Molecular phylogeny of extant megapode genera (after Harris et al., 2014); *Macrocephalon* is included here as a basal member of the 'scrubfowl' clade

The scrubfowl and brush-turkey clades were estimated in that study to have diverged ~18 million years ago (Ma) during the early Miocene (Harris, Birks, and Leaché 2014). However, a recent large-scale molecular phylogeny of birds, which estimated divergence dates of modern avian groups using clock-like genes, estimated that the branches leading to extant *Leipoa* and *Megapodius* (and by inference, the 'brush-turkey' and 'scrubfowl' clades) diverged at >25 Ma during the Oligocene (Claramunt and Cracraft 2015), some seven million years earlier than the prior estimate (Harris, Birks, and Leaché 2014). The oldest known fossil megapode, the tiny *Ngawupodius minya* from Lake Pinpa in central Australia, is of Late Oligocene age (c. 26–24 Ma) (Boles and Ivison 1999), and could therefore potentially be a crown-group megapode belonging either to the 'brush-turkey' or 'scrubfowl' clade if an Oligocene divergence date is correct. However, remains of this taxon are sparse, and its phylogenetic affinities are so far unknown.

There is currently no pre-Late Oligocene fossil record for the Megapodiidae, despite recent estimates for the family's divergence from other galliforms ranging from ~45 Ma in the Eocene (Prum et al. 2015) to as much as 70–75 Ma in the Late Cretaceous (Harris, Birks, and Leaché 2014). The more recent fossil record of megapodes is also sparse, with a 20-million-year gap in the record between *N. minya* and the next appearance of megapodes in the Pliocene. A few bones representing one or more species have been described from the Pliocene deposits of Bluff Downs (Boles and Mackness 1994) and the Chinchilla Sand (Louys and Price 2015) in Queensland. These are discussed below (see Systematic palaeontology).

The richest megapode fossil record is of Quaternary age. A few fragmentary bones of a species of *Aepypodius*, possibly *A. arfakianus*, are known from a site of possible Late Pleistocene age on Irian Jaya (Aplin, Pasveer, and Boles 1999). Four extinct Holocene taxa have been described from Islands in the Pacific: *Megapodius molistructor* is known from New Caledonia and Tonga (Balouet and Olson 1989; Steadman 1989); *Megapodius alimentum* from Tonga and Fiji (Steadman 1989; Worthy 2000); *Megapodius amissus* from Fiji (T.H. Worthy 2000); and *Mwalau walterlinii* from Vanuatu (T. Worthy et al. 2015). A large, undescribed species of *Megapodius* is also known from New Ireland off eastern New Guinea (Steadman 1999; Steadman 2006).

Two further extinct Holocene taxa from the Pacific that were previously thought to have been megapodes, *Sylviornis neocaledoniae* from New Caledonia (Poplin, Mourer-Chauviré, and Evin 1983) and *Megavitiornis altirostris* from Fiji (T.H. Worthy 2000) have since been referred to a separate family, the Sylviornithidae, which is now regarded as the sister group to all extant galliforms (Mourer-Chauviré and Balouet 2005; Worthy et al. 2016). The present study considers the increasingly rich fossil megapode record from the Plio-Pleistocene of Australia. 'Giant' extinct taxa in the genus *Progura* have been described from south-east Queensland, eastern New South Wales, and south-eastern South Australia (De Vis 1888; van Tets 1974; Boles 2008), but as we outline in greater detail below, the number of genera and species represented among these remains is controversial and requires clarification.

3.2.1 Australia's megapodes and their Late Cenozoic fossil record

Australia has three extant species of megapode: the endemic *Leipoa ocellata* and *Alectura lathami*, and *Megapodius reinwardt*, which is shared with Indonesia and New Guinea (Dickinson and Remsen 2013). The Malleefowl *Leipoa ocellata*, the only extant megapode adapted to arid environments, is found only in southern Australia (Jones and Göth 2008). The Australian Brush-turkey *A. lathami* has two subspecies: *A. lathami lathami* in high-rainfall eastern Australia in tropical, sub-tropical and temperate zones; and *A. l. purpureicollis* on Cape York Peninsula in far north Queensland (Dickinson and Remsen 2013). Although *M. reinwardt* is not endemic to Australia, three of its five recognised subspecies are. *Megapodius reinwardt tumulus* is found in north-western and central northern Australia, *M. r. yorki* on the Cape York Peninsula, and *M. r. castanonotus* in coastal north-eastern Queensland (Dickinson and Remsen 2013). A fossil record for all these taxa is essentially lacking. Megapodes, either extant or fossil, are not known from Tasmania.

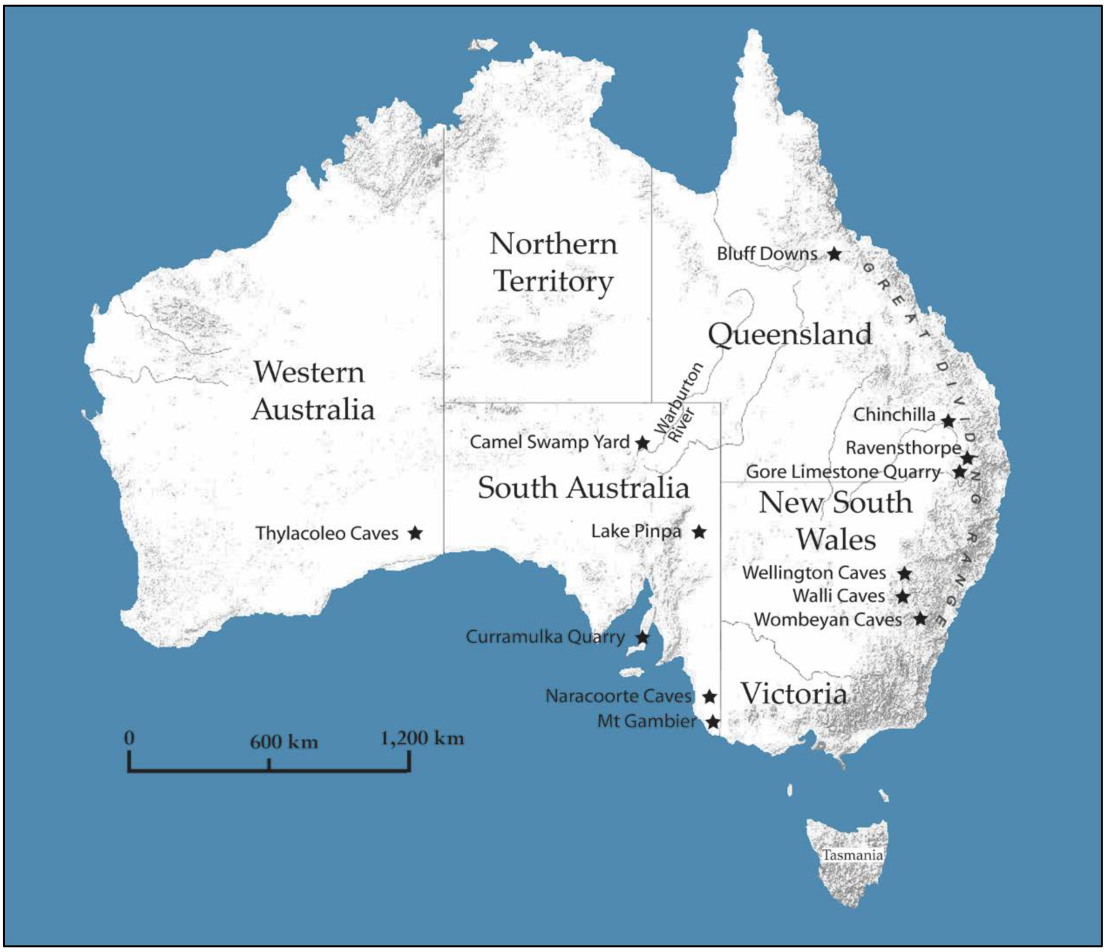


Figure 3.2: Key Australian fossil megapode localities

The earliest-described extinct megapode, the very large species *Progura gallinacea*, was described from deposits near the Condamine River in south-eastern Queensland (De Vis 1888) (Figure 3.2). The genus name was derived from De Vis's mistaken belief that the tarsometatarsi in the type series could be referred to a crowned pigeon ancestral to the *Goura* pigeons of New Guinea. *Progura gallinacea*, including several additional fossils from Queensland that de Vis erroneously referred to other avian families, was later placed in the Megapodiidae (van Tets 1974), along with more recently discovered Pleistocene remains from Walli Caves, Wellington Caves and Wombeyan Quarry in eastern New South Wales (Figure 3.2). In the same paper, van Tets described a second, somewhat smaller species, *P. naracoortensis*, from Pleistocene cave deposits in the Naracoorte region of south-eastern South Australia, and from Gore Limestone Quarry in south-eastern Queensland (Figure 3.2). However, he later informally revised his taxonomic decision, suggesting that the larger individuals were males and the smaller ones females of a single, sexually-dimorphic species, *P. gallinacea* (van Tets 1985). Conflicting with this, Olson (1985) commented that a cursory examination of fossils of *P. gallinacea* and *P. naracoortensis* led him to believe that they belonged in separate genera, but did not elaborate on why.

The identity of the two species of *Progura* was formally investigated by Boles (Boles 2008), who agreed with van Tets that fossils attributed to *Progura gallinacea* and *P. naracoortensis* belonged to one species. He concluded that apparent proportional differences within the skeleton between the two nominal species – namely the ratio of tarsometatarsus length to coracoid length given by van Tets (van Tets 1974) – were not valid due to the lack of associated skeletons. Boles (Boles 2008) argued that the coefficients of variation for lengths of tarsometatarsi and coracoids from modern specimens of *A. lathami* and *L. ocellata* were "not dissimilar to those of the *Progura* specimens collectively", and this was the primary reason given for synonymising *P. naracoortensis* with *P. gallinacea.* However, Boles' calculations of mean tarsometatarsus length excluded the type material of *P. gallinacea* from the Darling Downs, and were based only on tarsometatarsi of *P. naracoortensis* from Naracoorte. The study also lacked a morphological comparison of the type tarsometatarsi of the two nominal species. In our opinion, differences in the morphology and size of specimens referred to *P. gallinacea* and *P. naracoortensis* sensu van Tets (G. F. van Tets 1974) have not been satisfactorily addressed to date, and we aim to rectify this in our study.

A further matter to be resolved is the relationship between the large extinct megapodes and extant *L. ocellata*. Boles (2008) proposed that *Progura gallinacea* was a giant chronospecies of *L. ocellata*, the small size of the latter being the result of 'Late Pleistocene dwarfing', as purportedly observed in some other taxa (Marshall and Corruccini 1978). Noting no substantial differences in hind limb morphology between *Progura* and *Leipoa* besides size, Boles suggested that the large Pleistocene species should be referred to *L. gallinacea.* The nomen *Leipoa gallinacea* has subsequently been adopted in the literature for large Pleistocene megapode fossils (Louys and Price 2015; G. J. Prideaux et al. 2007; Reed and Bourne 2009). However, the dwarfing theory requires re-examination, in part because of the problematic synonymy of *P. gallinacea* and *P. naracoortensis*, but also because small Pleistocene fossils referred to *L. ocellata*, and large fossils referred to *P. naracoortensis*, have both been collected from the Main Fossil Chamber of Victoria Fossil Cave, Naracoorte (Reed and Bourne 2000), casting doubt on the chronospecies hypothesis.

The recent discovery of both large and small megapode fossils from Pleistocene deposits of the Thylacoleo Caves of the Nullarbor Plain, Western Australia, has prompted our re-examination of the Late Cenozoic megapode fossils from Queensland, New South Wales and south-eastern South Australia, and the first examination of previously unstudied megapode fossils from Curramulka and the Warburton River, South Australia (Figure 3.2). We address the generic and species diversity of Australia's Plio-Pleistocene megapodes, as well as the evolutionary relationships between the extinct taxa and extant megapodes.

3.3 Materials and methods

3.3.1 Abbreviations and definitions

Institutions: AM, Australian Museum, Sydney; AMNH, American Museum of Natural History, New York; ANWC, Australian National Wildlife Collection, Canberra; FU, Flinders University, Adelaide; KU, University of Kansas Natural History Museum, Lawrence; USNM, National Museum of Natural History, Washington DC; NHMUK, Natural History Museum, London; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington; NMV, Museum Victoria, Melbourne; QM, Queensland Museum; SAMA, South Australian Museum, Adelaide.

Geological timescale: Pliocene = 5.3–2.58 Ma; late Pliocene (Piacenzian) = 3.6–2.58 Ma; Early Pleistocene = 2.58–0.78 Ma; Middle Pleistocene = 780–126 thousand years ago (ka); Late Pleistocene = 126–11.7 ka; Quaternary = 2.58–0 Ma; Holocene = 11.7 ka–0 ka; Naracoortean = biocorrelated Australian land mammal age of Megirian *et al.* (2010), spanning max. 3.03–2.58 Ma to present; Tirarian = biocorrelated Australian land mammal age of Megirian *et al.* (2010), spanning 4.46 Ma–3.6 Ma.

Other terminology: CV = coefficient of variation; dL = distal left; dR = distal right; L = left; Ma = million years; m. = musculo (i.e. muscle, Latin); mm = millimetres; OSL = Optically Stimulated Luminescence; pL = proximal left; pR = proximal right; R = right; SD = standard deviation; troch. = trochlea/e; yr BP = years before present.

3.3.2 Comparative material

Modern skeletons of megapode taxa were examined as follows. Malleefowl *Leipoa ocellata*: SAM B.414, SAM B.1094, SAM B.5039, SAM B.11482, SAM B.55458, SAM B.11480, SAM B.11481, SAM B.47825, SAM B.48526, SAM B.48765, SAM B.49461, SAM B.51215, SAM B.55528, SAM B.58520, SAM B.58560; Australian Brush-turkey *Alectura lathami*: SAM B.46568, QM O.27218, QM O.27843, QM O.27844, QM O.27852, NMV B.2209, NMV B.4288, NMV B.11471, NMV B.19290, NMV B.23648, NMV B.23649, NMV B.23650; Moluccan Megapode *Eulipoa wallacei*, USNM 558275; Orange-footed Scrubfowl *Megapodius reinwardt*: ANWC O.22869; Melanesian Megapode *Megapodius eremita*: NMV B.20648, NMV B.20641, NMV B.20642, NMV B.20647, NMV B.24000, NMV B.24947, NMV B.24948, NMV B.24949, NMV B.24950, NMV B.24951, NMV B.24952, NMV B.25389; Black-billed Brush-turkey *Talegalla fuscirostris*: ANWC 03669, KU 97007; Collared Brush-turkey *Talegalla jobiensis*, ANWC 07567, USNM 146744; Wattled Brush-turkey *Aepypodius arfakianus*: ANWC O.26042; Waigeo Brush-turkey *Aepypodius bruijnii*, USNM 146767; Maleo *Macrocephalon maleo*, AMNH 12013 (by photographs taken 2000 by J. Palmer), NHMUK 1891.7.20.97, 1871.7.21.1, USNM 225130.

3.3.3 Key Locations

Key fossil-bearing localities mentioned in the Systematic Palaeontology section below are shown in Figure 3.2. Brief accounts of the localities are as follows.

3.3.3.1 Darling Downs, south-east Queensland

Megapode fossils have been recovered from three locations on the Darling Downs: Chinchilla, Ravensthorpe, and Gore Limestone Quarry (van Tets 1974). The Chinchilla Sand has not been directly dated, but its mammal fauna is dated to be of Pliocene age by biocorrelation with the Kanunka and Toolapinna Local Faunas of the Tirari Formation, Lake Eyre Basin, to be approximately 3.6 million years old (Louys and Price 2015), and thus fossils from the locality fall within the Tirarian land mammal age Megirian *et al.* (2010). Ravensthorpe, near Pilton, in the Clifton region east of King's Creek on the Eastern Darling Downs (Molnar and Kurtz 1997) is within in a river catchment where various fossil-bearing sites have been dated to the Late Pleistocene (Price et al. 2011). Fossils from Ravensthorpe are presumed to also be of Pleistocene age, and therefore within the Naracoortean land mammal age (Megirian et al. 2010). Fossils from Gore Limestone Quarry are mainly from fissure-fills, and are considered to be mainly Pleistocene in age (Bartholomai 1977).

3.3.3.2 Warburton River, north-eastern South Australia

A single megapode fossil has been collected from CAM 4 Quarry, Camel Swamp Yard (27°44.021'S, 137°45.196'E) (Worthy 2008), Warburton River, South Australia (Figure 3.2). This site contains a late Pliocene fossil fauna belonging to the Toolapinna Local Fauna within the Tirari Formation (Worthy 2008; Tedford, Wells, and Barghoorn 1992).

3.3.3.3 Thylacoleo Caves, Nullarbor Plain, Western Australia

A species of megapode is recorded in the faunal list for the Thylacoleo Caves (G. J. Prideaux et al. 2007), Nullarbor Plain, Western Australia (Figure 3.2). The three caves comprising this locality (Leaena's Breath Cave, Last Tree Cave and Flightstar Cave) are formed within the Early Miocene-aged Nullarbor Limestone and preserve a vertebrate fossil fauna of Early and Middle Pleistocene age (G. J. Prideaux et al. 2007), falling within the Naracoortean land mammal age (Megirian et al. 2010). Precise locations of the caves are registered with the Department of Earth and Planetary Sciences, Western Australian Museum, Perth. The fossil fauna is presumed to have accumulated via pitfall trapping through the solution pipe entrances to the caves, during intervals in the Pleistocene when they were open to the surface.

3.3.3.4 Naracoorte, south-eastern South Australia

The majority of megapode fossils recorded to date have been collected from various caves in the Naracoorte region (Figure 3.2). Some of the caves comprise the Naracoorte Caves World Heritage Area (Reed and Bourne 2000), while others are in the surrounding area. Caves in the region preserve Middle Pleistocene, Late Pleistocene and Holocene fossils (Reed and Bourne 2009, 2000). The majority of fossil megapode material comes from Henschke's Fossil Cave. This cave, which is formed within the Miocene-aged Gambier Limestone, was discovered within a working quarry and was eventually destroyed in 1981 following extensive excavation during the previous decade (Pledge 1990). It preserved a Pleistocene fauna, likely Middle or Pleistocene in age (Pledge 1990), falling within the Naracoortean land mammal age (Megirian et al. 2010).

3.3.3.5 Curramulka Quarry, Yorke Peninsula, South Australia

Curramulka Quarry (site RF 95) is a limestone quarry near the township of Curramulka (34°42'11.8"S 137°42'14.3"E), on the Yorke Peninsula, South Australia. The RF95 fissure-fill is considered to have accumulated vertebrate remains during the Pleistocene based on the presence of macropodid species that occur in deposits of this age elsewhere (Prideaux and Warburton 2008, 2009; Prideaux 2004).

3.3.4 Measurements

Measurements were taken with digital callipers and rounded to the nearest 0.1 mm. Long-bone circumferences used for body mass calculations were obtained by wrapping a thin strip of paper wrapped around the shaft, marking with a pen where the ends overlapped, and then straightening out the paper and measuring the distance between the marks with digital callipers. Measurements were made only on skeletally mature bones, identified by their smooth, non-porous surface and well-defined epiphyses.

3.3.5 Nomenclature

We follow the osteological terminology of Baumel *et al.* (1993) unless otherwise specified, and the taxonomic nomenclature of Dickinson and Remsen (2013) for extant taxa. Nomenclature of extinct taxa is addressed in the Systematic Palaeontology section.

3.3.6 Body-mass estimates

Where possible, body mass of extinct megapodes was estimated using regression equations based on minimum shaft circumferences of the femur and tibiotarsus (Campbell and Marcus 1992). We selected equations from the functional category of 'heavy-bodied birds', based on measurements of birds from 11 families, including some galliforms (Campbell and Marcus 1992). Where fossil femora or tibiotarsi were missing or too damaged to measure, we substituted an equation using the minimum width of the tarsometatarsus (Field et al. 2013). We elected not to use the preferred equation of Field *et al.* (2013), based on the maximum length of the humeral facet on the coracoid, because this facet has indistinct boundaries in megapodes, which would introduce measurement error.

3.3.7 Simpson log-ratio diagrams

We compared the body proportions of megapode species using the log-ratio method first described by Simpson (1941), and now used widely. In this study, we used the domestic chicken *Gallus gallus* as the arbitrary comparator. Relative size of different species is shown by their height on the y-axis.

3.3.8 Phylogenetic analysis

To test the validity of the extinct genera and species we identified via our morphological examinations, and to examine their relationships to extant megapode taxa, we scored them into a 285-character matrix for galloanseres, updated from Worthy *et al.* (2016). This matrix has 283 osteological characters, one behavioural character, and one non-osteological character of the foot, with palaeognaths and three species of Neoaves used as the outgroup. We undertook parsimony analyses in PAUP* 4.0b10 using standard settings (Swofford 2001), heuristic searches, tree bisection-reconnection branch swapping, and 1000 random addition replicates per search. Following Worthy *et al.* (2016), relationships between extant taxa were constrained using a backbone based on recent molecular data, but those of megapodes were altered to reflect the most recent phylogeny of the Megapodiidae (Harris, Birks, and Leaché 2014) (see Fig. 1). Support for the consensus tree was assessed in PAUP* via bootstrapping, using heuristic searches and the same options, and 1000 replications. Several non-Australian fossil taxa that were included in the consensus tree were excluded from the final bootstrap analysis because they were scored from incomplete fossil remains, and the resulting uncertainty led to reduced tree resolution and support. Trees were manipulated in FigTree 1.4.2 and labelled in Adobe Illustrator.

3.4 Results

3.4.1 Systematic Palaeontology

Galliformes Temminck, 1820

Megapodiidae Lesson, 1831

The fossil specimens described below are referred to Galliformes and therein to Megapodiidae based mainly on features noted by Mourer-Chauviré (1992), Worthy *et al*. (2015), Worthy *et al*. (2016), Mayr and Weidig (2004).

Humerus: the crista bicipitalis is more elongate and projects less ventrally than in Phasianidae; there dorsal fossa pneumotricipitalis is shallow, unlike in the stem-galliform *Gallinuloides* (Mayr and Weidig 2004); the impression for the insertion of m. coracobrachialis caudalis is dorsad of the incisura capitis, indents the crista incisura capitis distalis and abuts the midpoint of the caput humeri; the impression for the insertion of m. coracobrachialis caudalis is bound dorsally by a small tuberculum intermedium, rather than by a strongly-marked tuberculum; the caudal surface of the shaft is compressed into a distinct ridge (capital shaft ridge) level with the distal side of the crista bicipitalis; and the attachment of the m. latissimus dorsi is located dorsad of the margo caudalis (ventrally in all other galliforms except for the Sylviornithidae (Worthy et al. 2016).

Carpometacarpus: the facies articularis scapularis is flat to slightly convex, lacking the cup-like, concave facet seen in some stem-galliforms from the Northern Hemisphere (Mayr and Weidig 2004).

Tarsometatarsus: the eminentia intercotylaris is low and rounded, and barely projects further proximally than the area intercotylaris; the medial margin adjacent to the sulcus extensorius forms a sharp crest; the distal half of the facies dorsalis is convex, rather than flat or concave; the fossa metatarsi I is large and deep, with the rim of its articular facet projecting medially of the shaft margin. The hypotarsus has a single enclosed canal for m. flexor digitorum longus (Mayr 2016).

Progura De Vis, 1888

Progura De Vis, 1888 – type species *Progura gallinacea* De Vis, 1888 by monotypy.

> **Chosornis** De Vis, 1889: Proceedings of the Royal Society of Queensland 6: 55, Pl. IV – type Chosornis praeteritus De Vis, 1889 by monotypy, see van Tets (1974), Transactions of the Royal Society of South Australia, 98(4), p.214.
>
> **Palaeopelargus** De Vis, 1892: Proceedings of the Linnean Society of New South Wales (Ser. 2) 6: 441, Pl. XXIV – type Palaeopelargus nobilis De Vis, 1892 by monotypy, see van Tets (1974), Transactions of the Royal Society of South Australia, 98(4), p.214.

Included taxa: *Progura gallinacea* de Vis, 1888; *Progura campestris* sp. nov. (see below)

Revised diagnosis: *Progura* is distinguished from all other megapode genera by the following unique combination of features of the tarsometatarsus.

1) The shaft is elongate, the proximal and distal ends are proportionally narrow relative to length (PW = c. 19–22.8% length; DW = c. 20–22.6% length). 2) The shaft does not flare proximomedially into a convex profile in dorsal view as it widens to meet the cotyla medialis. 3) Dorsally, the lateral and medial foramina vascularia proximalia are of similar size and are about equidistant from the proximal end of the bone. 4) The sulcus infracotylaris dorsalis is a shallow depression bound by slightly raised areas of bone laterally and medially but not proximally. 5) The tuberositas m. tibialis cranialis comprises two short, broad tuberosities of about equal size, which are positioned symmetrically with respect to the midline of the shaft, are equidistant from the proximal end of the bone, diverge proximally, are separated from the foramina vascularia proximalia by a distinct gap, and are recessed in the sulcus extensorius thus do not protrude above the dorsal facies in lateral or medial aspect. 6) The impressiones retinaculi extensorii are low crests, unlike all other megapode genera, and both retinaculi, but especially the medial one, are located proximal of the level of the foramina vascularia proximalia. 7) The hypotarsus is dorsoplantarly shallow (proximal part of the medial hypotarsal ridge is approx. 40% of the depth of the medial cotyla). 8) The hypotarsus is slightly recurved distally into a hook in lateral/medial

aspects, and the junction between the distal part of the medial hypotarsal crest and the plantar facies is gradual. 9) Trochleae metatarsi II and IV are weakly grooved dorsally.

Differential diagnosis: The tarsometatarsi of extant genera of megapode differ from *Progura* as follows. 1) In *Leipoa* the shaft is proportionally shorter and stouter, the distal end is proportionally wider (*Leipoa* DW = 23–24% length. 2) In *Leipoa* and *Megapodius* the proximal end flares strongly medially from the shaft as it widens to meet the cotyla medialis, thus housing a larger fossa parahypotarsalis medialis, whereas the proximal end is more symmetrical, and the fossa smaller, in *Progura*. 3) In *Leipoa*, *Alectura*, *Megapodius* and *Eulipoa*, the foramen vascularis proximalis medialis is larger and placed a little more distally than its lateral counterpart (relative size and position of the foramina could not be accurately determined in *Aepypodius* due to immaturity of the available specimen; character state is variable in *Talegalla*). 4) In *Leipoa*, *Alectura* and especially so in *Megapodius*, the sulcus infracotylaris is deeper, and is bounded by raised areas of bone laterally, medially, and proximally (could not be accurately determined in *Aepypodius*; variable among species of *Talegalla*). 5) *Leipoa* is differentiated by having a single fused tuberositas m. tibialis cranialis rather than the tuberositas having two distinct parts. In *Talegalla* this character is variable among species. All other genera have an elongate tuberosity visibly divided into two parallel ridges (could not be determined in *Aepypodius*), and further differ from *Progura* by their placement and relative size: in *Megapodius*, *Eulipoa* and *Alectura*, the medial part of the tuberosity is broader and more elevated from the shaft than the lateral part; in *T. jobiensis* the tuberosities are particularly elongate and are laterally offset from the midline of the bone shaft. In *Megapodius*, *Eulipoa* and *Leipoa* the tuberositas is dorsally prominent and is visibly elevated above the shaft surface in lateral and/or medial aspect (character is variable among species of *Talegalla*). 6) In all compared genera, the impressiones retinaculi extensori are more prominent than in *Progura*, and are especially prominent in *Macrocephalon*. The placement of the retinaculi differs from *Progura* in other genera as follows: in *Megapodius* the proximo-distal placement of both retinaculi is roughly level with the foramen vascularis proximalis lateralis, with the lateral retinaculum abutting the sulcus infracotylaris; in *Alectura* both retinaculi are about level with one another and are placed slightly proximal of the level of the foramina; in *Leipoa* the medial retinaculum is placed further proximally than the lateral, with the lateral retinaculum placed immediately proximomedial to the foramen proximalis medialis, abutting the sulcus infracotylaris dorsalis; proximodistal placement of the retinaculi is variable in *Talegalla*, these being roughly level with the foramina in *T. fuscirostris* and proximal of the level of the foramina in *T. jobiensis.* 7) The hypotarsus is proportionally deeper dorsoventrally (approx. 50% of the depth of the cotyla medialis) in *Leipoa* and *Megapodius.* 8) In *Megapodius* and *Eulipoa*, the hypotarsus is strongly recurved distally, and has a deeply hooked appearance in lateral/medial aspect. The hypotarsus in *Talegalla* and *Alectura* is also hooked, although less strongly so. In *Megapodius* and

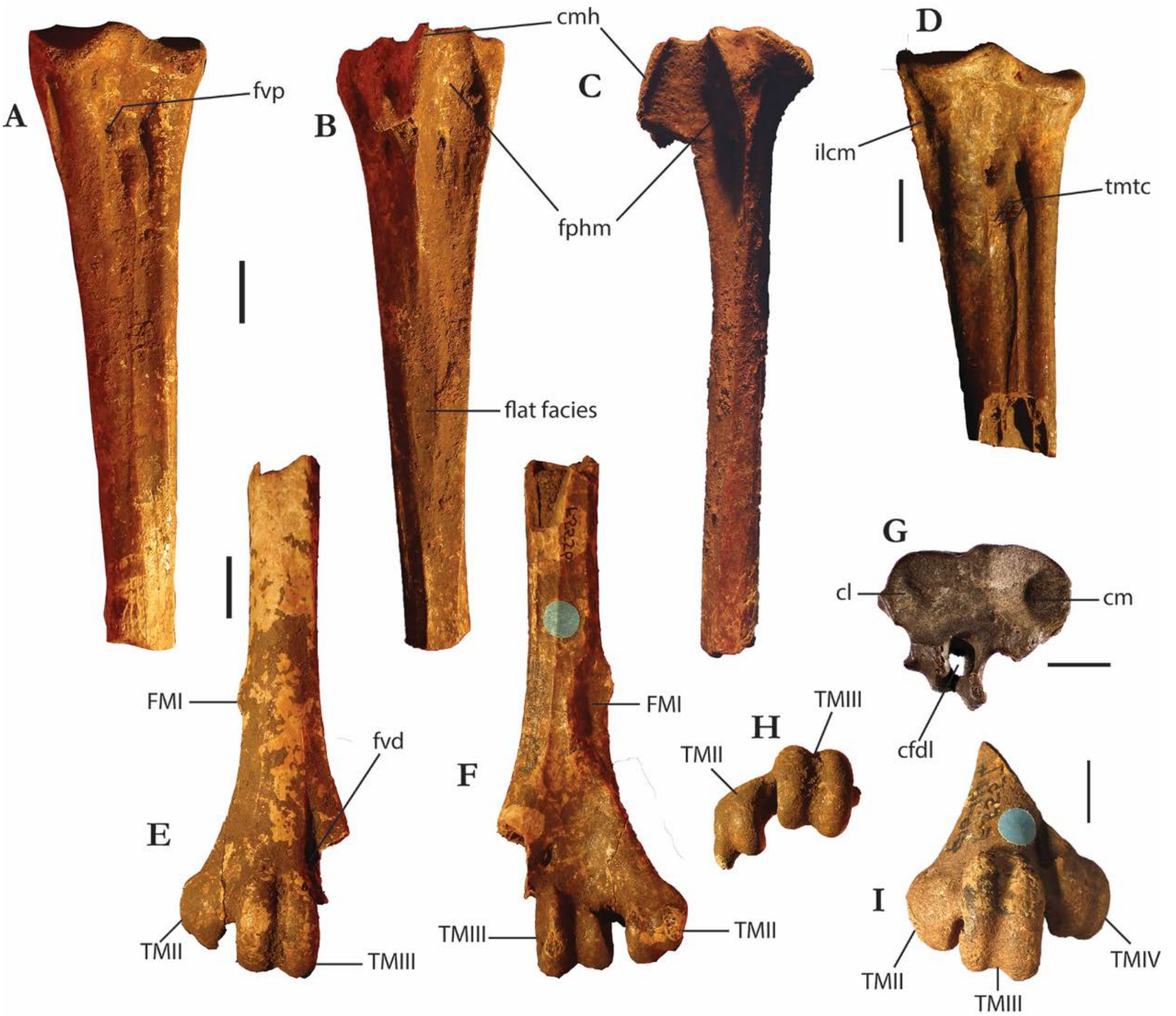


Figure 3.3: Tarsometatarsi of *P. gallinacea* De Vis, 1888. Lectotype (QM F1143, left) in dorsal (a), plantar (b) and medial (c) aspects; paralectotype (QM F1134, left) in dorsal (d) and proximal (g) aspects; paralectotype (QM F5556, right, images reversed) in dorsal (*e*), plantar (*f*) and distal (*h*) aspects; paralectotype (QM F5557, right, image reversed) in dorsal aspect (*i*). Scale bars, 10 mm. Abbreviations: cfdl, canal for m. flexor digitorum longus; cl, cotyla lateralis; cm, cotyla medialis; cmh, crista medialis hypotarsi; FMI, fossa metatarsi I; fphm, fossa parahypotarsalis medialis; fvd, foramen vasculare distale; fvp, foramina vascularia proximalia; ilcm, impressio lig. collateralis medialis; TMII, trochlea metatarsi II; TMIII, trochlea metatarsi III; TMIV, trochlea metatarsi IV; tmtc, tuberositas m. tibialis cranialis.

Aepypodius, the junction between the distal end of the medial hypotarsal crest and the plantar facies is abrupt rather than smoothly curved, meeting at approximately 90° in medial aspect. 9) Trochlea metatarsi II lacks a median groove distodorsally in *Leipoa*, *Macrocephalon*, *Megapodius*, *Eulipoa*, *Aepypodius*, *Alectura* and *Talegalla*. Trochlea IV is strongly grooved distodorsally in *Leipoa*, *Macrocephalon*, *Megapodius*, *Alectura*, and weakly so in *Aepypodius* and *Talegalla*.

Remarks: Our morphological observations indicate substantial differences between *Progura* and *Leipoa*. As per our generic diagnosis, compared with *Leipoa*, *Progura* has: a more elongate tarsometatarsus, lacking a marked medial flaring of the shaft proximally; similar-sized vascularia proximalia; a relatively shallow sulcus infracotylaris dorsalis; the tuberositas m. tibialis is paired and unfused rather than comprising a single fused tuberosity; weakly-marked and more proximally located impressiones retinaculi extensorii; less plantar extension of the hypotarsus; a trochlea metatarsi II that lacks a median groove; and a trochlea metatarsi IV that is more weakly grooved. Therefore, we reject the statement that "[o]ther than size, no differences could be found between these two genera that could not be attributed to individual variation within and among the samples" (Boles, 2008). These, and multiple other differences in other parts of the skeleton (see below), lead to our rejection of the synonymy of *Progura* with *Leipoa* (cf. Boles, 2008). This conclusion receives further support in our phylogenetic analysis (see below).

Geological range: late Pliocene (Louys & Price, 2015); Pleistocene (Prideaux, 2007; data herein).

Geographical range: The known geographical range of *Progura* includes south-eastern Queensland, north-eastern South Australia, and the Nullarbor Plain, Western Australia (see species accounts below).

Progura gallinacea **De Vis, 1888**

(Figures 3.3, 3.4 and 3.5 A, F, K, P, U)

Progura gallinacea **De Vis, 1888**: *Proceedings of the Royal Society of Queensland* 5: 131, Pl. VI – Ravensthorpe, near Pilton, Clifton region east of King's Creek, Eastern Darling Downs, south-eastern Queensland, Australia (see Molnar and Kurtz 1997); **Lectotype:** QM F1143, a pL tarsometatarsus (see Boles, 2008); **Paralectotypes:** QM F1134, a pL tarsometatarsus; QM F5556, a dR tarsometatarsus; QM F5557, a dR tarsometatarsus (see Boles, 2008).

Chosornis praeteritus De Vis, 1889: *Proceedings of the Royal Society of Queensland*, 6: 55, Pl. IV – Chinchilla, Darling Downs, Queensland, Australia; late Pliocene or Pleistocene; see van Tets (1974), p.214.

Palaeopelargus nobilis De Vis, 1892: *Proceedings of the Linnean Society of New South Wales* (Ser. 2) 6: 441, Pl. XXIV – Chinchilla, Darling Downs, Queensland, Australia; late Pliocene or Pleistocene; see van Tets (1974), pp. 214, 224.

L.[eipoa] (Progura) gallinacea (De Vis, 1888): Boles (2008), *Oryctos* 7: 204, in part.

Leipoa gallinacea (de Vis, 1888): Louys & Price (2015), *Acta Palaeontologica Polonica* 60[3]: 557.

Leipoa gallinacean (de Vis, 1888): Louys & Price (2015), *Acta Palaeontologica Polonica* 60[3]: 559, Fig. 5; unjustified emendation.

Referred material: QM F1132, pR carpometacarpus, Holotype *Chosornis praeteritus* De Vis, 1889, joins to QM F1139 (Chinchilla, Darling Downs, Queensland); **QM F1139**, dR carpometacarpus, Holotype

Palaeopelargus nobilis De Vis, 1892: joins to QM F1132, (Chinchilla, Darling Downs, Queensland); **QM F5553**, dR ulna (unknown locality, Darling Downs, Queensland); **QM F5558**, pR scapula (Chinchilla, Darling Downs, Queensland); **QM F7005**, pR carpometacarpus (unknown locality, Darling Downs, Queensland); **SAM P50028**, L coracoid, omal fragment (Warburton River, north-eastern South Australia).

Type locality: The lectotype and paralectotypes are from Ravensthorpe, Eastern Darling Downs, Queensland (see Key Locations) (Figure 3.2).

Stratigraphy, age and fauna: Stratigraphic information for the lectotype and paralectotypes was not recorded when the material was collected from Ravensthorpe in the late 19th Century, but the specimens share similar preservation, having been stained a uniform dark brown consistent with their being from one location, and are considered Pleistocene in age (see Key Locations). Referred specimens from Chinchilla, Darling Downs are of late Pliocene age if they arise from the Chinchilla Sand (see Key Locations). The partial coracoid was collected from CAM 4 Quarry, Camel Swamp Yard, Warburton River, South Australia, and is of late Pliocene age (Trevor H. Worthy 2008).

Revised diagnosis: A species of *Progura* with diagnostic features of the tarsometatarsus as for the genus, and distinguished from all other species of megapode, including the extinct '*Progura*' *naracoortensis,* which is transferred to a new genus below, by its very large size and the following unique combination of morphological features.

1) The shaft tapers evenly down its entire length, and is narrowest immediately proximal to fossa metatarsi I. 2) The medial edge of the shaft is dorso-plantarly compressed into a thin crest that is offset plantarly from the dorsal facies, and separated from the sulcus extensorius and foramina vascularia by a shallow sulcus on the dorsal facies, thus giving the shaft a somewhat twisted appearance in dorsal aspect. 3) The fossa parahypotarsalis medialis extends to about half the shaft length. 4) The impressio lig. collateralis medialis forms a very deep depression on the proximo-medial surface just distal of the medial cotyla. 5) The plantar surface of the midshaft is flattened. 6) The facet for metatarsal I is proportionally wide, extending to the midline of the shaft. 7) And in dorsal aspect, the rims of trochlea metatarsi III are parallel.

Description and comparisons: Only a few elements of this species are known (see Figures 3.3 and 3.4), and their morphology has not previously been described in detail. All are larger than in any other megapodid species. Some specimens previously referred to *P. gallinacea* (van Tets, 1974; Boles, 2008) are either not megapodes, or are megapodes that do not belong to this taxon. These are noted below following the descriptions.

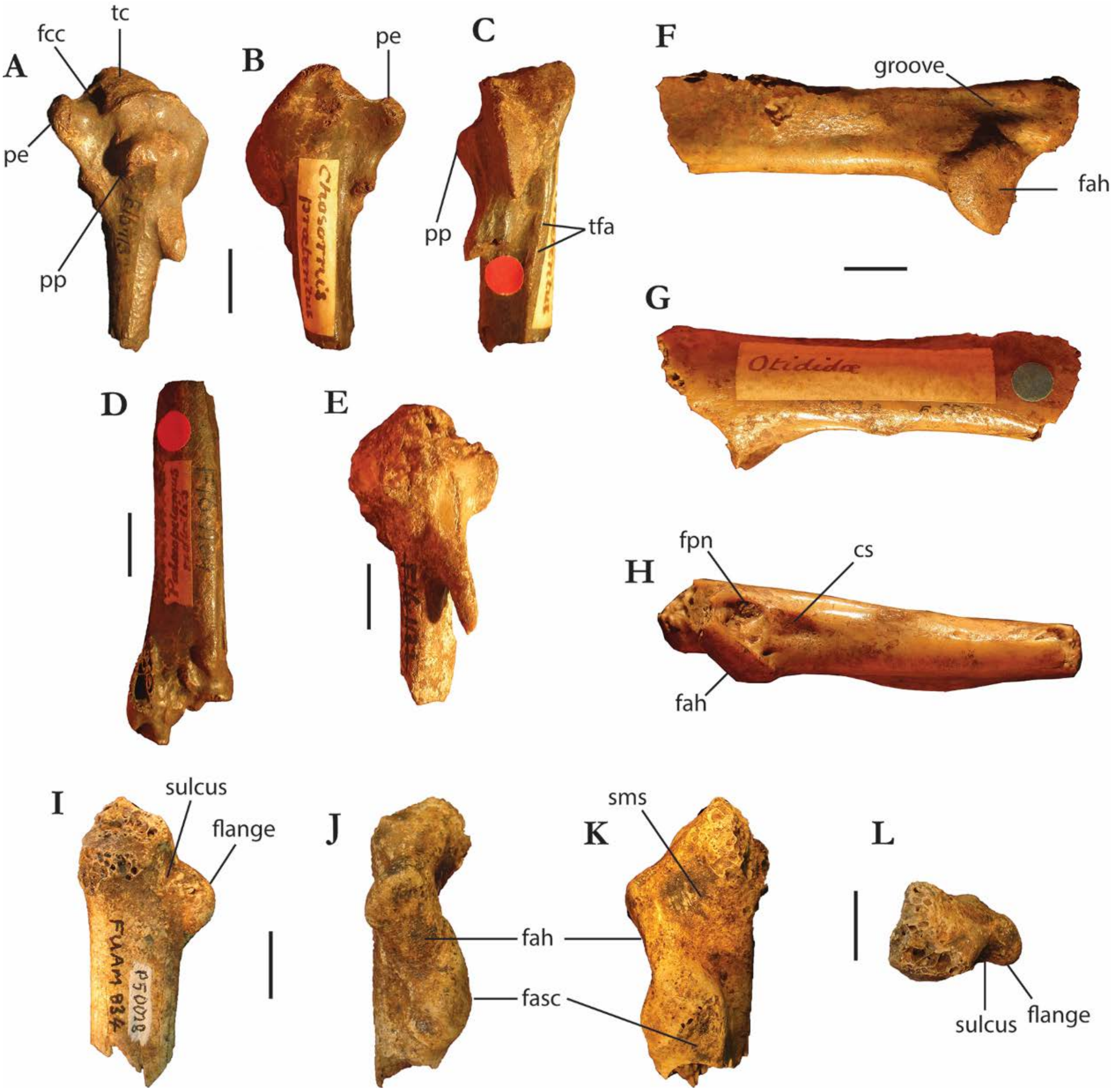


Figure 3.4: Pectoral elements of *P. gallinacea* De Vis, 1888. Carpometacarpus, QM F1132, holotype of *C. praeteritus* De Vis, 1889 (joins to QM F1139) in ventral (*a*), dorsal (*b*) andcaudal (*c*) aspects; carpometacarpus, QMF1139, holotype of *Pa. nobilis* De Vis, 1891 (joins to QMF1132) in caudal (*d*) aspect; carpometacarpus, QM F7005, in ventral (*e*) aspect; scapula, QM F5558, in lateral (*f*), medial (*g*) and ventral (*h*) aspects; coracoid, SAM P50028, in ventral (*i*), lateral (*j*), dorsal (*k*) and omal (*l*) aspects. Abbreviations: cs, collum scapulae; fah, facies articularis humeralis; fasc, facies articularis scapularis; fcc, fovea carpalis cranialis; fpn, foramen pneumaticum; pe, processus extensorius; pp, processus pisiformis; sms, sulcus m. supracoracoidei; tc, trochlea carpalis; tfa, tuberosity for flexor attachment. Scale bars, 10 mm.

Ulna: A portion of distal ulna approximately 50 mm long (QM F5553) from an unknown locality on the Darling Downs, south-east Queensland, was originally referred to *Palaeopelargus nobilis* by De Vis, and was referred to *P. gallinacea* by van Tets (2008). It is significantly eroded and is not sufficiently well preserved to make a detailed morphological description. We concur that it belongs to a very large megapode, but refer this bone to *P. gallinacea* only tentatively, based on its very large size and the fact that it was collected by De Vis from the Darling Downs in the 1880s or 1890s, as with other material of this species.

Carpometacarpus: Two carpometacarpi have previously been referred to *P. gallinacea*, under three catalogue numbers (see Referred material). A proximal specimen (QM F7005) is badly degraded (see Figure 3.4, E) and we refer this only tentatively. The other two bone fragments, QM F1132, a proximal right carpometacarpus (Figure 3.4, A–C), which is the holotype for *Chosornis praeteritus* De Vis, 1889, and QM F1139, a distal right carpometacarpus (Figure 3.4, D), which is the holotype of *Palaeopelargus nobilis* De Vis, 1892, join as a single bone, and so both nomina are synonyms of *P. gallinacea* (van Tets, 1974). The os metacarpale minus of this specimen is not preserved, but the two halves are in otherwise good condition and show that the carpometacarpus of this species is differentiated from those of all extant megapodes by its very much larger size. Total combined length of QM F1132 and QM F1139 is approximately 103 mm, longer than the carpometacarpi of all other extinct species of megapode (see species accounts below). Proximal and distal widths (Table 3.1) also exceed the size range of the other extinct species. The carpometacarpus has features as follows. The fovea carpalis cranialis is deep, as in *Alectura lathami* and *Leipoa ocellata*. The processus extensorius is cranially orientated. The ventral rim of the trochlea carpalis does not project much proximally past the tip of the processus extensorius, and is smoothly curved caudally. In dorsal aspect, the dorsal rim of the trochlea projects strongly proximally, and its caudal and cranial margins meet proximally at an approx. 90° angle. In caudal aspect, the ventral rim of the trochlea carpalis is orientated obliquely relative to the long axis of the bone, and thus converges distally with the dorsal rim of the trochlea at a point dorsal to the os metacarpale minus, as in *A. lathami* and *L. ocellata*. In proximal aspect, the processus extensorius is dorsoventrally thick (more than half the thickness of the adjacent carpal trochlea, whereas in *A. lathami* and *L. ocellata* the processus is less than half the width of the trochlea). The tuberosity for the flexor attachment forms two distinct scars on the proximo-caudal surface, one lying proximal of the spatium intermetacarpale, and the more distal one slightly overlapping the proximal synostosis of the metacarpals (i.e. mostly within the spatium intermetacarpale), whereas in *A. lathami* and *L. ocellata* there is a single, long tuberosity with its distal end lying within the spatium intermetacarpale, and overlapping the synostosis proximally. At the distal end, there is a short but very deep sulcus tendineus running longitudinally on the caudal surface of the os metacarpale majus. The facies articularis digitalis minor projects much further distally than facies articularis digitalis major, as in *A. lathami*, and differing from *L. ocellata* and *Talegalla fuscirostris*, in which there is little distal projection of the facies articularis dig. minor.

Coracoid: The coracoid of this species has not previously been described. We refer a very large Pliocene specimen (SAM P50028; Figure 3.4, I–L) to this species, previously noted in the literature under specimen number FU2655 (Worthy, 2008). We refer SAM P50028 to *P. gallinacea* rather than to any other large extinct taxon because of its very large size and the following morphological similarities with the coracoid of the smaller species of *Progura* described below: the ventro-lateral margin of the facies articularis humeralis projects strongly laterally as a rounded flange in ventral aspect; there is a deep sulcus on the ventral surface, between the ventro-lateral margin of the facies articularis humeralis and the processus acrocoracoideus, thus the depth of the bone here between the ventral and dorsal surfaces is shallow in omal aspect; and the facies articularis humeralis is deeply concave. It also has the following features: the dorsal part of the facies articularis clavicularis projects strongly cranially as in *L. ocellata* (less projection in *A. lathami*); and the ventral part of the facies articularis clavicularis does not project strongly over the ventral facies of the shaft. The very large size of the coracoid, and its wide shaft and large surface area for articulation with the scapula and humerus, is consistent with *P. gallinacea*, the largest known megapode species, having had a strong pectoral girdle, with no signs of reduction that would indicate flightlessness.

Scapula: A very large and robust specimen (QM F5558; Figure 3.3, F–H) from the late Pliocene Chinchilla Sand deposit, missing the acromion and most of the corpus scapulae, was originally referred to the Otididae by de Vis, and subsequently to *P. gallinacea* by van Tets (1974). As in all megapodes (Worthy *et al.* 2016), there is a pneumatic fossa immediately latero-ventral of the facies articularis humeralis. There is a broad, longitudinal groove latero-dorsal to the facies articularis humeralis. Insofar as the bone can be measured, its dimensions are outside the size range of other large extinct megapodes described below. Measurements (mm): width of the facies articularis humeralis, 15.1; width of collum scapulae immediately distal of the facies articularis humeralis, 13.7; depth of collum scapulae immediately distal of facies articularis humeralis, 10.5.

Tarsometatarsus: In addition to the diagnostic features noted above, tarsometatarsi of this species (Figure 3.3, A–I) have the following characteristics. They are far larger than those of any known megapode species, with the estimated length of a complete bone being approximately 147.5 mm, based on the length of the proximal fragment that is the lectotype (QM F1143) and the distal fragment with the longest preserved shaft (QM F5556, paralectotype) laid side by side with the shafts appropriately overlapped. This is of comparable length to tarsometatarsi of the giant flightless stem galliform *Sylviornis neocaledoniae*, but proximal width (28.4–28.9 mm) is some 10 mm narrower than in *S. neocaledoniae*, and distal width (29.5 mm; QM F5557) is around 12 mm narrower (Worthy *et al.* 2016). This is consistent with *P. gallinacea* having been a much lighter bird than the 27–34 kg *Sylviornis* (Worthy *et al.* 2016) (see Body-mass estimates). The trochleae are wide and deep, and are presumed to have articulated with very large phalanges, although none have been recovered. Measurements (mm): for TL, PW, SW and DW see Table 3.1; depth troch. metatarsi II, 11.6 (QM F5557), 11.9 (QM F5556); depth troch. metatarsi II, 14.4 (QM F5557), 14.2 (QM F5556); depth troch. metatarsi IV, 11.2 (QM F 5557).

Remarks on specimens previously referred to Progura gallinacea

All specimens from caves in the Naracoorte region (south-eastern South Australia), and a proximal tarsometatarsus (QM F2769) from Gore Limestone Quarry (Darling Downs, south-east Queensland), that were originally referred to *Progura naracoortensis* by van Tets (1974), but were included within the synonymy of *P. gallinacea* by Boles (2008), are transferred herein to a new genus (see below). A further six bones from Wombeyan Caves, eastern New South Wales, which were also originally referred to *P. gallinacea* (van Tets, 1974), and retained in that species by Boles (2008) are also transferred to this new genus.

A distal right tarsometatarsus (QM F7033, Ravensthorpe, Darling Downs, Queensland) was previously referred to *P. gallinacea* (van Tets, 1974) (where it was incorrectly reported as AM F7033). It is eroded and incomplete, but sufficiently well preserved to show that the trochleae do not match the morphology of the type specimens of *Progura gallinacea*. Trochlea III is much more elongate than in Megapodiidae; the incisura between trochleae III and IV is much wider; and trochlea IV is narrower and dorsoventrally flatter but more laterally flared. It is provisionally identified as a phoenicopteriform.

A distal right ulna (AM F54723, Walli Caves, New South Wales) previously referred to *P. gallinacea* (van Tets, 1974) does not belong to a megapode. Provisional examination suggests that it may belong to an undescribed eagle larger than extant Wedge-tailed Eagle *Aquila audax*.

A partial left coracoid missing both ends (BMNH A3244, from an unknown cave (likely either Cathedral or Mitchell [=Breccia] Cave) in Wellington Valley, near Wellington, New South Wales, was originally referred by Lydekker (1891), as his catalogue number 43879, to a species of *Alectura* (as *Talegalla*) larger than extant *A. lathami*. The specimen was later referred to *P. gallinacea* because of its large size (van Tets, 1974), but there is no other evidence that *P. gallinacea* inhabited the Wellington region (see below). The fossil may belong to the same genus and species as other large megapode fossils from Wellington, but a referral cannot be made without examining the specimen.

Figure 3.5: Tarsometatarsi of extinct Australian megapodes compared with extant malleefowl *L. ocellata*. *Progura gallinacea* (*a*, *f*, *k*, *p*, *u*); *P. campestris* sp. nov. WAM 15.9.5, holotype (*b*, *g*, *l*, *q*, *v*); *La. naracoortensis* (*c*, *r*, *w* = SAM P41731; *h*, *m* = SAM P51233, left, image reversed); *La. olsoni* sp. nov. WAM 15.9.6, holotype (*d*, *i*, *n*, *s*, *x*); *L. ocellata* SAM B.11482 (*e*, *j*, *o*, *t*, *y*). Bones in dorsal (top row), proximal (second row), medial (third row), plantar (fourth row) and distal (bottom row) aspects. (*a*) and (*p*) are reconstructed from photographs of two incomplete bones (proximal end = QM F1143, left, image reversed; distal end = QM F5556). (*f*), (*k*) = QM F1134, left, image reversed. (*u*) = QM F5556, right. Abbreviations: cfdl, canal for m. flexor digitorum longus; cl, cotyla lateralis; cm, cotyla medialis; cmh, crista medialis hypotarsi; FMI, fossa metatarsi I; fphm, fossa parahypotarsalis medialis; fvd, foramen vasculare distale; fvp, foramina vascularia proximalia; ilcm, impressio lig. collateralis medialis; re, impressiones retinaculi extensorii; sid, sulcus infracotylaris dorsalis; tmtc, tuberositas m. tibialis cranialis; TMII, trochlea metatarsi II; TMIII, trochlea metatarsi III; TMIV, trochlea metatarsi IV. Scale bars, 10 mm.

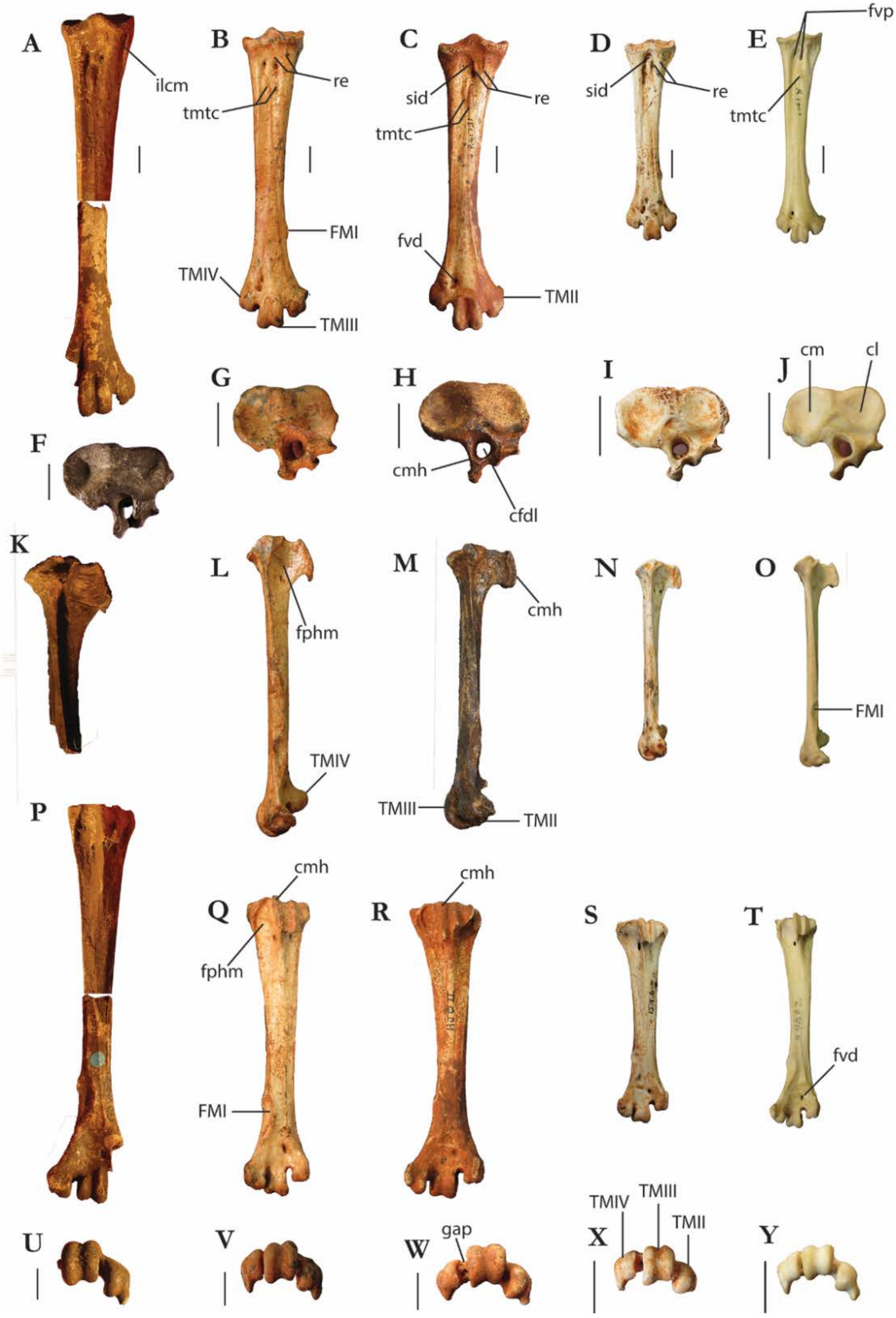

A
ilcm
B
re
tmtc
FMI
TMIV
TMIII
C
sid
re
tmtc
fvd
TMII
D
sid
re
E
fvp
tmtc
F
G
H
cmh
cfdl
I
J
cm
cl
K
L
fphm
TMIV
M
cmh
TMIII
TMII
N
O
FMI
P
Q
cmh
fphm
FMI
R
cmh
S
T
fvd
U
V
W
gap
X
TMIV
TMIII
TMII
Y

Table 3.1: Long bone measurements (mm) of *Progura gallinacea*; TL = total length; PW = proximal width; SW = midshaft width; DW = distal width; *estimated length of lectotype QM F1143 is based on measurement from proximal end to proximal edge of fossa metatarsi I (100 mm), added to distal length of slightly narrower syntype QM F5556 measured from proximal edge of fossa metatarsi I to distal end (47.5 mm) so TL of QM F1143 is estimated to be a minimum of 147.5 mm

Element/Side		Catalogue no.	TL	PW	SW	DW
Lectotype	Tarsometatarsus (pL)	QM F1143	est. 147.5*	28.4	12.7	-
Paralectotypes	Tarsometatarsus (pL)	QM F1134	-	28.9	-	-
	Tarsometatarsus (dR)	QM F5556	-	-	11.7	-
	Tarsometatarsus (dR)	QM F5557	-	-	-	29.5
Referred material	Carpometacarpus (pR)	QM F1132	-	26.9	-	-
	Carpometacarpus (dR)	QM F1139	-	-	-	19.0
	Ulna (dR)	QM F5553	-	-	-	20.0

Progura campestris Shute Prideaux & Worthy, sp. nov.

(Figure 3.5 B, G, L, Q, V, Figure 3.6, Figure 3.7 D–F, Figures 3.8–3.11)

Zoobank ID: urn:lsid:zoobank.org:act:02B438F7-C0F6-4B60-BA8D-C0F491D2CEB0

> ***Leipoa gallinacea*** (De Vis, 1888): Prideaux *et al.* (2007), *Nature*, 445: 423, Table 3.1. Not *Progura gallinacea* De Vis, 1888.
>
> ***Leipoa gallinaceae*** (De Vis, 1888): Wroe *et al.* (2013), *Proceedings of the National Academy of Sciences*, 110(22): 8779, Fig.3; Supp. Info. Table S1. Not *Progura gallinacea* De Vis, 1888.

Holotype (Figure 3.5 B, G, L, Q, V; Figure 3.6 E–H; Figure 3.7 D–F; Figure 3.8, Figure 3.9 D–O, Figure 3.10, Figure 3.11 A): WAM 15.9.5, associated remains of one adult individual, comprising the following elements: premaxilla, approx. 15 mm of the tip; right articular of mandible lacking tips of processus medialis and processus retroarticularis; vertebrae (cervicals 3 and 4, parts 5 others, 3 vertebral fragments, anterior fragment of synsacrum, pygostyle); sternum, preserving most of its length, the full depth of the keel and most of the rostrum sterni; two fragments of clavicula; R coracoid, sternal and omal fragments; R scapula, complete apart from missing distal tip; L humerus, missing caput humeri; dR ulna, approx. 3 cm fragment; L radius; L, R carpometacarpus; R os carpi ulnare; R phalanx I digiti majoris; R phalanx II digiti majoris; R femur; L, R tibiotarsus, L missing the crista cnemialis cranialis, R missing its proximal half; L, R tarsometatarsus, the L missing the hypotarsus and half of cotyla lateralis; 14 pedal phalanges (L: I.1, I.2, I ungual, II.1, II.2, III.1, IV.1, IV.2, IV.3, IV.4; R: III1, III.2, III.3, III ungual). Number of individual bones = 51.

Type locality: Leaena's Breath Cave, Thylacoleo Caves, Nullarbor Plain, Western Australia (Figure 3.2; see Key Locations).

Paratypes: ***Leaena's Breath Cave, Nullarbor Plain, Western Australia*** – WAM 15.9.16, 15.9.17, 15.9.18, 15.9.27, 15.9.28, 15.9.29, 15.9.30, 7 cervical vertebrae; WAM 15.9.13, dL humerus; WAM 15.9.14, pL humerus; WAM 15.9.15, pR humerus; WAM 15.9.32, L os carpi ulnare; WAM 15.9.9, R carpometacarpus; WAM 15.9.8, R coracoid; WAM 15.9.11, L tarsometatarsus; WAM 15.9.12, pR tarsometatarsus; WAM 15.9.1, dL tarsometatarsus; WAM 15.9.7, pL tarsometatarsus; WAM 15.9.31, phalanx I.1, L and R.

Referred material: *Last Tree Cave, Nullarbor Plain, Western Australia* – WAM 05.4.21, cranial vault (Figure 3.6 A–D); WAM 05.4.17, L ulna (Figure 3.8 C, D); WAM 04.6.1, dR tarsometatarsus.

Stratigraphy, age and fauna: The disarticulated but associated holotype material was excavated by G.J. Prideaux on 10–11 August 2011, from a depth of 110–115 cm below the current sediment floor, in stratigraphic Unit 3, Quadrat 3, Pit B, Leaena's Breath Cave. Reversed magnetic polarity and the composition of the vertebrate assemblage indicates that the Unit 3 sediments were deposited during the Matuyama Chron (2.58–0.78 Ma) (Early Pleistocene) (Prideaux *et al.* 2007). The paratypes were collected from the sediment floor of Leaena's Breath Cave by J.A. Long in July 2002, and are of unknown Pleistocene age. The referred specimens, including the referred cranium (WAM 05.4.21), were collected from the surface of The Ossuary deposit in Last Tree Cave by J.A. Long in July 2002, and are undated but of probable Pleistocene age given their co-deposition with extinct species of marsupial that occur only in Pleistocene deposits elsewhere (e.g., *Procoptodon goliah*).

Diagnosis: A species of megapode larger than any extant member of the Megapodiidae, with a tarsometatarsus conforming with *Progura*, but approximately one third shorter than that of the type species, and characterised by the following features. 1) The fossa parahypotarsalis medialis is shallow and restricted to the first 25% of length. 2) The medial margin of the shaft is thick, and lacks a shallow sulcus between it and the foramina vascularia-sulcus extensorius, lending the dorsal facies of the shaft a flat appearance in medial aspect. 3) The midshaft region is plantarly convex. 4) The shaft is robust (minimum width 10.1% of total length). 5) It lacks a deep depression for the impressio lig. collateralis medialis. 6) The facet for metatarsal I measures around one third of the width of the shaft (half the shaft width in *P. gallinacea*). 7) In dorsal aspect, the rims of trochlea metatarsi III converge proximally.

Differential diagnosis: Apart from much larger size, the tarsometatarsus of the type species *P. gallinacea* differs by having: 1) A deeper fossa parahypotarsalis medials extending to half the shaft length. 2) A thinner medial margin, and a twisted dorsal facies. 3) A flat plantar midshaft. 4) A more gracile, distally tapered shaft (minimum width 8.6% of total length). 5) A deep depression for the impressio lig. collateralis medialis. 6) A wider facet for metatarsal I (half the shaft width). 7) Parallel rims of trochlea metatarsi III in dorsal aspect.

Etymology: *campestris* = "from the plain" (campos = "plain" or "field", Latin), referring to the habitat of this species on the flat limestone plateau of the Nullarbor Plain.

Description and comparisons: The holotype skeleton preserves most major elements in excellent condition, with the paratypes and referred material preserving additional elements and anatomical detail. Features of the skeleton are described below and are compared with extinct and extant taxa. Long bone measurements are given in Table 3.2, and measurements of phalanges in Table 3.3. Additional measurements are given in text where applicable. Photographs of the tarsometatarsus are shown in Figure 3.5 B, G, L, Q and V and Figure 3.11, and other skeletal material in Figures 3.6–3.10.

Cranial bones: The articular mandible fragment of the holotype (Figure 3.6E) is relatively small and indicates that the bill of this species was gracile rather than robust (width of ramus immediately anterior of the cotyla lateralis, 2.3 mm; cf. 1.7 mm in *Leipoa ocellata*). The holotype also preserves the anterior portion of the rostrum maxillare (premaxilla) (Figure 3.6F–H), with approximately 0.5-cm long portion of the processus frontalis and a similar length of the left processus maxillaris. The shape of the anterior edge of the left naris is preserved, showing a wide opening. In size and shape the premaxilla is almost identical to that of *Alectura lathami*, and is considerably larger than in *L. ocellata* or *Megapodius reinwardt*. The tip is relatively elongate. A reconstruction of the shape of the anterior rostrum is shown in Figure 3.7.

The referred cranium (WAM 05.4.21; Figure 3.6 A–D) is similar in length and depth to that of *A. lathami*, but is broader. In lateral aspect, the shape of the braincase is dorsoventrally flattened and elongate as in *A. lathami*, rather than having the shorter, domed profile of *L. ocellata* and species of *Megapodius*, or having the bulging casque of *Macrocephalon maleo*. Unlike in *L. ocellata*, *A. lathami*, *M. reinwardt* or *M. maleo*, the lacrimals flare widely laterally anterior to the orbits and are wholly fused to the nasals, and the margo supraorbitalis flares laterally in the posterior section of the orbits, indicating bony protection of the eyes (Figure 3.6A). The occipital region is morphologically quite similar to that of *A. lathami*, although the condylus occipitalis is larger, and the foramen magnum is deeper than wide (wider than deep in *A. lathami* and *L. ocellata*). The processus basipterygoidei are about the same size as in *Alectura* and are also elongate (short in *L. ocellata*) but are placed slightly more posteriorly than in *Alectura*. Preserved on the left side, the processus postorbitalis and the processus zygomaticus are narrowly separated, allowing only a tiny fossa muscularis temporalis, but whether or not they were fused distally, or how large the aponeurosis zygomatica was, cannot be determined as the tips of both are broken. As in other species of megapode, the septum interorbitale is perforated by a large foramen nervi optici. A marked sulcus nervi olfactorii traverses the dorsal side of the septum interorbitalis (Figure 3.6C), which exits the braincase from a very small foramen nervi olfactorii, unlike the large and obvious foramen seen in *L. ocellata*, *A. lathami*, *M. reinwardt* and *M. maleo*.

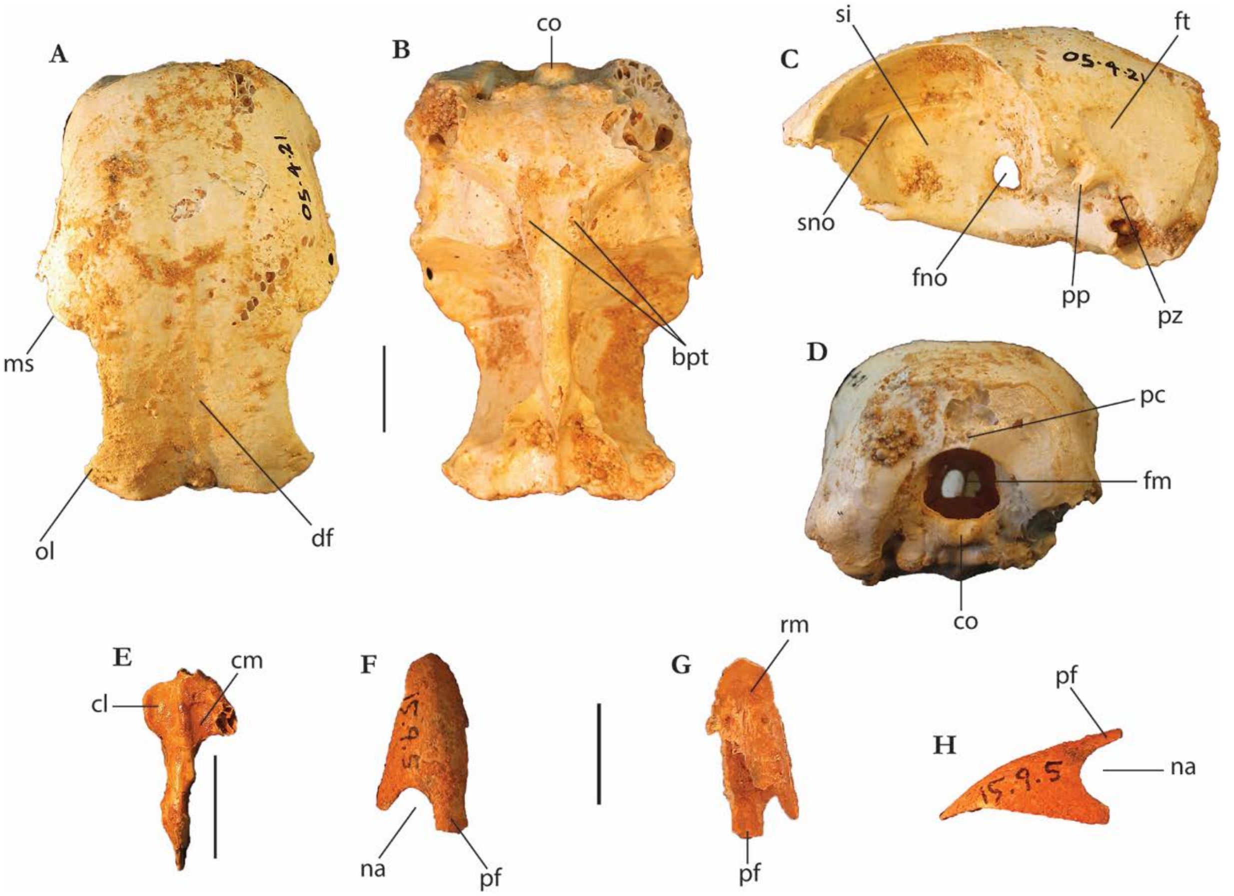


Figure 3.6: Cranial remains of P. campestris sp. nov. Cranium, WAM 05.4.21, in dorsal (a) ventral (b), lateral (c) and caudal (d) aspects; mandible,WAM15.9.5, holotype, right articular fragment, in dorsal aspect (e); premaxilla,WAM15.9.5, holotype, in dorsal (f), ventral (g) and lateral (h) aspects. Abbreviations: bpt, processus basipterygoidei; cl, condylus lateralis; cm, cotyla medialis; co, condylus occipitalis; df, depression frontalis; fm, foramen magnum; fno, foramen nervi optici; ft, fossa temporalis; ms, margo supraorbitalis; na, naris; ol, os lacrimale; pc, processus costalis; pf, processus frontalis; pp, processus postorbitalis; pz, processus zygomaticus; rm, rostrum maxillare; si, septum interorbitale; sno, sulcus nervi olfactorii. Scale bars, 10 mm.

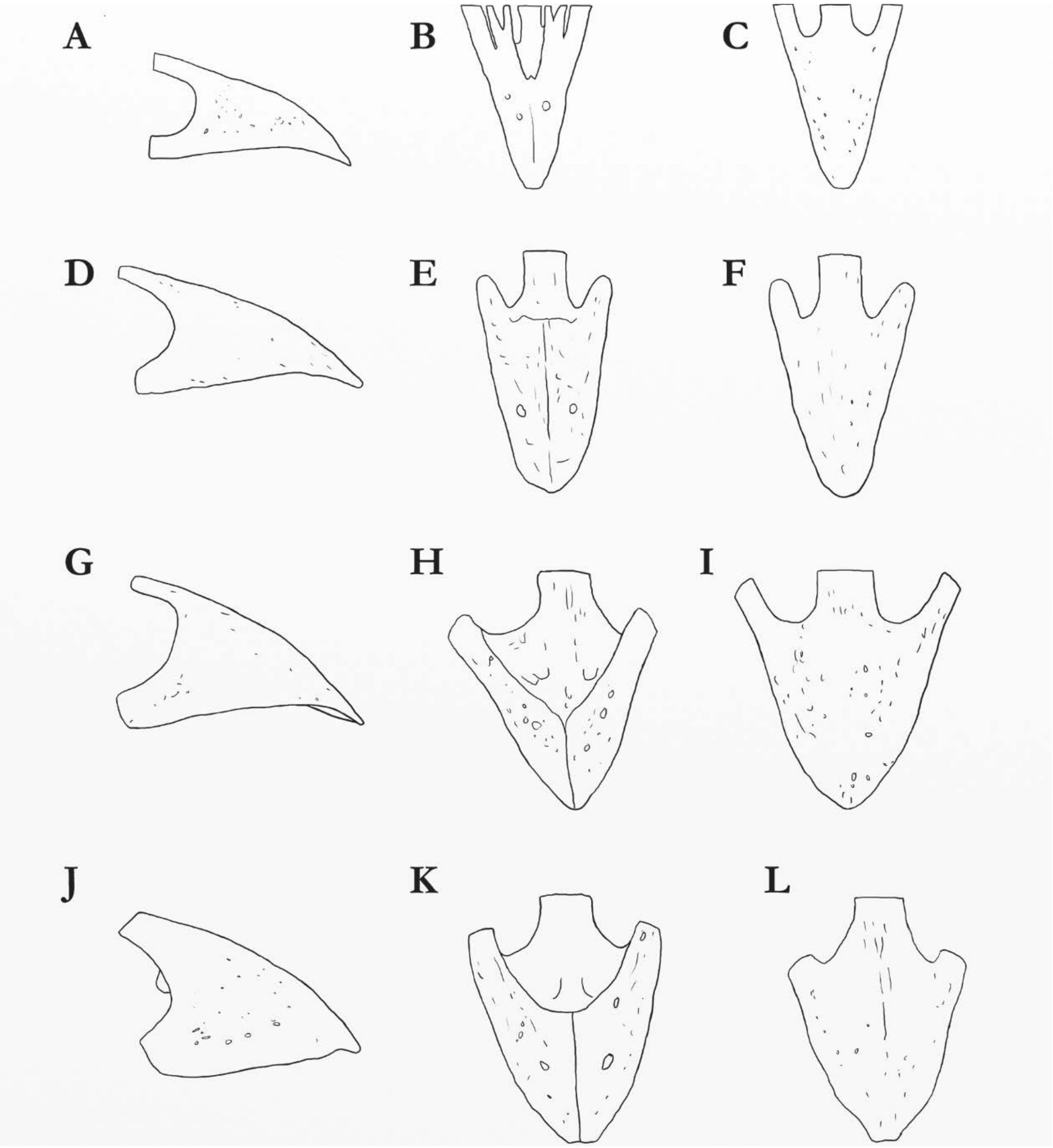


Figure 3.7: Shape comparison of megapode premaxillae: *L. ocellata* (*a–c*); *P. campestris* sp. nov. (*d–f*); *G. mcnamarai* sp. nov. (*g–i*); *La. naracoortensis* (*j–l*). (*a*, *d*, *g*, *j*) lateral view; (*b*, *e*, *h*, *k*) ventral view; (*c*, *f*, *i*, *l*) dorsal view. Outlines traced from photographs of specimens, with damaged portions mirrored from contralateral side where possible.

Measurements (mm): premaxilla, maximum depth measured at the level of the anterior edge of the naris, 7.2; preserved length of cranium, 47.6; maximum depth, 24.8; anterior width across fused lacrimals, 24.8; minimum interorbital width of osa frontales, 18.7; maximum diameter of the orbital fossa, 22.8; width of foramen magnum, 6.5; depth of foramen magnum, 6.9.

Vertebrae: The holotype and paratypic cervical vertebrae are morphologically similar to those of other megapodes. Cervical #4 is more elongate than in *L. ocellata* and anterior and caudal widths are the same

(*L. ocellata* is wider caudally). The pygostyle is about the same length as in *A. lathami*, but it is deeper and broader with more distinct, laterally projecting processus laterales anteriorly (smaller and more ventrally directed in *Alectura*; lacking entirely in *Leipoa*), and has a blunt rather than pointed caudal tip. The sides have large shallow sulci (absent entirely in *L. ocellata*). The distal end is directed dorsally at about 45° to the anterior section (Figure 3.9J), whereas in *A. lathami* the dorsal profile of the pygostyle is straight in lateral aspect, and in *L. ocellata* the pyogstyle is curved slightly downward. No thoracic vertebrae or notaria were recovered from the excavations.

Humerus: Most of the left humerus of the holotype is preserved but the proximal end, including the caput humeri, is missing (Figure 3.8 A, B). Two paratypic proximal fragments (WAM 15.9.14 and 15.9.15) preserve the caput, tuberculum ventrale and crista bicipitalis. Megapodes have relatively homogenous humeral morphology, and the humerus of *P. campestris* shares features typical of the Megapodiidae (see family diagnosis). It has distinguishing features as follows: the crista bicipitalis is relatively short proximodistally, as seen in WAM 15.9.14 and WAM 15.9.15; the tuberculum ventrale is not very prominent caudally and does not project further than the caudal facies of the caput humeri in proximal aspect; the shaft is relatively narrow in caudal aspect as it approaches the proximal end, but the margo caudalis is elevated as it approaches the proximal end because of a strong capital ridge, making the shaft proportionally thick here; the crista deltopectoralis has a thick base but forms a sharp crest in its distal section and the adjacent impression for m. pectoralis on the cranial surface is deeply concave; the distal end is relatively narrow; the condylus ventralis is prominent distally; and the tuberculum supracondylare ventrale is relatively small. Measurements: for PW, SW and DW see Table 3.2; if complete, total length of the holotype humerus would be approximately 144 mm.

Ulna: The holotype lacks a complete specimen, but the paratype ulna (WAM 05.4.17), is well preserved (Figure 3.8 C, D). The shaft is curved in dorsal aspect and is dorsoventrally compressed. The impression for the m. brachialis is deep, and the olecranon is orientated somewhat ventrally in cranial aspect. The condylus ventralis ulnaris does not protrude dorsally, as in most megapodes. Measurements: for TL, PW, SW and DW see Table 3.2.

Radius: The holotype preserves a complete L radius. Measurements (mm): for TL, PW, SW and DW see Table 3.2.

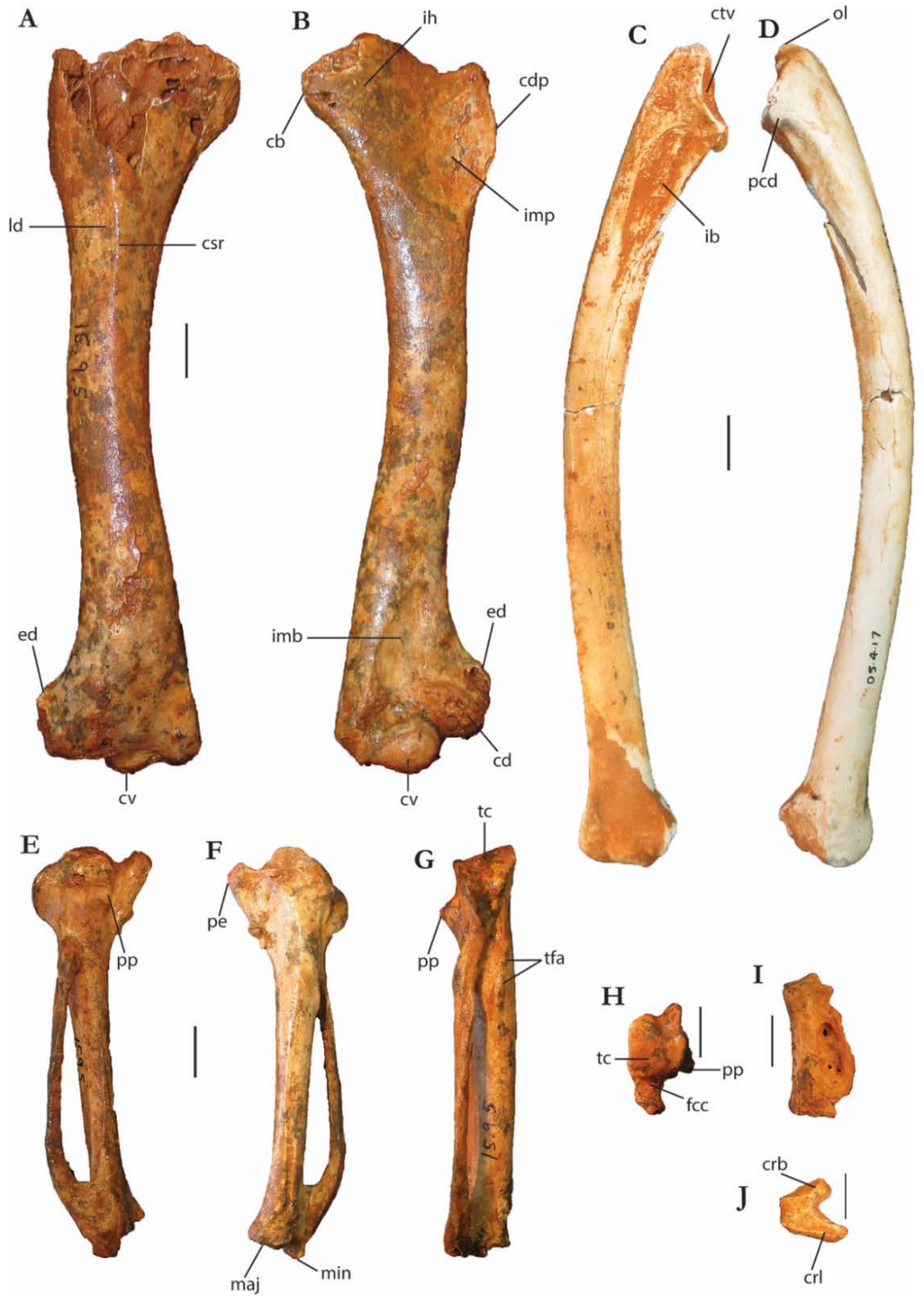


Figure 3.8: Wing elements of *P. campestris* sp. nov. Humerus, WAM 15.9.5 holotype, in caudal (a) and cranial (b) aspects; ulna, WAM 05.4.17, paratype, in ventral (c) and dorsal (d) aspects; carpometacarpus, WAM 15.9.5, holotype, left, in ventral (e) and dorsal (f) aspects, and WAM 15.9.5, holotype, right, in caudal (g) and proximal (h) aspects; phalanx dig. major, WAM 15.9.5, holotype (i); os carpi ulnare, WAM 15.9.5, holotype (j). Abbreviations: cb, crista bicipitalis; cd, condylus dorsalis; cdp, crista deltopectoralis; crb, crus breve of os carpi ulnare; crl, crus longum of os carpi ulnare; csr, capital shaft ridge; ctv, cotyla ventralis; cv, condylus ventralis; ed, epicondylus dorsalis; fcc, fovea carpalis cranialis; ib, impressio brachialis ulnaris; ih, intumescentia humeri; imb, impressiom. brachialis; imb, impressiomusculo brachialis; imp, impressio m. pectoralis; ld, attachment for m. latissimus dorsalis; maj, facies articularis digitalis major; min, facies articularis digitalis minor; ol, olecranon; pcd, processus cotylaris dorsalis; pe, processus extensorius; pp, processus pisiformis; tc, trochlea carpalis; tfa, tuberosity for flexor attachment. Scale bars, 10 mm.

Carpometacarpus: The carpometacarpi (Figure 3.8 E–H) are considerably smaller than those of *P. gallinacea* (approx. 25% shorter), but are morphologically quite similar, including having two distinct scars/tuberosities for the flexor attachment, the distal one being entirely within the spatium intermetacarpale, unlike the single tuberosity seen here in *Alectura lathami* and *Leipoa ocellata.* Carpometacarpi of *P. campestris* differ from *P. gallinacea* by having: a relatively longer, more proximally orientated processus extensorius that projects further proximally than the ventral rim of the trochlea carpalis (does not do so *P. gallinacea*); more caudal projection of the ventral rim of the trochlea carpalis; a more prominent processus pisiformis. In caudal aspect, the proximal end of the os metacarpale minus is directed ventrally, and the ventral rim of the trochlea carpalis cranialis diverges markedly from the long axis of the os metacarpus majus. The spatium intermetacarpale is relatively narrow. They differ from all species examined, including *P. gallinacea*, by having a shallow fovea carpalis cranialis. Measurements (mm): for TL, PW, DW, and maximum width (measured cranio-caudally at the widest arc of the os carpus minus), see Table 3.2.

Coracoid: The holotype includes omal and sternal coracoid fragments. Among the paratypes is a slightly more slender, coracoid (WAM 15.9.8), found in association with the holotype skeleton (Quadrat 3, Pit B, Unit 3, 110–115 cm, Leaena's Breath Cave) but belonging to another individual (Figure 3.9 A–C, F). It is complete apart from minor damage to the shaft and to the sternal end. Coracoids of this species are considerably smaller than that of *P. gallinacea*, and are small compared to other elements of the skeleton (see Simpson log-ratio diagram, Figure 3.22). They are further distinguished by the following features of the omal end (a sternal end is lacking for *P. gallinacea*): the dorsal part of the facies articularis clavicularis does not project as far cranially; and the ventral part of the facies articularis clavicularis projects more strongly above the ventral facies of the shaft. Other features of the coracoid of *P. campestris* include: a relatively slender shaft; a short processus acrocoracoideus (as in *Leipoa ocellata*, and differing from *Alectura*, in which it is elongate); a facies articularis clavicularis with little sternal projection (as in *L. ocellata*, differing from *A. lathami*, in which the facies projects); a ventromedial part of the facies articularis clavicularis that is prominent and overhangs the medial margin of the sulcus m. supracoracoidei; a dorsal portion of the facies articularis clavicularis that projects much further medially than the facies articularis scapularis in dorsal aspect; an angulus medialis that is smoothly contiguous with the medial shaft, rather than medially projecting; and a facies articularis sternalis with a relatively small surface area and a straight distal margin in dorsal aspect. Measurements (mm): for TL, SW, omal width and sternal width, see Table 3.2.

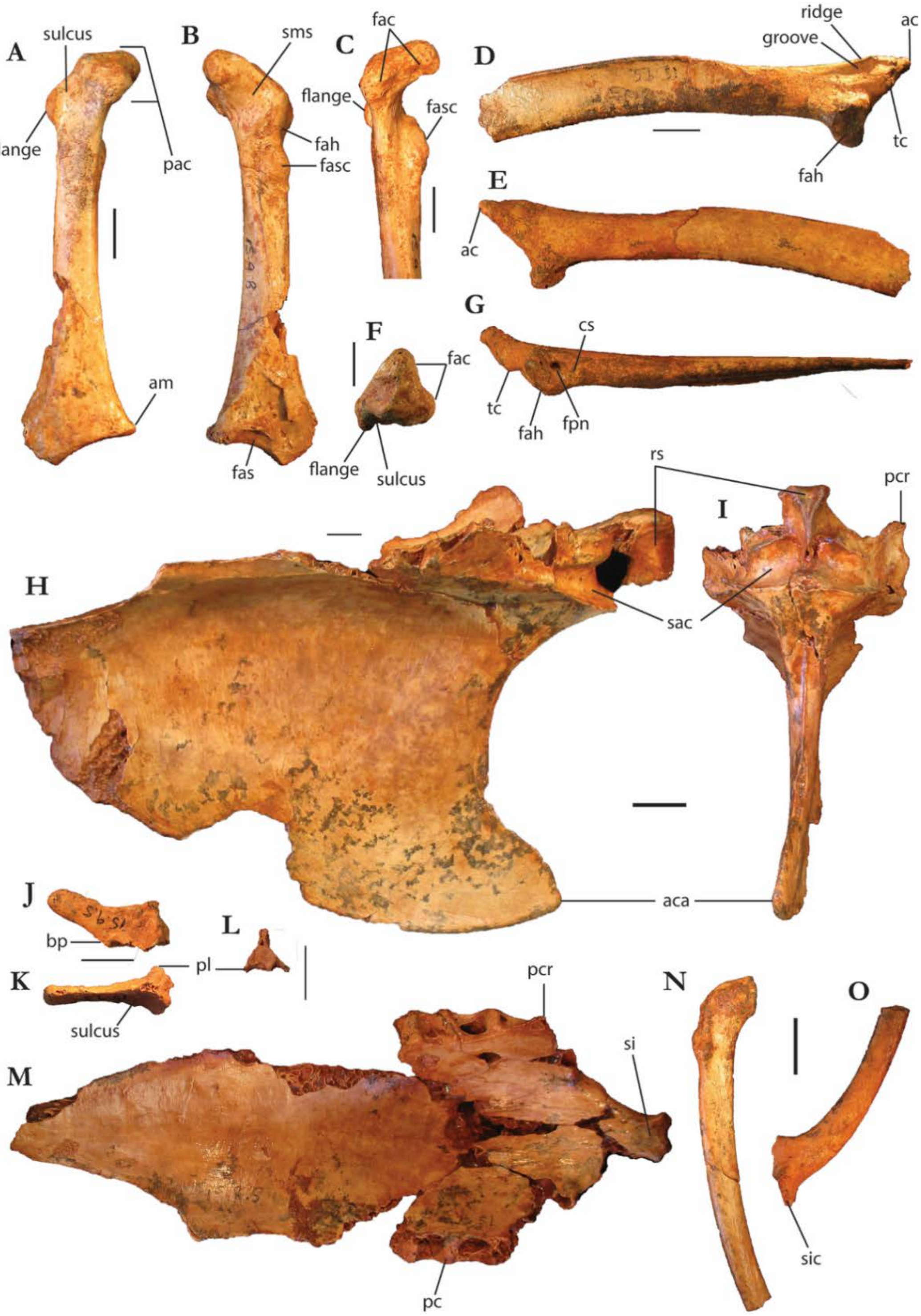


Figure 3.9: Pectoral and axial skeletal elements of P. campestris sp. nov. Coracoid, WAM 15.9.8, paratype, in ventral (a), dorsal (b), medial (c) and omal (f) aspects; scapula, 15.9.5, holotype, in lateral (d), medial (e) and ventral (g) aspects; sternum,WAM 15.9.5, holotype, in right lateral (h) cranial (i) and dorsal (m) aspects; pygostyle, 15.9.5, holotype, in lateral (j), dorsal (k) and cranial (l) aspects; clavicula, WAM 15.9.5, holotype, omal (n) and sternal (o) portions. Abbreviations: ac, acromion; aca, apex carinae; am, angulus medialis; bp, basis pygostyli; cs, collum scapulae; fac, facies articularis clavicularis; fah, facies articularis humeralis; fas, facies articularis sternalis; fasc, facies articularis scapularis; fpn, foramen pneumaticum; pac, processus acrocoracoideus; pc, processus costalis; pcr, processus craniolateralis; pl, processus lateralis; rs, rostrum sterni; sac, sulcus articularis coracoideus; si, spina interna; sic, synostosis interclavicularis; sms, sulcus m. supracoracoidei; tc, tuberculum coracoideum. Scale bars, 10 mm.

Scapula: The holotype skeleton preserves one nearly complete scapula, missing only the distal tip (Figure 3.9 D, E, G). It is much smaller than the scapula of its congener *P. gallinacea*. It has features as follows: the pneumatic fossa on the ventral surface immediately distal of the facies articularis humeralis is reduced; the acromion is quite short and is directed cranially; the process for attachment of the ligamentum acrocoraco-procoracoideum medially on the acromion is reduced; and there is a longitudinal groove latero-dorsal to the facies articularis humeralis, with the dorsal margin above it forming a narrow crest. Measurements (mm): for SW see Table 3.2; max. width of the facies articularis humeralis, 11.9; width distal of the facies articularis humeralis, 10.9; depth distal of the facies articularis humeralis, 8.1; length from distal rim of facies articularis humeralis to tip of acromion, 23.6 mm.

Sternum: The holotype includes a partial sternum (Figure 3.9 H, I, M), which preserves the rostrum sterni, the carina largely complete except for perhaps 25 mm of length caudally, most of the dorsal surface of the pars cardiaca, the sulci articularis coracoideii, three processus costali on each side (although presence of a fourth cannot be established due to breakage), but the specimen lacks the trabecula lateralis and left trabecula intermedia. The robust, and in dorsal view, triangular, spina interna is joined to the spina externa by a thin vertical blade of bone cranially as in other megapodes, enclosing a round foramen c. 6 mm in diameter. The carina is deep and cranially recurved at its tip (Figure 3.9H), as in extant megapodes. Caudally, on the right side the preserved trabecula intermedia encloses the original margin of the incisura medialis, with minimally c. 29 mm of that margin preserved caudal to it. Measurements (mm): maximum depth, measured from the top of the processus craniolateralis to the base of the carina, approx. 83; preserved length, 120; estimated total length, 145; length from spina interna to anterior margin of incisura medialis, 94; width at first processus costalis, 45.

Femur: The holotype preserves a complete right femur in excellent condition (Figure 3.10 A–D). It is comparatively short and stout, with its length about equal to that of the associated tarsometatarsi. Proximally, the cranial surface adjacent to the crista trochanteris and level with the caput has a deep, pneumatised fossa (Figure 3.10 A, C), as in most compared extant taxa, except for *T. fuscirostris* and *Macrocephalon maleo*. The caudal surface lacks the large pneumatic foramen adjacent to the facies articularis that is present in *T. fuscirostris*, but which is absent in all other extant taxa examined. The crista trochanteris is slightly damaged at its proximal end, but it appears to have been relatively short. At its proximal end, the crista is medially directed enclosing a fossa trochanteris, while its cranial margin is elevated from the shaft and drops steeply to the facies articularis antitrochanterica. In proximal aspect, the cranial edge of the crista trochanteris, the facies artic. antitrochanterica and the caput femoris form a smooth concave curve as in *A. lathami*, whereas in all other taxa examined the cranial edge of the facies artic. antitrochanterica forms a rather straight line between the crista and the caput. In proximal aspect, the caudo-medial edge of the facies artic. antitrochanterica projects strongly caudally adjacent to the caput femoris, forming an angle of approx. 120° with the caput as in *M.*

reinwardt and *A. lathami* (approx. 150° angle in *T. fuscirostris*, *L. ocellata*). The collum femoris is short and slightly constricted. At the distal end, the sulcus patellaris is proportionally broader and shallower than in all other taxa examined, and it has a more u-shaped profile in distal aspect. As in other megapodes, the impression of the m. gastrocnemialis lateralis is a large, deep pit on the caudo-lateral surface just proximal of the trochlea fibularis. The fossa poplitea is very shallow and bound medially by a short acute crista supracondylaris medialis. Measurements (mm): for TL, PW, SW and DW see Table 3.2; proximal depth, 24.5; min. shaft circumference, 43.9.

Tibiotarsus: The most complete specimen (L tibiotarsus of the holotype) is well preserved, missing only the crista cnemialis cranialis (Figure 3.10 E–H). The crista fibularis is very weakly expressed. Proximally, the crista cnemialis lateralis is proportionally wide as in *M. reinwardt* and *L. ocellata* (smaller in *T. fuscirostris*, *A. lathami* and *M. maleo*). In proximal aspect, the incisura tibialis is narrow, meaning that the facies articularis lateralis and the crista cnemialis lateralis are closely spaced. At the distal end, the pons supratendineus is proximodistally long as in *L. ocellata* and *A. lathami* (medial side of the pons is markedly more constricted in all other taxa). The epicondylus medialis is not highly protuberant, and is completely obscured by the condylus medialis in cranial aspect as in *T. fuscirostris*, *A. arfakianus* and *M. maleo* (highly protuberant and visible beyond the medial rim of the condylus medialis in all other species examined). The retinaculi m. fibularis are less marked than in all taxa examined apart from *T. fuscirostris*. In medial aspect, the disto-caudal rim of the trochlea cartilaginis tibialis terminates in a slight flange where it merges with the condylus medialis (Figure 3.10G), which is present but less exaggerated in other species. Just proximal of this flange, the caudal rim of the trochlea cartilaginis is slightly indented, whereas in all other species examined the rim is rounded here. Measurements (mm): for TL, PW, SW and DW see Table 3.2; width of proximal end without the crista cnemialis lateralis, i.e. the articular surfaces only, 20.8; depth of the condylus lateralis, 19.3; depth of the condylus medialis, 21.6; min. shaft circumference, 32.5.

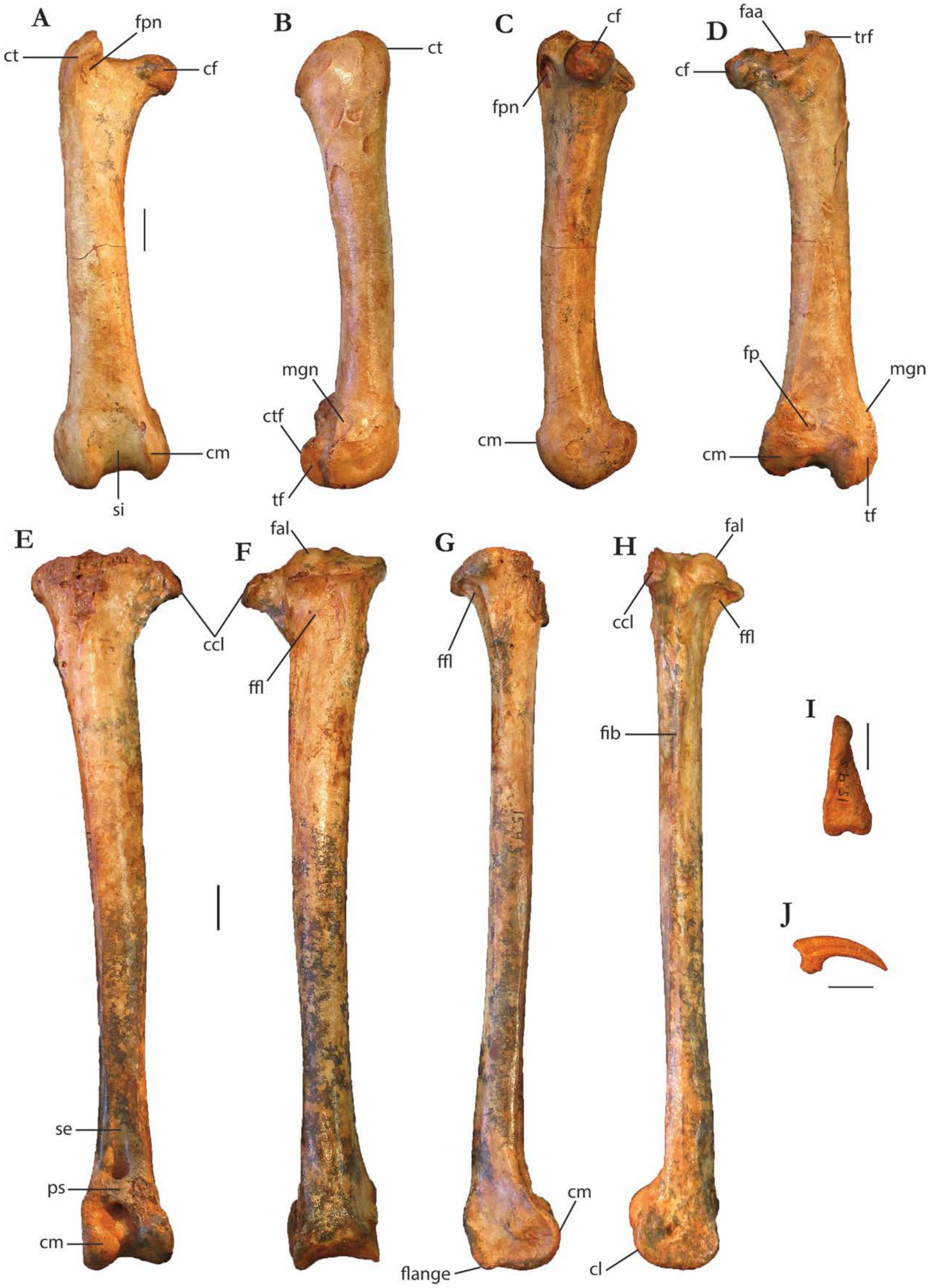


Figure 3.10: Leg and foot elements of the holotype of *P. campestris* sp. nov. WAM 15.9.5. Femur in cranial (a), lateral (b), medial (c) and caudal (d) aspects; tibiotarsus in cranial (e), caudal (f), medial (g) and lateral (h) aspects; os metatarsale I, left (i); ungual, dig. I, left (j). Abbreviations: ccl, crista cnemialis lateralis; cf, caput femoris; cl, condylus lateralis; cm, condylus medialis; ct, crista trochanteris; ctf, crista tibiofibularis; faa, facies articularis antitrochanterica; fal, facies articularis lateralis;ffl, fossa flexoria; fib, crista fibularis; fp, fossa poplitea; fpn, foramen pneumaticum; mgn, impression form. gastrocnemialis lateralis; ps, pons supratendineus; se, sulcus extensorius; si, sulcus intercondylaris; tf, trochlea fibularis; trf, trochanter femoris. Scale bars, 10 mm.

