

“There is nothing like geology; the pleasure of
the first day’s partridge shooting ... cannot be compared to finding
a fine group of fossil bones, which tell their story of former
times with almost a living tongue ...” - Charles Darwin
(*Correspondence*, v. 1, p. 379).

Diversification in the face of desertification: the evolution of Australian arid zone geckos



Heteronotia sp. nov., collected in Central Australia, 2010

Mitzy Rohani Pepper

March, 2011

A thesis submitted for the degree of
Doctor of Philosophy of The Australian National University.



Investigation in the face of description;

the evolution of Australia and some geology



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Declaration

The research presented in this thesis is my own original work except where due reference is given in the text. All the chapters were the product of investigations carried out jointly with others but, in all cases, I am the principal contributor to the work. No part of this thesis has been submitted for any previous degree.

A handwritten signature in dark ink, appearing to read 'Mitzy', written over a horizontal dotted line.

MITZY ROHANI PEPPER

March, 2011

This thesis is dedicated to my parents, Rex and Firzia.
Without any doubt, it could not have been done
without your love and support.

Diversification in the face of desertification: The evolution of Australian arid zone geckos

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Pepper, M., Ho, S.Y., Fujita, M.K., & Keogh, J.S. The genetic legacy of aridification: Miocene refugia fostered diversification while Pleistocene climate cycles erased diversity in desert lizards – *Molecular Phylogenetics and Evolution* (in revision).

Pepper, M., Doughty, P., Hutchinson, M., & Keogh, J.S. Ancient river systems divide recent species in Australia's arid zone: Morphological and multi-gene evidence for four new species of Beaked Geckos (*Rhynchoedura*) - *Molecular Phylogenetics and Evolution* (in review).

Pepper, M., Doughty, P., & Keogh, J.S. Endemism and genetic diversity in the iconic Australian Pilbara region: A review of landscape evolution and biotic responses in an ancient, heterogeneous refugium – *Manuscript*.

Thesis abstract

My thesis concerns gecko lizards and what their genes can tell us about the historical biogeography of the Australian arid zone. In contrast to the great antiquity of the continent, this immense xeric biome is surprisingly young. Evidence of arid conditions in palaeorecords appears around 15 million years ago (mya), with the inland sand deserts thought to have formed in the last million years. Such a drastic change over the majority of the continent would undoubtedly have had a profound influence on the evolution of the Australian biota, but at present studies are in their infancy. Why is there such high diversity of geckos in the arid zone? When did this diversity arise? Do some regions have more diversity than others? How did the formation of sand deserts affect the movement and distribution of species? To explore the evolutionary consequences of landscape and climate change following the onset and intensification of aridification, I examine genetic variation in various Australian geckos that have distributions spanning the arid regions of the continent, including topographically complex mountain ranges and the vast deserts of low-lying sand dunes. Using detailed molecular datasets, and drawing on information from geology and landscape history, I am able to shed light on the timing and mode of gecko diversification in the Australian desert.

The first chapter of my thesis investigates the presence and role of refugia in the arid zone, regions that retained climatic stability and allowed persistence of species during harsh climatic periods. Mountain ranges in central and western Australia are thought to have provided refugia for many species following widescale aridification, however this hypothesis has never been tested in a molecular framework. I assess divergence history among rock-dwelling geckos in the genus *Heteronotia* that have distributions confined to disjunct ranges in the arid zone. Were these gecko populations isolated from one another recently by the development of sand deserts between their rocky habitats, or were they relicts of an ancient, ancestral taxon driven into refugia by expanding arid conditions? I found that the age of divergence among the lineages was much older than the sand deserts, and the high levels of diversity within each taxa was indicative of persistence in refugia that likely was aided by topographic complexity in these areas.

Chapter II continues to explore arid zone mountain refugia using comparative datasets of other gecko taxa. In addition, I compare how levels of diversity differ between

mountainous regions and surrounding low-lying desert dunes. Again, I found strong evidence for the historical persistence of taxa in mountain refugia, but in stark contrast, gecko populations in the desert regions displayed very little genetic diversity, often over extremely large geographic areas. Using molecular dating, I inferred these population expansions to have occurred extremely recently (< 2 mya), and interpret this to be a result of population bottlenecks in response to extreme arid cycling that is known to have initiated in the mid Pleistocene. It appears that aridification had little effect on population demographics of mesic-adapted taxa in refugia, but profoundly influenced genetic diversity of geckos distributed in the desert regions most heavily impacted by aridification.

The third chapter of my thesis combines molecular systematics with detailed morphological data, to revise the classification of the arid zone beak-faced gecko, *Rhynchoedura ornata*. Formerly considered a single, widespread species, here I describe four new species and redescribe a fifth. The distributions of these species points to ancient biogeographic separations within the arid zone that appear to relate to a topographic divide between the western Australian uplands and eastern lowlands, with divisions in the latter correlated to dryland rivers and major drainage divisions. This result provides a unique contrast to existing studies of terrestrial arid zone vertebrates, and suggests the evolutionary histories of these desert geckos was shaped by wet periods as well as dry ones.

Chapter IV allowed me to apply a detailed focus on a poorly known region of biotic endemism in the arid zone, the Pilbara, in remote north-western Australia. To lay foundations for future molecular studies, I review the physical and biological history of the Pilbara and highlight general patterns that are beginning to emerge from the distribution of a variety of organisms. I provide a detailed review of geology, landscape history, and phytogeography to develop phylogeographic hypotheses, and I then test these predictions using large comparative datasets of seven Pilbara geckos. The molecular patterns I uncovered are consistent with those recently identified using species richness compositional patterns of invertebrates across the region. Together these concordant results across different taxa and at different levels of the genealogical hierarchy highlight the overarching (and underlying) influence of geology and landform on evolutionary processes in the Pilbara.

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Preface

My research interests lie in geology, and biology. The main objective when I started my doctoral research was to use my background in geological sciences to compliment a newly acquired curiosity of molecular evolution. By combining these disciplines I hoped to better understand the history of a part of Australia where neither alone was adequate – the arid zone. The chapters in my thesis reflect this goal.

Chapters have been prepared as stand alone scientific papers on various regions of the arid zone, each exploring how past landscape and climate change have structured genetic composition of the resident geckonid fauna.

In chapters I and II, I test key assumptions concerning whether topographically complex regions of the arid zone provided refugia following Miocene aridification. I do this by comparing levels of genetic diversity between mountain ranges and surrounding lowland deserts, assessing for evidence of population stability or expansions, and dating the age of coalescent events. Chapter III focuses on a taxonomic revision of the monotypic beak-faced gecko. Using multiple loci in conjunction with detailed morphological measurements, I describe four new species and raise a fifth from synonymy. The fine-scale sampling across the entire arid zone allows a detailed assessment of biogeographic patterns. Finally, in chapter IV, I carry out a comprehensive examination of phylogenetic patterns across multiple taxa in the remote Pilbara region of Western Australia. I provide a detailed review of the geology and landscape history to gain pivotal biogeographic insights into this ecologically and economically significant area.

A primary interest of mine throughout my candidature has been the development of effective science communication skills. Following chapters are short articles I prepared that were published in the Science pages of the Canberra Times newspaper, as part of a project to promote young scientists and their research in the ACT. These articles reflect aspects of each chapter of my thesis, in which I attempt to portray the nature of my research in the lab as well as in the field. Additional articles relating to other facets of herpetology I have included in the Appendix.

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The numerous funding sources and organisations who made my research possible and contributed to my broader PhD experiences: The Australian National University PhD stipend and Vice-Chancellors Fund, the Society for the Study of Evolution, the Australian Society of Herpetologists, the International Alliance of Research Universities, the Australian Museum, the Department of Environment and Conservation, the Wentworth Group of Concerned Scientists, the Australian Biological Resources Study, the ACT Herpetological Society, the ARC Environmental Futures Network and grants to JSK, and Craig Moritz and Fiona Hamer, for housing me for months on end in Berkeley.

The Department (it will always be BoZo to me) has been a very pleasant place to be. I would particularly like to thank the staff, Madeleine, Audra, Jan, Garry, Jim, Bob and Allan, for their help throughout my candidature. Also to all the students who created such a good vibe, but especially Mike, Brian and Sophie, for the many delightful chats on route to the lab or the bathroom.

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General Introduction

The large-scale distribution of organisms is fundamentally tied to ecology, evolution and historical biogeography (Avice 1998). By integrating these disparate but profoundly interrelated fields, biogeographers can view evolutionary processes in a “big picture” approach to test hypotheses concerning the influence of historical landscape and climatic processes in shaping the distribution of modern biological lineages (Crisp *et al.* 1999; Avice 2000).

A long-term interest of mine, both as a geologist and a biologist, is the Australian arid zone – the vast, xeric continental interior. Despite tens of thousands of years of human occupation, this remote and sparsely populated region remains, to a large extent, a scientific enigma. The non-depositional landscape has left continuous on-shore palaeo-records frustratingly incomplete, and extreme climate and inaccessibility means biological collections are limited. In an area where so little is known, it is necessary to use evidence from one field to inform the other – for geology to inform biology, and vice versa, to begin to piece together the history of the youngest, and largest, biome in Australia. This is precisely what the chapters of my thesis reflect.

Australia is an old and weathered continent that has been tectonically stable for a long period of time (Taylor 1994). This characteristic is particularly appealing for studies addressing the role of historical climate change on biotic diversification because in regions where active mountain building is ongoing, or has occurred in the very recent past, it can be difficult to distinguish the effects of geological activity from climatic fluctuations (ie. Brumfield & Capparella 1996; Pook *et al.* 2000; Trewick & Wallis 2001; Che *et al.* 2010), and testing competing hypotheses of tectonic versus climate induced diversification can be challenging. Australia attained its present outline between 50 and 150 million years ago (Mya) following rifting from Antarctica, but many landscapes are considerably older (Wasson 1982; Taylor 1994). Chapters I and IV explore evolutionary patterns across the oldest landscapes in the country (and some of the oldest in the world) – exposures of the ancient Australian Craton manifested in the rugged ranges and mountains of the Kimberley, Pilbara and Central Australia. The stability of these regions over tens of millions of years, combined with substantial

geological complexity relative to surrounding areas, is central to their importance in the evolutionary histories of arid zone organisms. I was fortunate during my candidature to have been able to explore the landscapes of the Pilbara, Kimberley and central Australia. While these mountainous regions are limited in elevation (<1500m) and appear relatively subdued on topographical maps, I was astounded at their magnitude, particularly in comparison to the adjacent low-lying and flat desert plains. Moist gullies support endemic palms and aquifer-fed springs, and clearly provide climatic refuges from the surrounding deserts. It is logical that these ranges would have provided refugia in the past during periods of continent-wide climatic instability, but few studies in the literature have tested this hypothesis in a molecular framework.

By far the greatest environmental change in recent times has been the development of the central arid zone in the late Miocene around 15 Mya (Martin 2006). This climatic discontinuity transformed the landscape across central Australia, with wide-scale contraction of temperate rainforests, unprecedented levels of erosion, cessation of drainages and the disappearance of extensive inland lakes (Bowler 1984; Frakes *et al.* 1987; Martin 2006). Intensifying aridification culminated in the mid-Pleistocene (~1 Mya) with the development of widespread sand dune systems across the central continent (Fujioka *et al.* 2009). The chronology of arid zone development is covered throughout this thesis, but Chapter II in particular explores the evolutionary consequences of recent and intense aridification in the low-lying deserts.

The Australian Squamate reptile fauna (snakes and lizards) is among the most diverse in the world, and the Australian geckonid fauna is particularly rich. Geckos occur in a wide variety of environments from rainforests to arid dune fields, and are well known for the extreme modifications to their feet and digits where specific morphologies have evolved for use in terrestrial, saxicolous and arboreal habitats (Greer 1989; Wilson & Swan 2003; Lamb & Bauer 2006). The arid zone in particular supports a spectacular diversity of geckos (Cogger & Heatwole 1981; Cogger 1984; Wilson & Swan 2003) that may in part be explained by the varied environments and complex climate history of the region. This extreme diversity coupled with relatively low vagility makes geckos a model system for addressing biogeographic and phylogeographic questions surrounding the effect of landscape and climate change on evolutionary history. Ideally, an approach that includes datasets from multiple independent taxa distributed across the

arid zone will provide the strongest means of addressing these types of questions. Comparative phylogeography allows the development of testable hypotheses regarding patterns of diversity, and has been fundamental in identifying pervasive and previously unrecognised biogeographic patterns that highlight the role of both ecologic and geologic vicariance in the development of modern biotic lineages (Arborgast & Kenagy 2001). Congruence among co-distributed species supports the notion of an evolutionary history derived from common landscape patterns and process, and provides evidence against genetic structure resulting purely from stochastic lineage sorting or random catastrophic events. However, taxa with different ecologies and physiological tolerances may be expected to show different patterns (Schneider *et al.* 1998; Moritz *et al.* 2000), particularly in a complex system such as the arid zone. This is examined in Chapter IV, where comparative datasets of six independent taxa sampled across the Pilbara region are used to explore the association between geologic and landscape variation, and patterns of genetic diversity.

A particularly important part of my research has been the identification of previously unrecognised diversity, including that of species level divergences. It is clear from a number of recent molecular studies that there is an extraordinary underestimation of reptile diversity in the arid zone, with many ‘species’ actually comprising complexes of multiple, morphologically similar, yet genetically distinctive taxa (Rabosky *et al.* 2004; Chapple & Keogh 2004; Pepper *et al.* 2006; Oliver *et al.* 2007b, 2009, 2010; Shoo *et al.* 2008; Fujita *et al.* 2010; Doughty *et al.* 2010). Chapters I, III, and IV present new genetic material consistent with this trend. Furthermore, Chapter III assembles these molecular results in conjunction with detailed morphological measurements to redescribe the monotypic Beak-faced gecko *Rhynchoedura* to include four new species. Taxonomic revisions based on other results from this thesis currently are in preparation in conjunction with museums and other collaborators.

Chapter I

Palaeoclimate change drove diversification among isolated mountain refugia in the Australian arid zone



Central Australian mountain ranges, Northern Territory.