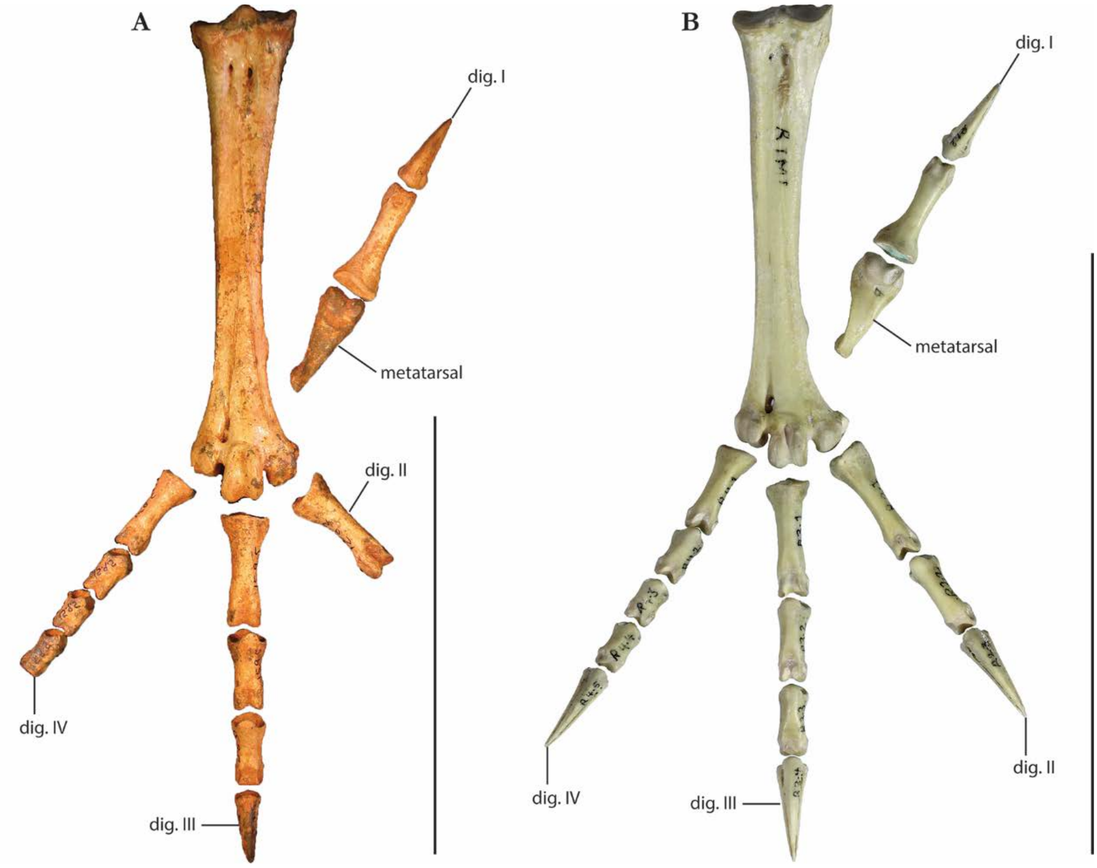


Figure 3.11: Reconstructed foot of extinct *P. campestris* sp. nov. (a) compared with foot of extant malleefowl *L. ocellata*, and scaled to the same size (scale bars, 10 cm). All bones of the extinct species are from the holotype skeleton WAM 15.9.5, with some images reversed to make a right pes. Note that the extinct species has a proportionally longer tarsometatarsus, but shorter digits, including shorter unguals on digits I and III. (Image of *L. ocellata* foot from Figure 11 in Worthy et al. 2016.)

Tarsometatarsus: In addition to the features noted above in the diagnosis, tarsometatarsi of *P. campestris* (Figures 3.5 and 3.11 A) have the following features. They are within the length range of *Alectura lathami* (86.8–95.4 mm) but are longer than in all other extant megapodes and both absolutely and proportionally much larger in other dimensions than in all other extant species (see proportional comparison in Appendix 1). Measurements (mm): for TL, PW, SW and DW see Table 3.2; width troch. metatarsi II, (WAM 15.9.5) 9.2, (WAM 15.9.1) 10.9; width troch. metatarsi III, (WAM 15.9.5) 12.8, (WAM 04.6.1) 11.1, (WAM 15.9.1) 11.7; width troch. metatarsi IV, (WAM 15.9.5) 9.0.

Phalanges: Most of the foot is represented, missing only one phalanx and ungual of digit II, and the ungual of digit IV. The pes in Figure 3.11A is reconstructed from left and right bones from the holotype. The toes are robust compared to all extant megapodes, but overall the reconstructed foot is of similar size to that of *A. lathami* despite *P. campestris* being a much larger bird, thus the foot is proportionally small compared to overall body size. The ungual of digit I is slightly longer than in *A. lathami*, but it is much stouter (deeper than wide) and has a more curved rather than a straight, elongate profile in lateral aspect. The ungual of digit III is slightly shorter than that of *A. lathami*, but is also deeply curved rather than elongate. Compared to the pes of *Leipoa ocellata* (Figure 3.11), the tarsometatarsus is proportionally long and the digits proportionally short as a proportion of overall length of the pes. The preserved unguals (digits I and III) are proportionally shorter and stouter than in *L. ocellata*. Overall, these observations indicate that this species was less well adapted for mound-building and may have been a burrow-nester. Measurements: see Table 3.3.

Table 3.2: Long bone measurements (mm) of *Progura campestris* sp. nov., holotype and referred material; TL = total length; PW = proximal width; SW = midshaft width; DW = distal width; *For coracoid, PW = omal width, DW = sternal width; †For the carpometacarpus, SW = maximum width measured cranio-caudally at the widest arc of the os carpus minus; ¥For tibiotarsus, PW is measured across the articular surface, and excludes the crista cnemialis lateralis

Element/Side	Catalogue no.	TL	PW	SW	DW
Holotype					
Coracoid, R	WAM 15.9.5	80.3	17.6*	9.8	>24*
Scapula, R	WAM 15.9.5	-	-	12.3	-
Humerus, L	WAM 15.9.5	-	34.6	14.6	29.0
Ulna, dR	WAM 15.9.5	-	-	-	17.8
Radius, L	WAM 15.9.5	140.7	9.5	6.3	13.1
Carpometacarpus, L	WAM 15.9.5	77.4	22.8	16.1†	14.4
Femur, R	WAM 15.9.5	106.6	27.5	14.0	26.2
Tibiotarsus, L	WAM 15.9.5	158.7	22.4¥	11.7	20.4
Tarsometatarsus, R	WAM 15.9.5	105.6	23.0	10.6	23.9
Referred material					
Coracoid, R	WAM 15.9.8	79.0	20.0*	9.8	>23.5*
Ulna, L	WAM 05.4.17	148.2	16.8	10.2	18.0
Carpometacarpus	WAM 15.9.9	75.1	21.0	-	-
Tarsometatarsus, dR	WAM 04.6.1	-	-	-	22.5
Tarsometatarsus, pL	WAM 15.9.7	-	23.3	-	-
Tarsometatarsus, L	WAM 15.9.11	93.4	21.3	10.0	-

Table 3.3: Measurements (mm) of pedal phalanges of *P. campestris* holotype; PW = proximal width; PD = proximal depth; SW = shaft width; DW = distal width; DD = distal depth; TL = total length

Phalanx	PW	PD	SW	DW	DD	TL
L I.1	3.8	5.3	6.8	10.2	6.5	26.3
L I.2	11.2	7.2	5.5	7.0	5.9	27.4
L I ungual	7.2	8.3	4.3	-	-	21.8
L II.1	10.2	8.6	5.5	6.9	6.9	26.7
L II.2	7.3	7.2	6.1	5.8	5.3	13.1
R III.1	10.9	10.5	5.8	7.9	6.7	26.2
R III.2	9.0	8.4	6.0	6.9	6.1	18.8
R III3.	8.0	8.1	5.7	6.7	5.2	16.6
R III ungual	6.1	7.4	3.8	-	-	18.6
L IV.1	9.2	7.8	5.2	7.0	6.5	20.6
L IV.2	7.1	7.3	6.0	6.0	5.4	12.9
L IV.3	7.1	6.6	6.1	6.1	4.7	11.2
L IV.4	6.4	6.4	5.2	6.2	4.7	12.0

Remarks: So far this is the only very large extinct species of megapode known from the western two-thirds of Australia. It differs in size and morphology from its larger congener *P. gallinacea* as noted in the diagnosis and description, and these appear to have been allopatric species. Thus there is no evidence that these represent members of a single sexually dimorphic species. Temporal overlap is more difficult to establish due to poor age constraints on Pleistocene material for *P. gallinacea* from the Darling Downs, thus an ancestral relationship between the two species cannot be ruled out (but see phylogenetic analysis below).

Latagallina Shute, Prideaux & Worthy, gen. nov.

Zoobank ID: urn:lsid:zoobank.org:act:8D617BBB-E082-442B-81A1-70AE6420B149

Type species: *Progura naracoortensis* van Tets, 1974

Included taxa: *Latagallina naracoortensis* (van Tets, 1974); *Latagallina olsoni* sp. nov. (see below)

Diagnosis: A genus of megapode distinguished from all other genera by the following unique combination of features of the tarsometatarsus and femur. **Tarsometatarsus:** 1) The shaft is stout and does not taper markedly towards the distal end, and the proximal and distal ends are proportionally wider than in other genera (proximal width = 23.6–26.0% of total length; distal width = 25.5–26.2% of total length). 2) The shaft flares widely proximomedially where it meets the cotyla medialis. 3) Dorsally, the foramen vascularis proximalis medialis is larger than its lateral counterpart, and is located slightly more distally. 4) The sulcus infracotylaris dorsalis is deep, and is confined by thick, raised areas of bone laterally, medially and proximally. 5) The tuberositas m. tibialis cranialis comprises two elongate, parallel ridges, the medial ridge being broader and more elevated from the shaft than the lateral. Both are offset laterally from the midline of the bone shaft, and are situated distal of the foramen vascularis proximalis medialis. 6) The lateral impressio retinaculum extensorii is placed slightly further distally than its medial counterpart, and is immediately proximo-medial to the foramen proximalis medialis, abutting the sulcus infracotylaris dorsalis. 7) The hypotarsus is plantarly extended (proximal part of medial hypotarsal ridge is about 50% of the depth of the cotyla medialis in medial aspect), and the junction between the medial hypotarsal crest and the plantar facies is abrupt, meeting the shaft more or less at 90° in medial aspect. 8) The fossa parahypotarsalis medialis is very wide and deep and extends just past midlength of the bone. **Femur:** 1) Femora of species of *Latagallina* are long relative to tarsometatarsus length (ratio of 1.2). 2) There is a large, round pneumatic foramen on the proximo-caudal facies, level with the caput femoris and immediately distal of the facies articularis antitrochanterica. This is considered an autapomorphy of the genus, convergent in *Talegalla*.

Differential diagnosis: The tarsometatarsi of extant and extinct genera of megapodes differ from *Latagallina* as follows. 1) The shaft is more elongate/gracile in *Progura*, *Macrocephalon*, *Megapodius*, *Talegalla*, *Aepypodius* and *Alectura.* 2) The shaft does not flare strongly proximomedially where it meets the cotyla medialis in *Progura*, *Macrocephalon*, *Aepypodius* or *Alectura*. 3) On the dorsal surface, the foramina vascularia proximalia are of equal size and are equidistant from the proximal end in *Progura*, *Macrocephalon* and *Talegalla*. 4) The sulcus infracotylaris dorsalis is shallow in *Progura* and *Macrocephalon* (variable among species of *Talegalla*), and in *Leipoa* the sulcus is bounded by thick ridges of bone laterally and medially, but not proximally. 5) In *Leipoa* the tuberositas m. tibialis cranialis comprises only a single short protuberance. In all other examined genera, the tuberositas comprises two parallel ridges. In *Progura*, *Macrocephalon* and *Alectura* these are short, of about equal size, and are placed symmetrically with respect to the midline of the shaft. In *Megapodius,* they are long and the medial is broader as in *Latagallina*, but both are placed centrally on the shaft rather than being offset laterally. In *Progura* and *Macrocephalon*, the tuberosities are separated from the foramina vascularia proximalia by a long gap. 6) In *Progura*, the impressiones retinaculi extensori are less prominent and both are placed well proximal of the level of the foramina vascularia proximalia. In *Macrocephalon*, they are more prominent, the medial one slightly more proximal than the lateral, and both are placed proximal of the level of the foramina vascularia proximalia. In *Alectura*, they are prominent, about level with one another, and slightly proximal of the level of the foramina vascularia proximalia. Position is variable between species of *Talegalla.* 7) The proximal part of the hypotarsus is dorsoplantarly shallower in all taxa apart from *Leipoa* and *Megapodius. Megapodius* is distinguished by having a hypotarsus that is strongly recurved distally, forming a deep hook in lateral/medial aspects. In *Leipoa*, the hypotarsus has a similar profile to *Latagallina*, but differs by having a medial hypotarsal crest that tapers distally where it meets the plantar shaft facies, rather than forming an abrupt 90° angle in medial aspect. 8) The fossa parahypotarsalis medialis is narrower, shorter and shallower in *Progura*, *Macrocephalon*, *Talegalla*, *Aepypodius* and *Alectura.* Femora of extant and extinct genera of megapode differ from *Latagallina* as follows. 1) The femur is shorter relative to the tarsometatarsus in *Alectura*, *Megapodius*, *Progura* and *Talegalla* (ratio of 1.0). 2) All extant megapode genera apart from *Talegalla*, and extinct *Progura*, lack a large pneumatic foramen on the proximo-caudal facies of the femur. In *Talegalla* the foramen is irregularly shaped and criss-crossed by trabeculae (a foramen is also seen here in members of some other galliform families on other continents, including the Miocene-aged *Ameripodius* in the Quercymegapodiidae and in extant *Argusianus* in the Phasianidae (Mourer-Chauviré 2000).

Etymology: *Latagallina* = “broad hen” (lata = ‘broad’, adjective, Latin; gallina = ‘hen’, noun, Latin). The name *Latagallina* refers to the stout, short-legged build of members of this genus. Gender is feminine.

Remarks: It was previously suggested that the type species for this genus was not morphologically separable from *Progura gallinacea* (Boles, 2008), and it was once interpreted as the smaller form (probably the female) of a single sexually dimorphic species (van Tets, 1985). In this paper we note substantial differences between *Progura* and *Latagallina* throughout the skeleton, further reflected in the results of our phylogenetic analysis (see below). Our observations support Olson’s remark that *Progura gallinacea* de Vis, 1888 and ‘*Progura*’ *naracoortensis* van Tets, 1974 belong in separate genera (Olson, 1985), and we have thus erected *Latagallina* as a new genus. Species of *Latagallina* are also readily distinguished from *Leipoa ocellata*, and we reject the proposed synonymy of *Progura/Latagallina* with *Leipoa*, which was based mainly on skeletal material of *L. naracoortensis* (cf. Boles, 2008).

Geological range: Early to Late Pleistocene (data herein).

Geographical range: Members of this genus are known to occur in south-eastern Queensland, eastern New South Wales, south-eastern South Australia, and the Nullarbor Plain, Western Australia.

Latagallina naracoortensis **(van Tets, 1974)**

(Figure 3.5 C, H, M, R, W; and Figures 3.12–3.16)

Synonyms:

Progura naracoortensis van Tets, 1974: *Transactions of the Royal Society of South Australia* 98(4): 214, Fig. 1–4; Henschke's Cave, near Naracoorte, south-eastern South Australia.

Progura gallinacea de Vis, 1888; Boles, 2008: *Oryctos* 7: 199, 205 Figs. 4, 5, in part; not *Progura gallinacea* De Vis, 1888.

Leipoa gallinacea Boles (2008): *Oryctos* 7: 204: in part, Fig. 6; not *Progura gallinacea* De Vis, 1888.

L.[eipoa] (Progura) gallinacea (De Vis, 1888); Boles, 2008: 204; not *Progura gallinacea* De Vis, 1888.

Holotype: SAM P17856, nearly complete, slightly immature, R tarsometatarsus, missing trochlea metatarsi IV.

Material originally referred to *Progura naracoortensis*: *Gore Limestone Quarry, Darling Downs, south-east Queensland:* QM F2769, pL tarsometatarsus; ***Naracoorte Caves, south-eastern South Australia: Main Fossil Chamber, Victoria Fossil Cave*** – SAM P16700, R coracoid; ***Henschke's Fossil Cave*** – SAM P17152, R tibiotarsus; SAM P17153, L humerus; SAM P17154, dL humerus; SAM P17857, pR femur; SAM P17876, dR tibiotarsus; SAM P17877, juvenile R ulna; SAM P17878, juvenile L humerus; SAM P17879, dL ulna; SAM P18181, cervical vertebra; SAM P18182, dL ulna; SAM P18183 – pR and dR humerus; SAM P18184, L radius; SAM P18185, pR tarsometatarsus; SAM P18186, dR femur; SAM P18187, cranial fragment of a synsacrum. We now explicitly refer all these specimens to *Latagallina naracoortensis*.

Newly referred material: The following specimens were previously referred to *Progura gallinacea* by van Tets (1974): ***Wombeyan Quarry, near Wombeyan Caves Reserve, New South Wales –*** AM F54720, R coracoid; AM F54721, pR ulna; AM F54722, dR ulna; AM F54724, pL tarsometatarsus; AM F54725, dL tarsometatarsus; AM F54726, dR tarsometatarsus

Newly identified material: *Kilsby's Hole, Mt Gambier, South Australia* – SAM P42079, pR ulna; SAM P42733, four pedal phalanges; ***Big Sink, Wellington Caves, New South Wales*** – NMNZ S46393, dL tarsometatarsus; ***Naracoorte Caves, South Australia*** – further to the holotype and referred specimens from Naracoorte listed above, we refer nearly 500 additional whole or partial specimens in the collection of the South Australian Museum (includes 6 crania, 3 rostra, 7 free vertebrae, 3 notaria, 16 synsacra, 3 ilia, 62 humeri, 46 ulnae, 14 radii, 33 carpometacarpi, 25 scapulae, 56 coracoids, 3 furculae, 15 sterna, 46 femora, 57 tibiotarsi, 67 tarsometatarsi; see Appendix 2) from various caves in the Naracoorte region, which were excavated subsequent to van Tets' (1974) description of *Progura naracoortensis*; and we also refer previously unregistered fossils from Buckridge Cave that were used in the analysis of Boles (2008), and were included in his synonymy of *Progura gallinacea* and '*Progura' naracoortensis*. There is evidence for only one large megapode in the Naracoorte region. All major skeletal elements are represented among the Naracoorte material, with most fossils being isolated elements, although three partial associated skeletons are known (***Big Bird Cave*** – SAM P51368; ***Komatsu Cave*** – SAM P51369; and ***Henschke's Fossil Cave*** – SAM P51370).

Type locality: Henschke's Fossil Cave, near Naracoorte, South Australia (van Tets, 1974) (Figure 3.2).

Stratigraphy, age and fauna: The holotype is of Pleistocene age (likely Middle or Late Pleistocene) (Pledge 1990). Most referred material comes Pleistocene-aged cave deposits in the Naracoorte area (Henschke's Fossil Cave, Victoria Fossil Cave, Buckridge Cave, Big Bird Cave and Komatsu Cave) and no caves here are known to have pre-Middle Pleistocene faunas (Reed and Bourne 2009). A small number of specimens come from deposits in other caves of uncertain age but which are presumed also to have a similar age range (Wombat Cave and Comaum Forest Cave near Naracoorte, and Kilsby's Hole, near Mt Gambier, approx. 100 km south of Naracoorte). Referred material from other locations (a proximal tarsometatarsus from Gore Limestone Quarry, south-east Queensland, and all bones from Wombeyan Quarry and Wellington Caves, New South Wales) are also presumed to be of Pleistocene age.

Revised diagnosis: A large species of megapode with diagnostic features of the tarsometatarsus and femur as noted for the genus, and further distinguished from other members of the genus by the following features: **Tarsometatarsi:** 1) These are large, ranging in length from 89.0 to 105.6 mm. 2) The fossa infracotylaris is moderately deep. 3) The medial hypotarsal ridge is dorsoplantarly very deep in proximal aspect. 4) The tuberositas m. tibialis cranialis is long and very protuberant, and the sulcus extensorius is shallow distally, such that the tuberositas is not recessed within the sulcus and is visible above the shaft in lateral and medial aspects. 4) In distal aspect, trochlea metatarsi IV is more plantarly depressed than trochlea metatarsi III. **Femora:** 1) The proximo-cranial surface adjacent to the crista trochanteris is relatively flat, lacking a fossa or with a fossa only very weakly developed.

Differential diagnosis: As well as differing from other taxa as per the generic diagnosis for *Latagallina*, tarsometatarsi of *L. naracoortensis* differ in size and proportion from extant and extinct species. Tarsometatarsi of *Leipoa ocellata* are approx. 25% shorter than those of *L. naracoortensis*. Shorter tarsometatarsi of *L. naracoortensis* are within the length range of some extant species of megapode (*Alectura lathami*, mean length 92.0 mm; *Talegalla jobiensis*, 90.1 mm; *Aepypodius arfakianus*, 96.8 mm), but these species are differentiated from *L. naracoortensis* by being much smaller in all width values and therefore being proportionally much more gracile (Appendix 1). Tarsometatarsi of *L. naracoortensis* are only approx. two-thirds of the estimated length of tarsometatarsi of *Progura gallinacea*, yet the proximal and distal widths of both species are similar, revealing the more robust nature of *L. naracoortensis*. Tarsometatarsi of *L. naracoortensis* are within the length range of *Progura campestris*, but are more robust, with the longest tarsometatarsus of *L. naracoortensis* (SAM P51231) being 2 mm shorter than the holotype tarsometatarsus of *P. campestris*, yet having a proximal width 2 mm (9%) wider, and a distal width 2.4 mm (13%) wider. The greater distal width seen in tarsometatarsi of *L. naracoortensis* is related to this species having wider individual trochlea, and also to having a wider incisura between trochleae III and IV than in *P. campestris*, which is evident in distal aspect (cf. Figure 3.5, V and W). The holotypic femur of *P. campestris* falls within the length range of femora of *L. naracoortensis*, but they differ by anatomical features as noted in the generic diagnoses, and are further distinguished by proportional differences: the holotypic femur of *P. campestris* is 96.2% the mean length, 92.9% of mean proximal width, 96.7% mean distal width, yet 107.7% of mean shaft width, of *L. naracoortensis*, thus *P. campestris* is characterised by having a proportionally more robust femur.

Description & comparisons:

Cranial bones: Several crania are preserved but all are in poor condition. No mandibles or quadrates are preserved. The tips of three premaxillae are preserved, showing that the ventral symphyseal zone is 7.8–8.2 mm long, thus shorter than in *Progura campestris* sp. nov. (>9 mm), and that the tip of the bill in *L. naracoortensis* was relatively short and wide (Figures 3.7 J–L and Figure 3.12 E–G). The cranium (Figure 3.12 A–D) is of similar width and depth to that of extant *A. lathami* and extinct *P. campestris*, and is therefore considerably larger than those of *L. ocellata* and *M. reinwardt*, but it has a relatively short, domed profile similar to that of *Leipoa ocellata.* Minimum interorbital width of the frontals (18.7 mm) is similar to *P. campestris*, but neither the lacrimals nor the margo supraorbitalis in the posterior part of the orbits appear to flare laterally to the same extent as they do in *P. campestris*, and so *Latagallina naracoortensis* apparently lacked the same degree of bony protection of the eyes. Unlike *L. ocellata*, *A. lathami*, *M. reinwardt* and *M. maleo*, but similar to *P. campestris*, the septum interorbitale has a small foramen nervi olfactorii posterior to the sulcus nervi olfactorii (Figure 3.12C). Measurements (mm): (SAM P41535), maximum depth, 26.6; length from posterior of cranium to the anterior of frontals, 41.9.

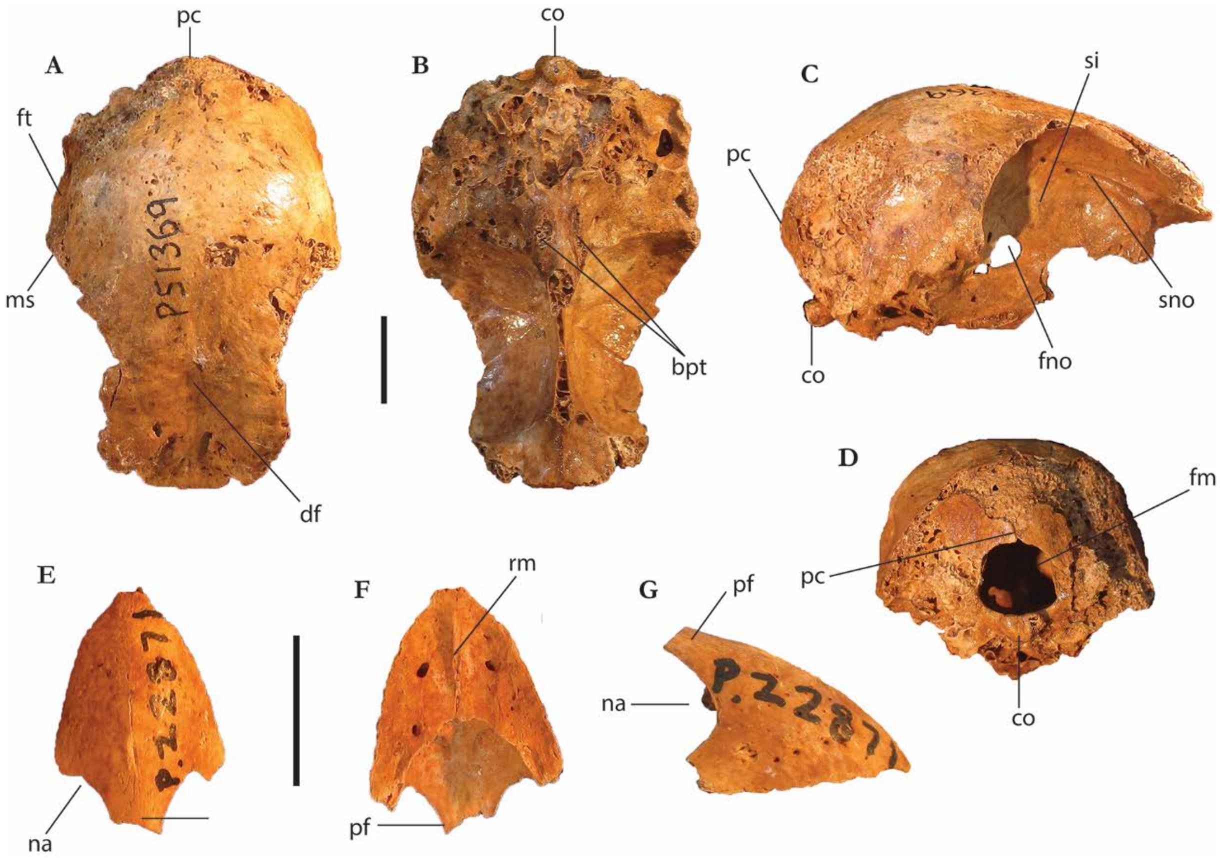


Figure 3.12: Cranial remains of La. naracoortensis; Cranium, SAM P.51369, in dorsal (a), ventral (b), lateral (c) and caudal (d) aspects premaxilla, SAM P.22871, in dorsal (e), ventral (f) and lateral (g) aspects. Abbreviations: bpt, processus basipterigoideus; co, condylus occipitalis; df, depressio frontalis; fm, foramen magnum; fno, foramen nervi optici; ft, fossa temporalis; ms, margo supraorbitalis; na, naris; pc, processus costalis; pf, processus frontalis; rm, rostrum maxillare; si, septum interorbitale; sno, sulcus nervi olfactorii. Scale bars, 10 mm.

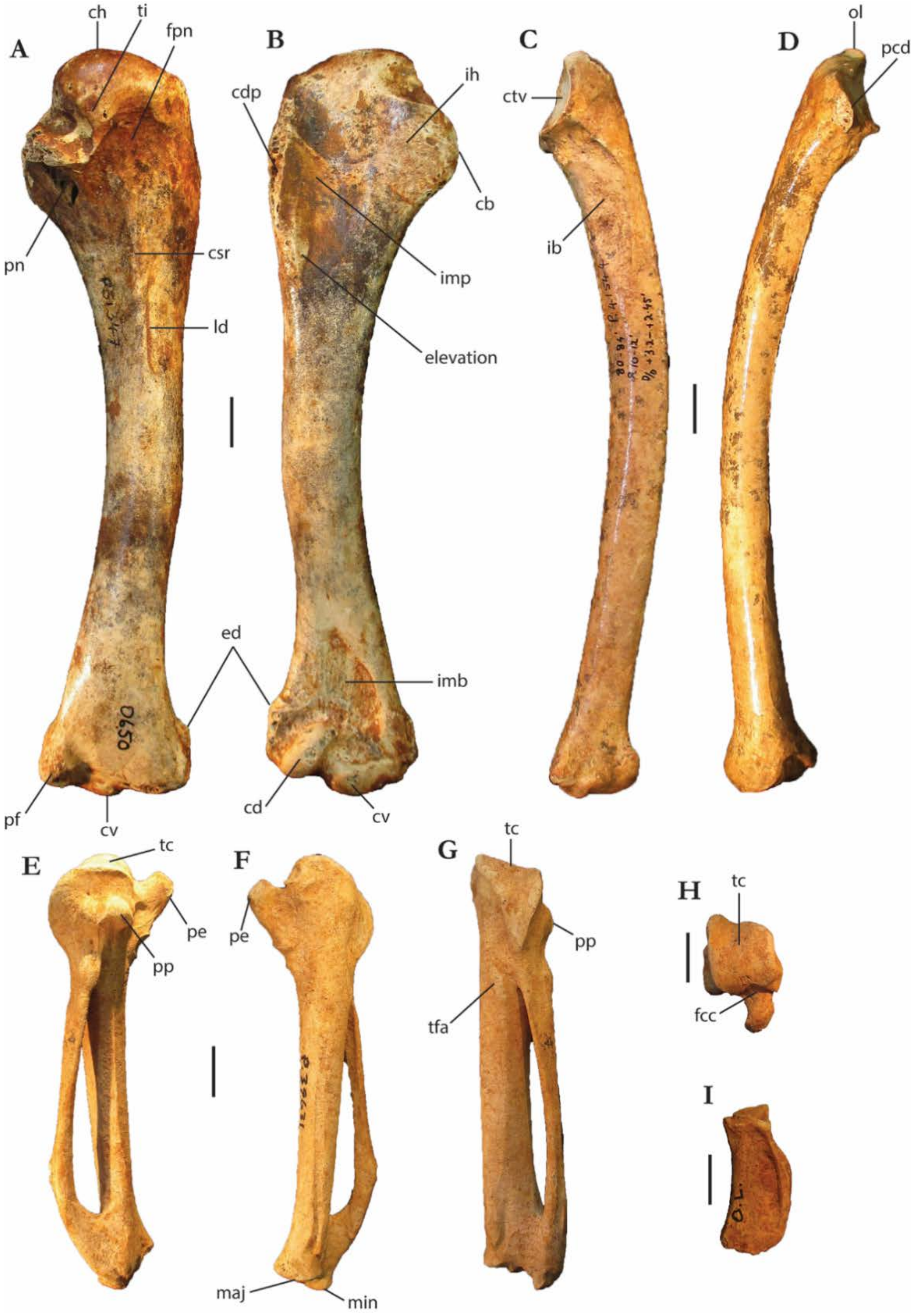
Humerus: Humeri of *L. naracoortensis* (Figure 3.13 A, B) are very large and robust, with deep muscle attachment scars, are well pneumatised, and are distinguished from those of other species of megapode as follows. They are much larger in all dimensions than the humeri of any extant megapode, being around 50% longer than in *Leipoa ocellata*, which has the longest humerus among extant species. It is further distinguished from extant megapodes by having: a tuberculum dorsale that is more swollen than in other species; a tuberculum intermedium that is not well pronounced, as in *T. fuscirostris* (prominent in *L. ocellata*, *A. lathami*, and less so in species of *Megapodius*); a tuberculum ventrale that projects caudally beyond the caput in proximal aspect (does not protrude like this in *L. ocellata*, *A. lathami*, *T. fuscirostris* or *M. reinwardt*); a crista bicipitalis that is long as in species of *Leipoa*, *Alectura* and *Talegalla*, rather than short as in those of *Megapodius* and *Macrocephalon*; a crista deltopectoralis with strong cranial projection as in species of *Leipoa*, *Talegalla* and *Megapodius* (shallow projection in *A. lathami*), with the adjacent scar for m. pectoralis on the cranial surface being strongly excavated (an elevated crescent of bone is seen here in species of *Leipoa*, *Alectura* and *Talegalla*); a processus flexorius that is blunter in shape in caudal aspect, as in *M. maleo* (more acute in species of *Leipoa*, *Alectura*, *Talegalla* and *Megapodius*) and a wider, deeper, more sharply demarcated impression for the m. brachialis.

The humerus of *L. naracoortensis* is only a little larger than that of *P. campestris*, and is distinguished from it by the following features: the tuberculum ventrale projects further caudally than the caput humeri in proximal aspect; the shaft is wider in caudal aspect; the capital shaft ridge is less elevated approaching the proximal end; the crista deltopectoralis is thicker ventrodorsally at its base, and the adjacent impression for m. pectoralis on the cranial surface is elevated adjacent to the crista, whereas this area is deeply excavated in *P. campestris*; the distal end is wider; the condylus dorsalis is longer and orientated more towards the long axis of the shaft; the condylus ventralis is oblong rather than spherical in cranial aspect, and does not protrude as far distally beyond the condylus dorsalis; the epicondylaris ventralis is proportionally larger; and the epicondylus dorsalis does not protrude as far dorsally.

Table 3.4: Summary statistics for humeri of *Latagallina naracoortensis* specimens from the Naracoorte Caves; TL = total length; PW = proximal width; SW = midshaft width; DW = distal width; measurements in mm. Measured specimens and source data in Appendix 2.

	TL	PW	SW	DW
Mean	150.6	38.1	15.5	30.7
SD	0.92	1.70	0.56	0.45
CV (%)	0.61	4.45	3.59	1.47
Minimum	135.5	33.6	13.8	27.2
Maximum	151.2	40.3	16.1	32.7
n	10	20	20	27

Figure 3.13: Wing elements of *La. naracoortensis*; Humerus, SAM P.51347, in caudal (a) and cranial (b) aspects; ulna, SAM P.41544, in ventral (c) and dorsal (d) aspects; carpometacarpus, SAM P.39631, in ventral (e), dorsal (f), caudal (g) and proximal (h) aspects; phalanx dig. major, SAM P.41844 (i). Abbreviations: cb, crista bicipitalis; cd, condylus dorsalis; cdp, crista deltopectoralis; ch, caput humeri; csr, capital shaft ridge; ctv, cotyla ventralis; cv, condylus ventralis; ed, epicondylus dorsalis; fcc, fovea carpalis cranialis; fpn, fossa pneumotricipitalis dorsalis; ib, impressio brachialis; ih, intumescentia humeri; imp, impressio m. pectoralis; ld, attachment for m. latissimus dorsalis; maj, facies articularis digitalis major; min, facies articularis digitalis minor; ol, olecranon; pcd, processus cotylaris dorsalis; pe, processus extensorius; pf, processus flexorius; pn, foramen pneumaticum in the fossa pneumotricipitalis ventralis; pp, processus pisiformis; tc, trochlea carpalis; tfa, tuberosity for flexor attachment; ti, tuberculum intermedium. Scale bars, 10 mm.


A
ch
ti
fpn
pn
csr
ld
ed
D650
pf
cv
B
cdp
ih
cb
imp
elevation
imb
cd
cv
C
ctv
ib
D
ol
pcd
E
tc
pe
pp
F
pe
maj
min
G
tc
pp
tfa
H
tc
fcc
I

Ulna: The ulna is larger and more robust than in any other species of megapode, extinct or extant (although it is of similar size to a distal ulna tentatively referred to *P. gallinacea*, see description for that species). In addition to its somewhat larger size, it is distinguished from the ulna of *P. campestris* by having a shaft that is straighter in dorsal aspect, a shallower impression for the m. brachialis, a less dorsoventrally compressed shaft, and an olecranon that is more aligned with the long axis of the shaft in caudal aspect. Measurements: for TL, PW, SW and DW, see Table 3.5.

Table 3.5: Measurements (mm) of ulnae of *Latagallina naracoortensis;* summary statistics are given for specimens from Naracoorte (Measured specimens and source data in Appendix 2); actual measurements are given for specimens from Wombeyan Quarry; TL = total length; PW = proximal width; SW = midshaft width; DW = distal width.

Naracoorte Caves		**TL**	**PW**	**SW**	**DW**
	Mean	154.2	18.7	10.9	19.5
	SD	8.68	1.33	0.79	0.06
	CV (%)	5.63	7.13	7.21	5.46
	Minimum	144.8	16.2	9.4	17.7
	Maximum	173.9	22.6	12.6	21.1
	n	11	23	22	22
Wombeyan Quarry	AM F54722	-	-	-	22.1
	AM F54721	-	20.7	-	-

Carpometacarpus: Carpometacarpi of *L. naracoortensis* are much larger than those of any extant megapode (mean length 79.3 mm, versus 52.8 mm in *Leipoa ocellata*). Carpometacarpi of *L. naracoortensis* are on average slightly longer than specimens of *P. campestris*, but their length ranges overlap (see Tables 3.2 and 3.6). In specimens of *L. naracoortensis* (SAM P39628; SAM P39631) that are of similar length to the holotype carpometacarpus of *P. campestris*, however, the maximum width of the carpometacarpus, measured at the widest arch of the os metacarpale minus, is c. 2.5–3.5 mm wider, thus the spatium intermetacarpale is relatively wider. In addition, carpometacarpi of *L. naracoortensis* are distinguished from those of *P. campestris* by having a single fused tuberosity for the flexor attachment that is entirely proximal to the spatium intermetacarpale (two scars in *P. campestris*, the proximal one within the spatium intermetacarpale), and a deeper fovea carpalis cranialis. Carpometacarpi of *Latagallina naracoortensis* are smaller than those of *P. gallinacea*, and are further distinguished by having: a dorsal rim of the trochlea carpalis that is rounded proximally rather than angular; a processus extensorius that is proportionally longer but less thick dorsoventrally (less than half the thickness of the adjacent carpal trochlea in *L. naracoortensis*, whereas in *P. gallinacea* it is more than half the thickness of the trochlea); a single tuberosity for the flexor attachment that is entirely proximal to the spatium intermetacarpale (two distinct scars in *P. gallinacea*, the distal one mostly within the spatium intermetacarpale); and a less distally extended facies articularis digiti minor.

Table 3.6: Summary statistics for carpometacarpi of *Latagallina naracoortensis* from the Naracoorte Caves; TL = total length; PW = proximal width; MW = metacarpal width, measured at widest arc of os metacarpale minus; DW = distal width; measurements in mm; Measured specimens and source data in Appendix 2.

	TL	**PW**	**MW**	**DW**
Mean	79.3	22.5	18.9	15.2
SD	4.86	1.76	1.45	1.08
CV (%)	6.13	7.81	7.67	7.13
Minimum	73.4	19.8	16.6	13.6
Maximum	90.8	25.8	20.5	17.0
n	25	27	5	26

Coracoid: Coracoids of this species (Figure 3.13 A–E) are very large and are further distinguished from extant species by the following features: the shaft is straight and robust and does not taper much towards the omal end (narrower and more tapered in *A. lathami*, *T. fuscirostris* and *M. reinwardt*, and arched slightly laterally in *T. fuscirostris*); the facies articularis scapularis is broad, flat to convex and well defined, with a long axis at approx. 45° to the long axis of the shaft (the facies is convex with less distinct edges in *A. lathami*, *T. fuscirostris* and *M. reinwardt*); the sulcus m. supracoracoidei is deep and is enclosed by the overhanging facies articularis clavicularis ventrally (in *A. lathami* and *T. fuscirostris*, the sulcus is shallow due to minimal overhang of the facies artic. clavicularis); the processus acrocoracoideus is proportionally long, and its apex is more or less in line with the medial facies of the shaft in ventral aspect as in *T. fuscirostris* and *M. reinwardt* (proportionally shorter in all other taxa, and apex placed further medially in *A. lathami* and *L. ocellata*); the facies articularis clavicularis is medially flattened with flat sternal margin in medial aspect, as in *A. lathami*, *T. fuscirostris* and *L. ocellata*, rather than notched as in *M. reinwardt*; the dorsal part of the facies articularis clavicularis projects a little beyond the medial margin of the shaft in dorsal view, as in *T. fuscirostris* and *A. lathami* and *M. reinwardt*, unlike the far greater projection in *L. ocellata*; the ventral side of the facies articularis clavicularis does not protrude medially of the shaft; the sterno-ventral facies is flat in sternal aspect (convex in *A. lathami*, *L. ocellata* and *T. fuscirostris*); and the distal margin of the processus lateralis is short relative to the length of the facies articularis sternalis (of about equal length in *M. reinwardt*).

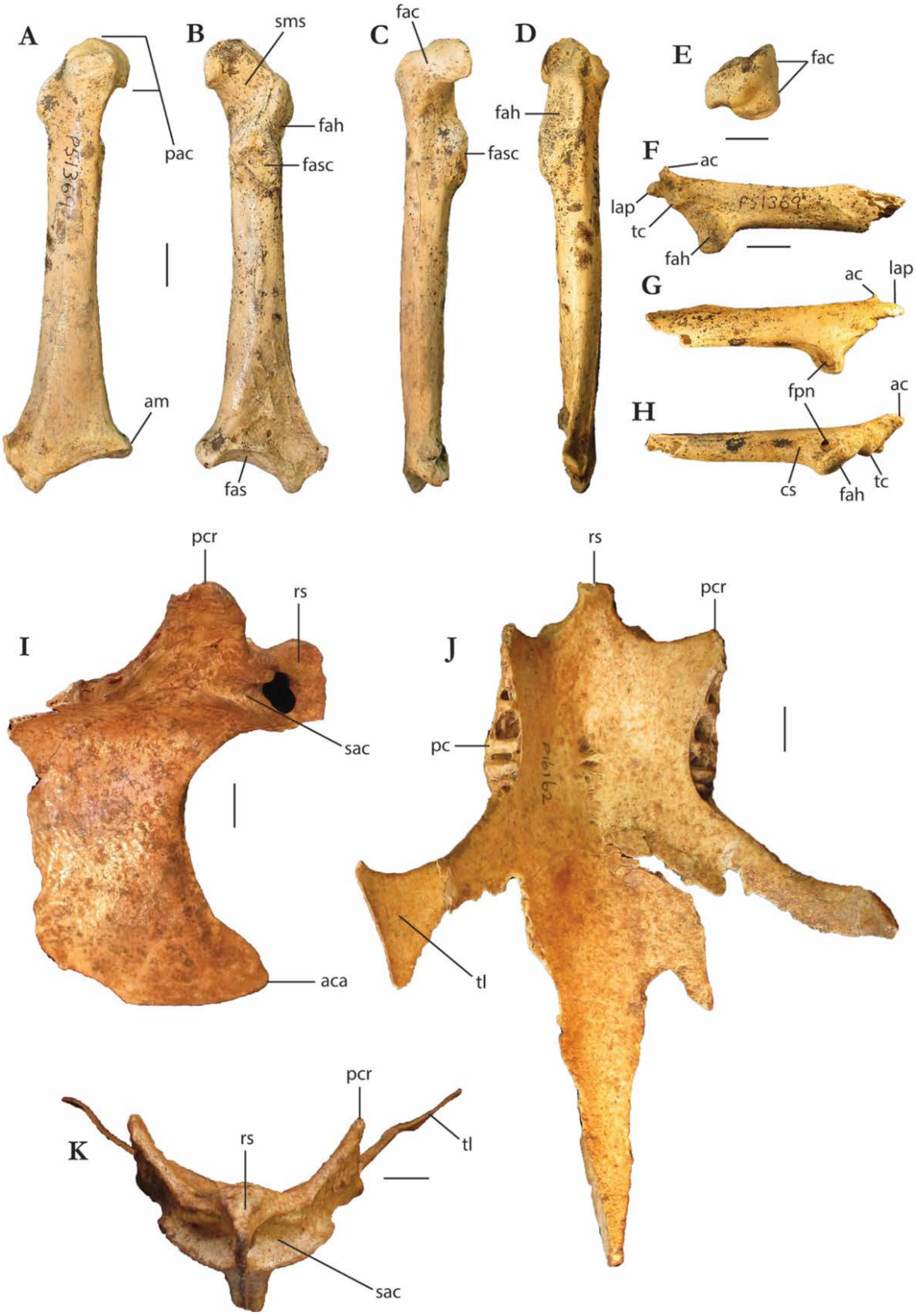


Figure 3.14: Pectoral and axial skeletal elements of *La. Naracoortensis*. Coracoid, SAM P.51369, in ventral (a), dorsal (b), medial (c) lateral (d) and omal (e) aspects; scapula, SAM P.51369, in lateral (f), medial (g) and ventral (h) aspects; sternum, SAM P.23125, in lateral (i) and cranial (k) aspects and SAM P.16162, in dorsal (j) aspect. Abbreviations: ac, acromion; aca, apex carinae; am, angulus medialis; cs, collum scapulae; fac, facies articularis clavicularis; fah, facies articularis humeralis; fasc, facies articularis scapularis; fas, facies articularis sternalis; fpn, foramen pneumaticum; lap, crista lig. acrocoraco-procoracoideum; pac, processus acrocoracoideus; pc, processus costalis; pcr, processus craniolateralis; rs, rostrum sterni; sac, sulcus articularis coracoideus; sms, sulcus m. supracoracoidei; tc, tuberculum coracoideum; tl, trabecula lateralis. Scale bars, 10 mm.

Mature specimens are intermediate in size between the coracoids of the two extinct species of *Progura* described above. They are distinguished from *P. gallinacea* by their somewhat smaller size, and the following features of the omal end (the distal coracoid of *P. gallinacea* is unknown): the ventrolateral margin of the facies articularis humeralis does not project as strongly laterally, and is more square (not as rounded) in ventral aspect; there is a shallower sulcus on the ventral surface between the ventrolateral margin of the facies articularis humeralis and the processus acrocoracoideus, resulting in a greater thickness of bone separating the ventral and dorsal surfaces here in omal aspect; and the facies articularis humeralis to the facies articularis scapularis is flatter (less concave). Coracoids of *L. naracoortensis* are differentiated from *P. campestris* by their larger size (mean length, 92.5 mm; 79.0 mm in the referred specimen of *P. campestris*), and the following morphological features: the facies articularis clavicularis has a long, medially flattened surface whose profile is triangular in medial aspect, and forms a distal hook that overhangs the sulcus dorsally (facies is short with a linear profile in *P. campestris*, and is less hooked); the ventromedial portion of the facies articularis clavicularis is not prominent medially in ventral aspect, whereas in *P. campestris* it projects strongly; the dorsal portion of the facies articularis clavicularis does not project much further medially than the facies articularis scapularis in dorsal aspect (projects strongly in *P. campestris*); at the sternal end, the angulus medialis projects medially, whereas in *P. campestris* it projects less and is smoothly contiguous with the medial shaft; the facies articularis sternalis has a large surface area dorsally and ventrally, and its sternal margin is deeply arched, providing a long, deep articulation with the sulcus artic. coracoideus of the sternum (shorter, shallower and straighter in *P. campestris*).

Table 3.7: Measurements (mm) of coracoids of *Latagallina naracoortensis;* summary statistics are given for specimens from Naracoorte (individual measurements are in Appendix 2); actual measurement given for the specimen from Wombeyan Quarry; TL = medial length; OW = omal width; SW = midshaft width; StW = sternal width

Naracoorte Caves		**TL**	**OW**	**SW**	**StW**
	Mean	92.5	21.8	11.0	28.7
	SD	1.06	1.19	0.28	1.63
	CV (%)	1.15	5.46	2.57	5.68
	Minimum	81.9	15.5	9.6	27.5
	Maximum	93.2	22.8	12.4	32.0
	n	16	20	19	7
Wombeyan Quarry	AM F54720	88.9	-	-	-

Scapula: The scapulae (Figure 3.14 F, H) are somewhat smaller and less robust than that of *P. gallinacea*, and are further distinguished from that species by having a convex dorso-lateral surface immediately distal of the acromion and dorsal to the facies articularis humeralis (*P. gallinacea* is grooved here). They are a little larger than scapulae of *P. campestris* and are further distinguished by having the following features: the pneumatic fossa on the ventral surface immediately distal of the facies articularis humeralis is larger; the acromion is more cranially extended; there is a large, costally directed process for attachment of the ligamentum acrocoraco-procoracoideum, which with the dorsal prominence on the acromion gives the proximal end a forked appearance (the dorsal process is much reduced in *P. campestris* and lacks this forked profile); and the dorso-lateral surface immediately distal of the acromion, and dorsal to the facies articularis humeralis, is convex rather than grooved, with the dorsal margin broadly rounded, not compressed into a narrow margin as in *P. campestris*. Measurements: see Table 3.8.

Table 3.8: Summary statistics for scapulae of *Latagallina naracoortensis* specimens from Naracoorte Caves (individual measurements are in Appendix 2); TL = total length; WA = width of facies artic. humeralis; WC = width of collum scapulae, measured immediately distal of the facies artic. humeralis; DC = depth of collum scapulae, measured immediately distal of the facies artic. humeralis; LAA = length from distal rim of facies artic. humeralis to tip of acromion; measurements in mm.

	TL	WA	WC	DC	LAA
Mean	-	12.3	10.8	7.6	24.1
SD	-	0.85	0.63	0.53	0.90
CV (%)	-	6.92	5.86	6.93	3.74
Minimum	-	10.3	9.7	6.7	22.6
Maximum	>100	13.7	12.0	8.5	25.8
n	1	22	23	20	18

Sternum: The best preserved specimen (SAM P16162) preserves almost the entire length of the sternum (Figure 3.14 J, K). It is 138.7 mm long, and has a cranial width of 44.5 mm, measured across the proc. craniolaterales. Depth of the carina is variable between individuals, with the largest sternum measuring 96.3 mm in carina depth, and the smallest 66.2 mm. Despite differences in carina depth, the sulci articularis coracoidei are consistently wide and deep in all individuals. The tip of the keel is ventrocranially recurved (Figure 3.14 I) as in extant megapodes and the extinct *P. campestris*. The deep carina of *L. naracoortensis*, along with other pectoral elements that show no signs of reduction, are consistent with adults of this species retaining the ability to fly, despite their large size.

Pelvis: Only fragmentary remains of the pelvis are preserved. The best preserved specimen (SAM P22818) is an approx. 80 mm-long fragment of a left ala postacetabularis ilii and ala ischia, preserving the foramen acetabuli, antitrochanter and foramen ilioischiadicum. The specimen does not preserve enough of the anatomy to allow a meaningful comparison with other species, but indicates that this species had a very large pelvis as would be expected.

Femur: Femora of *L. naracoortensis* (Figure 3.15 A–D) have features as follows. Mean femur length in this species is greater than mean tarsometatarsus length, unlike *P. campestris* in which femur and tarsometatarsus are of equal length. The proximo-cranial surface adjacent to the crista trochanteris is relatively flat, and it lacks a deep pneumatised fossa (e.g. SAM P51368) as seen in some other taxa. Though a fossa is lacking, pneumatism of this area is seen in some individuals (e.g. SAM P51262, SAM P51263). At the junction between the crista trochanteris, the cranial surface and the facies articularis antitrochanterica, the bone is compressed into a thin crest, as in *L. ocellata* and *M. reinwardt*. In proximal aspect, the cranial edge of the facies artic. antitrochanterica forms a straight line between the crista trochanteris and the caput femoris, as in all taxa examined except for *A. lathami* and *P. campestris*, in which it is concave. On the proximo-caudal surface there is a large, round pneumatic foramen adjacent to the caput femoris (see Generic Diagnosis). This feature can be seen in Figure 4*f* of Van Tets (1974) and Figures 2(9) and 5 of Boles (2008) but has not previously been noted or identified as a distinguishing character. However, we identify it as an autapomorphy that defines the genus *Latagallina* (see generic diagnosis above, and Phylogenetics results below). Distally, the rims of the cristae patellaris medialis and lateralis are broad, deep and long, and enclose a narrower, more v-shaped sulcus patellaris than in all extant species examined and *P. campestris*. The epicondylus lateralis flares more widely laterally than in all other species examined, and in caudal aspect this forms a buttress of bone laterad of the impression of the m. gastrocnemialis lateralis, which is absent in all other species. The crista tibiofibularis is proximodistally shorter but more caudally projecting than in similarly sized *P. campestris*. Measurements (mm): for TL, PW, SW and DW see Table 3.9; mean minimum shaft circumference, 41.2.

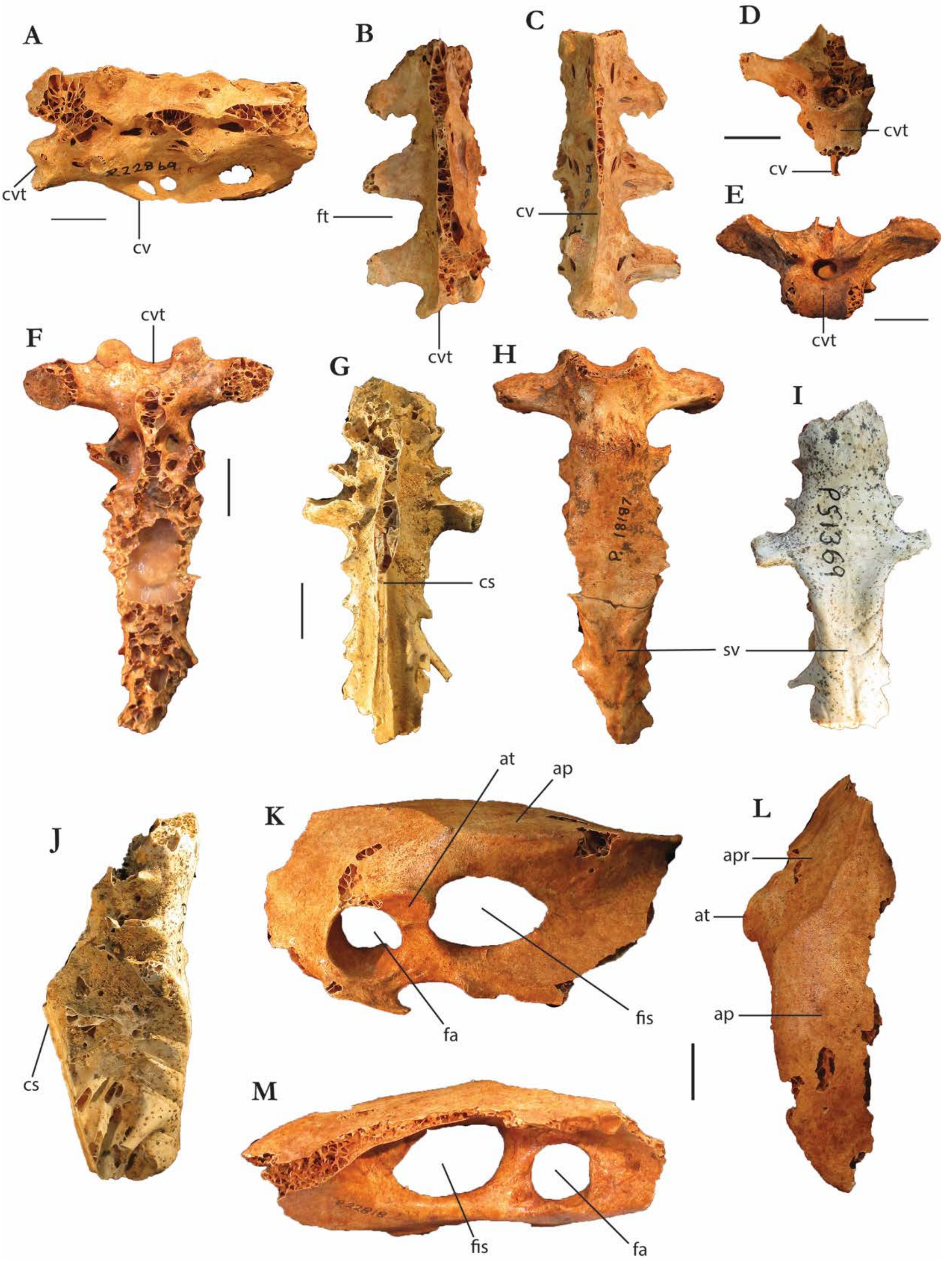


Figure 3.15: Pelvic and axial elements of *Latagallina naracoortensis*; notarium, SAM P22869, in lateral (a), dorsal (b), ventral (c) and cranial (d) aspects; synsacrum, SAM P18187, in cranial aspect (e), SAM P18187 (f) and SAM P51369 (g) in dorsal aspect, SAM P18187 (h) and SAM P51369 (i) in ventral aspect and SAM P51369 in lateral (j) aspect; ilium, SAM P22818, in lateral (k), dorsal (l) and medial (m) aspects. Abbreviations: ap, ala postacetabularis ilii; apr, ala preacetabularis ilii; at, antitrochanter; cs, crista spinosa synsacri; cv, crista ventralis; cvt, corpus vertebrae; fa, foramen acetabuli; fis, foramen ilioischiadicum; ft, fenestra transversaria; sv, sulcus ventralis synsacri. Scale bars, 10 mm

Table 3.9: Summary statistics for femora of *Latagallina naracoortensis* specimens from the Naracoorte Caves (individual measurements are in Appendix 2); TL = total length; PW = proximal width; SW = midshaft width; DW = distal width; measurements in mm

	TL	PW	SW	DW
Mean	110.8	29.6	13.0	27.1
SD	5.63	1.39	1.63	1.48
CV (%)	5.08	4.69	6.10	5.47
Minimum	102.4	27.8	11.8	25.2
Maximum	119.4	31.7	14.1	29.6
n	6	10	12	12

Tibiotarsus: Tibiotarsi of this species (Figure 3.15 E–H) are very large and robust. They are of similar length to the tibiotarsus in the holotype of *P. campestris*, but have more robust proximal and distal ends. Proximally, the crista cnemialis lateralis is as proportionally wide as in *P. campestris*, *M. reinwardt* and *L. ocellata*, unlike *T. fuscirostris*, *A. lathami* and *M. maleo*, in which this crista has less lateral extent. The proximal articular surface has a large surface area, and the incisura tibialis is wide, creating a greater separation between the facies articularis lateralis and the crista cnemialis lateralis, unlike *P. campestris* in which these are closer together. Distally, the epicondylus medialis is protuberant beyond the rim of the condylus medialis in cranial aspect, distinguishing it from *P. campestris*, *M. maleo* and *A. arfakianus*, in which the condylar rim occludes it. The proximodistal length of the pons supratendineus is much greater laterally than medially, and its distal margin is angled obliquely to the axis (rather more horizontal in *P. campestris*). The condylar width is relatively broad compared to the depth of the condylus medialis (subequal in *P. campestris*). Measurements (mm): for TL, PW, SW and DW, see Table 3.10; mean width of proximal end without the crista cnemialis lateralis, i.e. the articular surface only, 23.8; mean depth of the cotyla lateralis, 19.0; mean depth of the cotyla medialis, 19.7; mean minimum shaft circumference, 30.7.

Table 3.10: Summary statistics for tibiotarsi of *Latagallina naracoortensis* specimens from the Naracoorte Caves; TL = total length; PW = proximal width; SW = midshaft width; DW = distal width; measurements in mm; Measured specimens and source data in Appendix 2.

	TL	PW	SW	DW
Mean	157.5	23.8	10.9	21.0
SD	9.24	1.49	0.99	1.28
CV (%)	5.87	6.24	9.11	6.12
Minimum	144.2	21.6	9.1	19.1
Maximum	170.3	26.3	13.1	23.8
n	5	11	21	35

Tarsometatarsus: Diagnostic features are described above in the generic and species diagnoses and depicted in Figure 3.5 C, H, M, R and W. Measurements (mm): for TL, PW, SW and DW see Table 3.11; prox. depth including the hypotarsus, mean 22.2; depth of trochlea metatarsi II, mean 9.5; depth trochlea metatarsi III, mean 11.3; depth of trochlea metatarsi IV, mean 8.4.

Table 3.11: Summary statistics for tarsometatarsi of *Latagallina* naracoortensis specimens from the Naracoorte Caves; TL = total length; PW = proximal width; SW = midshaft width; DW = distal width; measurements in mm; measurements in mm; Measured specimens and source data in Appendix 2.

	TL	PW	SW	DW
Mean	97.3	23.1	10.1	24.8
SD	4.53	1.44	0.65	1.37
CV (%)	4.66	6.23	6.44	5.53
Minimum	89.0	19.7	9.2	22.7
Maximum	105.6	25.9	11.3	28.0
n	19	25	22	22

Phalanges: Relatively few pedal phalanges of this species are preserved, and given the abundance of other skeletal material from the Naracoorte Caves, it seems likely that they have generally been overlooked in the collection or processing of fossils. Six phalanges (L and R I.2; L III.1; R IV.1; and two unguals from unknown digits) belonging to an individual (SAM P51368) are preserved from Big Bird Cave, Naracoorte. All are of similar size to the equivalent bones in *P. campestris* but differ slightly in proportion from that species as follows: phalanx I.2 is slightly flatter dorso-ventrally; phalanx II.1 is a little wider proximally; and phalanx III.1 has a slightly wider shaft, a broader, more symmetrical proximal articular facet (lateral half of the facet is larger in *P. campestris*), and proximo-plantar surface is much more deeply excavated. The unguals are short, lateromedially compressed, and very deeply curved, and are not elongate or dorsoventrally flattened, unlike in specialised mound-building species such as *A. lathami* and *L. ocellata.*

Remarks on specimens previously referred to this species:
Two megapode fossils (QM F23258, a carpometacarpus; and QM F23259, a pL tarsometatarsus) from the early Pliocene Bluff Downs Local Fauna of north-eastern Queensland were tentatively referred by Boles and Mackness (1994) to *Latagallina* (as *Progura*) *naracoortensis* rather than to *P. gallinacea* because of their small size, but these authors commented that they could belong to a new species. Published measurements and photographs of these bones indicate that they are unlikely to belong to *L naracoortensis*, although the proximal width of the tarsometatarsus (19.5 mm) is closest in size to that species (Table 3.11). A photograph of QM F23259 (Boles and Mackness 1994) reveals the shaft of the tarsometatarsus to be very tapered towards the distal end. This is dissimilar to the stout shaft characteristic of species of *Latagallina*. The shaft is also more tapered than in *P. campestris*, but has a very similar shape to *A. lathami* albeit a bit larger, or *P. gallinacea* albeit very much shorter. However, estimated total length of the bone if complete (c. 90 mm), is only 60% of the length of the tarsometatarsus of *P. gallinacea* (approx. 147.5 mm), and is somewhat shorter than that of *P. campestris* (107 mm) and *L. naracoortensis* (mean 97.3 mm). This bone could be a large specimen of *A. lathami*, the tarsometatarsus of which can reach at least 101.9 mm in length (MV R4288; PW=17.1 mm), albeit one that is slightly more robust than modern specimens. The Bluff Downs fossils require further examination, and comparison with extant taxa and the extinct Plio-Pleistocene taxa that are known as a result of the present study.

Remarks: *L. naracoortensis* was a stout, robustly-built Pleistocene megapode larger and heavier than any extant member of the family, but was somewhat smaller than *P. gallinacea.* Although it was of similar size and mass to *P. campestris* (see Body-mass estimates), it had different body proportions (see species descriptions and Simpson log-ratio diagram), and fossils of these taxa are readily distinguishable based on morphology.

Latagallina olsoni Shute, Prideaux & Worthy, sp. nov.

(Figure 3.5 D, I, N, S, X; and Figures 3.17–3.19)

Zoobank ID: urn:lsid:zoobank.org:act:961E913A-9DF1-4FD0-B757-10CD65809220

Holotype (Figures 3.5 D, I, N, S; and Figures 3.17–3.19): WAM 15.9.6, associated remains of one adult individual, comprising the following elements: mandible, approx. 1.5 cm of tip; 2 vertebrae, 1 cervical, 1 caudal; 11 ribs and rib fragments; pelvis, disarticulated – complete synsacrum, portions of L and R ilia; notarium; L, a fragment of pR humerus; pR, L ulna; L radius, missing proximal end; R carpometacarpus; L os carpi ulnare; R os carpi radiales; L phalanx II digiti majoris II.1; L and R phalanx digiti majoris II.2; R femur, L femur missing lateral condyle; tibiotarsi, R with damaged midshaft, shaft and distal fragment L; L fibula; R and L (minus trochlea metatarsi IV) tarsometatarsus; os metatarsale I; 1 ungual digit unknown. Number of individual bones = 40.

Referred material: WAM 15.9.3, complete L carpometacarpus; WAM 15.9.4, fragment of a pR femur. Including the holotype skeleton, number of individual bones = 42, minimum number of individuals = 3.

Type locality: Leaena's Breath Cave, Thylacoleo Caves, Nullarbor Plain, Western Australia (Figure 3.2; see Key Locations).

Stratigraphy, age and fauna: All material comes from Leaena's Breath Cave. The associated holotype skeleton was found lying on the surface of the sediment floor. Surface sediments from elsewhere in the cave have been dated to the Middle Pleistocene, and so the holotype may also be of this age. The referred femoral fragment (WAM 15.9.4) was excavated from a depth of 5–10 cm below the sediment surface, in stratigraphic Unit 1, Quadrat 1, Pit B (Middle Pleistocene; Prideaux *et al.* 2007). The referred carpometacarpus (WAM 15.9.3) was excavated from 95–100 cm below the sediment floor, in stratigraphic Unit 3, Quadrat 2, Pit B (2.58–0.78 Ma, Early Pleistocene; Prideaux *et al.* 2007).

Diagnosis: A species of *Latagallina* as defined by generic features of the tarsometatarsus and femur, and distinguished from other members of the genus by its small size and by the following unique combination of features. **Tarsometatarsus:** 1) The fossa infracotylaris and sulcus extensorius are very deep. 2) The medial hypotarsal ridge is moderately deep in proximal aspect. 3) The tuberositas m. tibialis cranialis is relatively short and not protuberant, and completely recessed within the sulcus extensorius. 4) Trochlea metatarsi IV is only very slightly plantarly depressed relative to trochlea metatarsi III, as seen in distal aspect. **Femur:** 1) The proximo-cranial surface adjacent to the crista trochanteris has a deep pneumatic fossa.

Differential diagnosis: *Latagallina naracoortensis* is distinguished from the new species by its much larger size (tarsometatarsus approx. 38% longer on average), and by features as follows: Tarsometatarsi of *L. naracoortensis* have: a shallower fossa infracotylaris and sulcus extensorius; a longer, much more protuberant tuberositas m. tibialis cranialis that is elevated above the shaft rather than recessed in the sulcus extensorius; a dorso-plantarly deeper medial hypotarsal ridge in proximal aspect; and with greater plantar depression of trochlea metatarsi IV relative to trochlea metatarsi III. Femora of *L. naracoortensis* are differentiated by their much larger size, and by lacking a fossa on the proximo-cranial surface adjacent to the crista trochanteris, the bone here being rather flat and pneumatisation slight to absent, rather than excavated and well-pneumatised as in *L. olsoni*.

Measurements of holotype and referred material: See Table 3.12

Table 3.1: Long bone measurements (mm) of *Latagallina olsoni* holotype and referred material; TL = total length; PW = proximal width; SW = midshaft width; DW = distal width; *total length of femur would probably be 1 or 2 mm longer if the crista trochanteris was not eroded

Element/Side	Catalogue no.	TL	PW	SW	DW
Holotype					
Humerus, L	WAM 15.9.6	113.7	26.6	11.5	22.4
Ulna, L	WAM 15.9.6	~116	13.7	8.7	14.9
Carpometacarpus, R	WAM 15.9.6	61.5	17.7	-	12.8
Phalanx dig. majoris I	WAM 15.9.6	22.7			
Phalanx dig. majoris II	WAM 15.9.6	21.9			
Femur, R	WAM 15.9.6	87.1*	21.4	10.8	20.0
Tibiotarsus, R	WAM 15.9.6	117.1	16.8	-	15.0
Tibiotarsus, L	WAM 15.9.6	-	-	8.2	-
Tarsometatarsus, R	WAM 15.9.6	70.3	18.3	8.3	18.4
Referred material					
Carpometacarpus, L	WAM 15.9.3	63.0	19.7	14.1	11.2

Etymology: The species name honours Storrs Olson, of the Smithsonian National Museum of Natural History, Washington DC, who has worked extensively on fossil avifaunas in various parts of the world, including Australia, and who was the first author to note that *Progura gallinacea* and '*Progura*' *naracoortensis* could represent species in different genera (Olson, 1985). We honour him here with a new species in the same genus as the species from Naracoorte.

Description and comparisons:

The holotype skeleton preserves most postcranial elements, but lacks a skull. The bones of the tarsometatarsus are completely fused, and the surface of all bones lacks a porous texture, thus the holotype individual is an adult. Anatomical detail has excellent preservation. This species is considerably smaller than the other extinct Plio-Pleistocene species described herein. Its wing bones are longer and more robust than those of extant species, but its leg bones, while also robust, are of comparable size to those of extant species of megapode.

Cranial material: Only the tip of the mandible survives (Figure 3.18 A, B), with around 15 mm of the left and right rami preserved. Although most of the mandible is missing, the wide angle (approx. 30°) between the rami shows that the tip of the bill in this species was wider than in extant *L. ocellata* or *A. lathami* (approx. 20° in both) and had a shorter symphyseal zone.

Humerus: The left humerus of the holotype (Figure 3.17 A–C) preserves the complete length of the bone, with the only damage being slight erosion of the crista deltopectoralis. It is somewhat longer than humeri of *L. ocellata*, which has the longest humerus among extant megapodes, but is also considerably more robust overall, having proportionally wider proximal and distal ends and a wider shaft. It is further distinguished from humeri of *L. ocellata* by having a shallower, more enclosed fossa pneumotricipitalis ventralis, a fossa pneumotricipitalis dorsalis that is barely marked (broad, shallow fossa present in *L. ocellata*), a more dorsally prominent tuberculum dorsale, a capital ridge that is less compressed, an impressio m. brachialis in the fossa brachialis that is wider for its length, a condylus dorsalis that is broader proximally (dorsal and ventral edges converge proximally in *L. ocellata*), and a straighter (i.e. less sigmoid) shaft in dorsal aspect. The humerus of the holotype skeleton is longer compared to the length of associated leg elements than in extant Australian megapodes (see Simpson log-ratio diagram). It is approx. 25% shorter than humeri of *Latagallina naracoortensis*, and is further distinguished from its larger congener by having: a tuberculum ventrale that does not project caudally beyond the caput in proximal aspect; an intumescentia humeri that is less inflated; a more pronounced tuberculum intermedium; a proportionally shorter crista bicipitalis; no protuberance on the cranial surface where the crista deltopectoralis merges with the shaft distally (*L. naracoortensis* has a low protuberance here); and a more acute processus flexorius in caudal aspect (blunter in *L. naracoortensis*). Measurements (mm): for TL, PW, SW and DW see Table 3.12.

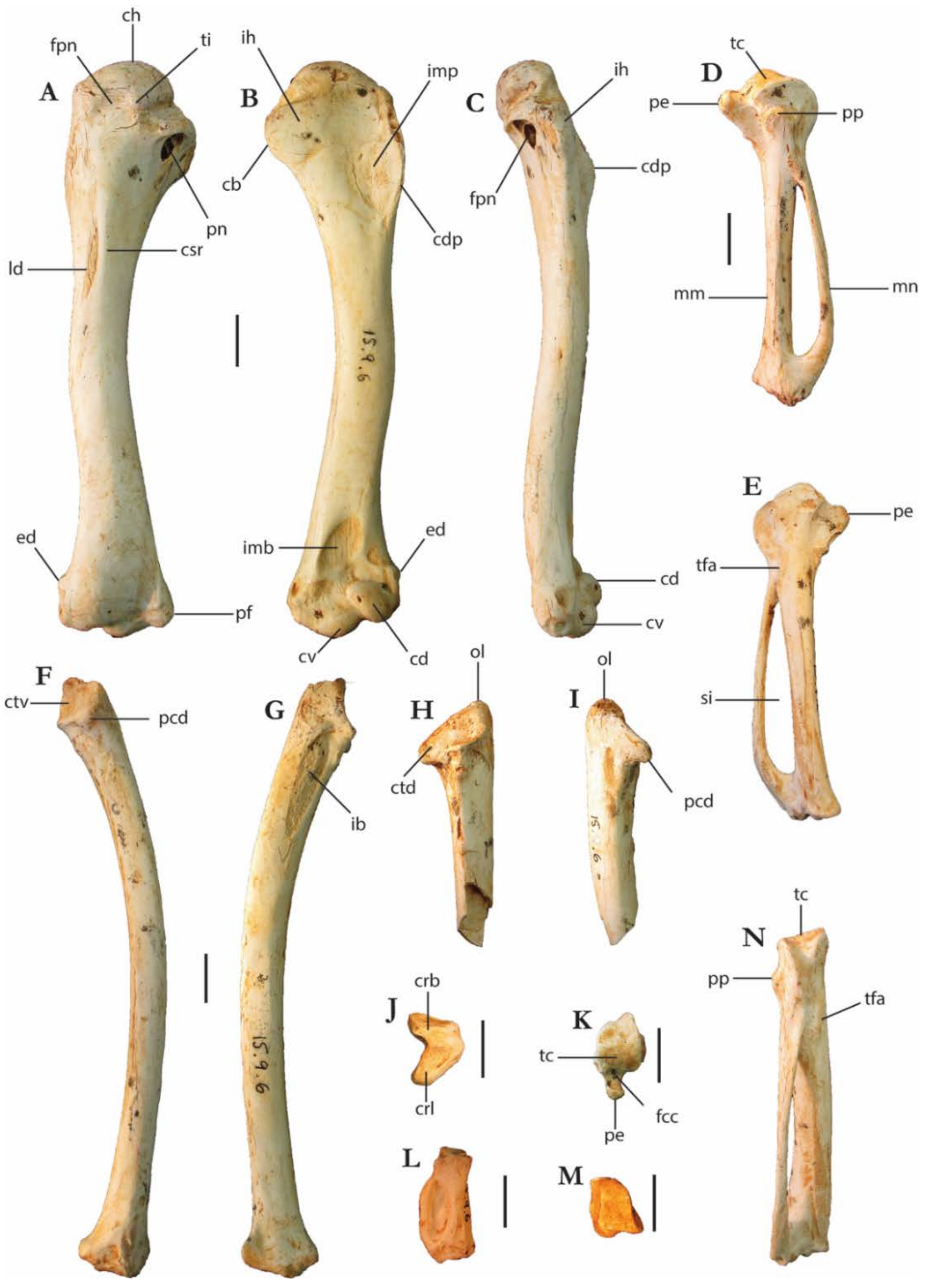


Figure 3.16: Wing bones of *Latagallina olsoni* sp. nov., WAM 15.9.6, holotype. Humerus in caudal (a), cranial (b) and ventral (c) aspects; carpometacarpus in ventral (d), dorsal (e) caudal (n) and proximal (k) aspects; ulna (left) in dorsal (f) and ventral (g) aspects and proximal ulna (right) in caudal (h) and dorsal (i) aspects; os carpi ulnare (j); phalanx dig. major (l); os carpi radialis (m). cb, crista bicipitalis; cd, condylus dorsalis; cdp, crista deltopectoralis; ch, caput humeri; crb, crus breve; crl, crus longum; csr, capital shaft ridge; ctd, cotyla dorsalis; ctv, cotyla ventralis; cv, condylus ventralis; ed, epicondylus dorsalis; fcc, fovea carpalis cranialis; fpn, fossa pneumotricipitalis dorsalis; ib, impressio brachialis; ih, intumescentia humeri; imb, impressio musculo brachialis; imp, impressio musuclo pectoralis; it, incisura tendineus; ld, attachment form. latissimus dorsalis; mm, os metacarpalemajus; mn, os metacarpaleminus; ol, olecranon; pcd, processus cotylaris dorsalis; fpn, foramen pneumaticum in fossa pneumotricipitalis ventralis; pe, processus extensorius; pf, processus flexorius; pn, foramen pneumaticum; pp, processus pisiformis; si, spatium intermetacarpale; tc, trochlea carpalis; tfa, tuberosity for flexor attachment; ti, tuberculum intermedium. Scale bars, 10 mm.

Ulna: The left ulna in the holotype (Figure 3.17 F, G) has an eroded olecranon, but this is preserved on the contralateral side (Figure 3.17 H, I). A total length of c. 116 mm is therefore estimated from the two bones of this individual. It is much smaller in all dimensions than the ulnae of *P. campestris* and *L. naracoortensis*. It is further distinguished from *P. campestris* by having a shallower impression for the m. brachialis, a shaft that is proportionally a little wider craniocaudally, a condylus dorsalis whose caudal margin protrudes ventrally much more sharply from the shaft (merges more smoothly with the margo caudalis of the shaft in *P. campestris*). Though only around 75% of the length of the ulnae of *L. naracoortensis* and considerably more slender, *L. olsoni* shares with its larger relative a shallow fossa brachialis, a proximodistally short tuberculum carpale whose profile is concave in ventral aspect (more elongate proximodistally and convex in *L. ocellata*), and a ventrally projecting condylus dorsalis. Measurements (mm): for TL, PW, SW and DW see Table 3.12.

Radius: The radius is missing the proximal third of its length, but the preserved portion shows that the facies articularis radiocarpalis slopes proximally towards the tip of the tuberculum aponeurosis ventralis rather than being at right angles to the axis as in *L. ocellata*.

Carpometacarpus: The holotype skeleton preserves a near complete right carpometacarpus, with slight erosion of the processus pisiformis and of the distal end (Figure 3.17 D, E, N). It is very similar to carpometacarpi of *L. ocellata*, but differs by its larger size (holotype carpometacarpus approx. 16.5% longer than those of *L. ocellata*) and by the tuberosity for the flexor attachment lying proximal to the spatium intermetacarpale (as in *L. naracoortensis*), not within it. The os metacarpale minus is broad and flattened proximally at the synostosis, and joins ventral to the ventral rim of the trochlea carpalis, which is aligned transversely to the shaft axis. The ventral rim of the trochlea carpalis is angled transversely at about a 30° angle to the long axis of the shaft in caudal aspect. Measurements (mm): see Table 3.12.

Pelvis: The entire length of the synsacrum is preserved (Figure 3.18 G–J), and is disarticulated from other portions of the pelvis. It comprises 15 synostosed vertebrae, as in *Leipoa ocellata*. Portions of the left and right ilia are preserved (right ilium pictured in Figure 3.18 K–M), but both lack most of the postacetabular section, the ischia and the pubes. The preserved portions reveal the pelvis to be much smaller than those of *L. naracoortensis.* The pelvis is pneumatic with foramina entering the corpus ischii both internally and externally (as in *Leipoa*), but there is also a pneumatic opening on the ala preacetabularis ilii anterior to the acetabulum on the internal surface (Figure 3.18 L), which is absent in *L. ocellata* and *M. reinwardt*, and is present but smaller and less distinct in *A. lathami* and *T. fuscirostris*. The synsacrum is deflected slightly ventrally in its caudal half (Figure 3.18 I), but less so than in *L. ocellata*, thus the ventral profile is flatter in lateral aspect. It is also longer and broader than in *L. ocellata* despite the two species having a similar leg length (sum of length of femur, tibiotarsus and tarsometatarsus in holotype of *L. olsoni* c. 274 mm, versus c. 277 mm in *L. ocellata* e.g. SAM B11483), thus *L. olsoni* was a larger-bodied and overall more robust species. The length of the synsacrum is almost identical to that of *T. fuscirostris*, but the synsacrum is deeper in *L. olsoni*, again suggesting larger overall body size. Measurements (mm): length of synsacrum, 98.5; depth measured at the level of the foramen acetabuli, 26.9.

Vertebrae: Most of the notarium is preserved in the holotype (Figure 3.18 C–F), with loss of the processus transversi on the left side. It includes 4 vertebrae, as in most megapodes (Worthy *et al.* 2016) although the centrum of the first is incompletely ankylosed. It is larger than the notarium of *L. ocellata*, as expected from its larger synsacrum and more robust leg bones. Measurements (mm): length, 49.2.

Femur: The holotypic femora (Figure 3.19 A–D) are of similar length to those of extant *T. fuscirostris*, *L. ocellata* and *M. maleo* and are slightly shorter than in *A. lathami*, but are considerably more robust than in any extant species. This is consistent with *L. olsoni* being more massive than extant megapodes (see Body-mass estimates). However, the femora are much smaller than those of extinct *P. campestris* and *L. naracoortensis.* As per the generic diagnosis, femora of *L. olsoni* have a large, round pneumatic foramen on the caudal surface adjacent to the facies articularis antitrochanterica (Figure 3.19D), which further distinguishes it from all extant Australian megapodes, and from *P. campestris*. The crista trochanteris is proportionally longer than in all species apart from *M. maleo* and *L. ocellata*, but in cranial aspect its medial edge is angled less medially, and so more proximally, than in those species. There is a well-marked fossa trochanteris. The proximo-cranial surface adjacent to the crista trochanteris has a deep, pneumatic fossa as in most other taxa (Figure 3.19 A, C), but distinct from its congener *L. naracoortensis* in which this fossa is absent or very weakly developed. The cranial margin of the fossa trochanteris comprises a thin crest (Figure 3.19C), as in *L. ocellata*, *M. reinwardt* and *L. naracoortensis*, and distinct from *T. fuscirostris*, *A. lathami* and *P. campestris*, where it is thicker. Distally, the fossa poplitea is enlarged proximomedially adjacent to the crista supracondylaris medialis, and is deeper than in all other species examined. The crista tibiofibularis projects proportionally further caudally relative to the trochlea fibularis than in all species examined apart from *L. naracoortensis*. Measurements (mm): for TL, PW, SW and DW, see Table 3.12; prox. depth, 17.9; minimum shaft circumference, 32.4.

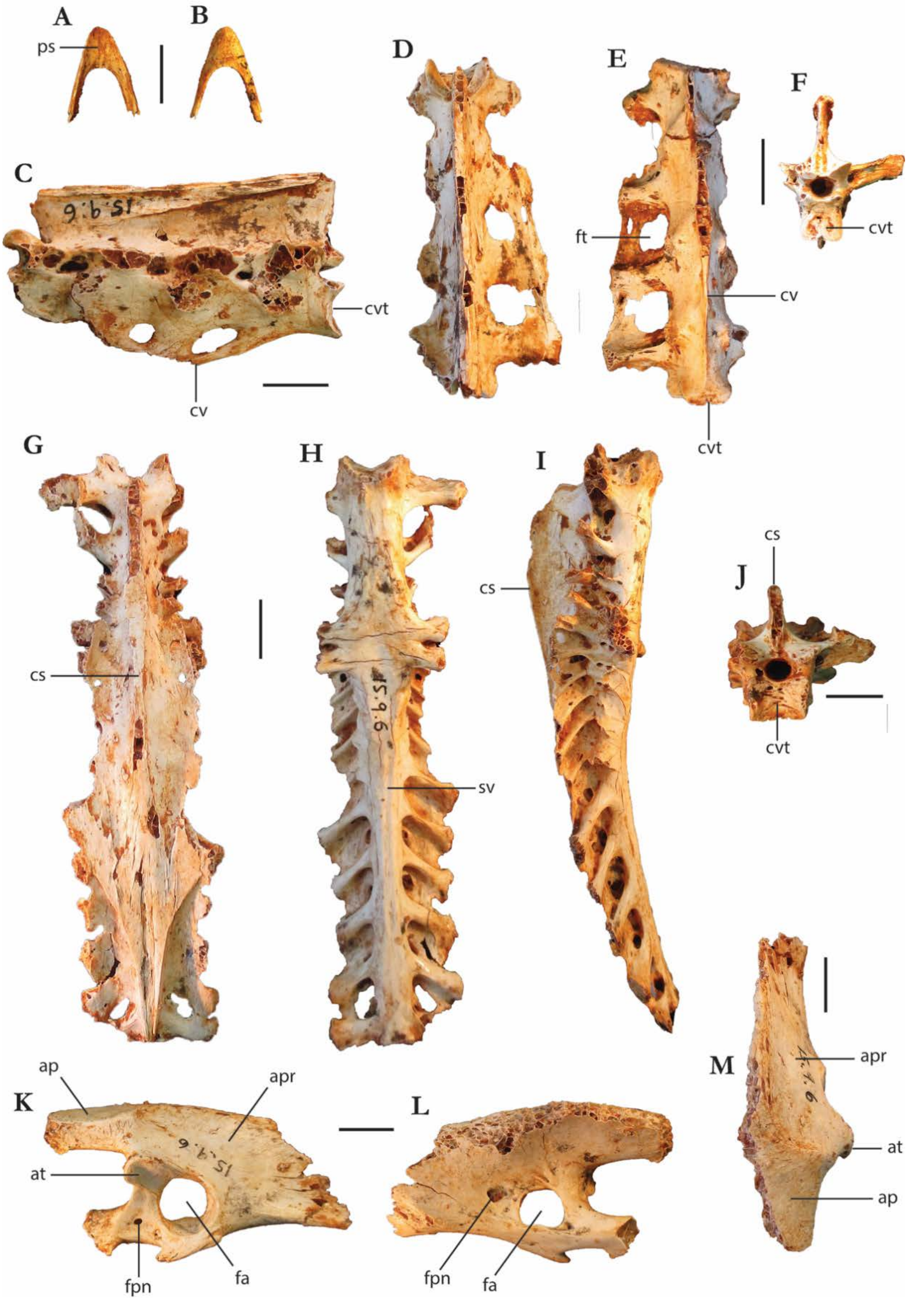


Figure 3.17: Cranial, axial and pelvic elements of *Latagallina olsoni* sp. nov., WAM 15.9.6, holotype. Mandible tip in dorsal (a) and ventral (b) aspects; notarium in right lateral (c), dorsal (d), ventral (e) and cranial (f) aspects; synsacrum in dorsal (g), ventral (h), lateral (i) and cranial (j) aspects; ilium in right lateral (k), medial (l) and dorsal (m) aspects. Abbreviations: ap, ala postacetabularis ilii; apr, ala preacetabularis ilii; at, antitrochanter; cs, crista spinosa synsacri; cv, crista ventralis; cvt, corpus vertebrae; fa, foramen acetabuli; fpn, foramen pneumaticum; ft, fenestra transversaria; ps, pars symphysialis; sv, sulcus ventralis synsacri. Scale bar, 10 mm.

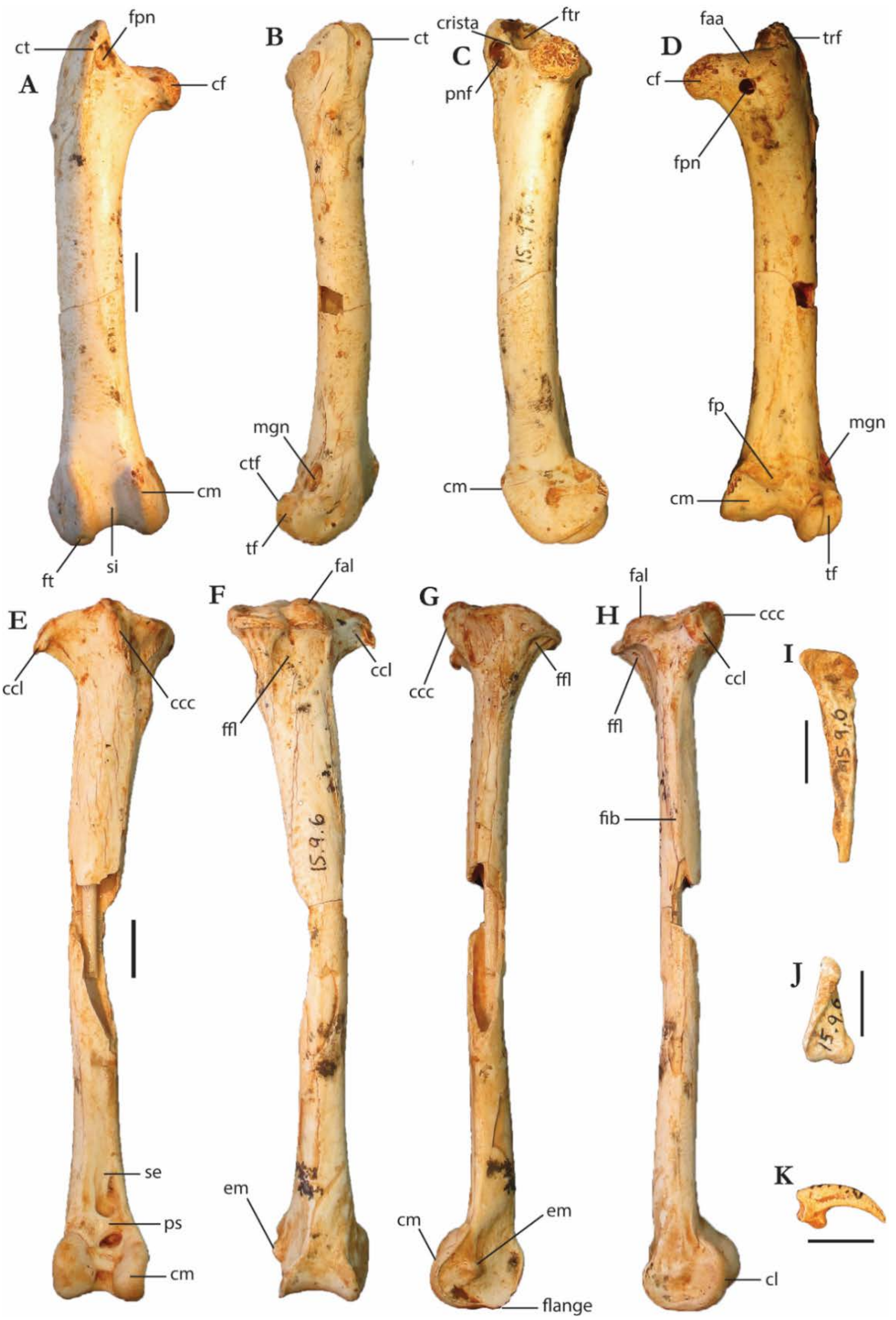


Figure 3.18: Leg and foot elements of *Latagallina olsoni* sp. nov., WAM 15.9.6, holotype. Femur in cranial (a), lateral (b), medial (c) and caudal (d) aspects; tibiotarsus in cranial (e), caudal (f), lateral (g) and medial (h) aspects; fibula (i); phalanx dig. I.1 (j); ungual (digit unknown) (k). Abbreviations: ccc, crista cnemialis cranialis; ccl, crista cnemialis lateralis; cf, caput femoris; cl, condylus lateralis; cm, condylus medialis; ct, crista trochanteris; ctf, crista tibiofibularis; em, epicondylus medialis; faa, facies articularis antitrochanterica; fal, facies articularis lateralis; ffl, fossa flexoria; fib, crista fibularis; fp, fossa poplitea; fpn, foramen pneumaticum; ft, fovea tendineus m. tibialis cranialis; ftr, fossa trochanteris; mgn, impression for m. gastrocnemialis lateralis; pnf, pneumatic fossa; ps, pons supratendineus; se, sulcus extensorius; si, sulcus intercondylaris; trf, trochanter femoris; tf, trochlea fibularis. Scale bar, 10 mm.

Tibiotarsus: The right tibiotarsus of the holotype (Figure 3.19 E–H) preserves the complete length and both proximal and distal ends, with some damage to the shaft. It approaches the length of tibiotarsi of *L. ocellata*, *M. reinwardt* and *T. fuscirostris*, but it is much more robust, consistent with *L. olsoni* being a stouter and more heavily built species overall (see Body-mass estimates). At the proximal end the crista cnemialis lateralis projects proportionally far laterally (Figure 3.19 E, F), as in *P. campestris*, *M. reinwardt*, *L. ocellata* and *L. naracoortensis*, and unlike *T. fuscirostris*, *A. lathami* and *M. maleo*, in which there is less lateral extent of the crista. The facies articularis medialis is of similar depth to that of *L. ocellata*, but the whole facies articularis is wider, giving it a larger proximal articular surface overall. The crista cnemialis cranialis does not protrude far cranially, is proximo-distally short, and is not deflected far laterally, as in *L. naracoortensis*, and unlike *Megapodius reinwardt*, *L. ocellata*, *A. lathami* , and *T. fuscirostris*, in which the crista is longer, projects further cranially, and is orientated more laterally. At the distal end, the epicondylus medialis is protuberant beyond the medial rim of the condylus medialis in cranial aspect, distinguishing it from *P. campestris*, *M. maleo* and *A. arfakianus*, in which the epicondylus is less protuberant. The proximodistal length of the pons supratendineus is much greater laterally than it is medially (Figure 3.19E), distinguishing it from *L. ocellata*, *A. lathami* and *P. campestris*. The crista fibularis is shorter than in *L. ocellata* and relatively shorter than in *L. naracoortensis*, and is more distinct than in *P. campestris*, in which the crista is very weakly expressed. The impressio lig. collateralis medialis is relatively more prominent than in *L. ocellata* (as in *L. naracoortensis* and *P. campestris*), and the distal width is wider for the depth of the condylus medialis (as in *L. naracoortensis*, unlike *P. campestris*). Measurements (mm): for TL, PW, SW and DW see Table 3.12; width of proximal articular surface measured without crista patellaris, 16.8; proximal depth including crista cnemialis cranialis, 19.7; depth of lateral trochlea, 14.0; depth of medial trochlea, 15.3; min. shaft circumference, 15.3.

Tarsometatarsus: As well as those mentioned in the diagnosis, the tarsometatarsus of this species (Figure 3.5 D, I, N, S and X; Appendix 1) has the following features. It is superficially similar to tarsometatarsi of *Leipoa ocellata*, being only slightly shorter, but it is considerably more robust, being broader overall and having a deeper shaft. The fossa infracotylaris dorsalis is much deeper and is surrounded laterally and proximally by thick ridges of bone (Figure 3.5D). On the plantar surface, the fossa parahypotarsalis medialis (Figure 3.5S) is proportionally wider than in *Leipoa*, as in the larger congener *L. naracoortensis*.

Pedal phalanges: Two phalanges are preserved (L I.1, Figure 3.19 J; and an ungual from an unknown digit, Figure 3.19 K). The I.1 is of similar size to that of *L. ocellata*. The ungual is shorter and more lateromedially compressed and deeply curved than those of any digit of *L. ocellata*, and the tuberculum extensorium is more prominent.

Remarks: This is one of two smaller species of megapode now known from southern Australia, the other being extant *Leipoa ocellata*. So far, *Latagallina olsoni* is known only from the Thylacoleo Caves, Nullarbor Plain. Its remains are rare within the Leaena's Breath Cave fossil assemblage, but bones of this species have been found in strata of both Early and Middle Pleistocene age. Remains of *L. ocellata* from the same cave deposit (see below) show that these smaller species overlapped geographically and temporally, which perhaps indicates niche partitioning. Although *Latagallina olsoni* shares many morphological similarities with its larger congener *L. naracoortensis*, morphological differences are noted throughout the skeleton (see diagnosis and description), and these species also appear to be allopatric. Thus there is no evidence that these taxa represent a single dimorphic species. That these species overlap temporally precludes the possibility that they are different-sized chronospecies.

Garrdimalga Shute, Prideaux & Worthy, gen. nov.

Zoobank ID: urn:lsid:zoobank.org:act:EF3C0068-4168-4A26-9504-99292BB2202E

Type species: *Garrdimalga mcnamarai* Shute, Prideaux & Worthy sp. nov. by monotypy.

Etymology: Garrdimalga, from which the name of the type locality derives, means 'emu waterhole' (garrdi = emu; malga = limestone/white waterhole) in the local Narungga (Nharangga) Aboriginal language of the Yorke Peninsula, South Australia (NAPA, 2006). Originally referring to a limestone depression where emus came to drink, the name, written as Curramulka, was later extended to the whole of the nearby township. Pronounced 'GA-ree-mal-ga', the '-rrd' of the first syllable is a soft 'r', made by the tongue slightly touching the roof of the mouth and forming a slight 'd' sound.

Diagnosis: A genus of megapode distinguished from all extant and extinct genera by unique morphology of the carpometacarpus and tibiotarsus as follows. **Carpometacarpus** 1) The processus extensorius (Figure 3.20 A, B, D) is short, dorso-ventrally narrow (less than half the width of the adjacent trochlea carpalis), and proximally directed. 2) The processus pisiformis is short, blunt, does not project over the extensor process, is placed relatively close to the proximal rim of the trochlea carpalis, and its caudal portion is highly protuberant (Figure 3.20 D). 3) The ventral rim of the trochlea carpalis has little caudal prominence relative to the os metacarpale minus in dorsal view (Figure 3.20 B), and in caudal aspect is more or less aligned with the long axis of the os metacarpale majus (Figure 3.20 C). 4) The distal margin of the articular facet of the trochlea carpalis is defined by the link between the caudal end of the dorsal rim and the distal end of the ventral rim, which traverses the caudal facies at a wide angle relative to the axis. **Tibiotarsus** 1) Just proximal of the epicondylus medialis and the condylus medialis there is a cranial protuberance of the shaft (Figure 3.20 H). 2) The pons supratendineus is placed proportionally further proximally than in all other taxa examined (i.e. there is no overlap of the pons and the condylus lateralis, and the pons is very constricted at its medial side, resulting in a very large distal opening of the canalis extensorius (Figure 3.20 E).

Differential diagnosis: Species in other genera differ from *Garrdimalga* as follows. **Carpometacarpus:** 1) In all other genera apart from *Progura*, the processus extensorius is orientated more cranially. *Progura* is distinguished by having a processus that is relatively wider dorsoventrally (more than half the width of the adjacent trochlea carpalis). 2) The processus pisiformis is relatively longer and more cranially protuberant in *Leipoa*, *Alectura* and *Megapodius*. In all extant and extinct genera examined, the caudal portion of the processus pisiformis is less protuberant relative to the cranial portion than in *Garrdimalga*, as seen in proximal aspect. 3) In all genera examined besides *Alectura*, the ventral rim of the trochlea carpalis projects further caudally relative to the os metacarpale minus, and in all genera the ventral rim of the trochlea is orientated about 30° to the long axis of the os metacarpale majus in caudal aspect, rather than aligned with the long axis as in *Garrdimalga*. 4) In all other genera examined, the distal margin of the articular facet of the trochlea carpalis traverses the caudal facies at a shallower angle. **Tibiotarsus:** In all other genera, 1) the shaft proximal of the epicondylus medialis and the condylus medialis is concave, and 2) the pons supratendineus overlaps proximodistally with the condylus lateralis. In all genera apart from *Progura,* the pons is placed relatively further distally on the shaft (proximal margin of the pons is a little further proximal in *Progura*). The only other genus in which the pons is constricted medially is *Latagallina*, but in this genus it is placed slightly further distally on the shaft, thus the distal opening of the canalis extensorius is relatively smaller. For visual comparison, the diagnostic material is depicted alongside the bones of other extinct species in the Supplementary Figure 3.1.

Garrdimalga mcnamarai Shute, Prideaux & Worthy, sp. nov.

(Figures 3.20 and 3.21)

Zoobank ID: urn:lsid:zoobank.org:act:336EEFFA-C49F-4186-9C8A-BF97A02CE94B

Holotype: SAM P42711 (R carpometacarpus, missing os metacarpale minus).

Paratypes: SAM P42709 (dL tibiotarsus); SAM P42710 (dR tibiotarsus).

Referred material: SAM P42712 (R radius); SAM P42713 (dR radius); SAM P42714 (pR radius); SAM P42715 (2 dL ulna); SAM P42716 (3 dR ulna); SAM P42717 (2L, 1R coracoid, omal fragments); SAM P42718 (R MII.1); SAM P42719 (1dL, 4dR tarsometatarsi); SAM P42720 (R, L fibulae); SAM P42721 (premaxilla); SAM P42722 (3 metatarsi); SAM P42723 (2R os carpi ulnare); SAM P42724 (pedal phalanges, 2L, 2R IV.1; 3L, 4R II.1; 1 I.1; 1R III.1; 4 other phalanges, 17 unguals undetermined to digit).

Type locality: Curramulka Quarry (site RF 95), Curramulka (34°42'11.8"S 137°42'14.3"E), Yorke Peninsula, South Australia (Figure 3.2).

Stratigraphy, age and fauna: All materials for this taxon was excavated from Curramulka Quarry (site RF 95) by J.A. McNamara between 1997 and 1999, and are considered Pleistocene in age (see Key Locations).

Diagnosis: As for the genus.

Etymology: The species name, *mcnamarai*, is in honour of Jim McNamara, formerly of the South Australian Museum, who collected the holotype and referred material of this species from Curramulka Quarry between 1997 and 1999.

Description and comparisons: The surface of all bones of this species are mottled with a fine dark grey mineral coating (Figures 3.20 and 3.21). With the exception of the holotype carpometacarpus and the pedal phalanges, most remains are fragmentary, with some apparently having been broken during collection. Key measurements are given in Table 3.13, with additional measurements given in the text where necessary. This is a species larger than any extant species of megapode and extinct *Latagallina olsoni*, and approaching the size of *Progura campestris*. It has a carpometacarpus that is of similar length to that of *Progura campestris*, but is proportionally larger compared to the leg elements.

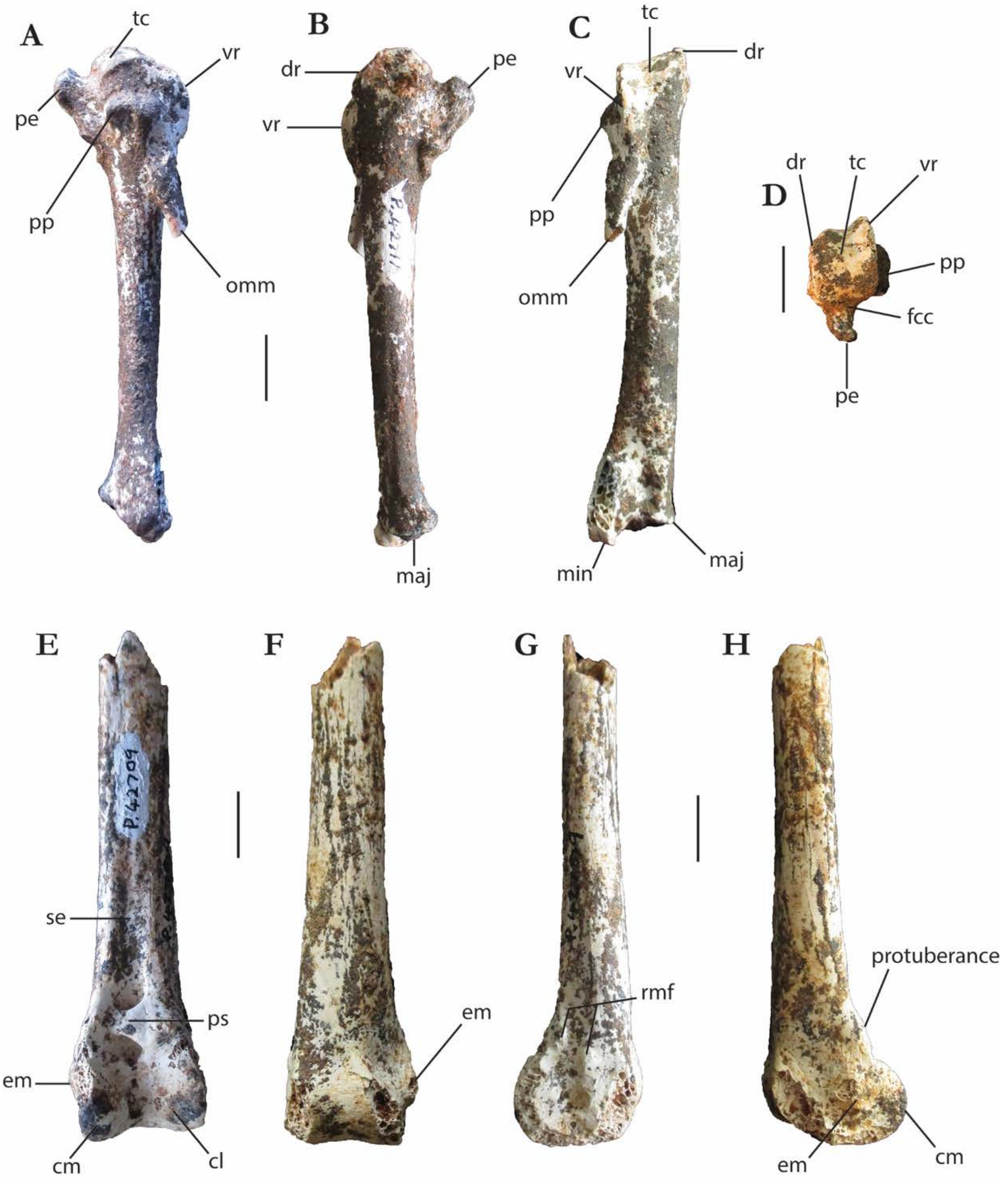


Figure 3.19: Type specimens of *Garrdimalga mcnamarai* gen. et sp. nov. Carpometacarpus, SAM P42711, holotype, in ventral (a), dorsal (b), caudal (c) and proximal (d) aspects; tibiotarsus, SAM P42709, paratype, in cranial (e), caudal (f), lateral (g) and medial (h) aspects. Scale bars, 10 mm. Abbreviations: cl, condylus lateralis; cm, condylus medialis; dr, dorsal rim of trochlea carpalis; em, epicondylusmedialis; fcc, fovea carpalis cranialis; maj, os metacarpale majus; min, facies articularis digitalis minor; omm, os metacarpale minus; pe, processus extensorius; pp, processus pisiformis; ps, pons supratendineus; rmf, retinaculi m. fibularis; tc, trochlea carpalis; se, sulcus extensorius; vr, ventral rim of trochlea carpalis.

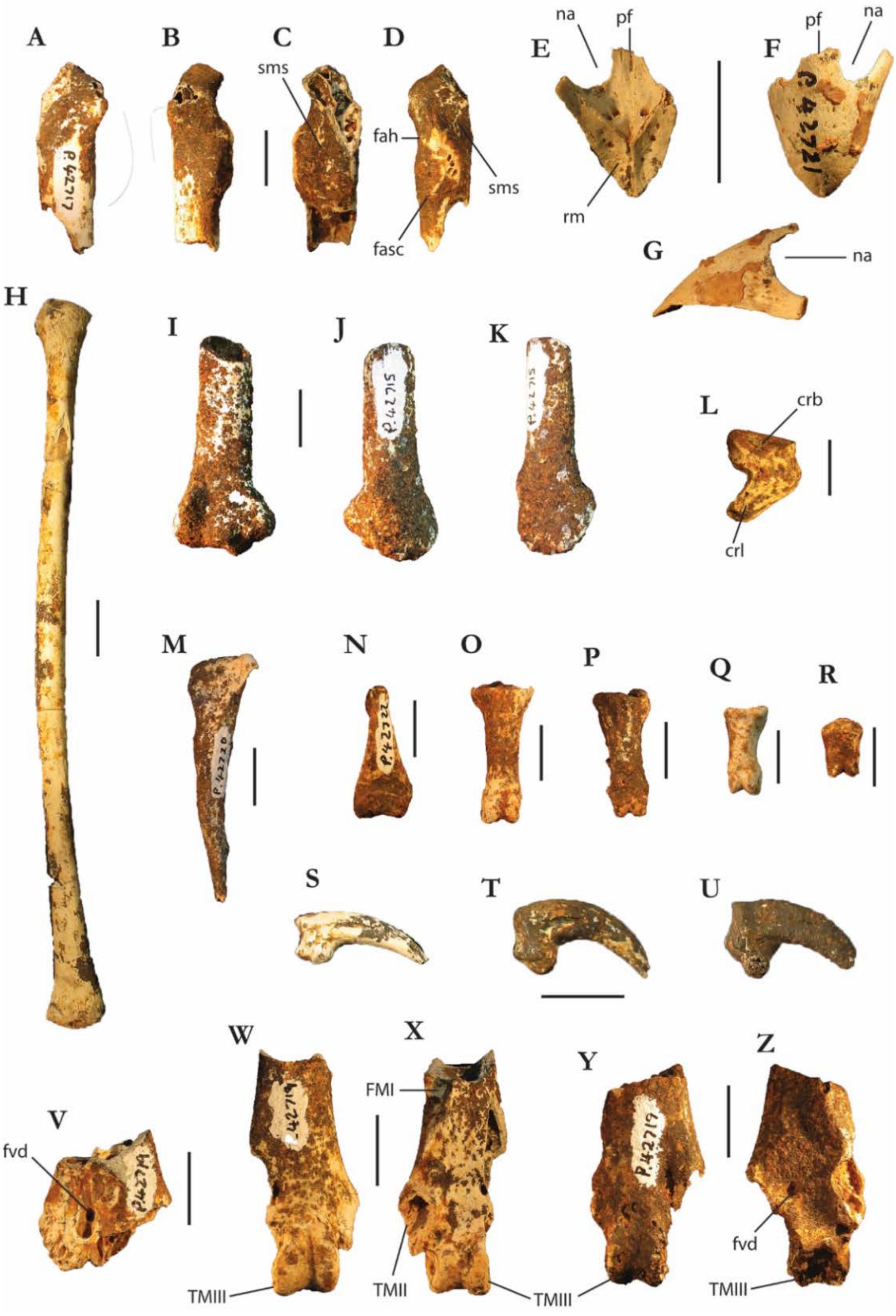


Figure 3.20: Referred material of *G. mcnamarai* sp. nov. Coracoid, SAM P42717, left omal fragment, in ventral (a), dorsal (b), medial (c) and lateral (d) aspects; premaxilla, SAM P42721, in ventral (e), dorsal (f) and lateral (g) aspects; radius, SAM P42712, (h); ulna, SAM P42715, in dorsal (i), caudal (j) and ventral (k) aspects; os carpi ulnaris, SAM P42723 (l); fibula, SAM P42720 (m); metatarsal, SAM P42722 (n); pedal phalanges (o–r) and unguals (s–u) (SAM P42724); tarsometatarsi, SAM P42719, right distal fragments (v–x), and left distal fragment (y,z). Scale bars, 10 mm. Abbreviations: crb, crus breve; crl, crus longum; fah, facies articularis humeralis; fasc, facies articularis scapularis; FMI, fossa metatarsi I; fvd, foramen vascularis distalis; maj, os metacarpale majus; min, facies articularis digitalis minor; na, naris; pf, processus frontalis; rm, rostrum maxillare; sms, sulcus m. supracoracoidei; TMII, trochlea metatarsi II; TMIII, trochlea metatarsi III.

Premaxilla: The anterior portion of a premaxilla (Figure 3.7 G–I; Figure 3.21 E–G), shows that the bill of this species was wider and deeper than in *L. ocellata* or *M. reinwardt*, and had a tip that was proportionally short, as in *L. naracoortensis*, rather than elongate as in *P. campestris*. The symphyseal zone is relatively short compared to *L. ocellata*, *P. campestris* and *L. naracoortensis* (Figure 3.7H; Figure 3.21E). For a shape comparison with selected taxa, see Figure 3.7. Measurements (mm): depth, measured at the level of the anterior edge of the nares, 7.6; width at the level of anterior edge of nares, 9.7; length of ventral symphyseal zone, 5.7.

Carpometacarpus: In addition to the diagnostic features noted for the genus (see above), the carpometacarpus of this species (Figure 3.20 A–D, and Supp. Figure 3.1) has the following characteristics. The proximal end is narrower relative to length than in the other large extinct species *P. campestris* and *L. naracoortensis*, and is proportionally more similar to carpometacarpi of *Leipoa ocellata* and *Alectura lathami* despite being much larger than both. As little of the os metacarpale minus is preserved, the extent of divergence from the os metacarpale major cannot be assessed relative to other species, but its proximal end differs from species of *Latagallina* and *Progura campestris* by being rotated ventrally, such that its broadest surface is orientated caudo-ventrally, rather than caudally. The scar for the flexor attachment is a single tuberculum, as in species of *Latagallina*, *L. ocellata* and *A. lathami*, and distinct from both species of *Progura* where the tuberculum has two distinct parts with the distal one placed partially or entirely within the spatium intermetacarpale. In *G. mcnamarai* this tuberculum is located immediately proximal to the spatium intermetacarpale, as in species of *Latagallina*, rather than overlapping the spatium intermetacarpale and the synostosis of the metacarpals as in *L. ocellata* and *A. lathami*. There is a discrete fovea carpalis caudalis as in *L. ocellata* and species of *Progura* (absent in species of *Latagallina*).

Os carpi ulnare: These are of similar size to those of *Progura campestris*, but in the mature specimen of *G. mcnamarai* (Figure 3.21 L) the crus breve and crus longum are a little broader than in that species.

Radius: The complete specimen (SAM P42712; Figure 3.21 H), which is from a slightly immature individual, is somewhat shorter and narrower than radii of *P. campestris* and *L. naracoortensis*, but is wider and presumably longer than that of *L. olsoni*. Measurements: for TL, PW, SW and DW see Table 3.13.

Ulna: Five fragments of distal ulnae are preserved, registered under two catalogue numbers. Total length is unknown, but based on length of a complete radius (above), a complete ulna would be approximately 140 mm, thus longer than in any extant species of megapode and the extinct *L. olsoni*, but slightly shorter than that of *P. campestris* (148.2 mm), and below the size range of *L. naracoortensis* (144.8–173.9 mm). The best preserved distal fragment (SAM P42715; Figure 3.21 I–K) is unusual in having a robust ridge extending dorsally from the tuberculum carpale, which defines a marked groove immediately proximal to it. This feature has not been seen in other megapodes. The distal fragments are a little wider than the distal ulna of *L. olsoni*, approach the size of *P. campestris*, and are much smaller than those of *L. naracoortensis.*

Coracoid: The omal fragments of the coracoid (e.g. Figure 3.21 A–D) are clearly larger than those of extant megapodes, but are smaller than those of *P. campestris* and *L. naracoortensis*, and seem small relative to other skeletal elements of this species. Given their fragmentary nature and state of preservation, it is not possible to tell whether the coracoid fragments belong to adults or juveniles, as observations of nearly 60 fossil coracoid specimens belonging to *L. naracoortensis* show that the omal end of the coracoid reaches osteological maturity (i.e. distinct morphology, absence of surface porosity) more quickly than does the sternal end. The facies articularis humeralis is slightly concave (Figure 3.21 D), a little less so than in *Progura campestris* but more so than in *L. naracoortensis.* Maximum dorsoventral depth measured at the facies articularis scapularis is 10.5 mm (cf. 12.2 mm in *Progura campestris* holotype, and 13.1 mm in a specimen of *L. naracoortensis* (SAM P51369).

Tibiotarsus: The two distal tibiotarsi (left pictured in Figure 3.20 E–H, and Supp. Figure 3.1), left and right but apparently not a pair, are somewhat eroded but preserve the distal anatomy quite well. They are much larger than the tibiotarsi of extant megapodes and of *L. olsoni*, but smaller than those of *L. naracoortensis*. In addition to the diagnostic features noted for the genus (see above), the tibiotarsus has features as follows. The distal shaft has similar dimensions to that of *P. campestris*, but terminates in smaller condyles, which indicates that the corresponding proximal articular surface of the tarsometatarsus of this species would also be narrower and shallower than in *P. campestris*. Lateral condylar depth (16.3 mm) approaches parity with distal width (17.5 mm). The epicondylus medialis is exceptionally large and protuberant (Figure 3.20 E, F, H), and is visible beyond the rim of the medial rim of the condylus medialis in cranial aspect, distinguishing it from *P. campestris*, *M. maleo* and *A. arfakianus*. The retinaculi m. fibularis form two parallel, longitudinal ridges that are strongly elevated on the lateral shaft facies immediately caudal to the condylus lateralis, and enclose a very deep sulcus, which opens proximally into a concave shaft surface. The retinaculi are less prominent in *L. ocellata*, *T. fuscirostris* and *P. campestris*, and while they are prominent in *L. naracoortensis*, *L. olsoni*, *A. lathami* and *M. reinwardt*, in those species the sulcus is somewhat shallower, and the shaft proximal of the sulcus is flat to convex. The lateral facies proximal to the retinaculi forms a plane that is angled more mediocranially/caudolaterally than in other taxa, exposing more of this facies in cranial aspect (Figure 3.20 E). The sulcus extensorius is proportionally longer and deeper than in all species examined apart from *Alectura lathami*. Measurements (mm): for SW and DW, see Table 3.13; depth of lateral condyle, (SAM P42709) 16.1, (SAM P42710) 17.1; depth of medial condyle (SAM P42709) 18.4.

Tarsometatarsus: The available tarsometatarsi of this species are poorly preserved (Figure 3.21 V–Z). One distal fragment (not pictured) is apparently a juvenile, and possibly also shows pathological modification to the shaft. The other bones are sufficiently well preserved to show that the plantar opening of the foramen vasculare distale (Figure 3.21 Z) is small, and on the dorsal surface the proximal end of the canalis interosseus distalis is visible in the same fossa as the foramen vasculare distale (Figure 3.21 V). Trochlea metatarsi III is of similar width and depth to those of *P. campestris*, but the distal shaft is more slender in *G. mcnamarai*, with trochleae II and IV not flaring so widely, thus the distal width of the tarsometatarsus would probably have been narrower if complete. This, combined with the smaller inferred size of the proximal end of the tarsometatarsus of *G. mcnamarai* compared to *P. campestris* (see description of tibiotarsus for *G. mcnamarai*), implies that *G. mcnamarai* had overall a smaller tarsometatarsus than *P. campestris.* However, shaft length is unknown, and so it is impossible to know whether the tarsometatarsus was proportionally robust or gracile compared to other taxa.

Pedal phalanges: Phalanges of this species are robust and are of similar size to those of *P. campestris* and *L. naracoortensis*, but since *G. mcnamarai* has somewhat smaller tarsometatarsi and tibiotarsi than those species, its feet were presumably proportionally larger. Phalanx III.1 is of similar length but a little narrower than that of *L. naracoortensis*. Like that species, it has a nearly symmetrical proximal articular facet (asymmetrical in *P. campestris*), and while the proximo-plantar surface is not as deeply excavated as in *L. naracoortensis*, it is more excavated than in *P. campestris*. Phalanx II.1 is slightly shorter than in *P. campestris*, with a proximal articular facet of similar overall size, although it is deeper than wide, not wider than deep as in *P. campestris*. Phalanx IV.1 is a little shorter than that of *P. campestris*. The unguals are short, deep, lateromedially compressed, deeply curved, and have very large extensor tubercles (Figure 3.21 S–U).

Table 3.13: Long bone measurements (mm) of *Garrdimalga mcnamarai* holotype and referred material; TL = total length; PW = proximal width; SW = midshaft width; DW = distal width

Element/Side	Catalogue no.	TL	PW	SW	DW
Holotype					
Carpometacarpus, R	SAM P42711	74.7	20.3	-	13.9
Referred material					
Radius, R	SAM P42712	130.6	9.2	5.3	10.9
Ulna, dL	SAM P42715	-	-	-	17.7
Ulna, dR	SAM P42716	-	-	-	17.3
Tibiotarsus, dL	SAM P42709	-	-	10.0	18.0
Tibiotarsus, dR	SAM P42710	-	-	-	17.3

Remarks: So far the remains of this species are insufficient to include it in a meaningful phylogenetic analysis, and its relationship to other genera of megapodes is unknown. Several features, including the single scar for the flexor attachment entirely proximal to the spatium intermetacarpale on the carpometacarpus, the broad trochlea carpalis, and the short, wide mandible, may suggest an affinity with species of *Latagallina*. However, the carpometacarpus shares other features in common with other taxa, including minimal caudal projection of the ventral rim of the trochlea carpalis as in *Alectura lathami*, and a distinct fovea carpalis caudalis as in species of *Progura*.

Leipoa ocellata Gould, 1840

Referred material: ***Leaena's Breath Cave, Nullarbor Plain*** – WAM 15.9.2, R humerus; ***Main Fossil Chamber, Victoria Fossil Cave, Naracoorte*** – SAM P25852, R tarsometatarsus, missing most of the hypotarsus and cotylae; SAM P41531, L humerus; SAM P41532, R tibiotarsus; SAM P42077, dR femur; SAM P42708, dL femur. ***Henschke's Fossil Cave, Naracoorte*** – SAM P41704, pL femur; SAM P41705, pL tarsometatarsus; SAM P41706, pL/dR tibiotarsus; SAM P417047, R tibiotarsus.

The above specimens, all of which belong to mature individuals, are referred to *Leipoa ocellata* because they do not differ appreciably in size or morphology from modern specimens of that species.

Stratigraphy, age and fauna: The humerus (WAM 15.9.2) was excavated from Leaena's Breath Cave, Nullarbor Plain, at a depth of 105–110 cm beneath the sediment floor, in stratigraphic Unit 3, Quadrat 2, Pit B (2.58–0.78 Ma, Prideaux *et al.* 2007; Early Pleistocene). The specimens from Victoria Fossil Cave, Naracoorte, all derive from stratigraphic layers that are of Middle Pleistocene age (>212 kyr, Prideaux *et al.* 2007). Specimens from Henschke's Fossil Cave are of Pleistocene age, probably Middle or Late Pleistocene (Pledge 1990) (see Table 3.14). The specimens from the Naracoorte Caves occur within the same deposit as fossils of *Latagallina naracoortensis*. Measurements: for TL, PW, SW and DW see Table 3.14. Measurements of modern specimens of *L. ocellata* are given in Table 3.15 for comparison.

Table 3.14: Measurements (mm) of Pleistocene *Leipoa ocellata* fossils from Leaena's Breath Cave, Nullarbor Plain (LBC) and Victoria Fossil Cave (VFC) and Henschke's Fossil Cave (HFC), Naracoorte

Element/Side	Catalogue no.	Provenance	Age	TL	PW	SW	DW
Humerus, R	WAM 15.9.2	LBC	>780,000 yr	97.9	22.1	9.1	17.9
Humerus, L	SAM P41531	VFC	>212,000 yr	106.1	24.8	9.4	21.1
Femur, pL	SAM P41704	HFC	(?)<126,000	-	-	-	-
Femur, dR	SAM P42077	VFC	>212,000 yr	-	-	-	19.4
Femur, dL	SAM P42708	Fossil Chamber, VFC	>212,000 yr	-	-	-	20.6
Tibiotarsus, R	SAM P41532	VFC	>212,000 yr	129.6	17.5	8.7	14.3
Tibiotarsus, pL/dR	SAM P41706	HFC	(?)<126,000	-	-	8.2	14.7
Tibiotarsus, R	SAM P41707	HFC	(?)<126,000	120.2	16.2	8.2	14.7
Tarsometatarsus, R	SAM P25852	VFC	>212,000 yr	75.8	-	8.1	17.4
Tarsometatarsus, pL	SAM P41705	HFC	(?)<126,000	16.7	-	-	-

Table 3.15: Summary data (mm) for modern skeletons of *Leipoa ocellata*; TL = total length; PW = proximal width; SW = shaft width; DW = distal width; data from Worthy *et al.* (2016, Supp. Info.)

Element		TL	PW	SW	DW
Humerus (n=2)	Range	100.2–100.5	22.3–23.1	8.5–8.8	19.2–19.5
Femur (n=12)	Mean (SD)	85.2 (2.8)	20.2 (0.9)	8.6 (0.6)	18.2 (0.3)
	Range	81.3–90.5	18.9–21.5	7.9–10.0	18.2–19.3
Tibiotarsus (n=13)	Mean (SD)	122.0 (5.9)	16.4 (0.3)	7.7 (0.5)	13.8 (0.4)
	Range	112.8–134.1	15.6–16.8	6.5–8.6	13.1–14.6
Tarsometatarsus (n=13)	Mean (SD)	73.5 (3.1)	15.3 (0.5)	8.9 (0.4)	16.7 (0.3)
	Range	67.8–79.2	14.3–15.9	8.1–9.8	15.9–17.1

Remarks:

It has previously been stated that modern-sized *L. ocellata* fossils do not occur in the same deposits as large extinct megapodes (Dekker 2007), and it has been proposed that the modern Malleefowl is a phyletic dwarf that evolved from the much larger *Progura gallinacea* during the Late Pleistocene (Boles, 2008). However, WAM 15.9.2, the humerus of *L. ocellata* from the Nullarbor Plain, demonstrates that modern-sized Malleefowl were already present in Australia during the Early Pleistocene, in sediments that pre-date the Late Pleistocene by at least half a million years. Furthermore, the humerus comes from the same stratigraphic unit in Leaena's Breath Cave as the holotype of *Progura campestris* and a referred carpometacarpus of *Latagallina olsoni* (see species accounts), thus the species was roughly coeval with two other taxa, one somewhat larger, and one very much so. At Naracoorte, modern-sized *L. ocellata* fossils (Table 3.14) occur in Middle and probable Late Pleistocene sediments, along with remains of the very much larger extinct species *Latagallina* (formerly *Progura*) *naracoortensis.* The phylogenetic relationship between *L. ocellata* and the extinct Plio-Pleistocene taxa is uncertain (see Phylogenetic analysis), but there is no evidence to support the proposal that *Leipoa ocellata* is a dwarf of any of the extinct taxa we have described herein.

3.4.2 Body-mass Estimates

In all species where both the femoral and tibiotarsal equations (Campbell and Marcus 1992) could be used, except for *Megapodius reinwardt*, estimates derived from the femur were greater than those from the tibiotarsus (Table 3.16). The magnitude of difference between femoral and tibiotarsal estimates varied greatly among species, being equal in *M. reinwardt* but differing by nearly a third in *Latagallina* *olsoni*, for example. Femoral equations also produced high estimates for three extant species (2.3 kg for *Talegalla fuscirostris* versus 1.4–1.6 kg recorded for modern specimens; mean 2.9 kg for *Alectura lathami* versus 2.2–2.5 kg for modern; and 1 kg for *Megapodius eremita* versus 0.64–0.71 kg for modern (Dunning 2008). This is consistent with our findings in other taxa (Handley *et al.* 2016; Shute, Prideaux, and Worthy 2016), where we identified an apparent tendency for femoral equations to overestimate body mass.

Estimates from the tibiotarsus for extinct species are probably more realistic because for most extant species they more closely approximate known body masses recorded in Dunning (2008). Thus the holotype of *P. campestris* is estimated to have weighed 6.2 kg, mature individuals of *L. naracoortensis* an average of 5.2 kg, *Garrdimalga mcnamarai* 5.2 kg (based on paratype tibiotarsus), and the holotype of *L. olsoni* 2.9 kg (Table 3.16). Estimated mass for *G. mcnamarai* is approximate, because the smallest measurable circumference was immediately distal of the broken midshaft, and it is not known if the shaft tapered proximal of this point. Given that neither a tibiotarsus nor a femur of *P. gallinacea* is known, the only estimate for this species was based on the minimum shaft width of the most complete tarsometatarsus (Field et al. 2013) (QM F1143), which produced an estimated mass of 7.7 kg for this species. These calculations show that all four extinct species for which we could estimate mass were heavier than extant megapodes, but even the largest species *P. gallinacea* was approximately 3.5–4.5 times lighter than the extinct flightless stem-galliform *Sylviornis neocaledoniae* (Worthy *et al.* 2016).

Table 3.16: Body-mass calculations for extinct and extant megapodes; † = extinct species; estimates based on femur circumference use the 'heavy-bodied birds' equation of Campbell & Marcus[42] as follows: $\log_{10}M = 2.293 \times \log_{10}LCf + 0.110$, where M=mass (g), and LCf = least shaft circumference of the femur (mm); estimates based on minimum circumference of the tibiotarsus use the 'heavy-bodied birds' equation of Campbell & Marcus (1992) as follows: $\log_{10}M = 2.416 \times \log_{10}LCt + 0.140$, where M = mass (g), and LCt = least shaft circumference of the tibiotarsus (mm); estimates based on the minimum width of the tarsometatarsus use an equation for the Galliformes derived from Figure 2 and Tables S2 and S4 of Field et al.[43] as follows: $\log_{10}(BM) = 2.069 (\log_{10}TW) + 3.709$, where BM = body mass (g), and TW = minimum shaft width of the tarsometatarsus (mm); all calculations expressed in kg

Species (No. specimens)		**Estimate from femur (kg)**	**Estimate from tibiotarsus (kg)**	**Estimate from tarso-metatarsus (kg)**
***Progura gallinacea*†** (n=1)		-	-	**7.7**
***Progura campestris*†**		**7.5**	**6.2**	**4.8–6.0**
(Femur & tibiotarsus, n=1; Tarsometatarsi, n=2)				
***Latagallina naracoortensis*†**	Mean (S.D.)	**5.8 (0.91)**	**5.2 (0.91)**	**6.1 (0.8)**
(Femora, n=7; Tibiotarsi, n=13; Tarsometatarsi, n=23)	Minimum	5.1	3.7	5.0
	Maximum	7.4	6.5	7.7
***Latagallina olsoni*†** (n=1)		**3.8**	**2.9**	**3.6**
***Garrdimalga mcnamarai*†** (n=1)		**-**	**5.2**	**-**
Talegalla fuscirostris (n=1)		**2.3**	**1.9**	**1.9**
Leipoa ocellata	Mean (S.D)	-	-	**2.9 (0.3)**
(Femora & tibiotarsi, n=2; Tarsometatarsi, n=13)	Minimum	2.0	1.8	2.2
	Maximum	2.3	2.2	3.5
Alectura lathami (Femora & tibiotarsi, n=5; Tarsometatarsi, n=12)	Mean (S.D.)	**2.9 (0.33)**	**2.4 (0.18)**	**3.1 (0.7)**
	Minimum	2.4	2.1	2.2
	Maximum	3.3	2.7	4.6
Aepypodius arfakianus (n=1)		-	**2.3**	**1.8**
Megapodius eremita (n=1)		**1.0**	**0.9**	**1.5**
Megapodius reinwardt (n=1)		**1.9**	**1.9**	**2.1**

3.4.3 Simpson Log-ratio Diagram

The Simpson log-ratio diagram (Figure 3.22) compares the proportions of the post-cranial skeleton for the three most complete extinct species (*Latagallina naracoortensis*, *L. olsoni* and *Progura campestris*) and the four extant species of megapode for which we had access to complete reference skeletons (*Leipoa ocellata*, *Megapodius reinwardt*, *Alectura lathami* and *Talegalla fuscirostris*). Measurements of *P. campestris* and *L. olsoni* are from the associated holotype skeletons (Tables 3.2 and 3.12), whereas measurements for *L. naracoortensis* are based on mean measurements of skeletal remains from the Naracoorte Caves (Tables 3.4–3.11). All measurements are standardised as a proportion of the reference species, the domestic chicken *Gallus gallus*, which is represented by a straight zero line on the horizontal axis.

Compared to *G. gallus*, the megapodes have: ulnae that are longer relative to their width; coracoids that have stouter shafts relative to length, and with the exceptions of *L. ocellata* and *T. fuscirostris*, a proportionally much wider omal end; carpometacarpi that have narrow proximal ends compared to distal ends; femora that are notably short relative to the size of the pectoral elements, and with a stout shaft in all species except *L. ocellata*; and tarsometatarsi that have exceptionally wide distal ends.

The three included extinct species (*L. naracoortensis, L. olsoni* and *P. campestris*) share body proportions that are more similar to one another than to extant species, with similarities between the two species of *Latagallina* (indicated by strong parallelism of their lines) being particularly striking. *Leipoa ocellata* has proportions seemingly dissimilar to all comparator species (e.g. long but gracile humerus, narrow femoral shaft, relatively robust coracoid). The diagram reveals proportional differences within the hindlimb between the two largest included species, *L. naracoortensis* and *P. campestris*, with *P. campestris* having a femur with a wider midshaft relative to its other dimensions, a narrower proximal tibiotarsus, and a longer tarsometatarsus relative to width. A further insight is the difference in relative proportions of the pectoral girdle versus the hindlimb in these two large species. The size of their leg elements overlaps (Figure 3.22), but the pectoral girdle of *Progura campestris* is somewhat smaller throughout, with the humerus, ulna and coracoid being shorter and narrower than in *L. naracoortensis*.

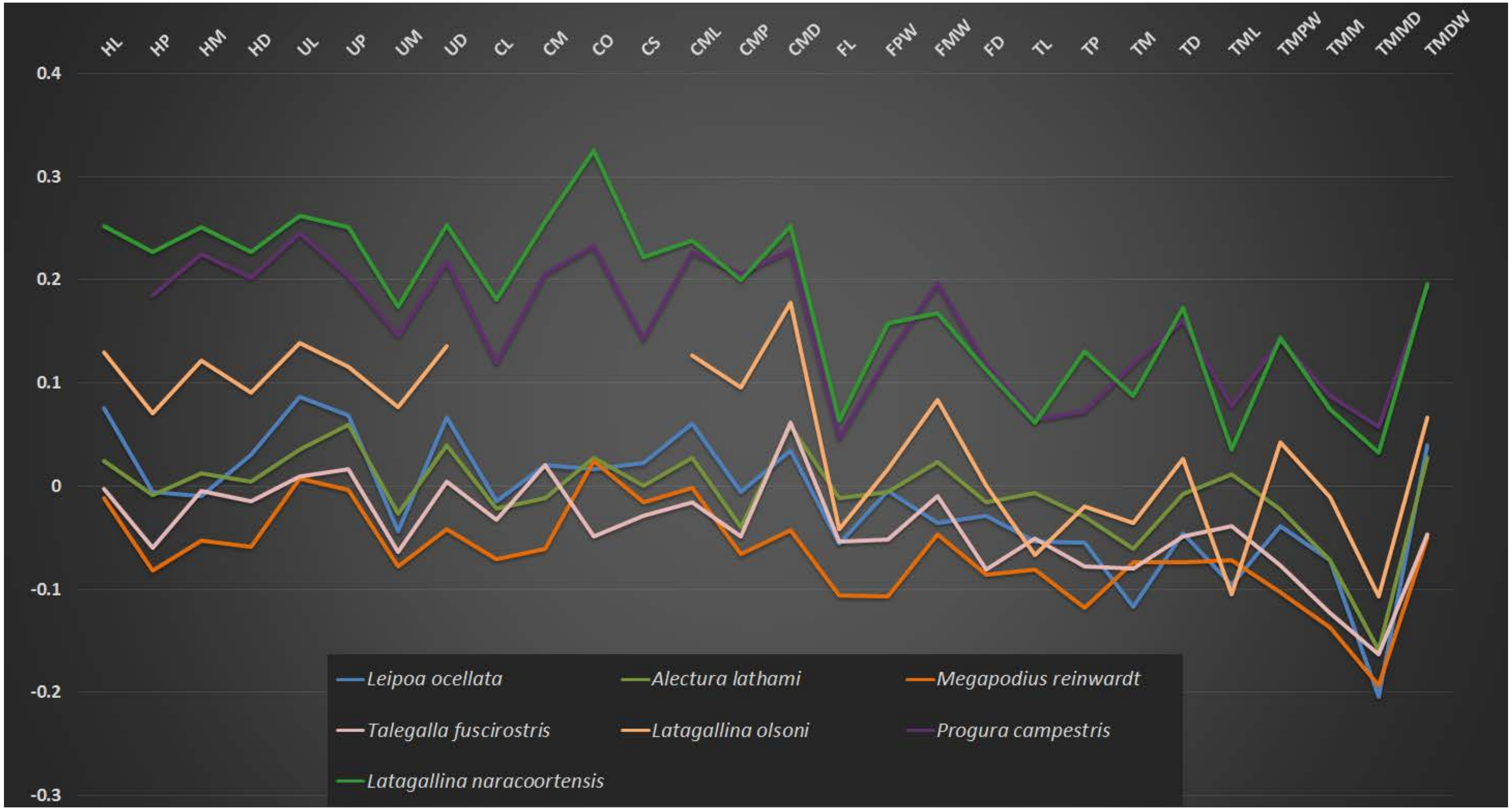


Figure 3.21: Log-ratio diagram showing proportions of the post-cranial skeleton in extinct and extant megapodes; all measurements in millimetres, log-transformed and expressed as a proportion of comparator galliform species, *Gallus gallus* (domestic chicken). HL, humerus length; HP, humerus proximal width; HM, humerus midshaft width; HD, humerus distal width; UL, ulna length; UP, ulna proximal width; UM, ulna midshaft width; UD, ulna distal width; CL, coracoid length; CM, coracoid midshaft width; CO, coracoid omal width; CS, coracoid sternal width; CML, carpometacarpus length; CMP, carpometacarpus proximal width; CMD, carpometacarpus distal width; FL, femur length; FPW, femur proximal width; FMW, femur midshaft width; FD, femur distal width; TL, tibiotarsus length; TP, tibiotarsus proximal width; TM, tibiotarsus midshaft width; TD, tibiotarsus distalwidth; TML, tarsometatarsus length; TMPW, tarsometatarsus proximal width; TMM, tarsometatarsus midshaft width; TMMD, tarsometatarsus midshaft depth; TMDW, tarsometatarsus distal width.

3.4.4 Phylogenetic Analysis

With the four most skeletally complete fossil megapode taxa added to the matrix (*Progura gallinacea*, *P. campestris*, *Latagallina naracoortensis* and *L. olsoni*), a parsimony analysis produced a consensus of one tree (tree length, 1453; Consistency Index, 0.27; Retention Index, 0.63) (Figure 3.23). As expected, the extinct taxa were all found to be included in the clade comprising the Megapodiidae.

With the inclusion of extinct taxa, the clade Megapodiidae and the constituent 'scrub-fowl' and 'brush-turkey' clades (Harris *et al.* 2014) retained high bootstrap support (75%, 90% and 75%, respectively) (Figure 3.23). All four of the extinct species were in a derived position within the brush-turkey clade, and strongly excluded from the scrubfowl clade. The two species of *Progura* and the two species of *Latagallina* formed their own clade with 70% bootstrap support, with a weakly supported sister relationship between this clade and *Leipoa ocellata* (53%). Furthermore, there was high support for the fossil megapode genera that we identified in our morphological examinations (see Systematic palaeontology): *P. gallinacea* and *P. campestris* formed a clade with 79% bootstrap support and *L. naracoortensis* and *L. olsoni* formed a clade with 92% support. Notably, neither species of the long-legged genus *Progura* was attracted to extant species with similarly elongate tarsometatarsi (*Macrocephalon*, *Aepypodius*, *Talegalla*, *Alectura*).

Our analysis found the following character state transformations for key clades and species as follows. The *Progura*/*Latagallina* clade is united by 14 synapomorphies, of which the following four character states of the postcranial skeleton are unambiguous (synapomorphic state in brackets): Character 138, CI = 0.25, 0 ==> 1 (distal humerus, tuber. supracondylare dorsale, in cranial view, not prominent from epicondylus dorsalis); Character 197, CI = 0.111, 1 ==> 0 (proximal femur, cranial facies, trochanter, elongate, extends distally past the level of the caput femoralis a distance exceeding the proximodistal width of the caput femoralis); Character 250, CI = 0.25, 0 ==> 1 (tarsometatarsus, cotyla medialis dorsoplantarly elongate, protruding dorsal to cotyla lateralis); Character 263, CI = 0.25, 0 ==> 1 (tarsometatarsus, tuberositas m. tibialis cranialis has two distinct tuberosities).

The extinct genus *Progura* is defined by seven synapomorphies of the postcranial skeleton, of which the following three are unambiguous: Character 97, CI = 0.167, 0 ==> 1 (coracoid, omal end, ventral facies, processus acrocoracoideus, depth of sulcus medial to facies artic. humeralis and sternal to impressio ligamentum acrocoracohumeralis is deep); Character 265, CI = 0.222, 1 ==> 0 (tarsometatarsus, foramina vascularis proximalis, of roughly equal size); Character 275, CI = 0.333, 0 ==> 1 (tarsometatarsus, anterior end of canalis interosseus distalis largely or completely exposed dorsally by reduction in bony covering). The larger species, *P. gallinacea*, is defined by three autapomorphies, two of which are unambiguous: Character 171, CI = 0.143, 0 ==> 1 (distal carpometacarpus, length synostosis metacarpals II and III, from distal end of spatium intermetacarpale to facies articularis digitalis minoris/facet for digit III, is ≥width of synostosis); Character 257, CI = 0.133, 1 ==> 0 (proximal tarsometatarsus, width hypotarsus adjacent to cotylae is distinctly less than half proximal width). The smaller species in this genus, *P. campestris*, is defined by two autapomorphies, one of which is unambiguous: Character 257, CI = 0.133, 1 ==> 2 (proximal tarsometatarsus, width hypotarsus adjacent to cotylae, distinctly more than half proximal width).

The extinct genus *Latagallina* is defined by six unambiguous synapomorphies of the postcranial skeleton: Character 193, CI = 0.25, 0 ==> 1 (femur, caudal facies, pneumatic openings adjacent to facies articularis antitrochanterica, present and large); Character 205, CI = 0.143, 0 ==> 1 (distal femur, cranial aspect, orientation of condylus lateralis markedly divergent); Character 212, CI = 0.286, 0 ==> 1 (femur, condylus medialis, profile in medial aspect is subangular between articular surface of condyle and its cranial surface); Character 213, CI = 0.091, 0 ==> 1 (distal femur, width of sulcus patellaris in cranial view, taken at half the depth of the bounding condyles, narrow and deep, less than width of condylus lateralis plus trochlea fibularis); Character 258, CI = 0.333, 0 ==> 1 (tarsometatarsus, hypotarsus, major hypotarsal ridge, distal end, ridge terminates abruptly, drops steeply to shaft); Character 262, CI = 0.286, 0 ==> 1 (tarsometatarsus, corpus tarsometatarsi, sulcus extensorius, shallow and broad proximally, flattens out distally). The larger species, *Latagallina naracoortensis*, is distinguished by five autapomorphies, of which the following four transformation are unambiguous: Character 118, CI = 0.333, 1 ==> 2 (proximal humerus, fossa pneumotricipitalis dorsalis, between incisura capitis and tuberculum dorsale, wide, shallow fossa ≥ width ventral pneumotricipital fossa); Character 144, CI = 144, 0 ==> 1 (humerus, width of space between the facet on the tuber. supracondylare ventrale and the proximoventral apex of the dorsal condyle is wide, gap wider than facet); Character 257, CI = 0.133, 1 ==> 2 (proximal tarsometatarsus, hypotarsus, width adjacent to cotylae, distinctly more than half proximal width); Character 264, CI = 0.20, 0 ==> 1 (tarsometatarsus, tuberositas m. tibialis cranialis dorsally prominent). Three unambiguous autapomorphies define the smaller species in this genus, *Latagallina olsoni*: Character 231, CI = 0.25, 1 ==> 0 (tibiotarsus, distal end, epicondylus medialis with internal ligamental prominence pronounced, visible in anterior view); Character 237, CI = 0.125, 1 ==> 0 (tibiotarsus, distal end, junction of crista trochlea cartilaginis tibialis and rim of condylus medialis, not marked by distinct shallow notch at mid-depth); Character 279, CI = 0.214, 1 ==> 0 (tarsometatarsus, foramen vasculare distale large).

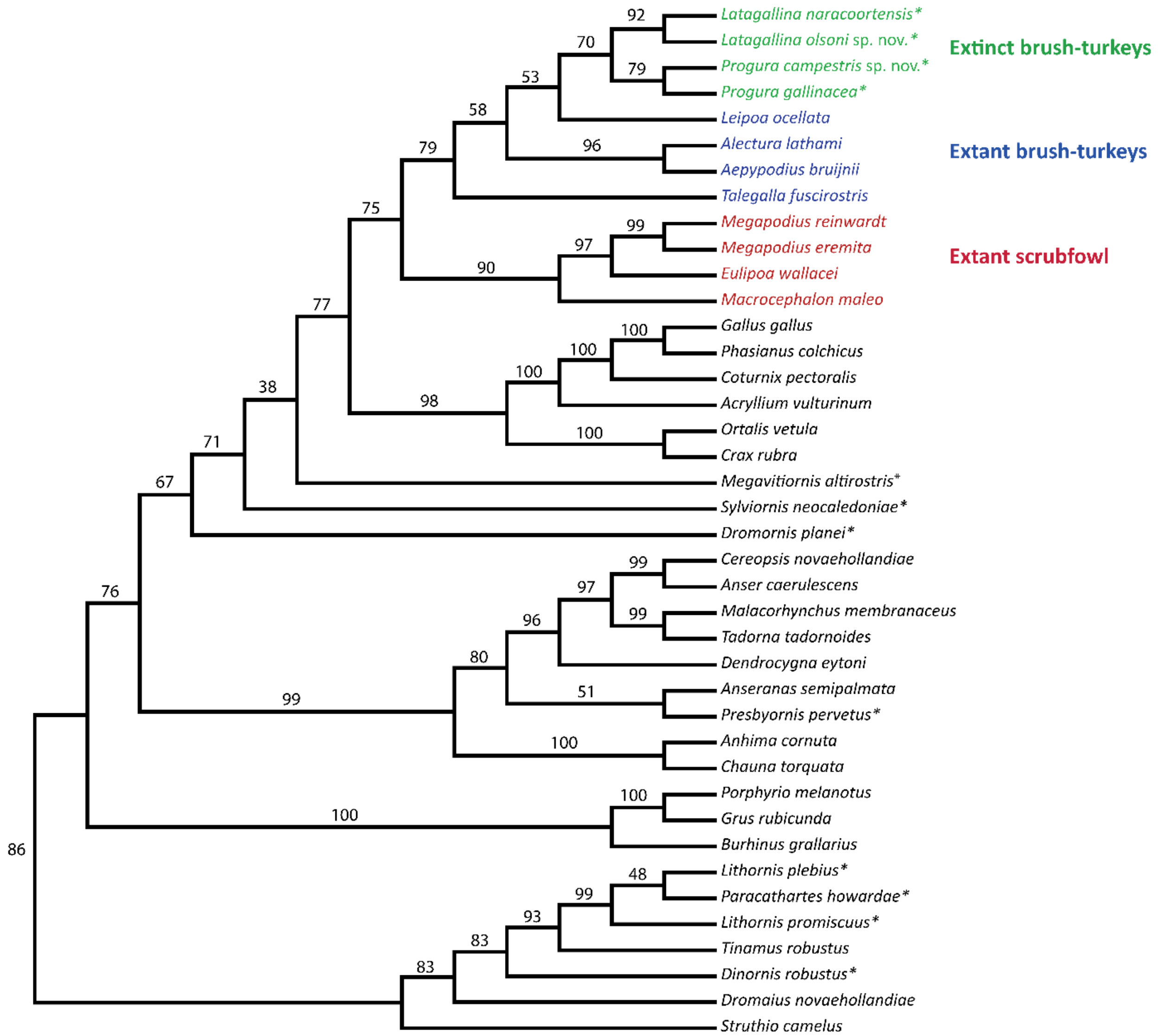


Figure 3.22: Bootstrap consensus tree with molecular backbone constraint for all extant taxa. Relationships between extant species of Megapodiidae were constrained based on a recent molecular phylogeny of that family (Harris *et al.* 2014), and all other extant non-megapode taxa as described by Worthy *et al.* (2016). Relationships of the fossil taxa were unconstrained, and they were therefore free to move to their optimal positions around this framework. *, Extinct taxon. Tree statistics: length, 1453; consistency index, 0.27; homoplasy index, 0.73; retention index, 0.63. Numbers are bootstrap probability values expressed as a percentage.

The relationships between the six ‘brush-turkey’ genera (*Talegalla*, *Leipoa*, *Alectura*, *Aepypodius*, *Progura* and *Latagallina*) show some conflict, with *Leipoa* being weakly supported (53%) as the sister taxon to the fossil genera. The more inclusive clade of (*Leipoa* + *Progura* + *Latagallina*) and the well supported (96%) pairing of *Aepypodius*/*Alectura* also had weak support (58%). This suggests that there is conflict in the data about whether *Leipoa* or the *Alectura*/*Aepypodius* clade is the sister group of the fossil clade. Discovery of more complete fossils of the new megapodes would likely resolve some of the ambiguity currently created by missing data. Nevertheless, the analysis supports the generic distinction of *Progura* and *Latagallina* and a sister-group relationship between these genera. The relationships between the *Progura*/*Latagallina* clade and *Leipoa*, and between *Progura*/*Latagallina* and the *Alectura*/*Aepypodius* clade, should be considered unresolved on present evidence.

3.5 Discussion

3.5.1 Late Cenozoic diversity

The last review of fossil megapodes concluded that there was evidence for just one late Cenozoic species in Australia, *Progura* (or *Leipoa*) *gallinacea* (Boles, 2008). We confirm that *P. gallinacea* is the only representative of the family recognised to date from Pliocene assemblages, but from Pleistocene deposits we record fossils of three extinct genera, comprising five species, plus extant *Leipoa ocellata*. The subspecific diversity of *Alectura lathami* and *Megapodius reinwardt* (Dickinson & Remsen, 2013) also implies their presence in the Pleistocene. Thus as a minimum, Australia was likely home to six genera and eight species of megapode during the late Cenozoic. This fundamentally alters our understanding of the recent history of the Megapodiidae, and shows that the estimated loss of half of the megapode species, mainly species of *Megapodius*, from Pacific islands during the Quaternary (Steadman, 1999) can also be extended to Australia.

3.5.2 Evolutionary relationships of extinct and extant taxa

While the phylogenetic character set that we used (Worthy *et al.* 2016) was designed to determine the relationships of galloanserine taxa in general and did not have a focus on crown group megapodes, our analysis nonetheless identified close relationships among the extinct species, and clarified evolutionary relationships between them and extant megapodes. The analysis identified two strongly supported species pairs among the extinct taxa – two of *Progura* and two of *Latagallina* – which accords with our generic distinctions (see Systematic Palaeontology). The analysis also placed the extinct *Progura + Latagallina* clade in a highly derived position within the 'brush-turkeys' (Harris *et al.* 2014), revealing previously obscure generic and species diversity within this endemic Australo-Papuan branch of the Megapodiidae. So far the affinities of *Garrdimalga mcnamarai* remain mysterious because of its fragmentary remains.

Relationships among extant taxa are well established based on molecular analyses, and were used as backbone constraints for the phylogenetic analysis. Thus low support for some of the clades comprising modern taxa indicates conflict in the signal from the morphological data for those clades, and there may be scope to optimise the character set for the Megapodiidae. Nevertheless, the analysis is informative about the hypothesis that modern Malleefowl *Leipoa ocellata* is a phyletic dwarf of *Progura gallinacea* (including *Latagallina naracoortensis* within the synonymy of *P. gallinacea*), with small-bodied *Leipoa* having evolved as a product of 'Late Pleistocene dwarfing' (Boles, 2008). Monophyly of the *Progura +*

Latagallina clade is well supported, and there is only very weak support (53%) for a sister taxon relationship between the *Progura* + *Latagallina* clade and *Leipoa*, so this relationship should be considered unresolved. These results provide neither support for a close relationship of *L. ocellata* to the fossil taxa, nor for an ancestral relationship between any of them and *L. ocellata* as the dwarfing idea implies. In fact, numerous morphological differences throughout the skeleton differentiate the extinct taxa from *Leipoa*. Furthermore, we have provided fossil evidence that small-bodied *Leipoa* had evolved by the Early Pleistocene at the latest, thus dwarfing in the Late Pleistocene is highly improbable. There is currently no fossil evidence to contradict an estimated divergence date of the *Leipoa* lineage from other members of the 'brush-turkey' clade in the Miocene (Harris *et al.* 2014).

Despite the apparent absence of dwarfing in the *Leipoa* lineage, we see evidence for body-size flexibility in other megapode lineages. The extinct Australian genera *Progura* and *Latagallina* each contained one 'giant' and one somewhat smaller, though still larger than modern, species. Marked size variation has been identified in the 'scrubfowl' clade as well: large body-size evolved within the genus *Megapodius* on islands (Steadman 1989; Steadman 1999; Balouet and Olson 1989). However, the smallest extant species of *Megapodius*, *M. pritchardii*, is also an island species, so this genus offers few clues as to the likely direction of body size trends in the extinct Australian lineages, particularly in a continental context.

3.5.3 Body mass

Previous estimates of body mass for *Progura gallinacea*, the largest known species of megapode, are invalid because they were based on skeletal material that does not belong to this species, or are based on possibly erroneous measurements. The original estimated mass for this species was 5–7 kg, based on the cube of the length of the coracoid AM F54720 from Wombeyan Caves, NSW (van Tets, 1974), but we have now referred this specimen to *Latagallina naracoortensis*. Later estimates for *P. gallinacea* (Boles, 2008) of 7.8–10.1 kg were also based on material from Naracoorte that we have now referred to *L. naracoortensis.* Furthermore, we could not replicate the measurements on which those estimates were based, regardless of taxon, and have no data to indicate that any of the extinct Australian megapodes weighed as much as 10 kg.

Our estimate for *P. gallinacea* of 7.7 kg (Table 3.15), based on minimum shaft width of the lectotype tarsometatarsus from the Darling Downs (QM F1143), is therefore the first published estimate based on material referrable to this species. A mass of nearly 8 kg for *P. gallinacea* is perhaps smaller than expected, given that bones of this species are in general considerably larger than those of *P. campestris*, *L. naracoortensis* and *Garrdimalga mcnamarai*, which all weighed in the region of 5 or 6 kg using our preferred equation for the tibiotarsus (Table 3.15). Minimum tarsometatarsus width correlates less well with body mass than some other skeletal measurements, though (Field et al. 2013), and the estimate for *P. gallinacea* should therefore be regarded as indicative only. Nevertheless, it is possible that this species was truly not much heavier than *P. campestris* or *L. naracoortensis*, with its long, distally tapered tarsometatarsus meaning that *P. gallinacea* stood exceptionally tall but was not a disproportionately bulky animal. Despite being the largest known species of megapode, *P. gallinacea* does not show signs of a reduced pectoral girdle indicative of flightlessness. It may have flown as well as the heaviest extant galliform, wild turkey *Meleagris gallopavo* of North America*,* males of which have an almost identical mean body mass of 7.8 kg (Dunning 2008). Similarities in their body masses may indicate that *M. gallopavo* and *P. gallinacea* approached the mass threshold for the retention of flight in galliforms.

Our preferred body-mass estimates for *P. campestris*, *Latagallina naracoortensis* and *Garrdimalga mcnamarai*, based on minimum circumference of the tibiotarsus, indicate that these taxa had overlapping body masses (*P. campestris*, 6.2 kg estimated from holotype; *L. naracoortensis*, mean 5.2 kg, range 3.7–6.5 kg, calculated from 13 specimens; *G. mcnamarai*, calculated from paratype tibiotarsus). The heaviest individual of *L. naracoortensis* had nearly twice the estimated mass of the smallest individual. All measurements were on skeletally mature individuals, so such a difference might indicate sexual dimorphism in this species. Assessing this was beyond the scope of this taxonomic study, but could be investigated in future research, as the large number of skeletal elements preserved for this species would allow statistical interrogation.

At 2.9 kg, our preferred estimate for *Latagallina olsoni*, based on circumference of the tibiotarsus, equalled that of the heaviest recorded extant megapode, a male individual of *Alectura lathami* (Dunning, 2008), but is above the mean for that species (*Alectura* females 2.2 kg, males 2.5 kg; Dunning, 2008). *Latagallina olsoni* was also heavier than Australia's other extant megapodes, being around two-and-a-half times heavier than *Megapodius reinwardt* (females 888 g, males 1.1 kg; Dunnig, 2008) and around one-and-a-half times heavier than *Leipoa ocellata* (females 1.8 kg, males 2.0 kg; Dunning, 2008). Although *L. olsoni* had legs of similar length to *L. ocellata*, considerably greater mass of the extinct species implies that it had a much stouter body, and this is borne out by the larger pelvis and notarium of the extinct species.

In summary, the extinct Plio-Pleistocene megapodes spanned an estimated mass range from 2.9 kg to 7.7 kg. This is on a par with the heaviest extant galliforms on other continents, including the curassows of the tropical Americas, turkeys of North America, and the largest grouse and pheasants of Eurasia (Dunning, 2008). Differences in body size may imply niche partitioning between the extinct species, which could help to explain the geographical/temporal overlap of three megapode species on the Nullarbor Plain during the Early Pleistocene (*Progura campestris*, *Leipoa ocellata* and *Latagallina olsoni*) and two at Naracoorte during the Middle to Late Pleistocene (*Latagallina naracoortensis* and *Leipoa ocellata*). However, exact contemporaneity of species is difficult to establish as the fossil deposits accumulated over periods of thousands of years.

3.5.4 Body proportions and flight ability

We note strong similarity between the skeletal proportions of congeners *Latagallina naracoortensis* and *L. olsoni* (Figure 3.22). This is despite their very different body sizes, and reinforces the conclusions of our anatomical observations and phylogenetic analysis that they are closely related. There is little allometric scaling despite *L. naracoortensis* approaching double the mass of *L. olsoni* (Table 3.16), demonstrating that body proportions within a megapode lineage can be independent of overall size.

Such similarities may be useful for testing any further apparent examples of gigantism/dwarfing within the megapodes. Pertinent to the question of whether *Leipoa ocellata* is a phyletic dwarf of one of the extinct taxa, the proportions of that species are rather dissimilar to those of *Latagallina naracoortensis*, *L. olsoni* and *Progura campestris* (Figure 3.22). *Progura gallinacea* was not included in the Simpson log-ratio diagram, but dissimilarity in proportions of the tarsometatarsus of *L. ocellata* and *P. gallinacea* are evident (Appendix 1). The balance of evidence, including the anatomical differences that we have documented, the results of our phylogenetic analysis, occurrence of *Leipoa* fossils in the same deposits as extinct taxa, and proportional differences revealed by the Simpson diagram, is that *Leipoa ocellata* does not belong to the same genus as any of the extinct taxa, and nor can it be descended from of any of them.

The Simpson diagram (Figure 3.22) and our morphological observations indicate that the included fossil species were volant, with strong pectoral girdles. The pectoral elements are not atrophied as they are in the extinct flightless stem-galliform *Sylviornis* (Worthy *et al.* 2016). *Garrdimalga mcnamarai* was not included in the Simpson diagram because its remains are so fragmentary, but it is likely that it, too, was volant given its proportionally long carpometacarpus relative to hind limb bone size (see Diagnosis).

3.5.5 Anatomy and ecology

The extinct taxa share some anatomical traits that may be associated with similarities in ecology and life history. Most notably, none of the four extinct Plio-Pleistocene taxa for which phalanges/unguals are preserved appears to have been specialised for mound-building: *Progura campestris*, both species of *Latagallina*, and *Garrdimalga mcnamarai* all have comparatively short, stout phalanges, and claws that are lateromedially compressed and deeply curved rather than dorsoventrally flattened as in extant mound-building species (e.g. *Leipoa*). They are similar to the proportionally short and laterally compressed unguals seen in burrow-nesting megapodes such as *Macrocephalon maleo*, which digs in sand, and the stem-galliform *Sylviornis neocaledoniae*, for which there is no evidence of egg-burying behaviour (Worthy *et al.* 2016).

In addition, some of the extinct taxa show further signs of adaptation away from mound-building, notably a short, shallow fossa parahypotarsalis medialis on the tarsometatarsus in both species of *Progura*, and proportionally shorter toes than those of specialist mound-builders (Figure 3.11). If our interpretation is correct and these taxa were all burrow-nesters, this would mean that burrow-nesting, which is a state currently only present in extant members of the 'scrub-fowl' clade (Harris *et al.* 2014), evolved or re-evolved independently within the Australian 'brush-turkeys'.

An ancestral state reconstruction using Bayesian analysis, Harris *et al.* (2014) determined that mound-building was the most probable ancestral nesting strategy in the megapodes, with burrow-nesting having evolved three times within the scrubfowl clade. That analysis was based on the prior that all members of the brush-turkey clade are mound-builders. However, if, as a result of our study appears to be the case, some brush-turkeys were burrow-nesters, repeating the ancestral state reconstruction with burrow-nesting taxa within the brush-turkey clade could produce more equivocal results. Note also that the sister taxon of all galliforms, *Sylviornis neocaledoniae*, was determined to be a non mound-builder and almost certainly an endothermic incubator (Worthy *et al.* 2016), and therefore ectothermic incubation is a synapomorphy of megapodes.

3.5.5.1 *Progura gallinacea*

Relatively few elements of *Progura gallinacea* are known (see species description), limiting interpretation of its functional anatomy. No cranial remains of this species are known and so nothing can be deduced about its feeding habits or its sensory abilities. Despite its limited remains, *Progura gallinacea* is clearly the largest known species of megapode, extant or extinct. The tarsometatarsus, reconstructed to have been nearly 150 mm long, is of similar length to that of the giant flightless stem galliform *Sylviornis neocaledoniae* from the Pacific (Worthy *et al.* 2016), but unlike *Sylviornis* the bones of the pectoral girdle of *P. gallinacea*, insofar as they are preserved, show no signs of reduction: the carpometacarpus, proximal scapula and coracoid are not gracile and have strong muscle attachments. We therefore presume that adults of this species could fly, even if only for short distances, and could have flown up into trees to roost as do extant megapodes (Jones and Göth 2008).

No phalanges or unguals of *P. gallinacea* are known, so it is more difficult to deduce the digging/nesting behaviour of this species compared to the other extinct species. However, the relatively small fossa parahypotarsalis medialis on the tarsometatarsus suggests that the musculature for the toes was reduced, which we consider to be a sign that this species was not particularly well adapted for using its feet to build mounds. It is possible that it buried its eggs in river sands or gravels, given that its remains in south-east Queensland and in northern South Australia its bones have been found in riverine depositional environments, but it is possibly more likely that it buried its eggs in adjacent sands or soils (Louys and Price 2015; Tedford, Wells, and Barghoorn 1992).

3.5.5.2 *Progura campestris*

Almost the entire skeleton of *P. campestris* is known, allowing a better appraisal of its functional anatomy than for *P. gallinacea*. This species has a pectoral girdle slightly reduced relative to its hindlimb compared to similarly-sized *L. naracoortensis* (Figure 3.22). Both species weighed in the region of 5–6 kg. Therefore slightly reduced pectoral elements suggest that *P. campestris* was a somewhat weaker flyer than *L. naracoortensis*. Typically there is a trade-off between the size/muscle mass of the hindlimb and forelimb in birds, with longer legs thought to compensate for weaker pectoral muscles by generating increasing forward force during take-off (Wright, Steadman, and Witt 2016). Thus *P. campestris* may have relied on its relatively more elongate tarsometatarsus to launch from the ground. Conversely, short distal legs are paired with longer wings in *L. olsoni* and *L. naracoortensis*, which may mean that these species generated greater forces with their wings/pectoral girdle to become airborne.

In *P. campestris*, the length of the femur is about equal to that of the tarsometatarsus, while in *L. naracoortensis* the tarsometatarsi are only about 88% of femoral length. This indicates that the two species, which had similar body masses, had different biomechanical properties of the hindlimb and may have differed in locomotory style and/or digging behaviour. This could be further investigated.

Cranial anatomy of *P. campestris* differs notably from that of other megapodes, in that the lacrimals and the margo supraorbitalis flare laterally (Figure 3.6 A), which would have provided bony protection to the eyes. This could signify that the species foraged in tough or spiny vegetation. Also of note is the very small foramen nervi olfactorii (Figure 3.6 C), similar to that of *Latagallina naracoortensis* (Figure 3.12 C), but dissimilar to the large and obvious foramina seen here in *L. ocellata*, *A. lathami*, *Megapodius reinwardt* and *Macrocephalon maleo*. This may mean that olfaction was of decreased importance in *P. campestris*. Given that the paratype cranium is well preserved (Figure 3.6), it should be possible to test this hypothesis by using computed tomography to reconstruct a virtual brain cast of this species and assess the size of the brain region corresponding to the processing of olfactory stimuli (Zelenitsky et al. 2011).

The tarsometatarsi of *P. campestris* and *L. naracoortensis* are of roughly similar length, but the distal end in *P. campestris* is relatively narrow, indicating it probably had a smaller foot span (Figure 3.5). As the unguals of both species are apparently adapted away from mound-building, differences in foot size may relate to differences in digging/nesting behaviour between these species, such as different preferred substrates for egg burial.

The shape of the pygostyle in *P. campestris* suggests that this species may have had elaborate tail feathers. The bone is flexed dorsally at an approximately 45° angle (Figure 3.9 J) and the lamina have a large surface area for muscular attachment, rather like the pygostyle of extant Silver Pheasant *Lophura nycthemera* (Wang and O'Connor 2017), which has a long trailing tail. By contrast, the pygostyle of *Alectura lathami*, which is noted for its short, vertically fanned tail (the name *Alectura* = cock-tail; Fraser and Gray 2013), is rather straight and lacks deep sulci on the laminae, and *Leipoa ocellata*, which has a short tail with a downward posture, has a pygostyle that is laterally compressed and points slightly downwards.

3.5.5.3 Latagallina naracoortensis

This was a stout, heavy, short-legged megapode, but despite this shows no signs of reduced volant ability (see above). It had long, strong wings, and large, robust coracoids, larger than those of *P. campestris*, and so it may have flown more strongly.

The cranium of *L. naracoortensis* (Figure 3.12) lacks bony protection of the eyes as is seen in *P. campestris* and it may therefore have fed in a different manner. This is further suggested by the different shapes of the beak in these species, (narrow, elongate tip in *P. campestris* – Figure 3.6 F–H; Figure 3.7 D–F; shorter and broad in *L. naracoortensis* – Figure 3.7 J–L; Figure 3.12 E–G). However, the diet of neither species is known. Despite these differences, an important similarity between *L. naracoortensis* and *P. campestris* is the small foramen for the olfactory nerve (Figure 3.12 C), posterior to the sulcus nervi olfactorii, meaning this species may also have had reduced olfactory capacity. This character is not captured in the character set that we used for our phylogenetic analysis, but seems to further confirm that *Progura* and *Latagallina* belong to the same clade.

The comparatively larger fossa parahypotarsalis medialis on the tarsometatarsus of *L. naracoortensis* (Figure 3.5) could mean that this species was a more powerful digger than *P. campestris*, but its short, laterally compressed, curved unguals (Figure 3.15 L) would have made it poorly adapted to mound-building compared to extant taxa like *L. ocellata*. If we have correctly interpreted this species to have been a burrow-nester, it may have buried its eggs in a more resistant substrate than did *P. campestris*.

3.5.5.4 Latagallina olsoni

As with its larger congener, *L. olsoni* had comparatively long wings and short legs (Figure 3.22) and was probably a strong flyer. The tibiotarsus and tarsometatarsus of *L. olsoni* were shorter than in extant *Leipoa ocellata*, but the femur was longer. This may mean that these similarly-sized species differed in locomotory style and may also have differed in how they used their legs and feet for digging. Articulation of the femur with the acetabulum of the pelvis shows that the leg was able to be splayed more widely than in *L. ocellata*, due to its more proximally-orientated crista trochanteris, perhaps indicating a generally wider stance in *L. olsoni* because of its greater body mass. A broad, deep pelvis could have allowed *L. olsoni* to lay larger eggs than *L. ocellata*. The only cranial remains of *L. olsoni*, the anterior portion of the mandible, shows that the angle between the left and right rami was comparatively wide (Figure 3.18, A and B), and the tip of the bill may therefore have had a similar shape to that of congener *L. naracoortensis* (Figures 3.7 J–L and 3.12 E–G).

3.5.5.5 Garrdimalga mcnamarai

Little can be deduced about the habits of this species due to its limited remains. However, compared to the similarly sized species *P. campestris* and *L. naracoortensis*, *G. mcnamarai* seems to have had large phalanges and unguals relative to the dimensions of its tarsometatarsi and tibiotarsi. This species may therefore have been a more powerful digger than those taxa. The humerus and most of the ulna are unknown, but the radius and carpometacarpus show that the distal wing was relatively long, and therefore this species may have been a strong flyer. Leg length, however, is not known and so relative length of the wing and leg cannot be determined. As in species of *Latagallina*, the tip of the bill in *G. mcnamarai* was short and wide (Figure 3.7 G–I; Figure 3.21 E–G), rather than elongate as in *P. campestris*.

3.5.6 Extinction and the possible role of humans

Here we have shown that the generic diversity of megapodes in Australia halved – and species diversity reduced by more than 60% – within the last few hundred-thousand years. Timing and reasons for extinction among the fossil taxa are not known, but based on current fossil evidence no small-bodied Australian megapode species went extinct during the Pleistocene, and there appears instead to have been a preferential loss of larger, heavier species. Large body size would have been a risk factor if it was associated with slow reproductive rates or susceptibility to hunting, as proposed for Australia's Pleistocene mammalian megafaunal extinctions (Johnson 2002). Nevertheless, there is currently no direct evidence that humans encountered or hunted any of the species in question. Pertinent to the issue of hunting, all of the extinct megapodes appear to have been able to fly (see above), and thus they may have been less vulnerable to hunting than might be supposed based on size alone. Given that at least four of the five species of megapode belonged to a single clade (see Phylogenetic analysis) it is also possible that other shared derived life-history or behavioural traits, such as diet or nesting behaviour, may have rendered them vulnerable to extinction.

Although evidence for hunting of adult birds is absent, fossil eggshell from various parts of Australia does indicate that humans consumed the eggs of at least one large extinct species of megapode during the Late Pleistocene. Eggshell fragments with characteristic burn patterns indicate that these eggs were cooked and consumed by people in various parts of Australia (Hamm et al. 2016; Miller et al. 2016). So far these eggs have not been attributed to any species in particular. Fossil eggshell of this type, formerly attributed to the giant extinct galloanseriform *Genyornis newtoni* (Miller et al. 2016; Miller et al. 2017), but since identified as belonging to one or more species of megapode (Grellet-Tinner, Spooner, and Worthy 2016), disappeared from the fossil record around 47 ka, within a few thousand years of first human arrival in Australia (Grellet-Tinner, Spooner, and Worthy 2016; Miller et al. 1999). All of the fossil bones that we have described are considerably older than 47 ka, so it is unknown if one or more of these taxa survived late enough into the Pleistocene to have been encountered by people. However, all the burnt eggshell material has been recovered from sandy environments, so given that we believe that all the large extinct taxa were burrow-nesters rather than mound-builders, the eggs could plausibly belong to one or more species of *Latagallina*, *Progura*, *Garrdimalga*, or perhaps other extinct taxa as yet unknown.

Egg size narrows down the possible candidate species for having laid these eggs. The best-preserved specimen, the 'Spooner Egg' (SAM P42421), was collected from dunes at the head of the Spencer Gulf in South Australia and was dated by optically stimulated luminescence to be 54.7 ± 3.1 kyr old (Grellet-Tinner, Spooner, and Worthy 2016). The volume of the Spooner Egg is roughly equivalent to that of the extant Emu *Dromaius novaehollandiae*, but is shorter and broader (Grellet-Tinner *et al.* 2016). Although some still dispute its identity as a megapode egg (Miller et al. 2017), the Spooner Egg, and other similar eggshell material from multiple localities, originally referred to *Genyornis newtoni* (Williams 1981), is almost certainly too small and too thin to have belonged to the giant stem-galliform *Genyornis* (Grellet-Tinner et al. 2017). Extant female megapodes lay exceptionally large eggs relative to body size (Watson, Anderson, and Olson 2015), and although the Spooner Egg is very large compared to eggs of extant megapodes, it was calculated that it would not be unusually long for a female megapode of approximately 5 kg in mass (Grellet-Tinner, Spooner, and Worthy 2016; Grellet-Tinner et al. 2017). Our body-mass estimates for extinct megapodes (Table 3.16) place two candidate species in this range (*Latagallina naracoortensis*, mean 5.2 kg; *Garrdimalga mcnamarai*, 5.2 kg), and two somewhat heavier (*Progura campestris,* 6.2 kg; *P. gallinacea*, 7.7. kg). Thus there is circumstantial evidence that at least one of these very large species could have survived until human arrival in the Late Pleistocene, only to then become extinct.

The Spooner Egg is notably broad for its length (Grellet-Tinner, Spooner, and Worthy 2016), which may indicate it was laid by a megapode with an especially large pelvis (Grellet-Tinner, Spooner, and Worthy 2016), given that egg size in birds is constrained by pelvis size (Varricchio and Jackson 2016). A proportionally long and broad pelvis was noted in *Latagallina olsoni* compared to *Leipoa ocellata*, despite these species having similar leg-length (see species description), and thus *L. olsoni* probably laid larger eggs than a Malleefowl. With an estimated body-mass of 2.9 kg (Table 3.16), *L. olsoni* is too small to have laid the Spooner Egg based on a 5-kg estimate for its parent bird (Grellet-Tinner, Spooner, and Worthy 2016). However, *L. olsoni'*s much larger congener *L. naracoortensis* probably also had a proportionally large pelvis, based on very similar body proportions of these two species throughout the rest of the postcranial skeleton (see Figure 3.21), and thus *L. naracoortensis* would be a plausible parent bird for the fossil eggshell. Based on fossils examined in this study, some skeletal remains of *L. naracoortensis* from Naracoorte are from deposits of likely Late Pleistocene age, thus it is probably the latest-known surviving species among our five extinct taxa. Future studies may elucidate whether the geographically widespread Pleistocene megapode eggshells derive from one or multiple species, and help clarify the geographical distribution and extinction history of large megapodes even in locations where fossil bones are absent.

3.5.7 Geographical and temporal distribution

Two of the species we have described, *Progura campestris* and *Latagallina olsoni*, are both known only from the Nullarbor Plain, south-central Australia, while *Garrdimalga mcnamarai* is only known from Yorke Peninsula in southern South Australia. These species may have had very limited geographical distributions, but it seems more likely that their remains are yet to be located further afield.

The known range of *P. gallinacea* has altered as a result of this study. We have confirmed its presence in riparian habitats both on the Darling Downs in south-eastern Queensland and on the Warburton River in the Lake Eyre Basin, northern South Australia. Similarities have previously been noted between the Pliocene marsupial faunas of the Tirari Formation in the Lake Eyre Basin, and the Chinchilla Sand on the Darling Downs (Louys and Price 2015; Tedford, Wells, and Barghoorn 1992), so the presence of *P. gallinacea* at both localities is further evidence of their faunal similarity. '*Progura' naracoortensis* (within the synonymy of *P. gallinacea*) was previously thought to also be present at Bluff Downs (Boles and Mackness 1994), and at several sites in eastern New South Wales (van Tets, 1974; Boles, 2008). However, we consider the Bluff Downs megapode fossils to be far too small to be *P. gallinacea*, and having examined the fossils from New South Wales we have referred these to *Latagallina naracoortensis*. At present, then, *P. gallinacea* is known only from two localities in Australia's mid-latitudes, one relatively close to the east coast and the other deep in the interior.

On current evidence, *Latagallina naracoortensis* had the widest geographical distribution of the extinct species. To this taxon we have referred specimens from Naracoorte and Mt Gambier in south-eastern South Australia, as well as three localities in eastern New South Wales, and one in south-east Queensland. Thus far, *L. naracoortensis* appears to have been a species of the south-eastern quarter of Australia. No fossils of this species are known from Victoria, but it seem likely to have inhabited the region intermediate between eastern NSW and south-eastern South Australia. In each known locality, it has been recovered from limestone caves or fissure fills in limestone, but this may be the result of preservation bias and may not indicate its true distribution or preferred substrate.

Further to the extinct taxa, we have also documented Pleistocene fossils of extant *Leipoa ocellata* from two southern localities: the Thylacoleo Caves of south-central Australia; and the Naracoorte Caves of south-eastern South Australia. These occurrences are in a similar geographical zone to where the species occurs today, perhaps indicating relative stability in the distribution of Malleefowl since the Pleistocene. The occurrence of *L. ocellata* in the heart of the Nullarbor Plain during the Early Pleistocene, however, is a modest range extension compared to today. There are no modern records of *L. ocellata* from the

Nullarbor Plain, although the species is recorded from woodlands peripheral to the Plain (Burbidge, Casperson, and Fuller 1987).

An implication of our findings for future palaeontological studies is that the identity of Australian fossil megapodes cannot safely be deduced from age, size and geography alone: identification based on morphology is essential. Just as the ranges of *Megapodius reinwardt* and *Alectura lathami* overlap in north-eastern Australia today, fossil evidence shows that *Leipoa ocellata*, *Progura campestris* and *Latagallina olsoni* all inhabited the Nullarbor Plain during the Early Pleistocene. Furthermore, on the Darling Downs in south-east Queensland, *Progura gallinacea* and *Latagallina naracoortensis* are present as fossils in the Pleistocene, and at Naracoorte *Leipoa ocellata* and *Latagallina naracoortensis* occur in the same Pleistocene deposits. The degree of temporal overlap between any of these species at a given location is uncertain, but spatial overlap is indisputable.

So far only one species of megapode – *Progura gallinacea* – has been confirmed from sites of Pliocene age. Although additional species from this epoch may yet be discovered, and the Bluff Downs fossils require reappraisal, current evidence indicates that megapode diversity reached its peak in Australia in the Pleistocene. During this epoch there is direct fossil evidence for four genera (*Leipoa*, *Progura*, *Latagallina* and *Garrdimalga*), and five species (*L. ocellata*, *P. gallinacea*, *P. campestris*, *L. naracoortensis*, *L. olsoni* and *Garrdimalga mcnamarai*), and *A. lathami* and *M. reinwardt* were also presumably resident.

3.5.8 Palaeoenvironments

This previously obscure diversity among the megapodes implies that the Pleistocene environment of Australia was particularly favourable for these mainly ground-dwelling birds. Occurrence of two or more species at three localities implies niche partitioning may have been at play, but as yet we know very little about how any of the extinct megapodes used their habitats.

Burrow-nesting is thought to have evolved in some species of *Megapodius* in response to their dispersal by flight into new habitats (Dekker 2007), in their case tropical islands with sandy substrates. In continental Australia, the rise of a burrow-nesting clade of *Progura* and *Latagallina* (and *Garrdimalga* if this genus also belonged to the same clade) could have been an evolutionary response to the spread of sandy habitats due to global trend towards aridification during the Plio-Pleistocene (Fujioka et al. 2009; Fujioka and Chappell 2010). However, at Chinchilla and on the Warburton River *P. gallinacea* inhabited riparian environments, seemingly at odds with aridification. The Pliocene habitat at Chinchilla has been interpreted as a mix of tropical forest, wetlands and grasslands, with estimated annual rainfall of around 1000 mm (Louys and Price 2015; Montanari, Louys, and Price 2013). The Pliocene environment of the Tirari Formation in the Lake Eyre Basin, on the other hand, whilst also riparian, has been described as highly evaporative (Tedford, Wells, and Barghoorn 1992). Thus the habitat and climatic tolerances of *P. gallinacea* are ambiguous.

Megapodes are omnivores, thus diet offers few clues for reconstructing the palaeoenvironments of the extinct taxa. However, it is likely that all the fossil megapodes required trees for roosting and for escaping predators, as with extant species (Jones and Göth 2008). Given that several of the fossil taxa weighed upwards of 5 kg, large trees were probably necessary to support their weight. Fossils of extant *Leipoa ocellata* are somewhat more informative about local Pleistocene habitats at Naracoorte and on the Nullarbor Plain because this species is a known habitat specialist of low open woodland, comprising in almost all cases an overstorey of multi-stemmed *Eucalyptus* trees, which provide the leaf litter with which it builds its nest mounds (Jones and Göth 2008). The local Pleistocene environment around the Thylacoleo Caves has previously been interpreted as a mosaic of grassland and woodland, based mainly on composition of the marsupial fossil fauna (Prideaux *et al.* 2007). The addition of *L. ocellata* to the species list for this locality corroborates the conclusion that the Nullarbor Plain, which today completely lacks a tree canopy, was at least at times an open woodland environment in the first half of the Pleistocene.

3.6 Conclusions

The trend in taxonomy over the last three decades has been towards a reduction of the number of extinct megapode taxa recognised from the Australian Cenozoic. First was the synonymy of *Progura gallinacea* and *P. naracoortensis*, then the suggestion that *P. gallinacea* was the megafaunal antecedent of modern *Leipoa ocellata*. The discovery of new fossil material from the Nullarbor Plain, Curramulka Quarry and the Warburton River has provided fresh perspective from which to re-evaluate previously known fossils from Naracoorte, New South Wales and south-east Queensland. As a result, this study has revealed that there was a previously unknown radiation – comprising three extinct genera and five extinct species – within the brush-turkey clade in Plio-Pleistocene Australia. All species appear to have been burrow-nesters rather than mound-builders, a behaviour previously unknown among the brush-turkeys.

Here we have demonstrated that *Progura gallinacea* and ‘*Progura*’ *naracoortensis* are generically distinct from each other, although they do belong in a single clade. Both these taxa differ from *Leipoa ocellata*, which was roughly contemporaneous with several larger taxa. We have found no evidence to support the claim that *Leipoa ocellata* is a phyletic dwarf. Evolutionary relationships of *Garrdimalga mcnamarai* remain to be determined. As a result of a clarification of taxonomy, we conclude that generic diversity of megapodes in Australia has halved in the last few hundred-thousand years, and species diversity has reduced by more than 60%, a startling loss. We hope that these discoveries provide perspective on the historical importance of these birds in the evolution and ecology of Australia. We hope also that our study prompts a renewed appreciation for the vulnerability of megapodes to the forces of extinction, and the need to conserve the species that still survive.

Data accessibility. All data are included in the manuscript, appendices or have been uploaded as part of the electronic supplementary material.

Authors' contributions. ES participated in the design of the study, made the skeletal comparisons for the systematic palaeontology, collected and analysed the skeletal measurements, conducted the phylogenetic analysis, prepared the photographic plates and drafted the manuscript. G.J.P. directed excavations of the Thylacoleo Caves and excavated much of the included material, provided direction and advice on the study design, edited the draft manuscript and directed the broader research project on the fossil fauna of the Thylacoleo Caves of which this study forms a part. T.H.W. provided direction and advice on the study design, developed the character set for the phylogeny on which this phylogenetic analysis is based, scored cranial material of the extinct Australian taxa for the phylogenetic analysis, oversaw the systematic palaeontology and data analysis and edited the draft manuscript. All authors gave final approval for publication.

3.7 References

Aplin, K.P., Pasveer, J.M., Boles, W.E. 1999. Late Quaternary vertebrates from the Bird's Head Peninsula, Irian Jaya, Indonesia, including descriptions of two previously unknown marsupial species. *Records of the Western Australian Museum* Suppl. 57, 351–387.

Balouet, J., Olson S. 1989. Fossil birds from late Quaternary deposits in New Caledonia. *Smithsonian Contributions to Zoology* 469, 1–38.

Bartholomai, A. 1977. The fossil vertebrate fauna from Pleistocene deposits at Cement Mills, Gore, southeastern Queensland. *Memoirs of the Queensland Museum* 18, 41–51.

Baumel, J., King, A., Breazile, J., Evans, H., Vanden Berge, J. 1993. *Handbook of avian anatomy: nomina anatomica avium*, 2nd edn. Cambridge, MA: Nuttall Ornithology Club.

Birks, S., Edwards, S. 2002. A phylogeny of the megapodes (Aves: Megapodiidae) based on nuclear and mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 23, 408–421.

Boles, W.E. 2008. Systematics of the fossil Australian giant megapodes *Progura* (Aves: Megapodiidae). *Oryctos* 7, 195–215.

Boles, W.E. Ivison, T. 1999. A new genus of dwarf megapode (Galliformes: Megapodiidae) from the Late Oligocene of Central Australia. *Smithsonian Contributions to Paleobiology* 89, 199–206.

Boles, W.E., Mackness, B. 1994. Birds from the Bluff Downs Local Fauna, Allingham Formation, Queensland. *Records of the South Australian Museum* 27, 139–149.

Burbidge, A., Casperson, K., Fuller, P. 1987. Birds. In *A biological survey of the Nullarbor Region, South and Western Australia in 1984*, pp. 153–178. Adelaide, Australia: South Australian Department of Environment and Planning, Western Australia Department of Conservation and Land Management, Australian National Parks and Wildlife Service.

Campbell, K., Marcus, L. 1992. The relationship of hindlimb bone dimensions to body weight in birds. In *Papers in Avian Palaeontology Honoring Pierce Brodkorb*, Natural History Museum of Los Angeles County, *Science Series* 36, 395–412.

Claramunt, S., Cracraft, J. 2015. A new time tree reveals Earth history's imprint on the evolution of modern birds. *Science Advances* 1, e1501005.

De Vis, C. 1888. Australian ancestry of the crowned pigeon of New Guinea. *Proceedings of the Royal Society of Queensland* 5, 127–131.

Dekker, R.W. 2007. Distribution and speciation of megapodes (Megapodiidae) and subsequent development of their breeding behaviour. In *Biogeography, time, and place: distributions, barriers, and islands* (ed. W. Renema), pp. 93–102. Dordrecht: The Netherlands: Springer.

Dickinson, E., Remsen, J.J. 2013. *The Howard and Moore complete checklist of the birds of the world*, 4th edn, vol. 1. Non-passerines. Eastbourne, UK: Aves Press.

Dunning, J. 2008. *CRC handbook of avian body masses*, 2nd edn. Boca Raton, FL: CRC Press.

Field, D.J., Lynner, C., Brown, C., Darroch, S.A.F. 2013. Skeletal correlates for body mass estimation in modern and fossil flying birds. *PLoS ONE* 8, e82000.

Fraser, I., Gray, J. 2013. *Australian bird names—a complete guide*. Victoria, Australia: CSIRO Publishing.

Fujioka, T., Chappell, J., Fifield, L.K., Rhodes, E.J. 2009. Australian desert dune fields initiated with Pliocene–Pleistocene global climatic shift. *Geology* 37, 51–54.

Fujioka, T., Chappell, J. 2010. History of Australian aridity: chronology in the evolution of arid landscapes. *Geologial Society Special Publications* 346, 121–139.

Grellet-Tinner, G., Spooner, N.A., Handley, W.D., Worthy, T.H. 2017. The *Genyornis* Egg: response to Miller *et al.*'s commentary on Grellet-Tinner *et al.*, 2016. *Quaternary Science Reviews* 161, 128–133.

Grellet-Tinner, G., Spooner, N.A., Worthy, T.H. 2016. Is the '*Genyornis*' egg of a mihirung or another extinct bird from the Australian dreamtime? *Quaternary Science Reviews* 133, 147–164.

Hamm, G., Mitchell, P., Arnold, L.J., Prideaux, G.J., Questiaux, D., Spooner, N.A., Levchenko, V.A., Foley, E.C., Worthy, T.H., Stephenson, B., Coulthard, V., Coulthard, C., Wilton, S., Johnston, D. 2016. Cultural innovation and megafauna interaction in the early settlement of arid Australia. *Nature* 539, 280–283.

Handley, W.D, Chinsamy, A., Yates, A.M., Worthy, T.H. 2016. Sexual dimorphism in the late Miocene mihirung *Dromornis stirtoni* (Aves: Dromornithidae) from the Alcoota Local Fauna of central Australia. *Journal of Vertebrate Paleontology* 36, e1180298.

Harris, R.B., Birks, S.M., Leaché, A.D. 2014. Incubator birds: biogeographical origins and evolution of underground nesting in megapodes (Galliformes: Megapodiidae). *Journal of Biogeography* 41, 2045–2056.

Johnson, C.N. 2002. Determinants of loss of mammal species during the Late Quaternary 'megafauna' extinctions: life history and ecology, but not body size. *Proceedings of the Royal Society B* 269, 2221–2227.

Jones, D,, Göth. A. 2008. *Mound-builders*. Victoria, Australia: CSIRO Publishing.

Jones, D.N., Dekker, R.W.R.J., Roselaar, C.S. 1995. *The megapodes*. Oxford, UK: Oxford University Press.

Louys, J., Price, G. 2015. The Chinchilla Local Fauna: an exceptionally rich and well-preserved Pliocene vertebrate assemblage from fluviatile deposits of south-eastern Queensland, Australia. *Acta Palaeontologica Polonica* 60, 551–572.

Lydekker, R. 1891. Catalogue of the fossil birds in the British Museum (Natural History). London, UK: British Museum (Natural History).

Marshall, L.G., Corruccini, R.S. 1978. Variability, evolutionary rates, and allometry in dwarfing lineages. *Paleobiology* 4, 101–119.

Mayr, G., Weidig, I. 2004. The early eocene bird *Gallinuloides wyomingensis*—a stem group representative of Galliformes. *Acta Palaeontologica Polonica* 49, 211–217.

Mayr, G. 2016. Variations in the hypotarsus morphology of birds and their evolutionary significance. *Acta Zoologica* 97, 143–266.

Megirian, D., Prideaux, G.J., Murray, P.F., Smit, N. 2010. An Australian land mammal age biochronological scheme. *Paleobiology* 36, 658–671.

Miller, G., Magee, J., Smith, M., Spooner, N., Baynes, A., Lehman, S., Fogel, M., Harvey, J., Williams, D., Clark, P., Florian, P., Holst, R., DeVogel, S. 2016. Human predation contributed to the extinction of the Australian megafaunal bird *Genyornis newtoni* ∼47 ka. *Nature Communications* 29, 10496.

Miller, G., Fogel, M., Magee, J., Gagan, M., Clarke, S., Johnson, B. 2005. Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction. *Science* 309, 287–290.

Miller, G.H., Fogel, M.L., Magee, J.W., Clarke, S.J. 2017. The *Genyornis* egg: a commentary on Grellet-Tinner *et al.*, 2016. *Quaternary Science Reviews* 161, 123–127.

Miller, G.H., Magee, J.W., Johnson, B.J., Fogel, M.L., Spooner, N.A., McCulloch, M.T., Ayliffe, L.K. 1999. Pleistocene extinction of *Genyornis newtoni*: human impact on Australian megafauna. *Science* 283, 205–208.

Molnar, R.E., Kurtz, C. 1997. The distribution of Pleistocene vertebrates on the eastern Darling Downs, based on the Queensland Museum collections. *Proceedings of the Linnean Society of New South Wales* 117, 107–134.

Montanari, S., Louys, J., Price, G.J. 2013. Pliocene paleoenvironments of southeastern Queensland, Australia, inferred from stable isotopes of marsupial tooth enamel. *PLoS ONE* 8, e66221.

Mourer-Chauviré, C., Balouet, J.C. 2005. Description of the skull of the genus *Sylviornis* Poplin, 1980 (Aves, Galliformes, Sylviornithidae new family), a giant extinct bird from the Holocene of New Caledonia. *Proceedings of the International Symposium 'Insular Vertebrate Evolution: the Palaeontological Approach', Monografies de la Societat d'Història Natural de les Balears* 12, 205–218.

Mourer-Chauviré, C. 1992. The Galliformes (Aves) from the Phosphorites du Quercy (France): systematics and biostratigraphy. *Papers in Avian Paleontology Honoring Pierce Brodkorb, Natural History Musuem of Los Angeles County*, *Science Series* 36, 67–95.

Mourer-Chauviré, C. 2000. A new species of *Ameripodius* (Aves: Galliformes; Quercymegapodiidae) from the Lower Miocene of France. *Palaeontology* 43, 481–493.

NAPA (Narungga Aboriginal Progress Association). 2006. *Nharangga Warra—Narungga Dictionary*. Adelaide, Australia: Wakefield Press.

Olson, S. 1985. The fossil record of birds. In *Avian biology* (ed. D Farner), pp. 79–238. New York, NY: Academic Press.

Pledge, N.S. 1990. The upper fossil fauna of the Henschke Fossil Cave, Naracoorte, South Australia. *Memoirs of the Queensland Museum* 28, 247–262.

Poplin, F., Mourer-Chauviré, C., Evin, J. 1983. Position systématique et datation de *Sylviornis neocaledoniae*, mégapode géant (Aves, Galliformes, Megapodiidae) éteint de la Nouvelle-Calédonie. *Comptes-rendus des séances de l'Académie des sciences Série II T.* 297, 301–304.

Price, G.J., Webb, G.E., Zhao, J., Feng, Y., Murray, A.S., Cooke, B.N., Hocknull, S.A., Sobbe, I.H. 2011. Dating megafaunal extinction on the Pleistocene Darling Downs, eastern Australia: the promise and pitfalls of dating as a test of extinction hypotheses. *Quaternary Science Reviews* 30, 899–914.

Prideaux, G. 2004. Systematics and evolution of the sthenurine kangaroos. *Geological Sciences* 146. Berkeley, CA: University of California Publications.

Prideaux, G.J. *et al.* 2007. An arid-adapted middle Pleistocene vertebrate fauna from south-central Australia. *Nature* 445, 422–425.

Prideaux, G.J., Warburton, N.M. 2008. A new Pleistocene tree-kangaroo (Diprotodontia: Macropodidae) from the Nullarbor Plain of south-central Australia. *Journal of Vertebrate Paleontology* 28, 463–478.

Prideaux, G.J., Warburton, N.M. 2009. *Bohra nullarbora* sp. nov., a second tree-kangaroo (Marsupialia: Macropodidae) from the Pleistocene of the Nullarbor Plain, Western Australia. *Records of the Western Australian Museum* 25, 165–179.

Prum, R., Berv, J., Dornburg, A., Field, D., Townsend, J., Lemmon, E.M., Lemmon, A.R. 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* 526, 569–573.

Reed, E.H., Bourne, S.J. 2000. Pleistocene fossil vertebrate sites of the South East region of South Australia. *Transactions of the Royal Society of South Australia* 124, 61–90.

Reed, E.H., Bourne, S.J. 2009. Pleistocene fossil vertebrate sites of the south east region of South Australia II. *Transactions of the Royal Society of South Australia* 133, 30–40.

Shute, E., Prideaux, G.J., Worthy, T.H. 2016. Three terrestrial Pleistocene coucals (*Centropus*: Cuculidae) from southern Australia: biogeographical and ecological significance. *Zoological Journal of the Linnean Society* 177, 964–1002.

Simpson, G. 1941. Large Pleistocene felines of North America. *The American Museum Novitates* 1131, 1–27.

Steadman, D. 1989. New species and records of birds (Aves: Megapodiidae, Columbidae) from an archaeological site on Lifuka, Tonga. *Proceedings of the Biological Society of Washington* 102, 537–552.

Steadman, D.W. 1999. The biogeography and extinction of megapodes in Oceania. *Zoologische Verhandelingen* 327, 7–22.

Steadman, D.W. 2006. *Extinction and biogeography of tropical Pacific birds*. Chicago, IL: University of Chicago Press.

Swofford, D.L. 2001. PAUP*: phylogenetic analysis using parsimony (*and other methods). Sunderland, MA: Sinauer Associates.

Tedford, R.H., Wells, R.T., Barghoorn, S.F. 1992. Tirari Formation and contained faunas, Pliocene of the Lake Eyre Basin, South Australia. *The Beagle: Records of the Museums and Art Galleries of the Northern Territory* 9, 173–194.

van Tets, G. 1985. *Progura gallinacea* De Vis, 1888—the Australian Giant megapode. In *Kadimakara—extinct vertebrates of Australia* (eds PV Rich, G van Tets, F Knight), pp. 195–199. Victoria, Australia: Pioneer Design Studio.

van Tets, G.F. 1974. A revision of the fossil Megapodiidae (Aves), including a description of a new species of *Progura* De Vis. *Transactions of the Royal Society of South Australia* 98, 213–224.

Varricchio, D.J, Jackson, F.D. 2016. Reproduction in Mesozoic birds and evolution of the modern avian reproductive mode. *Auk* 133, 654–684.

Wang, W., O'Connor, J.K. 2017. Morphological coevolution of the pygostyle and tail feathers in Early Cretaceous birds. *Vertebrata PalAsiatica* 55, online early.

Watson, D.M., Anderson, S.E., Olson, V. 2015. Reassessing breeding investment in birds: class-wide analysis of clutch volume reveals a single outlying family. *PLoS ONE* 10, e0117678.

Williams, D. 1981. *Genyornis* eggshell (Dromornithidae; Aves) from the Late Pleistocene of South Australia. *Alcheringa: An Australasian Journal of Palaeontology* 5, 133–140.

Worthy, T.H., Hawkin, S., Bedford, S., Spriggs M. 2015. Avifauna from the Teouma Lapita Site, Efate Island, Vanuatu, including a new genus and species of megapode. *Pac. Sci.* 69, 205–252.

Worthy, T.H., Mitri, M., Handley, W.D., Lee, M.S.Y., Anderson, A., Sand, C. 2016. Osteology supports a stem-galliform affinity for the giant extinct flightless bird *Sylviornis neocaledoniae* (Sylviornithidae, Galloanseres). *PLoS ONE* 11, e0150871.

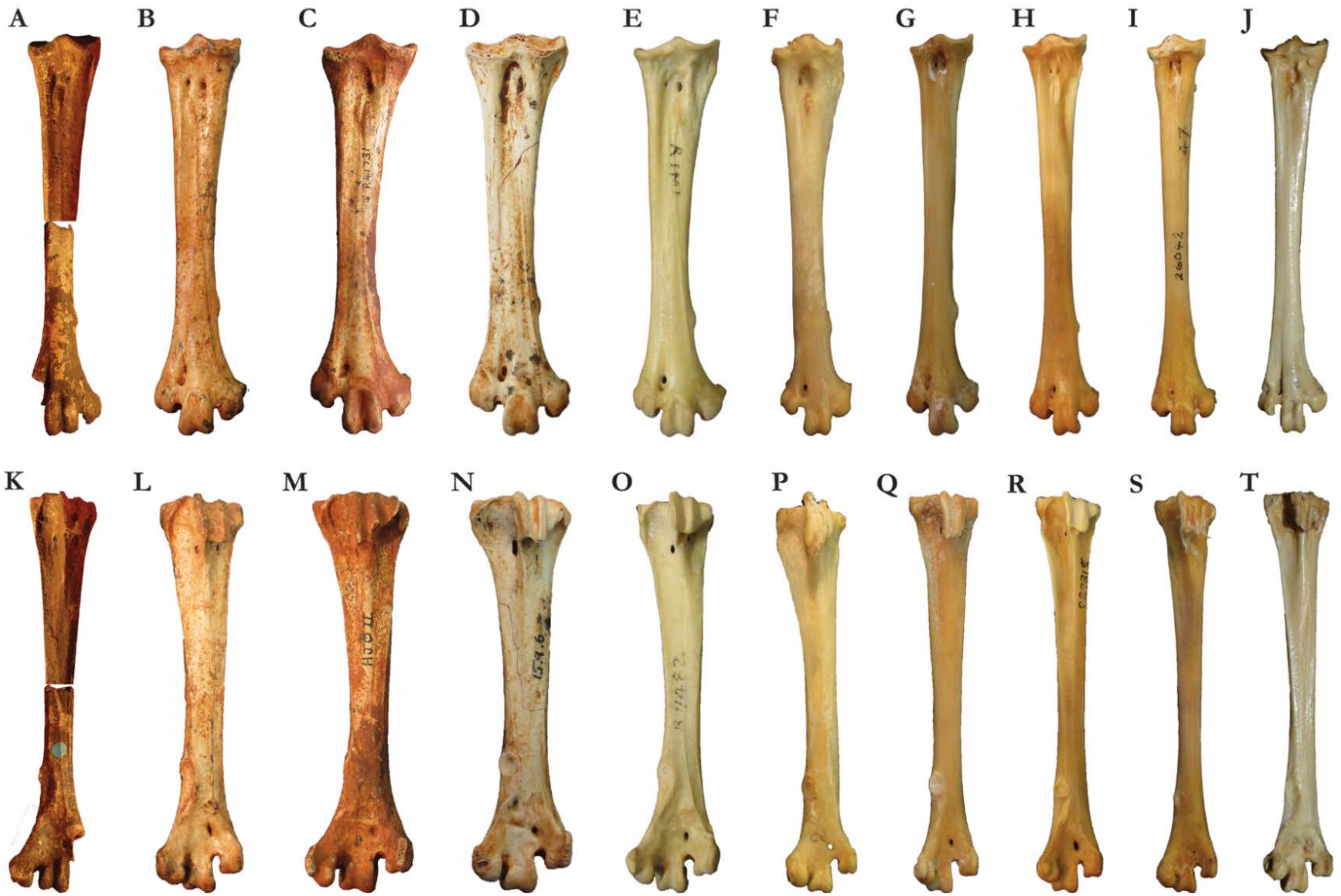
Worthy, T.H. 2000. The fossil megapodes (Aves: Megapodiidae) of Fiji with descriptions of a new genus and two new species. *Journal of the Royal Society of New Zealand* 30, 337–364.

Worthy, T.H. 2008. Pliocene waterfowl (Aves: Anseriformes) from South Australia and a new genus and species. *Emu* 108, 153–165.

Wright, N.A., Steadman DW, Witt CC. 2016. Predictable evolution toward flightlessness in volant island birds. *Proceedings of the National Academy of Sciences USA* 113, 4765–4770.

Zelenitsky, D.K., Therrien F, Ridgely RC, McGee AR, Witmer LM. 2011. Evolution of olfaction in non-avian theropod dinosaurs and birds. *Proceedings of the Royal Society B* 278, 3625–3634.

Appendix 3.A



Tarsometatarsi of extinct and extant megapodes in dorsal (top row) and plantar aspects (bottom row), scaled to the same length to reveal divergent proportions. *Progura gallinacea* (a,k) (reconstructed from two fragments); *Progura campestris* sp. nov. (b,l); *Latagallina naracoortensis* (c,m); *Latagallina olsoni* sp. nov. (d,n); *Leipoa ocellata* (e,o); *Megapodius reinwardt* (f,p); *Talegalla fuscirostris* (g,q); *Alectura lathami* (h,r); *Aepypodius arfakianus* (i,s); *Macrocephalon maleo* (j,t).

Appendix 3.B: *Latagallina naracoortensis* specimens from caves in the Naracoorte region examined for this study: specimen numbers and measurements

Crania

Henschke's Fossil Cave: SAM P22713; SAM P31773; SAM P31774; SAM P41861. **Komatsu Cave:** SAM P51369. **Victoria Fossil Cave:** SAM P41535; SAM P41536.

Premaxillae

Henschke's Fossil Cave: SAM P22871; SAM P23128; SAM P41397.

Notaria

Henschke's Fossil Cave: SAM P18186; SAM P22869; SAM P41687.

Pelves & synsacra

Buckridge Cave: SAM P51236; SAM P51237; SAM P51250; SAM P51355; SAM P51257; SAM P51258; SAM P51261. **Henschke's Fossil Cave:** SAM P18187; SAM P18635; SAM P22818; SAM P22819; SAM P22856; SAM P23117; SAM P23121; SAM P23154; SAM P23352; SAM P23370; SAM P23412; SAM P23413; SAM P23414; SAM P24146; SAM P24191; SAM P41366; SAM P41373; SAM P41688; SAM P41716; SAM P41845. **Victoria Fossil Cave:** SAM P41563; SAM P41564.

Sterna

Henschke's Fossil Cave: SAM P23125; SAM P23302; SAM P23323; SAM P23337; SAM P24190; SAM P39620; SAM P41699; SAM P41700; SAM P41751; SAM P41828; SAM P41857. **Victoria Fossil Cave:** SAM P16162; SAM P27528; SAM P28005; SAM P41545.

Furculae

Buckridge Cave: SAM P51259; SAM P51260. **Henschke's Fossil Cave:** SAM P23131; SAM P23149; SAM P41846.

Coracoids

Buckridge Cave: SAM P51245; SAM P51251; SAM P51352; SAM P51354; SAM P51364. **Fox Cave:** SAM P19027; SAM P19100. **Henschke's Fossil Cave:** SAM P18628; SAM P19071; SAM P19073; SAM P19076; SAM P22715; SAM P22817; SAM P22820; SAM P22858; SAM P22868; SAM P22872; SAM P23119; SAM P23120; SAM P23130; SAM P23336; SAM P24144; SAM P24161; SAM P24167; SAM P24172; SAM P24173; SAM P24187; SAM P24188; SAM P24189; SAM P24204; SAM P24212; SAM P39636; SAM P39637; SAM P39638; SAM P39645; SAM P39650; SAM P41486; SAM P41582; SAM P41586; SAM P41587; SAM P41588; SAM P41603; SAM P41609; SAM P41652; SAM P41653; SAM P41654; SAM P41657; SAM P41663; SAM P41664; SAM P41718; SAM P41733; SAM P41734; SAM P41735; SAM P41831; SAM P41840; SAM P41842. **Victoria Fossil Cave:** SAM P16700; SAM P P41538; SAM P41554.

Scapulae

Fox Cave: SAM P17373. **Henschke's Fossil Cave:** SAM P18630; SAM P19077; SAM P22863; SAM P23281; SAM P23408; SAM P23409; SAM P39634; SAM P39635; SAM P39648; SAM P39652; SAM P41374; SAM P41392; SAM P41481; SAM P41578; SAM P41591; SAM P41594; SAM P41657; SAM P41660; SAM P41696; SAM P41717; SAM P41730; SAM P41856; SAM P41686. **Victoria Fossil Cave:** SAM P41543.

Humeri

Buckridge Cave: SAM P51346; SAM P51347; SAM P51348; SAM P51350; SAM P51353; SAM P51363; SAM P51359. **Henschke's Fossil Cave:** SAM P17153; SAM P17154; SAM P17878; SAM P18183; SAM P18625; SAM P18627; SAM P18638; SAM P22714; SAM P22716; SAM P22719; SAM P22851; SAM P22865; SAM P23118; SAM P23133; SAM P23283; SAM P23293; SAM P23296; SAM P23297; SAM P23327; SAM P23374; SAM P23442; SAM P24143; SAM P24147; SAM P24148; SAM P24153; SAM P24159; SAM P24174; SAM P24175; SAM P24176; SAM P24202; SAM P24209; SAM P24210; SAM P24211; SAM P24219; SAM P39625; SAM P39629; SAM P39621; SAM P39639; SAM P41364; SAM P41367; SAM P41483; SAM P41648; SAM P41649; SAM P41650; SAM P41683; SAM P41684; SAM P41697; SAM P41714; SAM P41727; SAM P41728; SAM P41743; SAM P41750; SAM P41830; SAM P41833. **Victoria Fossil Cave:** SAM P41540; SAM P41551; SAM P41552; SAM P41553; SAM P42076; SAM P42706. **Wombat Cave:** SAM P18636.