Molecular Ecology
(2011)

Abstract

Refugia featured prominently in shaping evolutionary trajectories during repeated cycles of glaciation in the Quaternary, particularly in the northern hemisphere. The southern hemisphere instead experienced cycles of severe aridification but little is known about the temporal presence and role of refugia for arid-adapted biota. Isolated mountain ranges located in the Australian arid zone likely provided refugia for many species following Mio/Pliocene (<15 Mya) aridification, however the evolutionary consequences of the recent development of widespread sand deserts is largely unknown. In order to test alternative hypotheses of ancient versus recent isolation, we generated a 10 gene dataset to assess divergence history among saxicolous geckos in the genus *Heteronotia* that have distributions confined to major rocky ranges in the arid zone. Phylogenetic analyses show that each rocky range harbors a divergent lineage, and substantial intra-specific diversity is likely due to topographic complexity in these areas. Old divergences (~ 4 Mya) among lineages predate the formation of the geologically young sand deserts (<1 Mya), suggesting that Pliocene climate shifts fractured the distributions of biota long before the spread of the deserts.

Introduction

Changes in climate and landscape can drive speciation. The effects of these forces on evolutionary history often can be visualized in molecular phylogenies of extant taxa, which in turn can facilitate tests of diversification hypotheses (Hewitt 2004; Venditti *et al.* 2010). However, molecular studies repeatedly confirm that interpretation of the patterns and processes of organismal diversification requires simultaneous examination of genetic, climate and landscape histories (Ricklefs & Schluter 1993; Bermingham & Moritz 1998; Avise 2000; Hewitt 2000; Carstens & Knowles 2007). For example, the extension of ice-sheets during Pleistocene glacial cycles is well known to have structured the genetic signatures of boreal taxa through repeated contraction to southern mountain refugia (Taberlet *et al.* 1998; Hewitt 2004). In the un-glaciated tropics, fragmentation and expansion of forested habitats, also in response to climate cycling, is thought to have shaped congruent phylogenetic patterns across suites of taxa, both during the Pleistocene as well as in earlier time periods of the Miocene/Pliocene (Moritz *et al.* 2000; Thome *et al.* 2010). Studies of arid zone biotic diversification lag behind those of other biomes (Beheregaray 2008; Byrne *et al.* 2008). However, there are a number of studies that show the development of increasing aridity and the recent development of major sand dune systems has shaped diversification patterns of arid zone taxa (Scott *et al.* 2004; Sole *et al.* 2005; Murphy *et al.* 2006; Melville *et al.* 2009).

Tectonic uplift and mountain building also are known to influence species distribution and diversification independent of, or in conjunction with, climate shifts. In cases of the latter, it often can be difficult to distinguish the effects of geological activity from climatic fluctuations, particularly where active mountain building is ongoing, or has occurred in the very recent past, for example in the Andes (Brumfield & Capparella 1996; Elias *et al.* 2009), the Himalayas (Che *et al.* 2010) New Zealand (Trewick & Wallis 2001), and North American (Pook *et al.* 2000, Neiswenter & Riddle 2010). Therefore, while undeniably important, the role of recent uplift and topographic heterogeneity in the diversification of biota is complex, and testing competing hypotheses of geologic versus climate induced diversification can be challenging.

The Australian landmass is old and weathered and as a result its “mountainous” regions are more subdued than other continents. Recent tectonic events have been confined

largely to the leading edge of the Australia-New Guinea Plate and much of the continent has been geologically stable for hundreds of millions of years, enabling exclusive focus on climate driven evolutionary change. The palaeoclimatic history of Australia is characterized by erratic fluctuations, particularly from the mid Neogene (~23 - 2.5 Million years ago; Mya) and throughout the Quaternary (2.5 Mya - Present) when a major shift from a stable climate characterized by warm and wet environments to volatile climate cycling led to aridification of much of the continent (Bowler 1976; Frakes *et al.* 1987; Mabbutt 1988; Martin 2006). In the intensively studied rainforests of northeastern Australia, the repeated incursions of these dry conditions were paramount in the diversification of temperate biota as fragmentation and contraction of rainforests pushed biota into a number of mountain refugia (reviewed in Moritz *et al.* 2009).

But what of mountain ranges in xeric systems? Despite the immense size of the Australian arid zone, we still have much to learn about the effect of aridification on biotic diversification in this region (reviewed in Byrne *et al.* 2008), particularly regarding the presence and role of refugia, areas which promoted persistence of lineages throughout the Quaternary climate fluctuations. Fortunately, the physical origins of the arid zone and its landforms are well understood (Beard 1969; Wasson 1982; Mabbutt 1988; Fujioka *et al.* 2005, 2009), and, combined with regional palaeoecological inference, can provide the foundations to test evolutionary hypotheses concerning the spatial and temporal distribution and diversification of arid adapted biota (Byrne *et al.* 2008).

Geological evolution of the arid zone

While much of arid Australia is flat, several mountain ranges, albeit limited in elevation (<1500m), constitute prominent topographic features that rise above the surrounding lowlands (Figure 1). The rocky ranges of the Pilbara (Pilbara block), Kimberley (Kimberley block) and Central Australia (Arunta block) have been tectonically stable for more than 80 million years (van Kranendonk *et al.* 2002). They have a common geological history in that each is an uplifted remnant of the ancient Pre-Cambrian craton (or shield) that underlies the westernmost two-thirds of the Australian continent. The topography and rugged characteristics of these regions are heavily influenced by the geological composition of the craton, as considerable tectonic and igneous activity in the past has produced a complex mosaic of rock types that are hard and resistant to

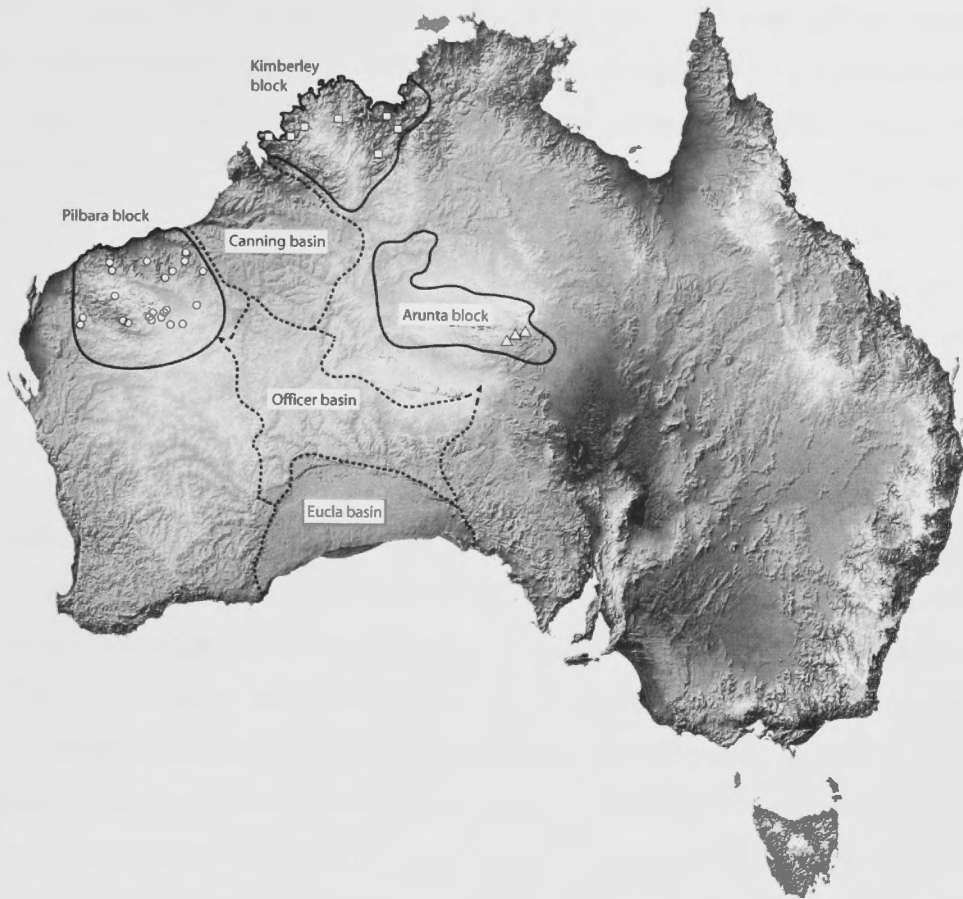


Figure 1. Topographic map of the Australian continent, adapted from the digital elevation maps produced by NASA and the National Geospatial-Intelligence Agency. The thick lines define the boundaries of the uplifted pre-Cambrian craton that forms the mountain ranges of the Pilbara (Pilbara block), Kimberley (Kimberley block) and central Australian ranges (Arunta block). Dashed lines define the boundaries of the sedimentary basins that underlie the present sand deserts. Circles represent Pilbara *H. spelea*, triangles represent Central *H. spelea* and squares represent *H. planiceps* specimens included in our molecular data set.

erosion (Beard 1979; Wasson 1982). In contrast, between these uplifted regions the craton is buried under much younger sediments of a number of lowland basins, with the Canning, the Officer and the Eucla Basins forming a north-south chain through the arid interior (Figure 1). The basins are comprised of younger, flat-lying sedimentary rocks laid down in a marine trough during the Palaeozoic when much of Western Australian was inundated by ocean (Wasson 1982). These sediments are strikingly different from those of the craton, and have had a profound influence on the subdued and uniform nature of what is now low-lying arid zone.

The onset of aridity played a major role in landscape physiognomy. In particular, the termination of the warm and wet conditions of the early Neogene (~ 20 Mya) followed by heightened levels of erosion initiated an immense change to the basins regions. The recent establishment of sand plains and dune fields isolated the mountain uplands with vast tracts of sandy soils. Knowledge of the timing of sand dune initiation and development is impeded by a historical difficulty in determining the age of sand dune landforms by direct dating methods (Fujioka *et al.* 2009), as the constant reworking of sand grains over time limits the use of luminescence methods for dating individual dunes to only a few hundred thousand years (Hesse *et al.* 2004). However, novel cosmogenic methods for dating arid-zone dune fields recently have been applied in the Simpson Desert in Central Australia, pushing back the age of dune field formation to a maximum of 1 Mya (Fujioka *et al.* 2009). The development of such an extensive and mobile landform system undoubtedly had a profound impact on the evolution and diversification of arid zone biota.

Biotic response to aridification

The lack of information on the relative age of contemporary clades against the age of the habitats in which they now and historically have lived is a fundamental gap in our knowledge (Byrne *et al.* 2008). Numerous authors have alluded to topographically complex regions in the Australian arid zone acting as mesic refuges during periods of extreme aridity (eg. Crocker & Wood 1947; Keast 1961; Shodde 1982; Heatwole 1987; Morton *et al.* 1995; Byrne *et al.* 2008), but we know little about the spatial and temporal scale of these putative refugia. Based on geology, topography and the associated influence on moisture and microclimate, the primary refuge regions should be the Pilbara, central Australian ranges and the Kimberley (Figure 1). These areas have been

highlighted to varying degrees for their high species diversity and endemism (ie. Cracraft 1991; Boden & Given 1995; Slatyer *et al.* 2007), but there have been surprisingly few attempts to explicitly test the assumption that these mountainous regions constitute major historic refugia, largely due to inadequate molecular sampling (Byrne *et al.* 2008). In particular, analyses of species endemism and phylogeny cast doubt on whether the central Australian ranges can be considered a long-term (>2 Mya) refuge and isolate (Crisp *et al.* 2001; Laffan & Crisp 2003). Furthermore, while we know that the central deserts constitute barriers to dispersal for mesic-adapted birds (Keast 1959; Ford 1971; Shodde 2006; Joseph & Omland 2009), frogs (Littlejohn 1961; Main 1968; Read *et al.* 2001; Morgan *et al.* 2007) and reptiles (Pianka 1972; Strasburg & Kearney 2005; Chapple & Keogh 2004; Shoo *et al.* 2008), the evolutionary consequences of developing the vast inland sand deserts <1 Mya in Australia has received little attention.

Study system and hypotheses

Testing hypotheses concerning the interaction between ancient topographically complex mountain systems and young, low lying desert regions ideally requires a group of organisms that currently span both landscapes. Geckos in the genus *Heteronotia* Wermuth, 1965 provide an ideal study system as their distributions span the Australian arid-zone, which includes the mountain regions of the Pilbara, Kimberley and Central Australia that are separated by intervening uniform desert lowlands. The genus currently comprises three described species (*binoei*, *spelea* and *planiceps*) with numerous recognized chromosomal and genetically divergent lineages within *H. binoei* (Moritz 1993; Fujita *et al.* 2010). Of the three described taxa, the *H. binoei* complex has the largest distribution and broadest ecological range, and is widespread throughout the Australian continent except the cooler southeast and southwest corners (Wilson & Swan 2008). In contrast, *H. spelea* and *H. planiceps* are rock-adapted specialists. *Heteronotia spelea* was described from the Pilbara region (Kluge 1963) with various populations from the Kimberley and central ranges also assigned to this taxon (Cogger 2000). *Heteronotia planiceps* is thought to occur in the Kimberley, with a purported disjunct population in the Pilbara (Storr 1989; Cogger 2000), while others extend its distribution into the Northern Territory (Wilson & Swan 2008).

The distribution of saxicolous *Heteronotia* across disjunct mountain ranges provides an ideal opportunity to examine the role of refugia and long-term aridification versus more recent development of sand dune deserts in shaping the evolution and diversification of the arid Australian biota. If the mountain ranges served as ancient refugia throughout the Mio/Pliocene aridification, and if saxicolous populations were isolated at this time, there should be high divergence among refugia. Conversely, if each taxon was previously widespread (as implied by current taxonomy) but subsequently isolated by mid-late Pleistocene development of dune systems, divergence among current isolates will date to the late Pleistocene (<1 Mya). To the extent that lineages maintained high effective population sizes, either as large connected populations or as multiple subdivided populations, through recent climate oscillations, we expect to see high within-lineage genetic diversity.

Here we use a multilocus, phylogenetic approach to carry out the first detailed genetic assessment of *H. spelea* and *H. planiceps* in order to distinguish between alternative hypotheses of ancient versus recent refugial isolation in the mountain ranges of the Pilbara, Kimberley and central Australia, and in doing so assess the role of mountain ranges and desert formation on their evolutionary histories. An analogous study, using the same suite of loci, on the widespread generalist *H. binoei* revealed mid Pleistocene divergence and recent (<0.5 Mya) population expansion for the lineages spanning the deserts that presently separate Central and Western populations of *H. spelea* (Fujita *et al.* 2010). A further prediction is that isolation of the saxicolous lineages (*H. spelea* and *H. planiceps*) is contemporaneous with expansion of the generalist *H. binoei* throughout the western deserts.