Ulnae

Buckridge Cave: SAM P51269; SAM P51270; SAM P51271; SAM P51272; SAM P51273; SAM P51343; SAM P51344; SAM P51345. **Henschke's Fossil Cave:** SAM P17817; SAM P17877; SAM P17879; SAM P18626; SAM P19069; SAM P19075; SAM P19079; SAM P23115; SAM P23126; SAM P23127; SAM P23132; SAM P23282; SAM P23284; SAM P23294; SAM P23375; SAM P24157; SAM P24160; SAM P24164; SAM P24178; SAM P24179; SAM P24180; SAM P24181; SAM P24182; SAM P39626; SAM P39627; SAM P39649; SAM P41363; SAM P41394; SAM P41589; SAM P41611; SAM P41612; SAM P41647; SAM P41658; SAM P41661; SAM P41678; SAM P41679; SAM P41680; SAM P41681; SAM P41711; SAM P41712; SAM P41713; SAM P41736; SAM P41752; SAM P41836. **Kilsby's Hole (Mt Gambier):** SAM P42079. **Victoria Fossil Cave:** SAM P41544.

Radii

Henschke's Fossil Cave: SAM P18099; SAM P18184; SAM P18629; SAM P18632; SAM P23376; SAM P23377; SAM P39640; SAM P39642; SAM P41585; SAM P41597; SAM P41599; SAM P41742; SAM P41922; SAM P41929.

Carpometacarpi

Buckridge Cave: SAM P51356; SAM P51357; SAM P51358; SAM P51362; SAM P51365; SAM P51366. **Fox Cave:** SAM P17364; SAM P17369. **Henschke's Fossil Cave:** SAM P22862; SAM P22870; SAM P23116; SAM P23110; SAM P23129; SAM P23324; SAM P23410; SAM P23443; SAM P24139; SAM P24140; SAM P24171; SAM P24183; SAM P24184; SAM P24203; SAM P24213; SAM P39628; SAM P39630; SAM P39631; SAM P39632; SAM P39641; SAM P39651; SAM P41583; SAM P41606; SAM P41584; SAM P41726; SAM P41655; SAM P41695. **Victoria Fossil Cave:** SAM P41537; SAM P28006.

Femora

Buckridge Cave: SAM P51244; SAM P51246; SAM P51247; SAM P51248; SAM P51249; SAM P51253; SAM P51254; SAM P51255; SAM P51262; SAM P51263; SAM P51351. **Fox Cave:** SAM P17366. **Henschke's Fossil Cave:** SAM P17857; SAM P18186; SAM P19068; SAM P19070; SAM P19074; SAM P19078; SAM P22712; SAM P22852; SAM P22854; SAM P23111; SAM P23112; SAM P23122; SAM P23134; SAM P23153; SAM P23325; SAM P23340; SAM P23371; SAM P23379; SAM P23445; SAM P24149; SAM P24165; SAM P24192; SAM P24205; SAM P39622; SAM P39633; SAM P41361; SAM P41362; SAM P41393; SAM P41476; SAM P41480; SAM P41482; SAM P41493; SAM P41494; SAM P41592; SAM P41593; SAM P41604; SAM P41682; SAM P41719; SAM P41729; SAM P41741; SAM P41834. **Victoria Fossil Cave:** SAM P41541; SAM P41549; SAM P41550; SAM P42707.

Tibiotarsi

Buckridge Cave: SAM P51238; SAM P51239; SAM P51240; SAM P51241; SAM P51242; SAM P51243. **Fox Cave:** SAM P17365; SAM P19042; SAM P19098. **Henschke's Fossil Cave:** SAM P17152; SAM P17876; SAM P18633; SAM P18792; SAM P23123; SAM P23152; SAM P23285; SAM P23286; SAM P23295; SAM P23298; SAM P23299; SAM P23326; SAM P23381; SAM P24142; SAM P24150; SAM SAM; SAM P24151; SAM P24162; SAM P24193; SAM P24194; SAM P24196; SAM P24197; SAM P24198; SAM P24206; SAM P31775; SAM P31776; SAM P39623; SAM P39624; SAM P41368; SAM P41372; SAM P41391; SAM P41396; SAM P41475; SAM P41477; SAM P41659; SAM P41690; SAM P41691; SAM P41692; SAM P41694; SAM P41720; SAM P41721; SAM P41722; SAM P41723; SAM P41724; SAM P41725; SAM P41737; SAM P41749; SAM P41835. **Victoria Fossil Cave:** SAM P41539; SAM P41547; SAM P41548. **No location data:** SAM P24195.

Tarsometatarsi

Buckridge Cave: SAM P51231; SAM P51232; SAM P51233; SAM P51234; SAM P51235; SAM P51349. **Fox Cave:** SAM P17361; SAM P17362; SAM P17363; SAM P17370; SAM P17371; SAM P19044. **Henschke's Fossil Cave:** SAM P17856; SAM P18185; SAM P19072; SAM P19099; SAM P22853; SAM P22866; SAM P22873; SAM P23109; SAM P23113; SAM P23124; SAM P23135; SAM P23287; SAM P23300; SAM P23301; SAM P23341; SAM P23382; SAM P23383; SAM P23384; SAM P23444; SAM P23446; SAM P23448; SAM P24152; SAM P24158; SAM P24199; SAM P24200; SAM P24201; SAM P24207; SAM P31772; SAM P31777; SAM P31778; SAM P31779; SAM P39643; SAM P39644; SAM P39646; SAM P39647; SAM P41479; SAM P41576; SAM P41577; SAM P41579; SAM P41600; SAM P41605; SAM P41607; SAM P41610; SAM P41685; SAM P41708; SAM P41709; SAM P41710; SAM P41731; SAM P41732; SAM P41740; SAM P41745; SAM P41746; SAM P41747; SAM P41748; SAM P41832; SAM P41837; SAM P41841; SAM P41843. **Victoria Fossil Cave:** SAM P25633; SAM P28007; SAM P41534.

Pedal phalanges & unguals

Henschke's Fossil Cave: SAM P23436; SAM P24156. **Kilsby's Hole (Mt Gambier):** SAM P42733.

Vertebrae

Buckridge Cave: SAM P51264; SAM P51265; SAM P51266; SAM P51267; SAM P51268. **Henschke's Fossil Cave:** SAM P18181; SAM P22821; SAM P22867; SAM P23358; SAM P24166; SAM P24169; SAM P41485.

Associated skeletons

Big Bird Cave: SAM P51368 (R femur, R ulna, R humerus, pR scapula, scapula fragment, pL tibiotarsus, fibula, 5 vertebrae, phalanx dig. major, phalanx dig. minor, synsacrum fragments, dL carpometacarpus, 6 pedal phalanges, rib fragment, sternum fragment, L coracoid sternal end).

Komatsu Cave: SAM P51369 (neurocranium, 3 vertebrae, synsacrum incomplete, pL scapula, L coracoid, R coracoid, dR femur, dL tarsometatarsus, pL humerus, pR humerus).

Henschke's Fossil Cave: SAM P51370 (R ulna, dL ulna, dR tarsometatarsus, dL tarsometatarsus, 3 coracoid fragments, 7 prox. phalanges, 3 distal phalanges, metatarsal 1, tibiotarsus distal fragment, R humerus incomplete, pL humerus, R femur, L femur, pR carpometacarpus, L carpometacarpus incomplete, R scapula, pL scapula, various fragments).

Measurements of Humeri* of *Latagallina naracoortensis (all measurements in mm)

SAM #	TL	PW	SW	DW
SAM P51347	149.9	36.2	15.6	31.1
SAM P51348	-	38.3	14.9	-
SAM P51346	-	-	-	30.2
SAM P51368	151.2	37.7	16.0	30.7
SAM P51369	-	40.3	-	-
SAM P41552	135.5	-	14.4	27.2
SAM P41551	149.4	36.2	15.2	29.2
SAM P39629	-	-	-	31.6
SAM P42706	-	35.9	-	-

SAM P39639	-	-	14.2	29.6
SAM P42076	-	-	13.9	30.1
SAM P39625	142.4	35.7	15.3	28.6
SAM P41727	-	35.6	-	-
SAM P41750	-	38.6	-	28.7
SAM P17154	-	-	-	31.5
SAM P17153	143.4	35.6	14.5	29.6
SAM P24219	-	35.2	-	-
SAM P41714	-	-	14.4	28.6
SAM P23296	-	-	-	29.4
SAM P24147	-	-	-	32.7
SAM P23283	-	-	-	29.5
SAM P18636	-	-	16.1	32.7
SAM P41649	-	-	13.8	-
SAM P41648	139.4	33.6	14.5	30.0
SAM P24143	-	36.9	15.7	-
SAM P24202	-	-	-	29.0
SAM P23133	-	-	-	29.4
SAM P22714	-	-	15.3	32.1
SAM P18625	-	39.0	-	-
SAM P24175	-	-	-	29.2
SAM P23442	-	35.0	-	-
SAM P22716	-	-	14.0	29.8
SAM P24210	-	34.1	-	-
SAM P24153	-	-	-	30.3
SAM P41650	148.9	36.9	15.0	30.6
SAM P23118	-	34.3	14.5	-
SAM P23327	150.4	35.6	15.8	30.2
SAM P22719	138.4	35.5	14.3	28.8

Ulnae

SAM #	TL	PW	SW	DW
SAM P51269	165	19.8	11.5	20.6
SAM P51272	-	20.1	11.6	-
SAM P51273	-	19.4	10.6	-
SAM P51345	-	-	11.1	19.9
SAM P51343	-	19.2	11.3	-
SAM P51368	159	20.4	11.8	20.5
SAM P51270	173.9	22.6	12.6	21.5
SAM P41752	-	18.5	11.2	-
SAM P41679	-	-	-	20.6
SAM P41680	152.4	19.1	11.6	19.4
SAM P41712	-	-	-	19.5
SAM P41711	144.8	18.2	10.2	18.3
SAM P4713	-	17.4	-	-
SAM P24179	-	17.9	10	-
SAM P41658	-	18.6	-	-
SAM P41612	-	18	-	-
SAM P19075	-	-	11.4	20
SAM P23294	-	-	9.4	18.1
SAM P41544	152.4	19.2	12	19.7
SAM P39627	149	19.2	11.1	18.3
SAM P39626	-	-	11.1	21.1
SAM P41589	-	17.2	-	-
SAM P41363	-	-	11	-
SAM P42079	-	19.3	-	-
SAM P24178	-	18	-	-
SAM P23115	150.4	-	10	19.4
SAM P23282	-	-	10.4	19.5
SAM P23132	145.6	16.2	10.3	18.2
SAM P41836	-	-	-	20.4
SAM P24181	-	-	-	18.2
SAM P24160	-	-	-	18.6
SAM P24180	-	17.4	-	-
SAM P19079	-	18.9	-	-
SAM P18626	153.2	18.2	10.2	19.1
SAM P19069	150.3	17.3	10.1	17.7

SAM P17879	-	-	-	19.3

Carpometacarpi (* = max. width at arch of os metacarpale minus)

SAM #	TL	PW	MW*	DW
SAMP51368	-	-	16.8	-
SAMP51367	-	25.8	-	-
0680	90.8	25.7	16.5	-
SAMP51358	85.7	25.3	17	-
SAMP51362	86.1	24.5	16.1	20.5
SAMP51357	87.3	25.7	17	-
SAMP23129	82.5	22.8	16.5	-
SAMP41584	-	21.2	-	-
SAMP17369	-	23.4	-	-
SAMP41726	-	-	15.5	-
SAMP23116	78.4	19.8	13.7	-
SAMP41655	77.3	22.7	14.2	-
SAMP41655	79.6	22.5	15.6	16.6
SAMP41695	75.7	22.1	14.4	-
SAMP39628	74.8	20.8	14.9	18.6
SAMP39631	74.8	20.8	14.9	19.5
SAMP39641	78.9	22.6	14.2	-
SAMP39632	80.9	-	14.1	-
SAMP39630	74.6	22.2	13.8	-
SAMP39651	-	22.3	-	-
SAMP41583	78.8	-	15.7	-
SAMP24184	77.1	-	14.8	-
SAMP41537	85.7	24.1	16.3	-
SAMP24213	79	20.6	14.7	19.2
SAMP23443	74.1	22.2	15.7	-
SAMP23110	74.8	21.5	-	-
SAMP17364	73	-	-	-
SAMP24171	80.3	21.4	14.3	-
SAMP24183	-	-	13.6	-
SAMP24139	-	21.4	-	-
SAMP24203	-	20.3	-	-
SAMP24140	-	-	14.9	-
SAMP22862	75.9	21.4	13.9	-

SAMP22870	82.4	23.4	15.8	-
SAMP41606	73.4	20.4	-	-

Coracoids (TL = total medial length; OW = omal width; SW = sternal width; MW = midshaft width)

SAM #	**TL**	**OW**	**SW**	**MW**
SAM P51354	91.7	22.8	27.5	10.8
SAM P51369	93.2	20.6	29.8	11.2
SAM P51352	-	20.9	-	-
SAM P51245	-	22.8	-	-
SAM P24187	81.9	17.8	-	9.6
SAM P41538	88.7	-	-	11.0
SAM P23120	86.3	16.7	-	10.5
SAM P19076	85.9	17.5	-	11.4
SAM P22820	90.6	18.6	27.5	10.9
SAM P23492	-	-	-	10.8
SAM P23336	92.1	17.3	-	12.0
SAM P41663	92.0	17.6	31.4	12.4
SAM P22868	89.6	17.3	-	11.2
SAM P24144	-	-	32.0	-
SAM P41842	-	-	-	10.5
SAM P39650	-	16.7	-	-
SAM P22715	84.2	16.5	-	10.5
SAM P41718	-	17.2	-	-
SAM P41654	-	17.2	-	10.8
SAM P22817	87.2	17.8	-	10.8
SAM P39636	86.9	17.8	-	11.2
SAM P39637	85.2	17.5	27.8	10.4
SAM P39638	84.9	15.5	27.7	10.5
SAM P39645	88.8	16.8	-	10.6

Scapulae (WA = width articularis humeralis;

SAM #	**WA**	**WC**	**DC**	**LAA**
SAM P51368	13.1	10.3	-	24.1
SAM P51369	12.2	11.0	-	25.2
SAM P51366	12.9	11.7	-	-
SAM P41374	12.6	10.3	7.3	-
SAM P41578	13.7	10.8	8.1	23.3

SAM P41696	11.2	10.5	7.6	-
SAM P41591	13.5	11.8	8.5	23.7
SAM P19077	12.2	10.8	8.2	23.7
SAM P39635	12.9	10.8	8.2	25.8
SAM P39652	12.2	12.0	8.1	24.9
SAM P41730	12.2	10.4	7.8	23.4
SAM P23281	12.5	11.0	7.1	24.4
SAM P39648	11.5	10.0	6.9	22.6
SAM P41543	11.0	10.5	7.4	22.7
SAM P41392	10.3	9.7	6.7	-
SAM P41481	12.1	11.8	8.2	24.3
SAM P39634	-	11.3	7.6	25.2
SAM P41717	12.8	10.6	7.2	23.3
SAM P41856	11.7	11.1	6.9	24.4
SAM P41594	12.5	10.0	7.3	23.2
SAM P41686	13.6	11.1	7.7	23.9
SAM P18630	11.7	10.1	7.2	24.8
SAM P22863	12.3	11.3	8.1	-

Femora (SC = minimum shaft circumference)

SAM #	TL	PW	SW	DW	SC
SAM P51368	119.4	30.5	14.1	28.2	42.2
SAM P51369	-	-	-	29.6	-
SAM P51263	-	31.7	14	-	44.3
SAM P19070	113.4	30.3	12.3	-	-
SAM P23445	110.7	27.8	12.2	26.5	-
SAM P17857	-	28.4	-	-	-
SAM P51254	-	-	-	-	45
SAM P51262	-	-	-	-	40.7
SAM P22712	108.1	-	12.1	-	37.2
SAM P22852	-	-	12.9	-	-
SAM P23122	102.4	28.6	11.8	25.3	37.2
SAM P23325	-	-	-	25.2	
SAM P23371	-	-	13.2	-	40.7
SAM P24192	-	28.7	-	-	-
SAM P39622	110.8	-	13.2	25.8	41.1
SAM P39633	-	-	-	29.5	-
SAM P41476	-	-	12.9	26.7	-

SAM P41482	-	-	-	27.9	-
SAM P41541	-	-	-	27.2	-
SAM P41592	-	29.8	-	-	-
SAM P41593	-	-	-	26	-
SAM P41729	-	-	14.1	-	43.6
SAM P41741	-	28.4	-	-	-
SAM P41834	-	31.5	13	-	-
SAM P42707	-	-	-	27.3	-

Tibiotarsi

SAM #	**TL**	**PW**	**SW**	**DW**	**MC**
SAM P51243	170.3	22.9	11.3	22.7	33
SAM P51242	158.3	24	12.4	23.6	34.3
SAM P51239	-	-	-	21.9	-
SAM P51241	-	-	-	22.1	31
SAM P51240	-	-	11.3	21.7	30.9
SAM P17876	-	-	10.7	20.5	-
SAM P17152	157.8	-	11.3	22.5	-
SAM P18633	-	-	-	19.1	-
SAM P19042	-	-	-	19.6	-
SAM P23123	-	-	-	19.8	-
SAM P23152	-	-	-	19.5	-
SAM P23285	-	-	10.5	21.2	28.5
SAM P23286	-	-	11.1	20.7	32.3
SAM P23298	-	21.6	10.5	-	30.7
SAM P23299	-	-	9.9	20.6	29.2
SAM P23326	-	-	-	20.6	-
SAM P24142	-	26.3	13.1	-	-
SAM P24150	-	-	-	23.8	-
SAM P24151	-	-	-	-	-
SAM P24162	-	-	-	21.2	-
SAM P24195	-	-	-	19.9	-
SAM P24197	-	25.2	-	-	-
SAM P24198	-	-	-	19.7	-
SAM P24206	-	-	9.1	19.5	27.4
SAM P31775	-	-	-	22.5	-
SAM P31776	-	-	-	20.7	30.9

SAM P39623	-	22.8	-	-	-
SAM P39624	-	-	-	20.1	-
SAM P41368	-	-	12.6	-	-
SAM P41475	157	25.5	11.4	22.1	31.4
SAM P41477	-	23.3	-	-	-
SAM P41539	-	-	-	19.1	-
SAM P41547	-	-	9.8	20.7	27.8
SAM P41548	-	-	9.4	20.4	26.2
SAM P41659	-	23.7	10.4	21.5	-
SAM P41690	-	-	-	21.8	-
SAM P41691	-	-	11.2	22.4	33.1
SAM P41692	-	-	11.3	-	-
SAM P41720	144.2	22	10.5	19.2	30
SAM P41721	-	-	-	21.1	-
SAM P41722	-	-	-	20	-
SAM P41724	-	24.7	-	-	-
SAM P41737	-	-	10.6	-	-
SAM P41749	-	-	10.5	19.7	31.2
SAM P41835	-	-	-	22.2	33.2

Tarsometatarsi (*midshaft width = minimum width in this taxon)

SAM #	TL	PW	SW*	DW
SAM P51369	-	-	-	25.6
SAM P51235	103.90	-	10.7	-
SAM P51231	105.60	25.00	11.3	27.1
SAM P51233	94.80	24.00	11	-
SAM P51234	97.70	24.30	10.6	26.2
SAM P41579	93.20	21.80	9.3	24.4
SAM P41843	94.60	19.70	9.6	22.8
SAM P41745	90.20	21.90	9.4	24
SAM P41731	104.70	25.30	10.6	28
SAM P41685	102.00	22.70	10	23.7
SAMP41709	96.80	23.00	10.5	26.4
SAM P31779	99.00	-	10.9	24.2
SAM P31778	96.00	21.80	9.8	23.4
SAM P23287	95.60	21.90	9.3	24
SAM P31772	98.90	23.10	-	-
SAM P18185	-	-	10.2	-

SAM P17856	95.30	21.70	9.2	-
SAM P39643	-	25.90	-	-
SAM P39644	-	-	-	24.5
SAM P41740	-	-	-	25.6
SAM P41837	-	-	-	25.4
SAM P41746	89.00	22.50	9.9	-
SAM P41841	-	-	-	24.2
SAM P41748	-	22.10	-	-
SAM P41479	-	25.00	-	-
SAM P24158	-	23.10	-	-
SAM P39646	-	22.50	-	-
SAM P41577	-	-	-	-
SAM P23301	-	-	-	24.1
SAM P22853	96.40	22.50	9.4	24.3
SAM P25633	100.50	24.20	10.4	-
SAM P17361	-	22.70	9.5	-
SAM P23109	-	-	10.2	26.4
SAMP23382	-	-	-	22.7
SAM P24152	-	25.40	10.7	-
SAM P31777	95.00	22.60	9.2	24
SAM P19044	-	22.50	9.6	-
SAM P24207	-	-	-	24.6
SAM P41605	-	22.70	-	-

Supplementary Figure 3.1

Type material of *Garrdimalga mcnamarai* sp. nov. compared with other extinct species

Supp. Figure 3.1: *Garrdimalga mcnamarai* carpometacarpus, SAM P42711, holotype (A, E, I) and tibiotarsus, SAM P42709, paratype (M, Q). Comparisons with *Latagallina naracoortensis* (B, F, J, N, R), *Latagallina olsoni* (C, G, K, O, S) and *Progura campestris* (D, H, L, P, T).

Chapter 4: The Early and Middle Pleistocene fossil avifauna of the Thylacoleo Caves: non-passerines

Manuscript enclosed

The following manuscript comprises work that has not been submitted for publication, and has not undergone external peer review.

Context

This manuscript documents the diversity of non-passerine birds preserved as fossils within the three Thylacoleo Caves, using a systematic palaeontological approach. Accounts of each identified taxon are given. The composition of the Early and Middle Pleistocene fossil assemblages from Leaena's Breath Cave are compared, and are used to make inferences about the Pleistocene palaeoecology of the Nullarbor Plain. The significance of the results for understanding the Pleistocene history of the Australian avifauna is discussed.

4.0 Abstract

The Early and Middle Pleistocene (2.58 Ma to 126 kyr ago) are intervals that are particularly poorly represented in the Australian fossil landbird record. Although dramatic climatic fluctuations during the Pleistocene are regarded as key drivers in the evolution of new species and subspecies of birds in Australia, the fossil record has so far provided little perspective on how closely the Pleistocene avifauna resembles that of the Holocene. The present study of fossil non-passerine birds from the Thylacoleo Caves, beneath the arid, treeless Nullarbor Plain, Western Australia, is the first in-depth investigation of an Australian landbird assemblage from either the Early or Middle Pleistocene. Nearly 60 taxa are represented, making this the most diverse Pleistocene avian assemblage yet discovered in Australia. Fourteen species (24.1%) are either known or suspected to be extinct, of which most were found only in the Early Pleistocene. The Early Pleistocene assemblage is diverse, with a mixture of woodland, open-habitat and wetland taxa represented. The Middle Pleistocene assemblage has fewer taxa and contains species characteristic of open habitats, indicating the loss of trees by this interval and a transition to a habitat similar to that of the modern Nullarbor. The transition from a moist, woodland habitat in the Early Pleistocene to an arid, open habitat in the Middle Pleistocene, with low bird diversity and the disappearance of most of the extinct taxa, raises the possibility that the 'mid-Pleistocene transition' caused range changes and species extinctions within the Australian avifauna. Extinction may have played a greater role in shaping the modern Australian avifauna than has previously been suspected.

Chapter 4: The Early and Middle Pleistocene fossil avifauna of the Thylacoleo Caves: non-passerines

4.1 Introduction

4.1.1 Australian birds during the Pleistocene

The diversity and geographical distribution of the modern Australian avifauna has long been viewed as a legacy of the climatic cycles of the Pleistocene epoch (2.58 Ma to 11.7 kyr ago). Since at least the mid-20th Century (e.g. Mayr 1944; Gentilli 1949; Keast, 1961), it has been recognised that the global glacial-interglacial cycles that characterise the Pleistocene must have had a profound influence on the diversity and distribution of Australian landbirds. Many extant taxa are thought to have evolved through the repeated isolation of populations by aridity barriers and habitat refugia as the Australian continent became more arid during the Plio-Pleistocene, and the distinctive regional species assemblages of today are also considered to have formed as a result of these processes (e.g. Cracraft, 1986; Ford 1987; Schodde and Mason 1999; Schodde 2006; Toon et al. 2007).

However, scientific understanding of the climatic complexity of the Pleistocene has undergone a revolution over the last few decades (Walker and Lowe 2007), transforming the lens through which modern faunas must be viewed. Consistent with knowledge at the time, Keast (1961) considered that the Australian climate, and thus the continental avifauna, had been influenced by just four major Northern Hemisphere glaciations during the Pleistocene. Today, more than 100 Pleistocene marine oxygen-isotope stages (MIS) have been defined, representing ~50 global glacial-interglacial cycles (Cohen and Gibbard 2011; Gibbard and Lewin 2016). Any attempts to understand the Pleistocene history of the Australian avifauna must now, therefore, take account of this much more complex palaeoclimatic framework. Genetic studies of bird evolution and geography are increasingly investigating the impacts of this complexity on the avifauna (e.g. Joseph and Wilke 2006; Toon et al. 2007; Joseph and Wilke 2007; Joseph et al. 2008; Kearns et al. 2010; Dolman and Joseph 2012; Toon et al. 2012; Joseph et al. 2013; Dolman and Joseph 2015, 2016; Toon et al. 2017).

While genetic studies inferring evolutionary and biogeographical trends among Australian landbirds during the Pleistocene have grown in number and sophistication over the last decade, there have been virtually no in-depth studies of fossil landbird assemblages over this same period. The most substantial investigations of Australian Quaternary fossil bird assemblages undertaken to date remain those on Late Pleistocene (126–11.7 kyr) and Holocene (11.7 kyr to present) cave sites from southern Australia by Robert F. Baird for his PhD thesis (Baird 1986, and associated publications). The avian components of some key Pleistocene fossil localities that have revealed much about Australia's extinct marsupial fauna, including the Wellington Caves in New South Wales (Dawson, 1985), the Mt Etna Caves in Queensland (Hocknull, 2007) remain virtually unstudied, and in the case of the Naracoorte Caves in south-eastern South Australia, bird fossils have only received cursory attention (e.g. van Tets and Smith, 1974).

There are major geographical and temporal gaps in the Pleistocene fossil record for Australian birds. Pleistocene-aged fossil localities that preserve diverse landbird assemblages are few, and are heavily biased towards sites in the mesic fringe of southern Australia. Just three localities that pre-date the Late Pleistocene are known to contain a fossil fauna preserving 10 or more bird species (Figure 4.1). Of these, the avian component of the Mt Etna Caves has not been published, the Middle- to Late Pleistocene Victoria Fossil Cave avifauna has been briefly documented (van Tets and Smith 1974) but has not been analysed within a temporal framework, and only a preliminary investigation of the Thylacoleo Caves avifauna has been published (Prideaux et al. 2007). Therefore, the Australian fossil landbird record during the Early Pleistocene (2.58 Ma to 780 kyr) and Middle Pleistocene (780–126 kyr), which together comprise the first 2.4 million years – nearly 95% – of the Pleistocene epoch – is very poorly understood. As a result, we still know remarkably little about which bird species lived where at different points during the Pleistocene, and have knowledge of how many bird taxa may have gone extinct during this epoch. Prior to 2016, only ten extinct Pleistocene Australian birds were known. Descriptions of new species of coucal and megapodes have increased this number by 50% (Shute et al. 2016, reproduced in Chapter 2; Shute et al. 2017, reproduced in Chapter 3).

We thus currently lack perspective on how closely the modern Holocene avifauna of Australia resembles that of the immediately preceding Pleistocene epoch, in terms of both diversity and geographical distribution. It is difficult, then, to discern what overall effects the climatic cycles of the Pleistocene had on the avifauna. Australia is not unique in this regard: over the last decade, debate has grown about what overall effects the Pleistocene climatic cycles had on the global diversity of birds (Nadachowska-Brzyska *et al.* 2015). Some authors (e.g. Johnson and Cicero, 2004; Weir and Schluter, 2004) have argued that the Pleistocene saw a net increase in the number of bird taxa due to high rates of vicariant speciation. Others (e.g. Zink *et al.*, 2004) have contended that speciation rates were lowered, or that high speciation rates were balanced out by extinctions for no net gain in the number of bird taxa.

There is reason for optimism that some of the major global avifaunal trends of the Pleistocene may ultimately be discernible from the fossil record. Renewed interest in studying fossil bird assemblages worldwide has led to the recent discovery of some previously cryptic range changes and extinctions that occurred during the Pleistocene, in both continental and island contexts, in northern Europe, the Americas and Asia (e.g. Meijer and Due 2010; Steadman and Mead 2010; Oswald and Steadman 2011;

Meijer et al. 2013; Holm and Svenning 2014; Meijer 2014; Meijer et al. 2015; Oswald and Steadman 2015; Steadman et al. 2015; Stewart and Jacobi 2015). The present study represents the first detailed examination of a diverse Pleistocene landbird assemblage from the Australian Pleistocene in nearly 30 years, contributing an antipodean perspective on the Pleistocene trajectory of the global avifauna.

Figure 4.1: Key Quaternary fossil bird sites of Australia. Numbers in brackets represent the number of avian taxa identified from each site or locality. Names in bold type are those known to preserve an Early or Middle Pleistocene fossil assemblage. Names in regular type are those dated to the Late Pleistocene, Holocene, or that are of unknown age.

4.1.2 Significance of the Thylacoleo Caves fossil avifauna

With the discovery in 2002 of the Thylacoleo Caves, beneath the Nullarbor Plain in south-central Australia, has come an unprecedented opportunity to study the Pleistocene history of Australian landbirds based on the fossil record. The caves contain: the most diverse Pleistocene vertebrate fauna yet known from the western half of Australia; the oldest vertebrate remains from the south-central region of the continent; and some of the best-preserved and complete specimens of extinct Pleistocene marsupials ever found (Prideaux et al. 2007). Bird remains are abundant in the deposit, and are very well preserved. Uniquely in Australia, the Thylacoleo Caves fossil fauna is known to span both the Early and Middle Pleistocene (Prideaux et al. 2007), allowing an investigation of a particularly turbulent interval of the Pleistocene, referred to as 'the mid-Pleistocene transition' or the 'mid-Pleistocene revolution' (Ford *et al.* 2016): at the end of the Early Pleistocene and beginning of the Middle Pleistocene, alterations in the Earth's orbit led to the 41-kyr glacial-interglacial cycles that had previously prevailed giving way to a pattern of longer, 100-kyr cycles. Although there was little glaciation in Australia, the mid-Pleistocene transition saw the continent affected by a heightening of arid conditions (Pillans and Bourman, 2001). Any effects this may have had on the avifauna on a continental scale are yet to be detected in the fossil landbird record, although increased aridity may have led to the extinction of aquatic taxa such as flamingos (e.g. Miller, 1963) and palaelodids (Baird and Vickers-Rich 1998) from central Australia.

In part, the importance of the Thylacoleo Caves fossil assemblage comes from the fact that it contains numerous new extinct vertebrate taxa unknown from any other locality to date. New species from the caves include seven kangaroos (Prideaux et al. 2007), most notably two species of tree-kangaroo (Prideaux and Warburton 2008, 2009), four species of bird (Shute, Prideaux, and Worthy 2016, 2017), and a species of tree-frog (Tyler and Prideaux 2016). However, another equally important aspect of the Thylacoleo Caves fauna is what it can reveal about the Pleistocene palaeoecology of the Nullarbor Plain, an arid, treeless region that has long been regarded as one of Australia's major Pleistocene aridity barriers, particularly for birds (e.g. Schodde, 2006).

The loss of woodland habitat from the Nullarbor Plain is thought to have occurred multiple times during the Pleistocene in response global climatic cycling, isolating animal populations in south-western and south-eastern Australia from each other, and driving vicariance events amongst many taxa including birds (e.g. Dolman and Joseph 2012). However, the date that trees were finally lost from the Nullarbor is unknown. Complicating matters, recent genetic studies have shown that the 'Nullarbor Barrier' appears to have prevented the dispersal of some animal taxa during the Pleistocene, whilst leaving others unaffected, as reviewed by Neaves et al. (2012). The Thylacoleo Caves fossil fauna, therefore, is of particular value for investigating the palaeoecology of the Nullarbor Plain, and the diversity of the regional avifauna, during a crucial but poorly understood window of time.

The preliminary palaeoecological study of the Thylacoleo Caves fauna, which focused primarily on the mammalian component, was based on a time-averaged assemblage considered to be of Middle Pleistocene age (Prideaux et al. 2007). The presence of numerous grazing, browsing and arboreal mammals, hollow-nesting parrots, along with isotopic evidence for low rainfall during the Middle Pleistocene, resulted in an interpretation of the local ecology as comprising a mosaic of floristically diverse woodland and shrubland, under an arid climatic regime. Importantly, the presence of arboreal taxa such as tree-kangaroos, possums and parrots indicated that trees persisted on the Nullarbor Plain into the Middle Pleistocene, while isotopic data from marsupial teeth showed that average rainfall on the Nullarbor Plain during the Middle Pleistocene was only a little higher than today (Prideaux et al. 2007). The apparent persistence of trees on the Plain despite relatively arid conditions does not fit the traditional view that the Nullarbor Plain lost its tree canopy due to increasingly arid conditions during the Pleistocene. The timing and reasons for the ultimate loss of trees from the Nullarbor Plain thus requires investigation and explanation.

Bird fossils were included as a minor component of the initial palaeoecological interpretation of the Thylacoleo Caves, with around 18 bird taxa from eight orders having originally been identified (Table 4.1), most of which were collected from surface deposits within the caves and are therefore of uncertain age. Further excavations at the locality have since uncovered a much larger collection of fossils spanning both the Early and Middle Pleistocene, including hundreds of bird bones. The assemblage now offers an unprecedented opportunity to analyse the diversity and ecology of birds at a key biogeographical location in southern Australia, during an interval that straddles the ‘mid-Pleistocene transition’.

4.1.3 Aims

The aims of this study are: 1) to document the diversity of the non-passerine birds from the Thylacoleo Caves locality during the Early and Middle Pleistocene using a systematic palaeontological approach; 2) to analyse the composition of the avifauna through time to determine whether it differs between the Early and Middle Pleistocene, and determine whether the avifauna supports the palaeoecological interpretation by Prideaux *et al.* (2007) that the local Pleistocene habitat comprised a mosaic of woodland/shrubland in an arid- to semi-arid climatic regime; and 3) to determine whether the Thylacoleo Caves fossil fauna records range changes in extant species of bird, with particular reference to the role of the Nullarbor Plain as a biogeographical barrier to the dispersal of birds in southern Australia during the Pleistocene.

Table 4.1: Bird taxa identified from initial excavations of the Thylacoleo Caves (from Prideaux *et al.* 2007); ***The genus name *Leipoa* was used by Prideaux *et al.* (2007) for this species; the name *Progura* is used here, in light of the taxonomic work by Shute et al. (2017) (see Chapter 3); **§**The genus name *Gallinula* was used for *Tribonyx ventralis* in the original publication

Order	Family	Genus/species	Common name
Casuariiformes	Casuariidae	*Dromaius novaehollandiae*	Emu
Galliformes	Megapodiidae	*Progura gallinacea**	Giant Malleefowl†
Accipitriformes	Accipitridae	Accipitridae indet.	Indeterminate bird of prey (small)
		Accipitridae indet.	Indeterminate bird of prey (medium)
Falconiformes	Falconidae	*Falco cenchroides*	Nankeen Kestrel
		Falco sp. indet.	Indeterminate kestrel/falcon
Gruiformes	Rallidae	*Tribonyx ventralis*§	Black-tailed Nativehen
Strigiformes	Tytonidae	*Tyto* sp. cf. *T. alba*	Barn Owl
		Tyto sp. indet. 1	Barn owl, indet. species 1
		Tyto sp. indet. 2	Barn owl, indet. species 2
Psittaciformes	Psittaculidae	*Barnardius zonarius*	Australian Ringneck parrot
		cf. *Melopsittacus undulatus*	Budgerigar
		Psittacidae indet.	Indeterminate parrot (medium)
Passeriformes	Corvidae	*Corvus mellori*	Little Raven
		Corvus orru	Torresian Crow
	Indet.	Passeriformes indet. (≥3)	Indeterminate passerines (≥3 spp.)
Totals 8	**≥9**	**≥18**	

4.2 Materials and methods

4.2.1 Locality data

Three limestone caves – Leaena's Breath Cave (hereafter LBC), Flightstar Cave (FSC) and Last Tree Cave (FSC) – collectively comprise the Thylacoleo Caves locality. They sit in a remote location beneath the surface of the Nullarbor Plain, Western Australia, in the arid climatic zone (Figure 4.2). Their exact locations are not publically disclosed, but coordinates of each cave are lodged with the Department of Earth and Planetary Sciences, Western Australian Museum, Perth. All three caves, which are within an approximately 20 km radius of one another, contain a similar Pleistocene vertebrate fossil fauna, and include a mixture of extant and extinct taxa (Prideaux *et al.* 2007).

LBC and FSC share a similar structure, and are accessed from the surface of the Nullarbor Plain through a small (<1 m diameter) opening in the calcrete cap that sealed their entrances until recently (Prideaux *et al.* 2007) (Figures 4.3 and 4.4). LTC has a different structure to the other two caves, and is accessible via a relatively large, sloping walk-in entrance within a shallow doline.

Both LBC and FSC are entered by abseiling down their single vertical solution pipe entrances, which descend through an approximately 10-m thick layer of limestone before opening into the caverns below. Both have an area of rockfall beneath the entrance (e.g. Figure 4.5), with a relatively flat-floored chamber comprising silty clay infill sediment opening out at the foot of the rockpile, beneath ceilings bearing stalactites.

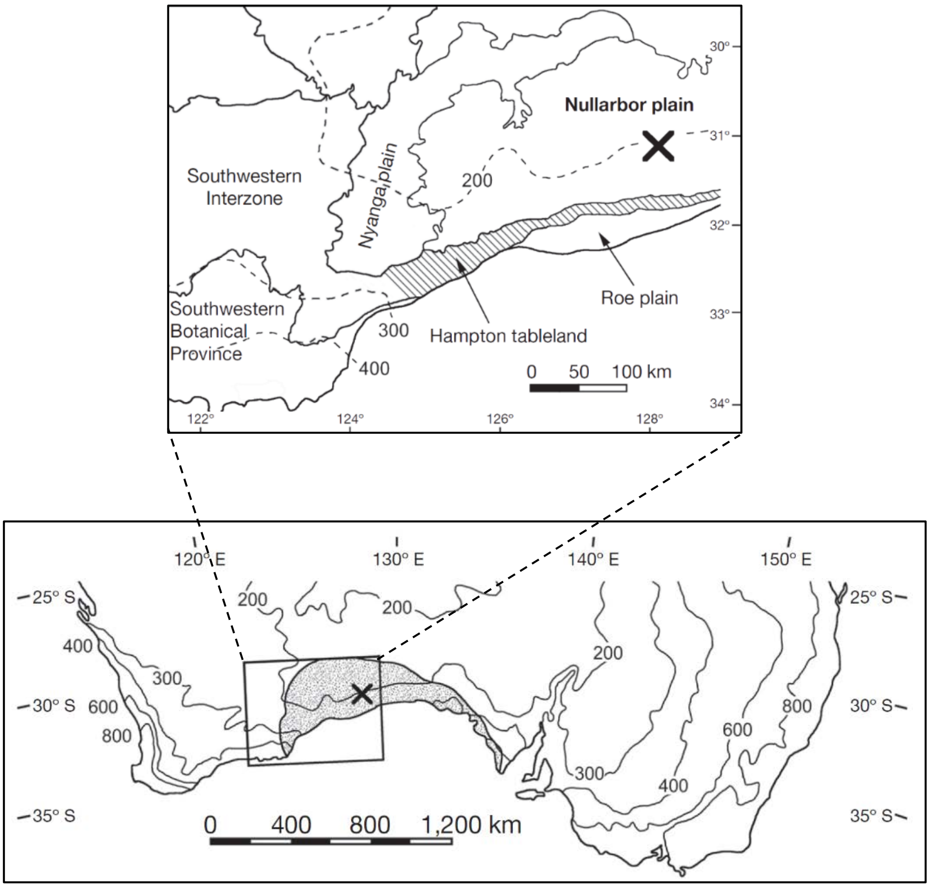


Figure 4.2: Location of the Thylacoleo Caves, Nullarbor Plain, Western Australia (marked by black X), showing the Eucla Basin (grey stippled area in lower map), and mean annual rainfall isohyets (mm) (adapted from Prideaux et al. 2007)

A map of LBC, based on a three-dimensional survey and reconstruction of the cave, can be found in Figure 4.6, and is marked with the numbered locations from which many surface specimens included in this study were collected. For a plan-view map of FSC, see Figure 4.7, and for LTC, Figure 4.8.

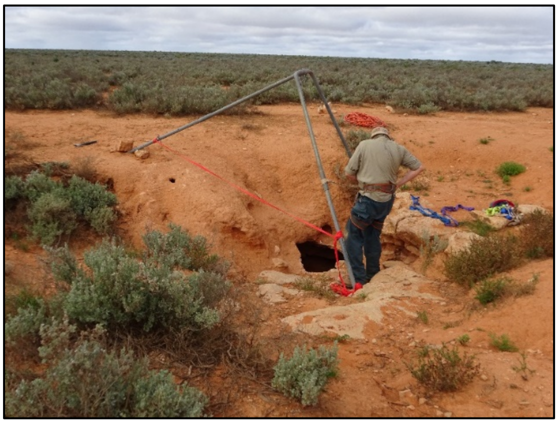


Figure 4.3: Entrance to Leaena's Breath Cave, 2014 (photograph courtesy of the Flinders University Palaeontology lab)

Figure 4.4: Entrance to Flightstar Cave, 2014 (photograph courtesy of the Flinders University Palaeontology lab)

Figure 4.5: Looking back towards the rockfall area beneath the solution pipe entrance to Leaena's Breath Cave, 2009. The partially-dug Pit B can be seen in the right foreground, at the foot of the floodlight. Ernie Lundelius for scale (photograph courtesy of the Flinders University Palaeontology lab)

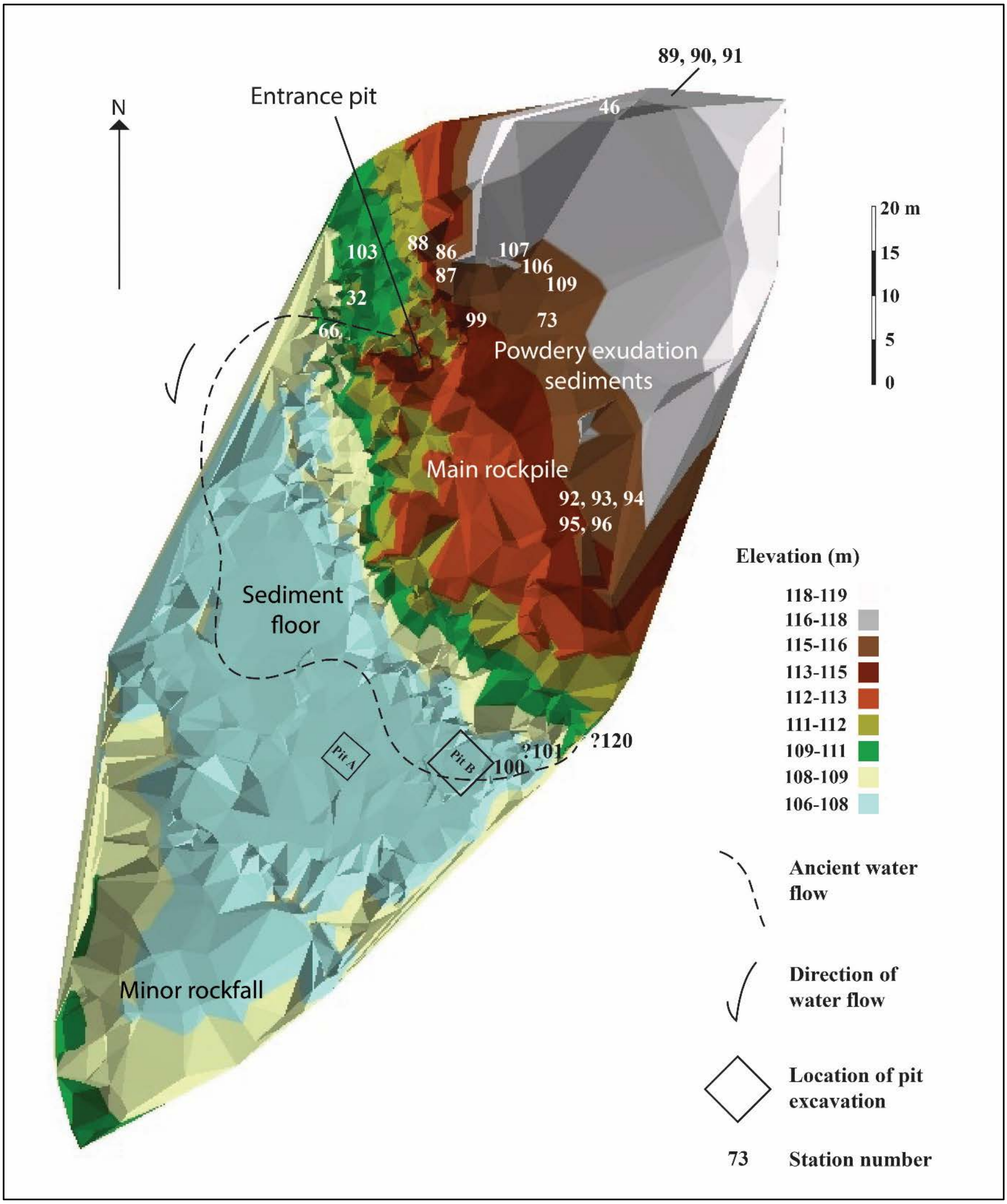
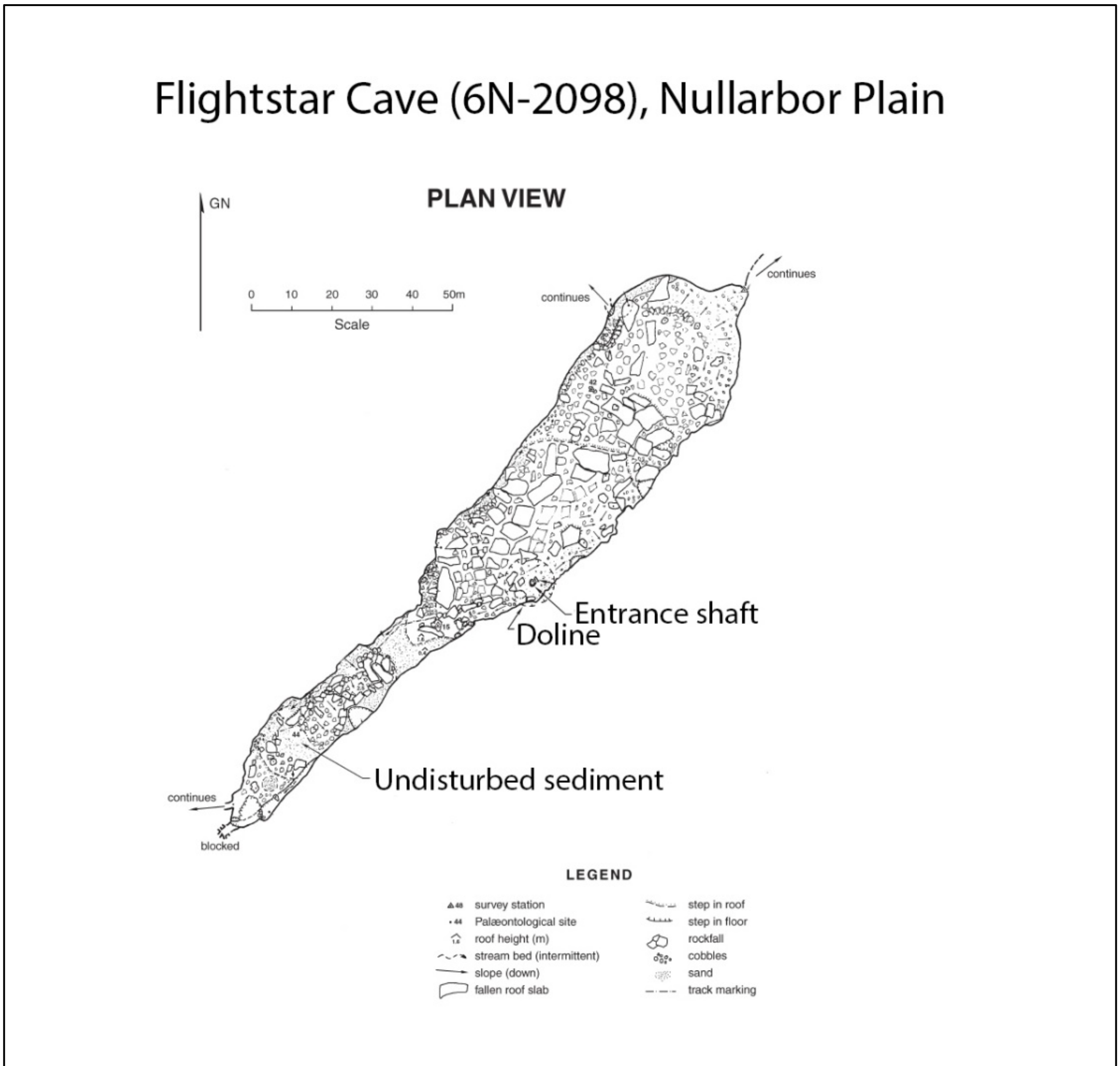


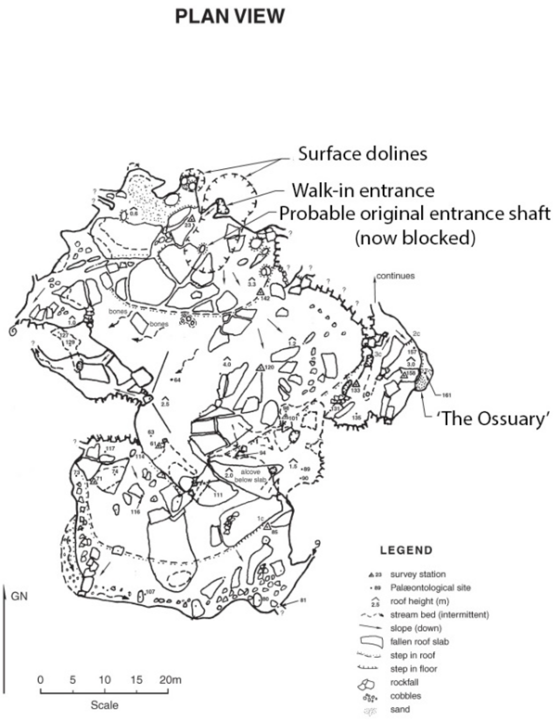
Figure 4.6: Map of Leaena's Breath Cave. Based on survey and 3D reconstruction by Samuel Arman (2017), geological interpretation of the cave by N. Mayman, K. Boland, P. Devine and M. Norton (2004), and field notes by Paul Devine.



Modified from ASF Map No. 6N2098.CEG3161, drawn by Peter Ackroyd, Nov. 2003
Surveyed by P. J. Ackroyd & R.A. Gibbons, of the Cave Exploration Group, South Australia, 18-19 July 2002
Survey length, 495 m. Cave depth, 36.5 m

Figure 4.7: Map of Flightstar Cave, in plan view

Last Tree Cave (6N-2121), Nullarbor Plain



Modified from ASF Map No. 6N2121.CEG3162, drawn by Peter Ackroyd, Nov. 2003
Surveyed by P. J. Ackroyd, R.A. Gibbons, K.M. Boland & P.D. Devine of the Cave Exploration Group, South Australia, 8-16 July 2002
Survey length, 696 m. Cave depth, 40.5 m

Figure 4.8: Map of Last Tree Cave, in plan view

Unlike LBC and FSC, LTC lacks an extensive sediment floor. The cave entrance leads into an entrance chamber with a low ceiling, beyond which the main chamber branches in two main directions (Figure 4.8). Directly ahead of the entrance lies the main chamber, which has a high ceiling and contains a steep area of rockfall comprising large limestone boulders, extending nearly to the far wall of the cavern. At the foot of the rockfall area, the chamber branches off into smaller side-chambers, from which some fossils were recovered. To the left of the cave entrance, a convoluted area of rockfall with a low ceiling winds down deep into the cave, with guide ropes needed to assist climbing down the boulders to reach "The Ossuary" (Figure 4.8), a small but bone-dense chamber with a low, overhanging ceiling, and a floor of powdery limestone breakdown material (Figure 4.9). The presence of associated and articulated marsupial skeletons (e.g. Figure 4.10) indicates that The Ossuary is a gravity lag deposit (Prideaux *et al.* 2007). It is unclear where fossils entered LTC during the Pleistocene, but they may have accumulated via a now blocked entrance about 8 m away from the present entrance (Figure 4.8) (Prideaux et al. 2007).

Figure 4.9: "The Ossuary", Last Tree Cave, 2002 (photograph courtesy of Clay Bryce, Western Australian Museum)

Figure 4.10: Articulated macropodid skeleton being excavated from The Ossuary, Last Tree Cave, 2004 (photo courtesy of the Flinders University Palaeontology lab)

4.2.2 Collection and curation of fossils

The fossil material examined in this study was collected over successive field seasons by teams of workers between 2002 and 2014. All previously examined material is re-appraised here, along with material that was excavated more recently and which has not previously been studied. Specimens included in this study are registered with a catalogue number from the Western Australian Museum, in the format e.g., WAM 15.9.215. All specimens will ultimately be deposited in the Department of Early and Planetary Sciences, Western Australian Museum, Perth.

Specimens included in this study come from two major depositional contexts: surface fossils, which lay exposed on top of or between boulders inside the caves, or on top of cave fill sediments; and those dug from pit excavations in the infill sediment floor of LBC. In general, larger bones, whether they were recovered from the surface or from pit excavations, were collected and treated individually as they were found. To prevent damage, they were treated immediately with Mowital® plastic consolidant dissolved in ethanol, allowed to dry, and were individually wrapped for transport. Smaller bones were removed in bulk sediment from the pit excavations in LBC and were processed above ground. After removing bulk sediment from the cave, it was first dry-sieved to remove loose material such as limestone clasts, and then wet-sieved to remove as much fine sediment as possible. The fossiliferous residue was then air-dried and transported to Flinders University in Adelaide.

Most surface fossils from the three caves were collected during the earliest field seasons. Their locations were recorded in notes by the late caving expert Paul Devine. Where possible, these locations have been determined based on field collection tags and the corresponding notes and sketches in his note books and on maps produced by cave explorers. Location data are reported along with specimen catalogue numbers (see Systematic Palaeontology). Some collection locations are referred to only by informal sub-site names (e.g. 'Metasthenurus Chamber', 'Two Bird Corner'). Other surface locations are recorded more precisely: The Ossuary sub-site in LTC was divided into a slightly irregular grid, with specimens having been labelled with the relevant grid number; while most of the surface specimens from the rockpile and sediment floor of LBC have an associated station number (e.g. Station 100), locations of which were either directly surveyed, or were annotated with reference to a surveyed location. Some of these station numbers were marked on a 2D map of LBC produced by N. Mayman, K. Boland, P. Devine and M. Norton in 2004. Approximate locations of stations from which bird remains were collected have been transferred from the 2D map onto a 3D reconstruction of the cave (Figure 4.6), along with additional station numbers for bird specimens that were collected during later fieldwork seasons and which were recorded in Paul Devine's notes but did not appear on the 2004 map.

Other specimens in this study were excavated from pits dug in the sediment floor of LBC. Two pits, Pit A and Pit B (locations shown in Figure 4.6), were dug over successive field seasons. Pit specimens are recorded with their pit name (e.g. B), the 1-m square quadrat from which they were excavated (e.g. 3), the depth from which they came (e.g. 120–125 cm below the sediment surface), and the sedimentary unit in which they were found (e.g. Unit 3), thus as an example, location data for a specimen are recorded in the format B3, 120–125 cm, Unit 3. Collection location is recorded along with taxonomic identifications in a specimen database (see Supplementary Information). More details about the pits and their stratigraphy are given below.

4.2.3 Age of fossils and stratigraphy of pit excavations

4.2.3.1 Surface fossils

Surface fossils from all three caves are of uncertain age. As with those excavated from pits, which have better age constraints, surface specimens comprise a mixture of extinct and extant taxa. Some bird specimens from the cave floors are obviously of very young Holocene age (e.g. mummified remains; these are not included in this study), but most are inferred to be of Pleistocene age. This inference is based on: the state of preservation of bone (disarticulated, chalky and lacking any collagen); co-deposition with the remains of mammalian megafaunal species that elsewhere went extinct during the Pleistocene; a Middle Pleistocene age of ~390 kyr obtained via Uranium-series dating on a sample of corraline calcite that was deposited on top of a marsupial bone from the surface of LBC; OSL ages of ~230 kyr obtained for sediments at a depth of 20 cm in FSC and ~101 kyr for sediments at a depth of 5 cm in LTC; and the fact that the caves were sealed until recently by a calcrete cap (Prideaux *et al.* 2007). However, a mixture of Pleistocene and Holocene ages for surface specimens cannot be ruled out.

4.2.3.2 Stratigraphy of infill sediment in LBC

The initial excavation of infill sediments in LBC comprised a 0.5 m^2 X 1.3m-deep test pit, which was dug down the sedimentary profile in depths (spits) of 10 cm (Prideaux *et al.* 2007). The test pit was used to quickly assay the depth and stratigraphy of the cave infill sediment, the quantity of bone contained within it, and to obtain sediment samples for dating. The test pit was later extended and incorporated into Pit A (Figure 4.6). The test pit revealed the sedimentary profile of the infill sediment to be divided into three relatively uniform, horizontal stratigraphic units comprising silty clay (Figure 4.11), interpreted to be alluvial in origin. No fine laminations were identified.

The sediment comprising Unit 1 (0–35 cm below the surface of the cave floor) has a smooth, compacted texture, and contains a moderate density of bone. Beneath this, Unit 2 sediment (35–55 cm) is slightly coarser and darker, and is almost barren of bone, perhaps suggesting more rapid deposition than Unit 1. Unit 3 (55–170 cm) sediment is slightly lighter in colour than Unit 2, but has a similarly coarse texture, and contains abundant bone. The same units that were identified within the test pit are also evident in Pit B, and deposition of sediment in the two pits is presumed to be contemporaneous.

4.2.3.3 Dating of infill sediments in LBC

OSL dating of a near-surface sediments sample from the test pit in LBC returned a Middle Pleistocene age (>195 ± 15 kyr), at a 68% confidence interval (Prideaux et al. 2007). Further specimens for single-grain OSL dating were collected from the wall of Pit A in 2014, the results of which are not yet available. Magnetostratigraphic assessment of test-pit sediments revealed an interval of reversed magnetic polarity between depths of 50–70 cm (Prideaux et al. 2007; Figure 4.12). This was interpreted as representing the last such reversal, the Matuyama-Brunhes boundary, dated worldwide at approximately 780 kyr. This designates the chronostratigraphic boundary between the Middle and Early Pleistocene (Pillans 2003). Thus, when evidence from OSL dating and magnetostratigraphy are combined, the infill sediments in LBC and the fossils they contain are considered to be ≥780 kyr old below a depth of 50 cm, and thus of Early Pleistocene age, while those shallower than 50 cm are between 780 kyr and 195 kyr old, and thus date to the Middle Pleistocene. The maximum age of the deepest sediments in the LBC sequence is unknown.

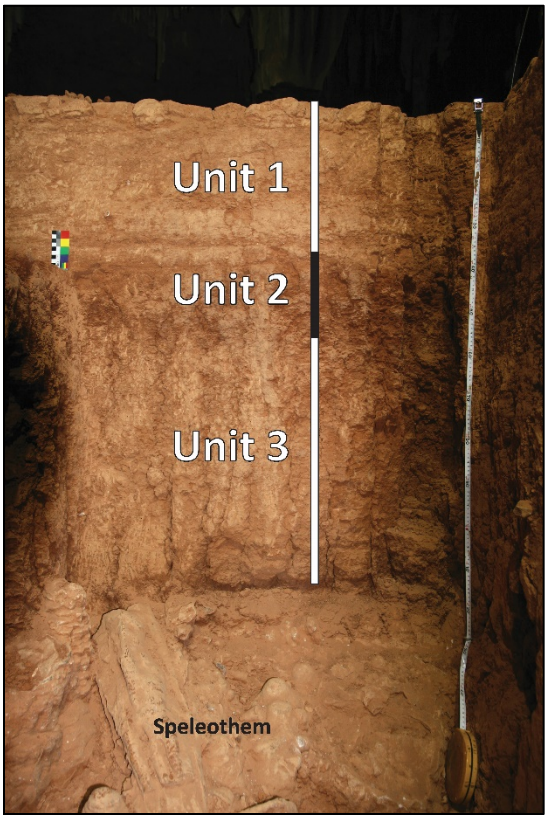


Figure 4.11: Stratigraphic units in the infill sediment of Leaena's Breath Cave (Pit A)

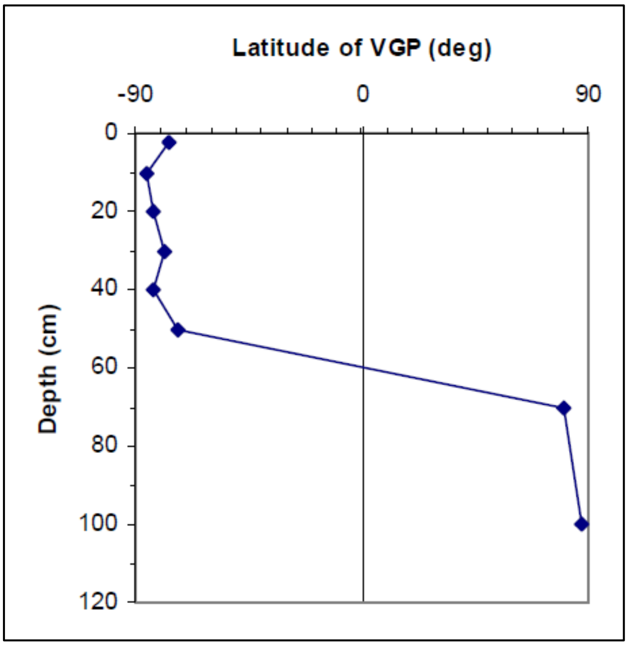


Figure 4.12: Palaeomagnetic signature from test pit excavation in Leaena's Breath Cave, plotted as latitude of Virtual Geomatgnetic Pole (VGP) against depth below sediment floor (from Prideaux et al. 2007, Supp. Info.)

Pit A is relatively small, measuring 2 x 2 m^2, and is divided into four 1-m^2 quadrats (Figure 4.13). As at the end of excavation in 2013, the four quadrats were dug to depths as follows: A1, 45 cm; A2, 155 cm; A3, 45 cm; A4, 180 cm. Pit B (Figure 4.14) was larger in area (3 x 3 m), with eight of its nine 1 m^2 quadrats having been dug to varying depths (the ninth was not excavated as at 2013). As at the end of excavation in 2013, the eight excavated quadrats were dug to depths as follows: B1, 130 cm; B2, 135 cm; B3, 145 cm; B4, 115 cm; B5, 140 cm; B6, 95 cm; B7, 40 cm; B8, 60 cm.

Due to the position of Pit B immediately at the modern foot of the rockpile, which extends beneath the sediment floor, quadrats in this pit contain large limestone boulders that were buried by the silty clay infill sediments during the Pleistocene. Although the boulders took up a considerable volume of some quadrats (Figure 4.14), fossils were abundant in the crevices between and beneath some of the boulders. It is unclear whether these fossils were already in place and were simply buried by alluvial sediments, or whether they were washed into the crevices by flood events. A mixture of both may have occurred.

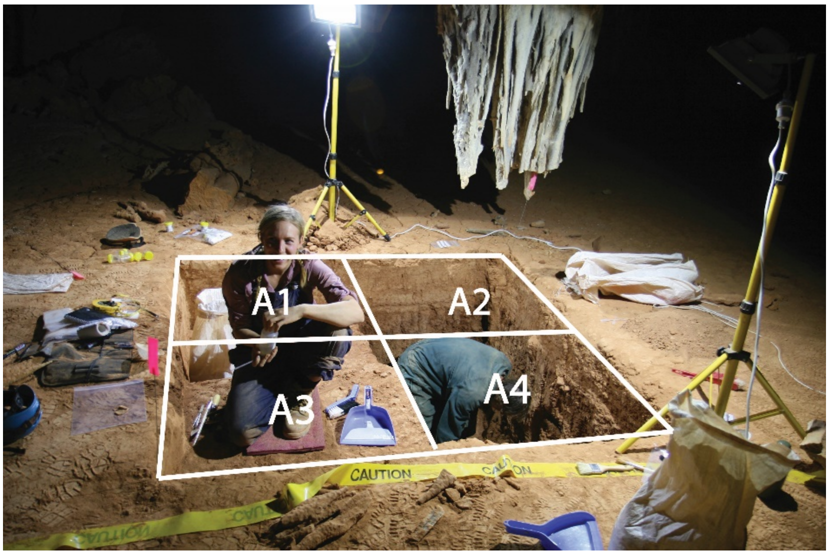


Figure 4.13: Quadrats in Pit A, Leaena's Breath Cave, 2013, looking south-east; pictured excavators – Rebecca Värttö left, Roger Matthews, right

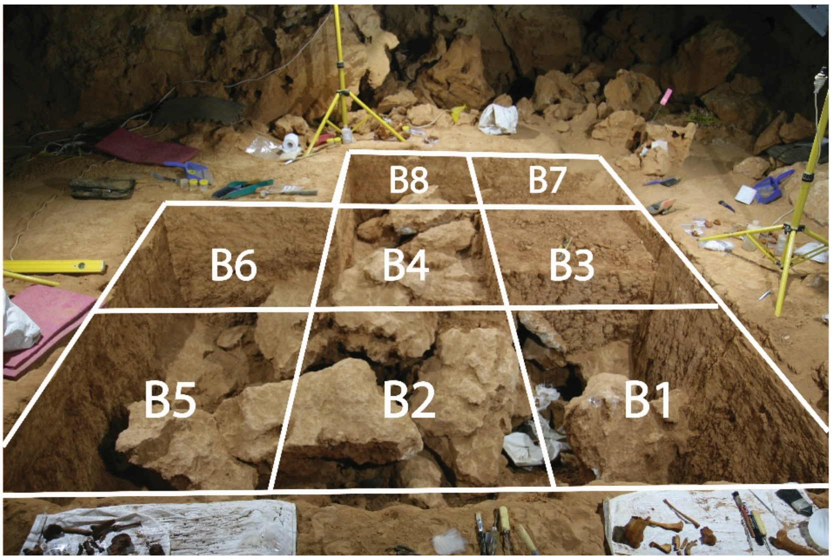


Figure 4.14: Quadrats in Pit B, Leaena's Breath Cave, 2013, looking north-east towards the foot of the rockpile, which can be seen in the background

With the exception of the portion of Pit A that comprised the original test pit, which was dug in spits of 10 cm, pits A and B were excavated in spits of 5 cm. The silty clay sediments were hard and dry, being above the modern water table, and had to be loosened with metal trowels. Fossiliferous sediment was loaded into sacks for transport using dustpans and brushes, ensuring that there was no mixing of material from different 5-cm spits. Sacks of sediment were labelled with a plastic tag noting the cave, pit, quadrat number, spit depth, and stratigraphic unit (1, 2 or 3). Care was taken at all stages of sediment processing and specimen identification to ensure that this stratigraphic information remained associated with the fossils. After processing of the sediment aboveground (see Section 4.2.2), fossils were later sorted from the remaining sediment using a small paintbrush ready for identification. The sorting process was carried out by various staff, students (myself included) and volunteers of the Flinders University Palaeontology Laboratory.

4.2.4 Abbreviations

ALA – Atlas of Living Australia; dL – distal left; dR – distal right; DW – distal width; FSC – Flightstar Cave; GBIF – Global Biodiversity Information Facility; HANZAB – Handbook of Australian, New Zealand and Antarctic Birds; LBC – Leaena's Breath Cave; LTC – Last Tree Cave; MNI – minimum number of individuals; NISP – number of individual specimens; NMV – National Museums of Victoria, Melbourne; pL – proximal left; pR – proximal right; PW – proximal width; QM – Queensland Museum, Brisbane; SAM – South Australian Museum, Adelaide; SW – shaft width; TL – total length; WAM – Western Australian Museum, Perth.

4.2.5 Analyses

4.2.5.1 Identification of fossils

I personally attempted identification of all fossil material included in this study. Where necessary, I sought expert advice on specimens that I could not readily identify. Identification effort focused on fossils from Pit B, which was the larger and more productive of the two pits and was selected for the palaeoecological analysis of the avifauna. A limited number of specimens from Pit A were also identified, and these are documented in the Systematic Palaeontology section. A comprehensive analysis of specimens from this pit will be completed at a later date.

The birds fossils identified during this study include some associated skeletons but mostly comprise isolated skeletal elements. I have attempted to identify all cranial and the main pelvic and pectoral girdle elements of the post crania. All identified specimens identified as belonging to non-passerine taxa are documented in the Systematic Palaeontology section. Hundreds of specimens identified as belonging to the order Passeriformes are not included and will form the basis of a separate study.

The specimen identification process was iterative, with each specimen examined multiple times. In the initial round of identification I referred specimens to order, by direct comparisons with skeletons of modern representatives of the orders of birds currently found in Australia. After the initial referral to order, I refined the identifications to as low a taxonomic level as possible by making comparisons with a wider range of modern skeletal specimens within each order, family, and genus. Where relevant, I also made comparisons with Quaternary fossil bird material in the Palaeontology collections of the South Australian, Australian, and Queensland Museums. If skeletal specimens of key taxa were not available, I consulted photographs if possible, including those in the primary literature, and those in the photographic archive of the Smithsonian National Museum of Natural History, available at https://collections.nmnh.si.edu/search/birds/. A list of comparative specimens used in this study is provided as Supplementary Information.

The level of taxonomic identification that was possible was limited by the availability of suitable comparative specimens. It was not possible in all cases to compare the fossils with a comprehensive set of reference specimens covering all relevant extant Australian genera or species. This was particularly the case for: 1) taxa that are rare and are thus poorly represented in museum collections; 2) taxa that only occur in locations geographically distant from South Australia, due to the majority of comparative specimens used in this study being those available in the South Australian Museum ornithology collection, which mostly holds local taxa; and 3) taxa that are particularly diverse at the level of family, genus or species, and for which a full suite of comparative specimens was therefore not available, particularly the Charadriiformes and Psittaciformes.

Taxonomy largely follows that of Dickinson and Remsen (2013). Where alternative taxonomy is used, this is specified in the systematic palaeontology section for that taxon or group of taxa. Osteological terminology follows Baumel et al. (1993) unless otherwise stated.

4.2.5.2 Distribution maps

For extant taxa that were identified as occurring outside of their current geographical range, modern distribution maps were generated using the Atlas of Living Australia's Spatial Portal, available at http://spatial.ala.org.au/. In the maps generated, which are included in the Systematic Palaeontology, individual occurrences of a species are shown as red dots, and the core range of the species is depicted as purple shading.

4.2.5.3 New taxa

Extinct and likely extinct taxa are noted as such in the Systematic Palaeontology. Complete differential diagnoses and descriptions were beyond the scope of this study, but notes on key distinguishing morphological features of these taxa are included to aid future systematic work.

4.2.5.4 Measurements

Where relevant, measurements of fossils and comparative specimens are reported in the Systematic Palaeontology. Measurements (mm) were taken with digital callipers, and rounded to one decimal place.

4.2.5.5 Abundance data

The minimum number of individuals (MNI) and number of individual specimens (NISP) for each identified taxon are reported. Associated skeletons that clearly represented a single individual, whether from the surface or from pit excavations, were counted as one individual and are catalogued under a single WAM number. For the majority of specimens, however, abundance data were based on dissociated remains. Isolated elements of the same taxon that could not reasonably be judged to belong to one individual – for example because they were found in different pits or caves, or a left and a right element that were found in close proximity but differed in size – were counted as separate individuals.

Within the pit excavations, MNI of a taxon was calculated based on the most abundant element of that taxon within a 5-cm spit inside each 1-m^2 quadrat. Quadrats and spits have arbitrary boundaries and individuals may have fallen across these boundaries, thus the MNI calculations should be regarded as indicative and not absolute. MNI is used for reporting on the Thylacoleo Cave fauna overall. The palaeoecological analysis of Pit B is based on NISP rather than MNI because most taxa are represented by few specimens. Because of the low abundance of many taxa, they were aggregated into functional guilds for the palaeoecological analyses, with the emphasis being on assessing broad ecological trends rather than trends within individual species.

4.2.5.6 Diversity of the assemblage

For each cave, and for each stratigraphic unit within Pit B of Leaena's Breath Cave, taxonomic diversity is compared at the level of order, family and genus, and where possible, species. The prevalence of extinct or probably extinct taxa in different depositional situations is compared.

4.2.5.7 Palaeoecological analysis of the avifaunal assemblage

The fossil bird assemblage from Pit B of LBC is used to make inferences about the ecology of the Nullarbor Plain during the Early and Middle Pleistocene. Specimens from this pit are relatively well constrained by age (see Section 4.2.3.3), by contrast to surface specimens which are of uncertain age and therefore cannot be used to assess palaeoecological trends through time. Specimens from only the four most productive quadrats in Pit B (Quadrats 1–4) were used for the analyses. The remaining quadrats produced very few specimens each, probably partly because the Pit B quadrats were dug to different depths, but possibly also due to the chance concentration of bone around certain boulders in this pit (see Figure 4.14).

The diversity and ecological characteristics of bird taxa from Pit B were analysed at two scales – firstly by sedimentary unit, and at a finer scale by 10-cm stratigraphic depths. The purpose of analysing the composition of the avifauna by sedimentary unit was to detect whether any broad-scale differences could be detected between the Early and Middle Pleistocene, before and after the ‘mid-Pleistocene transition’. Analysis at a finer scale (10-cm spits) was to investigate whether any shorter-term changes in faunal composition could be detected, bearing in mind that the climate, vegetation and fauna of the region could potentially have been subject to the effects of multiple glacial-interglacial cycles during the period of fossil accumulation (Gibbard and Lewin 2016). Also, it is currently unknown whether the sedimentary sequence in Pit B represents gradual deposition, or brief accumulation events with long hiatuses. Although Pit B was excavated in spits of 5 cm, specimen data were aggregated into increments of 10 cm for the analysis because there were few specimens of most individual bird taxa within any given 5-cm spit.

Ecological characteristics of the taxa identified in this study were determined from the primary literature and from compendium data sources, including the Atlas of Living Australia (ALA), Birdata, and the Global Biodiversity Information Facility (GBIF), all of which have overlapping datasets, as well as from volumes of the Handbook of Australian, New Zealand and Antarctic Birds (HANZAB). Palaeoecological interpretation is based on functional groupings (guilds) of taxa, rather than on individual taxa. Based on the literature, the ecological characteristics of each identified taxon were classified by: activity time (nocturnal, diurnal); feeding guild (carnivore, carnivore/insectivore, insectivore, omnivore, granivore/omnivore, strict granivore, nectarivore); preferred habitat type (aquatic/littoral, open/grassland, shrubland, woodland); and preferred nesting site (ground, dense brush, bushes, tree hollows, tree branches/caves).

Where possible, ecological characteristics of extinct taxa were inferred from closely related species. Similarly, as many ecological characteristics as possible are inferred for taxa that could not be identified to genus/species level, based on characteristics shared among close relatives (e.g. all accipitrids are classified as carnivores). Changes in the relative abundance of specimens from taxa with different ecological characteristics/requirements are used to make inferences about changes in habitat on the Nullarbor Plain through time during the Pleistocene. The ecological characteristics of taxa that comprise the assemblage are also used to detect potential taphonomic biases in the accumulation of fossils that could overprint and obscure an ecological signal.

4.2.5.8 Rarefaction analysis

Rarefaction curves, also known as species discovery curves, were calculated for the avifaunal fossil assemblage from Pit B of LBC, using the software package PAST version 3.0 (Hammer, Harper, and Ryan 2001). Rarefaction curves model the relationship between the number of specimens and the diversity of those specimens. Curves that climb steeply initially and then level off indicate that few additional taxa would be discovered by further sampling. Curves that continue to climb steeply without levelling off indicate that more taxa would be discovered by sampling a larger number of specimens. Rarefaction curves were calculated at the level of sedimentary unit (1, 3 and 3) and at a finer scale for 10-cm spits. In addition to the formal rarefaction analysis, the relationship between numbers of the most abundant taxa in the Pit B assemblage, *Turnix* sp. and *Melopsittacus undulatus*, and diversity of other taxa, was examined, to determine whether the abundance of these taxa could mask the diversity of other birds.

4.3 Results

4.3.1 Identified specimens

A total of 655 bird bone specimens from the Thylacoleo Caves were identified as belonging to non-passerine orders. Most of these (612 specimens; 93.4%) are from Leaena's Breath Cave (LBC), with smaller numbers from Last Tree Cave (LTC) (39; 5.6%) and Flightstar Cave (FSC) (4; 0.6%). Specimens from all three caves are documented in the Systematic Palaeontology section. Within the LBC assemblage of 612 identified specimens, 219 specimens (35.8%) were collected from the surface, and just over half were excavated from Pit B (341 specimens; 55.7%). A further 52 specimens from Pit A (8.5%) were opportunistically identified, and are included in the Systematic Palaeontology.

4.3.2 Summary of non-passerine diversity

4.3.2.1 Number of taxa

During this study, 14 orders, 18 families, and ~58 genera/species of non-passerine bird were identified from the Thylacoleo Caves (Tables 4.2, 4.3 and 4.4). Compared to the baseline avian diversity established for the Thylacoleo Caves by Prideaux *et al.* (2007), this increases the known diversity of non-passerine taxa from the caves at all taxonomic levels, but particularly at the level of genus/species, with an increase from 13 to around 58 taxa having now been identified from the locality (Figure 4.15). Of these, nearly a quarter (14; 24.1%) are either known or are likely to be extinct. Accounts of all identified taxa are given in the Systematic Palaeontology section below.

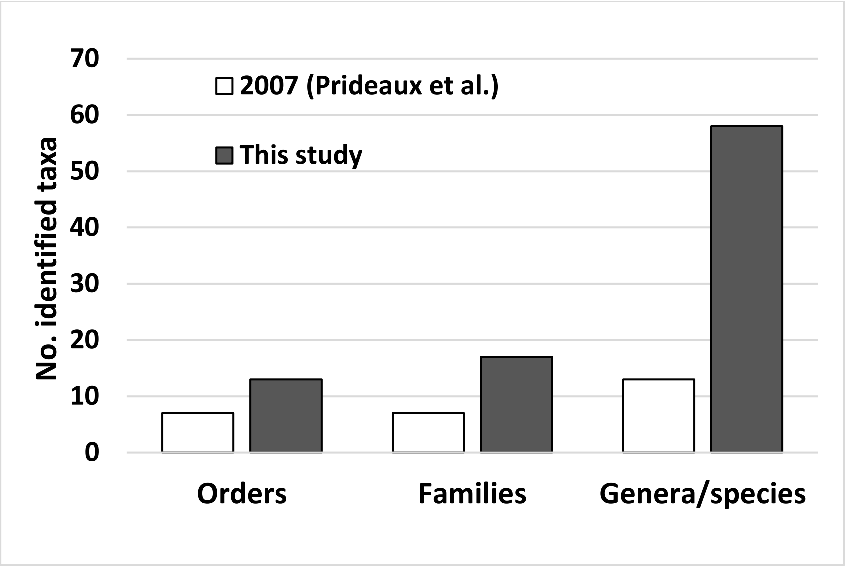


Figure 4.15: Comparison of the known diversity non-passerine birds from the Thylacoleo Caves, 2007 versus 2018

4.3.2.2 Representation of taxa within the three Thylacoleo Caves

By far the greatest number of taxa came from LBC, with 13 orders (Table 4.2), 17 families (Table 4.3) and ~56 genera/species having been identified (Table 4.4). LTC contributed one order (Casuariiformes) to the Thylacoleo Caves fauna that was not represented in LBC or FSC. While only two taxa were documented from FSC during this study, one of these was the new species of giant coucal, *Centropus maximus*, which was described by Shute *et al*. (2017; reproduced in Chapter 3), and which was a find unique to that cave.

4.3.2.3 Extant and extinct taxa

The majority of identifiable species in the Thylacoleo Caves avifauna are extant (Table 4.4). However, the faunal assemblage contains a relatively high proportion of bird taxa that are either extinct or are likely extinct (14 of ~58 taxa; 24.1%) (Table 4.4). Four of these taxa have already been described: two species of *Centropus* (coucals) (see Shute *et al.* 2016; reproduced in Chapter 2); and two species of megapode in the extinct genera *Progura* and *Latagallina* (see Shute *et al.* 2017; reproduced in Chapter 3). All the others remain to be formally described, or require confirmation that the fossil remains are those of extinct taxa (see accounts of individual taxa in Section 4.3.3).

Table 4.2: Orders of non-passerine birds represented in the Thylacoleo Caves fossil avifaunal assemblage; LBC = Leaena's Breath Cave; LTC = Last Tree Cave; FSC = Flightstar Cave

Order	Common name	LBC	LTC	FSC
Casuariiformes	Cassowaries & Emus	–	X	–
Anseriformes	Ducks & Geese	X	–	–
Galliformes	Landfowl	X	X	–
Columbiformes	Pigeons & Doves	X	X	–
Caprimulgiformes	Frogmouths & Nightjars	X	–	–
Apodiformes	Owlet-nightjars, Needletails & Swifts	X	–	–
Cuculiformes	Cuckoos	X	–	X
Gruiformes	Cranes, Crakes & Rails	X	X	–
Pelecaniformes	Storks, Herons, Ibis & Spoonbills	X	–	–
Charadriiformes	Waders & Shorebirds	X	–	–
Accipitriformes	Kites, Hawks, Harriers & Eagles	X	X	–
Strigiformes	Owls	X	X	–
Falconiformes	Falcons & Kestrels	X	X	X
Psittaciformes	Cockatoos & Parrots	X	–	–
	Total orders	**13**	**7**	**2**

Table 4.3: Families of non-passerine birds represented in the Thylacoleo Caves fossil avifaunal assemblage; LBC = Leaena's Breath Cave; LTC = Last Tree Cave; FSC = Flightstar Cave

Family	Common name	LBC	LTC	FSC
Casuariidae	Cassowaries & Emus	–	X	–
Anatidae	Ducks	X	–	–
Megapodiidae	Megapodes	X	X	–
Columbidae	Pigeons	X	X	–
Podargidae	Frogmouths	X	–	–
Aegothelidae	Owlet-nightjars	X	–	–
Cuculidae	Cuckoos	X	–	X
Rallidae	Rails	X	X	–
Ciconiidae	Storks	X	–	–
Charadriidae	Dotterels, Plovers & Lapwings	X	–	–
Pedionomidae	Plains-wanderers	X	–	–
Scolopacidae	Sandpipers	X	–	–
Turnicidae	Buttonquails	X		–
Accipitridae	Kites, Hawks, Harriers & Eagles	X	X	–
Tytonidae	Barn owls	X	X	–
Falconidae	Falcons & kestrels	X	X	X
Cacatuidae	Cockatoos	X	–	–
Psittacidae	Parrots	X	–	–
	Total families	**17**	**7**	**2**

Table 4.4: Non-passerine bird taxa represented in the Thylacoleo Caves fossil avifauna; MNI = minimum number of individuals; NISP = number of individual specimens; * = NISP includes at least one associated skeleton that is counted as a single specimen; LBC = Leaena's Breath Cave; LTC = Last Tree Cave; FSC = Flightstar Cave; taxa in **bold** type have been recorded in the Nullarbor bioregion as assessed from the Atlas of Living Australia; those with only a single regional record are marked with the '§' symbol, and are not considered resident; taxa highlighted in grey and marked with † are extinct or likely extinct (†)

Order	Family	Genus	Species	Common name	MNI	NISP	LBC	LTC	FSC
Casuariiformes	Casuariidae	***Dromaius***	***novaehollandiae***	**Emu**	**1**	**1***	**–**	**X**	**–**
Anseriformes	Anatidae	*Stictonetta*	*naevosa*	Freckled Duck	1	1*	X	–	–
		Anas	***gracilis***	**Grey Teal**	**1**	**1***	**X**	**–**	**–**
		Anas	***castanea***	**Chestnut Teal**	**1**	**1**	**X**	**–**	**–**
Galliformes	Megapodiidae	***Leipoa***	***ocellata***	**Malleefowl**	**1**	**1**	**X**	**–**	**–**
		Progura	*campestris*	Plains Megapode†	14	31	X	X	–
		Latagallina	*olsoni*	Olson's Megapode†	4	4*	X	–	–
Columbiformes	Columbidae	***Phaps***	***chalcoptera***	**Common Bronzewing**	**2**	**2**	**X**	**–**	**–**
		Phaps	***elegans***	**Brush Bronzewing§**	**4**	**8**	**X**	**–**	**–**
		Phaps	cf. *histrionica*	Flock Bronzewing	1	1	X	–	–
		Indet.	sp. 1	New species 1 (small)†	2	2	X	–	–
		Indet.	sp. 2	New species 2 (large)†	10	38	X	X	–
Caprimulgiformes	Podargidae	***Podargus***	***strigoides***	**Tawny Frogmouth**	**2**	**2**	**X**	**–**	**–**
Apodiformes	Aegothelidae	***Aegotheles***	***cristatus***	**Australian Owlet-Nightjar**	**2**	**2**	**X**	**–**	**–**
Cuculiformes	Cuculidae	*Centropus*	*bairdi*	Baird's Coucal†	6	12	X	–	–
		Centropus	*maximus*	Nullarbor Giant Coucal†	2	2*	–	–	X
		cf. Cuculidae	indet.	Cuckoo species (small)	1	1	X	–	–
Gruiformes	Rallidae	cf. *Hypotaenidia*	indet.	Rail, indeterminate species(†)	3	5	X	X	–
		cf. *Zapornia*	indet.	Crake, small species(†)	2	2	X	–	–
		cf. *Tribonyx*	indet.	Nativehen, indeterminate sp.(†)	3	3	X	X	–
		cf. *Fulica*	indet.	Coot, indeterminate species(†)	1	1	X	–	–
		Rallidae	indet.	Small/medium rails (≤ 2 spp.)(†)	2	3	X	–	–
		cf. Rallidae	indet.	Small indeterminate taxon	1	2	X	–	–
Pelecaniformes	Ciconiidae	Indet.	indet.	Stork, indeterminate sp.(†)	1	1	X	–	–

Charadriiformes	Charadriidae	***Peltohyas***	***australis***	**Inland Dotterel**	**4**	**4**	**X**	**–**	**–**
	Charadriidae	Indet.	indet.	Small plover/lapwing	1	1	X	–	–
		Indet.	indet.	Medium-sized plover/lapwing	1	1	X	–	–
	Pedionomidae	***Pedionomus***	***torquatus***	**Plains-wanderer§**	**1**	**1**	**X**	**–**	**–**
	Scolopacidae	Indet.	indet.	Sandpiper, indeterminate medium-large species	1	1	X	–	–
		Indet.	indet.	Sandpiper, indeterminate medium-sized species	1	1	X	–	–
		cf. *Numenius*	**indet.**	**Curlew/Whimbrel sp.§**	**1**	**1**	**X**	**–**	**–**
	Turnicidae	***Turnix***	**indet.**	**Button-quail (≥1 sp.)**	**38**	**80**	**X**	**–**	**–**
Accipitriformes	Accipitridae	Indet.	indet.	Extinct eagle (large)†	2	2	X	–	–
		Circus	indet.	Harrier sp.	3	3	X	–	–
		Circus	***assimilis***	**Spotted Harrier**	**2**	**2**	**X**	**X**	**–**
		Accipiter	***fasciatus***	**Brown Goshawk**	**3**	**4**	**X**	**–**	**–**
		Aquila	***audax***	**Wedge-tailed Eagle**	**1**	**1**	**X**	**–**	**–**
Strigiformes	Tytonidae	***Tyto***	**cf. *novaehollandiae***	**Masked Owl**	**1**	**1***	**X**	**–**	**–**
		Tyto	***delicatula***	**Australian Barn owl**	**1**	**1**	**X**	**–**	**–**
		Tyto	indet. (large)	‘Masked owl’, indet. species	42	79	X	X	–
Falconiformes	Falconidae	***Falco***	***cenchroides***	**Nankeen Kestrel**	**2**	**2**	**–**	**–**	**X**
		Falco	***berigora***	**Brown Falcon**	**35**	**47***	**X**	**X**	**–**
Psittaciformes	Cacatuidae	***Nymphicus***	***hollandicus***	**Cockatiel**	**1**	**1**	**X**	**–**	**–**
	Psittaculidae	Loriini	indet.	Lorikeet/lory species	4	4	X	–	–
		cf. *Glossopsitta*	indet.	Lorikeet species	1	1	X	–	–
		Melopsittacus	***undulatus***	**Budgerigar**	**50**	**103**	**X**	**–**	**–**
		cf. *Psephotus/ Psephotellus*	indet.	Small parrots (≥1 sp.)	15	18	X	–	–
		cf. *Northiella*	**indet.**	**Bluebonnet species**	**1**	**1**	**X**	**–**	**–**
		cf. *Purpureicephalus*	indet.	Red-capped Parrot	1	1	X	–	–
		Platycercus	magn. *elegans*	Crimson Rosella	3	3	X	–	–
		Platycercus	***icterotis***	**Western Rosella**	**8**	**10**	**X**	**–**	**–**
		Platycercus	indet.	Rosella species	6	8	X	–	–

Barnardius	**indet.**	**Ring-necked parrot sp. (≥1 sp.)**	**13**	**21***	**X**	**–**	**–**
cf. *Pezoporus*	sp. indet.	Night parrot species(†)	1	1	X	–	–
cf. *Neopsephotus*	***bourkii***	**Bourke's Parrot**	**3**	**4**	**X**	**–**	**–**
Neophema	**indet.**	**Grass parrot species**	**8**	**10**	**X**	**–**	**–**
Platycercini	indet.	Broad-tailed parrot species	6	7	X	–	–
cf. Pezoporini	indet.	Pezoporine parrot species	2	2	X	–	–
Psittaculinae	indet.	Psittaculine parrot species	1	36	X	–	–
cf. *Polytelis*	indet.	Long-tailed parrot species	1	1	X	–	–
Total taxa	**~58**	**Extinct/likely extinct taxa: 14**			**~56**	**8**	**2**

4.3.3 Systematic palaeontology

AVES

CASUARIIFORMES – CASSOWARIES & EMUS

CASUARIIDAE

Dromaius novaehollandiae (Latham, 1790) – Emu

Referred material – WAM 05.4.25, associated elements of a small juvenile (L/R femur; dL/R tibiotarsus; dL tarsometatarsus; vertebra) (Figure 4.16)

Site, stratigraphy and age – **Last Tree Cave:** ***Surface (probably Pleistocene)***, “Metasthenurus Chamber”

Measurements (mm): R tibiotarsus, TL 112.7, PW 12.1, DW 16.3; L femur, TL 69.4, PW 13.8, DW 17.1; tarsometatarsus, DW 16.9

Remarks – These associated bones of a small chick lack bony epiphyses so morphological detail is poorly preserved, but the remains are referred to *Dromaius novaehollandiae* based on gross morphology of the femur, which closely matches that of adult specimens (e.g. asymmetry of the distal condyles, pneumatic opening on the proximo-caudal surface adjacent to the caput femoris). Age of the animal at the time of death could not be estimated based on size because no modern juvenile skeletal specimens were available for comparison. Emu are present on the Nullarbor Plain today, and an adult bird was seen in the vicinity of Last Tree Cave during fieldwork in 2014 (*pers. obs*. 7 April, 2014). The fossil bones are of unknown geological age because they are from the cave floor of LTC, but they were found in a chamber along with extinct marsupials known only from the Pleistocene, so are likely contemporaneous.

Emu can inhabit areas with annual rainfall >60 mm, but in the north-west Nullarbor region have only been recorded breeding within 20 km of permanent water, as chicks require daily water (Marchant and Higgins 1990). Thus the skeleton of a very small chick, which implies that relatively local breeding took place, may mean that water was more available in the vicinity of Leaena’s Breath Cave than is the case today, whether that was permanent or the result of a particularly wet season.

Figure 4.16: Associated remains of a small juvenile Emu *Dromaius novaehollandiae* (WAM 05.4.25), from Last Tree Cave

ANSERIFORMES – DUCKS & GEESE

ANATIDAE Leach, 1819 – Ducks

Taxonomy for the Anatidae follows Christidis and Boles (2008), which recognises more Australian species of *Anas* than do Dickinson and Remsen (2013).

Stictonetta naevosa (Gould, 1841) – Freckled Duck

Referred Material – WAM 15.9.127, associated remains of one individual (cranium; mandible, anterior L/R, posterior L; rostrum, anterior; furcula; coracoid, L/R; vertebrae, 7; carpometacarpus, L/R; tibiotarsus, L/R; scapula, R; femur, L/R; humerus, L/R; ulna, L/R; radius, L/R; tarsometatarsus, dL, R missing distal end; synsacrum)

Site, stratigraphy and age – **Leaena's Breath Cave:** ***Surface (probably Pleistocene)*** – Station 86, "Two Bird Cavern" (Figure 4.6)

Remarks – This partial associated skeleton is morphologically indistinguishable from modern specimens of *S. naevosa*, which today is Australia's rarest species of duck. It inhabits inland water bodies in south-western, northern, and south-eastern Australia, but individuals may be found as vagrants elsewhere. There are no modern records of *S. naevosa* from the Nullarbor region, and today the species has a distribution on either side of the Nullarbor Plain (ALA, accessed 12-03-2018; Figure 4.17). Freckled Ducks are specialist dabbling filter-feeders that inhabit swampy waterbodies, and may congregate in their thousands in arid-zone wetlands (Read and Ebdon 1998). They feed mainly by wading in shallow (≤5cm deep) water (Marchant and Higgins 1990). This fossil individual may have been a vagrant attracted to the Nullarbor Plain during a Pleistocene flood event. However, age of the associated remains, which were collected from the rockpile of LBC, are unknown.

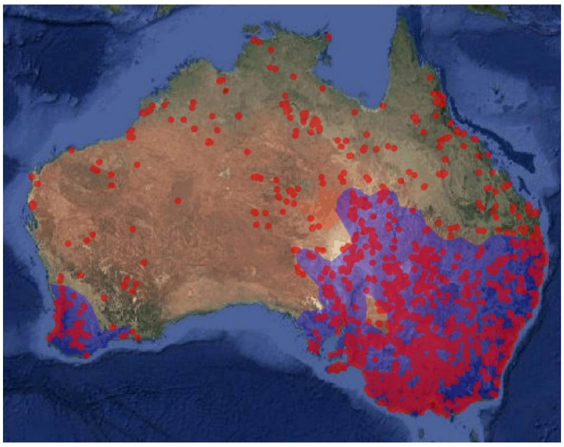


Figure 4.17: Distribution of Freckled Duck *Stictonetta naevosa*. Downloaded from ALA Spatial Portal, 12-03-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:cca72699-7f7e-4bdc-a915-8f39a20e9145#

Anas gracilis Buller, 1869 – Grey Teal

Referred Material – WAM 15.9.68, associated remains of an individual (humerus, L/R; coracoid, L; carpometacarpus, L; ulna, L/dR; tibiotarsus, L/dR; tarsometatarsus, R)

Site, stratigraphy and age – Leaena's Breath Cave: *Surface (probably Pleistocene)* – Station 120, "Upper Flood Shoot [sic.] Chamber" (Figure 4.9)

Remarks – This partial associated skeleton is referred to *A. gracilis* rather than to the closely related, and skeletally very similar, *A. castanea* based on skeletal proportions and on anatomical features of the coracoid. The pectoral elements are relatively smaller compared to the leg elements than in modern specimens of *A. castanea*, and the size and proportions of the fossil individual closely match a modern male specimen of *A. gracilis* (SAM B49080). The coracoid has a facies articularis clavicularis that is dorsoventrally narrower than in *A. castanea*, and diagonal muscular striations traverse the dorsal surface at a shallower angle (approx. 30°) relative to the long axis of the shaft as in specimens of *A. gracilis*, rather than approx. 45° in *A. castanea*. The right humerus shows possible signs of predation damage at the proximal and distal ends (Figure 4.19). *Anas gracilis* is an opportunistic species that is widespread throughout Australia (Marchant and Higgins 1990), and the Nullarbor region is within its modern range, although the eastern Nullarbor Plain constitutes a gap in its core range (Figure 4.18). A divergence date of around 105 kyr BP (Late Pleistocene) has been estimated for Grey Teal *A. gracilis* and

Chestnut Teal *A. castanea* based on nuclear and mitochondrial data (Dhami et al. 2013). Although both taxa are present in the Thylacoleo Caves fossil assemblage, the *A. gracilis* skeleton from LBC is an undated surface specimen and so does not shed light on the divergence date of the two species (but see comments for *A. castanea*, below).

Figure 4.18: Distribution of Grey Teal *Anas gracilis*. Downloaded from ALA Spatial Portal, 12-03-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:d6d85b3a-8cfa-4fbe-9d4e-9d1e5f6670dc#

Figure 4.19: Right humerus of *Anas gracilis* (WAM 15.9.68) from Leaena's Breath Cave, showing possible predation damage at the proximal and distal ends

Anas castanea (Eyton, 1838) – Chestnut Teal

Referred Material – WAM 15.9.76 (pL scapula)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – Pit B: 130–135 cm

Remarks – This specimen is referred to *A. castanea* rather than to *A. gracilis* because it has: an acromion that is orientated dorso-medially, rather than cranially as in *A. gracilis*; and a larger, more prominent muscle attachment on the lateral surface immediately dorsal of the facies articularis humeralis (weakly expressed in *A. gracilis*). Today *A. castanea* is found primarily in south-western and south eastern Australia, with the eastern population reaching as far west as the Eyre Peninsula. There are no records for the species from the central Nullarbor Plain, the closest known occurrences being a few isolated records from the southern coastal margin of the Nullarbor region (Figure 4.20). The Early Pleistocene fossil specimen may indicate that this sedentary species had a wider distribution across southern Australia then than it does today. This is consistent with the finding by Dhami et al. (2013) that genetic interchange between the *A. castanea* populations in mesic south-western and south-eastern Australia occurred up until 210 kyr BP (Middle Pleistocene, erroneously reported as late Pleistocene by Dhami *et al.* 2013). *Anas castanea* tolerates a wide range of wetland habitats, but feeds mainly at the edge of the water on recently flooded flats (Marchant and Higgins 1990). The individual from LBC may have been attracted to the vicinity of LBC by a heavy rainfall event.

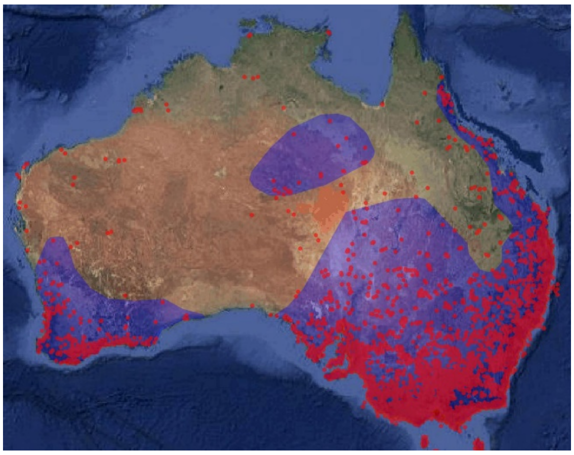


Figure 4.20: Distribution of Chestnut Teal *Anas castanea*. Downloaded from ALA Spatial Portal, 12-03-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:fbef87a7-34cc-4eca-9c32-b951c51c840c#

GALLIFORMES Temminck, 1820 – LANDFOWL

MEGAPODIIDAE Lesson, 1831 – MEGAPODES

Leipoa ocellata Gould, 1840 – Malleefowl

Referred Material – WAM 15.9.2 (R humerus) (Figure 4.21)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 105–110 cm

Measurements – see Shute *et al.* (2017) (reproduced in Chapter 3)

Remarks – The humerus, which is indistinguishable from modern specimens of *L. ocellata*, is discussed in Shute, Prideaux, and Worthy (2017) (reproduced in Chapter 3). Malleefowl have been recorded in mallee woodland habitat on the periphery of the Nullarbor Plain in historical times (Burbidge et al. 1987), but the species is unknown from the 'treeless plain'. Malleefowl have very specific habitat requirements, being found exclusively in woodlands that provide ample leaf litter for the construction of the large nest mounds that the species builds to incubate its eggs (Jones and Göth 2008). Today *L. ocellata* is found primarily in woodland dominated by an overstorey of mallee (short, multi-stemmed *Eucalyptus* spp. trees). It is found in the semi-arid zone (mean annual rainfall 200–450 mm), but is most closely associated with areas receiving rainfall at the upper end of that range (300–450 mm) that supports a floristically diverse mallee habitat with a dense, discontinuous canopy, and a diverse shrub and herb understorey, with *Acacia*, *Cassia*, *Bossiaea* and *Beyeria* being important food sources (Marchant and Higgins 1993). The specimen from LBC is the first fossil record of the species from the western half of Australia, and demonstrates that *L. ocellata*, a sedentary species, was widespread through southern Australia during the Pleistocene (see Shute *et al.* 2017). Presence of this species in Unit 3 of LBC therefore strongly indicates that a diverse woodland habitat, possibly dominated by a *Eucalyptus* overstorey, surrounded LBC when the specimen entered the fossil assemblage in the Early Pleistocene. The known rainfall tolerances of extant populations imply a mean annual rainfall on the Nullarbor Plain of between 200–450 mm for at least part of the Early Pleistocene, higher than the ~180 mm rainfall that the area receives today, and overlapping the 230–260 mm range that Prideaux et al. (2007) estimated for the Nullarbor Plain during the Middle Pleistocene.

Figure 4.21: Humerus of *Leipoa ocellata* (WAM 15.9.2) from Leaena's Breath Cave (left), with modern comparative specimen SAM B11480 (right). Scale bar = 10 cm

Progura campestris Shute Prideaux & Worthy, 2017 – Plains Megapode (extinct)

Type material – See Shute *et al.* (2017), reproduced in Chapter 3

Newly referred material – WAM 15.9.352 (phalanx dig. majoris), WAM 15.9.557 (immature L coracoid), WAM 15.9.579 (dR ulna), 15.9.580 (fragment of right ischium/ilium), WAM 15.9.561 (immature R humerus), 15.9.582 (dL/dR radii), WAM 15.9.625 (L tarsometatarsus, partial shaft)

Tentatively referred material – WAM 15.9.19 (cranial portion of notarium), 15.9.566 (phalanx)

Site, stratigraphy and age (NISP in brackets) – **Last Tree Cave:** ***"The Ossuary" (probably Pleistocene)*** – Unknown grid (1), Grid 9 (3); **Leaena's Breath Cave:** ***Surface (probably Pleistocene)*** – Unknown location (10), Station 73 (Figure 4.9) (2), "Devine Pit Site" (1); ***Unit 3 (Early Pleistocene)*** – 80–85 cm (1), 90–95 cm (2), 95–100 cm (1), 100–105 cm (1), 105–110 (1), 110–115 (52 – includes holotype with 51 associated elements), 115–120 (3), 120–125 (1), 115–130 (1)

Measurements – see Shute *et al.* (2017), reproduced in Chapter 3

Remarks – For details, see Shute *et al.* 2017; reproduced in Chapter 3. To date, the extinct Plains Megapode is the only 'giant' species of megapode known from the western two-thirds of Australia. According to the phylogenetic analysis in Chapter 3, it belonged to an extinct clade of burrow-nesting megapodes. Skeletal anatomy suggests that the species was volant, and it presumably needed to roost in trees to escape predators, as with all extant megapodes (Jones and Göth 2008; see Chapter 3). This supports the interpretation that trees were present in the vicinity of LBC in the Early Pleistocene. Remains of the species from LBC come exclusively from stratigraphic Unit 3 and from surface deposits, with none having been recovered from Units 2 or 1. Absence from the upper two stratigraphic units may be a taphonomic artefact, but could possibly indicate that the species had gone locally extinct by the later part of the Early Pleistocene or by the Middle Pleistocene.

Latagallina olsoni **Shute Prideaux & Worthy, 2017 – Olson's Megapode (extinct)**

Type material – See Shute *et al.* 2017 (reproduced in Chapter 3)

Tentatively referred material – 15.9.581 (furcula)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 100–105 cm (1), 110–115 cm (1); ***Unit 1 (Middle Pleistocene)*** – 5–10 cm (1); ***Surface (probably Pleistocene)*** – Station 100 (Figure 4.9) (holotype skeleton, 40 individual bones)

Measurements – See Shute *et al.* 2017 (reproduced in Chapter 3)

Remarks – For a description of this species, see Shute *et al*. 2017 (reproduced in Chapter 3). A fossil fragment (WAM 15.9.4) of *L. olsoni* was recovered from Unit 1 sediments in LBC, demonstrating that this species persisted on the Nullarbor Plain into the Middle Pleistocene. The diet and habitat preferences of the species are largely unknown, but as with *Progura campestris* (see above), *L. olsoni* was volant and presumably required trees for roosting.

Megapodiidae, gen. & sp. indet. – Extinct megapode, indeterminate species

Referred Material – WAM 15.9.562 (pL humerus, immature), WAM 15.9.571 (R coracoid, immature), WAM 15.9.604 (dR humerus, immature)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 90–95 cm (1), 95–100 cm (1), 110–115 cm (1)

Remarks – These immature specimens cannot be referred to genus with confidence. Both are larger than the equivalent element in any extant species of megapode, so probably belong to either *Progura campestris* or *Latagallina olsoni*, both of which are known from Unit 3 of LBC (see above).

COLUMBIFORMES Latham, 1790 – PIGEONS & DOVES

COLUMBIDAE Illiger, 1811 – PIGEONS

Phaps chalcoptera (Latham, 1790) – *Common Bronzewing*

Referred Material – WAM 15.9.455, WAM 15.9.456 (two R carpometacarpi)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 100–105 cm (1), 120–125 cm (1)

Remarks – These carpometacarpi are referred to *Phaps* rather than to the indeterminate large pigeon species from LBC (see below) because: the os carpus majus is compressed cranio-caudally into a ridge, rather than being rounded in dorsal aspect; the protuberant ridges distal of the sulcus tendineus are placed relatively caudally on the shaft, and are angled obliquely to the long axis of the os carpus majus, rather than placed centrally and angled longitudinally. They are referred to *P. chalcoptera* in particular rather than to another member of the genus because: there is a shallow fossa cranial to the processus pisiformis that does not extend caudally (fossa is deeper in *P. elegans;* fossa is moderately deep and extends caudally proximal to the processus pisiformis in *P. histrionica*); they lack a strong ridge linking the pisiform process to the proximo-ventral rim of the trochlea carpalis (distinct ridge in *P. elegans*); and the distal synostosis is relatively short proximo-distally (long in *P. histrionica*).

The Common Bronzewing, predominantly a woodland species, is not resident on the Nullarbor Plain today, but there are records for the species from the woodlands peripheral to the Plain (Figure 4.22). It is mainly granivorous, and is widespread in forest, woodland and savannah habitats with an open shrubby or grassy understorey, particularly with an *Acacia* overstorey, but also in other habitat types including mallee, or saltbush shrubland so long as there are some trees or tall shrubs and access to water (Higgins and Davies 1996).

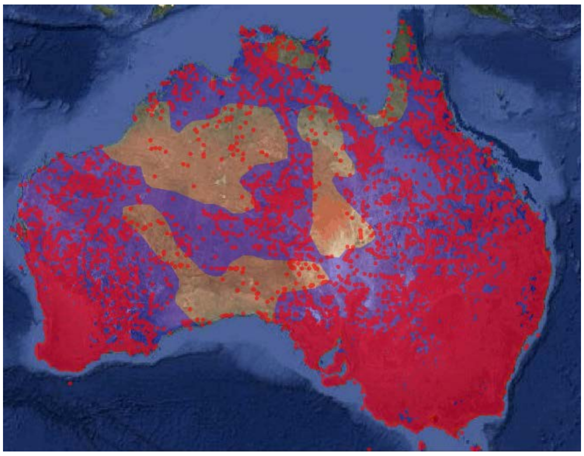


Figure 4.22: Distribution of Common Bronzewing *Phaps chalcoptera*. Downloaded from ALA Spatial Portal, 26-04-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:ef4a8336-a90b-4cdc-ae86-3842b3ec9da6#

Phaps elegans* (Temminck, 1809) – *Brush Bronzewing

Referred Material – WAM 15.9.451 (R humerus), WAM 15.9.452 (L humerus), WAM 15.9.459 pL tibiotarsus), WAM 15.9.461 (R carpometacarpus), WAM 15.9.464 (dR ulna), WAM 15.9.468 (R ulna)

Tentatively Referred Material – WAM 15.9.454 (R coracoid), WAM 15.9.458 (R tibiotarsus)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 90–100 cm (1), 100–105 cm (2), 110–115 cm (2), 115–120 (1), 125-130 cm (1), 130–135 cm (1)

Remarks – The humeri (WAM 15.9.451 and 15.9.452) are of similar size to humeri of *Ocyphaps* but are referred to *Phaps* because the processus supracondylaris dorsalis is placed relatively further proximally on the shaft than in *Ocyphaps*. They are referred to *P. elegans* in particular because of their small size, and because they have a relatively deep fossa m. brachialis disto-ventrally (shallow in *P. chalcoptera*), a moderately prominent crista deltopectoralis (highly protuberant and angular in *P. histrionica*), and a moderate-sized opening of the fossa pneumotricipitalis ventralis (large in *P. histrionica*). The humeri are different lengths and are thus from different individuals. The ulnae (WAM 15.9.464 and 15.9.468) are referred to *P. elegans* based on their small size, and the profile of the disto-dorsal condyle, whose proximal margin arises abruptly from the shaft, whereas in *P. chalcoptera* and *P. histrionica* the proximal margin of the condyle merges smoothly into the shaft. The carpometacarpus (15.9.461) is referred to *P. elegans* because of its relatively small size compared to *P. chalcoptera* and *P. histrionica*, and because it has a deep fossa on the ventral surface cranial of the processus pisiformis that does not extend caudally, and which is bounded caudally by a ridge of bone that forms a link from the processus pisiformis to the proximo-ventral rim of the trochlea carpalis (fossa is shallower in *P. chalcoptera* and a strong ridge is lacking; fossa is somewhat shallower and extends caudally proximal of the processus pisiformis in *P. histrionica*). The coracoid (15.9.454) is tentatively referred to *P. elegans* rather than to *P. chalcoptera* or *P. histrionica* because of its small size, and because the processus procoracoideus is narrow, angled obliquely to the long axis of the shaft, and originates relatively proximally on the shaft as in *P. elegans* (the processus is broader, angled more perpendicular to the shaft and originates further distally in *P. chalcoptera* and *P. histrionica*). However, the specimen is gracile compare to modern skeletons of *P. elegans*, has a smoothly rounded ventro-medial shaft (the ventral shaft is squared off into a slight medial ridge in all *Phaps* specimens examined), and the impressio musculi sternocoracoidei is more pneumatic and has more obvious muscular striations than in modern specimens of *P. elegans*. The tibiotarsi (WAM 15.9.458 and 15.9.459) are referred to *Phaps elegans* based on their relatively small size, prominent epicondylus medialis (not prominent in *P. chalcoptera*), smoothly rounded caudo-medial proximal shaft (ridge here in *P. histrionica*), and sloping profile of the crista cnemialis lateralis (proximal margin of the crista slopes more gradually distally in *P. chalcoptera*.

Phaps elegans has two extant subspecies, the nominate, which occurs in eastern Australia, and *P. e. occidentalis* in south-western Australia (Dickinson and Remsen 2013). The two populations are disjunct on either side of the Nullarbor region, at around the South Australian/Western Australian border (Figure 4.23). Only specimens representing the eastern population were examined during this study, so it was not possible to determine whether the fossils are referrable to one or other of the extant taxa. This exclusively granivorous woodland species has not been recorded from the heart of the Nullarbor Plain, but there are some records from wooded habitats at the southern margin of the Nullarbor region near the coast. The Brush Bronzewing, as the common name suggests, requires habitats with dense understorey, especially shrubs such as *Banksia*, *Acacia*, *Leptospermum*, *Melaleuca* and *Casuarina*, and it feeds and nests on the ground (Higgins and Davies 1996). Occurrence of the species in Unit 3 of LBC, but its modern absence from the ‘treeless plain’ of the Nullarbor, implies that there was a dense shrub layer in the vicinity of LBC during the Early Pleistocene.

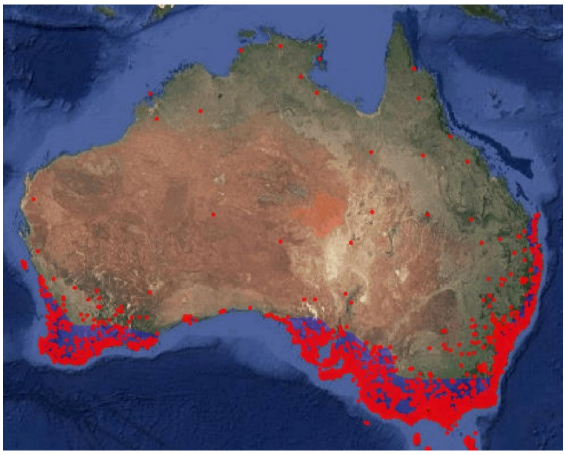


Figure 4.23: Distribution of Brush Bronzewing *Phaps elegans*. Downloaded from ALA Spatial Portal, 12-03-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:7d57fcdb-9179-47ea-8935-40caea987457#

Phaps cf. *histrionica* (Gould, 1841) – Flock Bronzewing

Tentatively Referred Material – WAM 15.9.295 (dR carpometacarpus)

Site, stratigraphy and age – **Leaena's Breath Cave: *Unit 3 (Early Pleistocene)*** – 105–110 cm

Remarks – A short distal fragment of the carpometacarpus is preserved. It is referred to *P. histrionica*, rather than to *P. chalcoptera*, *P. elegans* or the large indeterminate pigeon species from the Thylacoleo Caves (see below) because it is relatively large and has a long distal synostosis (synostosis is proportionally shorter in the other taxa). The Nullarbor Plain is hundreds of kilometres to the south of the modern range of the species (Figure 4.24). *Phaps histrionica* may have had a more southerly distribution during the Early Pleistocene. Today, this highly mobile granivorous species inhabits open grassy habitats, as well as chenopod shrublands, yet it does not occur on the Nullarbor Plain despite an apparently suitable vegetation type. This may mean it is absent for climatic reasons or because of a lack of water. It feeds, nests and rests on the ground, and although it needs to drink daily, sometimes flies several kilometres to drink (Higgins and Davies 1996).

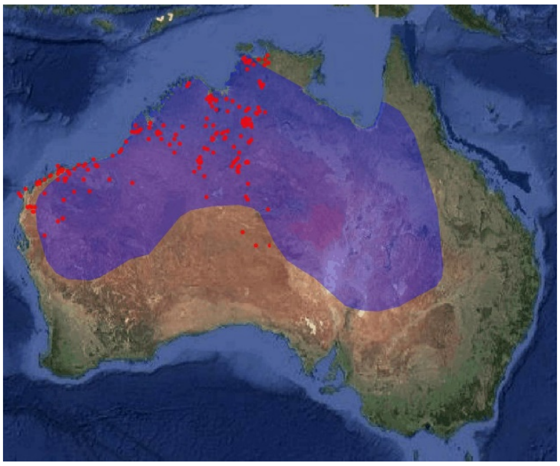


Figure 4.24: Distribution of Flock Bronzewing *Phaps histrionica*. Downloaded from ALA Spatial Portal, 12-03-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:6a686033-0629-4fa6-ac84-5e3f7cd2c2b9#

Phaps sp. indet. – Bronzewing pigeon, indeterminate species

Referred Material – WAM 15.9.453 (R coracoid, omal end), WAM 15.9.457 (L tarsometatarsus), WAM 15.9.466 (R coracoid), WAM 15.9.469 (pR tibiotarsus)

Site, stratigraphy and age – Leaena's Breath Cave: ***Unit 3 (Early Pleistocene)*** – 110–115 cm

Remarks – The partial coracoid (WAM 15.9.453) is similar to coracoids of species of *Phaps* but is too incomplete to refer to species. The complete coracoid (WAM 15.9.466) is tentatively referred to *Phaps* because it has a shaft typical of members of the genus (robust with a squared-off ventro-medial surface). However, it could not be referred to species because the omal end is proportionally smaller than in *P. chalcoptera* and *P. histrionica*, but the processus procoracoideus is broad and originates further down the shaft as in those two species, unlike *P. elegans.* The tarsometatarsus (WAM 15.9.457) is complete but was not referred to a species because I observed considerable morphological variation and overlap among species of *Phaps*. It may be possible to refer the tarsometatarsus to species with a wider range of comparative specimens to determine morphological and mensural criteria that distinguish each species in the genus. The proximal tibiotarsus (WAM 15.9.469) is of similar size and morphology to *P. chalcoptera* but the specimen is too incomplete to refer to species.

Columbidae, gen. and sp. indet. 1 – Indeterminate pigeon (small species)

Referred Material – WAM 15.9.462 (R tarsometatarsus with some damage to the hypotarsus), WAM 15.9.467 (L tarsometatarsus) (Figure 4.25)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave:** ***Unit 3 (Early Pleistocene)*** – 110–115 cm (1), 115–120 cm (1)

Measurements (mm): WAM 15.9.462 – TL, 26.8; PW, 5.3; SW, 2.5; DW, 6.1; WAM 15.9.467 – TL, 25.5; PW, 5.4; SW, 2.4; DW, 6.0

Remarks – The two tarsometatarsi, a left and a right, come from adjacent spits in Pit B of LBC, but are not of identical size (see measurements) and therefore represent two individuals. Both specimens preserve the complete length of the bone, but WAM 15.9.467 has better preservation of the hypotarsus. The specimens differ from all compared taxa (only two extant Australian genera, *Petrophassa* and *Lopholaimus*, were unavailable) and they may represent a new extinct species. The distinguishing combination of features of the tarsometatarsi include small size and gracile proportions, a hypotarsus that has very deep plantar extension (crista hypotarsalis medialis is dorsoplantarly deeper than the cotylae in proximal aspect, unlike any other taxon examined), a shallow fossa metatarsi I that does not indent the medial profile of the shaft in dorsal aspect, and strong plantar depression of trochlea metatarsi II relative to trochlea III in distal aspect.

Among the taxa examined, the fossils bore closest morphological similarity to the tarsometatarsus of the Wonga Pigeon *Leucosarcia melanoleuca*, although the fossils are very much smaller. The tarsometatarsus of *L. melanoleuca* is about 50% longer than the fossil bones (e.g. NMV B8879, TL 40.5, PW 8.9, SW 3.5, DW 9.4 mm), but shares the following features with the fossils: a relatively short fossa metatarsi I with a protuberant articular fact at its proximal end; strong plantar depression of trochlea metatarsi II relative to trochlea III (seen in distal aspect); and a gracile, elongate shaft. Besides its much larger large size, *L. melanoleuca* differs from the fossils by having a thin bridge of bone covering the canalis interosseus distalis plantarly, whereas this is open and uncovered in the fossils, and also by having a shaft that flares strongly towards the proximal end towards the articular surface, but this may be a feature associated with large body size in *Leucosarcia*.

Although comparisons were not made with *Lopholaimus* or *Petrophassa*, it is unlikely that the fossils belong to the extant members of these genera. *Lopholaimus antarcticus* (Topknot Pigeon), the only species in the genus, would be much too large to have a tarsometatarsus of this size, and furthermore belongs to the ptilinopine clade (*Ducula*, *Ptilinopus*, *Hemiphaga*, *Lopholaimus*, *Gymnophaps*), members of which are characterised by features of the tarsometatarsus that are not present in the fossil, including a very large medial foramen vasculare proximale (both proximal foramina small in the fossils), and a proportionally short shaft (fossils are gracile) (De Pietri *et al.* 2017). Based on published tarsus length measurements of *Petrophassa* spp. taken from museum skins (Crome and Johnstone 1979), the fossils are around the upper length limit for both members of the genus (White-quilled Rock-pigeon *P. albipennis*, 19.0–25.5 mm; Chestnut-winged Rock-pigeon *P. rufipennis*, 20.0–25.0 mm). Although these extant species would probably be in a similar size range to the fossil species, *Petrophassa* spp. are restricted to rocky outcrop habitats, a landform absent from the Nullarbor Plain, and thus the fossils are unlikely to belong to either species.

The fossils differ from tarsometatarsi of the other four species of pigeon identified in the Thylacoleo Caves deposits (*Phaps chalcoptera*, *P. elegans*, *P.* cf. *histrionica*, Columbidae sp. indet. 2 – see below) by being smaller in all dimensions and considerably more gracile, by having a hypotarsus with proportionally greater plantar extension, by having a proportionally smaller fossa metatarsi I that extends less far proximally on the shaft, and by having a more plantarly depressed trochlea metatarsi II. Comparisons with a full suite of modern comparative specimens are needed to confirm whether these tarsometatarsi represent a new taxon, and if so, what their affinities are.

Figure 4.25: Tarsometatarsus (WAM 15.9.467) of a small species of Columbidae from Leaena's Breath Cave, in dorsal (left), plantar (middle) and medial (right) aspects

Columbidae, gen. and sp. indet. 2 – Indeterminate pigeon (large species)

Referred Material – **Last Tree Cave**: WAM 15.9.556 (R coracoid). **Leaena's Breath Cave**: 15.9.470 (R coracoid), 15.9.471 (R carpometacarpus), WAM 15.9.472 (pR carpometacarpus), WAM 15.9.473 (R ulna), WAM 15.9.474 (L carpometacarpus), WAM 15.9.475 (R ulna), 15.9.476 (L tibiotarsus), 15.9.477 (pR humerus), 15.9.478 (L/R femur), 15.9.479 (L/R coracoid), 15.9.480 (L/R tarsometatarsus), 15.9.481 (pR tarsometatarsus), 15.9.482 (L/R ulna), 15.9.483 (L/R coracoid, omal ends), 15.9.484 (synsacrum), 15.9.485 (pL femur), 15.9.486 (pR femur), 15.9.487 (L/R carpometacarpus), 15.9.488 (dR carpometacarpus), 15.9.489 (L/R tibiotarsus), 15.9.490 (R tibiotarsus), 15.9.491 (pR humerus), 15.9.492

(dL ulna), 15.9.493 (R carpometacarpus), 15.9.494 (pL humerus), 15.9.495 (L coracoid), 15.9.496 (dL/R tibiotarsus), 15.9.497 (pL tarsometatarsus), 15.9.498 (pR scapula), 15.9.499 (R ulna), 15.9.500 (R ulna), 15.9.501 (pL humerus), 15.9.502 (dL humerus), 15.9.503 (R carpometacarpus), 15.9.504 (L/R carpometacarpus), 15.9.594 (sternum), 15.9.599 (R radius); NISP = 47

Site, stratigraphy and age (NISP in brackets) – **Last Tree Cave**: ***Surface (probably Pleistocene):*** "Offshoot of Metasthenurus Chamber" (1); **Leaena's Breath Cave**: ***Surface (probably Pleistocene):*** Station 46, "Tree Kangaroo Site" (2); Station 89, "4 Bird Corner, Tassie Devil Shoot [sic.]" (15); Station 90, "Pelvis Corner, Tassie Devil Shoot [sic.]" (10); Station 91, "US01 – Upper Dec Site" (4); Station 120, "Upper Flood Shoot [sic.] Chamber" (3); ***Unit 3 (Early Pleistocene)*****:** 100–105 cm (1), 110–115 cm (2)

Measurements – see Table 4.5

Remarks – Remains of a large pigeon of indeterminate genus and species are present in the Thylacoleo Caves fauna, and are the most abundant Columbidae remains in LBC. Most specimens are from the surface of LBC and are of unknown age. A few elements of Early Pleistocene age from Unit 3 of LBC put a minimum age bracket on the species of >780 kyr BP. Skeletal elements from the surface of LBC are catalogued under separate specimen numbers due to the bones of multiple individuals having been collected from the same locations, but among these are likely associated remains. It is likely that the remains are of a new undescribed taxon.

The bones could not be referred to any extant Australian genus after comparison with skeletons of all extant Australian pigeon genera apart from *Lopholaimus*, a specimen of which was not available for comparison. Nevertheless, *Lopholaimus* is ruled out by being a member of the 'ptilinopine' clade of pigeons, which have tarsometatarsi distinguished, amongst other features, by having a very large, open medial foramen vasculare proximale, whereas both proximal foramina are small in the fossil tarsometatarsi, as in 'phabine' taxa (De Pietri et al. 2017). Overall the taxon appears most skeletally similar to the Wonga Pigeon *Leucosarcia melanoleuca* and the Flock Bronzewing *Phaps histrionica*. The taxon is distinguished from species of *Phaps*, three of which are present in the Thylacoleo Caves deposit, *Ocyphaps lophotes*, *L. melanoleuca*, and Columbidae indet. 1 from LBC (see above), by proportional and morphological features as outlined below.

The leg elements are larger than in any species of *Phaps*, *Ocyphaps lophotes* of Columbidae indet. 1 (e.g. femora, Figure 4.26; tarsometatarsi, Figure 4.27). They are of similar size and robusticity to leg elements of *L. melanoleuca*, but the tarsometatarsus is rather shorter (e.g. *L. melanoleuca* NMV B8879, TL 40.5, PW 8.9, SW 3.5, DW 9.4 mm). Similar dimensions of the tibiotarsus suggest that the fossil taxon had a similar body size to *L. melanoleuca* (mean body mass of *L. melanoleuca* – males 410 g, females 448; Dunning 2008). The tarsometatarsus is longer than in any species of *Phaps* but the shaft is gracile (Figure 4.27), as in *Leucosarcia*. It has: moderately deep plantar extension of the hypotarsus as in *P. histrionica* (deeper than in *P. chalcoptera*, *P. elegans* and *L. melanoleuca*, though not as deep as in Columbidae indet 1; see above); a medial hypotarsal ridge that extends further proximally than the proximal articular surface and eminentia intercotylaris, and which meets the plantar shaft abruptly at its distal end as in *P. chalcoptera*; a single fully enclosed hypotarsal canal (two in *O. lophotes*); a trochlea metatarsi II that does not extend far laterally, with minor plantar depression as in *Ocyphaps* (troch. II is more plantarly depressed in *Phaps* spp., *L. melanoleuca* and Columbidae indet. 1), and the trochlea has a small plantarly-directed flange as in *P. histrionica* (flange on trochlea II is larger in *P. chalcoptera*, *P. elegans*, *L. melanoleuca*, and *O. lophotes*; and a small foramen vasculare distale (larger in *Phaps* spp.). Of the species examined, tarsometatarsi of the fossil taxon are most similar morphologically to those of *P. histrionica*.

The humeri (Figure 4.28) have a processus supracondylaris dorsalis that is placed relatively distally on the shaft as in *Leucosarcia*, and unlike the three species of *Phaps.* The carpometacarpi are most similar to those of *Leucosarcia*, sharing with that taxon: a deep fossa at the proximal end just cranial of the processus pisiformis (variable among species of *Phaps*); a link joining the processus pisiformis to the proximal rim of the trochlea carpalis (link somewhat less marked in *Leucosarcia*; variable among *Phaps* spp.); and two parallel ridges distal of the sulcus tendineus on the ventral surface of the os carpus majus that are placed centrally on the shaft, rather than more caudally in species of *Phaps.*

In observing similarities between the fossil taxon, *Phaps histrionica* and *Leucosarcia melanoleuca*, I note that there is considerable skeletal variation between the three extant species included in the genus *Phaps*, perhaps indicating deep divergence at species level, which is plausible if that genus diverged from its closest relatives around 30 Ma as estimated by Pereira et al. (2007). *Leucosarcia melanoleuca* is relatively basal in the phabine clade (Heupink et al. 2014) and *P. histrionica* (Flock Bronzewing) is the most basal species in its genus (Sweet et al. 2017). Thus similarities observed between the fossil taxon and these two taxa may mean it represents a relatively basal phabine taxon. Given the abundance and good preservation of the specimens, this hypothesis can be tested at a later date via a formal phylogenetic analysis.

Figure 4.26: Femur of Columbidae indet. 2 (left) compared to species of *Phaps* and *Ocyphaps lophotes*; from left to right, WAM 15.9.478 from Leaena's Breath Cave, *Phaps chalcoptera* SAM B56242, *Phaps histrionica* SAM B45943, *Phaps elegans* SAM B56023, *O. lophotes* B48075

Figure 4.27: Tarsometatarsus of Columbidae indet. 2 (left), compared to species of *Phaps* and *Ocyphaps lophotes*; from left to right, WAM 15.9.480 from Leaena's Breath Cave, *Phaps chalcoptera* SAM B56242, *Phaps histrionica* SAM B45943, *Phaps elegans* SAM B56023, *O. lophotes* B48075

Figure 4.28: Selected pectoral elements of Columbidae sp. indet (large species) from the Thylacoleo Caves. A, proximal humerus (WAM 15.9.477) in caudal aspect; **B**, distal humerus (WAM 15.9.502) in cranial aspect; **C**, ulna (WAM 15.9.475) in ventral aspect; D, coracoid (WAM 15.9.479) in ventral aspect; E, carpometacarpus (WAM 15.9.487) in ventral aspect

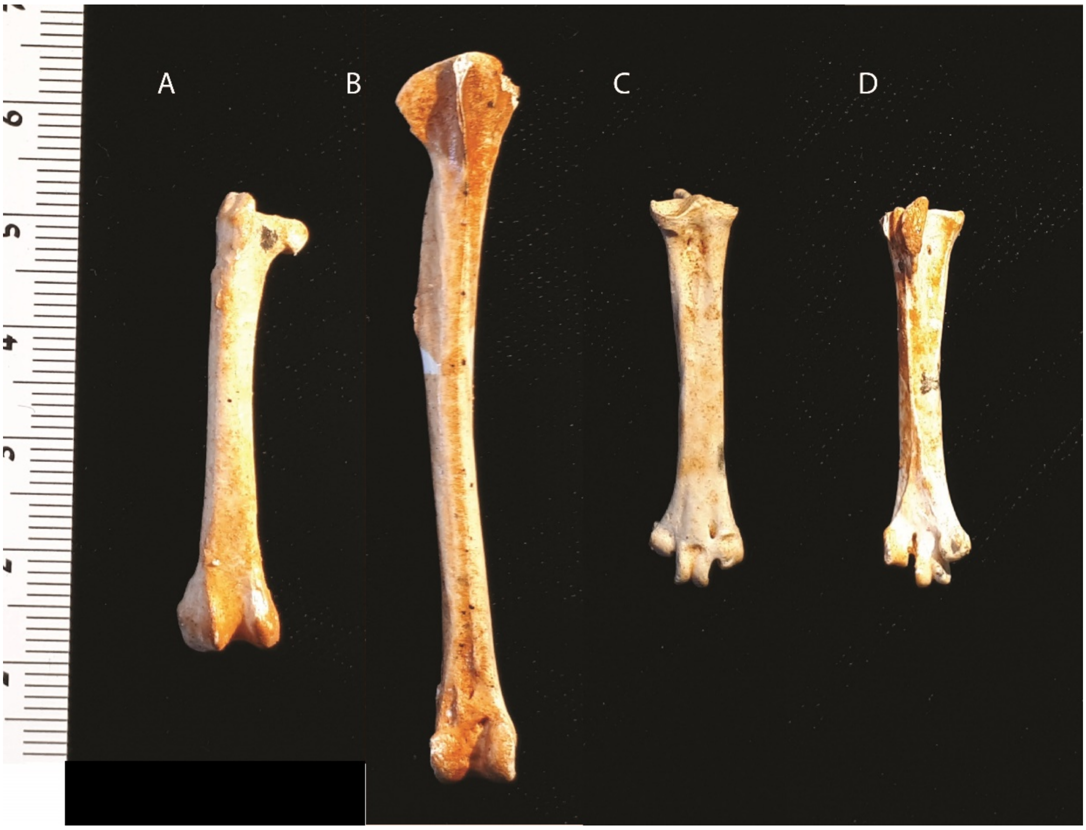


Figure 4.29: Selected leg elements of Columbidae sp. indet (large species) from the Thylacoleo Caves. A, femur (WAM 15.9.478) in dorsal aspect; **B**, tibiotarsus (WAM 15.9.490), in cranial aspect; **C** and **D**, tarsometatarsus (WAM 15.9.480) in dorsal (**C**) and plantar (**D**) aspects

Table 4.5: Long bone measurements (mm) of Columbidae indet. sp. 2; TL = total length; PW = proximal width; SW = midshaft width; DW = distal width’ *, length of coracoids is measured medially; †, ‘proximal’ width of coracoids is the omal width, and ‘distal’ width is sternal width; §, measurement is of the left of a pair; ø, measurement is of the right of a pair

Element/Side	Catalogue no.	TL	PW	SW	DW
Last Tree Cave					
Coracoid, R	WAM 15.9.556	34.3*	6.1†	3.9	–
Leaena’s Breath Cave					
Coracoid, R	WAM 15.9.470	31.0	5.7	3.5	–
Coracoid, L/R	WAM 15.9.479	33.0	6.3	4.0	–
Coracoid, omal ends L/R	WAM 15.9.483§	–	6.0	–	–
Coracoid, L	WAM 15.9.495	34.9	6.2	4.4	–
Scapula, pR	WAM 15.9.498	–	10.2	3.4	–
Humerus, pR	WAM 15.9.477	–	16.0	4.8	–
Humerus, pR	WAM 15.9.491	–	15.4	4.9	–
Humerus, pL	WAM 15.9.494	–	–	–	–
Humerus, pL	WAM 15.9.501	–	–	–	–
Humerus, dL	WAM 15.9.502	–	–	5.1	11.4
Ulna, R	WAM 15.9.473	44.1	6.6	3.3	5.9
Ulna, R	WAM 15.9.475	>51.0	8.1	4.1	>6.1
Ulna, L/R	WAM 15.9.482	–	–	3.9	7.0
Ulna, dL	WAM 15.9.492	–	–	3.8	6.6
Ulna, R	WAM 15.9.499	51.1	7.6	4.0	6.8
Ulna, R	WAM 15.9.500	>50.0	7.5	3.8	6.7
Radius, R	WAM 15.9.599	46.2	4.8	2.3	5.1
Carpometacarpus, R	WAM 15.9.471	29.9	8.9	7.1	6.0
Carpometacarpus, pR	WAM 15.9.472	–	8.2	–	–
Carpometacarpus, L	WAM 15.9.474	27.4	–	–	5.0
Carpometacarpus, L/R	WAM 15.9.487ø	30.4	8.8	7.1	6.2
Carpometacarpus, dR	WAM 15.9.488	–	–	–	6.2
Carpometacarpus, R	WAM 15.9.493	29.7	8.9	–	6.0
Carpometacarpus, R	WAM 15.9.503	30.7	8.6	–	6.0
Carpometacarpus, L/R	WAM 15.9.504§	30.7	8.7	7.3	6.0
Femur, L/R	WAM 15.9.478§	>40.0	9.1	3.9	9.1
Femur, pL	WAM 15.9.485	8.8	3.7	–	–
Femur, pR	WAM 15.9.486	–	–	3.9	–
Tibiotarsus, L	WAM 15.9.476	61.4	11.6	3.4	7.7
Tibiotarsus, L/R	WAM 15.9.489	–	7.5	3.3	7.0
Tibiotarsus, dL/R	WAM 15.9.496	–	–	3.7	7.0
Tibiotarsus, R	WAM 15.9.490	60.2	8.6	3.8	7.0
Tarsometatarsus, L/R	WAM 15.9.480§	31.6	7.2	3.6	7.9
Tarsometatarsus, pR	WAM 15.9.481	–	7.7	3.8	–
Tarsometatarsus, pL	WAM 15.9.497	–	7.9	4.0	–

CAPRIMULGIFORMES Ridgway, 1881 – FROGMOUTHS & NIGHTJARS

PODARGIDAE Vieillot, 1818 – FROGMOUTHS

Podargus strigoides Latham, 1801 – Tawny Frogmouth

Referred Material – WAM 15.9.446 (L tarsometatarsus), WAM 15.9.567 (L coracoid)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave:** ***Unit 3 (Early Pleistocene)*** – 80–85 cm (1), 95–100 cm (1)

Remarks – The tarsometatarsus and coracoid are indistinguishable from modern specimens of *P. strigoides*. This is a common and widespread woodland species of mainland Australia and Tasmania, and is found today in tropical, arid and temperate regions. It is mainly crepuscular/nocturnal, and eats a wide range of ground-dwelling invertebrates and small vertebrates, including lizards, frogs and rodents, and obtains most or all of its water from food (Kaplan 2007). Despite its ubiquity, and tendency to forage on the ground (Kaplan 2007), which should theoretically lead to pitfall trapping and fossilisation in cave deposits, the fossil record of the species is sparse. Rare exceptions are Scotts River (south-west Western Australia), Aiyenu Cave (Western Australia), Clogg's Cave (Victoria), and McEacherns Cave (Victoria) (Baird 1991). Modern records of the species from the Nullarbor region are sparse (GBIF, accessed 12-01-2017), but it was recorded in woodland in the Hampton Range at the southern edge of the Nullarbor Plain in the early 20th Century (McColl 1929), and in coastal woodlands/mallee, and peripheral woodlands to the west and east of the Nullarbor Plain in the late 20th Century (Burbidge et al. 1987). As a woodland species, *P. strigoides* is today absent from the heart of the Nullarbor Plain. A study of its roosting habits in the Northern Tablelands of New South Wales determined that the species selected only mature eucalypts with a girth of >0.5 m, with a preference for larger trees, and a roost height of 4.8–19.3 m above the ground (mean 12.8 ± 2.5 m). The birds did not roost in *Acacia* trees where those were present in their habitat, and of the three types of eucalypt present (gums – smooth bark; stringybarks – rough, dark-coloured bark; and box – flaky or scaly bark), *Podargus* showed a strong preference for stringybarks, these comprising more than three-quarters of trees chosen as roosts (Körtner and Geiser 1999). Although not conclusive, presence of *P. strigoides* may indicate tall eucalypt trees were present on the Nullarbor Plain during the Early Pleistocene.

APODIFORMES – OWLET-NIGHTJARS, SWIFTS, NEEDLETAILS

AEGOTHELIDAE Bonaparte, 1853 – OWLET-NIGHTJARS

Aegotheles cristatus (Shaw, 1790) – Australian Owlet-Nightjar

Referred material – WAM 15.9.445 (R coracoid); WAM 15.9.297 (L femur)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 90–95 cm (1), 115–120 cm (1)

Remarks – The coracoid (WAM 15.9.445) is morphologically similar to modern specimens of *A. cristatus*. Based on examination of several modern specimens, femora of this species appear to be quite variable in length, robustness and placement of muscle attachment scars. Thus to refer a femur to this species it is necessary to examine multiple reference specimens to determine the range of variation. The femur (WAM 15.9.297) is referred to *Aegotheles* rather than to *Hirundapus* because of its small size and because it has a condylus lateralis that projects strongly laterally (projects much less in *Hirundapus*). Owlet Nightjars are crepuscular/nocturnal, insectivorous woodland birds. According to Baird (1991), skeletal remains of *A. cristatus* are common in Australian cave deposits of Quaternary age because the species sometimes roosts in caves, but only two bones of the species were found in the LBC deposits. Richards (1971) recorded *A. cristatus* among the modern cave-dwelling fauna of the Nullarbor Plain, so the scarcity of fossils of this species are surprising. However, her observations of this species may not have included caves beneath the Nullarbor Plain *sensu stricto*, as most of the caves included in that study were peripheral to the Plain. A systematic bird survey recorded *A. cristatus* exclusively in woodlands peripheral to the Plain (Burbidge et al. 1987), but there are no records of the species from the Plain itself (GBIF data, accessed 24/01/2018). The species is strongly associated with woodland habitats, in particular woodland that has eucalypts bearing hollows for roosting (Brigham et al. 1998), and so the absence of *A. cristatus* from the plain today, and its occurrence during the Early Pleistocene, supports the presence of woodland habitat at that time.

CUCULIFORMES – CUCKOOS

CUCULIDAE – CUCKOOS

Centropus bairdi Shute, Worthy & Prideaux, 2016 – Baird's Coucal (extinct)

Type material – See Shute *et al*. (2016) (reproduced in Chapter 2)

Newly referred material – WAM 15.9.569 (L ulna), WAM 15.9.573 (R ulna), WAM 15.9.626 (R scapula), WAM 15.9.627 (L coracoid), WAM 15.9.628 (L carpometacarpus, proximal and distal ends, probably of the same individual), 15.9.629 (pygostyle)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 85–90 cm (1), 100–105 cm (1), 105–110 cm (1), 110–115 cm (5), 115–120 cm (2), 120–125 cm (2)

Measurements – For measurements of type material, see Shute et al. 2016, reproduced in Chapter 2
Measurements of newly referred specimens (mm) – WAM 15.9.626, TL 52.6, SW 4.9;
WAM 15.9.629, max. length 30.0, max. depth 18.8; WAM 15.9.628, TL approx. 26, PW 9.6, DW 7.1; WAM 15.9.627, TL 36.7, SW 3.3; WAM 15.9.569, TL 51.9, PW 9.0, SW 4.8, DW 7.4; WAM 15.9.573, TL 49.0, PW 8.2, 4.3, DW 6.4

Remarks – For a detailed treatment of this newly-described species, see Shute *et al*. (2016), reproduced in Chapter 2. When the description of the species was published (Shute *et al.* 2016), the elements then known were the humerus (holotype), femur, tibiotarsus and proximal tarsometatarsus. Here I refer additional elements to this species (scapula, coracoid, carpometacarpus, pygostyle; see Referred Material) because they closely match the morphology of other species of *Centropus*, are consistent with the size of *C. bairdi*, and were from the same sedimentary unit (Unit 3, Pit B) in LBC as the type material. A partial distal tarsometatarsus that joins to one of the previously described proximal tarsometatarsi (WAM 09.3.280) was also identified subsequent to the publication of Shute *et al*. (2016), and is now included under the same catalogue number. The ulnae, which are contralateral but non-identical and belong to different individuals, are of very similar size and morphology to the ulna of *C. violaceus* (Violaceous Coucal), from New Britain. The scapula and coracoid are approximately the same size as in the extant Pheasant Coucal *C. phasianinus*, and the carpometacarpus is only a little larger. This confirms that the entire pectoral girdle of this species was reduced relative to the leg elements, strengthening the interpretation that *C. bairdi* was probably terrestrial and flightless (Chapter 2). The newly identified pygostyle is larger than in *C. phasianinus*, and is also somewhat larger than that of the Violaceous Coucal *C. violaceus* from New Britain, which has leg and wing elements of similar size to those of *C. bairdi*. This suggests that *C. bairdi* had particularly well-developed muscles for controlling the tail. If this is correct, a strong, mobile tail may have been used as a rudder when running.

Centropus maximus Shute, Worthy & Prideaux 2016 – Giant Nullarbor Coucal (extinct)

Type material – see Shute *et al*. (2016), reproduced in Chapter 2

Site, stratigraphy and age – **Flightstar Cave:** ***Surface, unspecified location (probably Pleistocene)***

Remarks – For a detailed treatment and measurements of this newly-described extinct species, see Shute *et al.* (2016), reproduced in Chapter 2. In summary, *Centropus maximus* is the largest known cuckoo species from any part of the world, being a little larger than its extinct Australian congener *C. colossus*. It is presumed to have been largely terrestrial with very reduced capacity for flight, and probably required dense undergrowth as habitat.

cf. Cuculidae, gen. and sp. indet. (small species)

Referred Material – WAM 15.9.447 (R coracoid, omal end) (Figure 4.30)

Site, stratigraphy and age – **Leaena's Breath Cave:** ***Unit 1 (Middle Pleistocene)*** – 5–10 cm

Remarks – The coracoid is tentatively referred to the Cuculidae because it has a proportionally long, slender shaft that barely widens sternally, a sharply pointed apex of the processus acrocoracoideus, and an elongate, narrow processus procoracoideus that meets the shaft at an approximately 90° angle. Given its small size, likely candidates would be species of *Chalcites*, *Cacomantis* or *Cuculus*, among Australian taxa, but the specimen could not be referred to any of these during this study. The genus *Cacomantis* was ruled out by comparison with *Cacomantis flabelliformis* (Fan-tailed Cuckoo) and *Chalcites* was ruled out based on photographs of coracoids of *Ch. basalis* (AM O.64825), *Ch. ludicus* (AM O.59308) and *Ch. minutilus* (AM O.64699). Omal morphology somewhat resembled *Cuculus*, based on a photograph of *C. saturatus* (AM O.59413), which is extralimital to Australia (Dickinson and Remsen, 2013). The fossil differs from all examined cuckoo taxa by having a processus procoracoideus that is proportionally narrower, and is oriented very slightly sternally rather than omally with regard to the long axis of the shaft. The preserved portion is in good condition and should be readily identified to genus or species with a wider range of comparative specimens. It should be compared with *Cuculus optatus* (Oriental Cuckoo), which has a distribution that includes eastern Australia (Dickinson and Remsen, 2013).

Figure 4.30: WAM 15.9.447, a small coracoid from Leaena's Breath Cave, tentatively referred to the Cuculidae, in ventral (left) and dorsal (right) aspects. Divisions on scale bar = 1 mm.

GRUIFORMES Bonaparte, 1854 – CRANES, CRAKES & RAILS

RALLIDAE Rafinesque, 1815 – RAILS

cf*.* *Hypotaenidia* sp. indet. – Rail, indeterminate medium-sized species

Referred Material – WAM 15.9.131, WAM 15.9.134, (two dL tibiotarsi) (Figure 4.35); WAM 15.9.156 (dL/dR tibiotarsi) (Figure 4.31); WAM 15.9.157 (dR humerus) (Figure 4.31); WAM 15.9.158 (pR tibiotarsus) (Figure 4.31)

Site, stratigraphy and age (NISP in brackets) – **Last Tree Cave**: ***Surface (probably Pleistocene):*** – 'The Ossuary', Grid 15 (3); **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 115–120 cm (2)

Measurements (mm) – WAM 15.9.131, DW 6.9; WAM 15.9.134, DW 6.8; WAM 15.9.156, DW 6.9, SW 4.4; WAM 15.9.157, DW 8.2

Remarks – These remains from LTC did not match any extant species of Australian rail in size or morphology (all extant Australian taxa were compared, apart from *Rallina tricolor*, for which no comparative specimen was available), and may represent a new extinct taxon. The bones are congruent in size to be of one species, and some elements show particular affinity with *Hypotaenidia.* Here some preliminary observations of some distinguishing characters are made. The proximal tibiotarsus (WAM 15.9.158) was found in the same grid in 'The Ossuary' of LTC as two distal tibiotarsi (WAM 15.9.156), which are apparently a pair, but the proximal right fragment does not join to the distal right fragment, and although they are of congruent size, not enough length of the shaft is preserved to determine if they are ends of the same bone. WAM 15.9.156, a distal left tibiotarsus, preserves most of the shaft length, but is broken below the level of the crista fibularis. Laid alongside a modern specimen of *H. philippensis* (SAM B36299: TL 72.1 mm), the broken proximal end of the fossil reaches nearly to the proximal end of the crista fibularis of *H. philippensis*, thus total length of the tibiotarsus would have been longer, probably approaching the same length as in *Tribonyx ventralis* (e.g. SAM B47797, TL 88.3 mm). The distal tibiotarsi from LBC (WAM 15.9.131; WAM 15.9.134) are of similar size and morphology to the specimens from LTC. The proximal tibiotarsus (WAM 15.9.158) has similar morphology to *H. philippensis*, differing from *T. ventralis* by having a pair of longitudinal ridges bounding a deep sulcus on the caudal and caudo-medial surface of the shaft, immediately beneath the facies articularis medialis (visible in caudo-lateral view in Figure 4.31 B). These ridges, and the sulcus they define, are present in *H. philippensis*, but are much more marked in the fossil specimen. The distal humerus (WAM 15.9.157) is about the same size as humeri of *T. ventralis* (SAM B47797, DW 8.4 mm), and is a little larger than in *H. philippensis* (SAM B36299, DW 7.1 mm). As in *H. philippensis*, the processus epicondylus dorsalis is smaller and placed proportionally closer to the distal end than in *T. ventralis*, but the fossil differs from *H. philippensis* by having a broader, blunter processus flexorius. The form of the processus flexorius is more similar to *T. ventralis*, but it is a little shorter and blunter (longer and more finger-like in *T. ventralis*).

Figure 4.31: Rallidae specimens from Last Tree Cave, tentatively referred to *Hypotaenidia* sp.; (A = WAM 15.9.156; B = WAM 15.9.158 in cranial (left) and caudo-lateral (right) aspects; C = WAM 15.9.157, in caudal (left) and cranial (right) aspects

cf. *Zapornia* sp. indet. – Crake, indeterminate small species

Referred Material – WAM 15.9.138 (dR tibiotarsus) (Figure 4.32); WAM 15.9.450 (L carpometacarpus, missing the os metacarpale minus and processus extensorius) (Figure 4.37)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 1 (Middle Pleistocene)*** – 0–5 cm; ***Unit 3 (Early Pleistocene)***, 145–150 cm

Measurements (mm) – *WAM 15.9.138*, N/A; *WAM 15.9.450*: TL, 22.0, DW, 2.4

Remarks – The distal tibiotarsus has condyles too damaged to measure, but would have an estimated distal width of approximately 3–4 mm if complete. The specimen was compared to tibiotarsi of all extant Australian rallid taxa besides *Rallina tricolor*, for which no comparative specimen was available. It is distinguished from *Lewinia pectoralis*, *Hypotaenidia philippensis*, *Porzana fluminea*, *Amaurornis moluccana*, *Porphyrio porphyrio*, *Gallinula tenebrosa*, *Tribonyx ventralis*, *T. mortierii* and *Fulica atra* by its considerably smaller size, as well as various morphological differences. The only extant taxa with tibiotarsi in a similar size class are Baillon's Crake *Zapornia pusilla*, Spotless Crake *Z. tabuensis*, and White-browed Crake *Amaurornis cinerea*, but the fossil differs morphologically from each of these taxa. It is distinguished from *A. cinerea* by having: a proximodistally shorter pons supratendineus; a longer, ridge-like tuberositas retinaculi extensori proximal to the lateral condyle; a sulcus extensorius that is flat rather than rounded in profile; and a convex profile of the cranial shaft proximal of the sulcus extensorius (shaft is excavated proximal of the sulcus tendineus in *A. cinerea*). The fossil is distinguished from *Z. pusilla* by having: a shaft that flares more widely as it approaches the condyles; a much broader sulcus extensorius (approximately twice as wide as that of *Z. pusilla* despite similar overall size of the bone); a proximodistally shorter pons supratendineus; and a convex cranial shaft with a longitudinal ridge along its midline (flat in *Z. pusilla*). Despite its differences from *Z. pusilla*, the specimen is tentatively referred to *Zapornia* because it has morphology that most closely matches that of *Z. tabuensis* (Spotless Crake), sharing with that species the following features: a medial condyle that flares more widely medially than in any other rallid taxa examined; the lateral part of the tuberositas retinaculi extensori forming a continuous ridge of bone connecting the medial rim of the lateral condyle to the medial ridge of the retinaculum fibularis, creating a groove lateral to the pons supratendineus; and a central ridge running proximodistally along the midline of the cranial shaft, proximal of the sulcus extensorius. However, the fossil is distinguished from *Z. tabuensis* by having: a somewhat broader, flatter sulcus extensorius; a medial portion of the tuberositas retinaculi extensori that is placed relatively more distally on the shaft (sub-equal placement relative to the retinaculum m. fibularis), whereas in *Z. tabuensis* the medial portion of the tuberositas retinaculi extensori is further proximal than the retinaculum m. fibularis; and a smaller distal opening of the canalis extensorius.

The carpometacarpus, which has a slightly porous surface texture and is therefore from an immature individual, is referred tentatively to *Zapornia* based on its morphological similarity to extant taxa, *Z. pusilla* and *Z. tabuensis*, but it is considerably larger than both taxa (*Z. pusilla*, SAM B38159, TL, 14.2 mm; *Z. tabuensis*, SAM B45063, TL 14.8 mm). Features shared with *Zapornia* include: a relatively short proximal synostosis; a narrow proximal profile of the os metacarpale minus, revealing more of the caudal surface of the os metacarpalis majus in caudal aspect than in other taxa; relatively distal placement of the proximal muscular scar on the ventral side of the os metacarpale minus (more prominent in the fossil than in extant species).

It is likely that these specimens represent at least one undescribed extinct species of rail, which should be further investigated. The tibiotarsus is of similar size to extant Australian species of *Zapornia* (*Z. tabuensis* and *Z. pusilla*), while the carpometacarpus is rather larger than the carpometacarpi of those species, thus indicating either different skeletal proportions within one species, or two species may be present. Crakes are associated with wetland habitats, and there are no modern records of the genus from the Nullarbor Plain.

Figure 4.32: Small distal tibiotarsus (WAM 15.9.138) from Leaena's Breath Cave, tentatively referred to *Zapornia*, sp. indet. Small gradations on scale = 1 mm.

cf. Tribonyx sp. indet. – Nativehen, indeterminate small species

Referred Material – WAM 15.9.128 (L ulna), WAM 15.9.129 (dL tarsometatarsus), WAM 15.9.618 (dL tarsometatarsus) (Figure 4.33)

Site, stratigraphy and age (NISP in brackets) – **Last Tree Cave:** ***Surface (probably Pleistocene)*** – "The Ossuary", Grid 16 (1); **Leaena's Breath Cave:** ***Unit 2 (Middle Pleistocene)*** 45–50 cm (1); ***Unit 3 (Early Pleistocene)*** – 105–110 cm (1)

Measurements (mm) – *WAM 15.9.128*, TL 47.5, PW 5.5, SW 2.9, DW 5.1; *WAM 15.9.129*, SW 3.3, DW 7.6; *WAM 15.9.618*, DW 7.8

Remarks – Three rallid specimens that may or may not belong to one species, are tentatively referred to the genus *Tribonyx*, based on morphological similarity to the Tasmanian Nativehen *T. mortierii*, although they are much closer in size to bones of the Black-tailed Nativehen *T. ventralis.* The remains from LTC are probably the specimens on which an identification of *T. ventralis* was based in the preliminary analysis of the Thylacoleo Caves fauna by Prideaux *et al.* (2007), but no remains referrable to that species are confirmed here. Although placed in the same genus in current taxonomy (see Dickinson and Remsen, 2013), *T. ventralis* and *T. mortierii* appear to have rather different skeletal anatomy from one another, even allowing for *T. ventralis* being volant and *T. mortierii* flightless, and I would probably not have referred to the specimens to *Tribonyx* if I had only compared the fossils with *T. ventralis*. A dated phylogeny by Garcia-Ramirez *et al.* (2014) estimated that these taxa diverged in the Miocene or Pliocene, potentially explaining their morphological divergence.

The distal tarsometatarsi share with *T. mortierii* a rounded dorsal facies, a plantar ridge along the midline, and a depression of the latero-plantar facies at the level of fossa metatarsi I, but are distinguished from this species by their very much smaller size (e.g. *T. mortierii*, SAM B46032, DW 13.0 mm). They are closer in size to *T. ventralis* (e.g. SAM B47797, DW 8.6 mm), but differ morphologically by having: a slightly rounded dorsal profile (dorsal shaft is flat in *T. ventralis*); a well-defined ridge extending proximally along the midline of the plantar surface from trochlea metatarsi II (weakly expressed in *T. ventralis*); and a depression of the latero-plantar facies adjacent to fossa metatarsi I (more or less flat here in *T. ventralis*).

The ulna from LBC, which is complete apart from slight abrasion of the olecranon, is of similar size and proportions to that of *H. philippensis* (SAM B36299: TL 43.9 mm; PW 4.8; SW 2.7; DW 4.6), but is distinguished from that species by having a deep recess at the proximal end of the impressio brachialis and beneath the cotyla dorsalis, neither of which is present in *H. philippensis*. The ulna is somewhat smaller and more gracile than in *T. ventralis* (SAM B47797: TL 49.3 mm; PW 5.9; SW 3.6; DW 5.8). It is almost identical in length to a specimen of *T. mortierii*, but is more gracile (SAM B46032: TL 47.8; PW 7.3; SW 3.2; DW 6.1). As a flightless species, wing bones of *T. mortierii* are highly modified, including flattening of the ulnar shaft (the fossil has a round cross-section), but proximal morphology is similar to the fossil. Shared features include a deep depression at the proximal end of the impressio brachialis with an adjacent tuberculum on the ventral facies, a large protuberance on the proximo-cranial surface below the cotyla dorsalis, and a deep recess on the shaft below the cotyla dorsalis. The fossil differs from *T. ventralis* by having a less projecting rim of the cotyla ventralis, a deep recess on the shaft cranially beneath the cotyla dorsalis (absent in *T. ventralis*), the proximal end of the impressio brachialis deeply excavated (shallow in *T. ventralis*), and a larger, more proximally-paced tuberculum lig. collateralis ventralis.

Figure 4.33: Specimens tentatively referred to *Tribonyx* sp. (A = WAM 15.9129, in dorsal and plantar aspects; B = WAM 15.9.618, in dorsal aspect; C = WAM 15.9.128 in ventral and dorsal aspects)

cf. *Fulica* sp. indet. – Coot species

Referred Material – WAM 15.9.568 (L coracoid) (Figure 4.34)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)***, 115–120 cm

Measurements (mm) – TL, 26.4, omal width 5.0, SW 3.6, DW (facies sternalis only), 8.6

Remarks – The coracoid could not be referred to any extant species of rail, but is tentatively referred to *Fulica* based on morphological similarities to *F. atra*, although it is rather smaller (cf. *F. atra*, SAM B36791, TL 34.9). The fossil has: a distinctly waisted shape and a finger-like processus procoracoideus that has its tip pointing ventrally as in *Fulica* (Zelenkov, Panteleyev, and De Pietri 2017); a short, deep, more or less oval muscle scar on the ventro-medial shaft, about one-third of the way up the shaft from the omal end, which was observed to take this form in *F. atra*, but not in any other extant Australian taxon examined (all examined besides *Rallina tricolor*); and a very deep, pocket-liked depression of the impressio m. sternocoracoidei, undercutting the medial edge of the shaft in dorsal aspect (deep, but slightly less pocket-like, in *F. atra*). It also shares with *F. atra* a gently curved ventral facies that becomes narrow and ridge-like where it approaches the omal end, revealing the foramen nervi supracoracoidei in ventral aspect, and creating a broad sulcus m. supracoracoidei. Besides its smaller size, the fossil differs from *F. atra* by having a less elongate facies articularis clavicularis. Coots are associated worldwide with wetland habitats.

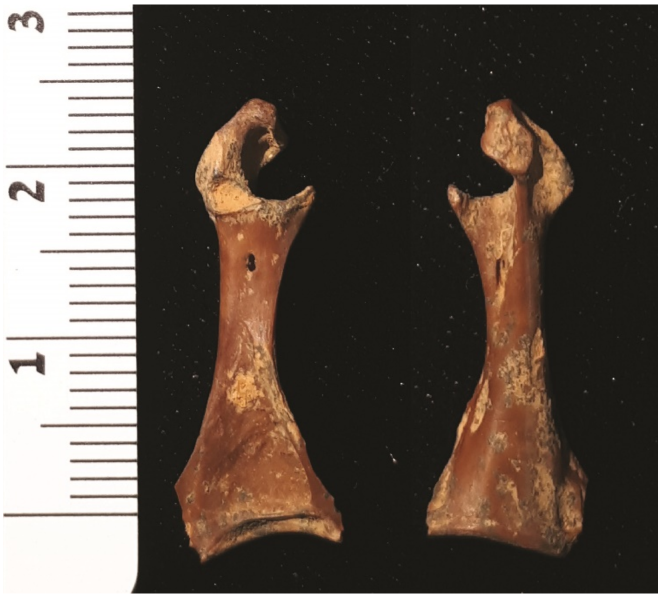


Figure 4.34: A coracoid (WAM 15.9.568) from Leaena's Breath Cave, tentatively referred to *Fulica* sp.

Rallidae, gen. & sp. indet. – Rail, indeterminate genus and species

Referred Material – WAM 15.9.133 (dL tibiotarsus) (Figure 4.35), WAM 15.9.136 (L carpometacarpus, missing os metacarpale minus) (Figure 4.37)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave:** ***Unit 3 (Early Pleistocene)*** – 75–80 cm (1), 140–145 cm (1)

Measurements (mm) – *WAM 15.9.133*, DW 6.9; *WAM 15.9.136*, TL 27.1, PW 5.9, DW 3.3

Remarks – These specimens are referred to the Rallidae but could not be referred to a modern genus or species during this study. The only extant Australian taxon for which a modern comparative skeleton was not available was *Rallina tricolor* (Red-necked Crake). More than one taxon may be represented. Among extant Australian species of rail, the carpometacarpus (WAM 15.9.136) is only of similar size to carpometacarpi of *Amaurornis moluccana* (Pale-vented Bush-hen, NMV B14162 TL, 27.4mm) and *Hypotaenidia philippensis* (Buff-banded Rail, SAM B36299 TL, 29.0 mm), but cannot be referred to either taxon. It differs from *A. moluccana* by having: longer proximal and distal synostoses, especially the proximal; a relatively flat surface of the os metacarpale majus in ventral aspect (in *A. moluccana* it is cranio-caudally broader and compressed into a ridge); a narrow processus alularis that does not have a pit beneath it on the cranial shaft (broader distally in *A. moluccana*, with a distinct facet beneath it on the cranial shaft); a processus pisiformis that is placed further distally relative to the rim of the trochlea carpalis ventralis; and the facies articularis dig. minoris and facies articularis dig. majoris that are more or less aligned (in *A. moluccana* the facies artic. minoris is displaced caudally relative to the facies artic. dig. minoris in distal aspect). It differs from *H. philippensis* by having: a shorter, slightly more proximally orientated processus extensorius, resulting in a narrower proximal width (SAM B36299, PW 6.3 mm); a smaller muscle scar on the cranio-ventral surface of the os metacarpale majus, just proximal of the facies artic. dig. majoris (scar is highly protuberant in *H. philippensis*); and a caudal rim of the trochlea carpalis dorsalis that slopes first caudally and then cranially towards the os metacarpale minus in dorsal aspect, whereas in *H. philippensis* the rim is more or less flat caudally and forms a straight line with the os metacarpale minus. The carpometacarpus is much larger than in Lewin's Rail *Lewinia pectoralis* (NMV B8661, TL 19.1 mm) and White-browed Crake *Amaurornis cinerea* (NMV B13773, TL 16.8 mm) but shares some morphological similarities with both. Morphology of *A. cinerea* is noted to be rather different to its congener *A. moluccana*.

A medium-sized distal tibiotarsus from LBC (WAM 15.9.133; Figure 4.35) is intermediate in size between those of *H. philippensis* (SAM B36299, DW 6.1 mm) and Black-tailed Nativehen *Tribonyx ventralis* (SAM B47797, DW 7.8 mm) but is not referrable to either taxon. *Tribonyx ventralis* is ruled out by larger size, and having a medial condyle that is rotated medially in cranial aspect (in the fossil, it is rotated slightly laterally), and a flat disto-lateral shaft (raised and rounded in fossil). *Hypotaenidia philippensis* is ruled out by its slightly smaller size, shallower sulcus extensorius, and flat disto-lateral shaft. Although of similar size to tibiotarsi tentatively referred to *Hypotaenidia* sp. (see above), the morphology of WAM 15.9.133 differs by having: a more protuberant tuberositas retinaculi extensori; a large epicondylus medialis that is visible beyond the rim of the condylus medialis in cranial aspect, a condition not observed in the other specimens; a more deeply excavated sulcus extensorius; and a lateral shaft adjacent to the sulcus extensorius that has a raised, rounded profile with the lateral surface falling away, rather than being relatively flat as in the other fossil specimens. These features are shared with *Lewinia pectoralis*, which is much smaller (NMV B8661, DW 4.4 mm) and *Tribonyx mortierii*, which is much larger (SAM B46032, DW 11.3 mm). These specimens require further study.

Figure 4.35: Distal tibiotarsi of one or more Rallidae taxa (WAM 15.9.134, left; WAM 15.9.131, centre; WAM 15.9.133, right)

cf. Rallidae

Referred Material – WAM 15.9.132 (dR tibiotarsus) (Figure 4.36); WAM 15.9.449 (L carpometacarpus, missing the os metacarpale minus) (Figure 4.37)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 1 (Middle Pleistocene)***, 0–5 cm

Measurements (mm) – WAM 15.9.132: DW 3.6, depth lateral condyle 3.0; WAM 15.9.449: TL, 18.9, PW, 4.5, DW, 2.6

Remarks – These specimens are tentatively referred to the Rallidae because they have some features that are similar to rails and could not be referred to any other family examined during this study. The very small distal tibiotarsus (WAM 15.9.132) has a slightly porous texture indicating that the bone is juvenile. The medial condyle is damaged and its morphology can't be assessed. The specimen is tentatively referred to the Rallidae because it has: a sulcus extensorius that is strongly medially displaced; a broad, flattened cranial shaft immediately proximal of the sulcus extensorius; prominent tuberositas retinaculi extensori laterally and medially; and prominent retinaculi m. fibularis enclosing a deep sulcus m. fibularis. Unlike the Rallidae, a pons supratendineus is absent, but it is unclear whether this is ontogenetic due to the juvenile age of the individual. The specimen is similar in size to smaller extant rallid taxa such as *Zapornia pusilla* (Baillon's Crake; cf. SAM B38159, DW 3.0 mm, depth lateral condyle 3.1 mm), but the fossil specimen could not be referred to any extant Australian taxon. The specimen differed from all rallid taxa examined, including the similarly-sized distal tibiotarsus from LBC tentatively referred to *Zapornia* sp. (WAM 15.9.138; see above) by having a lateral condyle that is proportionally narrow, particularly cranially, and which diverges more widely laterally relative to the medial condyle. The carpometacarpus, which is missing the os metacarpale minus, is referred tentatively to the Rallidae because of the elongate, cranio-caudally compressed profile of the trochlea carpalis. However, the distal morphology, insofar as it is preserved, does not seem particularly rail-like, having, for example, a rather short synostosis.

Figure 4.36: Tibiotarsus (WAM 15.9.132) from Leaena's Breath Cave, tentatively referred to the Rallidae

Figure 4.37: Carpometacarpi of specimens referred, or tentatively referred, to the Rallidae (WAM 15.9.450, left; 15.9.136, centre; 15.9.449, right)

PELECANIFORMES – Storks, Herons and Ibis

CICONIIDAE Gray, 1840 – Storks

Ciconiidae, gen. & sp. indet. – Stork, indeterminate species

Referred Material – WAM 15.9.135 (L carpometacarpus, missing most of the os metacarpale minus) (Figure 4.38)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 75–80 cm

Measurements (mm): TL, 102.1; PW, 21.4

Remarks – The carpometacarpus is referred to the Ciconiidae because it closely matches the morphology of that family, as determined from photographs (*Mycteria americana*, USNM 488620; http://n2t.net/ark:/65665/347993a9d-4248-4f61-9ad9-eb4f08405a4d). It is distinguished from carpometacarpi of the somewhat similar Gruidae by having a proportionally narrower proximal end relative to length, a more proximally orientated processus extensorius, a relatively short distal synostosis, and the lack of a foramen within the in the fossa infratrochlearis. The only extant species of stork resident in Australia today is *Ephippiorhynchus asiaticus* (Black-necked Stork), but the fossil is considerably smaller than in that species, being approximately 15% shorter and with a proximal end nearly 13% narrower, based on measurements in Louchart et al. (2005). A smaller extinct taxon, *Ciconia nana*, estimated to have been about the size of the extant extralimital species *Ciconia ciconia* (White Stork) based on leg elements, and is known from Plio-Pleistocene deposits on the Darling Downs and Cooper Creek (Boles 2005). No carpometacarpus of *C. nana* is known, and so the fossil cannot be compared with this taxon. However, published measurements of extant species of stork show that the fossil specimen from LBC is rather small compared to living and extinct taxa from around the world (Louchart et al. 2005), and so it is possible that the carpometacarpus belongs to *C. nana*. Throughout the world, storks are characteristic of wetland habitats. Today, the Ciconiidae are unknown from the south-western quarter of the Australian continent.

Figure 4.38: Carpometacarpus of Ciconiidae, gen. and sp. indet. (WAM 15.9.135) from Leaena's Breath Cave

CHARADRIIFORMES Huxley, 1867 – WADERS & SHOREBIRDS

CHARADRIIDAE Leach, 1820 – PLOVERS & LAPWINGS

Peltohyas australis Sharpe, 1896 – Inland Dotterel

Referred material – WAM 15.9.105 (L tarsometatarsus); WAM 15.9.115 (L coracoid, sternal portion, slightly immature); WAM 15.9.116 (R coracoid, omal portion); WAM 15.9.124 (L humerus)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave**: ***Unit 1 (Middle Pleistocene)*** – 0–5 cm (1), 15–20 cm (1), 20–25 cm (2)

Remarks – These specimens are referred to *Peltohyas australis* because they closely match comparative specimens of this monospecific genus in both size and morphology. *Peltohyas australis* is a common species of arid inland Australia, and is present on the Nullarbor Plain today (GBIF data, accessed 26/01/2018). The species is characteristic of open habitats with low, sparse vegetation, especially chenopods (Maclean 1976). All specimens are from Unit 1 of LBC (Middle Pleistocene), between depths of 0 and 25 cm beneath the sediment surface, and this may indicate that relatively arid conditions and an open chenopod shrubland habitat prevailed during this interval of accumulation.

Charadriidae, indet. 1 – Plover or Lapwing, indeterminate small species

Referred material – WAM 15.9.123 (sternum, anterior fragment)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)***, 135–140 cm

Remarks – Of the taxa examined, the fragment of a very small sternum most closely matched *Charadrius ruficapillus* (Red-capped Plover) and *Erythrogonys cinctus* (Red-kneed Dotterel) in both size and morphology, and is therefore referred to the Charadriidae. It is slightly smaller than those of *Peltohyas australis* and *Thinornis rubricollis*. It is distinguished from other similarly sized charadriiform taxa as follows. It has a rostrum sterni that is relatively shorter than in species of *Turnix*, but longer than in *Pedionomus torquatus*. It has a relatively flat dorsal surface immediately caudal of the rostrum, distinguishing it from *Stiltea*, in which the dorsal surface drops away steeply from the rostrum. Even if a full suite of small Charadriidae taxa were available for comparison, the specimen is probably too incomplete to identify to genus or species.

Charadriidae, indet. 2 (medium-sized species)

Referred material – WAM 15.9.114 (L humerus, missing the caput humeri) (Figure 4.39)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)***, 130–135 cm

Measurements (mm) – Preserved length 46.3, PW 11.6, SW 3.4, DW 7.3

Remarks – The humerus could not be referred to genus. Of the taxa examined, it most closely matched *Pluvialis* in both size and morphology, based on comparison with *P. apricaria* (European Golden Plover), which was used in the absence of comparative specimens of *Pluvialis* species that occur in Australia (Pacific Golden Plover, *P. fulva*; Grey Plover, *P. squatarola*). Features shared with *P. apricaria* include a slender shaft, prominent processus supracondylaris dorsalis, and a proximo-caudal facies compressed into a ridge where it approaches the caput. The humerus is not formally referred to the genus due to incomplete proximal morphology and incomplete series of reference taxa, but it may be identifiable at least to genus and possibly to species when assessed against more comparative taxa.

Figure 4.39: A Charadriidae humerus (WAM 15.9.114) from Leaena's Breath Cave, in caudal aspect

PEDIONOMIDAE – PLAINS-WANDERERS

Pedionomus torquatus Gould, 1840 – Plains-wanderer

Referred Material – WAM 15.9.126 (L coracoid, omal end and partial shaft, missing most of the processus procoracoideus) (Figure 4.41)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 1 (Middle Pleistocene)*** – 15–20 cm

Remarks – The partial coracoid is indistinguishable from modern specimens. It is distinguished from the Charadriidae because the shaft lacks a foramen nervi supracoracoidei, and differs from the Scolopacidae in having a rugosity for ligamental attachment on the dorso-medio edge of the shaft, immediately distal of the processus procoracoideus (De Pietri et al. 2015), visible in Figure 4.41. *Pedionomus torquatus* is an endemic, terrestrial Australian species with quail-like behaviour, and is the sole extant representative of the Pedionomidae (Dickinson and Remsen 2013). This critically endangered species has highly specialised habitat requirements, living only in low, sparse grassland with exposed soil (Baker-Gabb, Antos, and Brown 2016). The presence of this species in Unit 1 of LBC strongly suggests the availability of sparse, open grassland habitat near the Thylacoleo Caves during the Middle Pleistocene. A single Holocene record for the species is known from the eastern extreme of the Nullarbor region (Figure 4.40) but this is outside of the core range of the species. The specimen from LBC is the westernmost record for the species, and may indicate that its restriction to eastern Australia is a relatively recent phenomenon.

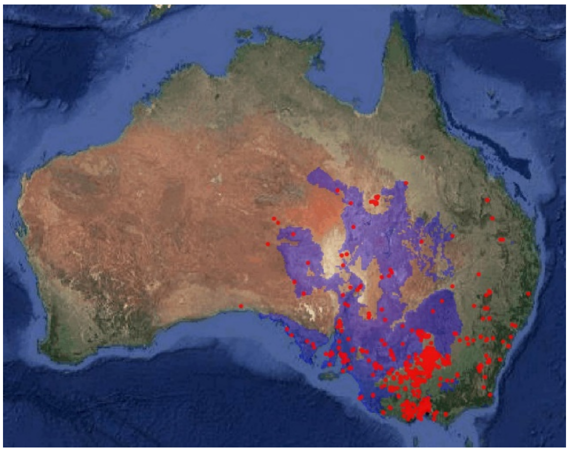


Figure 4.40: Distribution of Plains-wanderer *Pedionomus torquatus*. Downloaded from ALA Spatial Portal, 12-03-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:bc6f97c7-b94a-4622-8f13-bd063c02ff41#

Figure 4.41: Coracoid of Plains-wanderer *Pedionomus torquatus* (WAM 15.9.126; left) from Leaena's Breath Cave, in dorsal aspect (left) with a modern specimen (SAM B49157; right)

SCOLOPACIDAE Rafinesque, 1815 – SANDPIPERS

Scolopacidae, indet. 1 (medium-large species)

Referred Material – WAM 15.9.106 (L coracoid, omal portion)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 115–120 cm

Measurements (mm) – Omal width 7.3

Remarks – The specimen is relatively large for a charadriiform, and among the available comparative taxa the preserved portion was closest in size to *Cladorhynchus leucocephalus* (Banded Stilt). However, the coracoid is not referred to the Recurvirostridae, but rather to the Scolopacidae, because the shaft lacks a foramen nervi supracoracoidei. It was not referred to genus because a full suite of modern comparative specimens was not available during this study. However, the preserved portion is in good condition and should be identifiable to genus or species with access to a wider range of comparative specimens.

Scolopacidae, indet. 2 (medium-sized species)

Referred material – WAM 15.9.113 (dR femur, with damage to the medial condyle)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 60–65 cm

Measurements (mm) – N/A

Remarks – The femur could not be referred to genus. Of the taxa examined, it most closely matched *Tringa nebularia* (Common Greenshank) in size and morphology, but due to incompleteness of the specimen and lack of comparative specimens for other scolopacids the specimen is not referred to genus.

cf. *Numenius* Brisson, 1760, sp. indet. – Curlew or whimbrel, indeterminate species

Referred material – WAM 15.9.104 (L tarsometatarsus, complete apart from erosion of hypotarsus) (Figure 4.43)

Site, stratigraphy and age – **Leaena's Breath Cave:** ***Unit 3 (Early Pleistocene)*** – 110–115 cm

Measurements (mm) – TL 51.4, PW 6.7, SW, 2.6, DW 6.4

Remarks – The highly elongate tarsometatarsus is tentatively referred to *Numenius*, based on comparison with photographs of a Little Curlew *N. minutus* (USNM 347648). It is distinguished from *Rostratula*, in the family Rostratulidae, which has a tarsometatarsus that is superficially similar, based on comparison with photographs of Greater Painted Snipe *R. benghalensis* (USNM 613012), by having a proportionally more slender shaft, a more rounded eminentia intercotylaris (pointed in *Rostratula*), lateral and medial cotylae at a sub-equal proximodistal level (lateral cotyla placed relatively lower in dorsal aspect in *Rostratula*), a smaller foramen vascularis distalis, and relatively more distal extent of trochlea metatarsi II compared to trochlea IV. The fossil is of similar size to the tarsometatarsus of *N. minutus*, as assessed from photographs of USNM 347648, and shares with that species a slender, elongate shaft, a prominent and bulbous eminentia intercotylaris, a plantar shaft that is flat along most of its length but with a proximal ridge rising to meet the midline of the hypotarsus, a relatively small foramen vasculare distale recessed in a deep dorsal furrow, trochlea metatarsi II less distally extended than trochlea metatarsi IV, and a relatively indistinct fossa metatarsi I. However, the fossil appears to differ from *N. minutus* by having a deeper and longer sulcus extensorius. Throughout their range worldwide, curlews and whimbrels are associated with coastal and wetland habitats. In Australia, where the species that occur are non-breeding migrants, they have a mainly coastal distribution but may also be found inland. There are no modern records of the genus from the Nullarbor Plain, although there are three records from its periphery (Figure 4.42).

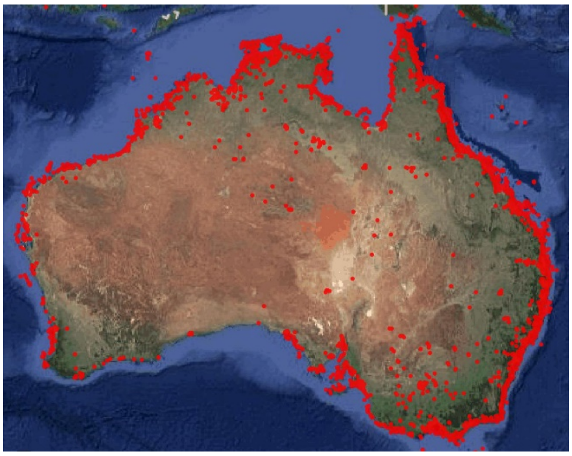


Figure 4.42: Distribution of curlews/whimbrels *Numenius* spp. Downloaded from ALA Spatial Portal, 12-03-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:cc8f0411-3009-47f5-8bcb-3e16b321144a#

Figure 4.43: Tarsometatarsus of cf. *Numenius* sp. (WAM 15.9.104) from Leaena’s Breath Cave, in dorsal (left) and plantar (right) aspects. Scale bar divisions = 1 cm

TURNICIDAE Gray, 1840 – BUTTONQUAILS

Turnix, sp. indet. – Buttonquail, indeterminate species

Referred specimens – WAM 15.9.108 (R femur); WAM 15.9.109 (pR femur); WAM 15.9.110 (dR femur); WAM 15.9.111 (R femur); WAM 15.9.112 (pL femur); WAM 15.9.119 (R tibiotarsus); WAM 15.9.120 (dL tibiotarsus); WAM 15.9.121 (dR tibiotarsus); WAM 15.9.122 (dR tibiotarsus); WAM 15.9.370 (L tarsometatarsus); WAM 15.9.371 (R tarsometatarsus); WAM 15.9.372 (dR tarsometatarsus); WAM 15.9.373 (L tarsometatarsus); WAM 15.9.374 (L tarsometatarsus); WAM 15.9.375 (dR tarsometatarsus); WAM 15.9.376 (R tarsometatarsus); WAM 15.9.377 (dL tarsometatarsus); WAM 15.9.378 (R tarsometatarsus); WAM 15.9.379 (R tarsometatarsus); WAM 15.9.380 (dR humerus); WAM 15.9.381 (dL humerus); WAM 15.9.382 (dR humerus); WAM 15.9.383 (dL humerus); WAM 15.9.384 (pR humerus); WAM 15.9.385 (pR humerus); WAM 15.9.386 (pL humerus); WAM 15.9.387 (pR humerus); WAM 15.9.388 (pL humerus); WAM 15.9.389 (pR humerus); WAM 15.9.390 (R humerus); WAM 15.9.391 (R humerus); WAM 15.9.392 (L humerus); WAM 15.9.393 (L humerus); WAM 15.9.394 (L humerus); WAM 15.9.395 (L humerus); WAM 15.9.397 (R humerus); WAM 15.9.398 (pL humerus); WAM 15.9.399 (pL humerus); WAM 15.9.400 (L coracoid, omal end); WAM 15.9.401 (L coracoid); WAM 15.9.402 (R coracoid); WAM 15.9.404 (pL coracoid); WAM 15.9.405 (L coracoid, omal end); WAM 15.9.406 (L coracoid, omal end); WAM 15.9.407 (R coracoid); WAM 15.9.408 (L coracoid, omal end); WAM 15.9.409 (R coracoid, omal end); WAM 15.9.410 (L coracoid, omal end); WAM 15.9.411 (L coracoid, omal end); WAM 15.9.412 (L coracoid, omal end); WAM 15.9.413 (L coracoid, omal end); WAM 15.9.414 (L coracoid, omal end); WAM 15.9.415 (R femur); WAM 15.9.416 (L femur); WAM 15.9.417 (L femur); WAM 15.9.419 (dL tibiotarsus); WAM 15.9.420 (dL tibiotarsus); WAM 15.9.421 (dL tibiotarsus); WAM 15.9.422 (dR tibiotarsus); WAM 15.9.423 (pL ulna); WAM 15.9.424 (pL ulna); WAM 15.9.425 (pL ulna); WAM 15.9.426 (pL ulna); WAM 15.9.427 (L ulna); WAM 15.9.428 (L ulna); WAM 15.9.429 (pL ulna); WAM 15.9.430 (R ulna); WAM 15.9.431 (sternum, anterior portion); WAM 15.9.432 (R coracoid, omal end); WAM 15.9.433 (pL carpometacarpus); WAM 15.9.435 (L carpometacarpus); WAM 15.9.436 (R carpometacarpus); 15.9.437 (R carpometacarpus); 15.9.438 (pL carpometacarpus); 15.9.439 (R carpometacarpus); 15.9.440 (R carpometacarpus); WAM 15.9.441 (L carpometacarpus); WAM 15.9.442 (R carpometacarpus); WAM 15.9.443 (pL carpometacarpus); WAM 15.9.444 (cR carpometacarpus); NISP = 81

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave:** ***Unit 1 (Middle Pleistocene)*** – 0–5 cm (4), 5–10 cm (10), 10–15 cm (1), 15–20 cm (3), 20–25 cm (5), 25–30 cm (9), 30–35 cm (6); ***Unit 2 (Middle Pleistocene)*** – 35–40 cm (3), 40–45 cm (2); ***Unit 2 (Early Pleistocene)*** – 50–55 cm (1); ***Unit 3 (Early Pleistocene)*** – 60–65 cm (2), 70–75 cm (2), 100–105 cm (1), 105–110 cm (1), 110–115 cm (7), 115–120 cm (19), 120–125 cm (2), 125–130 cm (1), 130–135 cm (2), 145–150 cm (1)

Remarks – Buttonquail fossils are among the most numerous bird remains in the LBC deposit, occurring in all three sedimentary units. The specimens are not referred to species because within the scope of this study it was not possible to determine morphological and size criteria for distinguishing between the seven extant Australian species, all of which are sexually dimorphic, with females being larger than males, and with size overlap between the skeletons of some species. As a preliminary assessment, the five complete fossil humeri from LBC were measured, and are longer (range 26.6–28.4 mm) than the available comparative specimen of Red-backed Buttonquail *T. maculosus* (NMV B20838; TL 23.8 mm), and shorter than the available specimen of Black-breasted Buttonquail *T. melanogaster* (NMV B30680; TL 33.6 mm). Mean length of the fossil humeri (27.3 mm) is longer than the mean length of Little Buttonquail *T. velox* (24.6 mm) and *T. pyrrhothorax* (25.6 mm) reported by Baird (1992), but there is overlap in length range of the fossils and these two species.

Based on modern geographical distributions, the most likely candidate species for the fossils would be *T. velox*, which is ubiquitous to all habitat types in the Nullarbor region today (Burbidge et al. 1987). *Turnix varius* may also be a plausible candidate given that it has a disjunct population across southern Australia and is apparently divided by the Nullarbor Plain (ALA data, accessed 12-03-2018), so may have had a contiguous distribution through southern Australia during at least parts of the Pleistocene. *Turnix pyrrhothorax* should also be considered, given that it should in theory inhabit much of the western portion of Australia, including the Nullarbor region, based on climatic modelling, with its current range apparently restricted by short-term weather trends as opposed to climate *per se* (Reside et al. 2010). All elements referred to this genus were recovered from the pit excavations in LBC, with no specimens having been found on the sediment floor or in the rockpiles beneath the cave entrances. The lack of modern skeletons of *T. velox* on the cave floor of LBC is difficult to account for, as the species is presumably resident around the caves today and is generally common in Quaternary cave deposits (Baird 1991).

Charadriiformes, indet. (medium-sized species)

Referred material – WAM 15.9.107 (L femur)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 115–120 cm

Measurements (mm): TL including crista trochanterica, 39.4; PW, 8.5; SW, 3.6; DW, 6.9

Remarks – The femur is well preserved but could not be referred to family based on the available comparative specimens. The femur is approximately the same size as femora of *Vanellus miles* (Masked Lapwing) but has a latero-medially curved shaft (straight in *V. miles*). It has a long crista trochanterica that is more or less aligned with the long axis of the shaft.

Note: the femur would be congruent in size with the tarsometatarsus referred to cf. *Numenius* sp. indet. (WAM 15.9.104; see below), also from Unit 3 in Pit B of LBC, but no femoral comparative specimens of that genus were available for comparison during this study. An extinct species of plover, *Vanellus liffyae*, has been described from the Pliocene of central Australia, but is known only from a coracoid (De Pietri *et al.* 2018), precluding a comparison.

ACCIPITRIFORMES Vieillot, 1816

ACCIPITRIDAE Vieillot, 1816 – KITES, HAWKS, HARRIERS & EAGLES

Accipitridae, indet. – Extinct eagle (large species)

Referred Material – WAM 15.9.72 (R coracoid, missing the omal end) (Figure 4.45); WAM 15.9.73 (pL tarsometatarsus, preserving approximately half the shaft length) (Figure 4.44)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 100–105 cm (1), 115–120 cm (1)

Measurements (mm) – WAM 15.9.72, SW 15.3, omal width N/A, DW 33.0; WAM 15.9.73, PW 12.8

Remarks – These elements of a large accipitrid were not found in association, but are both from Unit 3 (Early Pleistocene) of LBC, and may belong to the same extinct species. Neither is referrable to an extant taxon. The preserved portion of the coracoid is considerably larger than in any extant Australian accipitrid apart from the Wedge-tailed Eagle *Aquila audax*. It is more robust than a female specimen of *A. audax* (SAM B51219; Figure 4.45), and has a particularly stout shaft (*Aquila audax* SAM B46613, SW = 10.8 mm). It also differs morphologically from that species by having: a foramen nervi supracoracoidei that does not abut the medial margin; a shallow and indistinct cotyla scapularis (deep and cup-like in *A. audax*), and a proportionally wider facies articularis sternalis. Morphologically it shares some features in common with the much smaller Square-tailed Kite *Lophoictinia isura*, Black-breasted Buzzard *Hamirostra melanosternon* and Black Kite *Milvus migrans*. Features shared with these species include a proportionally stout shaft, and a large protuberance for a muscle attachment on the dorsal surface immediately proximo-lateral of the impressio m. sternocoracoidei, which is either absent or placed much further medially in all other extant Australian accipitrids. The omal end is missing, so presence and placement of a pneumatic fossa within the sulcus m. supracoracoidei cannot be assessed. The affinities of this specimen therefore remain unknown, but it likely represents a new extinct species, and requires further study. Initial assessment shows some similarity with a coracoid of the undescribed large accipitrid from Green Waterhole Cave (see Baird 1985).

The proximal tarsometatarsus is distinguished from all extant Australian accipitrid species besides *Aquila audax* by its much larger size. It is of similar size to the proximal tarsometatarsus of *A. audax* (e.g. SAM B46613, female, PW = 21.5 mm; Figure 4.44), but is morphologically highly divergent from that species, and is distinguished by having: a highly prominent and pointed eminentia intercotylaris (low and blunt in *A. audax*); a narrow hypotarsal canal with a round profile in proximal aspect (broad and more oval in *A. audax*); a much broader fossa parahypotarsalis medialis due to strong lateral deflection of the hypotarsus (medial hypotarsal crest is medially deflected in *A. audax*); a deeper fossa infracotylaris; a foramen proximalis vascularis medialis that is larger than its lateral counterpart and is placed more proximally (of sub-equal size, and with the medial foramen placed more distally than the lateral in *A. audax*); and a short, centrally-placed tuberositas m. tibialis cranialis that is immediately distal of the foramina vascularia proximalia, and which is completely recessed within the deep sulcus extensorius (tuberositas is longer, placed more distally, and sits above the facies of the shaft on its raised lateral edge in *A. audax*). The specimen is not referred to genus, but of the taxa examined it shows most morphological resemblance to *Hamirostra melanosternon* (Black-breasted Buzzard), particularly the central placement of the tuberositas m. tibialis cranialis, relative proximo-distal position of the foramina vascularia proximalia, the narrow, rounded shape of the hypotarsal canal, and strong lateral displacement of the medial hypotarsal crest. However, the fossil tarsometatarsus is approximately twice the size of that of *H. melanosternon* (Figure 4.44). Although the distal tarsometatarsus is not preserved, preliminary comparison with a fragmentary distal tarsometatarsus of a large Pleistocene accipitrid from Victoria Fossil Cave shows that they are incongruent in size, the LBC specimen likely belonging to a much smaller taxon, even allowing for sexual dimorphism among many raptors. Thus Australia likely had a minimum of two large extinct accipitrid taxa during the Pleistocene.

Figure 4.44: Tarsometatarsus of Accipitridae, indet. (large extinct species) (WAM 15.9.73; centre) from Leaena's Breath Cave in dorsal aspect, with modern specimens of Black-breasted Buzzard *Hamirostra melanosternon* (SAM B36200; left) and Wedge-tailed Eagle *Aquila audax* (SAM B46613; right)

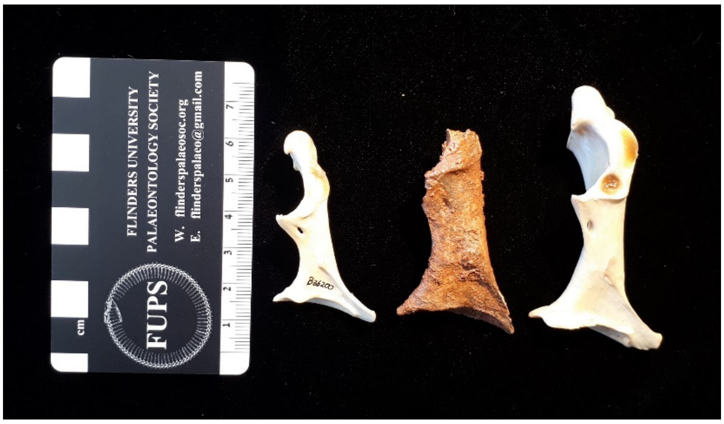


Figure 4.45: Coracoid of Accipitridae, indet. (large extinct species) (WAM 15.9.72, centre) from Leaena's Breath Cave, in dorsal aspect, with modern specimens of Black-breasted Buzzard *Hamirostra melanosternon* (SAM B36200; left) and Wedge-tailed Eagle *Aquila audax* (SAM B46613; right)

***Circus*, *sp.* indet. – Harrier, indeterminate species**

Referred Material – WAM 15.9.22 (L tarsometatarsus), WAM 5.9.70 (dL tarsometatarsus)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave: *Surface (unknown location, probably Pleistocene)*** (1); ***Unit 1 (Middle Pleistocene)*** – 0–5 cm (1)

Remarks – The tarsometatarsi are within the size range of both extant Australian species of harrier, the Spotted Harrier *Circus assimilis* and Swamp Harrier *C. approximans*, and no morphological features distinguishing the two taxa were identified during this study. Both species are widespread throughout Australia. *Circus assimilis* inhabits the Nullarbor Plain today, while *C. approximans* does not, with a few records of the species from the coastal margin to the south of the Nullarbor Plain (GBIF data, accessed 29/01/2018). Remains referred to *C. assimilis* are known from the Thylacoleo Caves (see below).

***Circus assimilis* Jardine & Selby, 1828 – Spotted Harrier**

Referred Material – WAM 15.9.71 (R humerus); WAM 15.9.78 (L/R distal tibiotarsi)

Site, stratigraphy and age (NISP in brackets) – **Last Tree Cave: *Surface (probably Pleistocene)*** – 'The Ossuary', Grid 9 (1); **Leaena's Breath Cave**: ***Surface (probably Pleistocene)*** – 'Corner Cluster' (1)

Remarks – These specimens are indistinguishable in size and morphology from modern specimens of *C. assimilis*, a species with a modern distribution that includes the Nullarbor Plain (GBIF data, accessed 29/01/2018). The humerus is referred to *C. assimilis* rather than to *C. approximans* (Swamp Harrier) because it has a shorter crus dorsale fossae, a round rather than slightly elongate opening of the fossa pneumotricipitalis ventralis, and a slight disto-dorsal rotation of the processus flexorius. The distal tibiotarsi were referred to *C. assimilis* rather than to *C. approximans* because the medial condyles are relatively shorter proximo-distally as seen in cranial aspect, thus creating a larger opening at the medial side of the pons supratendineus, and the bone is less expanded medio-distally such that the disto-medial shaft meets the medial condyle at a shallower angle than in *C. approximans. Circus assimilis* favours open and lightly wooded habitat that does not obstruct flight, and captures most of its prey on the ground, especially small ground-dwelling birds (Marchant and Higgins 1993).

Accipiter fasciatus (Vigors & Horsfield), 1827 – Brown Goshawk

Referred Material – WAM 15.9.75 (dL tarsometatarsus, missing trochlea II), WAM 15.9.77 (L scapula)

Tentatively Referred Material – WAM 15.9.583 (dL tibiotarsus), WAM 15.9.602 (dR tarsometatarsus)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 75–80 cm (1), 110–115 cm (1), 115−120 cm (1), 130−135 cm (1)

Measurements (mm) – WAM 15.9.602, DW 11.1; WAM 15.9.583, SW 4.4, DW 7.7

Remarks – This distal left tarsometatarsus is referred to *A. fasciatus* on the basis of size, being smaller than tarsometatarsi of *A. novaehollandiae* (Grey Goshawk) and larger than those of *A. cirrocephalus* (Collared Sparrowhawk), but distal width cannot be measured due to its missing trochlea metatarsi II. The scapula is distinguished from that of *A. novaehollandiae* by its slightly smaller size and because it has a larger pneumatic foramen on the proximo-medial surface. It is distinguished from *A. cirrocephalus* because in proximal aspect the facies of the acromion is more laterally expanded so has a proportionally larger surface area. The other two specimens are only tentatively referred. *Accipiter fasciatus* has a broad distribution throughout Australia, and while there are isolated records of the species from the Nullarbor Plain, the central Nullarbor and the Great Victoria Desert constitute the only geographical area considered to be outside the normal range of the species (Figure 4.46). *Accipiter fasciatus* has only rarely been recorded in treeless habitats, favouring woodland and forests, with the type and height of trees apparently unimportant. It hunts at all heights within wooded habitats from ground to canopy, and takes mainly birds, but also consumes other small vertebrates up to 2 kg (Marchant and Higgins 1993). Presence of this species on the Nullarbor Plain during the Early Pleistocene implies the likely presence of trees.

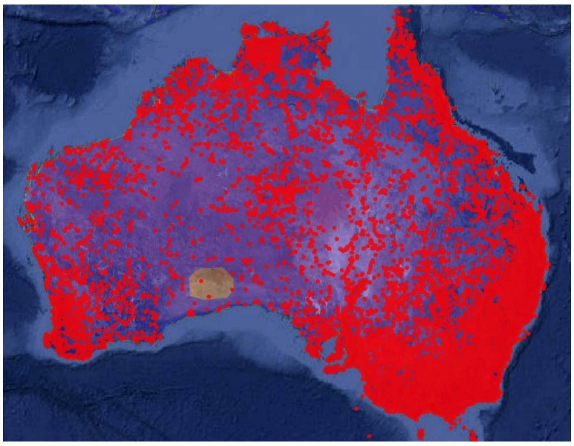


Figure 4.46: Distribution of Brown Goshawk *Accipiter fasciatus*. Downloaded from ALA Spatial Portal, 12-03-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:1cc98443-ce0f-47fd-a47e-912a3272bd71#

***Aquila audax* (Latham, 18012) – Wedge-tailed Eagle**

Referred Material – WAM 15.9.622 (partial pelvis) (Figure 4.47)

Site, stratigraphy and age – Leaena's Breath Cave: ***Surface (probably Pleistocene)*** 'Associated with 'Floor Skull #1'

Remarks – Insofar as it is preserved, the pelvis is of very similar size and morphology to a modern specimen of *A. audax* SAM B46613, female) (Figure 4.47). *Aquila audax* is the largest extant species of Australian eagle. It tolerates a wide range of habitats and is widespread throughout the mainland, including the Nullarbor region, but favours open and lightly timbered habitat where trees are available for nesting. The species takes live vertebrate prey including birds >100 g and mammals >500 g, as well as carrion (Marchant and Higgins 1993).

Figure 4.47: Pelvis of *Aquila audax* (WAM 15.9.622) from Leaena's Breath Cave, in ventral aspect, with a modern specimen (SAM B46613)

STRIGIFORMES Wagler, 1830

TYTONIDAE Ridgway, 1914 – BARN OWLS

Tyto cf. *T. novaehollandiae* Stephens, 1826 – Masked Owl

Referred Material – WAM 15.9.365 (partial associated skeleton)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Surface (probably Pleistocene):*** Station 91, "Upper Dec Site" (Figure 4.9)

Measurements – See Table 4.6 for measurements of main elements

Remarks – These associated skeletal remains from the surface of LBC are on the whole larger than other Pleistocene *Tyto* remains collected from the Thylacoleo Caves (see below), and have skeletal proportions more similar to modern specimens of *T. novaehollandiae novaehollandiae* from eastern Australia (NMV B.31181, zoo specimen; NMV B.25361, wild specimen; both of unknown sex). The leg elements of the fossil specimen are on the whole larger and more robust than other fossil remains from the Thylacoleo Caves (Table 4.7), with the tarsometatarsus, for example, more closely matching the size and proportions of *T. novaehollandiae novaehollandiae* than do the other fossils (Figure 4.48). Insofar as they can be measured, the pectoral elements of WAM 15.9.365 also appear larger than other Nullarbor fossil remains, with the ulna, which has a slightly damaged olecranon and thus would have been slightly longer than measured, measuring >120 mm, and thus being closer to the length of modern specimens of *T. n. novaehollandiae* (NMV B.25361, 119.2 mm; NMV B.311881, 116.3 mm) than to other measurable fossil specimens referred to *Tyto* sp. indet (see below; WAM 15.9.338, 103.2 mm; WAM 15.9.347, 113.5 mm). Preliminary observations also indicate that this specimen is more similar morphologically to *T. n. novaehollandiae* than to other large *Tyto* remains from LBC, with the synsacrum, for example, having a flat cranio-ventral surface rather than being latero-medially compressed into a ridge as in other fossil specimens (see below). For these reasons the skeleton is tentatively referred to *T. novaehollandiae.* Five extant subspecies of *T. novaehollandiae* are currently recognised, one occurring in New Guinea and the remaining four in Australia, with a taxon from Tasmania, *T. castanops*, now classified as a separate species rather than subspecies (Dickinson and Remsen, 2013). The extent of skeletal variation between these taxa is currently unknown, and determining this would aid in the referral of fossil specimens, and may shed light on relationships between 'Masked Owl' taxa, a review of which has been suggested by the International Ornithological Congress (Gill and Donsker 2018). See *Tyto* sp. indet. (large species) (below) for discussion of the identity and status of 'Masked Owls' that were resident on the Nullarbor Plain into the 20th Century.

Table 4.6: Measurements (mm) of main elements of WAM 15.9.365, a fossil specimen from the surface of Leaena's Breath Cave tentatively referred to *Tyto novaehollandiae*

Element/Side	TL	PW	SW	DW
Pelvis	50.4	–	–	–
Femur	66.6	13.3	6.7	14.2
Tibiotarsus	113.2	14.2	6.5	13.6
Tarsometatarsus	70.8	13.5	6.3	15.8
Humerus	–	–	–	17.2
Ulna	>120	10.4	5.4	–
Carpometacarpus, L	54.8	12.3	–	8.3

***Tyto delicatula delicatula* (Gould, 1837) – Australian Barn owl**

Referred Material – WAM 15.9.323 (L tibiotarsus, missing its distal condyles)

Site, stratigraphy and age – **Leaena's Breath Cave:** ***Unit 3 (Early Pleistocene)*** – 110–115 cm

Measurements (mm) – TL, N/A; PW, 10.8; SW, 5.2; DW, N/A

Remarks – The tibiotarsus closely matches the morphology and size of a modern specimen of *Tyto delicatula delicatula* (SAM B48664) (formerly included within *T. alba*; see Dickinson and Remsen, 2013). Total length of WAM 15.9.323 could not be measured as most of the distal end is missing, but would have been similar to length of the tibiotarsus of SAM B48664 (93.3 mm). The fossil specimen is smaller overall than other *Tyto* remains from the Thylacoleo Caves (see *T.* cf. *novaehollandiae*, above, and *Tyto* sp. indet., large species, below). Presence of *T. delicatula* in Unit 3 of LBC demonstrates that the species has been part of the Australian avifauna since at least the Early Pleistocene, but as the only specimen representing the taxon in the whole deposit – in contrast to the abundant remains of the indeterminate species (see below) – *T. delicatula* may have either been uncommon on the Nullarbor Plain in the Early and Middle Pleistocene, or else did not habitually roost or nest in cave entrances. There are few modern records of the Australian Barn Owl (as *T. alba* or *T. javanica*) from the Nullarbor region, with virtually all reports being from the periphery rather than from the Nullarbor Plain (ALA data, accessed 25-04-2018). It seems unlikely that the species contributed many small vertebrate remains to the Thylacoleo Caves fossil assemblage, unlike other Late Pleistocene and Holocene cave deposits in Australia, including some of those to the south of the Nullarbor Plain, where *T. alba* is thought to have been a major accumulating agent (Baird 1991).