Materials & Methods

Taxonomic sampling

Tissue samples were obtained from the Western Australian Museum, the South Australian Museum, and the Museum of Vertebrate Zoology at the University of California Berkeley for a total of 65 individuals (Table 1). This includes the best possible sampling given available tissues of the saxicolous members of the genus *Heteronotia* (*spelea* and *planiceps*) and representatives of the known major lineages of the *H. binoei* complex (Fujita *et al.* 2010). For all analyses, *Dixonius vietnamensis* (the

Table 1. Locality information for all individuals sampled in Chapter I.

Lab ID	Museum	Museum #	Genus	Species	Latitude (dec.)	Longitude (dec.)	Location (nearest)
31241	SAM	ABTC31241	<i>Heteronotia</i>	<i>binoei</i>	-11.96670	141.90000	Mapoon Mission, Qld
31253	SAM	ABTC31253	<i>Heteronotia</i>	<i>binoei</i>	-15.70000	126.36667	Drysdale, WA
32437	SAM	ABTC32437	<i>Heteronotia</i>	<i>binoei</i>	-27.00000	133.31700	Chandler, SA
MKF118	MVZ	MKF118	<i>Heteronotia</i>	<i>binoei</i>	-27.95000	134.31300	Copper Hills, SA
MKF302	MVZ	MKF302	<i>Heteronotia</i>	<i>binoei</i>	-26.13190	113.40334	Useless Loop, WA
Gko019	WAM	R96971	<i>Heteronotia</i>	<i>planiceps</i>	-15.71944	125.20694	Kings Cascade, WA
Gko020	WAM	R106220	<i>Heteronotia</i>	<i>planiceps</i>	-16.10000	124.63333	Red Cone Hill, WA
Gko021	WAM	R113996	<i>Heteronotia</i>	<i>planiceps</i>	-15.35000	126.61667	Carson Escarpment, WA
Gko022	WAM	R132761	<i>Heteronotia</i>	<i>planiceps</i>	-15.29111	128.66917	Carlton Hill Station, WA
Gko025	WAM	R158015	<i>Heteronotia</i>	<i>planiceps</i>	-16.11417	123.69417	Koolan Island, WA
Gko026	WAM	R158024	<i>Heteronotia</i>	<i>planiceps</i>	-16.14583	123.74917	Koolan Island, WA
Gko027	WAM	R158033	<i>Heteronotia</i>	<i>planiceps</i>	-16.14722	123.77056	Koolan Island, WA
Gko253	SAM	ABTC11740	<i>Heteronotia</i>	<i>planiceps</i>	-23.37300	120.14200	40km East of Mt. Newman, WA
Gko254	SAM	ABTC29848	<i>Heteronotia</i>	<i>planiceps</i>	-15.76806	129.09000	Jarmarm Escarpment, NT
Gko255	SAM	ABTC32937	<i>Heteronotia</i>	<i>planiceps</i>	-23.37300	120.14200	40km East of Newman, WA
Gko256	SAM	ABTC31418	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.69611	134.03556	Undoolya Homestead, NT
Gko257	SAM	ABTC31432	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.59000	134.47972	Ross River, NT
Gko258	SAM	ABTC31433	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.69611	134.03556	Undoolya Homestead, NT
Gko259	SAM	ABTC31434	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.59000	134.47972	Ross River, NT
Gko260	SAM	ABTC31435	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.69611	134.03556	Undoolya Homestead, NT
Gko261	SAM	ABTC32871	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.69611	134.03556	Undoolya Homestead, NT
Gko262	SAM	ABTC32988	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.69611	134.03556	Undoolya Homestead, NT
Gko280	SAM	ABTC31199	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.69611	134.03556	Undoolya Homestead, NT
Gko281	SAM	ABTC31436	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.69611	134.03556	Undoolya Homestead, NT
Gko282	SAM	ABTC31437	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.69611	134.03556	Undoolya Homestead, NT
Gko279	SAM	ABTC24118	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.89000	133.71972	Mulga Dam MacDonnell Range, NT
Gko283	SAM	ABTC31636	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.59000	134.47972	Ross River, NT
Gko284	SAM	ABTC31659	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.59000	134.47972	Ross River, NT
Gko285	SAM	ABTC31726	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.59000	134.47972	Ross River, NT
Gko286	SAM	ABTC31731	<i>Heteronotia</i>	<i>spelea</i> (central)	-23.59000	134.47972	Ross River, NT
Gko004	WAM	R110056	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-21.03590	117.10658	30km South of Roebourne, WA
Gko005	WAM	R110075	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-21.03590	117.10658	30km South of Roebourne, WA
Gko006	WAM	R110076	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-21.03590	117.10658	30km South of Roebourne, WA
Gko028	WAM	R97258	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-23.36667	120.13333	Wheelarra Hill, WA
Gko029	WAM	R102227	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-23.41139	115.89389	Barlee Range, WA
Gko030	WAM	R102380	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-23.40000	115.88333	Barlee Range, WA
Gko031	WAM	R102436	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-23.13056	115.99444	Goodeman Pool, WA
Gko032	WAM	R113545	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-22.83333	119.46667	Capricorn Roadhouse, WA
Gko033	WAM	R114561	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-23.08333	119.28333	Newman, WA
Gko034	WAM	R115832	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-23.11889	118.78278	The Governor, WA
Gko035	WAM	R115833	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-23.11889	118.78278	The Governor, WA
Gko036	WAM	R121394	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-22.86667	119.43333	Weeli Wolli, WA
Gko037	WAM	R132488	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-23.20000	117.66667	Paraburdoo, WA
Gko038	WAM	R132681	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-20.60028	120.29167	Shay Gap, WA
Gko039	WAM	R135010	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-23.38611	119.62944	Mount Whaleback, WA
Gko040	WAM	R135388	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-22.31056	117.32861	Mount Brockman Station, WA
Gko041	WAM	R135446	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-22.31056	117.32194	Mount Brockman Station, WA
Gko042	WAM	R135456	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-22.31056	117.32194	Mount Brockman Station, WA
Gko043	WAM	R145600	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-20.92860	118.67780	Port Hedland, WA
Gko044	WAM	R157546	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-23.19417	118.81500	West Angeles, WA
Gko045	WAM	R157719	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-22.94083	118.90500	Newman, WA
Gko278	SAM	ABTC11763	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-20.92000	120.20972	Bamboo Creek Mine, WA
Gko287	SAM	ABTC32832	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-20.92000	120.20972	Bamboo Creek, WA
Gko288	SAM	ABTC32922	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-20.92000	120.20972	Bamboo Creek, WA
Gko435	WAM	R111667	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-21.03640	117.10600	TCMBE*, WA
Gko436	WAM	R111927	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-22.60980	120.72900	BDRN09*, WA
Gko437	WAM	R111986	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-22.60980	120.72900	BDRN09*, WA
Gko438	WAM	R160085	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-21.32190	121.00200	NE09*, WA
Gko439	WAM	R160145	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-21.32190	121.00200	NE09*, WA
Gko440	WAM	R161285	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-21.32190	121.00200	NE09*, WA
Gko442	WAM	R165152	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-23.05380	119.17700	PW3*, WA
Gko443	WAM	R165222	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-21.34130	117.18900	DRC6*, WA
Gko444	WAM	R170295	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-21.03640	117.10600	TCMBC05*, WA
Gko445	WAM	R170828	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-23.31830	117.87000	MBE06*, WA
Gko446	WAM	R170892	<i>Heteronotia</i>	<i>spelea</i> (pilbara)	-21.50620	119.41800	MBE1*, WA

Note: Locality information for all individuals sampled in this study. Lab identification numbers (Lab ID#) were given to each sample and used in the figures. Museum # refers to the voucher specimens held in the South Australian Museum (SAM), the Western Australian Museum (WAM) and the Museum of Vertebrate Zoology, Berkeley (MVZ). Locality information is given to the nearest named location as provided by the museums. Localities marked with * refer to sample sites from the Pilbara Biological Surveys (2004) & 2 (2005) (unpublished reports).

sister taxon of *Heteronotia*) (Jackman *et al.* 2008), was used as the outgroup to root the phylogenetic trees.

Molecular data

Data used in this study were obtained from both mitochondrial DNA and multiple nuclear introns to provide robust inference of relationships and divergence history. Initially, the entire mitochondrial NADH dehydrogenase subunit 2 (*nad2*) gene and the flanking transfer RNA (tRNA) genes tRNA^{Met} (partial), and tRNA^{Trp} (entire), tRNA^{Ala} (entire) and tRNA^{Asn} (partial) was sequenced. In addition, nine nuclear introns were amplified using primers developed by Fujita *et al.* (2010). These include *bzw1*, *lztfl1*, *dncl1*, *frih*, *erh*, *nmes*, *rpl14*, *rpl35* and *snrpd3*. Information on primers and marker length is presented in Table 2. Full details of marker development as well as PCR and sequencing amplification are presented elsewhere (Fujita *et al.* 2010).

Sequences were edited in Sequencher 4.0 (Genes Codes Corporation). Where occasional heterozygous indels were found, we concatenated the forward and reverse reads at the indel position, and subsequently coded the indel as missing data. Multiple alignments were performed using MUSCLE (Edgar 2004), which were then refined by eye. Protein coding regions of *nad2* were translated into amino acid sequences using the vertebrate mitochondrial code, and were compared to *Gekko gecko* translations on GenBank to check for stop codons and frame shifts. We then used PHASE V2.1.1, running the algorithm 10 times, to phase the nuclear data into alleles (Stephens & Donnelly 2003), using the most probable reconstructed haplotypes for population genetic analyses. All sequences have been deposited in Genbank (Accession numbers HQ839864 - HQ840286).

Phylogenetic analyses

Phylogenetic relationships were inferred using maximum likelihood and Bayesian inference. Bayesian phylogenetic analyses were conducted in MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003), for individual genes using genotype data for the nuclear markers and for the concatenated dataset as a whole. For each marker, the best-fit models of molecular evolution were estimated under the Akaike Information Criterion (AIC) in MrModeltest v2.3 (Nylander 2004) (Table 2). For the concatenated dataset we calculated Bayes factors (Kass & Raftery 1995) to determine the best partitioning

Table 2. Marker information used in this study

Gene	Abbreviation	Intron	Size (bp) ^a	T _A (°C)	Primers (5'-3') ^b	Model ^c	Primer source
Small nuclear ribonucleoprotein D3	snrpd3	1	620	62	exon 1: ATATTGTGACTTGTGAGACCAATACG exon 2: CGAATGTACACTTGCTCTAACTGTG	HKY	Fujita et al. (2010) Fujita et al. (2010)
Enhancer of rudimentary homolog	erh	3	1750	62	exon 3: TTGATGATTGGCTGATCTTAGCTG exon 4: CCAGTCTTTATTGTAGGGCTGGTATG	GTR+G	Fujita et al. (2010) Fujita et al. (2010)
Ribosomal protein L14	rpl14	1	900	62	exon 1: ACTGGTAGCAATTGTGGATGTTATCG exon 2: GAACCTGAGAACGAAGTCAGTCAGTTG	HKY+G	Fujita et al. (2010) Fujita et al. (2010)
Ribosomal protein L35	rpl35	2	1500	72	exon 2: CAGAGTGCTGACAGTCATTAACCAGAC exon 3: GTCTTCAGACCTCTTCGTGCTTG	HKY+G	Fujita et al. (2010) Fujita et al. (2010)
Basic leucine zipper and W2 domain-containing protein 1	bzw1	2	700	70	exon 2: CTTCTGGAGCAAAGCTTGATTATCG exon 3: ATCGTTTCTAGGTCCTCCTGTGCTG	HKY+I	Fujita et al. (2010) Fujita et al. (2010)
Leucine zipper transcription factor-like 1	lztfl1	1	450	65	exon 1: TGAAGTAATTAACATACGCGATTGTCAC exon 2: TCCAGCATATCTGACACTTCATCTATTG	GTR	Fujita et al. (2010) Fujita et al. (2010)
Ferritin heavy chain	frih	5	1250	70	exon 5: AAGAACATCAACCAAGCTCTCTTGGAC exon 6: TGCTTGATAGCCTGCACTTGATCC	HKY+G	Fujita et al. (2010) Fujita et al. (2010)
Dynein light chain 1	dnc1	1	1500	65	exon 1: TGATCAAGAATGCGGATATGTCTGAG exon 2: TCTTCCCAACAATACAGTGCCAAGTAG	HKY+G	Fujita et al. (2010) Fujita et al. (2010)
Normal mucosa of esophagus-specific gene 1	nmes	3	1400	65	exon 3: ATAAACAACGTGGTAATCCGGAACC exon 4: CTCTTCAATGCGTTTCCACTCCTG	HKY+G	Fujita et al. (2010) Macey et al. (1998)
NADH dehydrogenase subunit 2	nd2		1200	65-42 ^d	L4437: AAGCTTTCGGGGCCCATACC rRNA ^{ASN} : CTAAATRTTRCGGGATCGAGGCC	GTR+I+G	Macey et al. (2000) (modified) Read et al. (2001)

^a Intron sizes are approximate as measured in sample MKF99 (see Fujita et al. 2010)

^b Primers anneal in the indicated exon

^c Model of molecular evolution as inferred in MrModelTest v2.3 (Nylander, 2004) using the AIC

^d Touchdown PCR

strategy (Brandley *et al.* 2005), comparing between (1) unpartitioned, (2) two partitions (partitioned by nDNA and mtDNA), (3) four partitions (partitioned by nDNA and by codon position for *nad2*), and (4) twelve partitions (partitioned by gene and by codon position for *nad2*). The ratio of the harmonic mean likelihoods for competing models were computed using Tracer v1.4.1 (Rambaut & Drummond 2007). For the concatenated analyses, some samples were missing one of the nine genes, but this appeared to have no effect on the ultimate topology. All Bayesian analyses consisted of 4 separate runs, each with 4 chains (3 heated, 1 cold, default heating parameters), for 20,000,000 generations sampled every 2,000 generations, and with 3,000,000 generations burnin. We assessed convergence of most of the Bayesian MCMC analyses in several ways. First, we examined the log-likelihood and parameter estimates over time using Tracer v1.4.1 (Rambaut & Drummond 2007). All runs had ESS values over 200 after discarding the burn-in, indicating we had at least 200 independent samples from the posterior for each analysis. Second, we examined the stability of posterior probabilities of nodes over time by plotting their values over the course of the analysis using Are We There Yet? (AWTY; Wilgenbusch *et al.* 2004). In all cases the posterior probabilities had stabilized after we discarded the burn-in. Finally, we also examined the correlation between the posterior probabilities of the separate runs using AWTY, and in each case the runs were visually strongly correlated. Partitioned maximum likelihood analyses of the combined nuclear data (partitioned by gene), and the mtDNA data (partitioned by codon position), were conducted using RAxML-VI-HPC v7.0.4 (Stamatakis 2006), using the GTR+G model of nucleotide substitution for each data partition. Support values were estimated from 1000 bootstrap replicates.