***Tyto*, sp. indet. – 'Masked owl', (indeterminate species)**

Referred Material – WAM 05.4.9 (R Carpometacarpus); WAM 05.9.22 (cranium); WAM 05.9.24 (R tarsometatarsus); WAM 05.9.26 (various associated elements); WAM 15.9.20 (R tarsometatarsus); WAM 15.9.23 (R femur); WAM 15.9.24 (L femur); WAM 15.9.69 (pR ulna); WAM 15.9.305 (cranium); WAM 15.9.306 (cranium); WAM 15.9.307 (L tarsometatarsus); WAM 15.9.308 (R tarsometatarsus); WAM 15.9.309 (L tarsometatarsus); WAM 15.9.310 (L tarsometatarsus); WAM 15.9.311 (pR tarsometatarsus); WAM 15.9.312 (L tarsometatarsus); WAM 15.9.313 (dL tarsometatarsus); WAM 15.9.314 (R tarsometatarsus); WAM 15.9.315 (R tibiotarsus); WAM 15.9.316 (pL carpometacarpus); WAM 15.9.317 (pR scapula); WAM 15.9.318 (dR humerus); WAM 15.9.319 (dL humerus); WAM 15.9.320 (R humerus); WAM 15.9.321 (dL humerus); WAM 15.9.322 (R coracoid); WAM 15.9.324 (dR ulna); WAM 15.9.325 (dR tarsometatarsus); 15.9.326 (dL carpometacarpus); WAM 15.9.329 (pelvis); WAM 15.9.330 (L/R tarsometatarsi); WAM 15.9.331 (L/R tibiotarsi); WAM 15.9.332 (synsacrum); WAM 15.9.333 (L/R femora); WAM 15.9.334 (pL/R femora); WAM 15.9.335 (L tibiotarsus, shaft); WAM 15.9.336 (dL tibiotarsus); WAM 15.9.337 (sternum); WAM 15.9.338 (L/R ulnae); WAM 15.9.339 (pL humerus); WAM 15.9.340 (L/R coracoid); WAM 15.9.341 (P, dL carpometacarpi); WAM 15.9.342 (pR scapula); WAM 15.9.343 (vertebra); WAM 15.9.344 (phalanges & unguals); WAM 15.9.345 (cranium); WAM 15.9.346 (rostrum); WAM 15.9.347 (associated remains, various); WAM 15.9.350 (L coracoid, omal); WAM 15.9.351 (L coracoid); WAM 15.9.355 (phalanx); WAM 15.9.356 (phalanx dig. majoris); WAM 15.9.357 (phalanx); WAM 15.9.358 (phalanx); WAM 15.9.359 (phalanx); WAM 15.9.360 (phalanx); WAM 15.9.361 (cranium); WAM 15.9.362 (L tarsometatarsus); WAM 15.9.364 (associated remains, various); WAM 15.9.366 (pL femur); WAM 15.9.367 (dL tibiotarsus); WAM 15.9.368 (dR humerus); WAM 15.9.369 (L coracoid); WAM 15.9.564 (R tibiotarsus); WAM 15.9.603 (L Humerus); WAM 15.9.607 (various associated elements); WAM 15.9.609 (L tarsometatarsus); WAM 15.9.610 (L coracoid); WAM 15.9.611 (pL humerus); WAM 15.9.617 (various associated elements)

Site, stratigraphy and age (NISP in brackets) – **Last Tree Cave**: ***Surface (probably Pleistocene)*** – "Nally Bin Site" (1); "The Ossuary", Grid 6 (1), Grid 7 (3), Grid 15 (1), Grid 16 (1); **Leaena's Breath Cave**: ***Surface***

(probably Pleistocene) – Station 32 (1); Station 86, “Two Bird Cavern” (18); Station 87 “Two Bird Cavern” (1); Station 88 “Two Bird Cavern, Rift Crevice Corner” (2); Station 94 (2); Station 107 “Powder Floor” (1); Station 120, “Upper Flood Shoot [sic.] Chamber” (1); “Corner Cluster” (1); unknown location (3); “Wallabia kitcheneri Corner” (1); ***Unit 1 (Middle Pleistocene)*** – 0–5 cm (2), 10–15 cm (2), 20–25 cm (3), 25–30 cm (3), 30–35 cm (1); ***Unit 2 (Middle Pleistocene)*** – 35–40 cm (2), 40–45 cm (1); ***Unit 3 (Early Pleistocene)*** – 70–75 cm (2), 75–80 cm (1), 80–85 cm (3), 95–100 cm (1), 110–115 cm (1), 115–120 cm (1), 115–130 cm (6)

Measurements – See Table 4.7 for measurements of main elements

Remarks – These remains are of a large species of *Tyto* intermediate in size between *T. delicatula* (Australian Barn Owl) and the nominate subspecies of *T. novaehollandiae* (Masked Owl) from eastern Australia. Although closer in size and robusticity to *T. n. novaehollandiae* than to *T. delicatula* (Table 4.7), including having considerably larger, more robust tarsometatarsi than *Tyto delicatula* (Figure 4.48), the specimens differ somewhat in both size and morphology from *T. n. novaehollandiae*. The tarsometatarsi are on average shorter than in *T. n. novaehollandiae*, and have proportionally narrower proximal and distal ends (Figure 4.48). Despite on average having a more gracile shaft, the fossil tarsometatarsi have a deeper sulcus extensorius and fossa infracotylaris than in *T. n. novaehollandiae.* Insofar as they can be measured, the distal wing elements (ulnae and carpometacarpi) of the fossil specimens appear somewhat smaller overall, and the carpometacarpi have a processus flexorius that is more proximally orientated (more cranially directed in *T. n. novaehollandiae*). The fossil synsacra also differ by having have a cranio-ventral surface that is lateromedially compressed into a ridge, whereas the ventral surface is flat in *T. n. novaehollandiae*. Overall, these difference indicate that the fossil specimens do not belong to the nominate subspecies of the Masked Owl *T. novaehollandiae*. Skeletal material of the other four mainland subspecies of *T. novaehollandiae*, which are noted to vary in size, was not available during this study, but all are distinguished from *Tyto delicatula* by having larger, more powerful legs and more massive feet (Higgins 1999). The large size of the fossil leg elements is consistent with these remains being of a ‘masked owl’ taxon.

A ‘Masked Owl’ taxon was recorded as inhabiting blowholes on the Nullarbor Plain into the early 20th Century, when it was apparently abundant (White 1919; McGilp 1932). There do not appear to be any modern skeletal specimens of Masked Owl from the Nullarbor Plain held in any museum collection, and so it is not possible to determine at present whether the Pleistocene fossils have anatomy matching that of the local Holocene Masked Owl population, which may now be extinct. However, the fossils do seem to have limb elements congruent in size with modern mummified *Tyto* specimens from the Nullarbor region (a featherless skin, SAM B38528, from Koonalda Cave, and two currently unregistered feathered specimens from Flightstar Cave), which are larger than *Tyto delicatula*, and have feathered tarsi and very large feet, as in *T. novaehollandiae* (Higgins, 1999).

At one time, the Nullarbor population of the Masked Owl was regarded as a unique subspecies, *T. n. troughtoni*, but this was later synonymised with the eastern taxon *T. n. novaehollandiae* (see review by Debus 1993). Given the anatomical and proportional differences between the Thylacoleo Caves specimens and eastern Australian specimens of *T. n. novaehollandiae*, it is worth reinvestigating the possibility that the fossil specimens, and the very limited amount of Holocene material collected from the Nullarbor Plain in the 20th and 21st Century, may be a distinct sub-species or species of 'masked owl'. Though once common, the Nullarbor population is now possibly extinct, although there were unconfirmed reports of its continued occurrence into the late 20th Century (Debus 1993). If the Nullarbor taxon were found to be a separate taxon on the basis of anatomical and/or genetic evidence, it would then be of considerable conservation significance to determine whether or not a small population persists in the region.

Table 4.7: Measurements (mm) of key skeletal elements of specimens referred to *Tyto* sp. indet. (large species), along with measurements of modern reference skeletons; TL = total length; PW = proximal width; SW = shaft width; DW = distal width

Specimens	Element/Side	TL	PW	SW	DW
Last Tree Cave					
WAM 05.4.24	Tarsometatarsus, R	65.0	11.4	5.3	12.3
WAM 05.4.26	Tibiotarsus, dR	–	–	6.0	11.6
	Tibiotarsus, pL	–	11.7	–	–
	Tarsometatarsus, R	66.1	11.7	5.4	13.3
	Coracoid, L	39.8	6.2	5.0	17.4
	Humerus, pL	–	–	6.4	–
	Ulna, pL	–	9.9	–	–
	Ulna, dR	–	–	–	7.5
	Carpometacarpus, L	49.5	11.2	7.5	7.8
WAM 15.9.351	Coracoid, L	45.1	5.5	5.6	–
WAM 15.9.609	Tarsometatarsus, L	66.2	11.8	5.6	13.6
WAM 15.9.610	Coracoid, R	38.7	5.3	4.7	–
WAM 15.9.617	Femur, R	69.1	13.7	6.2	13.8
	Pelvis	52.8	–	–	–
	Carpometacarpus	–	12.9	–	–
Leaena's Breath Cave					
Surface					
WAM 15.9.319	Humerus, L	96.4	17.1	6.4	15.0
WAM 15.9.329	Pelvis	44.6	–	–	–
WAM 15.9.330	Tarsometatarsus, L/R	63.8	10.5	5.2	12.8
WAM 15.9.331	Tibiotarsus, dL/dR	–	–	–	11.1
WAM 15.9.333	Femur, pL/pR	–	10.9	4.8	–
WAM 15.9.334	Femur, pL/pR	–	11.6	5.0	–
WAM 15.9.338	Ulna, L/R	103.2	9.5	4.3	7.8

WAM 15.9.340	Coracoid, L/R	35.3	6.1	4.7	–
WAM 15.9.341	Carpometacarpus	–	10.3	–	6.6
WAM 15.9.347	Ulna, dL	–	–	–	9.0
	Ulna, L	113.5	9.5	4.4	8.5
	Humerus, pR	–	–	6.7	–
	Tibiotarsus, R	–	–	5.1	11.7
WAM 15.9.362	Tarsometatarsus, L	68.2	11.3	5.4	12.7
WAM 15.9.364	Carpometacarpus, dR	–	–	–	6.9
	Ulna, pR	–	9.0	–	–
	Ulna, dR	–	–	4.1	7.6
	Humerus, dL/R	90.4	–	6.2	15.1
WAM 15.9.366	Femur, pL	–	10.7	4.6	–
Pit A					
WAM 05.4.9	Carpometacarpus, R	46.2	11.1	–	–
WAM 15.9.312	Tarsometatarsus, L	61.8	11.7	5.3	13.4
WAM 15.9.314	Tarsometatarsus, R	68.4	12.1	5.9	13.6
WAM 15.9.320	Humerus, R	–	16.0	6.5	–
WAM 15.9.350	Coracoid, dL	–	–	4.4	15.3
Pit B					
WAM 15.9.307	Tarsometatarsus, L	71.3	13.9	6.8	15.3
WAM 15.9.308	Tarsometatarsus, R	70.0	–	6.8	14.7
WAM 15.9.309	Tarsometatarsus, L	68.8	13.3	7.0	14.3
WAM 15.9.310	Tarsometatarsus, L	65.6	11.7	5.4	13.5
WAM 15.9.311	Tarsometatarsus, pR	–	11.2	5.8	–
WAM 15.9.313	Tarsometatarsus, dL	–	–	–	13.6
WAM 15.9.315	Tibiotarsus, R	–	–	5.0	11.1
WAM 15.9.316	Carpometacarpus, pL	–	10.4	–	–
WAM 15.9.318	Humerus, dR	–	–	–	14.9
WAM 15.9.322	Coracoid, R	39.4	4.7	4.6	16.1
WAM 15.9.323	Tibiotarsus, L	–	11.1	5.3	–
WAM 15.9.326	Carpometacarpus, dL	–	–	–	7.5
WAM 15.9.603	Humerus, L	>108	–	7.3	17.9
Modern					
Tyto n. novaehollandiae					
NMV B25361	Pelvis	51.0	–	–	–
	Femur	65.9	13.4	5.6	14.6
	Tibiotarsus	114.0	12.5	5.4	13.8
	Tarsometatarsus	72.5	14.3	6.6	15.7
	Coracoid	43.6	5.6	5.0	18.5
	Humerus	104.0	18.3	6.5	16.7
	Ulna	119.2	11.4	5.1	9.2
	Carpometacarpus	53.0	13.1	8.1	8.6
NMV B311881	Pelvis	53.0	–	–	–
	Femur	66.1	13.3	6.1	13.3
	Tibiotarsus	110.1	11.4	5.8	12.1
	Tarsometatarsus	71.1	14.0	6.4	15.6

	Coracoid	45.1	4.8	4.7	–
	Humerus	102.8	18.6	7.3	18.0
	Ulna	116.3	10.7	5.0	9.3
	Carpometacarpus	52.5	12.5	8.0	9.5
Tyto delicatula SAM B48664	Pelvis	41.3	–	–	–
	Femur	52.6	10.3	4.7	10.9
	Tibiotarsus	93.3	9.6	4.5	9.9
	Tarsometatarsus	62.6	10.1	4.3	11.3
	Coracoid	35.9	4.2	4.5	13.7
	Humerus	86.8	14.4	5.6	13.6
	Ulna	97.9	8.5	4.1	7.1
	Carpometacarpus	45.0	9.7	6.5	7.1

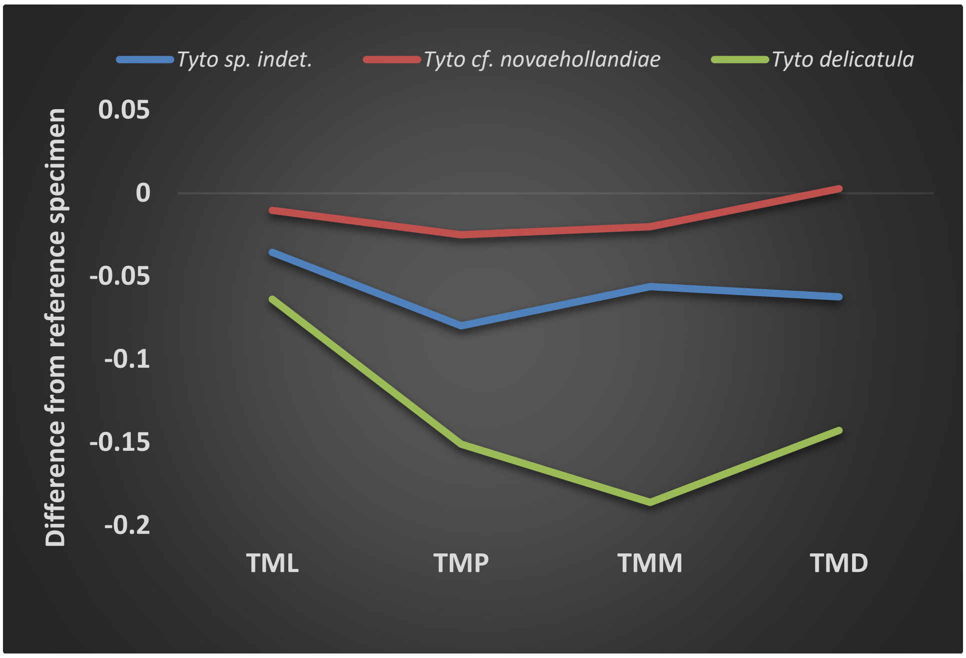


Figure 4.48: Log-ratio diagram comparing proportions of fossil tarsometatarsi of *Tyto* sp. indet. from the Thylacoleo Caves with a modern *Tyto novaehollandiae novaehollandiae* (NMV B25361) and *Tyto delicatula delicatula* (SAM B48664). For notes on methodology see Shute *et al*. 2016. The zero line represents measurements of modern reference specimen, NMV B25361, from East Gippsland, Victoria, eastern Australia. The blue line is based on mean measurements (mm) of fossil specimens from Leaena's Breath Cave and Last Tree Cave, referred to *Tyto* sp. indet. (large species), above. The red line is based on measurements of a single fossil specimen (WAM 15.9.365) from the surface of Leaena's Breath Cave, tentatively referred above to *Tyto novaehollandiae*. TML = tarsometatarsus length; TMP = tarsometatarsus proximal width; TMM = tarsometatarsus midshaft width; TMD = tarsometatarsus distal width.

cf. *Tyto* – Barn owl, indeterminate species

Referred Material – WAM 15.9.327 (synsacrum), WAM 15.9.328 (synsacrum), WAM 15.9.354 (phalanx, ungual), WAM 15.9.363 (pR humerus), WAM 15.9.578 (synsacrum), WAM 15.9.600 (sternum), WAM 15.9.619 (radius, fragment)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave**: ***Surface (probably Pleistocene)*** – Station 87 "Two Bird Cavern" (1); Station 120 "Upper Flood Shoot [sic.] Chamber" (1); ***Unit 1 (Middle Pleistocene)*** – 15–20 cm (1), 20–25 cm (1); ***Unit 3 (Early Pleistocene)*** – 115–120 cm (1), 120–125 cm (1)

Remarks – These fragmentary remains are tentatively referred to the Tytonidae because insofar as they are preserved, they are of similar size and morphology to other specimens of *Tyto* recovered from LBC. However, they are too incomplete for a confident referral.

FALCONIFORMES Sharpe, 1874

FALCONIDAE Vigors, 1824 – Falcons, kestrels and hobbies

Falco cenchroides Vigors, 1827 – Nankeen Kestrel

Referred Material – WAM 04.5.4, WAM 05.4.5 (two sterna)

Site, stratigraphy and age – **Flightstar Cave**: ***Surface (probably Holocene)*** – "Geoff's Big Bird" site

Remarks – *F. cenchroides* was included in the original taxon list for the Thylacoleo Caves fossil assemblage (Prideaux et al. 2007; Supp. Info.). Presence of this species is confirmed here based on two sterna collected from the surface of Flightstar Cave during the early explorations of the Thylacoleo Caves in 2004. These specimens appear to be modern (Holocene). Nankeen Kestrels are common on the Nullarbor Plain today, and they have been observed becoming trapped in Leaena's Breath Cave in recent times: mummified specimens complete with feathers litter the cave floors, a live bird was rescued from inside LBC during the 2012 excavation, and a mummified specimen was found in the bottom of Pit B in 2014, having fallen into the pit between the 2013 and 2014 excavations. Given how readily these birds become trapped inside the Thylacoleo Caves today, *F. cenchroides* fossils are notably absent from the pit excavations of LBC, while the larger *F. berigora* is found throughout the deposit (see below). Absence of *F. cenchroides* from Early and Middle Pleistocene sediments suggests the species was absent from the Nullarbor Plain during this interval. Molecular studies have estimated that *F. cenchroides* evolved during the Pleistocene, with estimated divergence dates for the species from its closest extralimital relatives of between 400–100 kyr (Groombridge et al. 2002) and 300–100 kyr ago (Fuchs et al. 2015), i.e. during the Middle to Late Pleistocene. The present study does not contradict this, and *F. cenchroides* may have been absent from the Australian avifauna during most of the Pleistocene.

Falco berigora Vigors and Horsfield, 1827 – Brown Falcon

Referred Material – **Last Tree Cave**: WAM 05.4.23 (L tarsometatarsus), WAM 05.4.27 (various associated elements), WAM 15.9.88 (dL humerus), WAM 15.9.91 (dL tibiotarsus), WAM 15.9.348 (pR tarsometatarsus), WAM 15.9.584 (various associated elements), WAM 15.9.585 (pelvis), WAM 15.9.586 (pR tibiotarsus), WAM 15.9.605 (R femur), WAM 15.9.606 (L tarsometatarsus), WAM 15.9.608 (L ulna), WAM 15.9.612 (L humerus), WAM 15.9.613 (sternum), WAM 15.9.614 (L tibiotarsus), WAM 15.9.615 (R ulna), WAM 15.9.616 (various associated elements); WAM 15.9.90 (L tarsometatarsus), WAM 15.9.92 (L coracoid), WAM 15.9.93 (dR tarsometatarsus); **Leaena's Breath Cave**: WAM 05.4.19 (various associated elements), WAM 15.9.80 (various associated elements), WAM 15.9.81 (dR tibiotarsus), WAM 15.9.82 (dR tibiotarsus), WAM 15.9.83 (dR tibiotarsus), WAM 15.9.84 (pL tarsometatarsus), WAM 15.9.85 (dR tarsometatarsus), WAM 15.9.86 (R tarsometatarsus), WAM 15.9.87 (dR tarsometatarsus), WAM 15.9.89 (R tarsometatarsus), WAM 15.9.94 (L tarsometatarsus), WAM 15.9.95 (pL tarsometatarsus), WAM 15.9.96 (L ulna), WAM 15.9.97 (L/R coracoid), WAM 15.9.98 (ulna, femur), WAM 15.9.99 (various associated elements), WAM 15.9.100 (R coracoid), WAM 15.9.101 (various associated elements), WAM 15.9.102 (various associated elements), WAM 15.9.103 (various associated elements), WAM 15.9.516 (frontal), WAM 15.9.559 (L humerus), WAM 15.9.563 (L tibiotarsus), WAM 15.9.565 (L tibiotarsus), WAM 15.9.587 (dR femur), WAM 15.9.588 (sternum), WAM 15.9.589 (various associated elements), WAM 15.9.590 (pR scapula), WAM 15.9.593 (R furcula), WAM 15.9.595 (sternum), WAM 15.9.596 (cranium), WAM 15.9.597 (L mandible), WAM 15.9.598 (R mandible), WAM 15.9.601 (R femur)

Site, stratigraphy and age (NISP in brackets) – **Last Tree Cave**: ***Surface (probably Pleistocene)*** – "Metasthenurus Chamber" (3) "The Ossuary", Grid 1 (1), Grid 2 (1), Grid 6 (3), Grid 15 (6), Grid 16 (1); **Leaena's Breath Cave**: ***Surface (probably Pleistocene)*** – Station 32 (2), Station 88 "Two Bird Cavern, Rift Crevice Corner" (4), Station 94 (1), Station 96 "Upper Dec Site" (1), Station 101 "Flood Shoot [sic.] Chamber" (5)(Station 103 (10), Station 106, "Powder Floor" (1), "Far eastern side of main rockpile" (1), "Associated with *B. nullarbora* holotype 05.4.70" (1); ***Unit 1 (Middle Pleistocene)*** – 30–35 cm (3); ***Unit 2 (Middle Pleistocene)*** – 35–40 cm (3), 40–45 cm (1); ***Unit 2 (Early Pleistocene)*** – 50–55 cm (2); ***Unit 3 (Early Pleistocene)*** – 75–80 cm (1), 85–90 cm (1), 90–95 cm (1), 95–100 cm (2), 115–130 (4)

Remarks – *Falco berigora* is one of the most abundant bird species within the Thylacoleo Caves assemblage. It is the only species of *Falco* that was excavated from Early and Middle Pleistocene sedimentary units in LBC, and is present in Units 1, 2 and 3. In recent times, three species of *Falco* – *F. berigora*, *F. cenchroides*, and *F. peregrinus* – have been recorded as inhabiting caves in the Nullarbor region, using them for shelter, roosting and nesting (Richards 1971). The abundance of fossil remains of *F. berigora* from the pit excavations in LBC, and the absence of other species of *Falco*, suggest that the species was the only common falcon in the region until recent times (see remarks about *F. cenchroides* above). Today it is a widespread and common species, being found throughout the Australian continent from temperate Tasmania to the northern tropics, and north into New Guinea in a wide range of habitats. In a systematic survey of birds in the Nullarbor region, *F. berigora* was one of few bird species noted to be ubiquitous to all habitat types surveyed, from the peripheral woodlands to the central Nullarbor Plain (Burbidge et al. 1987). It is an opportunistic hunter that takes small mammals, birds, reptiles and insects (Marchant and Higgins 1993).

PSITTACIFORMES Wagler, 1830 – Cockatoos and parrots

CACATUIDAE Gray, 1814 – Cockatoos

Nymphicus hollandicus (Kerr, 1792) – Cockatiel

Referred Material – WAM 15.9.237 (dR tibiotarsus, missing proximal end but preserving most of the shaft) (Figure 4.50)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 115–120 cm

Measurements (mm) – SW 1.9, DW 4.2

Remarks – The tibiotarsus is referred to *N. hollandicus* because it is indistinguishable from modern specimens of this species, having the following unique combination of features. The tuberculum retinaculum m. fibularis medialis is placed more proximally than its lateral counterpart; the pons supratendineus arises adjacent to the lateral retinaculum and is proximo-distally longer laterally than it is medially, creating a proximal edge of the pons that slopes disto-medially; and the epicondylus medialis is placed centrally in the depressio epicondylaris medialis, and is highly protuberant such that it is visible beyond the medial margin of the condylus medialis in cranial aspect. Although the proximal end of the bone is missing, placement of the crista fibularis is identical to modern specimens, suggesting it was of a similar overall length when complete. This fossil is the only specimen representing the Cacatuidae in the Thylacoleo Caves fauna. There are isolated records of the species from the periphery of the Nullarbor region, but the Nullarbor Plain is outside the core range of the species (Figure 4.49).

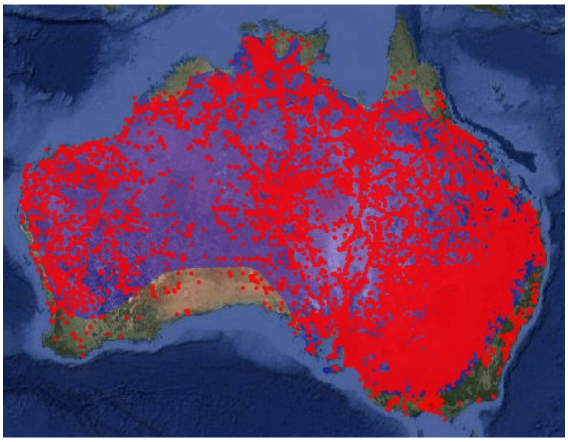


Figure 4.49: Distribution of Cockatiel *Nymphicus hollandicus*. Downloaded from ALA Spatial Portal, 12-03-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:b7a453b6-716e-4ba2-9e89-1f4b71abddef#

Figure 4.50: Tibiotarsus of *Nymphicus hollandicus* (WAM 15.9.237, left) with a modern specimen (SAM B3851, right)

PSITTACULIDAE Vigors, 1825 – Old World Parrots

Taxonomy of the Psittaculidae follows the subfamilies and tribes in Joseph *et al.* (2012).

Subfamily: Platycercinae

Tribe: Platycercini

Barnardius sp. indet. – Ringneck parrot, indeterminate species

Referred Material – WAM 15.9.45 (pR tarsometatarsus), WAM 15.9.47 (L tarsometatarsus), WAM 15.9.48 (R tarsometatarsus), WAM 15.9.162 (pR carpometacarpus), WAM 15.9.163 (pR carpometacarpus), WAM 15.9.241 (R coracoid), WAM 15.9.242 (R coracoid), WAM 15.9.243 (L coracoid), WAM 15.9.245 (L tarsometatarsus), WAM 15.9.256 (dR tibiotarsus), WAM 15.9.265 (L ulna), WAM 15.9.266 (dR ulna), WAM 15.9.267 (L ulna), WAM 15.9.269 (dL ulna), WAM 15.9.273 (L humerus), WAM 15.9.274 (L humerus), WAM 15.9.302 (R carpometacarpus), WAM 15.9.535 (L humerus), WAM 15.9.536 (L ulna), WAM 15.9.623 (various associated elements), WAM 15.9.624 (mandible)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave:** ***Surface (probably Pleistocene)*** – Station 46, "Tree Kangaroo Site" (4); Station 73 (1); "Far eastern side of main rockpile (1); Unknown location (1); ***Unit 3 (Early Pleistocene)*** – 90–95 cm (6), 95–100 cm (4), 101–115 cm (3), 115–120 cm (1)

Measurements (mm) – See Table 4.8

Remarks – The specimens are referred to *Barnardius* based on similarities to modern comparative specimens of this genus. Dickinson and Remsen (2013) recognise one species *B. zonarius*, with four sub-species, *B. z. semitorquatus*, *B. z. zonarius*, *B. macgillivrayi* and *B. z. barnardi*. However, however, some authors have tentatively suggested splitting the genus into two species, *B. zonarius* and *B. barnardi* (see Joseph and Wilke 2006; Forshaw and Joseph 2016). In addition, a further sub-species of *B. zonarius*, *B. z. parkeri*, was proposed by Forshaw and Joseph (2016). Preliminary examinations of the LBC fossils and comparative specimens of '*B. zonarius zonarius*', *B. z. semitorquatus* and '*B. barnardi'* indicate that at least some of their skeletal elements may be distinguishable based on skeletal morphology, and that more than one taxon may be represented among the fossil remains. On that basis, I have refrained from referring the fossil specimens to the only species currently recognised by Dickinson and Remsen (2013), until this is resolved.

Historically, *B. zonarius* has been recorded in woodlands surrounding the Nullarbor region (GBIF, accessed 05-01-2017), and although it was not recorded in the systematic surveys conducted in the Nullarbor region by Burbidge *et al.* (1987), McColl (1929) noted that Ringneck Parrots visited his camp approximately 50 km north of the Hampton Range, which is only around 50 km south-west of the Thylacoleo Caves. *Barnardius zonarius* was among the species originally identified within the Pleistocene avifauna of the Thylacoleo Caves (Prideaux *et al.* 2007), and the presence of the genus, if not necessarily the species, is confirmed here.

Table 4.8: Measurements (mm) of fossils from the Thylacoleo Caves referred to *Barnardius* sp.

Specimens	Element/Side	TL	PW	SW	DW
WAM 15.9.623	Coracoid (R)	28.8	6.2	3.0	7.0
(Associated skeleton)	Humerus (R)	39.0	12.1	3.8	8.3
	Ulna (R)	47.1	6.2	3.0	5.6
	Carpometacarpus (L)	30.2	7.6	5.3	4.5
	Femur (L)	33.3	6.7	2.8	6.4
	Tibiotarsus (R)	49.7	5.5	2.3	5.3
	Tarsometatarsus (R)	21.8	6.0	2.5	6.9
WAM 15.9.240	Coracoid (L)	30.4	6.5	2.7	6.9
WAM 15.9.241	Coracoid (R)	30.3	7.0	3.0	7.1
WAM 15.9.242	Coracoid (R)	28.9	6.3	2.7	7.0
WAM 15.9.243	Coracoid (L, omal end)	–	6.2	–	–
WAM 15.9.244	Coracoid (L, omal end)	–	5.9	–	–
WAM 15.9.273	Humerus (L)	40.5	11.4	4.2	9.0
WAM 15.9.274	Humerus (L)	40.3	11.4	3.9	8.7
WAM 15.9.535	Humerus (L)	39.7	11.6	4.0	8.6
WAM 15.9.536	Ulna (L)	46.6	6.2	3.0	5.6
WAM 15.9.265	Ulna (R)	48.2	6.0	3.2	5.6
WAM 15.9.266	Ulna (dR)	–	–	–	5.3
WAM 15.9.267	Ulna (R)	46.6	6.4	3.0	5.8
WAM 15.9.269	Ulna (dL)	–	–	–	5.7
WAM 15.9.162	Carpometacarpus (pR)	–	7.5	–	–
WAM 15.9.163	Carpometacarpus (pR)	–	7.0	–	–
WAM 15.9.302	Carpometacarpus (dR)	–	–	–	5.2
WAM 15.9.245	Tibiotarsus (dL)	–	–	2.4	5.9
WAM 15.9.246	Tibiotarsus (L)	50.3	5.6	2.5	5.0
WAM 15.9.256	Tibiotarsus (dR)	–	–	–	4.0
WAM 15.9.45	Tarsometatarsus (pR)	–	6.1	2.8	–
WAM 15.9.47	Tarsometatarsus (L)	21.3	5.6	2.6	6.9
WAM 15.9.48	Tarsometatarsus	22.7	6.2	2.6	7.6

Platycercus magn. *P. elegans* Gmelin, 1788 – Crimson Rosella

Referred Material – WAM 15.9.62 (sternum), WAM 15.9.143 (R humerus), WAM 15.9.144 (L carpometacarpus)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave:** ***Unit 3 (Early Pleistocene)*** – 90–95 cm (1), 95–100 cm (1), 100–110 cm (1)

Measurements (mm) – WAM 15.9.143, TL 38.4, PW 10.8, SW 3.9, DW 8.4; WAM 15.9.144, TL 30.4, PW 7.6, SW 4.9, DW 5.2

Remarks – These specimens are tentatively referred to *P. elegans* based on their similarity in size and morphology to that species (e.g. SAM B37406: humerus, TL 35.9, PW 10.1, SW 3.7, DW 7.9; carpometacarpus, TL 28.5, PW 6.9, SW 4.8, DW 4.3). However, it was not possible to compare the fossils to all members of the genus during this study, as skeletons of *P. venustus* (Northern Rosella, northern regions of Australia), *P. adscitus* (Pale-headed Rosella, tropical NE Australia) and the Tasmanian *P. caledonicus* (Green Rosella) were not available. Thus, the referral is tentative. The only species of rosella recorded in the Nullarbor region in recent times is the considerably smaller Western Rosella *P. icterotis*, fossil remains of which were also found in the LBC deposit (see below). If the identity of these specimens is confirmed to be *P. elegans*, this would provide insight into the Pleistocene biogeography of the species, which has been a question of considerable interest to recent researchers (Joseph et al. 2008). *Platycercus elegans* only occurs in eastern Australia today (Figure 4.51), and the Nullarbor Plain would constitute a major range change for this woodland species between the Early Pleistocene and today.

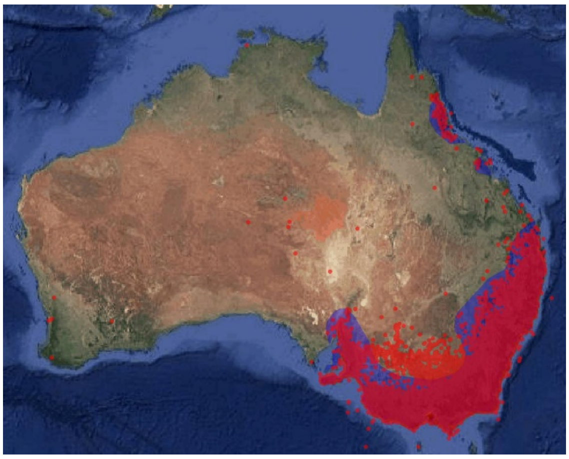


Figure 4.51: Distribution of Crimson Rosella *Platycercus elegans*. Downloaded from ALA Spatial Portal, 12-03-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:582310df-6f62-4032-b1f3-13e6e285b676#

Platycercus icterotis (Temminck & Kuhl, 1820) – Western Rosella

Referred Material – WAM 15.9.44 (L tarsometatarsus), WAM 15.9.66 (mandible), WAM 15.9.146 (R tarsometatarsus), WAM 15.9.147 (L tarsometatarsus), WAM 15.9.250 (dL tibiotarsus), WAM 15.9.251 (pL tibiotarsus), WAM 15.9.270 (R ulna), WAM 15.9.271 (p/d R ulna), WAM 15.9.284 (R humerus), WAM 15.9.291 (L carpometacarpus)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave:** ***Surface (probably Pleistocene)*** – Station 89, "4 Bird Corner – Tassie Devil Shoot [sic.]" (1); ***Unit 3 (Early Pleistocene)*** – 90–95 cm (3), 95–100 cm (4), 100–105 cm (1), 105–110 cm (1)

Measurements (mm) – See Table 4.9

Remarks – The specimens are referred to *P. icterotis* because they closely match that species in size and morphology (cf. SAM B47584). The Western Rosella is the smallest species of rosella, and today is restricted to forest habitats in the south-west corner of Western Australia (Figure 4.52). There are no recent records of the species from the Nullarbor region, but the species was reported to be present about 30 miles north of the Hampton Range in the early part of the 20th Century (McColl 1929).

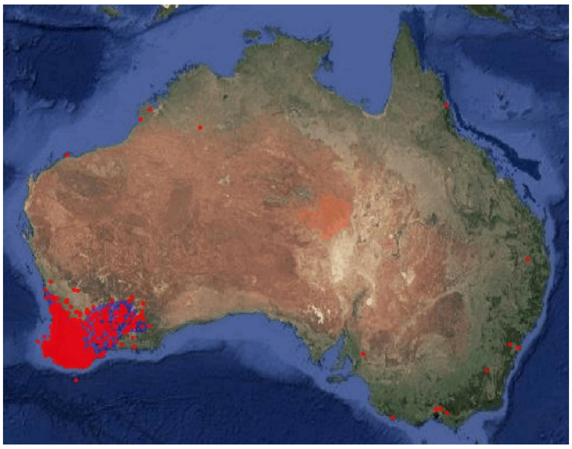


Figure 4.52: Distribution of Western Rosella *Platycercus icterotis*. Downloaded from ALA Spatial Portal, 12-03-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:9fa3d1ea-02e3-471d-b598-8761cbba9d3c#. Isolated records from eastern and northern Australia are likely erroneous identifications or due to aviary escapes.

Table 4.9: Measurements (mm) of *Platycercus icterotis* fossils from Leaena's Breath Cave

Specimens	Element/Side	TL	PW	SW	DW
WAM 15.9.284	Humerus (R)	28.6	7.8	2.8	6.3
WAM 15.9.270	Ulna (R)	33.1	4.7	2.4	4.2
WAM 15.9.271	Ulna (R)	32.8	4.7	2.1	4.4
WAM 15.9.291	Carpometacarpus (L)	22.3	5.6	–	4.1
WAM 15.9.250	Tibiotarsus (dL)	–	–	–	3.7
WAM 15.9.251	Tibiotarsus (pL)	–	3.8	1.8	–
WAM 15.9.44	Tarsometatarsus (pL/dL)	~18	4.6	1.5	5.5
WAM 15.9.146	Tarsometatarsus (R)	17.8	4.4	1.7	5.4
WAM 15.9.147	Tarsometatarsus (L)	17.9	4.6	1.9	5.6

***Platycercus*, sp. indet. – Rosella, indeterminate species**

Referred Material – WAM 15.9.46 (R tarsometatarsus), WAM 15.9.165 (dR carpometacarpus), WAM 15.9.275 (R/L humeri), WAM 15.9.296 (L femur), WAM 15.9.303 (pL ulna), WAM 15.9.518 (phalanx dig. maj.), WAM 15.9.233 (partial associated skeleton)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave: *Surface (probably Pleistocene)*** – Station 46 "Tree Kangaroo Site" (1, associated remains), Station 87 "2 Bird Cavern" (1, associated remains); ***Unit 3 (Early Pleistocene)*** – 90–95 cm (1), 95–100 cm (3), 100–105 cm (1), 110–115 cm (1)

Measurements (mm) – See Table 4.10

Remarks – These specimens could not be referred to species based on the available comparative *Platycercus* taxa (*P. elegans*, *P. icterotis*, *P. eximius*). They may be referrable with access to more comparative specimens. Probably more than one species is represented among these specimens.

Table 4.10: Measurements (mm) of specimens referred to *Platycercus* sp. indet. from LBC

Specimens	Element/Side	TL	PW	SW	DW
WAM 15.9.275	Humerus (R)	30.4	8.7	3.3	7.0
WAM 15.9.303	Ulna (pL)	–	6.1	3.1	–
WAM 15.9.165	Carpometacarpus (dR)	–	–	–	4.5
WAM 15.9.518	Phalanx dig. maj.	11.5	–	–	–
WAM 15.9.296	Femur (L)	25.2	5.0	2.2	4.7
WAM 15.9.43	Tarsometatarsus (R)	18.5	4.6	1.9	–
WAM 15.9.46	Tarsometatarsus (R)	22.3	5.6	2.9	7.2
WAM 15.9.233	Coracoid (L)	22.4	5.0	2.6	5.2
(associated skeleton)	Humerus (L)	27.7	7.6	3.3	6.3
	Ulna (R)	32.2	4.6	2.4	4.4
	Femur (R)	26.5	5.3	2.1	5.2
	Tibiotarsus (dR)	–	–	1.9	4.3
	Tarsometatarsus (L)	–	4.4	2.1	–

Platycercinae, cf. *Purpureicephalus spurius* (Kuhl, 1820) – Red-capped Parrot

Referred Material – WAM 15.9.532 (synsacrum)

Site, stratigraphy and age – **Leaena's Breath Cave:** ***Unit 3 (Early Pleistocene)*** – 100–105 cm

Remarks – Of the taxa examined, the synsacrum was most similar to that of *Purpureicephalus spurius*. However, it was not possible to make comparisons with all medium-sized members of the Platycercinae during this study, and the only available specimen of *P. spurius* (SAM B33091) was a slightly skeletally immature individual. Therefore, only a tentative referral to that species is made to facilitate future comparisons. If confirmed, the restriction of the species to the south-west corner of Western Australia (Figure 4.53) may have occurred at some point since the Early Pleistocene. The species is closely associated with the tree *Corymbia calophylla* (bloodwood, or marri) in its modern range (Forshaw 2011).

Figure 4.53: Distribution of Red-capped Parrot *Purpureicephalus spurius*. Downloaded from ALA Spatial Portal, 12-03-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:a94c442c-3257-46f2-aabc-b3580baa7dbe#. Isolated records from eastern and northern Australia are likely erroneous identifications or due to aviary escapes.

cf. *Psephotus* Gould, 1845/*Psephotellus* Mathews, 1913 – Small indeterminate parrot species

Referred Material – WAM 05.4.12 (L tarsometatarsus), WAM 15.9.49 (R tarsometatarsus), WAM 15.9.50 (dR tarsometatarsus), WAM 15.9.51 (dL tarsometatarsus), WAM 15.9.52 (pR tarsometatarsus), WAM 15.9.59 (cranium), WAM 15.9.234 (L tarsometatarsus), WAM 15.9.235 (dR tarsometatarsus), WAM 15.9.243 (L humerus), WAM 15.9.249 (dR tibiotarsus), WAM 15.9.262 (L ulna), WAM 15.9.277 (L humerus), WAM 15.9.278 (R humerus), WAM 15.9.281 (R humerus), WAM 15.9.285 (R humerus), WAM 15.9.289 (R carpometacarpus), WAM 15.9.298 (R femur), WAM 15.9.301 (dL tibiotarsus)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave:** ***Surface (probably Pleistocene)*** – Station 46 "Tree Kangaroo Site" (1); Station 89, "4 Bird Corner - Tassie Devil Shoot [sic.]" (3); Station 91, "Tassie Devil Shoot [sic.]" (1); ***Unit 1 (Middle Pleistocene)*** – 5–10 cm (1); ***Unit 3 (Early Pleistocene)*** – 90–95 cm (2), 95–100 cm (4), 100–105 cm (1), 105–110 cm (2), 115–120 cm (1), 160–165 cm (1)

Remarks – These specimens could not be referred to genus during this study. On the basis of their small size and reasonably similar morphology to *Psephotellus varius* (Mulga Parrot SAM B47689; species formerly in the genus *Psephotus*), they probably belong to one or more species of either *Psephotus* or *Psephotellus*. Based on the taxonomy of Dickinson and Remsen (2013), there are three other species in the genus *Psephotellus* besides *P. varius* – Hooded Parrot *P. dissimilis*, Golden-shouldered Parrot *P. chrysopterygius*, and the extinct Paradise Parrot *P. pulcherrimus*). However, Schweizer *et al.* (2013) found a putative '*Psephotus*' clade to be paraphyletic, with *P. varius* forming a clade with the larger species *Purpureicephalus spurius* (Red-capped Parrot). Without access to skeletons representing all the putative *Psephotus* and *Psephotellus* taxa, it is not possible to refer the specimens with confidence. All these specimens should be re-assessed against a wider range of comparative taxa. In terms of the modern fauna of the Nullarbor region, *P. varius* was noted to be a ubiquitous species in the woodlands peripheral to the Nullarbor Plain in a systematic survey in 1984 (Burbidge, *et al.* 1987).

cf. *Northiella haematogaster* Matthews, 1912 – Bluebonnet

Referred Material – WAM 15.9.142 (R coracoid)

Site, stratigraphy and age – **Leaena's Breath Cave**: ***Unit 3 (Early Pleistocene)*** – 120-125 cm

Measurements (mm) – TL 20.0, PW 4.0, SW 1.8, DW 4.9

Remarks – Of the taxa that were available for comparison, the coracoid most closely matched the morphology of *Northiella haematogaster*, and it is tentatively referred to this species. However, the fossil specimen was somewhat larger and more robust than the available comparative specimen (SAM B47577, R coracoid TL 24.2, PW 5.0, SW 2.4, DW 5.6), which represents the nominate sub-species. During this study, no specimens were available of the endemic Nullarbor taxon, *N. h. narethae*, which is arguably a separate species *N. narethae* according to analyses by Dolman and Joseph (2015). The Nullarbor taxon is smaller than its eastern counterpart, thus it seems unlikely that the relatively large fossil would belong to the Nullarbor taxon. It is noteworthy that this coracoid from the Early Pleistocene is the only specimen from the Thylacoleo Caves that may be referrable to *Northiella*, given that this genus includes a taxon that is today endemic to the Nullarbor region (see Figure 4.54 for current distribution).

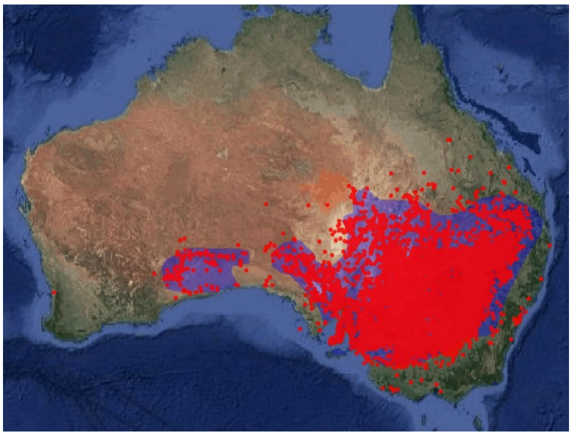


Figure 4.54: Distribution of Bluebonnet Parrot *Northiella haematogaster*. Downloaded from ALA Spatial Portal, 12-03-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:cb0bc816-19d5-4291-8f4f-006582bbdf50#

Platycercini, gen. & sp. indet. – Platycercine parrot, indeterminate genus and species

Referred Material – WAM 04.6.9 (cranium), WAM 15.9.35 (p/d L tarsometatarsus), WAM 15.9.248 (dR tibiotarsus), WAM 15.9.252 (dR tibiotarsus), WAM 15.9.257 (R ulna), WAM 15.9.258 (L ulna), WAM 15.9.259 (dR ulna)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave:** ***Surface (probably Pleistocene)*** – Station 120 "Upper Flood Shoot [sic.] Chamber" (1); "Collected with small wallaby found near 1st Thylacoleo site" (1); ***Unit 3 (Early Pleistocene)*** – 90–95 cm (1), 100–105 cm (1), 110–115 (3), 115–120 cm (1)

Remarks – These specimens are referred to the Platycercini but could not be referred to genus during the present study. They may be referrable with access to a wider range of comparative taxa.

Tribe: Pezoporini

cf. *Pezoporus* sp. indet. – 'Night parrot', indeterminate species

Referred Material – WAM 15.9.42 (R tarsometatarsus) (Figure 4.55)

Site, stratigraphy and age – **Leaena's Breath Cave:** ***Surface (probably Pleistocene)***, Station 99, "Upper Thylacoleo Rift"

Measurements (mm) – TL 20.6, PW 4.7, SW 1.8, DW 5.0

Remarks – The tarsometatarsus is referred to the Pezoporini because its morphology is highly divergent from that of all other Australian parrots besides *Pezoporus wallicus* and *Neopsephotus bourkii*, which belong to the pezoporine clade (Joseph et al, 2011). It is tentatively referred to *Pezoporus* on the basis of size and morphology. Its distal morphology is most similar to that of the very much smaller *N. bourkii,* sharing with that species a single opening of the foramen vascularis proximalis on the lateral plantar surface, an elongate trochlea metatarsi III, a trochlea metatarsi IV that has much less distal extent than trochlea metatarsi II, a narrow accessory trochlea on trochlea metatarsi IV, and a distinct fossa metatarsi I. However, it is very much larger than the tarsometatarsus of *N. bourkii* (SAM B45901, TL 13.1, PW 3.2, SW 1.3, DW 3.4). The fossil is closer in size to tarsometatarsi of the Eastern Ground Parrot *P. wallicus* (length range 21–27 mm, Ford, 1969), but has a stouter shaft and distal morphology is rather different (e.g. *P. wallicus* has a less elongate trochlea metatarsi III, and a longer/broader trochlea metatarsi IV in plantar aspect; Figure 4.55). It may therefore either belong to the related Night Parrot *P. occidentalis*, for which no modern comparative tarsi are known, but which has been noted to have a stouter tarsus than *P. wallicus* (Murie, 1868), or alternatively, to an unknown extinct relative. It is unlikely to belong to the Western Ground Parrot *P. flaviventris* (recently elevated to species based on mitochondrial DNA data; see Murphy *et al.* 2011), which has a tarsus length similar to its eastern relative *P. wallicus* (22.5–25.5 mm; Ford, 1969).

The specimen somewhat resembles a Late Pleistocene tarsometatarsus (MV P184907) from Madura Cave in the Nullarbor Region that was tentatively referred to *P. occidentalis* by Baird (1986) on the basis of size, but morphology of the Madura Cave and Leaena's Breath Cave specimens is not identical. As assessed from photographs in Plate 3–8 in Baird (1986), the two fossil specimens WAM 15.9.42 and MV P184907 have similar proportions, both having a relatively broad shaft that merges gradually with the distal end, and a similar shape of trochleae metatarsorum II and III in dorsal aspect. However, trochlea metatarsi IV differs markedly in the two specimens. In WAM 15.9.42, trochlea IV flares widely laterally, with the widest part of the trochlea being level with the distal end of the foramen vascularis distalis, whereas in MV P184907 trochleae II and IV are sub-equal in size, and the widest part of trochlea IV is well distal of the foramen. Overall evidence therefore suggests that two taxa are represented. One or other specimen may be referrable to the Critically Endangered Night Parrot *P. occidentalis*, but characterising the tarsometatarsus of this species will require CT-scanning a preserved skin from a museum collection, unless a skeletal specimen can be procured now that the species has been re-confirmed as extant (Pyke and Ehrlich 2014). I also note the existence of stout-shafted pezoporine tarsometatarsi from other Quaternary localities, those being a specimen from Victoria Fossil Cave, Naracoorte that was tentatively referred to *P. wallicus* (SAM P41879), an as-yet unregistered specimen from Komatsu Cave, Naracoorte, and two unregistered specimens from Bagalowie Caves, Flinders

Ranges, that are in the Palaeontology collection of the South Australian Museum. The morphology of all these specimens from disparate localities should ultimately be compared with each other, and with the tarsometatarsi of *P. occidentalis*, *P. wallicus* and *P. flaviventris*, to determine the number of pezoporine taxa represented in the Pleistocene and Holocene.

Note: cursory examination of a skeleton of a species of *Neophema* revealed this genus to be rather divergent from other members of the Pezoporini, which may be worth exploring further. Mayr (2008) has previously noted differences in morphology of the hypotarsus in *Neophema* and *Pezoporus*.

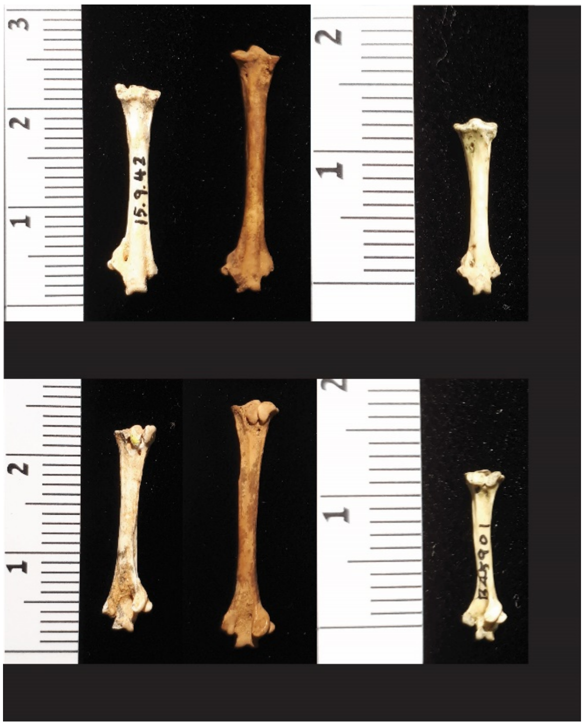


Figure 4.55: Tarsometatarsus of cf. *Pezoporus* sp. (WAM 15.9.42, left), from Leaena's Breath Cave, with a fossil specimen of *P. wallicus* (SAM P42937, centre) from Blanche Cave, Naracoorte, and a modern specimen of *Neopsephotus bourkii* (SAM B45901, right)

cf. *Neopsephotus bourkii* (Gould, 1841) – Bourke's Parrot

Referred Material – WAM 15.9.141 (R coracoid), WAM 15.9.153 (dR humerus), WAM 15.9.292 (R ulna), WAM 15.9.304 (pL ulna)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave:** ***Unit 1 (Middle Pleistocene)*** – 30–35 cm (1); ***Unit 3 (Early Pleistocene)*** – 115–120 cm (2), 120–125 cm (1)

Remarks – The specimens are tentatively referred to *N. bourkii* based on similarity in size and morphology to a modern reference specimen (SAM B45901). The humerus shares with *N. bourkii* a prominent muscle scar on the proximo-caudal surface of the shaft, running about 20° to the long axis of the shaft approaching the level of the muscle scar below the tuberculum dorsale, which was not observed in other taxa. The Nullarbor Plain is outside of the core range of the species (Figure 4.56), which is typically associated with *Acacia aneura* (mulga) woodlands (Forshaw 2011).

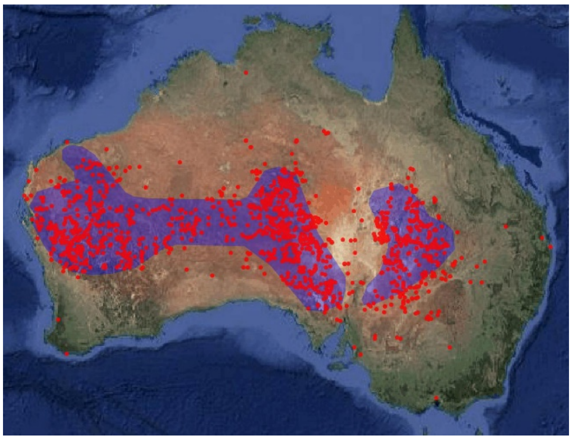


Figure 4.56: Distribution of Bourke's Parrot *Neopsephotus bourkii*. Downloaded from ALA Spatial Portal, 12-03-2018, using Google Maps: http://spatial.ala.org.au/?q=lsid:urn:lsid:biodiversity.org.au:afd.taxon:5ae56d81-0ab4-42b1-8ab8-c98c0345f5b2#

Neophema, sp. indet. – Grass parrots, indeterminate species

Referred Material – WAM 15.9.54 (rostrum), WAM 15.9.155 (R tarsometatarsus), WAM 15.9.167 (R coracoid), WAM 15.9.170 (R coracoid, omal end), WAM 15.9.171 (L coracoid), WAM 15.9.168 (R coracoid), WAM 15.9.172 (R coracoid), WAM 15.9.276 (pL humerus), WAM 15.9.288 (L carpometacarpus), WAM 15.9.539 (dL humerus)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave: *Unit 1 (Middle Pleistocene)*** – 0–5 cm (1); ***Unit 3 (Early Pleistocene)*** – 95–100 cm (1), 110–115 cm (2), 115–120 cm (5), 120–125 cm (1), 125–130 cm (1)

Remarks – These specimens are referred to the genus *Neophema* based on their similarity in size and morphology to *N. elegans* (Elegant Parrot). It may be possible to refer the remains to species with access to skeletons representing the other five species within this genus (*N. chrysostoma*, Blue-winged Parrot; *N. petrophila*, Rock Parrot; *N. chrysogaster*, Orange-bellied Parrot; *N. pulchella*, Turquoise Parrot; *N. splendida*, Scarlet-chested Parrot). There are records of members of the genus occurring in the woodlands peripheral to the Nullarbor Plain (GBIF data, 15/02/2018) but no species of *Neophema* is known to inhabit the treeless plain itself.

cf. Pezoporini, gen. & sp. indet. – Pezoporine parrot, indeterminate genus and species

Referred Material – WAM 15.9.247 (R tibiotarsus), WAM 15.9.521 (pL carpometacarpus)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave:** ***Surface (probably Pleistocene)*** – Station 89 "4 Bird Corner – Tassie Devil Shoot [sic.]" (1); ***Unit 3 (Early Pleistocene)*** – 115–120 cm (1)

Remarks – These specimens could not be referred to any extant species based on the available specimens, but most closely matched the morphology of members of the Pezoporini. Of the comparative specimens available, the tibiotarsus most closely matched the morphology of *Neophema elegans* but is considerably larger. The specimens should be compared with other pezoporine taxa.

Subfamily: Loriinae

Tribe: Loriini

Loriini, indet. – Lorikeet/lory, indeterminate (small species)

Referred Material – WAM 15.9.166 (R humerus), WAM 15.9.189 (L humerus), WAM 15.9.227 (R carpometacarpus), WAM 15.9.263 (L ulna)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave**: ***Unit 1 (Middle Pleistocene)*** – 0–5 cm (1); ***Unit 2 (Middle Pleistocene)*** – 40–45 cm (1); ***Unit 3 (Early Pleistocene)*** –110–115 cm (1), 110–115 cm (1)

Remarks – These specimens could not be referred to genus during this study, and may belong to one or more species of small lorikeet. They are approximately the same size as elements of *Melopsittacus undulatus* (Budgerigar) and were initially referred to this species, but were later observed to differ morphologically, and appear more similar to members of the Loriini tribe such as *Glossopsitta* and *Trichoglossus*. For example, the humeri have a margo caudalis that is compressed into a ridge where it approaches the caput, with a fossa on either side of this ridge, and with the fossa on the ventral side of the ridge undercutting the caput humeri (*Melopsittacus* has little compression of the margo caudalis, and the fossae are very weakly expressed and do not undercut the caput). At the distal end, the impression for the musculus brachialis proximal of the tuberculum supracondylare ventrale is deeper than in *M. undulatus*, and the adjacent ventral margin protrudes further beyond the shaft in cranial aspect (ventral margin here barely protrudes beyond the ventral margin of the shaft in *Melopsittacus*). The humeri share the features mentioned above with Purple-crowned Lorikeet *Glossopsitta porphyrocephala*, but are considerably smaller. They may therefore belong to a smaller relative such as the Little Lorikeet *Glossopsitta pusilla*, a comparative specimen of which was not available during this study. The specimens are well preserved and should be referrable to genus or species with access to a wider range of comparative specimens.

cf. *Glossopsitta* sp. – Lorikeet, indeterminate species

Referred Material – WAM 15.9.140 (L coracoid)

Site, stratigraphy and age – **Leaena's Breath Cave:** ***Unit 3 (Early Pleistocene)*** – 95–100 cm

Remarks – The coracoid is of similar size and morphology to those of *Glossopsitta porphyrocephala* (Purple-crowned Lorikeet), sharing with that species a groove on the medio-dorsal edge of the angulus medialis, which was not observed in any other available taxon. However, of the Loriinae sub-family, only *Melopsittacus undulatus*, *Glossopsitta porphyrocephala* and *Trichoglossus haematodus* were available for comparison during this study. The specimen should be identifiable to genus or species with a wider range of comparative specimens.

Tribe: Melopsittacini

Melopsittacus undulatus (Shaw, 1805) – Budgerigar

Referred Material – WAM 15.9.53 (rostrum), WAM 15.9.58 (cranium), WAM 15.9.60 (cranium and rostrum), WAM 15.9.63 (sternum), WAM 15.9.151 (R humerus), WAM 15.9.174 (L coracoid), WAM 15.9.175 (R coracoid), WAM 15.9.176 (R coracoid), WAM 15.9.177 (R coracoid), WAM 15.9.178 (L coracoid), WAM 15.9.179 (R coracoid), WAM 15.9.180 (R coracoid), WAM 15.9.181 (R coracoid), WAM 15.9.182 (L/R coracoid), WAM 15.9.183 (R coracoid), WAM 15.9.184 (L/R coracoid), WAM 15.9.185 R coracoid), WAM 15.9.200 (R ulna), WAM 15.9.201 (L/R ulna), WAM 15.9.202 (R ulna), WAM 15.9.203 (R ulna), WAM 15.9.204 (L ulna), WAM 15.9.205 (L/R ulna), WAM 15.9.206 (L ulna), WAM 15.9.207 (2 R ulnae), WAM 15.9.208 (R ulna), WAM 15.9.209 (R ulna), WAM 15.9.210 (R ulna), WAM 15.9.212 (R ulna), WAM 15.9.213 (L/R ulna), WAM 15.9.214 (pR carpometacarpus), WAM 15.9.215 (pR carpometacarpus), WAM 15.9.216 (pL carpometacarpus), WAM 15.9.217 (L carpometacarpus), WAM 15.9.218 (pL carpometacarpus), WAM 15.9.219 (pR carpometacarpus), WAM 15.9.221 (R carpometacarpus), WAM 15.9.222 (R carpometacarpus), WAM 15.9.223 (R carpometacarpus), WAM 15.9.224 (pL carpometacarpus), WAM 15.9.225 (R carpometacarpus), WAM 15.9.226 (L carpometacarpus), WAM 15.9.228 (pL carpometacarpus), WAM 15.9.229 (R carpometacarpus), WAM 15.9.230 (R carpometacarpus), WAM 15.9.231 (R carpometacarpus), WAM 15.9.232 (R carpometacarpus), WAM 15.9.244 (L tibiotarsus), WAM 15.9.255 (dR tibiotarsus), WAM 15.9.260 (R ulna), WAM 15.9.261 (L ulna), WAM 15.9.287 (R coracoid), WAM 15.9.290 (L carpometacarpus), WAM 15.9.293 (R ulna), WAM 15.9.299 (dR femur), WAM 15.9.300 (L carpometacarpus), WAM 15.9.505 (L humerus), WAM 15.9.506 (L humerus), WAM 15.9.507 (R humerus), WAM 15.9.508 (R humerus), WAM 15.9.509 (dR humerus), WAM 15.9.510 (R tarsometatarsus), WAM 15.9.519 (R carpometacarpus), WAM 15.9.523 (L ulna), WAM 15.9.524 (L ulna), WAM 15.9.525 (R coracoid), WAM 15.9.526 (rostrum), WAM 15.9.527 (rostrum), WAM 15.9.528 (R humerus), WAM 15.9.533 (pelvis), WAM 15.9.541 (L humerus), WAM 15.9.542 (L humerus), WAM 15.9.543 (pR humerus), WAM 15.9.544 (L carpometacarpus), WAM 15.9.545 (L coracoid), WAM 15.9.546 (L ulna), WAM 15.9.547 (L/R ulnae), WAM 15.9.548 (sternum), WAM 15.9.550 (cranium), WAM 15.9.591 (R carpometacarpus)

Tentatively Referred Material – WAM 05.9.64 (sternum), WAM 15.9.37 (pL tarsometatarsus), WAM 15.9.38 (R tarsometatarsus), WAM 15.9.39 (pL tarsometatarsus), WAM 15.9.40 (L tarsometatarsus), WAM 15.9.41 (dL tarsometatarsus), WAM 15.9.154 (dL humerus), WAM 15.9.515 (L carpometacarpus), WAM 15.9.529 (dR humerus), WAM 15.9.530 (R carpometacarpus), WAM 15.9.531 (pL carpometacarpus), WAM 15.9.533 (dR tarsometatarsus), WAM 15.9.536 (L ulna), WAM 15.9.537 (dL carpometacarpus), WAM 15.9.538 (dR humerus), WAM 15.9.540 (dL carpometacarpus), WAM 15.9.549 (dR tibiotarsus), WAM 15.9.56 (rostrum), WAM 15.9.620 (L carpometacarpus), WAM 15.9.65 (mandible), WAM 15.9.67 (mandible)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave**: ***Surface (probably Pleistocene)*** – Station 32 "Wallabia kitcheneri Corner" (1); Station 73 "Wallabia kitcheneri Corner" (5); Station 88 "2 Bird Cavern, Rift Crevice Corner" (6); Station 89 "4 Bird Corner, Tassie Devil Shoot [sic.] (9); Station 90 "Pelvis Corner, Tassie Devil Shoot [sic.]" (3); Station 91 "Tassie Devil Shoot [sic.]" (6); Station 92 (3); Station 93 (4); Station 94 (6); Station 95 (11); Station 96 (1); Station 99 "Upper Thylacoleo Rift" (1); Station 107 "Powder Floor" (1); ***Unit 1 (Middle Pleistocene)*** – 0–5 cm (1), 5–10 cm (6), 10–15 cm (5), 15–20 cm (3), 25–30 cm (3), 30–35 cm (1); ***Unit 3 (Early Pleistocene)*** – 90–95 cm (1), 95–100 (2), 100–105 cm (3), 110–115 cm (2), 115–120 cm (3), 120–125 cm (7), 125–130 cm (1)

Remarks – Remains of this species are among the most common bird remains in the LBC deposit, and are found through Unit 3 (Early Pleistocene), Unit 1 (Middle Pleistocene), and in surface deposits in LBC (presumed Pleistocene age). No specimens were recovered from Unit 2. The species is widespread throughout the arid zone, and the Nullarbor region is within its known range (ALA data, accessed 12-03-2018). Baird (1991) regarded *M. undulatus* as an indicator species, signifying arid conditions in the Quaternary fossil deposits where it is found. The species was tentatively identified in the preliminary analysis of the Thylacoleo Caves fauna by Prideaux *et al.* (2007), and it is confirmed here as a major element of the fossil fauna. The diet of *M. undulatus* consists almost exclusively of grass seeds, particularly tussock-grasses such as *Stipa* sp. and mitchell grass *Aristida* sp. (Higgins 1999). Significance of the species as an ecological indicator is discussed in the avifaunal analysis.

Subfamily: Psittaculinae

Tribe: Polytelini

cf. *Polytelis*, sp. indet. – Long-tailed parrot, indeterminate species

Referred Material – WAM 15.9.139 (R coracoid)

Site, stratigraphy and age – **Leaena's Breath Cave:** ***Unit 3 (Early Pleistocene)*** – 100–105 cm

Remarks – The coracoid is referred tentatively to *Polytelis*, based on its similarity to a specimen of *P. anthopeplus* (Regent Parrot; SAM B45906). It is of similar size to coracoids of *Barnardius* sp., which is also found in the LBC deposit (see above), but is distinguished from that taxon by having a dorsal margin of the sulcus m. supracoracoideus that runs at approximately 90° to the long axis of the shaft between the facies articularis humeralis and the facies articularis clavicularis, whereas in *Barnardius* the angle here is approximately 30°. This specimen should be referrable to species with access to more comparative taxa from the Psittaculinae.

Psittaculinae, gen. & sp. indet. – Psittaculine parrot, indeterminate genus and species

Referred Material – WAM 15.9.254 (pR tibiotarsus)

Site, stratigraphy and age – **Leaena's Breath Cave:** ***Unit 3 (Early Pleistocene)*** – 95–100 cm

Remarks – This specimen could not be referred to genus based on the available specimens. Of the taxa examined, it is most similar morphologically to the tibiotarsus of *Polytelis anthopeplus* (Regent Parrot), sharing with that species a crista fibularis that merges smoothly with the shaft proximally, and a crista cnemialis medialis that has a concave profile in cranial aspect, whereas in all other parrot taxa examined, the crista cnemialis medialis has a convex profile. However, the fossil is considerably smaller than *P. anthopeplus*, and is hence referred to the Psittaculinae, as no other members of this subfamily were available for comparison during this study. It may be referrable with access to further taxa representing the subfamily.

Psittaculidae, subfamily, tribe, gen. and sp. indet. – Indeterminate parrot species

Referred Material – 15.9.33 (L tarsometatarsus), 15.9.34 (dL tarsometatarsus), 15.9.55 (rostrum), 15.9.57 (rostrum), 15.9.61 (cranium), 15.9.148 (R humerus), 15.9.149 (dL humerus), 15.9.150 (L humerus), 15.9.152 (dL humerus), 15.9.159 (L/R carpometacarpi), 15.9.160 (L carpometacarpus), 15.9.161 (R carpometacarpus), 15.9.164 (L carpometacarpus), 15.9.169 (L coracoid), 15.9.236 (dR tarsometatarsus), 15.9.238 (L coracoid), 15.9.239 (L coracoid, omal end), 15.9.253 (pR tibiotarsus), 15.9.264 (dL ulna), 15.9.268 (pR ulna), 15.9.279 (pR humerus), 15.9.281 (dL humerus), 15.9.282 (dR humerus), 15.9.283 (dR humerus), 15.9.286 (R humerus), 15.9.511 (L tibiotarsus), 15.9.512 (R femur), 15.9.513 (R femur), 15.9.517 (synsacrum), 15.9.522 (L carpometacarpus), 15.9.570 (mandible), 15.9.572 (R femur), 15.9.574 (pR ulna), 15.9.575 (R humerus), 15.9.577 (pR ulna), 15.9.621 (R carpometacarpus)

Site, stratigraphy and age (NISP in brackets) – **Leaena's Breath Cave:** ***Surface (probably Pleistocene)*** – Station 46 "Tree Kangaroo Site" (1); Station 73 "Wallabia kitcheneri Corner" (1); Station 87 "Two Bird Cavern" (1); Station 88 "Two Bird Cavern, Rift Crevice Corner" (3); Station 90 "Pelvis Corner, Tassie Devil Shoot [sic.] (1); Station 92 (1); Station 93 (1); ***Unit 1 (Middle Pleistocene)*** – 0–5 cm (2), 5–10 cm (1), 23–30 cm (1); ***Unit 3 (Early Pleistocene)*** – 80–85 cm (1), 90–95 cm (4), 95–100 cm (9), 100–105 cm (3), 105–110 cm (1), 110–115 cm (3), 115–120 cm (5), 120–125 cm (1), 130–135 cm (2)

Remarks – The above specimens were determined to be parrots but could not be referred to genus or species during this study. Given the large quantity of indeterminate parrot material, it may be profitable to review these specimens at a future date along with a more complete series of reference specimens, as some referrals or tentative referrals may be possible based on morphological or mensural criteria.

4.3.4 Avifaunal analysis

4.3.4.1 Temporal representation of extinct and extant taxa

The greatest number of extinct taxa within the fossil fauna came from sedimentary Unit 3 (Early Pleistocene) in LBC (12 taxa; Table 4.11). Extinct/likely extinct taxa within this unit include two megapodes, two pigeons, a coucal, several rails, a stork, and a large eagle. A single element of a likely extinct rail, a species of *Tribonyx*, was found in Unit 2 sediments of LBC at a depth of 45–50 cm, above the Matuyama-Brunhes magnetostratigraphic boundary (Middle Pleistocene). Two extinct taxa, a megapode and a rail, appear in Unit 1 (Middle Pleistocene) assemblage, both of which were found within the upper 10 cm of sediments. In addition, seven extinct taxa were found within undated surface deposits in LBC, LTC and FSC (Table 4.11). Four of these taxa, a megapode, a pigeon and two rails, were also found in Unit 3 of LBC but not in Units 2 or 1, suggesting either that undated surface material may be coeval with Unit 3 and that these taxa went extinct in the Early Pleistocene, or that these taxa survived into the Middle Pleistocene but were excluded for geographical or taphonomic reasons from the younger sedimentary units in LBC. The timing of extinction for all of these taxa is unknown.

Table 4.11: Representation of extinct and likely extinct non-passerines within the Thylacoleo Caves fossil fauna. LBC = Leaena's Breath Cave; LTC = Last Tree Cave; LTC = Last Tree Cave

Species	LBC				LTC	FSC
	Unit 3	**Unit 2**	**Unit 1**	**Surface**		
Progura campestris	X	–	–	X	X	–
Latagallina olsoni	X	–	X	X	–	–
Columbidae, sp. 1	X	–	–	–	–	–
Columbidae, sp. 2	X	–	–	X	X	–
Centropus bairdi	X	–	–	–	–	–
Centropus maximus	–	–	–	–	–	X
cf. *Hypotaenidia* sp.	X	–	–	–	X	–
cf. *Zapornia* sp.	X	–	X	–	–	–
cf. *Tribonyx* sp.	X	X	–	–	X	–
cf. *Fulica* sp.	X	–	–	–	–	–
Rallidae, indet.	X	–	–	–	–	–
Ciconiidae, indet.	X	–	–	–	–	–
Accipitridae, indet.	X	–	–	–	–	–
cf. *Pezoporus* sp.	–	–	–	X	–	–
Total	**12**	**1**	**2**	**4**	**4**	**1**

4.3.4.2 Geographical ranges of non-passerine taxa in the Thylacoleo Caves fauna

Twenty-three of the ~58 non-passerine species identified from the Thylacoleo Caves fossil fauna (39.7%) have a modern known range that includes the Nullarbor bioregion, as determined from spatial data in the Atlas of Living Australia. A further three species (5.2%) have been recorded in the Nullarbor bioregion only once in modern times (Table 4.4), possibly as a result of vagrant individuals or erroneous species identifications, and are not considered resident. More than half the taxa in the fossil fauna (32 taxa; 55.2%) have no modern records from the Nullarbor bioregion, 14 of which are absent due to extinction (24.1%), and 18 (31%) are absent due to range changes presumed to stem from altered climate and/or vegetation on the Nullarbor Plain between the Pleistocene and today. Overall, the fossil record indicates that the composition of the Nullarbor avifauna has changed considerably between the Early to Middle Pleistocene and today. Only around 40% of the species in the assemblage have been recorded in the region in historic times, indicating likely local extirpation of the majority of taxa due to climatic and/or habitat change during or since the Pleistocene.

There is also relatively little overlap between the non-passerine genera/species identified from the Thylacoleo Caves fossil fauna and those that have previously been identified as fossils within Late Pleistocene or Holocene cave deposits in the region (Table 4.12). Only around ten of the non-passerine species have previously been recorded, and the Thylacoleo Caves fauna includes the first regional representation in the fossil record of the Casuariiformes, Megapodiidae, three species of Anatidae, the pigeons *Phaps chalcoptera*, *P. histrionica* and two extinct Columbidae taxa, the Caprimulgiformes, the genus *Centropus*, the Rallidae, Ciconiidae, Pedionomidae, a large extinct eagle of uncertain affinity, *Circus assimilis*, *Aquila audax*, an indeterminate species of tytonid owl, the Cacatuidae, and various genera and species of Psittaculidae, including the woodland genera *Platycercus* and *Barnardius* (Table 4.12). Some of this lack of overlap between taxa in Early to Middle Pleistocene and the Late Pleistocene to Holocene may be attributed to uncertain species identifications in this and previous fossil studies, but the possibility of range changes between the Early to Middle Pleistocene and the Late Pleistocene to Holocene must also be considered. A taxon that is common within Late Pleistocene/Holocene cave deposits in the region (Baird 1991) but is notably absent from the Early to Middle Pleistocene Thylacoleo Caves fauna, is the quail genus *Coturnix*, species of which are found in the Nullarbor region today.

Table 4.12: Representation of non-passerine bird taxa in Quaternary cave fossil deposits in the Nullarbor region: comparison of taxa found in prior studies, as summarised by Baird (1991), and taxa found in the Thylacoleo Caves (this study); † = extinct, (†) = likely extinct

Order	Family	Genus/species	Baird (1991)	This study
Casuariiformes	Casuariidae	*Dromaius novaehollandiae*	–	X
Anseriformes	**Anatidae**	*Stictonetta naevosa*	–	X
		Anas gracilis	–	X
		Anas castanea	–	X
		Indet.	X	–
Galliformes	Megapodiidae	*Leipoa ocellata*	–	X
		Progura campestris†	–	X
		Latagallina olsoni†	–	X
	Phasianidae	*Coturnix* sp.	X	–
Columbiformes	**Columbidae**	*Phaps chalcoptera*	–	X
		Phaps elegans	**X**	**X**
		Phaps cf. *histrionica*	–	X
		Indet. 1†	–	X
		Indet. 2†	–	X
		Geopelia cf. *striata*	X	–
		Ocyphaps lophotes	X	–
Caprimulgiformes	Podargidae	*Podargus strigoides*	–	X
Apodiformes	**Aegothelidae**	***Aegotheles cristatus***	**X**	**X**
Cuculiformes	**Cuculidae**	*Centropus bairdi*†	–	X
		Centropus maximus†	–	X
		Chrysococcyx sp.	X	–
		Chalcites basalis	X	–
Gruiformes	Rallidae	cf. *Hypotaenidia* sp.†	–	X
		cf. *Zapornia* sp. †	–	X
		cf. *Tribonyx* sp. †	–	X
		cf. *Fulica* sp. †	–	X

		Rallidae, indet.(†)	–	X
Pelecaniformes	Ciconiidae	Indet.†	–	X
	Threskiornithidae	*Platalea* sp.	X	–
Charadriiformes	**Charadriidae**	*Peltohyas australis*	–	X
		Indet.	X	X
	Pedionomidae	*Pedionomus torquatus*	–	X
	Scolopacidae	*Calidris* sp.	X	–
		Indet.	–	X
	Turnicidae	***Turnix* sp.**	**X**	**X**
		Turnix cf. *velox*	X	–
		Turnix varius	X	–
Accipitriformes	**Accipitridae**	Indet. extinct sp.†	–	X
		***Circus* sp.**	**X**	**X**
		Circus assimilis	–	X
		Accipiter fasciatus	**X**	**X**
		Accipiter cirrocephalus	X	–
		Aquila audax	–	X
Strigiformes	**Tytonidae**	***Tyto novaehollandiae***	**X**	**X**
		Tyto delicatula	**X**	**X**
		Tyto sp. indet.	–	X
Falconiformes	**Falconidae**	***Falco berigora***	**X**	**X**
		Falco cenchroides	**X**	**X**
Psittaciformes	Cacatuidae	*Nymphicus hollandicus*	–	X
	Psittaculidae	Loriini, indet.	–	X
		cf. *Glossopsitta*	–	X
		Melopsittacus undulatus	**X**	**X**
		cf. *Psephotus* sp.	–	X
		cf. *Northiella* sp.	–	X
		Northiella haematogaster	X	–
		cf. *Purpureicephalus* sp.	–	X
		Platycercus magn. *elegans*	–	X
		Platycercus icterotis	–	X
		Platycercus sp.	–	X
		Barnardius sp.	–	X
		Pezoporus occidentalis	X	–
		cf. *Pezoporus* sp.(†)	–	X
		cf. *Neopsephotus bourkii*	–	X
		Neophema sp.	–	X
		Neophema cf. *splendida*	X	–
		Platycercini, indet.	–	X
		cf. *Pezoporini* indet.	–	X
		Psittaculinae, indet.	–	X
		cf. *Polytelis*	–	X
		Polytelis anthopeplus	X	–

4.3.4.3 Numbers of specimens within the stratigraphic units of LBC

The number of individual specimens (NISP) identified from each of the three sedimentary units within Pit B differed considerably (Figure 4.57). Unit 3 (55–150 cm below the sediment surface; Early Pleistocene) was by far the most productive. Unit 2 (35–55 cm; Early to Middle Pleistocene) was almost barren of bone, producing only 10 non-passerine bird specimens. The reasons for the low yield from Unit 2 are yet to be determined. Unit 1 (0–35 cm; Middle Pleistocene) was moderately productive. In part the differences in NISP between the three sedimentary units may be attributed to the unequal depths of each unit (Unit 1, 35 cm deep; Unit 2, 20 cm; and Unit 3, ~95 cm), but is also due to some spits within the units being much more productive than others (Figure 4.58). For example, the 10-cm spit between a depth of 110–120 cm in Unit 3 contains more specimens than the whole of Unit 1 combined (Figure 4.58).

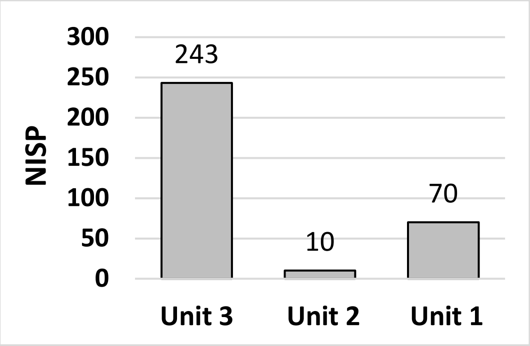


Figure 4.57: Number of individual specimens (NISP) of non-passerine birds found within the three stratigraphic units in Leaena's Breath Cave, Pit B

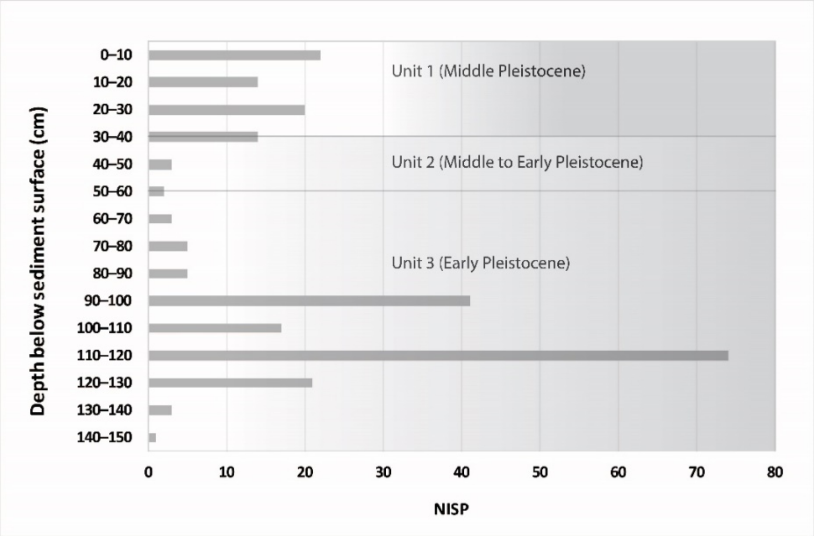


Figure 4.58: Number of individual specimens (NISP) of non-passerine birds found within 10-cm spits in Leaena's Breath Cave, Pit B (Quadrats 1–4)

4.3.4.4 Comparison of avian diversity in the Early and Middle Pleistocene sediments of Pit B, LBC

Unit 2 of LBC is not considered further here because it yielded so few specimens and only three taxa (*Turnix* sp., *Tyto* sp. and *Falco berigora*) (Figure 4.59). The analyses that follow compare the taxon assemblages within the more productive units – the Early Pleistocene sediments in Unit 3 and Middle

Pleistocene sediments in Unit 1. Taxonomic diversity differed greatly between stratigraphic units. Unit 3 (Early Pleistocene) had by far the highest number of taxa (12 orders, 15 families, 36 genera). Unit 1 (Middle Pleistocene) sediments contained roughly two-thirds as many orders and families as Unit 3 (8 orders, 9 families), but only one third the number of genera (12) (Figure 4.59). The composition of the avifauna in the two most diverse units (Units 3 and 1) are analysed further below.

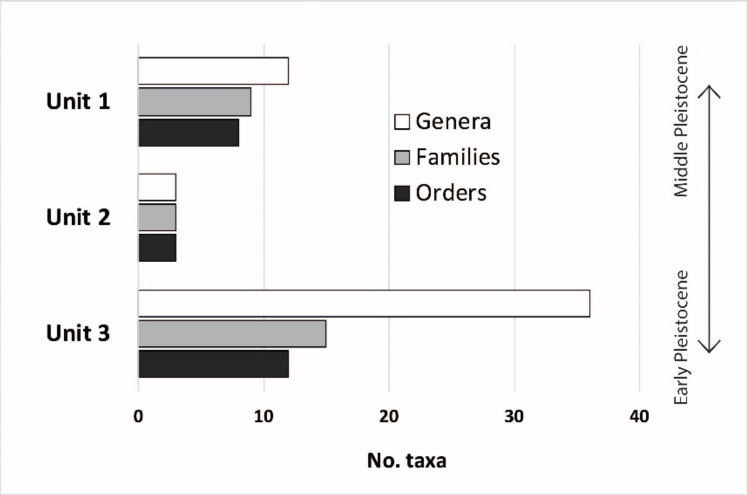


Figure 4.59: Taxonomic diversity of non-passerines in Units 1, 2 and 3 of Leaena's Breath Cave, Pit B (Quadrats 1–4)

Eight non-passerine orders (Galliformes, Cuculiformes, Gruiformes, Charadriiformes, Strigiformes, Falconiformes and Psittaciformes) were common to both Units 3 and 1, while the Anseriformes, Columbiformes, Caprimulgiformes and Apodiformes were unique to Unit 3. No orders were unique to Unit 1 (Figure 4.60). The representation of families between the units followed a similar pattern to the orders, since only one family represented most orders in the Pit B assemblage. The only exceptions to this were slightly greater representation in Unit 3 of Charadriiformes families (≥4 families in Unit 3; ≥2 families in Unit 1) and Psittaciformes families (2 families in Unit 3; 1 family in Unit 1).

Greater difference in avifaunal composition between Units 3 and 1 was evident at the level of genus and species, with the Early Pleistocene assemblage from Unit 3 being much more speciose (Figure 4.59; Table 4.13). Diversity in Unit 3 was higher among the Megapodiidae (3 genera/3 species in Unit 3; 1 genus/species in Unit 1), Columbiformes (3 genera/5 species in Unit 3; none in Unit 1) and Charadriiformes (≥3 genera/species in Unit 3; ≥2 genera/species in Unit 1), but the most marked difference was the high diversity of Psittacidae taxa in the Early Pleistocene of Unit 3 (~15 genera/species) versus only ~5 in the Middle Pleistocene of Unit 1 (Figure 4.60; Table 4.13).

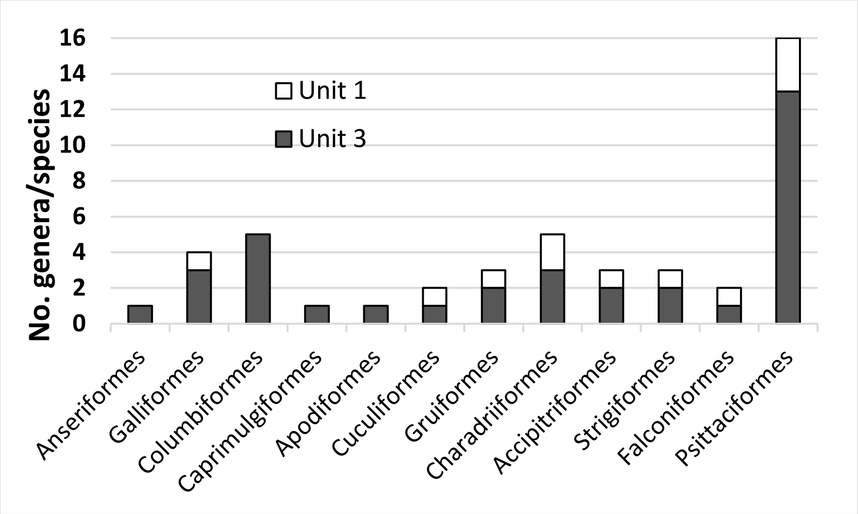


Figure 4.60: Number of genera/species within non-passerine orders: comparison between Unit 3 (Early Pleistocene) and Unit 1 (Middle Pleistocene) of Leaena's Breath Cave, Pit B

4.3.4.5 Relative abundances of taxa in the Early and Middle Pleistocene sediments of Pit B, LBC

The non-passerine assemblages in the Early Pleistocene sediments of Unit 3 and the Middle Pleistocene sediments of Unit 1 are both dominated by specimens referred to the Charadriiformes and Psittaciformes (Figure 4.61). The high abundance of Charadriiformes is mostly accounted for in both units by specimens in the genus *Turnix* (buttonquails), which comprise about 15% of the Unit 3 assemblage, and more than 44% of the Unit 1 assemblage (Table 4.13). The Psittaciformes comprise more than 30% of non-passerine specimens in Unit 1, and nearly 45% of specimens in Unit 3. However, the composition of the parrot assemblage differs considerably between units. The Early Pleistocene assemblage in Unit 3 has high parrot diversity, comprising ~15 genera/species of mainly platycercine species, while the Middle Pleistocene assemblage in Unit 1 has low diversity of parrots, and consists almost entirely of specimens of *Melopsittacus undulatus* (Budgerigar) (Table 4.13).

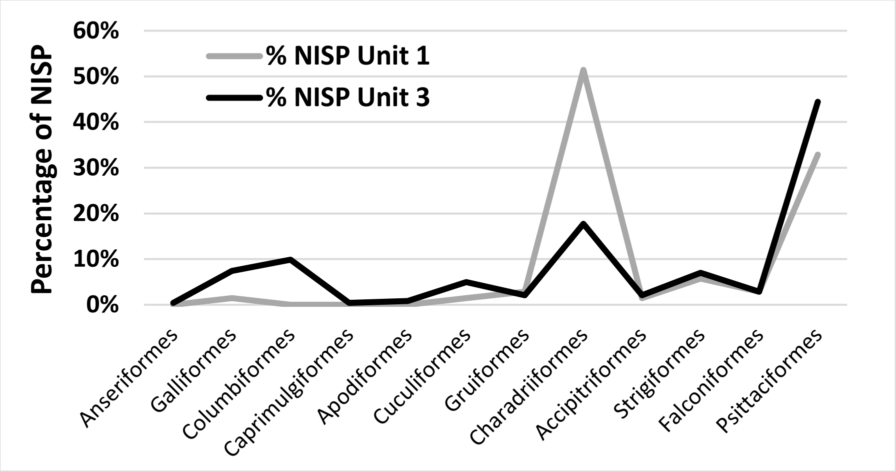


Figure 4.61: Relative abundance of specimens referred to non-passerine orders in Unit 3 (Early Pleistocene) and Unit 1 (Middle Pleistocene) of Leaena's Breath Cave, Pit B

Notably, the taxa that dominate Unit 1 in terms of relative abundance – *Turnix* and *Melopsittacus* – have almost identical absolute abundances in Units 1 and Units 3 (Table 4.13). The much lower relative abundances of *Turnix* and *Melopsittacus* specimens in Unit 3 suggest that the non-passerine avifauna from the Early Pleistocene assemblage is truly more diverse than the Middle Pleistocene assemblage in Unit 1, and that the relatively low diversity of genera/species seen in Unit 1 is not simply due to other taxa being masked for taphonomic reasons by an accumulation bias towards *Turnix* and *Melopsittacus*. This is borne out by Figure 4.62, which shows that the Early Pleistocene spit with the highest number of *Turnix* specimens (110–120 cm) also has by far the highest generic diversity of any 10-cm spit within Pit B of LBC, while moderate numbers of *Turnix* and *Melopsittacus* specimens in other 10-cm spits are associated with relatively higher generic diversity in Unit 3 (Early Pleistocene) than in Unit 1 (Unit 1). Thus there appears to be a loss of generic diversity in the Pit B assemblage from the Early into Middle Pleistocene.

Unit 3 contains a high diversity of woodland taxa, such as megapodes, pigeons, frogmouths, coucals and platycercine parrots, as well as some water-dependent taxa such as ducks and rails, while Unit 1 contains a low diversity of taxa, being mainly ones that prefer more open habitat. Although they are low in abundance, Unit 1 of LBC contains the only specimens of the Inland Dotterel *Peltohyas australis*, which is an indicator species of very open, sparsely vegetated habitats dominated by chenopods (see Section 4.3.3), and probably indicate that during the Middle Pleistocene interval represented in Unit 1, the Nullarbor Plain had a similar habitat structure to that of today.

Table 4.13: Non-passerine genera in Units 1 and 3 of LBC, Pit B; numbers = number of individual specimens (NISP) and percentage of NISP for each unit; grey = found in both units

			Early Pleistocene	**Middle Pleistocene**
Order	**Family**	**Genus**	**Unit 3** (n=232)	**Unit 1** (n=70)
Anseriformes	**Anatidae**	*Anas*	1 (0.4)	-
Galliformes	**Megapodiidae**	*Latagallina*	3 (1.3)	1 (1.4)
		Leipoa	1 (0.4)	-
		Progura	13 (5.6)	-
Columbiformes	**Columbidae**	*Phaps*	15 (6.5)	-
		Columbidae indet. 1	2 (0.9)	-
		Columbidae indet. 2	2 (0.9)	-
Caprimulgiformes	**Podargidae**	*Podargus*	1 (0.4)	-
Apodiformes	**Aegothelidae**	*Aegotheles*	2 (0.9)	-
Cuculifomes	**Cuculidae**	cf. Cuculidae indet.	-	1 (1.4)
		Centropus	12 (5.2)	-
Gruiformes	**Rallidae**	cf. *Zapornia*	-	1 (1.4)
		cf. *Hypotaenidia*	2 (0.9)	-
		cf. *Tribonyx*	1 (0.4)	-
		Rallidae indet.	2 (0.9)	1 (1.4)
Charadriiformes	**Charadriidae**	*Peltohyas*	-	3 (4.3)
		Charadriidae indet.	1 (0.4)	-
	Scolopacidae	Scolopacidae indet.	3 (1.3)	-
	Turnicidae	*Turnix*	35 (15.1)	31 (44.3)
	Charadriiformes, indet.	Charadriiformes indet.	4 (1.7)	2 (2.9)
Accipitriformes	**Accipitridae**	*Circus*	-	1 (1.4)
		Accipiter	3 (1.3)	-
		Accipitridae indet.	2 (0.9)	-
Strigiformes	**Tytonidae**	*Tyto*	17 (7.3)	4 (5.7)
Falconiformes	**Falconidae**	*Falco*	7 (3.0)	2 (2.9)
Psittaciformes	**Cacatuidae**	*Nymphicus*	1(0.4)	-
	Psittaculidae	Loriinae indet.	2 (0.9)	1 (1.4)
		Melopsittacus	18 (7.8)	19 (27.1)
		Glossopsitta	1 (0.4)	-
		Psittaculinae indet.	1 (0.4)	-
		Polytelis	1 (0.4)	-
		Psephotus/Psephotellus	10 (4.3)	1 (1.4)
		Neopsephotus	3 (1.3)	1 (1.4)
		Barnardius	14 (6.0)	-
		Platycercus	18 (7.8)	-
		Platycercinae indet.	1(0.4)	-
		Purpureicephalus	1(0.4)	-
		Northiella	1(0.4)	-
		Neophema	8 (6.0)	-
		Pezoporini indet.	1(0.4)	-
		Psittaculidae indet.	22 (9.5)	1 (1.4)

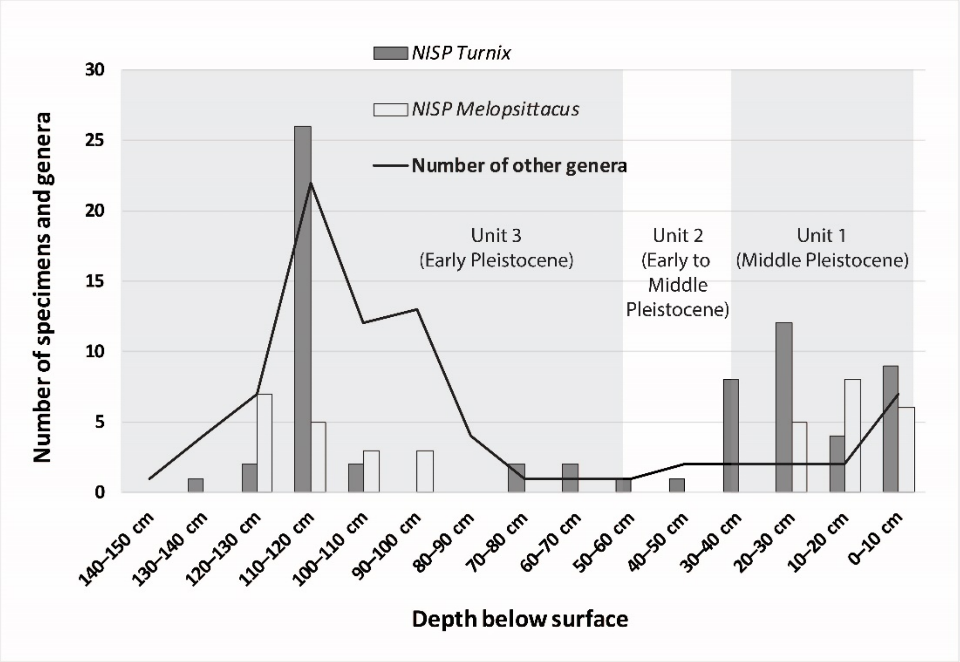


Figure 4.62: Number of individual specimens (NISP) of *Turnix* and *Melopsittacus* versus generic diversity of other non-passerines in Pit B, Leaena's Breath Cave

4.3.4.6 Rarefaction curves for genera in the Early and Middle Pleistocene sediments of Pit B, LBC

Rarefaction curves for the more diverse stratigraphic units in Pit B (Units 1 and 3; Figure 4.63), calculated at the level of genus, did not reach asymptote. This indicates that the numbers of taxa identified within Unit 1 (12 genera) and Unit 3 (36 genera) are likely to be an underestimate of true diversity for those units, and that if sampling increased, so would the number of identified taxa within both units. The diversity currently known for Units 1 and 3 is thus considered to be a minimum baseline diversity for the Thylacoleo Caves locality during the Early and Middle Pleistocene. The curve for Unit 2 does reach asymptote, but this is unlikely to be meaningful since this is based on few specimens and just three taxa, and is unlikely to represent true diversity of the living avifaunal assemblage around the Thylacoleo Caves at the time of accumulation.

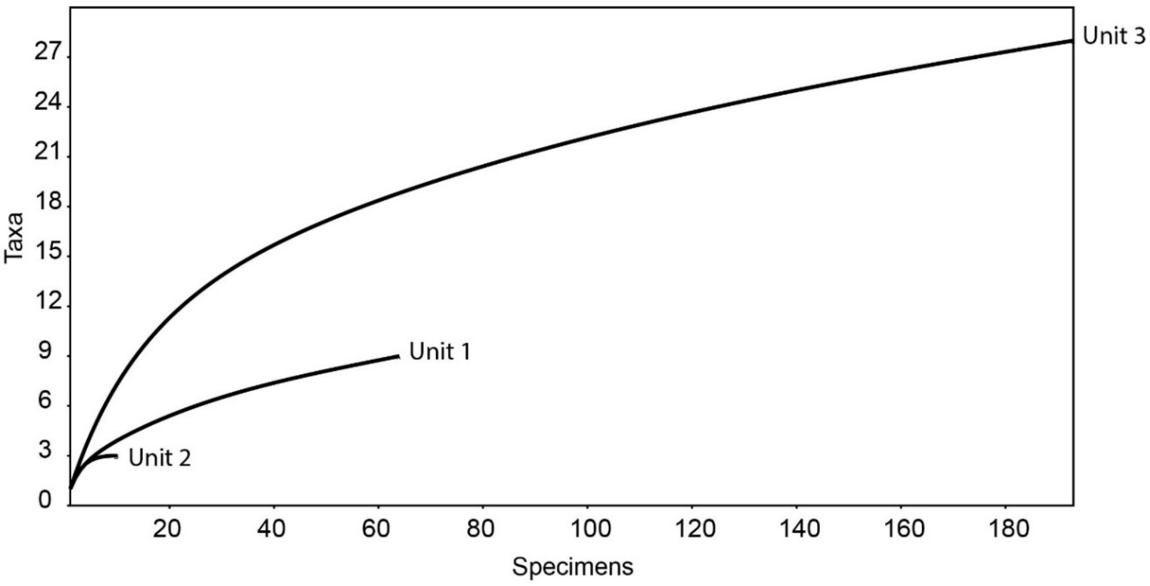


Figure 4.63: Individual rarefaction curves for genera in Units 1, 2 & 3, Pit B, Leaena's Breath Cave. Curves were calculated in PAST version 3.0. Calculations were based on genus because some taxa could not be identified beyond the level of genus, and few genera in the assemblage were represented by more than one species. Taxa of uncertain generic affinity were included if they were clearly distinct from taxa that were identified to the level of genus.

Given large differences in the number of specimens excavated from 10-cm spits within the three sedimentary units (Figure 4.64), a rarefaction analysis was also carried out within these spits. For spits between 20 and 80 cm depth below the sediment surface, the diversity curves approach asymptote, but these spits contained very few taxa and specimens, and seem unlikely to reflect diversity of the living avian community from which they derived. On the other hand, spits with the greatest numbers of specimens, which were within Unit 3 (90–100 cm, 14 genera; and 110–120 cm, 24 genera), did not reach asymptote, suggesting that even more taxa would be discovered within these high-diversity spits by increased sampling at these depths.

Although overall Unit 1 has lower generic diversity than Unit 3, the finer-scale analysis by spit shows that the uppermost 10 cm of Unit 1 contains higher diversity than the deeper spits within Unit 1 (Figure 4.62), and that some woodland taxa are present, albeit in very low abundance (e.g. single specimens of an extinct megapode, a possible cuckoo taxon, a lorikeet taxon and a *Psephotus* species). Although it is difficult to draw inferences from such low numbers of specimens, it is possible that the upper 10-cm spit of Unit 1 represents an interval of the Middle Pleistocene where trees were present on the Plain, before the cave entrance became sealed until it reopened in the Holocene.

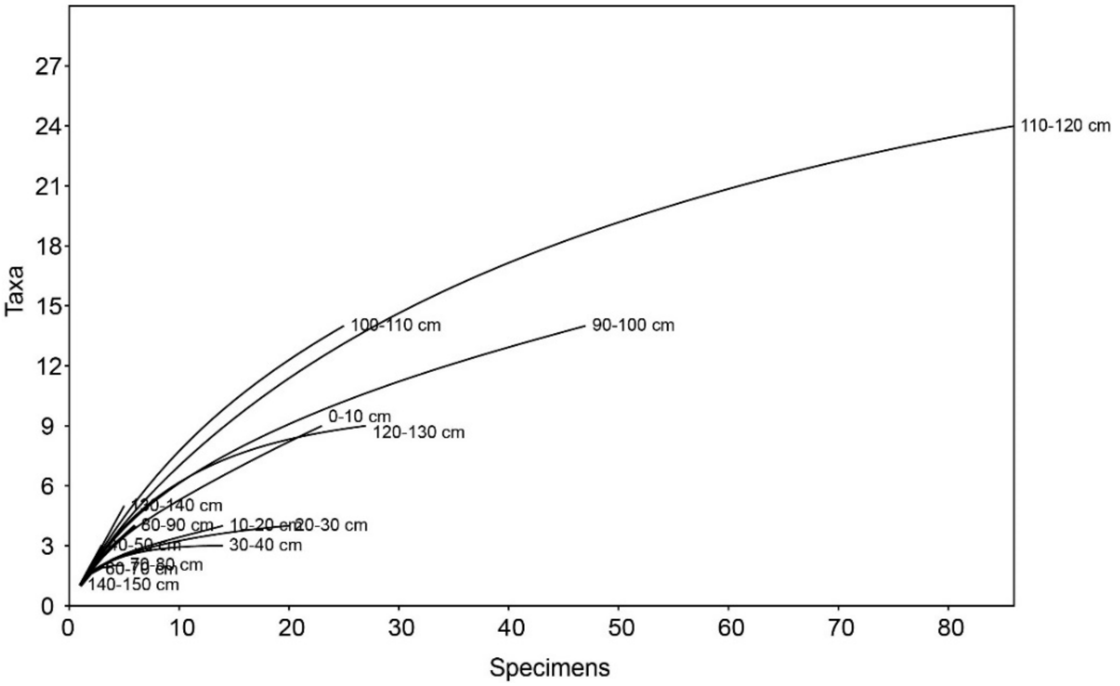


Figure 4.64: Individual rarefaction curves for genera within 10-cm spits in Pit B, Leaena's Breath Cave. Curves were calculated in PAST version 3.0. Calculations were based on genus because some taxa could not be identified beyond the level of genus, and few genera in the assemblage were clearly represented by more than one species. Taxa of uncertain generic affinity were included if they were clearly distinct from taxa that were identified to the level of genus.

In summary, some spits within the Early Pleistocene assemblage in Unit 3 appear to represent a highly diverse woodland community, with the Middle Pleistocene assemblage of Unit 1 representing a less diverse, open-habitat assemblage. However, differences in the numbers of specimens recovered from different stratigraphic depths make it difficult to determine whether the apparent loss of taxonomic diversity from the Early into the Middle Pleistocene represents avian responses to changes in climate and habitat, or whether it reflects differences in fossil accumulation for other reasons. In order to further investigate the possible palaeoecological significance of differences observed between the Unit 1 and Unit 3 avian assemblages, the ecological characteristics of the taxa from these units are examined in further detail below.

4.3.4.7 Habitat guilds of taxa in the Early and Middle Pleistocene of Pit B, LBC

Distinct trends in the habitat spectrum in Figure 4.65 indicate that the species assemblages represented in the Early Pleistocene of Unit 3 and the Middle Pleistocene of Unit 1 differ in their preferred habitat types. Both units contain some taxa that require aquatic and/or littoral habitats, but each taxon (rails, ducks) occur in very low abundances, suggesting that water-dependent taxa were a relatively minor component of the avifauna during both accumulation intervals. Unit 3 (Early Pleistocene) contains roughly equal abundances of specimens from taxa that prefer open habitats and woodland habitats

(~40% each), with those preferring shrubland forming a relatively minor component (13.6%). The Middle Pleistocene assemblage from Unit 1, however, is heavily dominated by specimens from taxa that prefer open/grassland habitat (87.5%), with a much reduced component of taxa that prefer wooded habitats (7.8%), and a very minor component of taxa that prefer shrubland (1.6%). This is broadly suggestive of a transition from a structurally diverse habitat on the Nullarbor Plain during the Early Pleistocene, towards a more uniform, open habitat in the Middle Pleistocene. The higher structural diversity of habitat indicated by the taxa in Unit 3 corresponds with higher avian diversity during this interval (see Section 4.3.4.4), while the structurally simpler habitat indicated for Unit 1, presumably with fewer trees and shrubs, corresponds with low avian diversity during that accumulation interval.

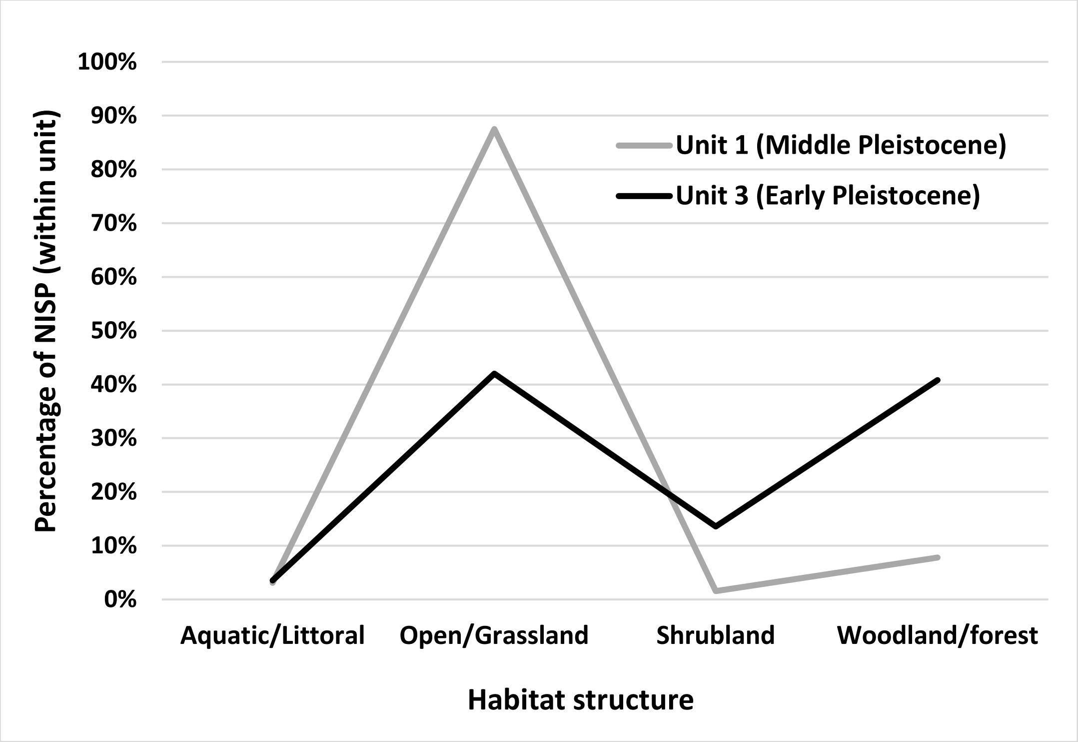


Figure 4.65: Primary preferred habitat of taxa in Pit B, Leaena's Breath Cave, Units 1 & 3

4.3.4.8 Dietary niches of taxa in the Early and Middle Pleistocene of Pit B, LBC

Differences were seen in the dietary niches of taxa in Units 1 and 3, based on specimens that could be identified to a high enough taxonomic level to determine likely diet (Unit 3, n = 198; Unit 1, n = 65). The remains of mixed feeders (plant + animal food) were relatively high in both units, comprising nearly 60% of NISP, but the proportions of taxa with an exclusively animal- or plant-based diet differed between units: Unit 3 had roughly equal numbers of both, while Unit 1 had fewer predators (10.8%) and more plant-eaters (30.8%) (Figure 4.66).

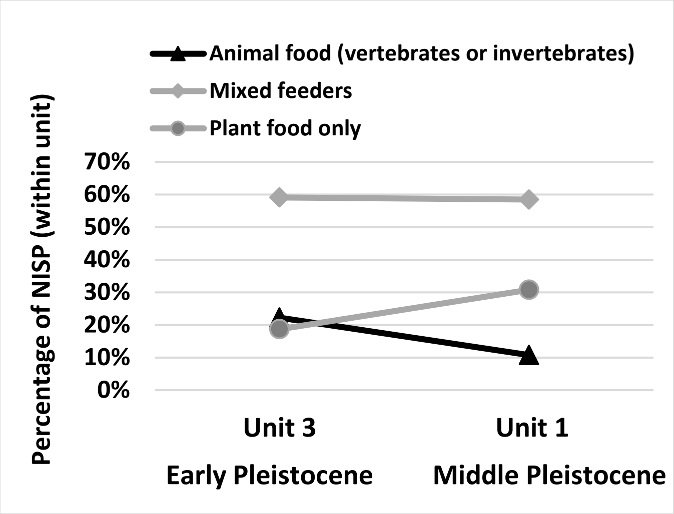


Figure 4.66: Broad dietary categories of taxa in Pit B of Leaena's Breath Cave, Units 1 & 3

Dissecting these feeding niches further, the dietary spectrum in Figure 4.67 shows that that both Units 3 and 1 have fairly low proportions of strict carnivores, although Unit 3 has slightly more of these, virtually no strict insectivores, and virtually no nectarivores. Unit 3 (Early Pleistocene) has higher proportions of specimens from taxa with a mixed carnivorous/insectivorous diet (mainly specimens of *Centropus*; see Chapter 2), relatively fewer true omnivores, more taxa that are primarily granivores but that also eat other foods (mainly platycercine parrots), and relatively fewer strict granivores. Unit 1 (Middle Pleistocene) comprises mainly omnivores (56.9%) due to the dominance of *Turnix* specimens in this unit (Table 4.13), but with a relatively high component of strict granivores (~30%) due mainly to the abundance of *Melopsittacus undulatus*. Overall, the differences between the dietary niches observed for the two units imply higher availability of animal-based food resources during the Early Pleistocene, perhaps reflecting a more productive environment with more complex food webs during this interval, and a higher prevalence of a seed-based diet in the Middle Pleistocene.

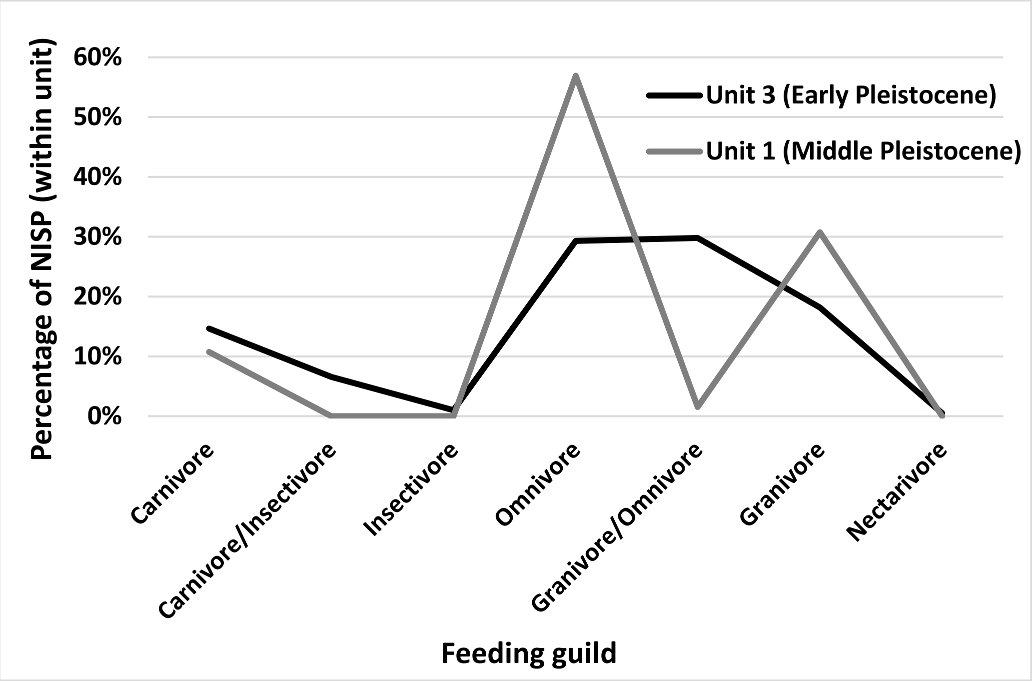


Figure 4.67: Feeding guilds of taxa in Pit B, Quadrats 1–4, Leaena's Breath Cave, Units 1 & 3

4.3.4.9 Nesting requirements of taxa in the Early and Middle Pleistocene of Pit B, LBC

The taxon assemblages in both the Early and Middle Pleistocene units showed similar patterns of nesting requirements, with few taxa in either unit preferring to nest in dense brush or bushes, and relatively high proportions of ground-nesters and tree-hollow nesters present in both units (Figure 4.68). However, Unit 3 (Early Pleistocene) has a higher proportion of tree-nesting taxa, while Unit 1 (Middle Pleistocene) has a high relative abundance of ground-nesters (nearly 60% of NISP), and a somewhat lower proportion of taxa that nest in tree hollows or tree branches, consistent with the Middle Pleistocene habitat having become more open with fewer available trees.

Despite evidence for the presence of trees on the Nullarbor Plain during the Early Pleistocene, ground-nesting was still the single most common nesting mode in the Unit 3 assemblage, with nearly 40% of Early Pleistocene specimens deriving from ground-nesting taxa. Furthermore, although ground-nesting taxa comprised a lower percentage of NISP in the Unit 3 assemblage overall, this unit had a higher diversity of ground-nesting taxa (e.g. *Turnix* and other charadriiform taxa; a coucal presumed to be ground-nesting, see Chapter 2; three megapodes, *Leipoa ocellata*, *Progura campestris* and *Latagallina olsoni*; rails) than did Unit 1. Presence of trees in the Early Pleistocene, therefore, should not be interpreted as precluding a ground-dwelling niche, but rather as providing of a more diverse habitat structure that supported both arboreal and strongly ground-dwelling taxa.

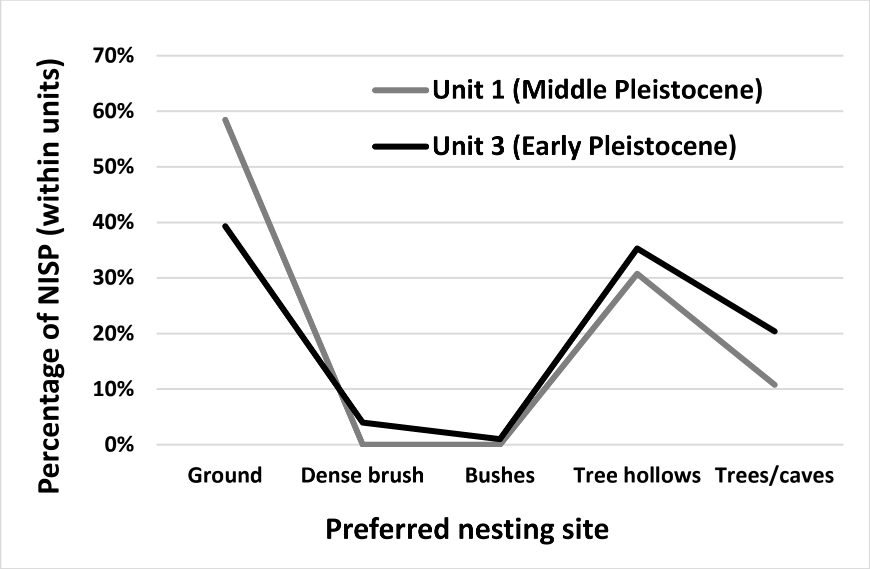


Figure 4.68: Preferred nesting site of taxa in Pit B, Leaena's Breath Cave, Units 1 & 3

4.3.4.10 Habitat guilds of taxa within 10-cm spits in Pit B, LBC

In order to investigate whether differences in the composition of the LBC avifauna could be detected at a finer scale than unit, the Pit B assemblage was also analysed in spits of 10 cm to examine change through time. Within Unit 3 (Early Pleistocene), three habitat phases appear to be indicated (Figure 4.69):

1) a relatively open-habitat phase at 110–120 cm, but with shrubland and woodland taxa also present (genera and indeterminate higher taxonomic level taxa that are present are: *Accipiter*, *Aegotheles*, *Barnardius*, *Centropus*, Columbidae indet. 1, Columbidae indet. 2, *Falco*, cf. *Hypotaenidia*, cf., *Latagallina*, Loriinae, *Melopsittacus*, *Neophema*, *Neopsephotus*, *Nymphicus*, cf. Pezoporini, cf. Platycercini, *Phaps*, Platycercini, *Platycercus*, *Progura*, cf. *Psephotus*/*Psephotellus*, *Turnix*, and *Tyto*);
2) a phase between 80–100 cm where there is a decline in abundance of open-habitat and shrubland taxa (no *Turnix* specimens, only three *Melopsittacus* specimens) and a concomitant rise in the abundance of woodland taxa (taxa present are: *Aegotheles*, *Barnardius*, *Centropus*, *Falco*, cf. *Glossopsitta*, *Melopsittacus*, *Neophema*, *Phaps*, Platycercini, *Platycercus*, *Podargus*, *Progura*, cf. *Psephotus*/*Psephotellus*, Psittaculinae, cf. Scolopacidae); and
3) a decline in abundance of all taxa from above about 80 cm, which may be for taphonomic reasons, such as the cave entrance becoming blocked.

Low specimen numbers continue through the shallower depths of Unit 3 into Unit 2, with an increase in the number of specimens characteristic of open habitats into the Middle Pleistocene of Unit 1 (Figure 4.69) (mostly *Melopsittacus* and *Turnix*, with a few specimens of *Peltohyas*, with single specimens of *Circus*, *Latagallina*, Loriinae, cf. *Neopsephotus*, cf. *Psephotus*/*Psephotellus*, and cf. *Zapornia*).

This trajectory broadly agrees with the analysis at the level of Unit (see Section 4.3.4.7), which indicated that woodland taxa dominate the assemblage in the Early Pleistocene and more open-habitat taxa in the Middle Pleistocene, but the finer-scale analysis reveals that possible phases of ecological succession are represented within the Early Pleistocene of Unit 3. The initial more open habitat phase during the Early Pleistocene (Figure 4.69) followed by a phase where more woodland taxa are present, may have occurred quickly or over successive glacial-interglacial cycles within the Early Pleistocene. Without better dating of the LBC sediments, it is not possible to determine the rate at which this apparent habitat transition occurred.

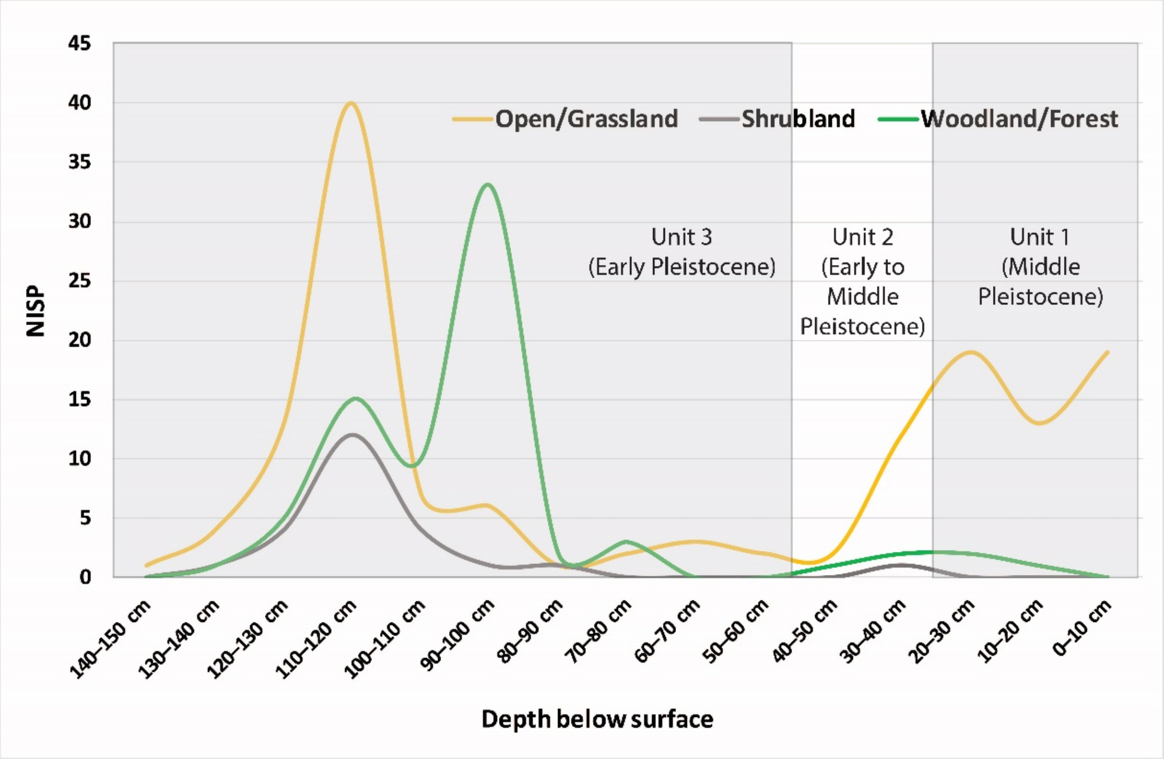


Figure 4.69: Primary preferred habitat of taxa in Pit B, Leaena's Breath Cave, analysed by 10-cm spits

4.3.4.11 Dietary niches of taxa within 10-cm spits in Pit B, LBC

The abundance of the remains of taxa within broad dietary categories (those consuming animal foods only, those consuming a mixture of animal and plant foods, those consuming plant foods only) showed marked fluctuations within Unit 3 (Early Pleistocene), with mixed feeders showing particularly large changes in abundance between different 10-cm spits in the Early Pleistocene (Figure 4.70). Taxa reliant entirely on plant foods appear to decline gradually throughout Unit 3, but their absolute numbers are low. At a depth of 110–120 cm, the high abundance of mixed-feeders, comprising mainly parrots, buttonquails and megapodes, appears related to higher numbers of predators (Figure 4.70). However, the next highest abundance of mixed-feeders, at 90–100 cm, is not matched by a similarly high number of predators. Therefore, fluctuations in the numbers of mixed-feeders seems more likely to reflect changes in habitat availability and/or food resources, rather than being due to accumulation bias from predation. The peaks in abundance of mixed feeders in Unit 3 correspond with the apparent habitat signals evident in Figure 4.69, which shows evidence for a transition from a more mixed open/shrubland/woodland habitat at 110–120 cm to a more closed woodland structure at 90–100 cm.

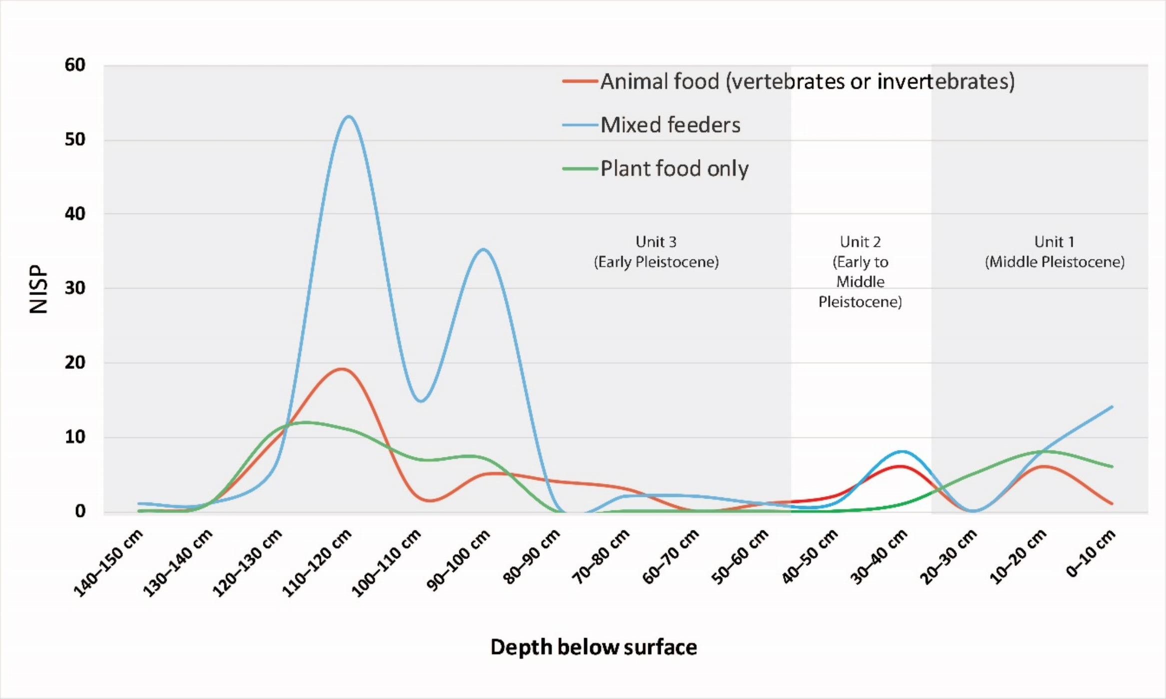


Figure 4.70: Broad dietary categories of taxa in Pit B, Leaena's Breath Cave, within 10-cm spits

Examining the dietary preferences of taxa that consume plant foods more closely, both Units 3 and 1 contain a guild of strict granivores. In Unit 3 (Early Pleistocene), the initial dominance of this guild (Figure 4.71) is followed by a decline in strict granivores, and an increase in taxa that are primarily granivores but which also consume other foods. This may signal either seasonal fluctuations in seed availability over a short period of time, initially favouring seed-eaters, but later favouring taxa with greater dietary flexibility, or it may signify a longer-term vegetation succession, with a transition from open grassland with abundant seed towards a more closed habitat with more diverse food sources. In Unit 3 (Early Pleistocene), the granivore guild at 120–130 cm comprises the parrot taxa *Melopsittacus* and *Neopsephotus*, and at least two species of pigeons in the genus *Phaps.* In this unit, the granivore guild gradually declines, and is absent above a depth of 80 cm, but taxa that eat seeds as well as other foods have two peaks of abundance after this, at 110–120 cm (the parrot taxa *Nymphicus*, *Barnardius*, *Psephotus*, *Neophema*, *Platycercus* and indeterminate platycercine parrots), and at 90–100 cm (parrots taxa *Barnardius*, *Psephotus*, *Platycercus*, *Neophema* and an indeterminate platycercine parrot). The only specimen of a nectarivore taxon in Unit 3, an indeterminate lorikeet species, also occurs at 90–100 cm. The strict granivore guild in the Middle Pleistocene of Unit 1 comprises *Melopsittacus* and *Neopsephotus*, but unlike this guild in Unit 3, pigeons are absent from Unit 1, and there are no taxa present that are primarily granivores but which also consume other foods, apart from a single specimen of a *Psephotus/Psephotellus* parrot species.

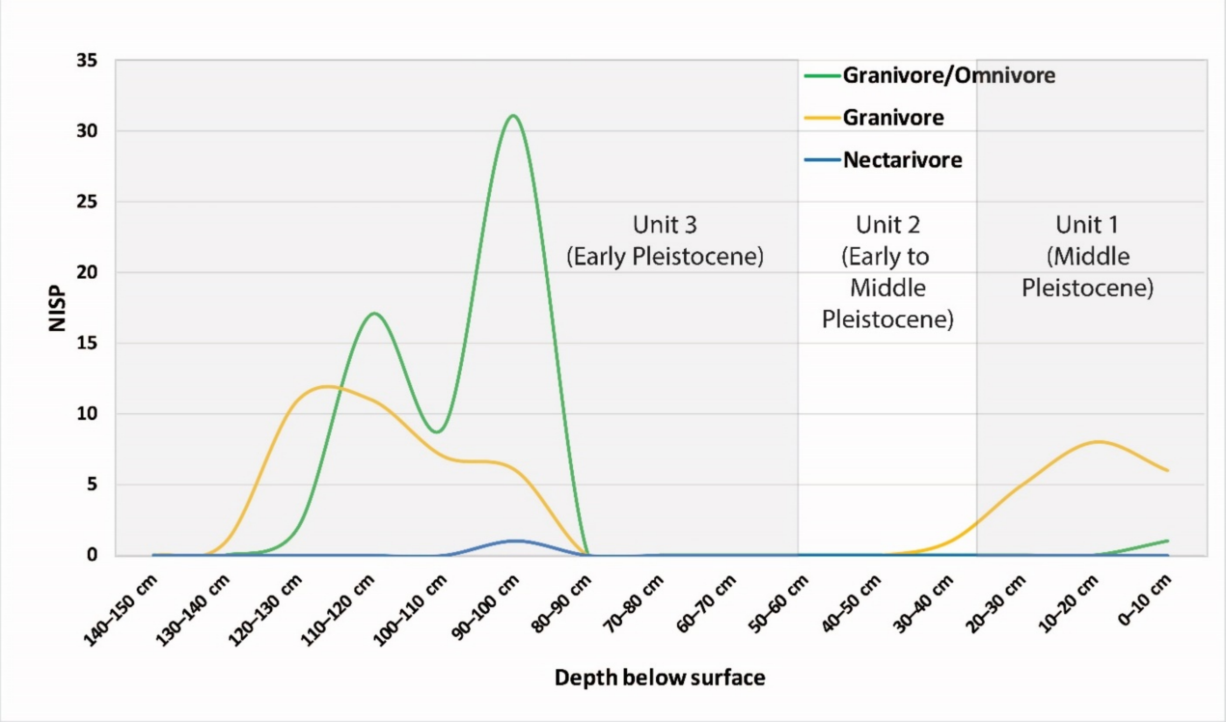


Figure 4.71: Diet categories of plant-consuming taxa in Pit B, Leaena's Breath Cave, within 10-cm spits

4.3.4.12 Nocturnal and diurnal taxa in the LBC assemblage

For taxa where daily activity cycle is known, or can be inferred from related taxa, the avifaunal assemblages in the Early Pleistocene of Unit 3 and Middle Pleistocene of Unit 1 are very similar with regard to the representation of nocturnal versus diurnal taxa, with a bias in both units towards taxa that are active at night (Figure 4.72). This is the case regardless of whether nocturnal and diurnal raptors are included or excluded, and the assemblages in both units contain almost identical proportions of nocturnal and diurnal raptors (>60% owls, <40% falcons and accipitrids). The implications of this for site taphonomy are discussed below.

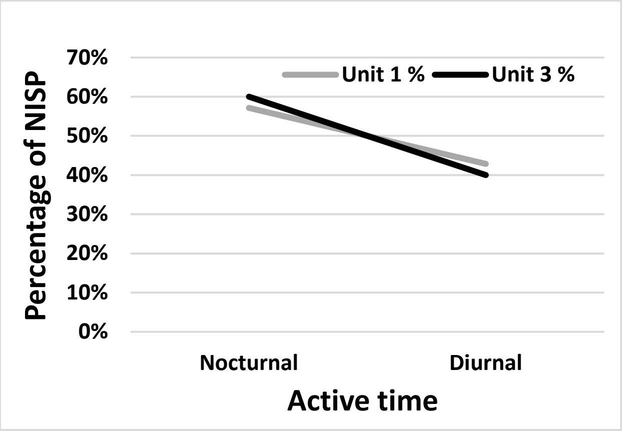


Figure 4.72: Daily activity patterns of bird taxa represented in Pit B, Leaena's Breath Cave, during the Early Pleistocene (Unit 3) and Middle Pleistocene (Unit 1); NISP = number of individual specimens

Table 4.14: Number of individual specimens (NISP) of non-passerine bird taxa identified from Leaena's Breath Cave, Pit B, Quadrats 1–4

Taxon	Early Pleistocene Unit 3									Middle Pleistocene Unit 1			
Depth (cm)	140–150	130–140	120–130	110–120	100–110	90–100	80–90	70–80	60–70	30–35	20–30	10–20	0–10
Anatidae													
Anas castanea		1											
Megapodiidae													
Latagallina olsoni†				1	1								1
Leipoa ocellata					1								
Progura campestris†			3	5	1	3	1						
Columbidae													
Phaps chalcoptera			1		1								
Phaps elegans		1	1	3	2	1							
Phaps indet.			1	1		2							
Columbidae indet. 1†				2									
Columbidae indet. 2†				2	1								
Podargidae													
Podargus strigoides						1							
Aegothelidae													
Aegotheles cristata				1		1							
Cuculidae													
Centropus bairdi†			2	7	2		1						
cf. Cuculidae indet. †													1
Rallidae													
cf. *Zapornia* sp. †													1
cf. *Hypotaenidia* sp. †				2									

Tribonyx sp. †					1									
Rallidae indet.	1													
cf. Rallidae				1										1
Charadriidae														
Peltohyas australis												1	1	1
Charadriidae indet.		1												
Scolopacidae														
Scolopacidae indet.				1		1			1					
Charadriiformes														
Charadriiformes, indet.		1		3								1		1
Turnicidae														
Turnix sp.		1	2	26	2			2	2		6	12	4	9
Accipitridae														
Circus sp.														1
Accipiter sp.		1		2										
Accipitridae indet.†				1										
Tytonidae														
Tyto sp.			5	5		1	2	3			1	2	1	
Falconidae														
Falco berigora			3	1		2	1				2			
Cacatuidae														
Nymphicus hollandicus				1										
Psittacidae														
Loriinae indet.				2										1
Melopsittacus undulatus			7	5	3	3						5	8	6
Glossopsitta sp.						1								
Psittaculinae indet.						1								
cf. *Polytelis* sp.				1										
Psephotus/Psephotellus				2	2	6								1
Neopsephotus			1	2							1			

Barnardius sp.				4		10								
Platycercus magn. *elegans*					1	2								
Platycercus icterotis					2	7								
Platycercus indet.				1	1	4								
Platycercinae indet.					1									
cf. *Purpureicephalus spurius*					1									
cf. *Northiella haematogaster*			1											
Neophema sp.			1	6		1								
Pezoporini indet.				1										
Psittaculidae indet.			1	8	2	10	1							1
No. specimens	**1**	**6**	**29**	**106**	**25**	**57**	**6**	**5**	**3**					
No. taxa	**1**	**6**	**13**	**28**	**17**	**18**	**5**	**2**	**2**					

4.4 Discussion

4.4.1 Diversity

4.4.1.1 Comparison with other Australian Quaternary fossil localities

One of the aims of this investigation was to document the taxonomic diversity of non-passerine birds in the Early and Middle Pleistocene fossil fauna from the Thylacoleo Caves. As a result of this study, nearly 60 non-passerine taxa have now been identified within the fauna, around four-and-a-half times more non-passerine taxa than were identified in the preliminary assessment of the fauna from these caves (Prideaux et al. 2007). Based on the results of this study, more avian taxa have now been documented from the Thylacoleo Caves than from any other Australian Quaternary fossil locality. The diversity of the passerine component of the fauna remains to be determined, and so the total number of avian taxa from the locality is expected to well exceed 60 taxa in total, once the passerines are also included.

The only locality known to approach a similar level of avian diversity is the Late Pleistocene to Holocene deposit in Clogg's Cave near Buchan in eastern Victoria (Figure 4.1), from which 55 taxa have been identified (Baird 1986). However, 32 of the total taxa from Clogg's Cave were non-passerines, thus the Thylacoleo Caves fauna preserves almost double the number of non-passerines. Further, the higher diversity of taxa from the Thylacoleo Caves is based on only around one third the number of specimens (656 bones versus 1,817 from Clogg's Cave; Baird, 1986). The next most diverse Quaternary locality after Clogg's Cave – Mable Cave, also in the Buchan district (Figure 4.1) – is a Holocene deposit comprising 46 avian taxa, of which 30 are non-passerine taxa. Therefore again, the Thylacoleo Caves preserve around twice as many non-passerine taxa, based in this case on fewer specimens (576 from Mabel Cave; Baird 1986).

The Thylacoleo Caves also far outstrip the avian diversity of the Late Pleistocene and Holocene cave deposits in the Nullarbor region that were studied by Baird (1986) (Figure 4.1; Table 4.7), the Middle Pleistocene deposits from Mt Etna in Queensland, and the Middle to Late Pleistocene deposits of Victoria Fossil Cave in south-eastern South Australia (Figure 4.1). By these measures, the locality represents an exceptional record of the Australian avifauna during the Pleistocene. Most importantly, it comprises the first record of a diverse landbird assemblage from the Early Pleistocene.

4.4.1.2 Why do the Thylacoleo Caves contain so many avian taxa?

In some respects it seems unsurprising that the Thylacoleo Caves should contain a more diverse avian assemblage than other Quaternary localities, given that the deposit includes depositional intervals spread over a period spanning hundreds of thousands of years of the Early to Middle Pleistocene.

However, diversity is not spread evenly throughout the deposits. By far the greatest number of taxa were recovered from the Early Pleistocene sediments in Unit 3 in LBC (Figure 4.59), and even within Unit 3 the number of avian taxa varied considerably at different depths: diversity was highest by far between 110 and 120 cm (Figure 4.62), with 24 genera represented, whereas the next most diverse spits (90–100 cm; 100–110 cm) both contained ten fewer genera.

Therefore the diversity recorded for LBC does not seem to be simply a function of a relatively long sedimentary sequence that resulted in the gradual accumulation of an exceptionally large number of specimens, and alternative explanations are needed for the variable number of specimens and taxa found at different depths. This is discussed further below (see Section 4.4.2). Until better dating of the LBC sediments are available, it is not possible to determine with certainty whether the infill sediments in LBC accumulated gradually or rapidly, and whether the sequence contains long hiatuses in deposition, but some observations on taphonomy are provided below.

4.4.1.3 Accumulation of avian fossils

Although the Thylacoleo Caves avifauna is particularly diverse relative to other Quaternary fossil localities, the rarefaction analyses for Pit B suggest that the number of taxa identified to date is an underestimate, and that more taxa would be discovered with further sampling within LBC. Twenty-four taxa – around 40% of all taxa in the Thylacoleo Caves fauna – are represented by just a single element or associated skeleton (Table 4.4). In addition, three taxa were found only in FSC or LTC and not in LBC, (Table 4.4), one of which was the newly described extinct species *Centropus maximus* (see Chapter 2), further indicating that the LBC assemblage as studied to date did not capture all local taxa during the sampled intervals.

In future, therefore, it will be important to identify and analyse the specimens from Pit A of LBC to determine whether additional taxa are represented. In addition, not all specimens examined in this study have yet been identified to the level of genus or species, and it is likely that the number of identified taxa will increase, particularly among the parrots and charadriiforms, once comparisons are made with complete sets of reference specimens.

Although a formal taphonomic analysis was not conducted for this study, some observations on the Thylacoleo Caves deposits are warranted, as this has a bearing on how well the fossil fauna represents the living avian community of the Nullarbor Plain during the Pleistocene. Little is yet known about the accumulation of birds in FSC as only two bird species have so far been documented from this cave. LTC is also poorly understood. Pitfall trapping is one likely mode of accumulation for both caves given that some large terrestrial taxa are present in both, notably specimens of the extinct megapode *Progura* *campestris* in LTC, which had an estimated body mass of ~ 6 kg (Shute et al. 2017; see Chapter 3), and two associated skeletons of the large extinct coucal *Centropus maximus* in FSC, estimated to have weighed upwards of 1 kg (Shute et al. 2016; see Chapter 2).

More can be determined about patterns of avian fossil accumulation in LBC. Birds with a wide range of body sizes are represented, indicating possible mixed modes of accumulation (Baird 1986). The assemblage includes a strongly terrestrial component (e.g. *Turnix* and other charadriiform taxa, *Centropus*, *Leipoa ocellata*, *Progura campestris*, *Latagallina olsoni*, various rails), indicative of pitfall trapping (Baird 1991). The assemblage also includes ground-feeding taxa such as granivorous parrots and pigeons, which may also have been particularly prone to pitfall trapping.

The silty clay infill sediments in LBC are not laminated, indicating relatively rapid accumulation via flooding, which may have resulted in the inclusion of an allochthonous fossil component (e.g. Baird 1991). There is evidence of ancient water flow that scoured a path through the upper sediments (Figure 4.6), with the modern configuration of the entrance pit in the cave preventing overflow of flood waters onto the sediment floor of the cave (Prideaux et al. 2007). Heavy Pleistocene rainfall events resulting in regional flooding may account for the incorporation of aquatic/littoral taxa into the assemblage, including three species of duck, several rails and a stork, although any of these could also have accumulated via pitfall trapping, and damage to a humerus of *Anas gracilis* indicates possible predation damage (Figure 4.19). Temporary flooding after heavy rain has previously been suggested as the reason that remains of a spoonbill *Platalea* sp. were found in Weeke's Cave in the Nullarbor region (Baird 1990).

Differences in the numbers of specimens found in the three sedimentary units in LBC may mean that different flood events varied in severity, season, or even occurred during different glacial/interglacial intervals. Better dating of LBC sediments may further illuminate which is more likely. Unit 3 contains many woodland taxa, and relatively high densities of bone, particularly at some depths within Unit 3, and this may indicate relatively slow accumulation: a woodland habitat would be expected to have relatively stable soils, and flooding might not have scoured the landscape severely. Unit 2, on the other hand, which based on magnetostratigraphy straddles the Early to Middle Pleistocene, is almost barren of bird bones. It may represent a particularly intense flood event where much sediment but little bone was incorporated, or an interval when the woodland of the Early Pleistocene had been lost, and soils were less stable resulting in heavy sedimentation. Although the taxon assemblage in Unit 1 (Middle Pleistocene) is indicative of more open habitat than Unit 3, density of bird bones and taxonomic diversity is much higher than in Unit 2. This could mean that sediment accumulation was slower than in Unit 2, either due to dryer conditions or more stable soils.

A degree of fossil accumulation by avian predators is possible, particularly from Brown Falcon *Falco berigora* and species of *Tyto* owls, fossils of which are found throughout the deposit from the Early Pleistocene onwards. Nocturnal and diurnal non-raptorial birds in the Pit B assemblage appear in more or less identical proportions to nocturnal and diurnal raptors (Figure 4.72), indicating either that bones of non-raptors accumulated independently of raptors, or that falcons contributed diurnal prey and owls contributed nocturnal prey to the assemblage in exact proportion to their own abundance. *Falco berigora* has a diet that includes small birds (Marchant and Higgins 1993), but diet of the most common owl in the LBC assemblage, an indeterminate species of 'masked owl', is unknown. Elsewhere, Masked Owls *Tyto novaehollandiae* specialise on mammalian prey but also take other prey including birds (Debus 1993). However, the Nullarbor owls, which may be a distinct taxon (see Systematic Palaeontology), cannot be assumed to have a similar diet.

Relatively high numbers of *Turnix* sp. and *Melopsittacus undulatus*, which together comprise almost exactly one third (33.2%) of specimens in Pit B, may indicate that these were prey species of falcons and/or owls. This is similar to proportions of key small prey species found within, for example, Clogg's Cave (*Coturnix* sp., 37%), and Mabel Cave (*Coturnix* sp., *Turnix varius* and *Trichoglossus haematodus*, 36%) (Baird 1986). This could be formally investigated by studying the representation of various skeletal elements and breakage patterns of *Turnix* and *Melopsittacus* (e.g. Baird 1986, 1991), and could also help illuminate the relative contributions of *Tyto* and *Falco* species in the accumulation of other small vertebrates, which are abundant in LBC. Mammalian predators are very unlikely to have contributed to the avian fossil assemblage of LBC, as the structure of the cave, with a long drop from the bottom of the solution pipe to the rockpile below, would have prevented non-volant mammals from entering and leaving the cave.

One further accumulation mode to be considered is that birds sheltering in the cave entrance may have been sucked down the solution pipe by the strong downdraughts that occur during changes in atmospheric pressure, and then been unable to fly back up the near-vertical pipe. This process appears to happen today, with fresh specimens of Nankeen Kestrel *Falco cenchroides*, for example, accumulating in LBC in between fieldwork seasons.

Given the possible mixed modes of accumulation in LBC, with pitfall trapping, flooding, raptor predation and downdraughts as plausible contributors to the avian fossil assemblage, a wide range of taxa from the Pleistocene avifaunal assemblage of the Nullarbor Plain have probably been sampled. A formal assessment of body sizes, representation of skeletal elements, and breakage patterns of bird bones would, however, enhance our understanding of patterns of accumulation, and potential biases, in the avian fossil assemblage from LBC.

4.4.1.4 Representation of taxa

Almost all of non-passerine taxa that were originally identified from the locality based on material collected in the earliest fieldwork seasons (Prideaux et al. 2007) were confirmed in this study. The only bird taxa removed from the original species list for the locality are: *Leipoa gallinacea*, with the large megapode remains formerly attributed to that species having now been referred to the new taxon *Progura campestris* (see Shute et al. 2017; reproduced in Chapter 3); and *Tribonyx* (=*Gallinula*) *ventralis*, with all Rallidae specimens from the Thylacoleo Caves having been tentatively referred to other taxa (see Systematic Palaeontology). Nevertheless, one specimen from LTC and two from LBC were tentatively referred to the genus *Tribonyx*, although the remains could not be attributed to either of the extant members of the genus, *T. ventralis* or *T. mortierii.* Many additional taxa, both extant and extinct, have now been added to the species list for the Thylacoleo Caves locality (see Figure 4.15 and Table 4.4).

4.4.1.5 Absent taxa

Some taxa that are common elements of the Holocene avifauna of Australia are surprisingly absent from the Thylacoleo Caves assemblage, most notably quails in the genus *Coturnix*. These are near-ubiquitous in other Quaternary fossil cave assemblages (Baird 1986), and inhabit the Nullarbor Plain today. It is possible that this genus, species of which are often among the most abundant birds in Late Pleistocene and Holocene cave fossil deposits in Australia (Baird 1991), may not have entered Australia until the Late Pleistocene. As the sole representatives in Australia of the Phasianidae, this galliform family may therefore have been entirely absent from Australia until sometime within the last 126 kyr.

Almost entirely absent, too, are cockatoos, with a single Early Pleistocene specimen of the smallest Australian species, the Cockatiel *Nymphicus hollandicus*, being the only bone of a species in the Cacatuidae family (see Systematic Palaeontology). Although cockatoos are not common in most Australian Quaternary cave fossil sites, they are represented in some deposits, notably species of black cockatoo in the genus *Calyptorhynchus*, Galah *Cacatua roseicapilla* and Gang-gang Cockatoo *Callocephalon fimbriatum* at Mabel Cave in eastern Victoria (Baird 1986), and *Calyptorhynchus*, *Callocephalon*, and species of Corella in the genus *Cacatua* from Green Waterhole Cave in south-eastern South Australia (Baird 1985). Absence of larger cockatoos from the Thylacoleo Caves is surprising given the abundance of woodland parrots in the Psittacidae within LBC. Species of *Cacatua* and *Calyptorhynchus* are large, often feed on the ground, and form large flocks, so the occasional individual might be expected to have been subject to pitfall trapping if present. White et al. (2011) estimated that species of *Calyptorhynchus*/*Zanda* in south-western and south-eastern Australia diverged as a result of isolation on either side of the Nullarbor Plain at around 1.3 Ma, which is possibly earlier than the accumulation of Unit 3 in LBC. The present study does not provide any evidence to contradict this, although it is possible that species of cockatoo may have been present on the Nullarbor Plain and been excluded from the Thylacoleo Caves fossil record for taphonomic reasons. No specimens of any cockatoo species were found in Late Pleistocene or Holocene deposits from the Nullarbor region by Baird (1986; 1991; Table 4.7) either, but only two species, Galah *Eolophus roseicapilla* and Major Mitchell's Cockatoo *Cacatua leadbeateri* are found in the Nullarbor region today, and are only found at the periphery of the plain (ALA data, accessed 20-05-2018).

One of the few characteristic taxa of the Nullarbor Plain today, the Bluebonnet Parrot *Northiella* sp. was only tentatively identified from a single specimen from the Early Pleistocene. Given the dominance of parrots in the assemblage (Figure 4.61), this taxon might have been expected to be more prominent, particularly given that the endemic Nullarbor population probably constitutes a separate species (Dolman and Joseph 2015). As a species favouring arid, open habitat, its absence from Middle Pleistocene sediments in Unit 1 is surprising. This raises questions about how recently the taxon evolved, and whether it evolved *in situ* on the Nullarbor Plain, or evolved elsewhere and only colonised the Nullarbor Plain relatively recently.

Entirely absent from the Early and Middle Pleistocene record in LBC, too, is the now-ubiquitous Nankeen Kestrel *Falco cenchroides* (see Systematic Palaeontology), despite the fact that these birds readily become trapped in LBC today. Entry of kestrels into Australia in the Late Pleistocene would be consistent with genetic evidence that this is a species that evolved only in the last few hundred-thousand years (Fuchs et al. 2015). As Australia's smallest raptor, the success of this species may relate to its ability to exploit small prey not targeted by larger raptors.

No specimens from the Thylacoleo Caves were referred to the Coraciiformes in this study, despite their current widespread distribution through varied climatic zones and habitat types in Australia, and despite the representation of species of kingfishers in Late Pleistocene/Holocene localities elsewhere in Australia (Baird 1986). They may have been excluded from the Thylacoleo Caves deposits for taphonomic reasons, or by reason of absence from the locality.

4.4.2 Temporal change in the composition of the avifauna

4.4.2.1 Extinctions

Research in this study and that by Shute et al. (2016, 2017; see Chapters 2 and 3) has revealed that the Thylacoleo Caves fauna contains a diversity of extinct avian taxa that is unparalleled at any Australian Pleistocene locality. Four of the extinct species, and one new genus, have already been formally described from the locality (Chapters 2 and 3), but during this study ten more species of uncertain generic identity have been identified as extinct or likely extinct, including two pigeons, several rails, a stork, a large eagle, and a pezoporine parrot, for a total of 14 (see Table 4.4 and Systematic Palaeontology).

All the suspected new taxa require further study, but prior to the inception of this research project, only around 10 taxonomically sound extinct avian species had previously been described from the Pleistocene record for the entire Australian continent. That more than double the number of extinct taxa is now known or suspected based on just one locality suggests that Pleistocene extinctions played a greater role in shaping the modern Australian avifauna than has generally been assumed. We now stand on the cusp of being able to ask – and hopefully ultimately answer – questions that have been applied to avifaunas on other continents (e.g. Johnson and Cicero 2004; Weir and Schluter 2004; Zink, Klicka, and Barber 2004): did the climatic and habitat fluctuations of the Pleistocene epoch result in a net generation or net loss of diversity among the Australian avifauna?

The apparent loss of nearly a quarter of non-passerine species from the Thylacoleo Caves fauna begs the question whether the Nullarbor Plain formerly had an especially diverse or unique avifauna compared to the rest of the continent, or whether Australia as a whole lost a large suite of bird taxa during the Pleistocene in a hitherto undetected extinction ‘event’. The marsupial fauna from the Thylacoleo Caves also revealed numerous new species that had not previously been found elsewhere (Prideaux et al. 2007; Prideaux and Warburton 2008, 2009), which could on one hand be interpreted as indicating an unusual fauna. However, it seems more likely that the extinct taxa identified from the locality also occurred further afield, and have only been recorded from the Nullarbor Plain because of the extraordinary quality of fossil preservation in the Thylacoleo Caves.

An analysis by Hawkins *et al.* (2005), which included both passerine and non-passerine taxa, identified the modern Nullarbor region as having a particularly derived avifaunal assemblage at the level of family. It would provide valuable perspective on the results of this fossil study if the methods of Hawkins *et al.* (2005) were applied to non-passerine taxa alone. This would help to determine whether the non-passerine fauna of the Nullarbor region has lost more basal families than comparable parts of the arid zone, and thus whether the high rate of extinctions observed in the Thylacoleo Caves fauna is due to high rates of extinction within an exceptionally diverse avifauna, or whether this pattern is likely to typify the rest of the continent.

Highest losses seem to have been sustained among strongly terrestrial taxa, including megapodes (two genera and species) and coucals (two species), which may be due to loss of trees and associated understorey, and among taxa that were probably water-dependent (rails and a stork). As discussed by Shute et al. (2016) in relation to the coucals *Centropus bairdi* and *C. maximus*, the impact on the fauna of the loss of dense understorey from the Nullarbor Plain during the Pleistocene has not generally been considered, with discussions of vegetation change in the region having always centred on the loss of trees. A loss of complexity of habitat structure must be considered in examining the fossil record of other taxa from the Thylacoleo Caves, including the passerine birds and small mammals, and in considering the role of the Nullarbor Plain as a biogeographical barrier more generally.

Extinction of rails is not entirely unexpected, since they are a group that has been shown worldwide to be characterised by rapid turnover (e.g. Garcia-Ramirez 2014; Mather 2018). However, the present study provides the first evidence that the Australian rail fauna may have undergone high species turnover since the Early to Middle Pleistocene, given that no fossil specimens examined in this study could be referred to an extant species. Even though rail taxa may have been replaced by new species, it is telling that modern rails have never been recorded as present on the Nullarbor Plain. All else being equal, it might be expected that living species would occasionally have been recorded on the Plain after heavy rainfall. The fact that they have not, whereas multiple taxa occurred there during the Early Pleistocene, implies greater availability of standing water in the landscape, even if ephemeral.

4.4.2.2 A signature of the 'mid-Pleistocene transition'?

The LBC fossil assemblage shows an apparent reduction in non-passerine diversity on the Nullarbor Plain between the Early and Middle Pleistocene. Most of the distinctively woodland taxa and rails are present in Unit 3 (Early Pleistocene), and the majority of extinct taxa are also found in this unit. Unfortunately Unit 2, which according to magnetostratigraphic dating by Prideaux et al. (2007) encompasses both the Early and Middle Pleistocene, reveals virtually nothing about the nature of either the avifauna or the palaeoecology of the Nullarbor Plain more generally during this time due to a lack of bird specimens preserved. However, by the Middle Pleistocene, represented in Unit 1, a much less diverse fauna apparently associated with a more open habitat, and with few extinct species, is evident.

Although the apparently lower diversity of non-passerines in Unit 1 may be partly be an artefact of smaller sample size compared to Unit 3 (see Section 4.3.4.3), the absence of most woodland taxa, the dominance of open-habitat taxa, as well as the much reduced representation of now-extinct species in Unit 1, are difficult to ignore. The question emerges: was there a regional, or even continental-scale reduction in avian diversity associated with the 'mid-Pleistocene transition'?

Pillans and Bourman (2001) found evidence for markedly elevated aridity throughout southern Australia during the first half of the Middle Pleistocene, from 350–700 ka, following changes in Earth's orbit that forced the globe into longer glacial/interglacial cycles. This arid interval likely coincides with the accumulation of an open-habitat avifaunal assemblage in Unit 1. Aridity associated with longer glacial-interglacial cycles could be implicated in the loss of littoral/aquatic birds (rails, storks) from the Nullarbor Plain, as well as the loss of trees from the Plain during this interval, which could in turn explain an apparent loss of avian taxa. In support of this interpretation, fossil frogs from LBC indicate that conditions on the Nullarbor Plain were moister during the Early Pleistocene, with three species of frog, including a species of tree-frog, having been described from Unit 3, whereas only arid-adapted burrowing frogs have been found in Units 1 and 2 (Tyler and Prideaux 2016). Thus evidence is building for Unit 3 representing a more mesic interval during the Early Pleistocene, and Unit 1 a more arid one during the Middle Pleistocene.

Given that the accumulation of sediment in LBC ceased in the Middle Pleistocene, unfortunately it is not possible to tell at present whether more mesic conditions returned later in the Pleistocene, and thus whether the apparent loss of now-extinct bird species by the Middle Pleistocene was due to continent-wide extinction of taxa during the 'mid-Pleistocene transition', or whether the extinct/likely extinct species in Table 4.4 were only extirpated locally at this time. Some extinct and woodland taxa are present in the rockpile in LBC, and may be younger than specimens in Unit 3, but they could equally well be contemporaneous. Many rockpile specimens were collected upslope of the entrance pit (see Systematic Palaeontology, and 3D map in Figure 4.8) and could not have been washed in by floodwater, and thus could be Early Pleistocene specimens that accumulated via pitfall trapping, and which remained in situ during the presumed floods that led to accumulation of the Unit 1 infill sediments during the Middle Pleistocene.

Although evidence from additional localities is needed to provide a continental perspective on the effects on the avifauna of the 'mid-Pleistocene transition', LBC nevertheless represents the first known Australian fossil site where an Early and Middle Pleistocene landbird fauna exist in superposition, and where, *prima facie*, there is evidence for both species attrition and local extirpation of extant taxa across the Early/Middle Pleistocene boundary. Currently little is known about what impacts – if any – the 'mid-Pleistocene transition' had on global avifaunas. Finlayson et al. (2012) reviewed transitions in Pleistocene faunal composition in the Palaearctic, but primarily examined the transition from the Middle into the Late Pleistocene. Although they did not quantify extinctions from the Early into the Middle Pleistocene, their analysis showed that the later transition from the Middle into the Late Pleistocene resulted in the loss of only a very small proportion of bird genera and species from the Palaearctic, with 1.6% of bird genera and 5.9% of bird species apparently having gone extinct from the region. By contrast, 20% of mammal genera and 40% of mammal species went extinct. Although not contemporaneous with the present study, their analysis provides some perspective on the nearly 25% loss of non-passerine taxa observed at the Thylacoleo Caves locality.

If the unexpected species loss evident from the fossil record of the Thylacoleo Caves is not a signature of extinctions at around the time of the 'mid-Pleistocene transition', and some or all of the now-extinct species in the fossil fauna survived elsewhere in Australia into the Middle Pleistocene or later, then alternative explanations for the later demise of these taxa must still be sought: were these species lost gradually from the Australian landscape, or did they all disappear rather suddenly due to a later period of particularly harsh climatic change, or after the arrival of humans in the Late Pleistocene? These are not questions that can be answered by studying a single fossil locality, but the Thylacoleo Caves fossil record is sufficient to establish that higher-than-expected species extinctions occurred among Australian Pleistocene landbirds. This can now serve as an impetus to further investigate the Quaternary fossil record of Australian birds, including key fossil localities that have received scant attention to date, such as the Wellington Caves in New South Wales, and the Naracoorte Caves in South Australia.

4.4.3 Palaeoecology of the Nullarbor Plain

The preliminary study of the Thylacoleo Caves fauna by Prideaux et al. (2007) concluded that the Middle Pleistocene habitat of the Nullarbor Plain comprised a mosaic habitat of woodland and shrubland, under an arid- to semi-arid climatic regime. That conclusion was based mainly on the marsupial fauna from the locality, and was based on a time-averaged analysis of fossils from the thee Thylacoleo Caves. One of the aims of this study was to use the non-passerine fossil assemblage from the Thylacoleo Caves to determine whether the composition of the avifauna supports that palaeoecological interpretation.

One key difference between the present study and that of Prideaux et al. (2007) is that the avifaunal analysis is based not on a time-averaged assemblage, but rather on specimens form a relatively well age-constrained sediment sequence from LBC. This allows for a more nuanced interpretation of the palaeoecology of the Nullarbor Plain, including a temporal dimension.

4.4.3.1 Vegetation

The avifaunal assemblage from Leaena's Breath Cave is consistent with the conclusion of Prideaux et al. (2007) that both woodland and open habitats were present on the Nullarbor Plain during the Pleistocene, but this study provides evidence for a general transition from a more complex woodland habitat structure in the Early Pleistocene towards a simpler, more open habitat in the Middle Pleistocene. In Unit 3 (Early Pleistocene), the NISP of woodland and open-habitat taxa are both ~40% of the assemblage, whereas in Unit 1, nearly 90% of specimens are from taxa that prefer open habitats, indicating that trees were probably all but absent.

At a finer scale, though, analysis of habitat guilds of birds within Unit 3 indicates that the Early Pleistocene assemblage contains two main pulses of specimen accumulation, but with different composition in each (Figure 4.69). The earliest such pulse (110–120 cm) comprises a mixture of taxa with preferences for open habitat, shrubland and woodland/forest, with open-habitat specimens being the most numerous. At a slightly shallower depth (90–100 cm), these proportions are inverted, with woodland/forest taxa becoming the most numerous, and numbers of open/shrubland taxa dropping to almost nothing. An examination of dietary guilds shows that these accumulation intervals coincide with a gradual decline in the number of strict granivores (*Melopsittacus undulatus* and species of *Phaps*) and a stepped increase in taxa that primarily eat seeds but that also consume other foods (platycercine parrots) (Figure 4.71).

Further dating of the sediments are required to determine with certainty whether these apparent habitat/dietary pulses in the Early Pleistocene were rapid, the result of seasonal fluctuations in food resources, or whether they occurred gradually over a period of thousands of years in response to climatic/habitat change. Gradual change seems perhaps more likely given the increase in the absolute abundance of sedentary woodland/forest taxa (platycercine parrots) during the Early Pleistocene, since tree-dominated habitats are unlikely to have emerged or declined rapidly, and may have occurred over hundreds or even thousands of years.

4.4.3.1.1 Overstorey during the Early Pleistocene

Based on the most abundant sedentary woodland parrots identified in Unit 3 (*Platycercus icterotis*, *Platycercus* magn. *elegans*, *Barnardius* sp.), the floristic composition of the overstorey during the Early Pleistocene is most likely to have comprised species of *Eucalyptus* as all three taxa, and particularly *P. elegans*, are most commonly found in eucalypt associations (Higgins 1999). However, *P. icterotis* and *B. zonarius* are sometimes found in *Acacia* scrubs or other associations (Higgins 1999). A single specimen of a Malleefowl *Leipoa ocellata* at 105–110 cm is most likely to indicate an overstorey of low multi-stemmed *Eucalyptus* trees, but this species is not found exclusively in eucalypt-dominated habitats (Marchant and Higgins 1993). Many hollow-nesting parrots are present in the Early Pleistocene assemblage, suggesting availability of mature trees in the landscape, particularly during the depositional interval at 90-100 cm in Unit 3 of LBC. Unit 3 also contains the only specimens of the Brown Goshawk *Accipiter fasciatus*, which hunts in woodland and forest habitats (Marchant and Higgins 1993).

It is not currently possible to independently verify that a specifically *Eucalyptus* overstorey was present on the Nullarbor Plain in the Early Pleistocene, because there is a temporal gap in the speleothem pollen record for the region during this interval (Sniderman et al. 2016). However, there is pollen evidence that in the preceding Pliocene epoch, the vegetation in the region comprised mesic forest of *Eucalyptus* and other myrtaceous taxa (*Corymbia* and *Angophora*), as well as *Banksia* and *Doryanthes* (spear-lilies). It is possible that any of these taxa could have persisted or re-colonised the Nullarbor during the Early

Pleistocene if conditions were sufficiently moist. In eastern Australia, recently-discovered plant macrofossils have revealed a previously unknown, but highly floristically diverse, vegetation association from the Early Pleistocene (Sniderman et al. 2013). That study revealed that a regional mass extinction of a diverse flora had previously gone undetected in pollen studies because the taxa involved had the same palynomorphs as surviving related taxa. This highlights how poorly known the Early Pleistocene vegetation of Australia is, and raises the possibility that a floristic community with no modern analogue was present in the Nullarbor region during the Early Pleistocene.

The non-passerine fauna from the Thylacoleo Caves provides no evidence to suggest that nectar was an abundant food source on the Nullarbor Plain during the Early Pleistocene, given the almost total absence of nectarivores from the fossil assemblage (Figure 4.71). The only remains of nectar-eating taxa were a few isolated bones of parrots in the Loriini tribe (lorikeets), which is surprising given the abundance of the remains of other parrots in the Early Pleistocene of Unit 3, and given that lorikeets are common in some other Quaternary fossil assemblages (e.g. *Trichoglossus moluccana* in Mabel Cave; Baird 1986). However, no lorikeet species inhabit the Nullarbor region today, and only one species, the Purple-Crowned Lorikeet *Glossopsitta porphyrocephala* is native to the south-western quarter of Australia (Rainbow Lorikeet *Trichoglossus moluccana* is a recent introduction; Higgins, 1999).

The few specimens of lorikeets in the LBC assemblage may represent vagrant individuals of these highly mobile taxa, and may mean that the Nullarbor Plain, despite having a habitat that was more floristically and structurally diverse during the Early Pleistocene than today, did not have nectar as an abundant resource. The ready availability of nectar in the Australian landscape, for example from flowering eucalypts, has been hypothesised to have been a major factor in the evolution of the continent's avifauna (Lowe, 2014). If eucalypts were the main overstorey plants of the habitat surrounding the Thylacoleo Caves as suggested above, there may have been reasons for the absence of lorikeets other than a lack of nectar. The availability of nectar in the Nullarbor landscape during the Pleistocene should be investigated via the fossil record – or lack thereof – for other nectar-dependant taxa, such as honeyeaters (Meliphagidae) and small mammals like pygmy possums in the genus *Cercartetus*, none of which were identified in the fauna during the preliminary assessment of the Thylacoleo Caves fauna (Prideaux et al. 2007).

4.4.3.1.2 Understorey during the Early Pleistocene

It is likely given the diversity of non-passerines in the Early Pleistocene that the Early Pleistocene habitat of the Nullarbor Plain was floristically and structurally diverse. Initially abundant but then declining numbers of *Turnix* and *Melopsittacus undulatus* specimens through Unit 3 (Figure 4.62), both of which favour open habitats, may indicate that earlier in the unit a relatively more open habitat with more grasses existed, later giving way to a more closed canopy and/or a more dense understorey.

The most abundant pigeon species in Unit 3, *Phaps elegans*, which is found between depths of 95–135 cm in Pit B, prefers habitats that include dense shrubs, such as *Banksia*, *Acacia* and *Leptospermum* (Higgins and Davies, 1996), of which only *Acacia* spp. occur in the vicinity of the Nullarbor Plain today (GBIF data, accessed 23-05-2018). Another taxon in the Early Pleistocene that favours a diverse shrub and herb understorey is the Malleefowl *Leipoa ocellata*, with *Acacia*, two genera of pea-plants *Cassia* and *Bossiaea*, and *Beyeria* (turpentine bushes) being important food sources (Marchant and Higgins 1993). Although only one specimen of *L. ocellata* was found in Pit B, adult Malleefowl are sedentary and poor flyers, and an individual is highly unlikely to have been present in the vicinity of LBC if unsuitable woodland habitat with shrubs and herbs was not present. The diet and habitat requirements of the extinct megapodes *Progura campestris* and *Latagallina olsoni*, which were also found in Unit 3, is unknown other than the presumption that they required relatively large trees for roosting (see Chapter 3).

The exact floristic requirements of extinct *Centropus bairdi* are also unknown, but as a species thought to be flightless and ground-dwelling it probably relied on dense grass and shrubs for cover, feeding and nesting, like its extant counterpart *Centropus phasianinus* in northern and eastern Australia (see Chapter 2 and Systematic Palaeontology). Specimens of *C. bairdi* were recovered between depths of 85–120 cm in Pit B, likely indicating dense ground cover was available at these depths. It is not clear whether its larger relative, *C. maximus*, was contemporaneous, as remains of this species were only found in an undated context in FSC (see Chapter 2).

In considering the impacts of Pleistocene habitat change on the Nullarbor Plain on the fauna, it has historically been the loss of trees from the landscape that has always been the focal point of discussion. While the present study provides evidence for a woodland habitat during the Early Pleistocene, and indicates that trees were largely or entirely absent by the Middle Pleistocene, this study highlights the importance of understorey, and terrestrial niches in general, for supporting a diverse avifauna: a greater diversity of strongly terrestrial taxa, including the extinct coucals and megapodes described in Chapters 2 and 3, were found in Early Pleistocene woodland than in the open habitat of the Middle Pleistocene, once trees were lost from the landscape (Figure 4.68). Turning the focus away from trees, and towards considering the entire Nullarbor palaeocommunity, may provide a fruitful new paradigm for investigating the evolution of the southern Australian flora and fauna.

4.4.3.1.3 Middle Pleistocene vegetation

The non-passerine fossil assemblage from Unit 1 of LBC contains low species diversity, and overall the species assemblage indicates an open habitat with trees absent or virtually absent. A few isolated specimens of likely tree-dependent taxa (e.g. *Latagallina olsoni*, *Psephotus* sp.), as well as abundant specimens of *Melopsittacus undulatus*, which feeds only in open habitat but nests in tree hollows, indicates that there may still have been some trees in the region. However, most woodland taxa that were present in Unit 3, such as platycercine parrots, pigeons, frogmouths and coucals, were not recorded in Unit 1.

Further indicative of an open habitat structure, Unit 1 contains the only specimens of the open-habitat indicator species, the Inland Dotterel *Peltohyas australis* and the Plains-Wanderer *Pedionomus torquatus* (see Systematic Palaeontology). *Peltohyas australis* in particular is known to feed on chenopods (Maclean 1976), and it is possible that the vegetation community reflected in the avifauna of Unit 1 had similar floral composition to that of the Nullarbor Plain today. Supporting this interpretation, pollen from a speleothem from LBC, dated to 410 ± 70 ka (Middle Pleistocene), shows a signature of vegetation that was strongly dominated by chenopods (saltbush/bluebush), with Poaceae (grasses), Asteraceae (daisies) and Myoporeae, but without *Eucalyptus* pollen (Sniderman, 2016).

4.4.3.2 Arid or mesic?

In their preliminary analysis of the Thylacoleo Caves fauna, Prideaux et al. (2007) interpreted the time-averaged fossil assemblage as arid-adapted, based on modern rainfall tolerances of living taxa in the assemblage, and isotopic data from marsupial teeth. Combined evidence led to the conclusion that the Thylacoleo Caves fauna existed under a mean annual rainfall regime of 230–260 mm – slightly but not dramatically higher than rainfall received on the northern part of the Plain today (~180 mm per year), and still arid to semi-arid.

The present study of birds reveals a curious mixture of arid and mesic taxa. Overall, evidence from the avifauna, as well as from the fossil record of frogs from LBC (Tyler and Prideaux 2016), suggests that the Early Pleistocene interval(s) captured in Unit 3 was somewhat wetter than the Middle Pleistocene interval in Unit 1. In Unit 3, woodland taxa are relatively abundant, such as rosellas, which now only inhabit mesic woodlands and forests in south-western, south-eastern, eastern, and northern Australia. However, these mesic parrots co-occur in Unit 3 with specimens of *Barnardius*, which are found in both arid and mesic habitats, and *Melopsittacus undulatus*, a true arid-zone species (Higgins 1999). In addition, although none is abundant individually, Unit 3 contains a relatively high diversity of littoral/aquatic taxa, including various species of rails, a duck, a stork, a specimen of a curlew/whimbrel, and unidentified specimens of the Scolopacidae, which is a charadriiform family of largely littoral/aquatic taxa.

This mixing of arid-adapted taxa, mesic woodland taxa, as well as the occurrence of taxa like ducks, rails and charadriiforms that were likely mobile and responsive to heavy rainfall, could mean that conditions on the Nullarbor Plain during the Early Pleistocene were somewhat wetter than today, and wetter than indicated by the time-averaged analysis of the Thylacoleo Caves fauna by Prideaux et al. (2007). The Nullarbor Plain could have hosted a non-analogue avifaunal community, Pleistocene exemplars of which have be found on other continents (e.g. Holm and Svenning 2014; Oswald and Steadman 2015; Stewart and Jacobi 2015). However, it is also possible that time-averaging within the LBC assemblage could also account for an apparently mixed arid/mesic fossil fauna, but a more detailed chronology for the cave fill sediment in LBC is needed to properly examine the likelihood of this. Even if time-averaging were a factor, the occurrence of mesic taxa indicates that conditions were wetter on the Nullarbor Plain during at least part, or parts, of the Early Pleistocene than today.

By contrast, the Middle Pleistocene assemblage in Unit 1 seems to represent a relatively more arid ecosystem similar to that of the Nullarbor Plain today, with few or no trees, and a low diversity of non-passerines. However, the rare occurrence of rails and non-*Turnix* charadriiforms in Unit 1 may mean that occasional heavy rainfall events still attracted littoral/aquatic taxa to the region even if conditions were more arid overall than in the Early Pleistocene. The occurrence of arid-adapted burrowing frogs on the Nullarbor Plain during the Middle Pleistocene, but their modern exclusion from the region, was identified as a conundrum by Tyler and Prideaux (2016), given that burrowing frogs occur elsewhere in the modern arid zone. Periodic heavy rainfall, even if not annual, would likely have been required to maintain populations of these burrowing frogs.

Today, rainfall in the northern Nullarbor region is low, unreliable, and falls mainly on the Plain as a result of summer storms with heavier rainfall in some years due to monsoonal activity (James et al. 2012). The occurrence of water-dependent taxa like frogs, rails and charadriiforms, even in the Middle Pleistocene when vegetation appears to have been similar to today, may indicate that conditions then were more humid than today, or that mean annual rainfall was low, but perhaps fell with either greater frequency or greater reliability than it does today. Geological evidence from the Gregory Lakes in the Great Sandy Desert, around 1,300 km north of the Nullarbor Plain, shows that monsoonal activity was particularly high in northern Australia during the Middle Pleistocene at around 300 kyr. Lacustrine activity later reduced, in the later Middle Pleistocene and into the Late Pleistocene (~200–100 kyr), which coincided with the expansion of arid dune fields in the Western Deserts region, north of the Nullarbor (Bowler et al. 2001).

Greater penetration of monsoonal rainfall from northern Australia onto the Nullarbor Plain during the Middle Pleistocene than occurs today might explain the occurrence in Unit 1 of LBC of water-dependant taxa like frogs, rails and charadriiforms. Enhanced climatic, and perhaps habitat connections with north-western Australia during parts of the Pleistocene might also help explain the occurrence in the fossil record of the Thylacoleo Caves of taxa that now occur somewhat further north, including rare specimens of the Flock Bronzewing *Phaps histrionica*, Cockatiel *Nymphicus hollandicus*, Bourke's Parrot *Neopsephotus bourkii*, and extinct taxa like a stork and two species of coucal, whose living Australian relatives occur in the arid but monsoon-influenced north-west of the continent.

4.4.4 Range changes and the role of the Nullarbor Plain as a biogeographical barrier during the Early to Middle Pleistocene

Given the pivotal role that has often been attributed to the Nullarbor Plain as an arid-habitat barrier that shaped the evolution and biogeography of the southern Australian avifauna during the Pleistocene, more species that now have disjunct populations in south-western and south-eastern Australia might have been expected to be present in the fossil fauna of the Thylacoleo Caves. The few examples of this are: Freckled Duck *Stictonetta naevosa*; Chestnut Teal *Anas castanea*; and the Brush Bronzewing *Phaps elegans*. Of these taxa, *S. naevosa* and *A. castanea* are each represented by a single individual, while *Phaps elegans* is represented from various specimens from between depths of 90–135 cm in LBC. This provides preliminary evidence that the species may have had a contiguous population across southern Australia until at least the Early Pleistocene, potentially shedding light on the divergence of the western and eastern sub-species.

Besides the general confirmation that there was woodland habitat on the Nullarbor Plain during the Early Pleistocene, which is not unexpected based on other lines of evidence (e.g. Dolman and Joseph 2012), there is little obvious fossil evidence from the Thylacoleo Caves locality that illuminates what role the Nullarbor Plain played as a biogeographic barrier (or conversely, a corridor) for extant taxa with vicariant distributions, during the Early and Middle Pleistocene. Overall, the fossil fauna carries a greater signature of species extinction than it does of vicariance.

Around 40% of taxa in the assemblage have been recorded in the Nullarbor region in the late Holocene (Table 4.4), and their Pleistocene presence on the now-treeless part of the Nullarbor Plain represents either no geographical change or only a very modest range change relative to today. Taxa with modern records from the region include Emu *Dromaius novaehollandiae*, species of teal *Anas* spp., Malleefowl *Leipoa ocellata*, Common Bronzewing *Phaps chalcoptera*, Tawny Frogmouth *Podargus strigoides*, Australian Owlet-Nightjar *Aegotheles cristatus*, Inland Dotterel *Peltohyas australis*, buttonquails *Turnix* spp., Spotted Harrier *Circus assimilis*, Brown Goshawk *Accipiter fasciatus*, Wedge-tailed Eagle *Aquila* *audax*, tytonid owls, Nankeen Kestrel *Falco cenchroides*, Brown Falcon *Falco berigora*, Cockatiel *Nymphicus hollandicus*, Budgerigar *Melopsittacus undulatus*, Bluebonnet parrot *Northiella* sp., Western Rosella *Platycercus icterotis*, Ring-necked Parrot *Barnardius* sp., Bourke's Parrot *Neopsephotus bourkii*, and grass parrots *Neophema* sp.

A smaller number of extant taxa (18; 31%) in the Thylacoleo Caves fauna were found to be outside their current range, but most of these are present in the fossil assemblage only in very low numbers. Some of these are woodland taxa that are considered relatively mobile (e.g. *Glossopsitta* sp., *Polytelis* sp., cf. *Purpureicephalus spurius*, *Phaps histrionica*) (Higgins and Davies, 1996; Higgins, 1999), and the Nullarbor Plain during the Early Pleistocene may have provided temporary habitat for them or facilitated their movement in southern Australia without necessarily supporting resident populations. Other mesic woodland taxa that are present in the fossil deposit in higher abundances (*Phaps elegans*, *Platycercus* spp.) are more sedentary (Higgins and Davies, 1996; Higgins, 1999) and these seem more likely to have been resident on the Nullarbor Plain during the Early Pleistocene.

The sympatry of species of *Platycercus* during the Early Pleistocene is of biogeographical and evolutionary interest, given the complex genetic and Pleistocene biogeographical history of this genus (Joseph et al. 2008; Schweizer et al. 2013). A minimum of three species appear to be present in LBC, those being Western Rosella *Platycercus icterotis*, Crimson Rosella *P. elegans*, and an unidentified species. Today, the range of *P. icterotis* does not overlap with any other member of the genus, and it is confined to the south-western corner of Australia (historically, it was recorded in the Nullarbor region by McGilp, 1932, but no longer occurs this far east). The *Platycercus elegans* species complex today inhabits mesic south-eastern and eastern Australia, where it overlaps with other species in the genus. Why the range of *P. icterotis* should ultimately have contracted to the west and that of *P. elegans* to the east of the Nullarbor Plain after the Early Pleistocene is a mystery.

At higher taxonomic levels, certain other taxa in the fossil record are far outside of the current range of their nearest living Australian relatives, including coucals in the genus *Centropus*, whose living relative *C. phasianinus* is considered a characteristically Torresian species (see Shute *et al.* 2016), the Rallidae, which do not occur on the Plain although they occur elsewhere in the arid zone, and the Ciconiidae, which are unknown from the south-west quarter of the continent. The Rallidae and Ciconiidae taxa would be expected to be highly mobile and responsive to rainfall events, but poorly volant species of *Centropus* would not. Presumably the southern distribution of *Centropus* during the Pleistocene was a legacy of historical habitat connections between northern and southern Australia (Shute et al. 2016).

4.5 Conclusions

This study represents the first in-depth assessment of an Early and Middle Pleistocene fossil landbird fauna from any Australian locality. Much work remains to be done on the fossil avifauna from the Thylacoleo Caves, including the description of new taxa identified in this study, refining the identifications of some specimens, and the analysis of the passerine component of the fauna. Nevertheless, the diversity of the Thylacoleo Caves avifauna as currently understood is exceptional relative to other Australian Pleistocene fossil localities. The non-passerine avifauna reveals a transition on the Nullarbor Plain from a woodland habitat in the Early Pleistocene to an open habitat in the Middle Pleistocene. The timings of this transition, how it relates to individual climatic cycles and monsoon activity, and the timing of the final loss of trees from the Plain, is currently unclear, but *prima facie* there appears to be evidence for species extinctions and lowered avian diversity in south-central Australia across the 'mid-Pleistocene transition'. These factors can be further investigated in future, particularly once dating of the sediment sequence in LBC is refined, and when the complete avifauna is analysed along with other vertebrates in the assemblage.

At the inception of this research project, it was expected that the fossil avifauna would contain many taxa that today have allopatric ranges in south-western and south-eastern Australia, thus providing a framework for better understanding the timing of vicariance for taxa in southern Australia, and the operation of the 'Nullarbor barrier' as a biogeographical filter during the Pleistocene. Surprisingly few examples of this were found in the present study, and what has instead been revealed are unexpectedly high rates of extinction. These results open up broader questions about rates of extinction among birds across the entire Australian continent over the course of the Quaternary. Molecular studies will continue to reveal much about the impacts of the Pleistocene on the living Australian avifauna, but questions of extinction will only be answered by the fortuitous discovery of other diverse fossil avifaunas in other parts of the country, and by giving under-exploited fossil bird collections in museums the attention they deserve.

4.6 References

Baird, R.F. 1985. 'Avian fossils from Quaternary deposits in "Green Waterhole Cave", South-Eastern South Australia'. *Records of the Australian Museum* 37(6): 353–70.

Baird, R.F. 1986. 'The avian portions of the Quaternary cave deposits of southern Australia and their biogeographical and palaeoenvironmental interpretations'. PhD thesis, Monash University, Melbourne.

Baird, R.F. 1991. 'The taphonomy of Late Quaternary cave localities yielding vertebrate remains in Australia'. In *Vertebrate Palaeontology of Australasia*, edited by P. Vickers-Rich, J. Monaghan, R.F. Baird, and T. Rich, 267–301. Pioneer Design Studio, Melbourne.

Baird R.F. and Vickers-Rich P. 1998. '*Palaelodus* (Aves: Palaelodidae) from the Middle to Late Cainozoic of Australia.' *Alcheringa: An Australasian Journal of Palaeontology* 22(2): 135–151.

Baird, R.F., Vickers-Rich P., and van Tets, G. 1991. 'Appendix II: localities yielding avian assemblages of Quaternary age in Australia'. In *Vertebrate Palaeontology of Australasia*, 850–67. Pioneer Design Studio, Melbourne.

Baker-Gabb D., Antos M., and Brown G. 2016. 'Recent decline of the critically endangered Plains-Wanderer (*Pedionomus torquatus*), and the application of a simple method for assessing its cause: major changes in grassland structure'. *Ecological Management & Restoration* 17(3): 235–42.

Baumel, J., King A., Breazile J., Evans H. and Vanden Berge J. 1993. *Handbook of Avian Anatomy: Nomina Anatomica Avium*. Second Edition. Publications of the Nuttall Ornithological Club 23: Nuttall Ornithology Club, Cambridge, Massachusetts.

Boles, W.E. 2005. 'A review of the Australian fossil storks of the genus *Ciconia* (Aves: Ciconiidae), with the description of a new species'. *Records of the Australian Museum* 57(2): 165–178.

Bowler, J.M., Wyrwoll K-H. and Lu Y. 2001. 'Variations of the northwest Australian summer monsoon over the last 300,000 years: the paleohydrological record of the Gregory (Mulan) Lakes System'. *Quaternary International* 83–85: 63–80.

Brigham, R., Debus S.J.S., and Geiser F. 1998. 'Cavity selection for roosting, and roosting ecology of forest-dwelling Australian Owlet-Nightjars (*Aegotheles cristatus*)'. *Austral Ecology* 23(5): 424–429.

Burbidge, A., Casperson K., and Fuller P. 1987. 'Birds'. In *A Biological Survey of the Nullarbor Region, South and Western Australia in 1984*, 153–78. Adelaide: South Australian Department of Environment and Planning, Western Australia Department of Conservation and Land Management, Australian National Parks and Wildlife Service.

Byrne, M. 2008. 'Evidence for multiple refugia at different time scales during Pleistocene climatic oscillations in southern Australia inferred from phylogeography'. *Quaternary Science Reviews* 27 (27–28): 2576–85.

Christidis, L., and W. Boles. 2008. *Systematics and Taxonomy of Australian Birds*. CSIRO Publishing, Victoria.

Cohen, K., and Gibbard P. 2011. '2011 global chronostratigraphical correlation table for the last 2.7 million years.' Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy), Cambridge, England.

Cracraft, J. 1986. ‘Origin and evolution of continental biotas - speciation and congruence within the Australian avifauna’. *Evolution* 40(5): 977–96.

Crome, F.H.J., and Johnstone R.E. 1979. ‘Geographical variation in the Australian rock pigeons’. *Records of the Western Australia Museum* 8: 117–133.

Dawson, L. 1985. ‘Marsupial fossils from Wellington Caves, New South Wales; the historic and scientific significance of the collections in the Australian Museum, Sydney’. *Records of the Australian Museum* 37(2): 55–69.

De Pietri, V.L., Camens A.B., and Worthy T.H. 2015. ‘A Plains-Wanderer (Pedionomidae) that did not wander plains: a new species from the Oligocene of South Australia’. *Ibis* 157(1): 68–74.

De Pietri V.L. 2017. ‘The diversity of early Miocene pigeons (Columbidae) in New Zealand’. In *Proceedings of the 9th International Meeting of the Society of Avian Palaeontology and Evolution, Diamante (Argentina), 1–6 August 2016*. Paleontologia y Evolucion de las Aves: Contribuciones del Museo Argentino de Ciencias Naturales No. 7: 49–68

De Pietri, V.L., Scofield R.P., Prideaux G.J., and Worthy T.H. 2018. ‘A new species of lapwing (Charadriidae: *Vanellus*) from the Late Pliocene of central Australia’. *Emu - Austral Ornithology*, May: 1–10.

Debus, S.J.S. 1993. ‘The mainland Masked Owl *Tyto Novaehollandiae*: a review’. *Australian Bird Watcher* 15: 168–91.

Dhami, K.K., Joseph, L., Roshier D.A., Heinsohn R., and Peters J.L.. 2013. ‘Multilocus phylogeography of Australian teals (*Anas* spp.): a case study of the relationship between vagility and genetic structure’. *Journal of Avian Biology* 44(2): 169–78.

Dickinson, E.C., and Remsen Jr, J.V., eds. 2013. *The Howard and Moore Complete Checklist of the Birds of the World*. 4th ed. Volume 1: Non-passerines. 2 vols. Aves Press, Eastbourne.

Dolman, G., and Joseph L. 2012. ‘A species assemblage approach to comparative phylogeography of birds in southern Australia’. *Ecology and Evolution* 2(2): 354–69.

Dolman, G., and Joseph, L. 2015. ‘Evolutionary history of birds across southern Australia: structure, history and taxonomic implications of mitochondrial DNA diversity in an ecologically diverse suite of species’. *Emu* 115: 35–48.

Dolman, G., and Joseph, L. 2016. ‘Multi-locus sequence data illuminate demographic drivers of Pleistocene speciation in semi-arid southern Australian birds (*Cinclosoma* spp.)’. *BMC Evolutionary Biology* 16 (1).

Dunning, J. 2008. *CRC Handbook of Avian Body Masses*. 2nd ed. CRC Press, Boca Raton, Florida.

Ford, H.L., Sosdian S.M., Rosenthal Y., and Raymo M.E. 2016. ‘Gradual and abrupt changes during the Mid-Pleistocene Transition’. *Quaternary Science Reviews* 148 (September): 222–33.

Ford, J. 1969. Distribution and taxonomic notes on some parrots from Western Australia. *South Australian Ornithologist*, *25*: 99–105.

Ford, J. 1987. ‘Minor isolates and minor geographical barriers in avian evolution in continental Australia’. *Emu* 87: 90–102.

Forshaw, J.M. 2011. *Parrots of the World.* CSIRO Publishing, Collingwood.

Forshaw, J.M., and Joseph L. 2016. ‘A new subspecies of the Australian Ringneck (*Barnardius zonarius*) from the upper Cooper Creek drainage, Lake Eyre Basin, Central Australia’. *Emu* 116 (4): 440.

Fuchs, J., Johnson J.A., and Mindell D.P. 2015. ‘Rapid diversification of falcons (Aves: Falconidae) due to expansion of open habitats in the Late Miocene’. *Molecular Phylogenetics and Evolution* 82 (January): 166–82.

Garcia-Ramirez, J, Gibb G., and Trewick S. 2014. ‘Deep global evolutionary radiation in birds: diversification and trait evolution in the cosmopolitan bird family Rallidae’. *Molecular Phylogenetics and Evolution* 81: 96–108.

Gentilli, J. 1949. ‘Foundations of Australian bird geography’. *Emu* 49: 85–129.

Gibbard, P.L., and Lewin J. 2016. ‘Partitioning the Quaternary’. *Quaternary Science Reviews* 151 (November): 127–39.

Gill, F., and Donsker D. 2018. ‘Owls’. *IOC World Bird List, v8.1*. doi: 10.14344/IOC.ML.8.1.

Groombridge, J.J., Jones C.G., Bayes M.K., van Zyl A.J., Carrillo J., Nichols R.A., and Bruford M.W. 2002. ‘A molecular phylogeny of African kestrels with reference to divergence across the Indian Ocean’. *Molecular Phylogenetics and Evolution* 25(2): 267–277.

Hammer, Ø, D.A.T. Harper, and P.D. Ryan. 2001. *Palaeontologica Electronica* 4(1): 9.

Heupink, T.H., van Grouw H., and Lambert D.M. 2014. ‘The mysterious Spotted Green Pigeon and its relation to the Dodo and its kindred’. *BMC Evolutionary Biology* 14(1): 136.

Higgins, P.J. 1999. *Handbook of Australian, New Zealand and Antarctic Birds, Volume 4, Parrots to Dollarbird*. Oxford University Press, Melbourne.

Higgins, P.J., and S.J.J.F. Davies. 1996. *Handbook of Australian, New Zealand and Antarctic Birds, Volume 3, Snipe to Pigeons*. Oxford University Press, Melbourne.

Hocknull, S.A, Zhao, J.X. , Feng, Y.X., and Webb, G.E. 2007. ‘Responses of Quaternary rainforest vertebrates to climate change in Australia’. *Earth and Planetary Science Letters* 264: 317–31.

Holm, S.R., and Svenning, J.C. 2014. ‘180,000 years of climate change in Europe: avifaunal responses and vegetation implications’. Edited by M. Hofreiter. *PLoS ONE* 9(4): e94021.

James, J.M., Contos, A.K. and Barnes, C.M. 2012. ‘Nullarbor Caves, Australia’. *Chemical Geology* 179 (1): 167–186.

Johnson, N., and Cicero, C. 2004. ‘New mitochondrial DNA data affirm the importance of Pleistocene speciation in North American Birds’. *Evolution* 58(5): 1122–1130.

Jones, D, and A Göth. 2008. *Mound-Builders*. Australian Natural History Series. CSIRO Publishing, Victoria, Australia.

Joseph, L., Dolman G., Donnellan S., Saint K.M., Berg M.L., and Bennett A.T.D. 2008. ‘Where and when does a ring start and end? Testing the ring-species hypothesis in a species complex of Australian parrots’. *Proceedings of the Royal Society B: Biological Sciences* 275(1650): 2431–40.

Joseph, L., Toon, A., Schirtzinger, E.E., and Wright, T.F. 2011. ‘Molecular systematics of two enigmatic genera *Psittacella* and *Pezoporus* illuminate the ecological radiation of Australo-Papuan parrots (Aves: Psittaciformes)’. *Molecular Phylogenetics and Evolution* 59(3): 675–684.

Joseph, L., and Wilke T. 2007. ‘Lack of phylogeographic structure in three widespread Australian birds reinforces emerging challenges in Australian historical biogeography’. *Journal of Biogeography* 34: 612–24.

Joseph, L., Edwards, S.V., and McLean, A.J. 2013. ‘The Maluridae: inferring avian biology and evolutionary history from DNA sequences’. *Emu* 113 (3): 195–207.

Joseph, L., and Wilke T. 2006. ‘Molecular resolution of population history, systematics and historical biogeography of the Australian Ringneck Parrots *Barnardius*: are we there yet?’ *Emu* 106(1): 49.

Kaplan, G. 2007. *Tawny Frogmouth*. Australian Natural History Series. CSIRO Publishing, Collingwood.

Kearns, A.M., Joseph L., and Cook L.G. 2010. ‘The impact of Pleistocene changes of climate and landscape on Australian birds: a test using the Pied Butcherbird (*Cracticus nigrogularis*)’. *Emu* 110(4): 285.

Keast, JA. 1961. ‘Bird speciation on the Australian continent’, *Bulletin of the Museum of Comparative Zoology* (123): 303–495.

Körtner, G., and Geiser F. 1999. ‘Roosting behaviour of the Tawny Frogmouth (*Podargus strigoides*)’. *Journal of Zoology* 248(4): 501–507.

Louchart, A., Vignaud P., Likius A., Brunet M., and White T.D. 2005. ‘A large extinct marabou stork in African Pliocene hominid sites, and a review of the fossil species of *Leptoptilos’*. *Acta Palaeontologica Polonica* 50(3): 549–563.

Lowe T. 2014. *Where Song Began: Australia’s Birds and How They Changed the World*. Viking, Melbourne.

Maclean, G.L. 1976. ‘A field study of the Australian Dotterel’. *Emu - Austral Ornithology* 76(4): 207–15.

Marchant, S., and Higgins P.J. 1990. *Handbook of Australian, New Zealand and Antarctic Birds: Volume 1, Ratites to Ducks*. Oxford University Press, Melbourne.

Marchant, S., and Higgins P.J. 1993. *Handbook of Australian, New Zealand and Antarctic Birds, Volume 2, Raptors to Lapwings*. Oxford University Press, Melbourne.

Mather E.K., Tennyson A.J.D., Scofield R.P., De Pietri V.L., Hand S.J., Archer M., Handley W.D. and Worthy T.H. 2018. ‘Flightless rails (Aves: Rallidae) from the early Miocene St Bathans Fauna, Otago, New Zealand’. *Journal of Systematic Palaeontology* February: 1–27. DOI: 10.1080/14772019.2018.1432710

Mayr, E. 1944. ‘Timor and the colonization of Australia by birds’. *Emu* 44(2): 113–30.

Mayr, G. 2008. ‘The phylogenetic affinities of the parrot taxa *Agapornis*, *Loriculus* and *Melopsittacus* (Aves: Psittaciformes): hypotarsal morphology supports the results of molecular analyses’. *Emu* 108(1): 23–27.

McColl, W.S. 1929. ‘Avifauna of the Hampton Tableland, Hampton Low-Lands and Nullabor Plain.’ *Emu* 29 (2): 91–100.

McGilp, J.N. 1932. ‘Birds of the Nullarbor Plain and far west coast of South Australia.’ *South Australian Ornithologist* 11(5): 146–151.

Meijer, H.J.M., Sutikna, T., Saptomo, E.W., Awe, R.D., Jatmiko, Wasisto, S., James, H.F., Morwood, M.J., and Tocheri, M.W. 2013. 'Late Pleistocene-Holocene non-passerine avifauna of Liang Bua (Flores, Indonesia)'. *Journal of Vertebrate Paleontology* 33(4): 877–94.

Meijer, H.J.M. 2014. 'The avian fossil record in insular southeast Asia and its implications for avian biogeography and palaeoecology'. *PeerJ* 2 (March): e295.

Meijer, H.J.M., and Due, R.A. 2010. 'A new species of giant marabou stork (Aves: Ciconiiformes) from the Pleistocene of Liang Bua, Flores (Indonesia)'. *Zoological Journal of the Linnean Society* 160(4): 707–24.

Meijer, H.J.M., Tocheri, M.W. Due, R.A., Sutikna, T., Saptomo, E.W. and James, H.F. 2015. 'Continental-style avian extinctions on an oceanic island'. *Palaeogeography, Palaeoclimatology, Palaeoecology* 429 (July): 163–70.

Miller A. 1963. 'The fossil flamingos of Australia'. *The Condor* 65(4): 289–299.

Murie, J. 1868. 'On the nocturnal Ground-Parrakeet (*Geopsittacus occidentalis*, Gould)'. *Proceedings of the Scientific Meetings of the Zoological Society of London* Feb. 27th: 158-168.

Murphy, S.A., Joseph, L., Burbidge, A.H. and Austin, J. 2011. 'A cryptic and critically endangered species revealed by mitochondrial DNA analyses: the Western Ground Parrot'. *Conservation Genetics* 12(2): 595–600.

Nadachowska-Brzyska, K., Li, C., Smeds, L., Zhang, G. and Ellegren, H. 2015. 'Temporal dynamics of avian populations during Pleistocene revealed by whole-genome sequences'. *Current Biology* 25(10): 1375–80.

Neaves, L.E., Zenger, K.R., Prince, R.I.T., and Eldridge, M.D.B. 2012. 'Impact of Pleistocene aridity oscillations on the population history of a widespread, vagile Australian mammal, *Macropus fuliginosus*'. *Journal of Biogeography* 39(8): 1545–63.

Oswald, J.A., and Steadman, D.W. 2011. 'Late Pleistocene passerine birds from Sonora, Mexico'. *Palaeogeography, Palaeoclimatology, Palaeoecology* 301(1–4): 56–63.

Oswald, J.A., and Steadman, D.W. 2015. 'The changing diversity and distribution of dry forest passerine birds in northwestern Peru since the last ice age'. *The Auk* 132(4): 836–62.

Pillans, B., and Bourman, R. 2001. 'Mid Pleistocene arid shift in southern Australia, dated by magnetostratigraphy'. *Soil Research* 39(1): 89–98.

Pillans, B. 2003. 'Subdividing the Pleistocene using the Matuyama–Brunhes Boundary (MBB): an Australasian perspective'. *Quaternary Science Reviews* 22(15–17): 1569–77.

Prideaux, G.J., and Warburton, N.M. 2008. 'A new Pleistocene tree-kangaroo (Diprotodontia: Macropodidae) from the Nullarbor Plain of south-central Australia'. *Journal of Vertebrate Paleontology* 28(2): 463–478.

Prideaux, G.J., and Warburton, N.M. 2009. '*Bohra nullarbora* sp. nov., a second tree-kangaroo (Marsupialia: Macropodidae) from the Pleistocene of the Nullarbor Plain, Western Australia'. *Records of the Western Australian Museum* 25: 165–79.

Prideaux, G.J., Long, J.A., Ayliffe, L.K., Hellstrom, J.C., Pillans, B., Boles, W.E., Hutchinson, M.N., Roberts, R.G., Cupper, M.L., Arnold, L.J., Devine, P.D. and Warburton, N.M. 2007. 'An arid-adapted middle Pleistocene vertebrate fauna from south-central Australia'. *Nature* 445(7126): 422–25.

Pyke, G., and P. Ehrlich. 2014. 'Conservation and the Holy Grail: The story of the Night Parrot'. *Pacific Conservation Biology* 20(2): 221–26.

Read, J.L., and Ebdon F.R. 1998. 'Waterbirds of the Arcoona Lakes, an important arid-zone wetland complex in South Australia'. *Australian Bird Watcher* 17: 234–44.

Reside, A.E., VanDerWal J.J., Kutt A.S., and Perkins G.C. 2010. 'Weather, not climate, defines distributions of vagile bird species'. *PLoS ONE* 5(10): e13569.

Rich, P.V., and McEvey A.R. 1977. 'A new owlet nightjar from the Early to Mid–Miocene of eastern New South Wales'. *Memoirs of the National Museum of Victoria* 38: 247–53.

Richards, A. 1971. 'An ecological study of the cavernicolous fauna of the Nullarbor Plain southern Australia'. *Journal of Zoology* 164: 1–60.

Schodde, R., and Mason, I. 1999. *The Directory of Australian Birds: Passerines - A Taxonomic and Zoogeographic Atlas of the Biodiversity of Birds in Australia and Its Territories*. CSIRO Publishing, Canberra.

Schodde, R. 2006. 'Australasia's bird fauna today - origins and evolutionary development'. In *Evolution and Biogeography of Australasian Vertebrates*, edited by J.R. Merrick, M. Archer, G.M. Hickey, and M.S.Y. Lee, 413–58. Auscipub, Sydney.

Schweizer, M., Güntert M., and Hertwig S.T. 2013. 'Out of the Bassian province: historical biogeography of the Australasian platycercine parrots (Aves, Psittaciformes)'. *Zoologica Scripta* 42(1): 13–27.

Shute, E., Prideaux G.J., and Worthy T.H. 2016. 'Three terrestrial Pleistocene coucals (*Centropus*: Cuculidae) from southern Australia: biogeographical and ecological significance'. *Zoological Journal of the Linnean Society* 177(4): 964–1002.

Shute, E., Prideaux G.J., and Worthy T.H. 2017. 'Taxonomic review of the late Cenozoic megapodes (Galliformes: Megapodiidae) of Australia'. *Royal Society Open Science* 4(6): 170233.

Sniderman J.M.K., Jordan G.J. and Cowling R.M. 2013. 'Fossil evidence for a hyperdiverse sclerophyll flora under a non-Mediterranean-type climate'. *Proceedings of the National Academy of Sciences* 110(9): 3423–3428.

Sniderman, J.M.K., Woodhead, J.D., Hellstrom, J., Jordan, G.J., Drysdale, R.N., Tyler, J.J. and Porch, N. 2016. 'Pliocene reversal of Late Neogene aridification'. *Proceedings of the National Academy of Sciences*, 201520188.

Steadman, D.W., and Mead, J.I. 2010. 'A Late Pleistocene bird community at the northern edge of the tropics in Sonora, Mexico'. *The American Midland Naturalist* 163(2): 423–41.

Steadman, D.W., Oswald, J.A. and Rincón, A.D. 2015. 'The diversity and biogeography of Late Pleistocene birds from the lowland neotropics'. *Quaternary Research* 83(03): 555–64.

Stewart, J.R., and Jacobi, R.M. 2015. 'The long term response of birds to climate change: new results from a cold stage avifauna in Northern England'. *PLOS ONE* 10(5): e0122617.

Sweet, A.D., Chesser R.T., and Johnson K.P. 2017. 'Comparative cophylogenetics of Australian phabine pigeons and doves (Aves: Columbidae) and their feather lice (Insecta: Phthiraptera)'. *International Journal for Parasitology* 47(6): 347–56.

Toon, A., Mather, P.B., Baker, A.M., Durrant, K.L., and Hughes, J.M. 2007. 'Pleistocene refugia in an arid landscape: analysis of a widely distributed Australian passerine'. *Molecular Ecology* 16(12): 2525–2541.

Toon, A., Austin, J.J., Dolman, G., Pedler, L. and Joseph, L. 2012. 'Evolution of arid zone birds in Australia: leapfrog distribution patterns and mesic-arid connections in quail-thrush (*Cinclosoma*, Cinclosomatidae)'. *Molecular Phylogenetics and Evolution* 62(1): 286–95.

Toon, A., Drew A., Mason I.J., Hughes J.M., and Joseph L. 2017. 'Relationships of the New Guinean subspecies, *Gymnorhina tibicen papuana*, of the Australian Magpie: an assessment from DNA sequence data'. *Emu-Austral Ornithology*, 1–11.

Tyler, M.J., and Prideaux, G.J. 2016. 'Early to middle Pleistocene occurences of *Litoria*, *Neobatrachus* and *Pseudophryne* (Anura) from the Nullarbor Plain, Australia: first frogs from the "frog-free zone"'. *Memoirs of Museum Victoria* 74: 403–8.

van Tets, G., and Smith M. 1974. 'Small fossil vertebrates from Victoria Fossil Cave, Naracoorte, South Australia, III. Birds (Aves)'. *Transactions of the Royal Society of South Australia* 98(4): 225–27.

Walker, M., and Lowe J. 2007. 'Quaternary Science 2007: a 50-year retrospective'. *Journal of the Geological Society* 164(6): 1073.

Weir, J.T., and Schluter, D. 2004. 'Ice sheets promote speciation in boreal birds'. *Proceedings of the Royal Society B: Biological Sciences* 271(1551): 1881–87.

White, S. 1919. 'Four ornithological trips to the Nullarbor Plains'. *Emu* 18: 189–98.

White N., Phillips M., Gilbert M.T., Alfaro-Nunez A., Willerslev E., Mawson P., Spencer P. and Bunce M. 2011. 'The evolutionary history of cockatoos (Aves: Psittaciformes: Cacatuidae)'. *Molecular Phylogenetics and Evolution* 59: 615–622.

Zelenkov, N.V., Panteleyev A.V., and De Pietri V.L. 2017. 'Late Miocene rails (Aves: Rallidae) from southwestern Russia'. *Palaeobiodiversity and Palaeoenvironments*, 97(4): 791-805.

Zink, R.M., Klicka J., and Barber B.R. 2004. 'The tempo of avian diversification during the Quaternary'. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 359(1442): 215–220.

Chapter 5: General Discussion & Conclusions

5.1 Introduction

The overarching aim of this project was to use the fossil avifaunal assemblage from the Thylacoleo Caves to investigate the diversity and distribution of non-passerine birds on the Nullarbor Plain during the Early and Middle Pleistocene by:

1. Documenting the non-passerine avifauna using a systematic palaeontological approach;
2. Analysing the composition of the avifauna to detect whether its composition changed through time;
3. Using the fossil avifauna to make palaeoecological inferences and determine whether these support the existing interpretation;
4. Investigating whether the data indicate range changes for extant bird species since the middle Pleistocene, with particular reference to the role of the Nullarbor Plain as a biogeographical barrier;
5. Identifying and describing new extinct bird species where applicable; and
6. Discussing how the findings advance knowledge about the diversity, distribution and evolutionary history of the Australian avifauna.

Here I discuss the key findings of the earlier chapters through which these aims have been addressed, discuss how this study has advance our state of knowledge about the Quaternary avifaunal history of Australia, and suggest further avenues for research building on the original work presented in the thesis and the questions it has raised about the Australian avifauna.

5.2 Has Australia’s Pleistocene bird diversity been underestimated?

At the outset of this project, the objective of describing any new species of birds that might be found within the Thylacoleo Caves fossil fauna was included ‘just in case’, on the expectation that perhaps one or two new species might be discovered from the locality, based on experience from other Australian Quaternary cave deposits. For example, Baird (1985) identified three extinct species from the Pleistocene deposit of Green Waterhole Cave, and two from Pyramids Cave (Baird 1993).