Recent arguments have been made that concatenation across loci may not be the most reliable approach to inferring the species phylogeny (Kolaczkowski & Thornton 2006; Edwards 2009) particularly when there is rate heterogeneity across loci (Carstens & Knowles 2007). Therefore, in addition to our concatenated approach, we used the hierarchical model implemented in *BEAST v. 1.6.0 (Heled & Drummond 2010), that coestimates the species tree and all gene trees in one Bayesian MCMC analysis, to estimate the species tree phylogeny. This method requires *a priori* designation of species, so we divided our data based on the monophyletic groups that were consistent between mitochondrial and concatenated nuclear analyses resulting in four “species”. Because species tree methods are more sensitive to missing data than supermatrix

approaches (Edwards 2009), we only used individuals in our ingroup represented by complete data, resulting in a dataset of 23 individuals for which each species was represented by at least five samples, with the exception of *H. planiceps* where we only had two. Our outgroup sample, BLS11160 *Dixonius vietnamensis*, contained missing data for one intron, *erh*. We partitioned our data by gene using models inferred in MrModeltest v2.3 (Nylander 2004) under the Akaike Information Criterion (Table 2). We conducted 4 separate runs, with samples drawn every 5,000 steps over a total of 50,000,000 steps, with the first 10% discarded as burn-in. Acceptable convergence to the stationary distribution was checked by inspecting the posterior samples using the diagnostic software Tracer v1.5 (Rambaut & Drummond 2007). Effective sample sizes were >200 for all parameters. All runs produced the same topology with very similar posterior probabilities, so we combined runs to generate a single consensus tree.

To estimate genetic diversity within and between *H. binoei*, *H. planiceps*, and *H. spelea* (“central” and “Pilbara”), we calculated average sequence divergence (Dxy, Nei 1987) using the Tamura-Nei model for mtDNA and concatenated nuclear data separately, using individuals sequenced for all genes, as implemented in Arlequin v3.1.1 (Excoffier *et al.* 2005).

Divergence dating

Using molecular data to place a time frame on divergence events is an active area in phylogenetics, yet there is little agreement on how best to do this. Most of these methods require fossil calibration points to put bounds on internal divergence events (Ho & Phillips 2009), but the reality for most data sets is that the fossil record is limited or non-existent or the fossils are poorly dated themselves (Heads 2005). The fossil record of geckos is particularly poor and there are no fossils available of *Heteronotia* or any closely related genera. In addition, the problems associated with incorporating calibrations have received much attention (Graur & Martin 2004; Hedges & Kumar 2004; Benton & Donoghue 2007; Ho 2007; Ho & Phillips 2009), and it is becoming increasingly apparent that the type of calibrating information used in the dating analysis can significantly affect estimates of divergence times (Ho *et al.* 2008).

For a direct comparison with the analyses performed in Fujita *et al.* (2010) for divergences among lineages of *H. binoei*, we used a relaxed molecular clock in BEAST

v1.5.2 (Drummond & Rambaut 2007), calibrated using a fixed calibration point from an inferred date of divergence within the *H. binoei* lineage (Strasburg & Kearney 2005), which itself is based on the *nd2* substitution rate in agamid lizards of Macey *et al.* (1998). We used our concatenated nDNA dataset that included only those individuals that had complete data. We unlinked loci and substitution models, and assigned the most appropriate model of sequence evolution based on the results provided above. To allow for rate heterogeneity among lineages we employed an uncorrelated lognormal relaxed clock (Drummond *et al.* 2006). We used a coalescent tree prior because of the recent relationships of the individuals. The constant population size model was chosen based on results from Bayesian Skyline Plots (not shown). For the prior age of the *H. binoei* node, we specified a normal distribution with a mean of 5.47 Mya and standard deviation of 0.7 (Fujita *et al.* 2010). We also specified a prior age for the root node using a gamma distribution (offset 19 Mya, shape=2.0, scale=0.5), corresponding to the estimated time when faunal exchange initiated between Southeast Asia and Australia (Heatwole 1987). Posterior estimates of parameters were obtained via Markov chain Monte Carlo (MCMC) sampling. We conducted three independent runs, with samples drawn every 20 000 steps over a total of 200,000 000 steps, with the first 10% discarded as burn-in. Acceptable convergence to the stationary distribution was checked by inspecting the posterior samples using the diagnostic software Tracer v1.5 (Rambaut & Drummond 2007).

There are a number of limitations and problems associated with this type of dating analysis, the most important of which are the use of a tertiary calibration point (Graur & Martin 2004) and the application of a date calibration based on a mtDNA substitution rate that we used on our combined nDNA data, which assumes the nuclear loci share the same time to most recent common ancestor (TMRCA) as the mtDNA locus. To explore the effect of incorporating different calibration methods, we also used two alternative approaches to estimate the approximate timing of diversification events within *Heteronotia*, which we briefly outline below.

First, we used the Dxy mtDNA genetic distances between lineages and applied the mtDNA substitution rate of 1.3% pair-wise divergence / million years as derived by Macey *et al.* (1998). This rate estimation has been applied widely in dating phylogenies for many groups of vertebrates, particularly reptiles (Schulte *et al.* 2000; Melville *et al.*

2004; Glor *et al.* 2005; Oliver *et al.* 2009). This rate also was used in several previous phylogeographic studies on *Heteronotia* based on the same region of mtDNA (Strasburg & Kearney 2005; Strasburg *et al.* 2007). In addition, we used a relaxed molecular clock in BEAST v1.5.2 calibrated using the mitochondrial substitution rate of 0.57 % per lineage per Mya as determined by Macey *et al.* (1999) based on *Teratiscincus* geckos, rather than using an inferred date. With no information on the evolutionary rates of the nuclear introns utilized in this study, we excluded the nDNA data and used the mtDNA data only. We assigned the GTR+I+G nucleotide substitution model with 6 rate categories for the discrete gamma distribution. Given the variation in topology from the nDNA data, we constrained the topology to that of the combined mtDNA and nDNA tree from MrBayes. We ran the same analysis without the topology constraints to assess any difference in divergence date estimates. To allow for rate heterogeneity among lineages we employed an uncorrelated lognormal relaxed clock (Drummond *et al.* 2006). We used a constant-size coalescent prior for the tree. We specified a normally-distributed prior (mean 6.5×10^{-9} subs/site/yr, standard deviation 2.55×10^{-10} subs/site/yr) for the *mean of branch rates parameter* (ucl.d.mean). Default priors were used for the remaining parameters. An important difference from the previous dating analysis is that we did not specify a prior age for the root node, which could result in discrepancies between the analysis methods. We conducted 4 independent runs, each for 50,000,000 steps.

Results

Following the removal of ambiguously-aligned nucleotide sites, the final mtDNA dataset consisted of 1041 base pairs (bp) and the nDNA dataset consisted of 7872 bp. For the concatenated analyses, we compared partitioning strategies using Bayes factors. Comparing between (1) unpartitioned, (2) two partitions (partitioned by nDNA and mtDNA), (3) four partitions (partitioned by nDNA and by codon position for *nad2*), and (4) twelve partitions (partitioned by gene and by codon position for *nad2*), support is strongest for the twelve partition model (Table 3). The partitioned Bayesian analyses of the concatenated nDNA (Figure 2) and the combined (mtDNA + nDNA) (Figure 3) trees strongly support the monophyly of the three described species of *Heteronotia* (with 100% posterior probability support; pp 1.00). The mtDNA tree corroborated this result but with lower support for the monophyly of *H. binoei* and *H. planiceps* (pp 0.82

Table 3. Bayes factors comparisons of different data partitions for the concatenated data. Standard errors (S.E.) were estimated using a bootstrap procedure with 1,000 replicates in Tracer v.1.4 (Rambaut and Drummond, 2007). Negative values indicate support for the alternative model.

Concatenated Data	Ln P(model data) (harmonic mean)	S.E.	Alternative Model			
			Unpartitioned	2-Partitions (nDNA & mtDNA)	4-Partitions (nDNA & mtDNA by codons)	12-Partitions (by genes & codons)
Unpartitioned	-30959.225	+/- 0.248	—	-77.752	-157.163	-182.058
2-Partitions (nDNA & mtDNA)	-30780.194	+/- 0.266	77.752	—	-79.411	-104.306
4-Partitions (nDNA & mtDNA by codons)	-30597.344	+/- 0.331	157.163	79.411	—	-24.895
12-Partitions (by genes & codons)	-30540.02	+/- 0.311	182.058	104.306	24.895	—

and 0.92, respectively) (Figure 4). All central Australian samples variously identified as *Heteronotia* sp. (Moritz *et al.* 1990), *H. spelea* (Cogger 2000) or *H. binoei* (Wilson & Swan 2003) group together in our phylogenies as a highly divergent sister-clade to *H. spelea*. This relationship is strongly supported in both the concatenated nDNA tree as well as the combined tree (pp 1.00) but has poor support in the mtDNA tree (pp. 0.67). Samples of *H. planiceps* recorded from Newman in the Pilbara region are nested within the *H. spelea* clade in all analyses. The relationship between the lineages of *H. spelea*, *H. planiceps* and *H. binoei* were not resolved despite the large data set. The very short branch lengths in this part of the phylogeny suggests that the poor resolution is most likely due to rapid speciation of the three major clades over a short period of time (eg. Willerslev *et al.* 2009). The partitioned maximum likelihood analyses of both the concatenated nuclear data and the mtDNA data recovered the same topology as the partitioned Bayesian analyses (not shown), but the relationships between species are not strongly supported, with the exception of the sister relationship of the two *H. spelea* clades for which there is good support. The species tree estimated using *BEAST recovered a topology identical to the combined concatenated mtDNA and nDNA, again with support for the sister relationship of the two *H. spelea* clades (pp. 0.96) but with similarly weak support for the sister relationship of the *H. spelea* clades to *H. planiceps* (pp. 0.75)(Figure 3).

Our sampling across the lineages of *Heteronotia* has revealed that rather than existing across multiple mountain ranges, *H. spelea* and *H. planiceps* have geographic distributions confined to separate mountain ranges (Figure 1). *Heteronotia planiceps* is restricted to the Kimberley region, despite the morphologically similar individuals found in the Pilbara. The two divergent clades of *H. spelea* have disjunct distributions, with one restricted to the Pilbara (herein referred to as Pilbara *H. spelea*) and the other found only in the central Australian ranges (herein referred to as Central *H. spelea*). Taxonomic revisions based on the results presented here are currently in preparation.

A substantial amount of variation was found within each of the three major lineages of saxicolous *Heteronotia*. Despite limited sampling, we found high genetic diversity across the Kimberley range of *H. planiceps*, with mtDNA diversity almost equal to that across the entire continental range of *H. binoei* (Table 4) (Fujita *et al.* 2010). Our sampling is greatest for Pilbara *H. spelea* and also highlights substantial genetic

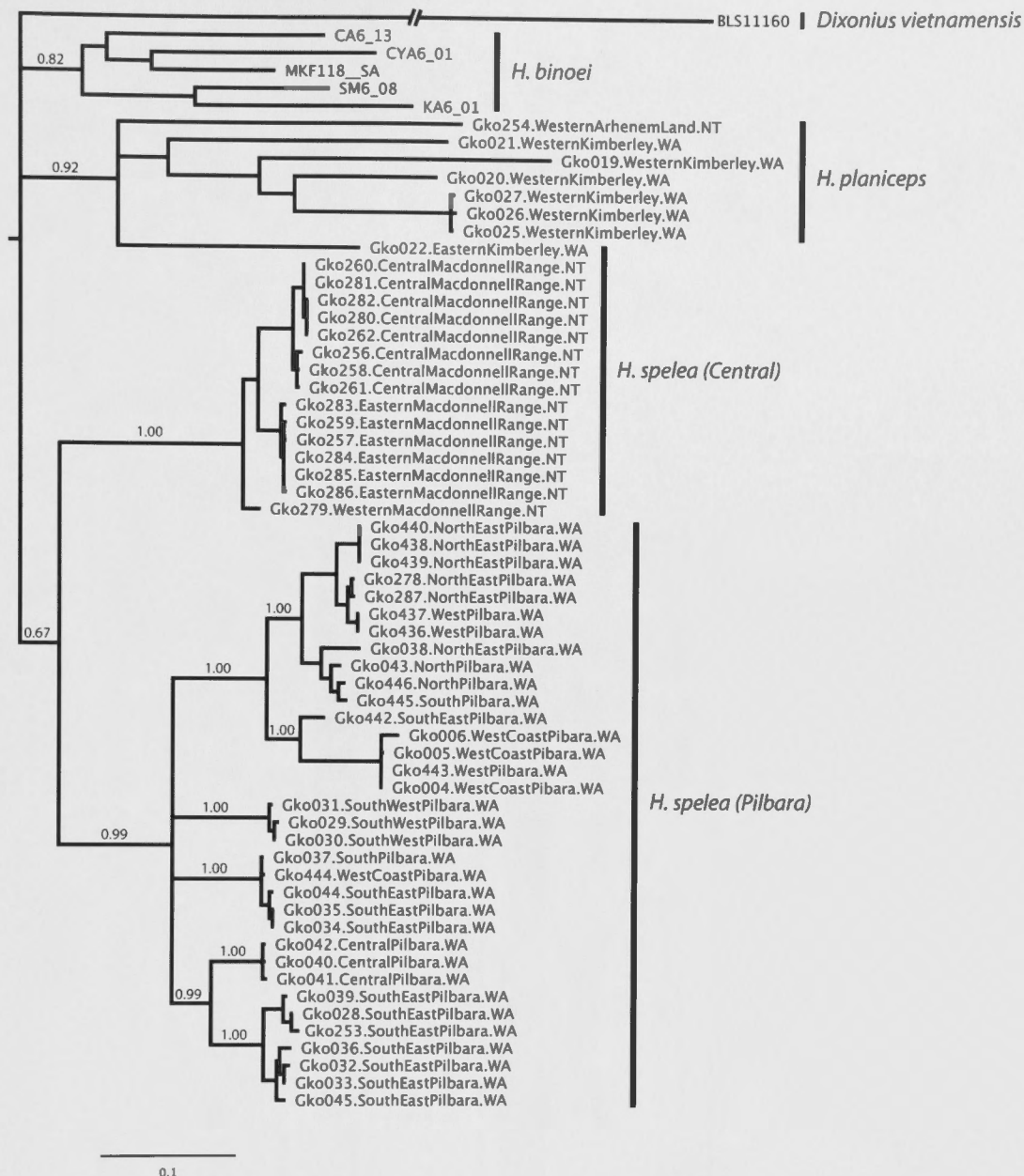


Figure 4. Representative phylogram based on Bayesian analyses of the mitochondrial set. Values refer to Bayesian posterior probabilities.

Table 4. Measures of diversity and divergence

Taxon	mtDNA uncorrected "P" distance	mtDNA corrected Tamura-Nei diversity	Combined nDNA uncorrected "P" distance	Combined nDNA corrected Tamura-Nei diversity
<i>H. binoei</i> (n = 4)	0.1287 (0-0.1402)	0.1467	0.0167 (0-0.0207)	0.0162
<i>H. planiceps</i> (n = 6)	0.1146 (0-0.1623)	0.1323	0.0097 (0-0.0153)	0.0023
Central <i>H. spelea</i> (n = 14)	0.0218 (0-0.0365)	0.0226	0.0039 (0-0.0094)	0.0041
Pilbara <i>H. spelea</i> (n = 29)	0.0710 (0-0.1047)	0.0777	0.0082 (0-0.0164)	0.0078

Taxon	mtDNA uncorrected "P" distance	mtDNA corrected Tamura-Nei Dxy	Combined nDNA uncorrected "P" distance	Combined nDNA corrected Tamura-Nei Dxy
<i>H. binoei</i> and <i>H.planiceps</i>	0.1615 (0.1422-0.1787)	0.1887	0.0202 (0.0159-0.0233)	0.0205
<i>H. binoei</i> and Pilbara <i>H.spelea</i>	0.1382 (0.1201-0.1575)	0.1582	0.0211 (0.0156-0.0272)	0.0215
<i>H. binoei</i> and Central <i>H.spelea</i>	0.1437 (0.1239-0.1595)	0.1666	0.0199 (0.0151-0.0255)	0.0209
<i>H. planiceps</i> and Pilbara <i>H.spelea</i>	0.1575 (0.1431-0.1739)	0.1834	0.0197 (0.0144-0.0274)	0.0186
<i>H. planiceps</i> and Central <i>H.spelea</i>	0.1593 (0.1479-0.1691)	0.1862	0.0179 (0.0160-0.0228)	0.0182
Pilbara <i>H. spelea</i> and Central <i>H. spelea</i>	0.1340 (0.1076-0.1537)	0.1537	0.0129 (0.0087-0.0215)	0.0136

structure across the region. Six major clades were identified in the mtDNA tree, with an overall average nucleotide diversity of 7.77%. The geographically limited sampling of Central *H. spelea* revealed less genetic diversity than in the Pilbara population (dxy = 2.3%), and this result holds with recent extended mtDNA sampling across the species distribution (Fujita, Pepper & Moritz, unpublished data). Pairwise mitochondrial sequence divergences between the three major lineages ranged from 15.37% (Pilbara-Central *H. spelea*) to 18.87% (*H. binoei*-*H. planiceps*). Corresponding nuclear divergences ranged from 0.77% (Pilbara-Central *H. spelea*) to 1.51% (*H. planiceps*-Central *H. spelea*).

Divergence dating

Each of our dating approaches produced different age estimates, and this is expected given the different ways in which calibration points and rates of molecular evolution were incorporated into the analyses. Dividing the genetic distance between lineages with the substitution rate of Macey *et al.* (1998) estimated major *Heteronotia* lineages diverged between 12 and 15 Mya. The relaxed lognormal clock analysis of the mtDNA dataset using the substitution rate calibration produced the oldest date estimates, as expected because no age was specified on the root node. Divergence times from this method suggest that *Heteronotia* lineages split between 26 to 34 Mya. To facilitate comparison with divergence dynamics in *H. binoei*, we largely restrict our discussion to the dates derived via the relaxed lognormal clock analysis of the combined nDNA and a fixed calibration point (Figure 5). Using this method, estimated divergence times between the major lineages (*H. planiceps*, *H. spelea* and *H. binoei*) occurred in the Pliocene between 3.9 and 4.2 Mya (2.5 – 5.7 Mya, 95% HPD estimate). The split between Pilbara and Central *H. spelea* occurred in the late Pliocene/early Pleistocene, around 2.9 Mya (1.9 – 4.0 Mya, 95% HPD estimate) (Figure 5). Our results exclude the hypothesis that these lineages separated in conjunction with the development of sand dune systems and at the same time as expansion of arid lineages *H. binoei* (<1 Mya, Fujita *et al.* 2010).

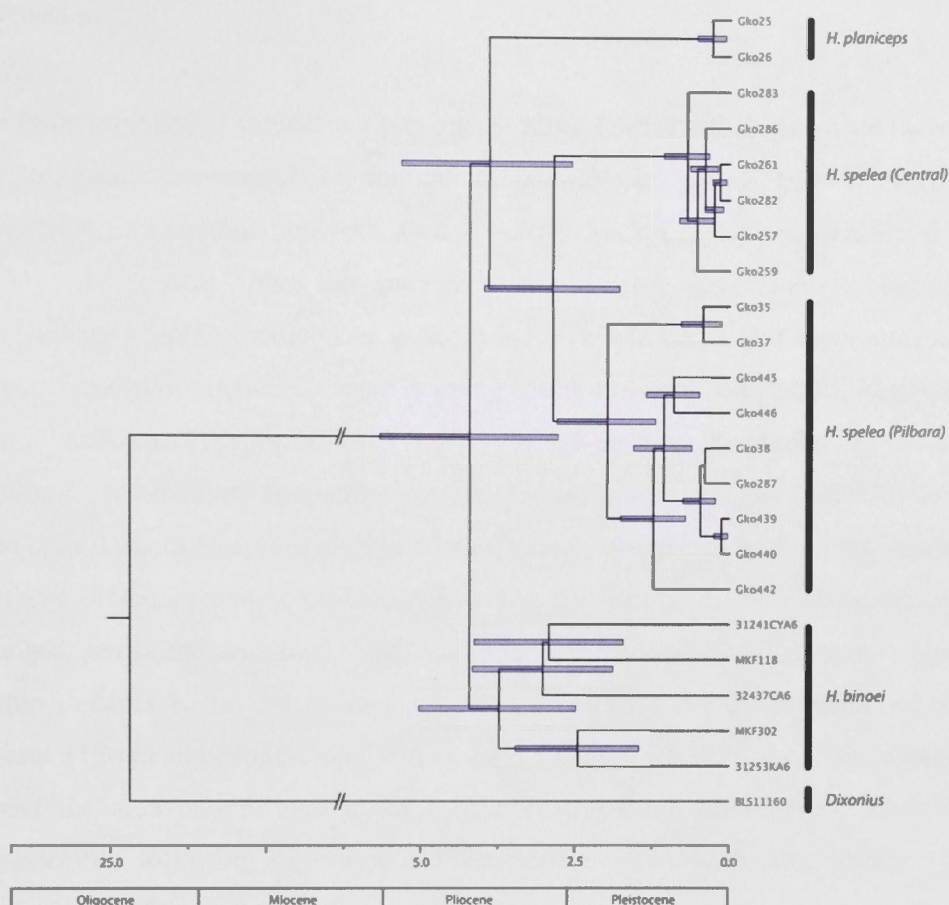


Figure 5. Cladogram inferred using a relaxed molecular clock implemented in BEAST v. 1.5.3 using a subset of the nuclear data, with time axis indicated on the bottom. Node bars represent 95% confidence intervals.

Discussion

We have produced a multilocus phylogeny using both mtDNA and nine independent nuclear genes allowing us to confidently identify the genealogical lineages within *Heteronotia*. In combination with what already is known of the geological and climate history of the arid zone, our molecular results give important insights into the mechanisms shaping biodiversity in the Australian arid zone. Our topologies show no recent connectivity between the saxicolous populations from the Pilbara, Kimberley and central Australian ranges, as each region harbors its own divergent lineage of rock-dwelling *Heteronotia*. Furthermore, large amounts of genetic structure within *H. planiceps*, Pilbara *H. spelea* and, to a lesser extent, Central *H. spelea* indicate that each of these mountain ranges enabled population persistence as climates and landscapes changed across the arid zone. Finally, the timing of diversification both between and within lineages is too old to have arisen as a result of the development of the sand deserts >1 Mya and expansion of arid *H. binoei* lineages. Rather, the climate and habitat across the area presently occupied by the central sand deserts must have changed considerably following the onset and development of aridification through the late Miocene and Pliocene to fragment populations of *Heteronotia* ancestors early in the history of arid zone development.

Biogeography and diversification of the rocky endemics

The rock-specialized habit of both *H. spelea* and *H. planiceps* highlights the relevance of an understanding of the geological setting around which these species have evolved. The regions where *H. spelea* and *H. planiceps* are found are geologically and topographically diverse compared to surrounding areas, primarily due to the unique geological structure of the Pre-Cambrian Australian craton. The landforms of the Kimberley are rugged, characterized by intensely folded and faulted rocks, steeply scarped sandstone-capped hills and mountains and limestone gorges (Bridgewater 1987) that are bound to the south by the monotonous expanse of linear sand ridges of the inland deserts (Beard 1979). The south and central Pilbara is composed of two major mountain ranges, with deep gorges incised into the ironstone hills, while the northern Pilbara is dominated by gently rolling hills of deeply weathered granites. This region is bound on its north and eastern sides by the inland deserts. The central Australian ranges are comprised of rugged strike ridges and valleys of granites and limestones, with large

Salinas and numerous dry-bed river systems (Mabbutt 1988; Boden & Given 1995). These inland ranges are entirely surrounded by desert lowlands, which has a strong influence on the extreme climates experienced in this region.

Contrary to previously reported distributions, *H. planiceps* and *H. spelea* (Pilbara *H. spelea* and Central *H. spelea*) have entirely disjunct distributions with each lineage confined to a separate mountain system within and peripheral to the arid zone. The sister relationship between lineages of *H. spelea* in the Pilbara and those in the central Australian ranges is concordant with the genetic results of a recent study on a dragon lizard (*Tympanocryptis*; Shoo *et al.* 2008) and gecko (“CA6” *Heteronotia binoei*; Kearney *et al.* 2003, Fujita *et al.* 2010) where both show disjunct distributions across the central deserts. Similarly, Cracraft’s (1991) assessment of the area relationships within a number of Australian vertebrate groups found the arid zone regions of the Pilbara and “Central Highlands” (included in his “Western Desert”) to be most closely associated, while the Kimberley region always is more distantly associated (Cracraft 1991). This genetic clustering agrees with what is known of the landscape history in the area. Despite the geological similarities of the Kimberley, central Australian ranges and the Pilbara, the climate of the Kimberley is substantially different to the southern mountain ranges, largely due to the dominating influence of the summer monsoon (Wyrwoll & Miller 2001). Accordingly, vegetation in the Kimberley also is very different compared to the Pilbara and central Australian ranges, with large areas dominated by tropical high-grass and woodland savanna (Beard 1979). In contrast, the shrubby *Acacia* habitat that dominates the Pilbara and central Australian ranges also exists in a very narrow belt through the sand deserts that separate these regions. Known as the ‘Giles Corridor’ (Pianka 1972) the extent of this habitat juncture is thought to have expanded and contracted in response to past changes in climate, periodically connecting the mountain ranges via a corridor of favorable habitat. Increased wind activity potentially could enable sandy top-soils to be swept away, exposing harder sub-soils underneath that allowed the spread of shrubby habitat. However, increased aridity could easily have tipped the balance in favor of *Triodia* grass habitat, which would isolate the Pilbara and central Australian ranges from one another with tracts of unsuitable habitat (Pianka 1972, Shoo *et al.* 2008). The large genetic distance between Pilbara and Central *H. spelea* lineages suggests that if the Giles Corridor promoted connectivity between the Pilbara and central Australian ranges for these species, it must

have been insufficient to allow gene-flow between these regions early in the speciation of the lineage that has persisted to the present time.

Persistence within mountain systems

The large amount of intraspecific diversity within the Pilbara lineages of *H. spelea* and Kimberley/Ord range of *H. planiceps* and their long-isolated distributions in different mountain ranges provides strong evidence that the Pilbara and Kimberley provided refugia during the unfavorably hyper-arid cycles during the Neogene and Quaternary. The ability of these regions to provide more thermally buffered climatic conditions is a direct result of topography, which in turn is intimately tied to the history and geological composition of the Australian craton. While only represented by a small number of samples, *H. planiceps* displays extraordinarily high sequence diversity across its small geographic range of the Kimberley, on par with the diversity found across the entire continental range of *H. binoei* (Fujita *et al.* 2010). This may in part be explained by the particularly heterogeneous nature of the Kimberley landscape, with plateaus, gorges, rivers, and numerous islands providing ample barriers to dispersal for non-vagile organisms (Phillips *et al.* 2009). Our data further support that the Kimberley has been an important centre of diversification and endemism for terrestrial biota (Bowman *et al.* 2010) and highlights the need for further genetic studies in the area. Our sampling is greatest for Pilbara *H. spelea* and this too shows substantial genetic diversity across the region, consistent with what already has been found for other Pilbara reptiles (Pepper *et al.* 2006, 2008; Shoo *et al.* 2008). The central Australian uplands are a major topographic feature in Australia's arid region, further emphasized because they are completely isolated by surrounding deserts. While coastal mountain ranges such as the Pilbara or Kimberley would have been wetter and more thermally buffered (Byrne *et al.* 2008), the ranges in central Australia experienced more severe arid conditions, as well as temperatures that were much colder than at present (Miller *et al.* 1997). This hyper-arid climatic history is thought to have repeatedly extinguished narrowly endemic taxa in central Australia during the Pleistocene (Crisp *et al.* 2001). A similar pattern was identified by Linder (2000) of plant endemism in sub-Saharan Africa, where the expansion of deserts during arid cycles promoted a series of extinctions, even in apparently suitable mountain refugia. The low level of genetic diversity within Central *H. spelea* compared to lineages in other rocky ranges provides further support for a loss

of genetic diversity in this region of Australia during periods of extreme aridity, but not for regional extinction in this case.