This aspect of the project evolved to become a much more important component than anticipated because of the sheer diversity of the extinct taxa that were uncovered. Up to 14 extinct non-passerine species are now either known or suspected to be represented within the Thylacoleo Caves avifauna. Four of these have so far been formally described: the coucals *Centropus bairdi* and *C. maximus* (Chapter 2);

and the megapodes *Progura campestris* and *Latagallina olsoni* (Chapter 3). The description of the two megapodes also necessitated a thorough re-appraisal of fossil megapodes from other Australian localities. The results of this review were: confirmation that the two previously-described species of '*Progura*' were indeed separate species, and furthermore belonged in separate genera; the first appraisal of remains from Curramulka Quarry in South Australia, which revealed another new species in its own genus; and a phylogenetic analysis showing that four of the five extinct Cenozoic megapodes from Australia formed an extinct clade of burrow-nesting 'brush-turkeys'.

In addition to the descriptions of two new genera and five new species in Chapters 2 and 3, ten more taxa from the Thylacoleo Caves are documented in Chapter 4 that are likely to represent new species. These were: two pigeon taxa, one large and one small; up to five species of rail of varying sizes; a stork, which may be referrable to *Ciconia nana* (see Boles, 2005); a large eagle, which will require appraisal along with remains of an undescribed large extinct accipitrid from Green Waterhole Cave (Baird 1985); and a pezoporine parrot.

These all require a thorough appraisal along with their fossil and extant relatives, but the number of fossils that could not readily be referred to extant species was unexpected. Among the known and putative extinct taxa, ground-dwelling taxa, particularly large ones, are over-represented. This could be partly the result of taphonomic bias, because large ground-dwelling birds are particularly prone to pitfall trapping (Baird 1991), but could also be because the ecological characteristics of large, ground-dwelling birds rendered them vulnerable to palaeoecological change. Boles (2006) speculated that the large size of extinct Australian birds from the Pleistocene had perhaps been over-emphasised in the past because of a bias towards the discovery and study of large species. While I admit to finding 'giant' megapode bones much more enjoyable to study than tiny rail bones that must be viewed under a microscope, the large size of some of the extinct species compared to their extant relatives cannot entirely be explained away.

There may be cause to consider why a growing cast of large, ground-dwelling birds may have been preferentially extirpated from the Australian avifauna. Two of the extinct species of *Centropus* considered in Chapter 2 are the largest, heaviest species of cuckoo known from anywhere in the world. All five of the megapodes described or re-described in Chapter 3 are larger than their living counterparts. The largest, *Progura gallinacea*, is estimated to have weighed as much as the largest living galliforms on other continents, and may have reached the limits of body mass for a galliform bird to retain flight (see Chapter 3). Elsewhere in Australia, ground-dwelling taxa that have been described include two species of logrunner, *Orthonyx* spp., one of which is larger than its living relative (Baird 1985), and a species of pilotbird *Pycnoptilus fordi*, in the currently monospecific genus (Baird 1993). The closest relatives of all these taxa forage in thick leaf litter in closed forest formations (Baird 1985; 1993).

A loss of dense understorey may be one plausible explanation for the extinction of relatively large, ground-dwelling species such as those noted from the Thylacoleo Caves and from other Quaternary deposits, as discussed in Chapters 2 and 4. The higher diversity of strongly ground-dwelling taxa identified in the relatively moist, Early Pleistocene unit of Leaena's Breath Cave, when trees were still present on the Nullarbor Plain (see Chapter 4), and lower diversity of ground-dwelling taxa in the drier, open-habitat phase in the Middle Pleistocene, lend support to this possibility. Aridity may have been a direct or indirect factor. In the case of coucals, loss of dense understorey may have played a role in their demise. The apparent extinction of tree-frogs from the Nullarbor Plain after the Early Pleistocene, possibly due to more arid conditions and associated loss of frog habitat, may also have eliminated a key food resource for these birds (see Chapter 2).

Plant biomass, controlled by moisture availability, has been identified as the ecological correlate that best explains modern Australian bird diversity (Hawkins *et al.* 2005). The results of the avifaunal analysis in Chapter 4 indicate, *prima facie*, that the loss of avian diversity from the Nullarbor Plain – whether due to range changes, extinctions, or both – may be a result of increased aridity on the Nullarbor Plain during the 'mid-Pleistocene transition'. Various localities in southern Australia are known to have become more arid during this time, between the end of the Early Pleistocene and the late Middle Pleistocene (Pillans and Bourman 2001). A weakening of the northern monsoon is suggested as another possible reason for increased aridity on the Nullarbor Plain after ~300 kyr (see Chapter 4, and Bowler et al. 2001). A weaker monsoon may also have had a severe impact on avian populations in what is now the Western Deserts region, to the north of the Nullarbor, whose pre-Holocene avifauna is completely unknown.

Debate has long centred on the role – or lack thereof – that humans may have played in the extinction of most of Australia's megafaunal species in the Late Pleistocene (e.g. Wroe and Field 2006; Grün *et al.* 2010; Johnson *et al.* 2016). Although none of the extinct birds identified in this research project is strictly megafaunal, many are notably large, and almost all are ground-dwellers – features that might conceivably render them disproportionately vulnerable to human hunting. It is possible that at least one of the 'giant' species of megapode described in Chapter 3 survived late enough for its eggs to be eaten by people, based on charred fossil eggshell spread through the arid interior of Australia (see Chapter 3). However, the large coucals, assuming they tasted and smelled like their living relatives, were unlikely targets for early hunters (see Chapter 2), and effects of habitat loss seem more likely to have contributed to their demise, at least.

The Thylacoleo Caves fossil deposits are too old to coincide with human arrival, and so are not well placed to address the issue of possible human impacts on the avifauna directly. However, the apparent extirpation of multiple non-passerine taxa from the Nullarbor Plain between the Early and Middle Pleistocene, possibly up to 700 kyr before the arrival of humans, indicates likely sensitivity of multiple bird taxa to changes in climate and vegetation, even in the absence of hunting. Prideaux et al. (2007)

speculated that the Nullarbor Plain could have been converted to its modern, treeless state following burning of the landscape by people after 40 kyr ago. However, the avifaunal analysis in Chapter 4 indicates that trees were lost from the Plain by, or during, the Middle Pleistocene, well before the peopling of the region. Woodlands could potentially have returned to the Plain later in the Pleistocene, after the entrances to the Thylacoleo Caves became sealed, so human impacts on the region's flora and fauna cannot be ruled out, but there is currently no evidence to support this.

Regardless of cause, there is now growing evidence that diversity within the Australian avifauna may have been higher during the Pleistocene than has previously been realised. The Holocene mammalian fauna of Australia is known to be depauperate due to the extinction of the Pleistocene 'megafauna' (Prideaux 2007). We must now consider the possibility that the continent's avifauna may not have come through the Pleistocene unscathed either. Eventually we may be in a better position to assess the net effects of the Pleistocene on the avifauna as a whole, and judge whether species losses were balanced out by the evolution of new taxa. These are questions that are yet to be resolved for other continents as well (e.g. Zink *et al.* 2004; Nadachowska-Brzyska *et al.* 2015). Ultimately, a clearer understanding of the Pleistocene fossil record may enable us to better identify which taxa may be at greatest risk of extinction under future predicted climate and habitat change, and prioritise conservation planning accordingly.

5.3 Avian biogeography of southern Australia

The Plio-Pleistocene avian biogeography of southern Australia has piqued the interest of many researchers over a course of decades. Originally, inferences about the history of the southern Australian avifauna were based on observations of modern distributions of species and subspecies. Increasingly, genetic techniques are being deployed to detect complex patterns of vicariance related to the many glacial-interglacial cycles of the Pleistocene (Chapter 1). Until now, the fossil record has contributed little to our understanding of the role that the Nullarbor Plain may have played as a barrier – and conversely a habitat corridor – at different intervals of the Pleistocene.

The present study of Early and Middle Pleistocene bird fossils from the Nullarbor Plain fills a geographical and temporal gap in the fossil record for Australian landbirds, and provides new insight into the nature and extent of palaeoecological change in the Nullarbor region over the course of the Pleistocene. Range changes compared to the late Holocene are evident for some extant taxa, indicating a certain amount of reorganisation of the Australian avifauna has occurred since the Early and Middle Pleistocene, but rather less than might have been expected given the emphasis that has generally been placed on the importance of the Nullarbor Plain as an arid-habitat barrier for birds from the Pleistocene onwards.

Few taxa that today have allopatric populations on either side of the Nullarbor Plain were found in the fossil assemblage, and although some other species were found to be outside of their current ranges (see

Chapter 4), these were mostly present in low abundances, and not drastically out of range. The apparent absence of large populations of now-allopatric woodland taxa provides little support for the Nullarbor Plain having been a major conduit for these during the Early Pleistocene woodland phase captured in the Leaena's Breath Cave fossil assemblage. Increasingly, the importance of the Nullarbor Plain as a biogeographical barrier in southern Australia is being questioned, with genetic data showing that different southern Australian taxa have had very different Pleistocene demographic histories, possibly as a result of quirks of habitat requirements (e.g. Byrne et al. 2008; Kearns et al. 2010; Dolman and Joseph 2012). It will be crucial to investigate whether the passerine bird assemblage from the Thylacoleo Caves also records a similar lack of now-allopatric species.

A few taxa were, however, notably out of range. The occurrence of extinct rails, a stork, and at least one species of coucal in the Early Pleistocene, as well as a diversity of charadriiform birds which have yet to be fully identified, may indicate that increased aridity in southern Australia during the Pleistocene may have had an underappreciated impact on the distribution, and to some extent the diversity, of water-dependent taxa. The Pleistocene habitat(s) of the Nullarbor Plain have not generally been considered for their role in supporting wetland taxa, but this study highlights that, at least during certain intervals of the Pleistocene, it may have supported much more than a woodland species assemblage.

Perturbations to the southern Australian avifauna during the Pleistocene have historically been considered mainly from the point of view of extant woodland species. The results of this fossil study, while in accord with the general consensus that increasing aridity during the Pleistocene led to the disappearance of trees from the Nullarbor Plain, reveals that the impacts of this may to a degree have been misunderstood. The past avian diversity of the Nullarbor Plain has clearly been underestimated, and species extinctions were an important part of ecosystem change in the region.

5.4 Suggestions for future research

5.4.1 Systematics and taxonomy

As already noted, around ten species from the Thylacoleo Caves avifauna will require review, and where appropriate, description as new taxa. The abundant *Tyto* specimens from the Thylacoleo Caves should also be reviewed along with such Holocene material as exists of the Nullarbor 'masked owl', as observations made in Chapter 4 indicate that the Pleistocene and Holocene remains may be of one species, and that it may be a taxon distinct from the nominate subspecies of the Masked Owl *Tyto novaehollandiae*.

Besides the taxa already noted from the Thylacoleo Caves, some fossil material from other Australian localities should also be reviewed. These include Pliocene megapode fossils from Bluff Downs in

Queensland, which Boles and Mackness (1994) flagged as a possible new taxon, and some specimens from Queensland and New South Wales that had previously been referred to the Megapodiidae but have now been identified as likely including phoenicopteriforms and accipitrids (see Chapter 3).

5.4.2 Systematic palaeontology

Although the Thylacoleo Caves represents the most diverse Quaternary fossil bird assemblage yet discovered in Australia, diversity curves for Pit B of Leaena's Breath Cave indicate that the currently known diversity of the non-passerine assemblage is likely to underestimate the true diversity of birds living on the Nullarbor Plain during the Pleistocene. Many taxa are represented by just a single bone. The most obvious way of increasing the sample size for this locality would be to identify the fossil bird bones that have been recovered from Pit A of Leaena's Breath Cave, and then to re-analyse the assemblage having pooled the specimens from both pits. This may result in a more accurate representation of the diversity of the Early and Middle Pleistocene avifauna of the Nullarbor Plain. Increasing the sample size may also enable analysis of the avifaunal assemblage based on MNI rather than NISP, at least for some taxa. This would allow for a more robust palaeoecological interpretation.

Additional work is also required to refine the identifications of some of the taxa documented in the Systematic Palaeontology section of Chapter 4. This is particularly the case for the Charadriiformes and the Psittaciformes, both of which are large and diverse orders containing numerous families or sub-families. Given time constraints within this project, the large number of specimens that required identification, the unavailability of complete series of comparative specimens, and in some cases taxonomic uncertainty for extant species, some taxa could not be identified to genus or species. It is highly likely that with further work, and in particular if more complete series of modern comparative specimens can be examined, that the known diversity of the Thylacoleo Caves assemblage will increase.

One of the major limitations of this project is that only non-passerine birds are included within its scope. Although this is a common approach to the study of fossil avifaunas (e.g. Campbell 1979; Olson and James 1991; Meijer 2013), it is not optimal for palaeoecological interpretation. The ecological reconstruction of the Nullarbor Plain would be greatly enhanced by analysing the non-passerine and the passerine taxa together. Preliminary work is already underway on the passerine taxa, and data on both groups should ultimately be pooled and analysed together.

Further to this, data on the avian taxa should also be analysed along with data on the mammalian and other vertebrate fauna from the Thylacoleo Caves. This would produce a much richer understanding of the palaeoecology of the Nullarbor Plain during the Early and Middle Pleistocene, and would allow for comparisons of regional species turnover in different vertebrate classes. A comparison between the avifauna and the small mammal fauna could be particularly fruitful for the palaeoecological interpretation of the locality, as sedentary small mammals may produce a more local palaeoecological signal, while the birds, because of the inherent mobility of many taxa, may reflect briefer environmental events such as floods.

5.4.3 Enhanced dating

The results presented in Chapters 2–4 were interpreted within the temporal framework for the Thylacoleo Caves reported by Prideaux *et al.* (2007). During the fieldwork season of 2014, further samples were collected from Leaena's Breath for single-grain optically stimulated luminescence (OSL) dating. The results of this are pending as at May 2018, but when available, the new OSL dates may shed new light on the chronology of the accumulation of sediments and fossils in Leaena's Breath Cave. This should enhance the interpretation of the fossil deposit, since the temporal windows during which the fossils accumulated are currently understood only in broad brackets. With a more refined chronology, it may be possible to trace ecological signals in the fauna across individual glacial-interglacial cycles. Data on the avifauna presented in Chapter 4 should be re-analysed and re-interpreted when the new dates become available.

5.4.5 Studies of other Australian fossil bird assemblages

It could be beneficial to re-appraise the Late Pleistocene and Holocene avian fossil collections from other cave localities in the Nullarbor region that were studied by Baird (1986), most of which remain unpublished. Also, further to his study of Weeke's Cave (Baird 1990), an additional, and as yet unstudied, collection of fossil bird bones collected from this cave in the 1960s exists in the Field Museum in Chicago.

In-depth studies of fossil collections from other key Pleistocene localities should also be a research priority, in order to increase the geographical scope of our knowledge of Australian Pleistocene avifaunas. Much bird material has been excavated from various caves in the Naracoorte region and has yet to be properly studied or published. An examination of fossil birds from the Wellington Caves, which are virtually unstudied so far, would provide a valuable eastern Australian perspective on Pleistocene and Holocene avian diversity and distribution. A new excavation of Cathedral Cave, Wellington, has recently been completed by students and staff at Flinders University, and contains bird material referable to species of various sizes.

5.5 Conclusions

This study has provided an unprecedented window into the diversity and distribution of the southern Australian avifauna during the Pleistocene, an epoch that has long been considered crucial to the development of the modern bird fauna, but for which the Australian fossil record is sparse. Through the work presented in this thesis, I have demonstrated that extinction rates among Australian non-passerine birds appear to have been considerably higher during the Pleistocene than previously suspected. The true extent and significance of these extinctions may be elucidated in future with the discovery of new fossil deposits in other localities, with the re-excavation of known sites, and by exploiting the full potential of avian fossil material already in museum collections. In the meantime, much work remains to be done on the Thylacoleo Caves avifauna, including the description of further new taxa, and a combined avifaunal analysis of non-passerine and passerine taxa to enhance the palaeoecological interpretation of the Nullarbor Plain during the Pleistocene. Thankfully we have come a long way since the avian components of Australia's Quaternary fossil faunas were considered the uninteresting bycatch of marsupial megafauna excavations that were ignored, or worse still, discarded.

5.6 References

Baird, R.F. 1985. ‘Avian fossils from Quaternary deposits in “Green Waterhole Cave”, South-Eastern South Australia’. *Records of the Australian Museum* 37(6): 353–70.

Baird, R.F. 1986. Tasmanian Native-hen *Gallinula mortierii*: the first Late Pleistocene record from Queensland. *Emu* 86: 121–122.

Baird, R.F. 1990. ‘The fossil avian assemblage from Weekes Cave (N-15), Nullarbor Plain, South Australia: corrections, additions and reinterpretation’. *South Australian Ornithologist* 31: 29–35.

Baird, R.F. 1991. ‘The taphonomy of Late Quaternary cave localities yielding vertebrate remains in Australia’. In *Vertebrate Palaeontology of Australasia*, edited by P. Vickers-Rich, J. Monaghan, R.F. Baird, and T. Rich, 267–301. Pioneer Design Studio, Melbourne.

Baird, R.F. 1993. ‘Pleistocene avian fossils from Pyramids Cave (M-89), Eastern Victoria, Australia’. *Alcheringa: An Australasian Journal of Palaeontology* 17(4): 383–404.

Boles, W.E. 2005. ‘A review of the Australian fossil storks of the genus *Ciconia* (Aves: Ciconiidae), with the description of a new species’. *Records of the Australian Museum* 57(2): 165–178.

Boles, W.E. 2006. ‘The avian fossil record of Australia: an overview’. In *Evolution and Biogeography of Australasian Vertebrates*, 387–411. Australian Scientific Publishing, Sydney.

Boles, W.E., Mackness, B. 1994. Birds from the Bluff Downs Local Fauna, Allingham Formation, Queensland. *Records of the South Australian Museum* 27, 139–149.

Bowler, J.M., Wyrwoll K-H. and Lu Y. 2001. ‘Variations of the northwest Australian summer monsoon over the last 300,000 years: the paleohydrological record of the Gregory (Mulan) Lakes System’. *Quaternary International* 83–85: 63–80.

Campbell, K.E. 1979. *The non-passerine Pleistocene avifauna of the Talara Tar Seeps, Northwestern Peru*. Toronto. *Life Sciences Contribution 118*, Royal Ontario Museum.

Grün, R., Eggins, S., Aubert, M., Spooner, N., Pike, A.W.G., and Müller, W. 2010. ‘ESR and U-Series analyses of faunal material from Cuddie Springs, NSW, Australia: implications for the timing of the extinction of the Australian megafauna’. *Quaternary Science Reviews* 29(5–6): 596–610.

Hawkins, B., Diniz-Filho, J., and Soeller, S. 2005. ‘Water links the historical and contemporary components of the Australian bird diversity gradient’. *Journal of Biogeography* 32: 1035–42.

Johnson, C.N., Alroy, J., Beeton, N.J., Bird, M.I., Brook, B.W., Cooper, A., Gillespie, R., Herrando-Perez, S., Jacobs, Z., Miller, G.H., Prideaux, G.J., Roberts, R.G., Rodriguez-Rey, M., Saltre, F., Turney, C.S.M. and Bradshaw, C.J.A. 2016. 'What caused extinction of the Pleistocene megafauna of Sahul?' *Proceedings of the Royal Society B: Biological Sciences* 283(1824): 20152399.

Meijer, H.J.M., Sutikna, T., Saptomo, E.W., Awe, R.D., Jatmiko, Wasisto, S., James, H.F., Morwood, M.J., and Tocheri, M.W. 2013. 'Late Pleistocene-Holocene non-passerine avifauna of Liang Bua (Flores, Indonesia)'. *Journal of Vertebrate Paleontology* 33(4): 877–94.

Olson, S.L., and James, H.F. 1991. 'Descriptions of Thirty-Two New Species of Birds from the Hawaiian Islands'. *Ornithological Monographs, No.* 45. American Ornithologists' Union, Washington, D.C.

Pillans, B., and Bourman, R. 2001. 'Mid Pleistocene arid shift in southern Australia, dated by magnetostratigraphy'. *Soil Research* 39(1): 89–98.

Prideaux, G.J. 2007. 'Mid-Pleistocene Vertebrate Records'. In *Encyclopedia of Quaternary Science*, edited by S.A. Elias, 1st ed., 1518–37. Elsevier, online edition.

Wroe, S. and Field, J. 2006. 'A review of the evidence for a human role in the extinction of Australian megafauna and an alternative interpretation'. *Quaternary Science Reviews* 25: 2692–2703.

6. Bibliography

1. Aplin, K.P., Pasveer, J.M., Boles, W.E. 1999. Late Quaternary vertebrates from the Bird's Head Peninsula, Irian Jaya, Indonesia, including descriptions of two previously unknown marsupial species. *Records of the Western Australian Museum* Suppl. 57, 351–387.
2. Ayliffe, L.K., and Veer H.H. 1988. 'Uranium-series dating of speleothems and bones from Victoria Cave, Naracoorte, South Australia'. *Chemical Geology: Isotope Geoscience Section* 72(3): 211–234.
3. Ayliffe, L.K., Marianelli P.C., Moriarty K.C., Wells R.T., McCulloch M.T., Mortimer G.E., and Hellstrom J.C. 1998. '500 ka precipitation record from southeastern Australia: evidence for interglacial relative aridity'. *Geology* 26 (2): 147–150.
4. Baird R.F. and Vickers-Rich P. 1998. '*Palaelodus* (Aves: Palaelodidae) from the Middle to Late Cainozoic of Australia.' *Alcheringa: An Australasian Journal of Palaeontology* 22(2): 135–151.
5. Baird, R.F. 1984. 'The Pleistocene distribution of the Tasmanian Native-Hen *Gallinula mortierii mortierii*'. *Emu* 84(2): 119–123.
6. Baird, R.F. 1985. 'Avian fossils from Quaternary deposits in "Green Waterhole Cave", South-Eastern South Australia'. *Records of the Australian Museum* 37(6): 353–70.
7. Baird, R.F. 1986. 'The avian portions of the Quaternary cave deposits of southern Australia and their biogeographical and palaeoenvironmental interpretations'. PhD thesis, Monash University, Melbourne.
8. Baird, R.F. 1986. Tasmanian Native-hen *Gallinula mortierii*: the first Late Pleistocene record from Queensland. *Emu* 86: 121–122.
9. Baird, R.F. 1989. 'Fossil bird assemblages from Australian Caves: precise indicators of late Quaternary Environments?' *Palaeogeography, Palaeoclimatology, Palaeoecology* 69: 241–44.
10. Baird, R.F. 1990. 'The fossil avian assemblage from Weekes Cave (N-15), Nullarbor Plain, South Australia: corrections, additions and reinterpretation'. *South Australian Ornithologist* 31: 29–35.
11. Baird, R.F. 1991. 'The taphonomy of Late Quaternary cave localities yielding vertebrate remains in Australia'. In *Vertebrate Palaeontology of Australasia*, edited by P. Vickers-Rich, J. Monaghan, R.F. Baird, and T. Rich, 267–301. Pioneer Design Studio, Melbourne.
12. Baird, R.F. 1993. 'Pleistocene avian fossils from Pyramids Cave (M-89), Eastern Victoria, Australia'. *Alcheringa: An Australasian Journal of Palaeontology* 17(4): 383–404.
13. Baird, R.F. and Vickers-Rich, P. 1998. '*Palaelodus* (Aves: Palaelodidae) from the Middle to Late Cainozoic of Australia'. *Alcheringa: An Australasian Journal of Palaeontology* 22(2): 135–51.

14. Baird, R.F., Vickers-Rich P., and van Tets, G. 1991. 'Appendix II: localities yielding avian assemblages of Quaternary age in Australia'. In *Vertebrate Palaeontology of Australasia*, 850–67. Pioneer Design Studio, Melbourne.

15. Baker-Gabb D., Antos M., and Brown G. 2016. 'Recent decline of the critically endangered Plains-Wanderer (*Pedionomus torquatus*), and the application of a simple method for assessing its cause: major changes in grassland structure'. *Ecological Management & Restoration* 17(3): 235–42.

16. Balouet, J., Olson S. 1989. Fossil birds from late Quaternary deposits in New Caledonia. *Smithsonian Contributions to Zoology* 469, 1–38.

17. Barnosky, A., Koch, P.L., Feranec R.S., Wing, S. and Shabel, A. 2004. 'Assessing the causes of Late Pleistocene extinctions on the continents'. *Science* 306: 70–75.

18. Barnosky, A.D, and Lindsey, E.L. 2010. 'Timing of Quaternary megafaunal extinction in South America in relation to human arrival and climate change'. *Quaternary International* 217 (1–2): 10–29.

19. Barrows, T.T., Stone J.O., Fifield L.K., and Cresswell R.G. 2001. 'Late Pleistocene glaciation of the Kosciuszko Massif, Snowy Mountains, Australia'. *Quaternary Research* 55(2): 179–89.

20. Bartholomai, A. 1977. The fossil vertebrate fauna from Pleistocene deposits at Cement Mills, Gore, southeastern Queensland. *Memoirs of the Queensland Museum* 18, 41–51.

21. Baumel, J., King A., Breazile J., Evans H. and Vanden Berge J. 1993. *Handbook of Avian Anatomy: Nomina Anatomica Avium*. Second Edition. Publications of the Nuttall Ornithological Club 23: Nuttall Ornithology Club, Cambridge, Massachusetts.

22. Beard, J.S., Beeston G.R., Harvey J.M., Hopkins A.J.M., and Shepherd D.P. 2013. 'The vegetation of Western Australia at the 1:3,000,000 Scale. Explanatory Memoir. Second Edition'. *Conservation Science Western Australia* 9(1): 1–152.

23. BirdLife Australia. 2017. 'The BirdLife Australia working list of Australian Birds, Version 2.1'. BirdLife. Available: http://www.birdlife.org.au/documents/BWL-BirdLife_Australia_Working_List_v2.1.xlsx

24. Birks, S., Edwards, S. 2002. A phylogeny of the megapodes (Aves: Megapodiidae) based on nuclear and mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 23, 408–421.

25. Blyth, A.J., Watson J.S., Woodhead J., and Hellstrom J. 2010. 'Organic compounds preserved in a 2.9 million year old stalagmite from the Nullarbor Plain, Australia'. *Chemical Geology* 279(3): 101–105.

26. Boles, W.E. 1993. A logrunner *Orthonyx* (Passeriformes, Orthonychidae) from the Miocene of Riversleigh, north-western Queensland. *Emu* 93: 44–49.

27. Boles, W.E. 1995. 'A preliminary analysis of the Passeriformes from Riversleigh, northwestern Queensland, Australia, with the description of a new species of lyrebird'. *Courier Forschungsinstitut Senckenberg* 181: 163–70.

28. Boles, W.E. 2001. ‘A swiftlet (Apodidae: Collocaliini) from the Miocene of Riversleigh, Northwestern Queensland’. *Memoirs of the Association of Australasian Palaeontologists* 25: 45–52.

29. Boles, W.E. 2005. ‘A review of the Australian fossil storks of the genus *Ciconia* (Aves: Ciconiidae), with the description of a new species’. *Records of the Australian Museum* 57(2): 165–178.

30. Boles, W.E. 2006. ‘The avian fossil record of Australia: an overview’. In *Evolution and Biogeography of Australasian Vertebrates*, 387–411. Australian Scientific Publishing, Sydney.

31. Boles, W.E. 2006. The avian fossil record of Australia: an overview. In: Merrick, J.R., Archer, M., Hickey, G.M., Lee, M.S.Y., eds. *Evolution and biogeography of Australasian vertebrates*. New South Wales, Australia: Auscipub, 387– 411.

32. Boles, W.E. 2008. Systematics of the fossil Australian giant megapodes *Progura* (Aves: Megapodiidae). *Oryctos* 7: 191– 211.

33. Boles, W.E. 2010. ‘A revision of C.W. De Vis’ fossil cormorants (Aves: Phalacrocoracidae). In *Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution*, Ed. W.E. Boles and T.H. Worthy’. *Records of the Australian Museum* 62(1): 145–55.

34. Boles, W.E. Ivison, T. 1999. A new genus of dwarf megapode (Galliformes: Megapodiidae) from the Late Oligocene of Central Australia. *Smithsonian Contributions to Paleobiology* 89, 199–206.

35. Boles, W.E., Mackness, B. 1994. Birds from the Bluff Downs Local Fauna, Allingham Formation, Queensland. *Records of the South Australian Museum* 27, 139–149.

36. Bowler, J.M., Wyrwoll K-H. and Lu Y. 2001. ‘Variations of the northwest Australian summer monsoon over the last 300,000 years: the paleohydrological record of the Gregory (Mulan) Lakes System’. *Quaternary International* 83–85: 63–80.

37. Brigham, R., Debus S.J.S., and Geiser F. 1998. ‘Cavity selection for roosting, and roosting ecology of forest-dwelling Australian Owlet-Nightjars (*Aegotheles cristatus*)’. *Austral Ecology* 23(5): 424–429.

38. Brooker, M.G., Ridpath M.G., Estbergs J.A., Bywater J., Hart D.S., and Jones M.S. 1979. ‘Bird observations on the north-western Nullarbor Plain and neighbouring regions, 1967–1978’. *Emu* 79(4): 176–190.

39. Burbidge, A., Casperson K., and Fuller P. 1987. ‘Birds’. In *A Biological Survey of the Nullarbor Region, South and Western Australia in 1984*, 153–78. Adelaide: South Australian Department of Environment and Planning, Western Australia Department of Conservation and Land Management, Australian National Parks and Wildlife Service.

40. Burgoyne, I. 2000. *The Mirning - We Are the Whales*. Magabala Books Aboriginal Corporation, Broome, Western Australia.

41. Burnett, S., Webb J.A., and White S. 2013. 'Shallow caves and blowholes on the Nullarbor Plain, Australia — flank margin caves on a low gradient limestone platform'. *Geomorphology* 201: 246–53.

42. Byrne, M. 2008. 'Evidence for multiple refugia at different time scales during Pleistocene climatic oscillations in southern Australia inferred from phylogeography'. *Quaternary Science Reviews* 27 (27–28): 2576–85.

43. Byrne, M., Steane D.A., Joseph L., Yeates D.K., Jordan G.J., Crayn D., Aplin K., Cantrill, D., Cook L.G, Crisp, M., Keogh, J.S., Melville, J., Moritz, C., Porch, N., Sniderman, J.M.K., Sunnucks, P., and Weston, P. *et al.* 2011. 'Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota'. *Journal of Biogeography* 38: 1635–56.

44. Byrne, M., Yeates D.K., Joseph L., Kearney M., Bowler J., Williams M.A.J., Cooper S., Donnellan, S.C., Keogh, J.S., Leys, R., Melville, J., Murphy, D.J., Porth, N. and Wyrwoll, K-H. 2008. 'Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota'. *Molecular Ecology* 17(20): 4398–4417.

45. Campbell, K., Marcus, L. 1992. The relationship of hindlimb bone dimensions to body weight in birds. In *Papers in Avian Palaeontology Honoring Pierce Brodkorb*, Natural History Museum of Los Angeles County, *Science Series* 36, 395–412.

46. Campbell, K.E. 1979. *The non-passerine Pleistocene avifauna of the Talara Tar Seeps, Northwestern Peru*. Toronto. *Life Sciences Contribution 118*, Royal Ontario Museum.

47. Campbell, K.E., Marcus, L. 1992. The relationship of hindlimb bone dimensions to body weight in birds. In: K. Campbell, ed. *Papers in avian palaeontology honouring Pierce Brodkorb*. Natural History Museum of Los Angeles County, Science Series, 395–412.

48. Campos, P.F., Sher A., Mead J.I., Tikhonov A., Buckley M., Collins M., Willerslev E., and Gilbert M.T.P. 2010. 'Clarification of the taxonomic relationship of the extant and extinct ovibovids, *Ovibos*, *Praeovibos*, *Euceratherium* and *Bootherium'*. *Quaternary Science Reviews* 29 (17–18): 2123–2130.

49. Christidis, L., and W. Boles. 2008. *Systematics and Taxonomy of Australian Birds*. CSIRO Publishing, Victoria.

50. Claramunt, S., Cracraft, J. 2015. A new time tree reveals Earth history's imprint on the evolution of modern birds. *Science Advances* 1, e1501005.

51. Cohen, K., and Gibbard P. 2011. '2011 global chronostratigraphical correlation table for the last 2.7 million years.' Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy), Cambridge, England.

52. Cohen, T.J., Nanson G.C., Jansen J.D., Jones B.G., Jacobs Z., Treble P., Price D.M., May, J.H., Smith, A.M., Ayliffe, L.K. 2011. 'Continental aridification and the vanishing of Australia's megalakes'. *Geology* 39(2): 167–170.

53. Commonwealth of Australia. 2012. 'Interim Biogeographic Regionalisation for Australia, Version 7'. Commonwealth of Australia.

http://www.environment.gov.au/parks/nrs/science/bioregion-framework/ibra/maps.html.

54. Cowles, R.B. 1959. *Zulu Journal: Field Notes of a Naturalist in South Africa*. Los Angeles, California: University of California Press.

55. Cracraft, J. 1986. 'Origin and evolution of continental biotas - speciation and congruence within the Australian avifauna'. *Evolution* 40(5): 977–96.

56. Crisp, M., and Cook L. 2007. 'A congruent molecular signature of vicariance across multiple plant lineages'. *Molecular Phylogenetics and Evolution* 43: 1106–17.

57. Crome, F.H.J., and Johnstone R.E. 1979. 'Geographical variation in the Australian rock pigeons'. *Records of the Western Australia Museum* 8: 117–133.

58. Dawson, L. 1985. 'Marsupial fossils from Wellington Caves, New South Wales; the historic and scientific significance of the collections in the Australian Museum, Sydney'. *Records of the Australian Museum* 37(2): 55–69.

59. Dawson, L. 2006. 'An ecophysiological approach to the extinction of large marsupial herbivores in Middle and Late Pleistocene Australia'. *Alcheringa: An Australasian Journal of Palaeontology* 30 (sup1): 89–114.

60. De Pietri V.L. 2017. 'The diversity of early Miocene pigeons (Columbidae) in New Zealand'. In *Proceedings of the 9th International Meeting of the Society of Avian Palaeontology and Evolution, Diamante (Argentina), 1–6 August 2016*. Paleontologia y Evolucion de las Aves: Contribuciones del Museo Argentino de Ciencias Naturales No. 7: 49–68

61. De Pietri, V.L., Camens A.B., and Worthy T.H. 2015. 'A Plains-Wanderer (Pedionomidae) that did not wander plains: a new species from the Oligocene of South Australia'. *Ibis* 157(1): 68–74.

62. De Pietri, V.L., Scofield R.P., Prideaux G.J., and Worthy T.H. 2018. 'A new species of lapwing (Charadriidae: *Vanellus*) from the Late Pliocene of central Australia'. *Emu - Austral Ornithology*, May: 1–10.

63. De Vis, C. 1888. Australian ancestry of the crowned pigeon of New Guinea. *Proceedings of the Royal Society of Queensland* 5: 127–131.

64. Debus, S.J.S. 1993. 'The mainland Masked Owl *Tyto Novaehollandiae*: a review'. *Australian Bird Watcher* 15: 168–91.

65. Dekker, R.W. 2007. Distribution and speciation of megapodes (Megapodiidae) and subsequent development of their breeding behaviour. In *Biogeography, time, and place: distributions, barriers, and islands* (ed. W. Renema), pp. 93–102. Dordrecht: The Netherlands: Springer.

66. Dhami, K.K., Joseph, L., Roshier D.A., Heinsohn R., and Peters J.L.. 2013. 'Multilocus phylogeography of Australian teals (*Anas* spp.): a case study of the relationship between vagility and genetic structure'. *Journal of Avian Biology* 44(2): 169–78.

67. Diamond, J. 1994. Stinking birds and burning books. *Natural History* 103: 4–12.

68. Diamond, J. 2002. Dispersal, mimicry, and geographic variations in northern Melanesian birds. *Pacific Science* 56: 1– 22.

69. Dickinson, E.C., Remsen, J.J. 2013. *The Howard and Moore complete checklist of the birds of the world*, 4th ed., Volume 1. Non-passerines. Eastbourne, UK: Aves Press.

70. Dickinson, E.C., and Christidis L., eds. 2014. *The Howard and Moore Complete Checklist of the Birds of the World*. 4th ed. Volume 2: Passerines. Aves Press, Eastbourne.

71. Doerr, S.H., Davies R.R., Lewis A., Pilkington G., Webb J.A., Ackroyd P.J., and Bodger O. 2011. 'Origin and karst geomorphological significance of the enigmatic Australian Nullarbor Plain "blowholes"'. *Earth Surface Processes and Landforms*, October. https://doi.org/10.1002/esp.2233.

72. Dolman, G., and Joseph L. 2012. 'A species assemblage approach to comparative phylogeography of birds in southern Australia'. *Ecology and Evolution* 2(2): 354–69.

73. Dolman, G., and Joseph, L. 2015. 'Evolutionary history of birds across southern Australia: structure, history and taxonomic implications of mitochondrial DNA diversity in an ecologically diverse suite of species'. *Emu* 115: 35–48.

74. Dolman, G., and Joseph, L. 2016. 'Multi-locus sequence data illuminate demographic drivers of Pleistocene speciation in semi-arid southern Australian birds (*Cinclosoma* spp.)'. *BMC Evolutionary Biology* 16 (1).

75. Doube, M., Yen, S.C.W., Klosowski, M.M., Farke, A.A., Hutchinson, J.R., Shefelbine, S.J. 2012. Whole-bone scaling of the avian pelvic limb. *Journal of Anatomy* 221: 21–29.

76. Dunkley, J.R. 1967. 'The geographical and historical background'. In *Caves of the Nullarbor - A Review of Speleological Investigations in the Nullarbor Plain, Southern Australia*, 1–12. The Speleological Research Council, Sydney.

77. Dunning, J. 2008. *CRC Handbook of Avian Body Masses*. 2nd ed. CRC Press, Boca Raton, Florida.

78. Elzanowski, A., Stidham, T.A. 2010. Morphology of the quadrate in the Eocene anseriform Presbyornis and extant galloanserine birds. *Journal of Morphology* 271: 305–323.

79. Environmental Resources Information Network. 2013. 'Terrestrial Ecoregions in Australia'. Environmental Resources Information Network, Australian Government Department of the Environment.

80. Erritzøe, J., Mann, C.F., Brammer, F.P., Fuller, R.A. 2012. *Cuckoos of the world*. Helm identification guides. London: Christopher Helm.

81. Faith, J.T. 2011. 'Late Pleistocene climate change, nutrient cycling, and the megafaunal extinctions in North America'. *Quaternary Science Reviews*.

82. Field, D.J., Lynner, C., Brown, C., Darroch, S.A.F. 2013. Skeletal correlates for body mass estimation in modern and fossil flying birds. *PLoS ONE* 8: e82000.

83. Field, J., and Wroe, S. 2012. 'Aridity, faunal adaptations and Australian Late Pleistocene extinctions'. *World Archaeology* 44(1): 56–74.

84. Field, J., Wroe, S., Trueman C.N., Garvey J., and Wyatt-Spratt S. 2013. ‘Looking for the archaeological signature in Australian megafaunal extinctions’. *Quaternary International* 285 (February): 76–88.

85. Fillios, M., Field J., and Charles, B. 2010. ‘Investigating human and megafauna co-occurrence in Australian prehistory: mode and causality in fossil accumulations at Cuddie Springs’. *Quaternary International* 211(1–2): 123–143.

86. Finlayson, C., Monclova, A., Carrion, J.S., Fa., D.A., Finlayson, G., Rodriguez-Vidal, J., Fierro, E., Fernandez, S., Bernal-Gomez, M., Giles-Pacheco, F.. 2011. Ecological transitions – but for whom? A perspective from the Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 329: 1–9.

87. Ford, H.L., Sosdian S.M., Rosenthal Y., and Raymo M.E. 2016. ‘Gradual and abrupt changes during the Mid-Pleistocene Transition’. *Quaternary Science Reviews* 148 (September): 222–33.

88. Ford, H.L., Sosdian S.M., Rosenthal Y., and Raymo M.E. 2016. ‘Gradual and abrupt changes during the Mid-Pleistocene Transition’. *Quaternary Science Reviews* 148 (September): 222–33.

89. Ford, J. 1969. Distribution and taxonomic notes on some parrots from Western Australia. *South Australian Ornithologist*, *25*: 99–105.

90. Ford, J. 1987. ‘Minor isolates and minor geographical barriers in avian evolution in continental Australia’. *Emu* 87: 90–102.

91. Forshaw, J.M. 2011. *Parrots of the World*. CSIRO Publishing, Collingwood.

92. Forshaw, J.M., and Joseph L. 2016. ‘A new subspecies of the Australian Ringneck (*Barnardius zonarius*) from the upper Cooper Creek drainage, Lake Eyre Basin, Central Australia’. *Emu* 116 (4): 440.

93. Fraser, I., Gray, J. 2013. *Australian bird names – a complete guide*. CSIRO Publishing, Victoria, Australia.

94. Fu, X., Cohen T.J., and Arnold L.J. 2017. ‘Extending the record of lacustrine phases beyond the last interglacial for Lake Eyre in Central Australia using luminescence dating’. *Quaternary Science Reviews* 162 (April): 88–110.

95. Fuchs, J., Johnson J.A., and Mindell D.P. 2015. ‘Rapid diversification of falcons (Aves: Falconidae) due to expansion of open habitats in the Late Miocene’. *Molecular Phylogenetics and Evolution* 82 (January): 166–82.

96. Fujioka, T., and Chappell, J. 2010. ‘History of Australian aridity: chronology in the evolution of arid landscapes’. *Geological Society Special Publications* 346: 121–39.

97. Fujioka, T., Chappell, J., Fifield L.K., and Rhodes E.J. 2009. ‘Australian desert dune fields initiated with Pliocene–Pleistocene global climatic shift’. *Geology* 37(1): 51–54.

98. Fujioka, T., Chappell, J., Honda M., Yatsevich I., Fifield K., and Fabel D. 2005. ‘Global cooling initiated stony deserts in central Australia 2–4 Ma, Dated by Cosmogenic ^{21}Ne-^{10}Be’. *Geology* 33(12): 993–996.

99. Garcia-Ramirez, J, Gibb G., and Trewick S. 2014. ‘Deep global evolutionary radiation in birds: diversification and trait evolution in the cosmopolitan bird family Rallidae’. *Molecular Phylogenetics and Evolution* 81: 96–108.

100. Garnett, S., Szabo J., and Dutson G. 2011. *The Action Plan for Australian Birds 2010*. CSIRO Publishing, Birds Australia, Victoria.

101. Gentilli, J. 1949. ‘Foundations of Australian bird geography’. *Emu* 49: 85–129.

102. Gibbard, P.L., and Lewin J. 2016. ‘Partitioning the Quaternary’. *Quaternary Science Reviews* 151 (November): 127–39.

103. Gibbard, P.L., Head M.J., Walker M.J.C., and the Subcommission on Quaternary Stratigraphy. 2010. ‘Formal ratification of the Quaternary system/period and the Pleistocene series/epoch with a base at 2.58 Ma’. *Journal of Quaternary Science* 25 (2): 96–102.

104. Gill, F., and Donsker D. 2018. ‘Owls’. *IOC World Bird List, v8.1*. doi: 10.14344/IOC.ML.8.1.

105. Gilliard, E.T., LeCroy M. 1967. Results of the 1958-1959 Gilliard New Britain expedition: 4. Annotated list of birds of the Whiteman Mountains, New Britain. *Bulletin of the American Museum of Natural History* 135: 173–216.

106. Gillieson, D., Wallbrink P., and Cochrane A. 1996. ‘Vegetation change, erosion risk and land management on the Nullarbor Plain, Australia’. *Environmental Geology* 28(3): 145–153.

107. Gillieson, D.S., Cochrane J.A., and Murray A. 1994. ‘Surface hydrology and soil movement in an arid karst: the Nullarbor Plain, Australia’. *Environmental Geology* 23(2): 125–133.

108. Gmelin, J.F. 1788. Caroli a Linne, *Systema Naturae per Regna Tria Naturae: Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis*. Leipzig: Georg Emanuel Beer.

109. Goede, A., Harmon R.S., Atkinson T.C., and Rowe P.J. 1990. ‘Pleistocene climatic change in southern Australia and its effect on speleothem deposition in some Nullarbor caves’. *Journal of Quaternary Science* 5(1): 29–38.

110. Gray, G.R. 1840. *A list of the genera of birds with an indication of the typical species of each genus compiled from various sources*. London: Richard and John Taylor.

111. Grellet-Tinner, G., Spooner, N.A, and Worthy T.H. 2016. ‘Is the “*Genyornis*” egg of a mihirung or another extinct bird from the Australian dreamtime?’ *Quaternary Science Reviews* 133 (February): 147–64.

112. Grellet-Tinner, G., Spooner N.A., Handley W.D., and Worthy T.H. 2017. ‘The *Genyornis* egg: response to Miller *et al.*’s commentary on Grellet-Tinner *et al.* 2016’. *Quaternary Science Reviews*, February.

113. Groombridge, J.J., Jones C.G., Bayes M.K., van Zyl A.J., Carrillo J., Nichols R.A., and Bruford M.W. 2002. ‘A molecular phylogeny of African kestrels with reference to divergence across the Indian Ocean’. *Molecular Phylogenetics and Evolution* 25(2): 267–277.

114. Groucutt, H.S., Petraglia, M.D., Bailey, G., Scerri, E.M.L., Parton, A., Clark-Balzan, L., Jennings, R.P. Lewis, L., Blinkhorn, J., Drake, N.A., Breeze, P.S., Inglis, R.H., Deves, M.H.,

Meredith-Williams, M., Boivin, N., Thomas, M.G. and Scally, A. 2015. 'Rethinking the dispersal of *Homo sapiens* out of Africa'. *Evolutionary Anthropology: Issues, News, and Reviews* 24 (4): 149–64.

115. Grün, R., Eggins, S., Aubert, M., Spooner, N., Pike, A.W.G., and Müller, W.. 2010. 'ESR and U-Series analyses of faunal material from Cuddie Springs, NSW, Australia: implications for the timing of the extinction of the Australian megafauna'. *Quaternary Science Reviews* 29(5–6): 596–610.

116. Guthrie, D.R. 2006. 'New carbon dates link climatic change with human colonization and Pleistocene extinctions'. *Nature* 441 (7090): 207–9.

117. Guthrie, R.D. 2000. 'Origin and causes of the Mammoth Steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia'. *Quaternary Science Reviews* 20: 549–74.

118. Hamm, G., Mitchell, P., Arnold, L.J., Prideaux, G.J., Questiaux, D., Spooner, N.A., Levchenko, V.A., Foley, E.C., Worthy, T.H., Stephenson, B., Coulthard, V., Coulthard, C., Wilton, S., and Johnston, D. 2016. 'Cultural innovation and megafauna interaction in the early settlement of arid Australia'. *Nature* 539(7628): 280–83.

119. Hammer, Ø, D.A.T. Harper, and P.D. Ryan. 2001. *Palaeontologica Electronica* 4(1): 9.

120. Handley, W.D, Chinsamy, A., Yates, A.M., Worthy, T.H. 2016. Sexual dimorphism in the late Miocene mihirung *Dromornis stirtoni* (Aves: Dromornithidae) from the Alcoota Local Fauna of central Australia. *Journal of Vertebrate Paleontology* 36, e1180298.

121. Harris, R.B., Birks, S.M., Leaché, A.D. 2014. Incubator birds: biogeographical origins and evolution of underground nesting in megapodes (Galliformes: Megapodiidae). *Journal of Biogeography* 41, 2045–2056.

122. Hawkins, B., Diniz-Filho, J., and Soeller, S. 2005. 'Water links the historical and contemporary components of the Australian bird diversity gradient'. *Journal of Biogeography* 32: 1035–42.

123. Hedges, R., Stevens, R., and Koch, P.L. 2005. 'Isotopes in bones and teeth'. In *Isotopes in Palaeoenvironmental Research*, edited by M.J. Leng, 117–45. Springer, The Netherlands.

124. Heinsohn, T., Hope, G. 2006. The Torresian connections: zoogeography of New Guinea. In: Merrick, J.R., Archer, M., Hickey, G.M., Lee, M.S.Y., eds. *Vertebrate zoogeography and evolution in Australasia*. New South Wales, Australia: Auscipub, 71–93.

125. Helgen, K.M., Portela Miguez R., Kohen, J. and Helgen, L. 2012. 'Twentieth Century occurrence of the long-beaked echidna *Zaglossus bruijnii* in the Kimberley Region of Australia'. *ZooKeys* 255 (December): 103–32.

126. Helgen, K.M., Wells, R.T., Kear, B.P. Gerdtz, W.R. and Flannery, T.F. 2006. 'Ecological and evolutionary significance of sizes of giant extinct kangaroos'. *Australian Journal of Zoology* 54(4): 293.

127. Heupink, T.H., Huynen, L., and Lambert, D.M. 2011. ‘Ancient DNA suggests dwarf and ‘giant’ emu are conspecific’. *PloS One* 6(4): e18728.

128. Heupink, T.H., van Grouw H., and Lambert D.M. 2014. ‘The mysterious Spotted Green Pigeon and its relation to the Dodo and its kindred’. *BMC Evolutionary Biology* 14(1): 136.

129. Higgins, P., ed. 1999. *Centropus phasianinus*, Pheasant Coucal. In: Parrots to Dollarbird. *Handbook of Australian New Zealand and Antarctic birds*. Vol. 4, Melbourne, Australia: Oxford University Press, 793–806.

130. Higgins, P.J. 1999. *Handbook of Australian, New Zealand and Antarctic Birds, Volume 4, Parrots to Dollarbird*. Oxford University Press, Melbourne.

131. Higgins, P.J., and S.J.J.F. Davies. 1996. *Handbook of Australian, New Zealand and Antarctic Birds, Volume 3, Snipe to Pigeons*. Oxford University Press, Melbourne.

132. Hindwood, K.A. 1954. The distribution of the Coucal (*Centropus phasianinus*) in Australia. Emu 54: 1–6.

133. Hocknull, S.A, Zhao, J.X., Feng, Y.X., and Webb, G.E. 2007. ‘Responses of Quaternary rainforest vertebrates to climate change in Australia’. *Earth and Planetary Science Letters* 264: 317–31.

134. Hocknull, S.A, Zhao, J.X., Feng, Y.X., and Webb, G.E. 2007. ‘Responses of Quaternary rainforest vertebrates to climate change in Australia’. *Earth and Planetary Science Letters* 264: 317–31.

135. Hocknull, S.A. 2009 (unpub.). *Late Cainozoic Rainforest Vertebrates from Australopapua: Evolution, Biogeography and Extinction.* PhD Thesis, University of New South Wales, Sydney.

136. Holm, S.R., and Svenning, J.C. 2014. ‘180,000 years of climate change in Europe: avifaunal responses and vegetation implications’. Edited by M. Hofreiter. *PLoS ONE* 9(4): e94021.

137. Hope, J.H., Lampert, R.J., Edmondson, E., Smith, M.J., and van Tets, G.F. 1977. ‘Late Pleistocene faunal remains from Seton Rock Shelter, Kangaroo Island, South Australia’. *Journal of Biogeography*, 363–385.

138. Horsfield, T. 1823. *Zoological researches in Java and the neighbouring islands*, Vol. 6. London: Kingsbury, Parbury & Allen.

139. Horton, D.R. 1996. ‘The AIATSIS Map of Indigenous Australia’. Australian Institute of Aboriginal and Torres Strait Islander Studies. https://aiatsis.gov.au/explore/articles/aiatsis-map-indigenous-australia.

140. Hughes, J.M. 1997. *Systematics of new world cuckoos (Aves, Cuculidae) and the evolution of brood parasitism*. PhD thesis, Ontario, Canada: University of Toronto.

141. Hughes, J.M. 2000. Monophyly and phylogeny of cuckoos (Aves, Cuculidae) inferred from osteological characters. *Zoological Journal of the Linnean Society* 130: 263–307.

142. Hughes, J.M. 2006. Phylogeny of the cuckoo genus Coccyzus (Aves: Cuculidae): a test of monophyly. *Systematics and Biodiversity* 4: 483–488.

143. Illiger, J.K.W. 1811. *Prodromus Systematis Mammalium et Avium: Additis Terminis Zoographicis Utriusque Classis*, Eorumque Versione Germanica. Berlin: Sumptibus C. Salfeld.

144. James, J.M., Contos, A.K. and Barnes, C.M. 2012. 'Nullarbor Caves, Australia'. *Chemical Geology* 179 (1): 167–186.

145. Jankowski, N.R., Gully, G.A., Jacobs, Z., Roberts, R.G. and Prideaux, G.J. 2016. 'A late Quaternary vertebrate deposit in Kudjal Yolgah Cave, south-western Australia: refining regional Late Pleistocene Extinctions'. *Journal of Quaternary Science* 31(5): 538–50.

146. Jarvis, E.D., Mirarab, S., Aberer, A.J., Li, B., Houde, P., Li, C., Ho, S.Y.W., Faircloth, B.C., Nabholz, B., Howard, J.T., Suh, A., Weber, C.C., da Fonseca, R.R., Li, J., Zhang, F., Li, H., Zhou, L., Narula, N., Liu, L., Ganapathy, G., Boussau, B., Shamsuzzoha, Bayzid, M., Zavidovych, V., Subramanian, S., Gabaldon, T., Capella-Gutierrez, S., Huerta-Cepas, J., Rekepalli, B., Munch, K., Schierup, M., Lindow, B., Warren, W.C., Ray, D., Green, R.E., Bruford, M.W., Zhan, X., Dixon, A., Li, S., Li, N., Huang, Y., Derryberry, E.P., Frost Bertelsen, M., Sheldon, F.H., Brumfield, R.T., Mello, C.V., Lovell, P.V., Wirthlin, M., Cruz Schneider, M.P., Prosdocimi, F., Samaniego, J.A., Vargas Velazquez, A.M., Alfaro-Nunez, A., Campos, P.F., Petersen, B., Sicheritz-Ponten, T., Pas, A.N., Bailey, T., Scofield, P., Bunce, M., Lambert, D.M., Zhou, Q., Perelman, P., Driskell, A.C., Shapiro, B., Xiong, Z., Zeng, Y., Liu, S., Li, Z., Liu, B., Wu, K., Xiao, J., Yinqi, X., Zheng, Q., Zhang, Y., Yang, H., Wang, J., Smeds, L., Rheindt, F.E., Braun, M., Fjeldsa, J., Orlando, L., Barker, F.K., Jønsson, K.A., Johnson, W., Koepfli, K.P., O'Brien, S., Haussler, D., Ryder, O.A., Rahbek, C., Willerslev, E., Graves, G.R., Glenn, T.C., McCormack, J., Burt, D., Ellegren, H., Alstrom, P., Edwards, S.V., Stamatakis, A., Mindell, D.P., Cracraft, J., Braun, E.L., Warnow, T., Jun, W., Gilbert, M.T.P., Zhang, G. 2014. Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* 346: 1320–1331.

147. Johnson, C.N. 2002. 'Determinants of loss of mammal species during the late Quaternary "megafauna" extinctions: life history and ecology, but not body size'. *Proceedings of the Royal Society B: Biological Sciences* 269(1506): 2221–27.

148. Johnson, C.N., Alroy, J., Beeton, N.J., Bird, M.I., Brook, B.W., Cooper, A., Gillespie, R., Herrando-Perez, S., Jacobs, Z., Miller, G.H., Prideaux, G.J., Roberts, R.G., Rodriguez-Rey, M., Saltre, F., Turney, C.S.M. and Bradshaw, C.J.A. 2016. 'What caused extinction of the Pleistocene megafauna of Sahul?' *Proceedings of the Royal Society B: Biological Sciences* 283(1824): 20152399.

149. Johnson, K.P., Goodman, S.M., Lanyon, S.M. 2000. A phylogenetic study of the Malagasy *Coua*s with insights into cuckoo relationships. *Molecular Phylogenetics and Evolution* 14: 436–444.

150. Johnson, N., and Cicero, C. 2004. ‘New mitochondrial DNA data affirm the importance of Pleistocene speciation in North American Birds’. *Evolution* 58(5): 1122–1130.

151. Jones, D, and A Göth. 2008. *Mound-Builders*. Australian Natural History Series. CSIRO Publishing, Victoria, Australia.

152. Jones, D.N., Dekker, R.W.R.J., Roselaar, C.S. 1995. *The megapodes*. Oxford, UK: Oxford University Press.

153. Joseph, L., and Omland, K.E. 2009. ‘Rowley Review – Phylogeography: its development and impact in Australo-Papuan ornithology with special reference to paraphyly in Australian birds’. *Emu* 109(1): 1–23.

154. Joseph, L., and Wilke T. 2006. ‘Molecular resolution of population history, systematics and historical biogeography of the Australian Ringneck Parrots *Barnardius*: are we there yet?’ *Emu* 106(1): 49.

155. Joseph, L., and Wilke T. 2007. ‘Lack of phylogeographic structure in three widespread Australian birds reinforces emerging challenges in Australian historical biogeography’. *Journal of Biogeography* 34: 612–24.

156. Joseph, L., Dolman G., Donnellan S., Saint K.M., Berg M.L., and Bennett A.T.D. 2008. ‘Where and when does a ring start and end? Testing the ring-species hypothesis in a species complex of Australian parrots’. *Proceedings of the Royal Society B: Biological Sciences* 275(1650): 2431–40.

157. Joseph, L., Edwards, S.V., and McLean, A.J. 2013. ‘The Maluridae: inferring avian biology and evolutionary history from DNA sequences’. *Emu* 113 (3): 195–207.

158. Joseph, L., Slikas, B., Alpers, D. and Schodde, R. 2001. ‘Molecular systematics and phylogeography of New Guinean logrunners (Orthonychidae)’. *Emu* 101(4): 273–280.

159. Joseph, L., Toon, A., Schirtzinger, E.E., and Wright, T.F. 2011. ‘Molecular systematics of two enigmatic genera *Psittacella* and *Pezoporus* illuminate the ecological radiation of Australo-Papuan parrots (Aves: Psittaciformes)’. *Molecular Phylogenetics and Evolution* 59(3): 675–684.

160. Kaal, J., Schellekens, J., Nierop, K.G.J., Martínez Cortizas, A. and Muller, J. 2014. ‘Contribution of organic matter molecular proxies to interpretation of the last 55ka of the Lynch’s Crater Record (NE Australia)’. *Palaeogeography, Palaeoclimatology, Palaeoecology* 414 (November): 20–31.

161. Kaplan, G. 2007. *Tawny Frogmouth*. Australian Natural History Series. CSIRO Publishing, Collingwood.

162. Kearns, A.M., Joseph L., and Cook L.G. 2010. ‘The impact of Pleistocene changes of climate and landscape on Australian birds: a test using the Pied Butcherbird (*Cracticus nigrogularis*)’. *Emu* 110(4): 285.

163. Keast, JA. 1961. ‘Bird speciation on the Australian continent’, *Bulletin of the Museum of Comparative Zoology* (123): 303–495.

164. Körtner, G., and Geiser F. 1999. ‘Roosting behaviour of the Tawny Frogmouth (*Podargus strigoides*)’. *Journal of Zoology* 248(4): 501–507.

165. Lambeck, K., and Chappell, J. 2001. ‘Sea level change through the last glacial cycle’. *Science* 292: 679–86.

166. Laslett, T., 2006 (unpub.). *A Palaeoecological Study of a Quaternary Vertebrate Fossil Deposit in Blanche Cave, Naracoorte, South Australia* (Honours Thesis). Flinders University, Adelaide.

167. Leach, W.E. 1819. Eleventh room, upper floor. In: Anonymous, ed. *Synopsis of the contents of the British Museum*, 15th edn. London: British Museum, 63–67.

168. Lipar, M., and Ferk, M. 2015. ‘Karst pocket valleys and their implications on Pliocene–Quaternary hydrology and climate: examples from the Nullarbor Plain, Southern Australia’. *Earth-Science Reviews* 150 (November): 1–13.

169. Lipar, M., Webb, J.A., Cupper, M.L., and Wang, N. 2017. ‘Aeolianite, calcrete/microbialite and karst in southwestern Australia as Indicators of Middle to Late Quaternary palaeoclimates’. *Palaeogeography, Palaeoclimatology, Palaeoecology* 470 (March): 11–29.

170. Louchart, A., Vignaud P., Likius A., Brunet M., and White T.D. 2005. ‘A large extinct marabou stork in African Pliocene hominid sites, and a review of the fossil species of *Leptoptilos’*. *Acta Palaeontologica Polonica* 50(3): 549–563.

171. Louys, J., Price, G. 2015. The Chinchilla Local Fauna: an exceptionally rich and well-preserved Pliocene vertebrate assemblage from fluviatile deposits of south-eastern Queensland, Australia. *Acta Palaeontologica Polonica* 60, 551–572.

172. Lowe T. 2014. *Where Song Began: Australia’s Birds and How They Changed the World*. Viking, Melbourne.

173. Lowry, D.C, and Jennings, J.N. 1974. ‘The Nullarbor karst, Australia’. *Zeitschrift Für Geomorphologie* 18(1): 35–81.

174. Lundelius, E.L., and Turnbull, W.D. 1978. ‘The mammalian fauna of Madura Cave, Western Australia, Part III’. *Fieldiana Geology* 38: 1–120.

175. Lydekker, R. 1891. Catalogue of the fossil birds in the British Museum (Natural History). London, UK: British Museum (Natural History).

176. Maclean, G.L. 1976. ‘A field study of the Australian Dotterel’. *Emu - Austral Ornithology* 76(4): 207–15.

177. Marchant, S., and Higgins P.J. 1990. *Handbook of Australian, New Zealand and Antarctic Birds: Volume 1, Ratites to Ducks*. Oxford University Press, Melbourne.

178. Marchant, S., and Higgins P.J. 1993. *Handbook of Australian, New Zealand and Antarctic Birds, Volume 2, Raptors to Lapwings*. Oxford University Press, Melbourne.

179. Marki, P.Z., Jønsson, K.A., Irestedt, M., Nguyen, J.M.T., Rahbek, C., and Fjeldså, J. 2017. ‘Supermatrix phylogeny and biogeography of the Australasian Meliphagides Radiation

(Aves: Passeriformes)'. *Molecular Phylogenetics and Evolution* 107 (February): 516–29.

180. Marshall, L.G., Corruccini, R.S. 1978. Variability, evolutionary rates, and allometry in dwarfing lineages. *Paleobiology* 4, 101–119.

181. Martin, H. A. 2006. 'Cenozoic climatic change and the development of the arid vegetation in Australia'. *Journal of Arid Environments* 66(3): 533–563.

182. Martin, H.A. 1973. 'Palynology and historical ecology of some cave excavations in the Australian Nullarbor'. *Australian Journal of Botany* 21(2): 283–316.

183. Mason, I.J., McKean, J.L., Dudzinski, M.L. 1984. Geographical variation in the Pheasant Coucal *Centropus phasianinus* (Latham) and a description of a new subspecies from Timor. *Emu* 84: 1–15.

184. Mather E.K., Tennyson A.J.D., Scofield R.P., De Pietri V.L., Hand S.J., Archer M., Handley W.D. and Worthy T.H. 2018. 'Flightless rails (Aves: Rallidae) from the early Miocene St Bathans Fauna, Otago, New Zealand'. *Journal of Systematic Palaeontology* February: 1–27. DOI: 10.1080/14772019.2018.1432710

185. Maurer, G. 2008. Who cares? Males provide most parental care in a monogamous nesting cuckoo. *Ethology* 114: 540– 547.

186. Maurer, G., Double, M.C., Milenkaya, O., Süsser, M., Magrath, R.D. 2011. Breaking the rules: sex roles and genetic mating system of the Pheasant Coucal. *Oecologia* 167: 413–425.

187. Mayr, E. 1944. 'Timor and the colonization of Australia by birds'. *Emu* 44(2): 113–130.

188. Mayr, G. 2008. 'The phylogenetic affinities of the parrot taxa *Agapornis*, *Loriculus* and *Melopsittacus* (Aves: Psittaciformes): hypotarsal morphology supports the results of molecular analyses'. *Emu* 108(1): 23–27.

189. Mayr, G. 2016. Variations in the hypotarsus morphology of birds and their evolutionary significance. *Acta Zoologica* 97, 143–266.

190. Mayr, G., Weidig, I. 2004. The early eocene bird *Gallinuloides wyomingensis*—a stem group representative of Galliformes. *Acta Palaeontologica Polonica* 49, 211–217.

191. McColl, W.S. 1929. 'Avifauna of the Hampton Tableland, Hampton Low-Lands and Nullabor Plain.' *Emu* 29 (2): 91–100.

192. McCracken, K., Fullagar, P., Slater, E., Paton, D.C., and Afton, A.D. 2002. 'Advertising displays of male Musk Ducks indicate population subdivision across the Nullarbor Plain of Australia'. *Wildfowl* 53: 137–54.

193. McDowell, M.C., and Medlin, G.C. 2010. 'Natural resource management implications of the pre-European non-volant mammal fauna of the southern tip of Eyre Peninsula, South Australia'. *Australian Mammalogy* 32(2): 87.

194. McGilp, J.N. 1932. 'Birds of the Nullarbor Plain and far west coast of South Australia.' *South Australian Ornithologist* 11(5): 146–151.

195. McLaren, S., and Wallace, M.W. 2010. ‘Plio-Pleistocene climate change and the onset of aridity in southeastern Australia’. *Global and Planetary Change* 71(1–2): 55–72.

196. McLaren, S., Wallace, M.W., and Reynolds, T. 2012. ‘The Late Pleistocene evolution of Palaeo Megalake Bungunnia, southeastern Australia: a sedimentary record of fluctuating lake dynamics, climate change and the formation of the modern Murray River’. *Palaeogeography, Palaeoclimatology, Palaeoecology* 317–318: 114–127.

197. McLean, A.J., Toon, A., Schmidt, D.J., Joseph, L. and Hughes, J.M. 2012. ‘Speciation in Chestnut-Shouldered Fairy-Wrens (*Malurus* spp.) and rapid phenotypic divergence in Variegated Fairy-Wrens (*Malurus lamberti*): a multilocus approach’. *Molecular Phylogenetics and Evolution* 63(3): 668–78.

198. Megirian, D., Prideaux, G.J., Murray, P.F., Smit, N. 2010. An Australian land mammal age biochronological scheme. *Paleobiology* 36: 658–671.

199. Meijer, H.J.M. 2014. ‘The avian fossil record in insular southeast Asia and its implications for avian biogeography and palaeoecology’. *PeerJ* 2 (March): e295.

200. Meijer, H.J.M., and Due, R.A. 2010. ‘A new species of giant marabou stork (Aves: Ciconiiformes) from the Pleistocene of Liang Bua, Flores (Indonesia)’. *Zoological Journal of the Linnean Society* 160(4): 707–24.

201. Meijer, H.J.M., Sutikna, T., Saptomo, E.W., Awe, R.D., Jatmiko, Wasisto, S., James, H.F., Morwood, M.J., and Tocheri, M.W. 2013. ‘Late Pleistocene-Holocene non-passerine avifauna of Liang Bua (Flores, Indonesia)’. *Journal of Vertebrate Paleontology* 33(4): 877–94.

202. Meijer, H.J.M., Tocheri, M.W. Due, R.A., Sutikna, T., Saptomo, E.W. and James, H.F. 2015. ‘Continental-style avian extinctions on an oceanic island’. *Palaeogeography, Palaeoclimatology, Palaeoecology* 429 (July): 163–70.

203. Miller A. 1963. ‘The fossil flamingos of Australia’. *The Condor* 65(4): 289–299.

204. Mille, C.R., James, N.P., and Bone, Y. 2012. ‘Prolonged carbonate diagenesis under an evolving Late Cenozoic climate; Nullarbor Plain, southern Australia’. *Sedimentary Geology* 261–262 (June): 33–49.

205. Miller, G., Fogel, M., Magee, J., Gagan, M., Clarke, S., Johnson, B. 2005. Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction. *Science* 309, 287–290.

206. Miller, G., Fogel, M., Magee, J.W., Gagan, M., Clarke, S. and Johnson, B. 2005. ‘Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction’. *Science* 309: 287–90.

207. Miller, G., Magee, J., Smith, M., Spooner, N., Baynes, A., Lehman, S., Fogel, M., Johnston, H., Williams, D., Clark, P., Florian, C., Holst, R., DeVogel, S. 2016. ‘Human predation contributed to the extinction of the Australian megafaunal bird *Genyornis newtoni* ~47 Ka’. *Nature Communications* 7 (January): 10496.

208. Miller, G., Magee, J., Smith, M., Spooner, N., Baynes, A., Lehman, S., Fogel, M., Harvey, J., Williams, D., Clark, P., Florian, P., Holst, R., DeVogel, S. 2016. Human predation

contributed to the extinction of the Australian megafaunal bird *Genyornis newtoni* ~47 ka. *Nature Communications* 29, 10496.

209. Miller, G.H., Fogel, M.L., Magee, J.W., Clarke, S.J. 2017. The *Genyornis* egg: a commentary on Grellet-Tinner *et al.*, 2016. *Quaternary Science Reviews* 161, 123–127.

210. Miller, G.H., Magee, J.W., Johnson, B.J., Fogel, M.L., Spooner, N.A., McCulloch, M.T. and Ayliffe, L.K. 1999. ‘Pleistocene extinction of *Genyornis newtoni*: human impact on Australian megafauna’. *Science* 283(5399): 205–208.

211. Molnar, R.E., Kurtz, C. 1997. The distribution of Pleistocene vertebrates on the eastern Darling Downs, based on the Queensland Museum collections. *Proceedings of the Linnean Society of New South Wales* 117, 107–134.

212. Montanari, S., Louys, J., Price, G.J. 2013. Pliocene paleoenvironments of southeastern Queensland, Australia, inferred from stable isotopes of marsupial tooth enamel. *PLoS ONE* 8, e66221.

213. Moriarty, K.C., McCulloch, M.T., Wells, R.T., and McDowell, M.C. 2000. ‘Mid-Pleistocene cave fills, megafaunal remains and climate change at Naracoorte, South Australia: towards a predictive model using U-Th dating of speleothems’. *Palaeogeography, Palaeoclimatology, Palaeoecology* 159(1–2): 113–143.

214. Mourer-Chauviré, C. 1992. The Galliformes (Aves) from the Phosphorites du Quercy (France): systematics and biostratigraphy. *Papers in Avian Paleontology Honoring Pierce Brodkorb, Natural History Musuem of Los Angeles County*, *Science Series* 36, 67–95.

215. Mourer-Chauviré, C. 2000. A new species of *Ameripodius* (Aves: Galliformes; Quercymegapodiidae) from the Lower Miocene of France. *Palaeontology* 43, 481–493.

216. Mourer-Chauviré, C., Balouet, J.C. 2005. Description of the skull of the genus *Sylviornis* Poplin, 1980 (Aves, Galliformes, Sylviornithidae new family), a giant extinct bird from the Holocene of New Caledonia. *Proceedings of the International Symposium ‘Insular Vertebrate Evolution: the Palaeontological Approach’, Monografies de la Societat d’Història Natural de les Balears* 12, 205–218.

217. Moyle, R.G., Oliveros, C.H., Andersen, M.J., Hosner, P.A., Benz, B.W., Manthey, J.D., Travers, S.L., Brown, R.M. and Faircloth, B.C. 2016. ‘Tectonic collision and uplift of wallacea triggered the global songbird radiation’. *Nature Communications* 7 (August): 12709.

218. Murie, J. 1868. ‘On the nocturnal Ground-Parrakeet (*Geopsittacus occidentalis*, Gould)’. *Proceedings of the Scientific Meetings of the Zoological Society of London* Feb. 27th: 158-168.

219. Murphy, B.P., Williamson, G.J., and Bowman, D.M.J.S. 2012. ‘Did central Australian megafaunal extinction coincide with abrupt ecosystem collapse or gradual climate change?: Megafaunal extinction and climate change’. *Global Ecology and Biogeography* 21(2): 142–51.

220. Murphy, S.A., Joseph, L., Burbidge, A.H. and Austin, J. 2011. 'A cryptic and critically endangered species revealed by mitochondrial DNA analyses: the Western Ground Parrot'. *Conservation Genetics* 12(2): 595–600.

221. Murray, P.F., and Vickers-Rich, P. 2004. *Magnificent Mihirungs: The Colossal Flightless Birds of the Australian Dreamtime*. Indiana University Press.

222. Murray, P.F., Vickers-Rich, P. 2004. *Magnificent mihirungs: the colossal flightless birds of the Australian dreamtime*. Bloomington, Indiana: Indiana University Press.

223. Nadachowska-Brzyska, K., Li, C., Smeds, L., Zhang, G. and Ellegren, H. 2015. 'Temporal dynamics of avian populations during Pleistocene revealed by whole-genome sequences'. *Current Biology* 25(10): 1375–80.

224. NAPA (Narungga Aboriginal Progress Association). 2006. *Nharangga Warra—Narungga Dictionary*. Wakefield Press, Adelaide, Australia.

225. Neaves, L.E., Zenger, K.R., Prince, R.I.T., and Eldridge, M.D.B. 2012. 'Impact of Pleistocene aridity oscillations on the population history of a widespread, vagile Australian mammal, *Macropus fuliginosus*'. *Journal of Biogeography* 39(8): 1545–63.

226. Nguyen, J., Boles, W., Worthy, T., Hand, S. and Archer, M. 2014. 'New specimens of the Logrunner *Orthonyx kaldowinyeri* (Passeriformes: Orthonychidae) from the Oligo-Miocene of Australia'. *Alcheringa: An Australasian Journal of Palaeontology* 38(2): 245–55.

227. Nguyen, J.M.T. 2016. 'Australo-Papuan treecreepers (Passeriformes: Climacteridae) and a new species of sittella (Neosittidae: *Daphoenositta*) from the Miocene of Australia'. *Palaeontologia Electronica* 19(1): 1–13.

228. Nguyen, J.M.T., Boles, W.E., Worthy, T.H., Hand, S.J., Archer, M. 2014. New specimens of the logrunner *Orthonyx kaldowinyeri* (Passeriformes: Orthonychidae) from the Oligo-Miocene of Australia. *Alcheringa: An Australasian Journal of Palaeontology* 38: 245–255.

229. Nguyen, J.M.T., Hand, S.J., and Archer, M. 2016. 'The Late Cenozoic passerine avifauna from Rackham's Roost Site, Riversleigh, Australia'. *Records of the Australian Museum* 68(5): 201–30.

230. O'Connell, L.G., James, N.P., and Bone, Y. 2011. 'The Miocene Nullarbor Limestone, Southern Australia; deposition on a vast subtropical epeiric platform'. *Sedimentary Geology* 53: 1–16.

231. Olson, S.L. 1975. 'The fossil rails of CW De Vis, being mainly an extinct form of *Tribonyx mortierii* from Queensland'. *Emu* 75(2): 49–54.

232. Olson, S.L. 1977. 'The identity of the fossil ducks described from Australia by CW De Vis'. *Emu* 77(3): 127–131.

233. Olson, S.L. 1985. The fossil record of birds. In *Avian biology* (ed. D Farner), pp. 79–238. New York, NY: Academic Press.

234. Olson, S.L., and James, H.F. 1991. 'Descriptions of Thirty-Two New Species of Birds from the Hawaiian Islands'. *Ornithological Monographs, No.* 45. American Ornithologists' Union, Washington, D.C

235. Olson, S.L., Rasmussen, P.C. 2001. Miocene and Pliocene birds from the Lee Creek Mine, North Carolina. pp. 233–365 in: Ray C, Bohaska D, eds. Geology and paleontology of the Lee Creek Mine, North Carolina, III. Vol. 90: *Smithsonian Contributions to Paleobiology*. Smithsonian Institution Press, Washington, D.C.

236. Orenstein, R.I. 1976. Birds of the Plesyumi area, central New Britain. *Condor* 78: 370–374.

237. Oswald, J.A., and Steadman, D.W. 2011. 'Late Pleistocene passerine birds from Sonora, Mexico'. *Palaeogeography, Palaeoclimatology, Palaeoecology* 301(1–4): 56–63.

238. Oswald, J.A., and Steadman, D.W. 2015. 'The changing diversity and distribution of dry forest passerine birds in northwestern Peru since the last ice age'. *The Auk* 132(4): 836–62.

239. Pereira, S.L., Johnson, K.P., Clayton, D.H. and Baker, A.J. 2007. 'Mitochondrial and nuclear DNA sequences support a Cretaceous origin of Columbiformes and a dispersal-driven radiation in the Paleogene'. *Systematic Biology* 56(4): 656–72.

240. Pillans, B. 2003. 'Subdividing the Pleistocene using the Matuyama–Brunhes Boundary (MBB): an Australasian perspective'. *Quaternary Science Reviews* 22(15–17): 1569–77.

241. Pillans, B., and Bourman, R. 2001. 'Mid Pleistocene arid shift in southern Australia, dated by magnetostratigraphy'. *Soil Research* 39(1): 89–98.

242. Pledge, N.S. 1980. Macropodid skeletons, including *Simosthenurus* Tedford, from an unusual 'drowned cave' deposit in the south east of South Australia. *Records of the South Australian Museum* 18: 131–141.

243. Pledge, N.S. 1990. The upper fossil fauna of the Henschke Fossil Cave, Naracoorte, South Australia.*Memoirs of the Queensland Museum* 28, 247–262.

244. Polly, P.D., and Eronen, J.T. 2011. 'Mammal associations in the Pleistocene of Britain: implications of ecological niche modelling and a method for reconstructing palaeoclimate'. In *The Ancient Human Occupation of Britain*, edited by N. Ashton, S. Lewis, and C. Stringer, 279–304. Developments in Quaternary Science 14. Elsevier, Amsterdam.

245. Poplin, F., Mourer-Chauviré, C., Evin, J. 1983. Position systématique et datation de *Sylviornis neocaledoniae*, mégapode géant (Aves, Galliformes, Megapodiidae) éteint de la Nouvelle-Calédonie. *Comptes-rendus des séances de l'Académie des sciences Série II T.* 297, 301–304.

246. Posso, S.R., Donatelli, R.J. 2006. Análise filogenética e implicações sistemáticas e evolutivas nos Cuculiformes (Aves) com base na osteologia, comportamento e ecologia. *Revista Brasileira de Zoologia* 23: 608–629.

247. Price, G.J., Webb, G.E., Zhao, J., Feng, Y., Murray, A.S., Cooke, B.N., Hocknull, S.A., Sobbe, I.H. 2011. Dating megafaunal extinction on the Pleistocene Darling Downs, eastern

Australia: the promise and pitfalls of dating as a test of extinction hypotheses. *Quaternary Science Reviews* 30, 899–914.

248. Prideaux, G. 2004. Systematics and evolution of the sthenurine kangaroos*. Geological Sciences* 146. Berkeley, CA: University of California Publications.

249. Prideaux, G.J. 2007. 'Mid-Pleistocene Vertebrate Records'. In *Encyclopedia of Quaternary Science*, edited by S.A. Elias, 1st ed., 1518–37. Elsevier, online edition.

250. Prideaux, G.J. *et al.* 2007. An arid-adapted middle Pleistocene vertebrate fauna from south-central Australia. *Nature* 445, 422–425.

251. Prideaux, G.J., and Warburton, N.M. 2008. 'A new Pleistocene tree-kangaroo (Diprotodontia: Macropodidae) from the Nullarbor Plain of south-central Australia'. *Journal of Vertebrate Paleontology* 28(2): 463–478.

252. Prideaux, G.J., and Warburton, N.M. 2009. '*Bohra nullarbora* sp. nov., a second tree-kangaroo (Marsupialia: Macropodidae) from the Pleistocene of the Nullarbor Plain, Western Australia'. *Records of the Western Australian Museum* 25: 165–79.

253. Prideaux, G.J., Long, J.A., Ayliffe, L.K., Hellstrom, J.C., Pillans, B., Boles, W.E., Hutchinson, M.N., Roberts, R.G., Cupper, M.L., Arnold, L.J., Devine, P.D. and Warburton, N.M. 2007. 'An arid-adapted middle Pleistocene vertebrate fauna from south-central Australia'. *Nature* 445(7126): 422–25.

254. Prideaux, G.J., Long, J.A., Ayliffe, L.K., Hellstrom, J.C., Pillans, B., Boles, W.E., Hutchinson, M.N., Roberts, R.G., Cupper, M.L., Arnold, L.J., Devine, P.D. and Warburton, N.M. 2007. 'An arid-adapted middle Pleistocene vertebrate fauna from south-central Australia'. *Nature* 445(7126): 422–25.

255. Prideaux, G.J., Warburton, N.M. 2008. A new Pleistocene tree-kangaroo (Diprotodontia: Macropodidae) from the Nullarbor Plain of south-central Australia. *Journal of Vertebrate Paleontology* 28: 463–478.

256. Prideaux, G.J., Warburton, N.M. 2009. *Bohra nullarbora* sp. nov., a second tree-kangaroo (Marsuplialia: Macropodidae) fromthe Pleistocene of the Nullarbor Plain, Western Australia. *Records of the Western Australian Museum* 25: 165–179.

257. Prideaux, G.J., Warburton, N.M. 2009. *Bohra nullarbora* sp. nov., a second tree-kangaroo (Marsupialia: Macropodidae) from the Pleistocene of the Nullarbor Plain, Western Australia. *Records of the Western Australian Museum* 25, 165–179.

258. Prum, R., Berv, J., Dornburg, A., Field, D., Townsend, J., Lemmon, E.M., Lemmon, A.R. 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* 526, 569–573.

259. Pyke, G., and P. Ehrlich. 2014. 'Conservation and the Holy Grail: The story of the Night Parrot'. *Pacific Conservation Biology* 20(2): 221–26.

260. Read, J.L., and Ebdon F.R. 1998. 'Waterbirds of the Arcoona Lakes, an important arid-zone wetland complex in South Australia'. *Australian Bird Watcher* 17: 234–44.

261. Reed, E.H., and Bourne, S.J. 2000. ‘Pleistocene fossil vertebrate sites of the south east region of South Australia’. *Transactions of the Royal Society of South Australia*, no. 124: 61–90.

262. Reed, E.H., Bourne, S.J. 2000. Pleistocene fossil vertebrate sites of the South East region of South Australia. *Transactions of the Royal Society of South Australia* 124, 61–90.

263. Reed, E.H., Bourne, S.J. 2009. Pleistocene fossil vertebrate sites of the south east region of South Australia II. *Transactions of the Royal Society of South Australia* 133, 30–40.

264. Reside, A.E., VanDerWal J.J., Kutt A.S., and Perkins G.C. 2010. ‘Weather, not climate, defines distributions of vagile bird species’. *PLoS ONE* 5(10): e13569.

265. Rich, P.V., and McEvey A.R. 1977. ‘A new owlet nightjar from the Early to Mid–Miocene of eastern New South Wales’. *Memoirs of the National Museum of Victoria* 38: 247–53.

266. Rich, P.V., McEvey, A.R., Baird, R.F. 1985a. Osteological comparison of the scrub-birds, *Atrichornis*, and lyrebirds, *Menura* (Passeriformes: Atrichornithidae and Menuridae). *Records of the Australian Museum* 37: 165–191.

267. Rich, P.V., van Tets G.F., Knight, F. 1985b. *Kadimakara: extinct vertebrates of Australia*. Lilydale, Victoria: Pioneer Design Studio.

268. Rich, P.V., van Tets, G.F., Rich, T. and McEvey, A.R. 1987. ‘The Pliocene and Quaternary flamingos of Australia’. *Memoirs of the Queensland Museum* 25(1): 207–25.

269. Richards, A. 1971. ‘An ecological study of the cavernicolous fauna of the Nullarbor Plain southern Australia’. *Journal of Zoology* 164: 1–60.

270. Roberts, R.G., Spooner, N.A., Jones, R., Cane, S., Olley, J.M., Murray, A.S. and Head, M.J. 1996. ‘Preliminary luminescence dates for archaeological sediments on the Nullarbor Plain, South Australia’. *Australian Archaeology* 42(1): 7–16.

271. Rubenson, J., Marsh, R.L. 2009. Mechanical efficiency of limb swing during walking and running in Guinea Fowl (*Numida meleagris*). *Journal of Applied Physiology* 106: 1618–1630.

272. Ryan, K., Page, B., Brandle, R., Jay, J., Ehmann, H. and Armstrong, D. 2012. ‘Trends in the biodiversity of the Nullarbor region: a comparison between 1984 and 2012’. Department of Environment, Water and Natural Resources, Government of South Australia, Adelaide.

273. Sandom, C., Faurby, S., Sandel, B. and Svenning, J.C. 2014. ‘Global late Quaternary megafauna extinctions linked to humans, not climate change’. *Proceedings of the Royal Society B: Biological Sciences* 281(1787): 20133254–20133254.

274. Sarnthein, M., Bartoli, G., Prange, M., Schmittner, A., Schneider, B., Weinelt, M., Andersen, N., and Garbe-Schönberg, D. 2009. ‘Mid-Pliocene shifts in ocean overturning circulation and the onset of Quaternary-style climates’.

275. Scanlon, J.D., and Lee, M. 2000. ‘The Pleistocene serpent *Wonambi* and the early evolution of snakes’. *Nature* 403: 416–20.

276. Schodde, R. 2006. ‘Australasia’s bird fauna today - origins and evolutionary development’. In *Evolution and Biogeography of Australasian Vertebrates*, edited by J.R. Merrick, M. Archer, G.M. Hickey, and M.S.Y. Lee, 413–58. Auscipub, Sydney.

277. Schodde, R. 2006. ‘Australasia’s bird fauna today - origins and evolutionary development’. In *Evolution and Biogeography of Australasian Vertebrates*, edited by J.R. Merrick, M. Archer, G.M. Hickey, and M.S.Y. Lee, 413–58. Auscipub, Sydney.

278. Schodde, R. 2006. Australasia’s bird fauna today – origins and evolutionary development. In: Merrick, J.R., Archer, M., Hickey, G.M., Lee, M.S.Y., eds. *Evolution and biogeography of Australasian vertebrates*. Sydney, Australia: Auscipub, 413–458.

279. Schodde, R., and Mason, I. 1999. *The Directory of Australian Birds: Passerines - A Taxonomic and Zoogeographic Atlas of the Biodiversity of Birds in Australia and Its Territories*. CSIRO Publishing, Canberra.

280. Schweizer, M., Güntert M., and Hertwig S.T. 2013. ‘Out of the Bassian province: historical biogeography of the Australasian platycercine parrots (Aves, Psittaciformes)’. *Zoologica Scripta* 42(1): 13–27.

281. Schweizer, M., Seehausen, O., and Hertwig, S. 2011. ‘Macroevolutionary patterns in the diversification of parrots: effects of climate change, geological events and key innovations’. *Journal of Biogeography* 38: 2176–94.

282. Shipham, A., Schmidt, D.J., Joseph, L., and Hughes, J.M. 2015. ‘Phylogenetic analysis of the Australian rosella parrots (*Platycercus*) reveals discordance among molecules and plumage’. *Molecular Phylogenetics and Evolution* 91 (October): 150–59.

283. Shute, E., Prideaux G.J., and Worthy T.H. 2016. ‘Three terrestrial Pleistocene coucals (*Centropus*: Cuculidae) from southern Australia: biogeographical and ecological significance’. *Zoological Journal of the Linnean Society* 177(4): 964–1002.

284. Shute, E., Prideaux G.J., and Worthy T.H. 2017. ‘Taxonomic review of the late Cenozoic megapodes (Galliformes: Megapodiidae) of Australia’. *Royal Society Open Science* 4(6): 170233.

285. Shute, E., Prideaux, G.J., Worthy, T.H. 2016. Three terrestrial Pleistocene coucals (*Centropus*: Cuculidae) from southern Australia: biogeographical and ecological significance. *Zoological Journal of the Linnean Society* 177, 964–1002.

286. Simpson, G. 1941. Large Pleistocene felines of North America. *The American Museum Novitates* 1131, 1–27.

287. Smith, M.A., Williams, A.N., Turney, C.S.M., and Cupper, M.L. 2008. ‘Human—environment Interactions in Australian drylands: exploratory time-series analysis of archaeological records’. *The Holocene* 18 (3): 389–401.

288. Sniderman J.M.K., Jordan G.J. and Cowling R.M. 2013. ‘Fossil evidence for a hyperdiverse sclerophyll flora under a non-Mediterranean-type climate’. *Proceedings of the National Academy of Sciences* 110(9): 3423–3428.

289. Sniderman, J.M.K., Woodhead, J.D., Hellstrom, J., Jordan, G.J., Drysdale, R.N., Tyler, J.J. and Porch, N. 2016. 'Pliocene reversal of Late Neogene aridification'. *Proceedings of the National Academy of Sciences*, 201520188.

290. Sobbe, I.H., Price, G. and Knezour, R.A. 2013. 'A ziphodont crocodile from the Late Pleistocene King Creek Catchment, Darling Downs, Queensland'. *Memoirs of the Queensland Museum: Nature* 56(2): 601–6.

291. Sorenson, M.D., Payne, R.B. 2005. A molecular genetic analysis of cuckoo phylogeny. In: Payne RB, ed. *The cuckoos*. New York, New York: Oxford University Press, 68–94.

292. Steadman, D. 1989. New species and records of birds (Aves: Megapodiidae, Columbidae) from an archaeological site on Lifuka, Tonga. *Proceedings of the Biological Society of Washington* 102, 537–552.

293. Steadman, D.W. 1999. The biogeography and extinction of megapodes in Oceania. *Zoologische Verhandelingen* 327, 7–22.

294. Steadman, D.W. 2006. *Extinction and biogeography of tropical Pacific birds*. Chicago, IL: University of Chicago Press.

295. Steadman, D.W., and Mead, J.I. 2010. 'A Late Pleistocene bird community at the northern edge of the tropics in Sonora, Mexico'. *The American Midland Naturalist* 163(2): 423–41.

296. Steadman, D.W., Oswald, J.A. and Rincón, A.D. 2015. 'The diversity and biogeography of Late Pleistocene birds from the lowland neotropics'. *Quaternary Research* 83(03): 555–64.

297. Steadman, D.W., White, J.P., Allen, J. 1999. Prehistoric birds from New Ireland, Papua New Guinea: extinctions on a large Melanesian island. *Proceedings of the National Academy of Sciences*, USA 96: 2563–2568.

298. Stewart, J.R., and Jacobi, R.M. 2015. 'The long term response of birds to climate change: new results from a cold stage avifauna in Northern England'. *PLOS ONE* 10(5): e0122617.

299. Stringer, C. 2016. 'The origin and evolution of *Homo Sapiens*'. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371(1698): 20150237.

300. Sweet, A.D., Chesser R.T., and Johnson K.P. 2017. 'Comparative cophylogenetics of Australian phabine pigeons and doves (Aves: Columbidae) and their feather lice (Insecta: Phthiraptera)'. *International Journal for Parasitology* 47(6): 347–56.

301. Swofford, D. 2001. PAUP*: phylogenetic analysis using parsimony (* and other methods) (version 4.0b10). Sunderland, Massachusetts: Sinauer Associates.

302. Taplin, A., Beurteaux, Y. 1992. Aspects of the breeding biology of the Pheasant Coucal *Centropus phasianinus*. *Emu* 92: 141–146.

303. Tedford, R.H., Wells, R.T., Barghoorn, S.F. 1992. Tirari Formation and contained faunas, Pliocene of the Lake Eyre Basin, South Australia. *The Beagle: Records of the Museums and Art Galleries of the Northern Territory* 9, 173–194.

304. Thomson, V.A., Mitchell, K.J., Eberhard, R., Dortch, J., Austin, J.J. and Cooper, A. 2018. ‘Genetic diversity and drivers of dwarfism in extinct island emu populations’. *Biology Letters* 14(4): 20170617.

305. Tindale, N.B. 1974. *Aboriginal Tribes of Australia: Their Terrain, Environmental Controls, Distribution, Limits, and Proper Names, with an Appendix on Tasmanian Tribes by Rhys Jones*. Australian National University Press, Canberra.

306. Toon, A., Austin, J.J., Dolman, G., Pedler, L. and Joseph, L. 2012. ‘Evolution of arid zone birds in Australia: leapfrog distribution patterns and mesic-arid connections in quail-thrush (*Cinclosoma*, Cinclosomatidae)’. *Molecular Phylogenetics and Evolution* 62(1): 286–95.

307. Toon, A., Drew A., Mason I.J., Hughes J.M., and Joseph L. 2017. ‘Relationships of the New Guinean subspecies, *Gymnorhina tibicen papuana*, of the Australian Magpie: an assessment from DNA sequence data’. *Emu-Austral Ornithology*, 1–11.

308. Toon, A., Mather, P.B., Baker, A.M., Durrant, K.L., and Hughes, J.M. 2007. ‘Pleistocene refugia in an arid landscape: analysis of a widely distributed Australian passerine’. *Molecular Ecology* 16(12): 2525–2541.

309. Treble, P.C., Baker, A., Ayliffe, L.K., Cohen, T.J., Hellstrom, J.C., Gagan, M.K., Frisia, S., Drysdale, R.N., Griffiths, A.D., and Borsato, A. 2017. ‘Hydroclimate of the Last Glacial Maximum and deglaciation in southern Australia’s arid margin interpreted from speleothem records (23–15 Ka)’. *Climate of the Past* 13(6): 667–87.

310. Turney, C.S.M., Bird, M.I., and Roberts, R.G. 2001. ‘Elemental δ^{13}C at Allen’s Cave, Nullarbor Plain, Australia: assessing post-depositional disturbance and reconstructing past environments’. *Journal of Quaternary Science* 16(8): 779–84.

311. Tyler, M.J., and Prideaux, G.J. 2016. ‘Early to middle Pleistocene occurences of *Litoria*, *Neobatrachus* and *Pseudophryne* (Anura) from the Nullarbor Plain, Australia: first frogs from the “frog-free zone”’. *Memoirs of Museum Victoria* 74: 403–8.

312. van Tets, G. 1974. ‘A revision of the fossil Megapodiidae (Aves), including a description of a new species of *Progura* De Vis’. *Transactions of the Royal Society of South Australia* 98(4): 213–24.

313. van Tets, G. 1974. ‘Fossil birds (Aves) from Weekes Cave, Nullarbor Plain, South Australia’. *Transactions of the Royal Society of South Australia* 98(4): 229–30.

314. van Tets, G. 1985. *Progura gallinacea* De Vis, 1888—the Australian Giant megapode. In *Kadimakara—extinct vertebrates of Australia* (eds PV Rich, G van Tets, F Knight), pp. 195–199. Victoria, Australia: Pioneer Design Studio.

315. van Tets, G., and Smith M. 1974. ‘Small fossil vertebrates from Victoria Fossil Cave, Naracoorte, South Australia, III. Birds (Aves)’. *Transactions of the Royal Society of South Australia* 98(4): 225–27.

316. van Tets, G., and Vickers-Rich, P. 1980. ‘A review of the De Vis fossil pigeons of Australia’. *Memoirs of the Queensland Museum* 20(1): 89–93.

317. van Tets, G., and Vickers-Rich, P. 1990. ‘An evaluation of De Vis’ fossil birds’. *Memoirs of the Queensland Museum* 28(1): 165–68.

318. Varricchio, D.J, Jackson, F.D. 2016. Reproduction in Mesozoic birds and evolution of the modern avian reproductive mode. *Auk* 133, 654–684.

319. Voris, H.K. 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* 27: 1153–1167.

320. Wagler, J.G. 1830. *Natürliches System der Amphibien: mit vorangehender Classification der Säugethiere und Vögel: Ein Beitrag Zur Vergleichenden Zoologie*. Munich: J. G. Cotta.

321. Walker, M., and Lowe J. 2007. ‘Quaternary Science 2007: a 50-year retrospective’. *Journal of the Geological Society* 164(6): 1073.

322. Wang, W., O’Connor, J.K. 2017. Morphological coevolution of the pygostyle and tail feathers in Early Cretaceous birds. *Vertebrata PalAsiatica* 55, online early.

323. Warren, D.L., Cardillo, M., Rosauer, D.F., and Bolnick, D.I. 2014. ‘Mistaking geography for Biology: inferring processes from species distributions’. *Trends in Ecology & Evolution* 29(10): 572–80.

324. Watson, D.M., Anderson, S.E., Olson, V. 2015. Reassessing breeding investment in birds: class-wide analysis of clutch volume reveals a single outlying family. *PLoS ONE* 10, e0117678.

325. Webb, J.A., James, J.M. 2006. Karst evolution of the Nullarbor Plain, Australia. In: Special paper 404: Perspectives on karst geomorphology, hydrology, and geochemistry – a tribute volume to Derek C. Ford and William B. White, Vol. 404: *Geological Society of America*, 65–78.

326. Webb, S. 2010. ‘Palaeotrophic reconstruction and climatic forcing of Mega-Lake Eyre in Late Quaternary central Australia: a review’. *Boreas* 39(2): 312–24.

327. Weir, J.T., and Schluter, D. 2004. ‘Ice sheets promote speciation in boreal birds’. *Proceedings of the Royal Society B: Biological Sciences* 271(1551): 1881–87.

328. White N., Phillips M., Gilbert M.T., Alfaro-Nunez A., Willerslev E., Mawson P., Spencer P. and Bunce M. 2011. ‘The evolutionary history of cockatoos (Aves: Psittaciformes: Cacatuidae)’. *Molecular Phylogenetics and Evolution* 59: 615–622.

329. White, S. 1919. ‘Four ornithological trips to the Nullarbor Plains’. *Emu* 18: 189–98.

330. Williams, A.N., Ulm, S., Cook, A.R., Langley, M.C., and Collard, M. 2013. ‘Human refugia in Australia during the Last Glacial Maximum and terminal Pleistocene: a geospatial analysis of the 25–12 ka Australian archaeological record’. *Journal of Archaeological Science* 40(12): 4612–25.

331. Williams, D. 1981. *Genyornis* eggshell (Dromornithidae; Aves) from the Late Pleistocene of South Australia. *Alcheringa: An Australasian Journal of Palaeontology* 5, 133–140.

332. Williams, J.W., and Jackson, S.T. 2007. ‘Novel climates, no-analog communities, and ecological surprises’. *Frontiers in Ecology and the Environment* 5(9): 475–82.

333. Woinarski, J.C.Z., Burbidge, A.A., and Harrison, P.L. 2015. ‘Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement’. *Proceedings of the National Academy of Sciences* 112(15): 4531–40.

334. Woodhead, J., Hellstrom, J., Maas, R., Drysdale, R., Zanchetta, G., Devine, P. and Taylor, E. 2006. ‘U-Pb geochronology of speleothems by MC-ICPMS’. *Quaternary Geochronology* 1: 208–21.

335. Worthy, T.H. 2000. The fossil megapodes (Aves: Megapodiidae) of Fiji with descriptions of a new genus and two new species. *Journal of the Royal Society of New Zealand* 30, 337–364.

336. Worthy, T.H. 2008. Pliocene waterfowl (Aves: Anseriformes) from South Australia and a new genus and species. *Emu* 108, 153–165.

337. Worthy, T.H. 2012. A new species of Oligo-Miocene darter (Aves: Anhingidae) from Australia. *The Auk* 129: 96–104.

338. Worthy, T.H. 2012a. ‘A phabine pigeon (Aves : Columbidae) from Oligo-Miocene Australia’. *Emu* 112(1): 23–31.

339. Worthy, T.H., Hand, S.J., Worthy, J.P., Tennyson, A.J.D., and Scofield, R.P. 2009. ‘A large fruit pigeon (Columbidae) from the Early Miocene of New Zealand’. *The Auk* 126(3): 649–56.

340. Worthy, T.H., Hawkins, S., Bedford, S., Spriggs, M. 2015. Avifauna from the Teouma Lapita Site, Efate Island, Vanuatu, including a new genus and species of megapode. *Pacific Science* 69: 205–252.

341. Worthy, T.H., Mitri, M., Handley, W.D., Lee, M.S.Y., Anderson, A., Sand, C. 2016. Osteology supports a stem-galliform affinity for the giant extinct flightless bird *Sylviornis neocaledoniae* (Sylviornithidae, Galloanseres). *PLoS ONE* 11, e0150871.

342. Wright, N.A., Steadman DW, Witt CC. 2016. Predictable evolution toward flightlessness in volant island birds. *Proceedings of the National Academy of Sciences USA* 113, 4765–4770.

343. Wroe, S. 2002. ‘A review of terrestrial mammalian and reptilian carnivore ecology in Australian fossil faunas, and factors influencing their diversity: the myth of reptilian domination and its broader ramifications’. *Australian Journal of Zoology* 50(1): 1–24.

344. Wroe, S., Crowther, M., Dortch, J., and Chong, J. 2004. ‘The size of the largest marsupial and why it matters’. *Proceedings of the Royal Society B: Biological Sciences* 271(Supp.3): S34–36.

345. Wroe, S. and Field, J. 2006. ‘A review of the evidence for a human role in the extinction of Australian megafauna and an alternative interpretation’. *Quaternary Science Reviews* 2

2692–2703.

346. Wroe, S., Myers, T.J., Wells, R.T., and Gillespie, A. 1999. ‘Estimating the weight of the Pleistocene Marsupial Lion, *Thylacoleo carnifex* (Thylacoleonidae: Marsupialia): implications for the ecomorphology of a marsupial super-predator and hypotheses of

impoverishment of Australian marsupial carnivore faunas'. *Australian Journal of Zoology* 47(5): 489–98.

347. Yokoyama, Y., Purcell, A., Lambeck, K. and Johnston, P. 2001. 'Shore-Line reconstruction around Australia during the Last Glacial Maximum and late glacial stage'. *Quaternary International* 83: 9–18.

348. Zeffer, A., Johansson, L.C., Marmebro, A. 2003. 'Functional correlation between habitat use and leg morphology in birds (Aves).' *Biological Journal of the Linnean Society* 79: 461–484.

349. Zeffer, A., Norberg, U.M.L. 2003. 'Leg morphology and locomotion in birds: requirements for force and speed during ankle flexion.' *The Journal of Experimental Biology* 206: 1085–1097.

350. Zelenitsky, D.K., Therrien F, Ridgely RC, McGee AR, Witmer LM. 2011. 'Evolution of olfaction in non-avian theropod dinosaurs and birds.' *Proceedings of the Royal Society B* 278, 3625–3634.

351. Zelenkov, N.V., Panteleyev A.V., and De Pietri V.L. 2017. 'Late Miocene rails (Aves: Rallidae) from southwestern Russia'. *Palaeobiodiversity and Palaeoenvironments*, 97(4): 791-805.

352. Zink, R.M., Klicka J., and Barber B.R. 2004. 'The tempo of avian diversification during the Quaternary'. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 359(1442): 215–220.