Divergence dating

The inland sand deserts of the Australian arid zone represent recently derived landforms, thought to only have existed for the last million years. Prior to this time, the landscape would most likely have consisted of hard, lateritic soils (Beard 1969; R. Wasson, pers com). Contraction of the sclerophyll and wet forest that extended across inland Australia would have been concomitant with the initiation and spread of arid conditions from the mid Neogene (<15 Mya) onwards (Martin 2006). Results from our dating analysis following the method of Fujita *et al.* (2010) suggest the divergence between *H. binoei*, *H. planiceps* and *H. spelea* conservatively dates to the Pliocene/early Pleistocene, with short branch lengths and largely overlapping confidence intervals suggesting near simultaneous diversification. This timing is much older than the postulated maximum age of 1 Mya for the development of the sand deserts, implying the mobile desert landform was not responsible for isolating historical *Heteronotia* populations in the mountains. Similar ages were estimated for divergences between major lineages of the *H. binoei* complex (Fujita *et al.* 2010). These divergence times coincide with a time of extreme environmental change associated with deepening aridity and increased seasonality (reviewed in Byrne *et al.* 2008). In particular, the basin areas separating the uplands experienced a major termination of the warmer, wetter conditions experienced in the early Miocene, with the cessation of palaeodrainage channels in central and western Australia as well as unprecedented levels of erosion across the landscape (Martin 2006). While precise palaeoclimate reconstructions may never become available for the late Miocene due to a loss of a continuous geological record (Hill 1994; Byrne *et al.* 2008) it is likely that conditions in central and western Australia previously considered favorable by *Heteronotia* ancestors, would have changed sufficiently in the lowlands to fragment populations into the moister refuges of the rocky uplands of the Pilbara, Kimberley and central Australia. Our dating exercise suggests the split between Pilbara and Central *H. spelea* occurred more recently around 2.9 Mya, and possibly much earlier, which is also older than the geological age of desert formation. In contrast to the saxicolous *Heteronotia*, divergences within the arid zone lineages of *H. binoei*, a habitat generalist, were dated between 0.69 and 2.27 Mya (SM6) and 0.3 and 1.14 Mya (CA6) Mya, with strong signatures of recent population

expansion <1 Mya (Fujita *et al.* 2010). This timing is consistent with the opening and spread of sand desert landforms in the arid interior, highlighting the recent connectivity between populations of this closely related species. Together, our studies on *Heteronotia* illuminate the contrasting roles of geological, landscape and climate evolution on the diversification of saxicolous and desert lineages, and make an important contribution to our understanding of wide-scale biogeography in the Australian arid zone.

A species of the rock-loving *Heteronotia* gecko.

Photo: Patrick Cullen

The genes of the gecko

Over the past 50 million years the Australian continent has weathered a storm of extreme climate changes. Huge areas of Western Australia were once covered by an extensive inland sea. In the centre, tropical vegetation flourished like a verdant oasis, replaced over time by dunes of windblown sand. The effects of these climatic fluctuations on the natural world can be seen in the immense diversity of species that have evolved in response.

I study extant organisms (ones that are alive today) and it is relatively easy to get a genetic sample that can provide a window into the past evolutionary history of my study animal. Using complicated computer models that use information on the variation between strands of DNA from different individuals, I can graphically depict the genetic diversity that exists within a species. I use this genetic "tree" in conjunction with known geographic distributions to get an idea about which areas of Australia contain a lot of genetic diversity, and are therefore important for conservation.

Over the years, scientists that study completely different types of organisms have identified the same areas in Australia where there are higher levels of genetic diversity within their study organisms than elsewhere. They call these regions "glacial refugia", and according to evolutionary biologists these areas have been tremendously important in the diversification and speciation of plants and animals in Australia.

The idea is that during the many ice ages that have occurred in the past (every 100 thousand years or so in the last two million years), the climate in Australia became significantly drier and more inhospitable. During these times, plants and animals that needed moister environments retracted their distributions into "refuge" areas (commonly mountain ranges)



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where they were able to persist during these unfavourable conditions that often lasted for tens of thousands of years. When populations of the same species were isolated in different refugia, they temporarily evolved separately from one another, sometimes so much that when the arid conditions eased and the populations became connected again, they no longer recognised each other. Reproductive isolation and speciation had occurred. If you imagine this happened every time there was an ice age, you can see how these refugia facilitated such spectacular diversification of organisms.

Without knowledge of past climate change in Australia, evolutionary biologists cannot make sense of the genetic patterns that exist in the plants and animals we see today. While I primarily study genetics, the full story about how a species evolved doesn't emerge until you mix this genetic information with other fields. A big part of my research focuses on understanding what happened to climate patterns and landscape changes that could have affected the way species evolved in the Australian deserts.

I have spent the past two years studying the genetic patterns within and among three species of closely related geckos, all in the same Genus (or group) called *Heteronotia*. Each of these species likes rocky habitats, and occurs in different mountainous regions; one in the Pilbara in Western Australia, another in the Kimberley in the far north-west, and the third in the Central Ranges in the middle of the continent. Despite their current distance from one another, each species is very closely related,

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1. True or false? Stomach ulcers are caused by stress and lifestyle factors.
2. What is the only human infectious disease to have been completely eradicated?
3. The movie *The Dish* is based on what astronomical instrument located in Parkes, NSW?
4. Which Australian scientist appears on the fifty dollar note?
5. How much coal do you need to burn to run a single bar radiator for one hour?

Answers: 1. False. Stomach ulcers are caused by *Helicobacter pylori*, a bacterial infection treatable by antibiotics. This was discovered in 1984 by Australian scientists Barry Marshall and J. Robin Warren. 2. Smallpox. 3. CSIRO's Radio Telescope. The Dish was involved in broadcasting the 1969 moon landing. 4. Sir Howard Florey. Regarded as Australia's greatest scientist, he produced modern day antibiotics in 1940. 5. Half a kilogram of black coal or 1.5kg of lower quality brown coal.

and they all arose from a common ancestor. Why did these geckos evolve into three different species? And were they driven into these mountainous regions because of climate change?

It is amazing what the genes of modern organisms can reveal about the evolution of ancestors that haven't existed for millions of years. With knowledge of the speed at which some genes evolve, we can even work out (albeit crudely) when different species diverged from one another. My research shows that the three species of gecko split from one another around seven

million years ago. How can I use this to start piecing together the puzzle?

Palaeo-climate scientists know that the arid zone in Australia started to develop around 15 million years ago, and following this onset were pulses of wetter times during the ever-increasing trend towards permanent aridity. The area most affected by this changing climate was central and north-western Australia, the region in between the three mountain refugia where the geckos are currently found. Scientists in the Department of Nuclear Physics at the Australian National University have used cosmogenic techniques (measuring the speed of decay of certain isotopes) to date the sand dunes in Australia, and believe they formed about one million years ago.

While a certain amount of arm-waving and story telling is inherent, it is hypothesised that during the harshest arid periods, the once widespread species of gecko retracted its distribution into different mountain ranges. Over millions of years, these populations became more and more different, until they stopped mixing their genes around seven million years ago. These geckos may not always have been rock specialists, but the development of vast sand deserts in between their refugia was enough to isolate them completely.

With more than one million years of evolution gone by, trapped in the mountains by a barrier of impenetrable sand, who knows when they will move out of their rocky refuges and start the cycle again? In the meantime, in evolutionary timescales, the opportunity for sand loving geckos to colonise the deserts and speciate has only just begun.

■ Mitzy Pepper is a third-year PhD student in the School of Botany and Zoology at the Australian National University, studying the evolution of geckos in the Australian deserts.

Chapter II

**The genetic legacy of aridification: Miocene refugia fostered
diversification while Pleistocene climate cycles erased
diversity in desert lizards**



Red sand dunes on the outskirts of the SW Pilbara, Western Australia

Molecular Phylogenetics and Evolution
(in revision)

Abstract

It is a widely held assumption that populations historically restricted to mountain refugia tend to exhibit high levels of genetic diversity and deep coalescent histories, while populations distributed in surrounding low-lying regions tend to be genetically depauperate following recent expansion from refugia. These predicted genetic patterns are based largely on our understanding of glaciation history in Northern Hemisphere systems, yet remain poorly tested in analogous Southern Hemisphere arid systems because few examples in the literature allow the direct comparison of widespread taxa distributed across mountain and desert biomes. We demonstrate with multiple data sets on Australian reptiles that topographically complex mountain regions harbor extremely high nucleotide diversity, up to 18 times higher than that of the surrounding deserts.

We further demonstrate that taxa in topographically complex areas have substantially older coalescent histories than those in the geologically younger deserts, and that both ancient and more recent aridification events have contributed to these patterns. Our results show that, despite differences in the details of climate and landscape changes that occurred in the Northern and Southern hemispheres (ice-sheets versus aridification), similar patterns emerge that illustrate the profound influence of the Pleistocene on contemporary genetic structure.

Introduction

Considerable research attention has focused on the evolution of Northern Hemisphere taxa in response to glacial cycles (Shafer *et al.* 2010), driven in part by the classic review by Hewitt (2000). In particular, an increasing number of molecular studies have highlighted the importance of Pleistocene refugia in generating and sustaining genetic diversity in boreal and temperate systems (Stewart *et al.* 2010), as species repeatedly contracted their distributions in response to the periodic extension of ice sheets (Hewitt 1999), or the contraction and dissection of tropical and temperate forests (Moritz *et al.* 2000). Despite this recent work, we are only just beginning to scratch the surface in our understanding of climate-induced biotic diversification in arid systems (Beheregaray 2008). Few examples in the literature have directly addressed the impact of aridification on evolutionary history (Bowie *et al.* 2006), or the role of refugia in arid biomes recently inundated by sand deserts (Toon *et al.* 2007).

Arid conditions are thought to have been prevalent during the Mid-Miocene associated with global Cenozoic cooling (Flower & Kennett 1994), so processes underpinning modern evolutionary patterns of arid-zone taxa are likely to have a deep history (Melville *et al.* 2009). However, the initiation of glacial cycles in the Plio/Pleistocene caused immense global change (Clark *et al.* 2006), and the spread of continental ice-sheets across the Northern Hemisphere during glacial cycles was concomitant with cool, arid periods over mid-latitude continental regions. In addition, the transition from high-frequency, low-amplitude glaciations (every 40 thousand years (ka)) that characterized the late Pliocene/early Pleistocene, to the low-frequency, high-amplitude glaciations (every 100 ka) that became established in the middle Pleistocene (Huybers 2007) led to increasingly severe aridification and the development of sand deserts on immense scales (Hartley & Chong 2002; Fujioka *et al.* 2009; McLaren & Wallace 2010). Such dynamic landscape changes over large continental areas would have had a profound effect on the evolution of biota that inhabited these regions, with refugia undoubtedly playing a major role.

Refugia typically occur in regions with heterogeneous topography and serve as centers of persistence for both warm and cold-adapted species by retaining relative climatic stability during periods of hostile climate (Hewitt 1999). While the refugial concept

implicitly involves a reduction in population size (bottleneck) (Bennett & Provan 2008), diversity has been shown to accumulate over time through the repeated movement of populations both in and out of the refugium, as well as over altitudinal gradients. The resulting pattern is one of increased genetic diversity in topographically complex regions, with taxa displaying deep coalescent histories (Hewitt 1999). Refugia also serve as sources from which adjacent regions were recolonized following amelioration of climatic conditions during interglacial periods. Examination of genetic signatures of Northern Hemisphere post-glacial colonizers has revealed insights into routes of colonization and the mode and tempo of dispersal (Taberlet *et al.* 1998). The most recent expansion episode followed the retreat of ice-sheets and permafrost after the Last Glacial Maximum < 20 000 years ago (Clark *et al.* 2009). Coupled with this recent history, where post-glacial expansion occurs rapidly, leading-edge expansion can result in large geographic areas that contain low genetic diversity (Mila *et al.* 2000).

Despite the different environmental agents driving changes in species distributions (permafrost and ice-sheets versus aridity and deserts), we might expect some similarities between temperate and boreal taxa, and their arid-zone counterparts, in their genetic response to major climatic change. Assuming that the expansion of arid systems was unfavorable for mesic biota, the distribution of mesic taxa would have been fragmented as these organisms retreated into moister pockets that typically occur in areas of higher elevation and topographic complexity. Indeed, rocky ranges in present-day arid zones often harbour discrete genealogical lineages (e.g. Smit *et al.* 2007). However, in contrast to Northern Hemisphere refugial scenarios, where expansion and contraction of species distributions occurred regularly throughout the last three million years, the onset and development of arid conditions during the Miocene eventuated in increasing and permanent aridification, potentially isolating mesic taxa in refugia for extremely long periods of time. We would therefore predict that populations restricted to mountain refugia in arid zones, and thus unaffected by severe aridification, should show high levels of genetic diversity and deep phylogeographic structure among disjunct refugia, with deep coalescence histories resulting from many millions of years in isolation. For arid-zone taxa distributed throughout desert regions, we would expect populations to be less diverse than their rocky relatives due to the geologically young nature of the desert biomes. Furthermore, in regions most affected by Plio/Pleistocene aridification and the advancement of sand dunes, we expect populations to have very

shallow coalescence histories due to recent bottlenecks, as well as strong signatures of population expansion as arid-adapted taxa expanded their distributions with the opening of new desert biomes (Fujita *et al.* 2010).

These predictions are intuitively obvious yet remain poorly tested because few examples in the literature incorporate appropriate sampling of widespread taxa that allows the direct genetic comparison of taxa distributed across both mountain and desert biomes. Here we use new and published genetic data from three wide-ranging gekkonid radiations that span the vast arid zone of Australia, a biome larger than the area of Europe, to test hypotheses on refugial isolation and arid zone diversification. This region presents an ideal system because it contains a number of ancient, stable, topographically complex areas that are isolated by a continuous expanse of low-lying sand deserts that are thought to have existed for less than one million years (Figure 1; Fujioka *et al.* 2009). We analyse large mitochondrial DNA (mtDNA) datasets to evaluate the genetic patterns and evolutionary histories of mountain and desert dwelling clades in response to changing climates since the Miocene, specifically to address the following questions: (1) Do mountain ranges harbour more diversity than the surrounding deserts? (2) Is the diversity in mountain ranges older than in the deserts? We consider our results for these questions, along with the inferred demographic history, in light of the climatic and landscape history of the Australian arid zone to address a third question: (3) How did populations respond to increasing aridity and more severe glacial cycles of the mid-Pleistocene? Our results imply very different evolutionary outcomes for taxa in mountain versus desert landscapes, and suggest the deepening aridity of the Pleistocene had a profound influence on the genetic architecture of desert clades.

Materials & Methods

Sampling and sequencing

We generated large mtDNA datasets from three gekkonid radiations, providing us with three independent estimates of coalescent histories. Recent genetic sequencing of nuclear loci supports the major mtDNA phylogroups in each of the taxa (Pepper *et al.* 2006; Oliver *et al.* 2007; Fujita *et al.* 2010; Pepper *et al.* 2011 [Chapter I]). The gekkonine genus *Heteronotia* consists of three described species, of which *H. binoei* has

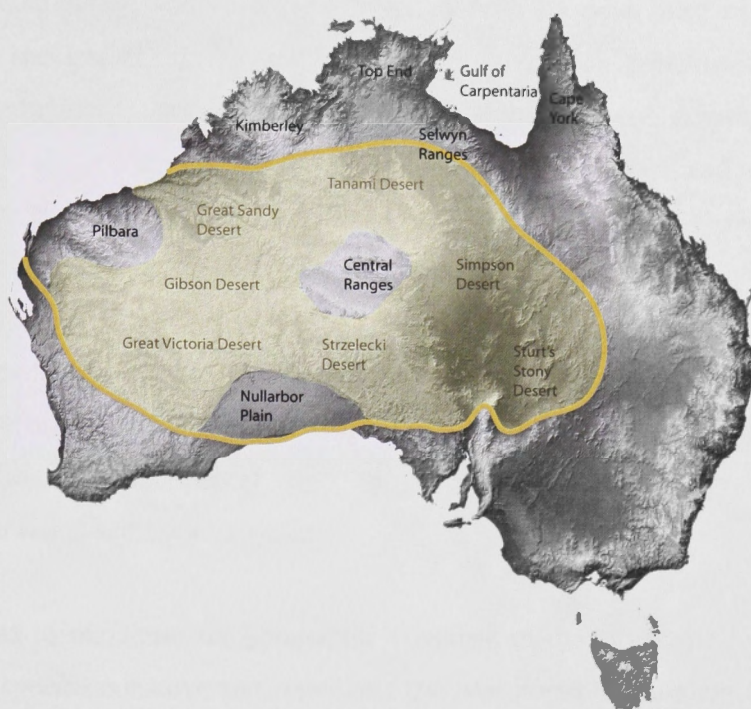


Figure 1. Elevation map of Australia showing the extent of the arid zone (solid line), the distribution of sand deserts (shaded yellow) and major geographical features mentioned in the text.

the largest distribution and ecological range and occurs over most of Australia. A further two species, *H. spelea* and *H. planiceps*, are rock specialists restricted to mountainous regions in western and central Australia. Previous genetic work on *H. spelea* showed this species is comprised of two genetically divergent and geographically disjunct populations, herein referred to as Pilbara *H. spelea* and Central *H. spelea* (Pepper *et al.* 2011 [Chapter I]) (Figure 2c & 3d). The diplodactyline genus *Lucasium* comprises a number of species largely confined to the arid zone. Of these, *L. stenodactylum* has the broadest distribution, which spans the arid zone and also extends into the Kimberley and Northern Territory. The monotypic *Rhynchoedura* is closely related to *Lucasium* (Pepper *et al.* 2006; Oliver *et al.* 2007) and is distributed throughout arid and semi-arid Australia.

We attempted to maximise the geographic coverage of the target species and for the majority of species our coverage represents the best possible sampling from existing collections of the Western Australian Museum, the South Australian Museum, the Australian Museum, and the Museum of Vertebrate Zoology at the University of California, Berkeley (Figure 3). Our datasets consist of 179 *Heteronotia*, 220 *Lucasium stenodactylum*, and 189 *Rhynchoedura ornata* individuals. Our *Heteronotia* dataset consists of previously published sequences from the three described species, *H. binoei*, *H. spelea*, and *H. planiceps* (Fujita *et al.* 2010; Pepper *et al.* 2011 [Chapter I]). Details of all the chromosome races of *H. binoei* can be found in Fujita *et al.* (2010). The majority of our *L. stenodactylum* samples represent previously published material (Pepper *et al.* 2006; Pepper *et al.* 2008); however, we extended our sampling, particularly in South Australia, to provide a clearer picture of the distribution of genetic diversity across the southern arid zone. Our *Rhynchoedura* dataset largely consists of sequences generated for this study. Museum accession numbers and collection localities are given in Table 1.

DNA sequencing and alignment

For all samples, a ~1200 bp fragment of the mitochondrial genome was targeted, extending from tRNA^{Met} through the entire protein-coding gene *nd2* (NADH dehydrogenase subunit II) and the genes encoding tRNA^{Trp}, tRNA^{Ala}, and tRNA^{Asn}. For details of PCR amplification and sequencing, including reactions and primer combinations, see Pepper *et al.* (2006) and Fujita *et al.* (2010). Alignment of the

A) *Lucasium stenodactylum*

B) *Rhynchoedura ornata*

C) *Heteronotia*

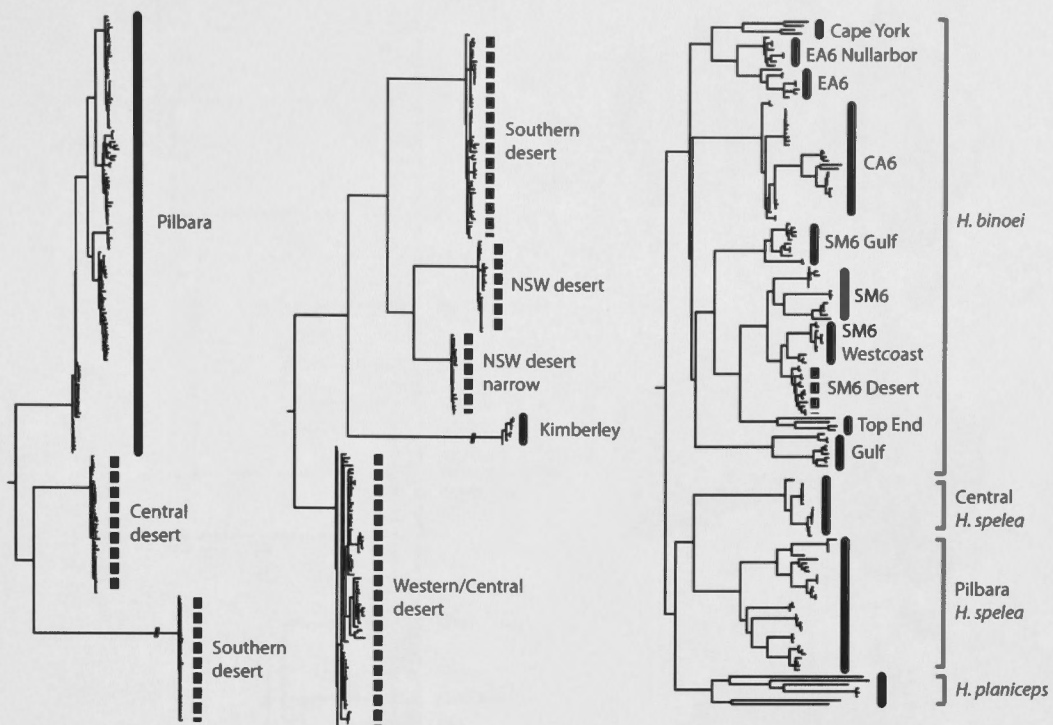


Figure 2. Maximum-likelihood trees inferred from mtDNA sequences using RAxML. Solid lines beside clades indicate a rocky/mountain range clade, while dashed lines indicate a desert clade.

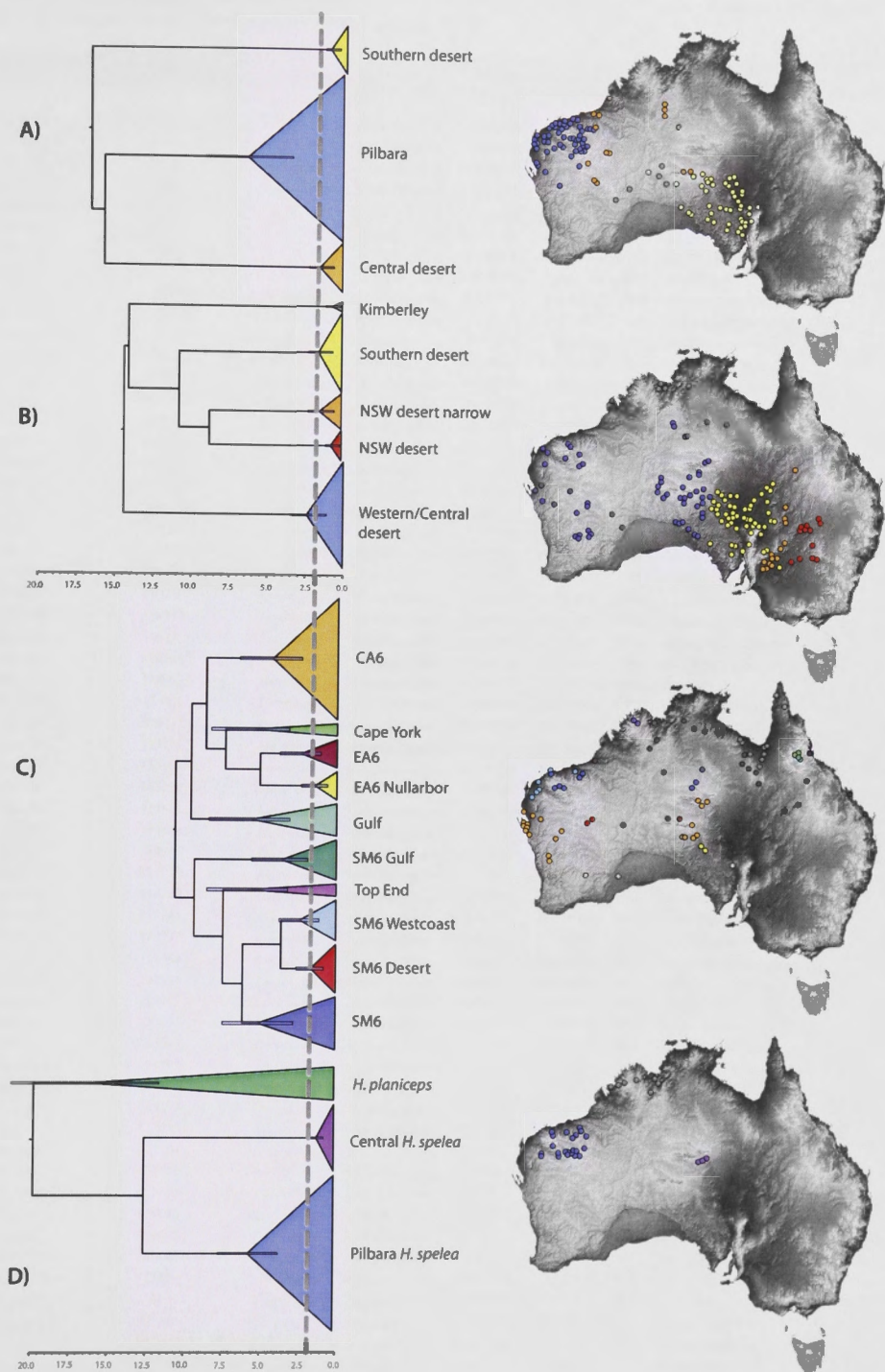


Figure 3. Chronograms inferred using Bayesian molecular clocks in BEAST v.1.6 using only 3rd codon positions of mtDNA, alongside the distribution of each major clade. Time axis in millions of years is indicated on the bottom. Nodal bars are 95% confidence intervals. Dashed grey line indicates the beginning of the Pleistocene.

Table 1. Museum accession numbers and collection localities. Localities marked with "*" refer to sample sites from the Pilbara Biological Surveys (CALM-WA unpublished report).

Lab ID	Museum #	Genus	Species	Latitude	Longitude	State	Locality (nearest)
Gko101	90635	<i>Lucasium</i>	<i>stenodactylum</i>	-21.60944	118.97444	WA	Woodstock Station
Gko102	90671	<i>Lucasium</i>	<i>stenodactylum</i>	-21.60944	118.97444	WA	Woodstock Station
Gko103	90702	<i>Lucasium</i>	<i>stenodactylum</i>	-21.60972	119.02139	WA	Woodstock Station
Gko104	97256	<i>Lucasium</i>	<i>stenodactylum</i>	-23.38333	120.15000	WA	Wheelarra Hill
Gko105	97257	<i>Lucasium</i>	<i>stenodactylum</i>	-23.38333	120.15000	WA	Wheelarra Hill
Gko106	102053	<i>Lucasium</i>	<i>stenodactylum</i>	-20.31667	119.25000	WA	Degray River
Gko107	102181	<i>Lucasium</i>	<i>stenodactylum</i>	-22.60000	118.51194	WA	Mt Windell
Gko108	102185	<i>Lucasium</i>	<i>stenodactylum</i>	-22.60000	118.51194	WA	Mt Windell
Gko109	102481	<i>Lucasium</i>	<i>stenodactylum</i>	-23.04472	115.78722	WA	Barlee Range Nature Reserve
Gko111	102752	<i>Lucasium</i>	<i>stenodactylum</i>	-24.53194	120.29111	WA	Little Sandy Desert
Gko112	104001	<i>Lucasium</i>	<i>stenodactylum</i>	-21.61167	118.95556	WA	Woodstock Station
Gko113	106155	<i>Lucasium</i>	<i>stenodactylum</i>	-23.86667	118.56667	WA	Turee Creek Homestead
Gko116	108803	<i>Lucasium</i>	<i>stenodactylum</i>	-19.70000	121.23333	WA	Sandfire Roadhouse
Gko117	108807	<i>Lucasium</i>	<i>stenodactylum</i>	-18.15000	122.55000	WA	Thangoo Homestead
Gko118	108835	<i>Lucasium</i>	<i>stenodactylum</i>	-24.70000	119.60000	WA	Kumarina
Gko119	108846	<i>Lucasium</i>	<i>stenodactylum</i>	-21.03333	116.81667	WA	Cherralta Homestead
Gko120	108847	<i>Lucasium</i>	<i>stenodactylum</i>	-21.03333	116.81667	WA	Cherralta Homestead
Gko121	110584	<i>Lucasium</i>	<i>stenodactylum</i>	-19.88917	128.86000	WA	Tanami Desert
Gko122	110588	<i>Lucasium</i>	<i>stenodactylum</i>	-19.85694	128.84806	WA	Tanami Desert
Gko124	110591	<i>Lucasium</i>	<i>stenodactylum</i>	-19.89861	128.86583	WA	Tanami Desert
Gko125	110592	<i>Lucasium</i>	<i>stenodactylum</i>	-19.59333	128.86111	WA	Tanami Desert
Gko126	110593	<i>Lucasium</i>	<i>stenodactylum</i>	-19.89972	128.82694	WA	Tanami Desert
Gko127	110706	<i>Lucasium</i>	<i>stenodactylum</i>	-22.58861	117.23639	WA	Mount Brocreekman
Gko128	110710	<i>Lucasium</i>	<i>stenodactylum</i>	-22.61750	117.18139	WA	Mount Brocreekman
Gko129	110723	<i>Lucasium</i>	<i>stenodactylum</i>	-22.43778	117.28444	WA	Mount Brocreekman
Gko130	110741	<i>Lucasium</i>	<i>stenodactylum</i>	-22.51806	117.28444	WA	Mount Brocreekman
Gko131	112692	<i>Lucasium</i>	<i>stenodactylum</i>	-21.68778	115.09194	WA	Onslow
Gko134	113026	<i>Lucasium</i>	<i>stenodactylum</i>	-20.28056	118.88056	WA	Lesley Salt Works
Gko135	113031	<i>Lucasium</i>	<i>stenodactylum</i>	-20.24722	118.84722	WA	Lesley Salt Works
Gko136	113181	<i>Lucasium</i>	<i>stenodactylum</i>	-24.70000	119.58333	WA	Kumarina
Gko137	113194	<i>Lucasium</i>	<i>stenodactylum</i>	-23.33333	119.86667	WA	Newman
Gko138	113229	<i>Lucasium</i>	<i>stenodactylum</i>	-21.70000	116.16667	WA	Deepdale
Gko140	113591	<i>Lucasium</i>	<i>stenodactylum</i>	-21.98333	118.83333	WA	Auski Roadhouse
Gko141	113601	<i>Lucasium</i>	<i>stenodactylum</i>	-21.98333	118.83333	WA	Auski Roadhouse
Gko145	114918	<i>Lucasium</i>	<i>stenodactylum</i>	-21.16667	119.81667	WA	Marble Bar
Gko146	114919	<i>Lucasium</i>	<i>stenodactylum</i>	-21.16667	119.81667	WA	Marble Bar
Gko147	114920	<i>Lucasium</i>	<i>stenodactylum</i>	-21.16667	119.81667	WA	Marble Bar
Gko148	115245	<i>Lucasium</i>	<i>stenodactylum</i>	-21.63333	114.38333	WA	South Muiron Island
Gko149	119277	<i>Lucasium</i>	<i>stenodactylum</i>	-26.43333	117.15000	WA	Mt Levra Station Homestead
Gko152	122758	<i>Lucasium</i>	<i>stenodactylum</i>	-24.40556	114.44417	WA	Mardathuna Homestead
Gko153	123831	<i>Lucasium</i>	<i>stenodactylum</i>	-25.08806	115.38000	WA	Gascoyne Junction
Gko154	125017	<i>Lucasium</i>	<i>stenodactylum</i>	-22.70972	118.98194	WA	Yandicoogina
Gko155	125031	<i>Lucasium</i>	<i>stenodactylum</i>	-22.70972	118.98194	WA	Yandicoogina
Gko156	125037	<i>Lucasium</i>	<i>stenodactylum</i>	-22.72056	118.99056	WA	Yandicoogina
Gko158	126773	<i>Lucasium</i>	<i>stenodactylum</i>	-24.44306	114.51167	WA	Mardathuna Homestead
Gko159	127444	<i>Lucasium</i>	<i>stenodactylum</i>	-21.75000	115.08333	WA	Onslow
Gko160	127493	<i>Lucasium</i>	<i>stenodactylum</i>	-21.73333	115.08333	WA	Onslow
Gko161	127515	<i>Lucasium</i>	<i>stenodactylum</i>	-21.73333	115.08333	WA	Onslow
Gko162	127518	<i>Lucasium</i>	<i>stenodactylum</i>	-21.73333	115.08333	WA	Onslow
Gko163	127703	<i>Lucasium</i>	<i>stenodactylum</i>	-22.79917	117.77639	WA	Mount Tom Price Mine
Gko164	127776	<i>Lucasium</i>	<i>stenodactylum</i>	-22.79917	117.77639	WA	Mount Tom Price Mine
Gko165	129656	<i>Lucasium</i>	<i>stenodactylum</i>	-22.99583	119.09167	WA	Newman
Gko166	131012	<i>Lucasium</i>	<i>stenodactylum</i>	-21.13833	117.11583	WA	Millstream-Chichester
Gko167	131487	<i>Lucasium</i>	<i>stenodactylum</i>	-23.37167	119.62889	WA	Mount Whaleback Creek
Gko168	132239	<i>Lucasium</i>	<i>stenodactylum</i>	-21.77778	114.87056	WA	Urala Station
Gko169	132240	<i>Lucasium</i>	<i>stenodactylum</i>	-21.76167	114.85278	WA	Urala Station
Gko170	132528	<i>Lucasium</i>	<i>stenodactylum</i>	-20.67222	116.75611	WA	Burrup Peninsula
Gko171	132533	<i>Lucasium</i>	<i>stenodactylum</i>	-20.67222	116.75611	WA	Burrup Peninsula
Gko172	132556	<i>Lucasium</i>	<i>stenodactylum</i>	-20.62611	116.78972	WA	Burrup Peninsula
Gko175	135006	<i>Lucasium</i>	<i>stenodactylum</i>	-23.33750	119.69667	WA	Mount Whaleback Creek
Gko176	135007	<i>Lucasium</i>	<i>stenodactylum</i>	-23.40306	119.69611	WA	Mount Whaleback Creek
Gko178	139043	<i>Lucasium</i>	<i>stenodactylum</i>	-19.81222	121.47361	WA	Mandora
Gko179	139232	<i>Lucasium</i>	<i>stenodactylum</i>	-21.26639	120.45528	WA	Meentheena Homestead
Gko182	145077	<i>Lucasium</i>	<i>stenodactylum</i>	-27.05194	125.15861	WA	Officer Basin
Gko183	145195	<i>Lucasium</i>	<i>stenodactylum</i>	-22.24306	114.03472	WA	Learmonth Airstrip
Gko184	145196	<i>Lucasium</i>	<i>stenodactylum</i>	-22.24306	114.03472	WA	Learmonth Airstrip
Gko186	145566	<i>Lucasium</i>	<i>stenodactylum</i>	-20.70000	118.64000	WA	Port Hedland
Gko187	145592	<i>Lucasium</i>	<i>stenodactylum</i>	-20.78000	118.64000	WA	Port Hedland
Gko188	145703	<i>Lucasium</i>	<i>stenodactylum</i>	-22.82083	119.28694	WA	Weeli Wolli Creek
Gko189	145704	<i>Lucasium</i>	<i>stenodactylum</i>	-22.83389	119.27278	WA	Weeli Wolli Creek
Gko190	145742a	<i>Lucasium</i>	<i>stenodactylum</i>	-21.94000	118.96083	WA	Chichester Range
Gko191	145742b	<i>Lucasium</i>	<i>stenodactylum</i>	-21.94000	118.96083	WA	Chichester Range
Gko195	151440a	<i>Lucasium</i>	<i>stenodactylum</i>	-26.20083	121.30361	WA	Lorna Glen Station
Gko196	151440b	<i>Lucasium</i>	<i>stenodactylum</i>	-26.20083	121.30361	WA	Lorna Glen Station
Gko197	151484a	<i>Lucasium</i>	<i>stenodactylum</i>	-26.26250	121.51083	WA	Lorna Glen Station

Lab ID	Museum #	Genus	Species	Latitude	Longitude	State	Locality (nearest)
Gko198	151484b	<i>Lucasium</i>	<i>stenodactylum</i>	-26.26250	121.51083	WA	Lorna Glen Station
Gko199	151743	<i>Lucasium</i>	<i>stenodactylum</i>	-21.94000	118.96083	WA	Chichester Range
Gko200	154249	<i>Lucasium</i>	<i>stenodactylum</i>	-22.29917	119.02278	WA	Munjina Roadhouse
Gko201	154560	<i>Lucasium</i>	<i>stenodactylum</i>	-23.37917	120.10528	WA	Newman
Gko202	157145	<i>Lucasium</i>	<i>stenodactylum</i>	-22.70583	120.53806	WA	Roy Hill
Gko203	157156	<i>Lucasium</i>	<i>stenodactylum</i>	-22.78389	120.50056	WA	Roy Hill
Gko204	157189	<i>Lucasium</i>	<i>stenodactylum</i>	-22.16417	114.58972	WA	Yanrey
Gko205	157273	<i>Lucasium</i>	<i>stenodactylum</i>	-22.25750	114.60000	WA	Yanrey
Gko206	157539	<i>Lucasium</i>	<i>stenodactylum</i>	-21.74778	116.07528	WA	Pannawonica
Gko207	157573	<i>Lucasium</i>	<i>stenodactylum</i>	-21.74778	116.07528	WA	Pannawonica
Gko208	157732	<i>Lucasium</i>	<i>stenodactylum</i>	-19.57944	128.86806	WA	Larranganni Bluff
Gko209	157733	<i>Lucasium</i>	<i>stenodactylum</i>	-19.57944	128.86806	WA	Larranganni Bluff
Gko210	157945	<i>Lucasium</i>	<i>stenodactylum</i>	-23.29833	122.70167	WA	Lake Views
Gko211	157946	<i>Lucasium</i>	<i>stenodactylum</i>	-23.29833	122.70167	WA	Lake Views
Gko212	157947	<i>Lucasium</i>	<i>stenodactylum</i>	-23.23417	122.70139	WA	Lake Disappointment
Gko213	157948	<i>Lucasium</i>	<i>stenodactylum</i>	-23.23417	122.70139	WA	Lake Disappointment
Gko214	157949	<i>Lucasium</i>	<i>stenodactylum</i>	-23.35194	122.66667	WA	Savory Creek Mouth
Gko215	157950	<i>Lucasium</i>	<i>stenodactylum</i>	-23.35194	122.66667	WA	Savory Creek Mouth
Gko216	158319	<i>Lucasium</i>	<i>stenodactylum</i>	-22.65778	114.39194	WA	Giralia
Gko217	158320	<i>Lucasium</i>	<i>stenodactylum</i>	-22.62167	114.39250	WA	Giralia
Gko307	R139897	<i>Lucasium</i>	<i>stenodactylum</i>	-16.00000	127.96667	WA	El Questro Station
Gko313	R110130	<i>Lucasium</i>	<i>stenodactylum</i>	-21.88230	117.79436	WA	PE02*
Gko314	R110195	<i>Lucasium</i>	<i>stenodactylum</i>	-21.38408	117.06078	WA	PW12*
Gko315	R110251	<i>Lucasium</i>	<i>stenodactylum</i>	-22.67519	119.84078	WA	RHNE05*
Gko316	R110270	<i>Lucasium</i>	<i>stenodactylum</i>	-22.11789	119.87647	WA	RHNE10*
Gko317	R110294	<i>Lucasium</i>	<i>stenodactylum</i>	-22.67519	119.84078	WA	RHNE05*
Gko318	R110298	<i>Lucasium</i>	<i>stenodactylum</i>	-22.76608	119.63069	WA	RHNE02*
Gko319	R110305	<i>Lucasium</i>	<i>stenodactylum</i>	-22.81983	119.61389	WA	RHNE01*
Gko320	R110310	<i>Lucasium</i>	<i>stenodactylum</i>	-22.67519	119.84078	WA	RHNE05*
Gko321	R158064	<i>Lucasium</i>	<i>stenodactylum</i>	-21.31010	117.27561	WA	PW13*
Gko322	R158067	<i>Lucasium</i>	<i>stenodactylum</i>	-21.67752	116.97497	WA	PW06*
Gko323	R158092	<i>Lucasium</i>	<i>stenodactylum</i>	-21.38408	117.06078	WA	PW12*
Gko324	R158093	<i>Lucasium</i>	<i>stenodactylum</i>	-21.38408	117.06078	WA	PW12*
Gko325	R158186	<i>Lucasium</i>	<i>stenodactylum</i>	-22.29453	119.06136	WA	RHNW11*
Gko327	R159841	<i>Lucasium</i>	<i>stenodactylum</i>	-20.94990	117.85017	WA	DRE11*
Gko328	R159850	<i>Lucasium</i>	<i>stenodactylum</i>	-20.60730	118.15700	WA	DRE07*
Gko329	R159851	<i>Lucasium</i>	<i>stenodactylum</i>	-20.52552	118.07728	WA	DRE06*
Gko331	R159884	<i>Lucasium</i>	<i>stenodactylum</i>	-20.91968	117.86092	WA	DRE10*
Gko332	R159891	<i>Lucasium</i>	<i>stenodactylum</i>	-20.86988	117.85847	WA	DRE09*
Gko333	R159895	<i>Lucasium</i>	<i>stenodactylum</i>	-20.94990	117.85017	WA	DRE11*
Gko334	R159906	<i>Lucasium</i>	<i>stenodactylum</i>	-20.96942	118.04792	WA	DRE13*
Gko338	R159919	<i>Lucasium</i>	<i>stenodactylum</i>	-20.86988	117.85847	WA	DRE09*
Gko339	R159920	<i>Lucasium</i>	<i>stenodactylum</i>	-20.86988	117.85847	WA	DRE09*
Gko342	R159941	<i>Lucasium</i>	<i>stenodactylum</i>	-20.91968	117.86092	WA	DRE10*
Gko343	R159942	<i>Lucasium</i>	<i>stenodactylum</i>	-20.91968	117.86092	WA	DRE10*
Gko346	R160024	<i>Lucasium</i>	<i>stenodactylum</i>	-20.52552	118.07728	WA	DRE06*
Gko347	R160061	<i>Lucasium</i>	<i>stenodactylum</i>	-21.28844	121.23761	WA	NE12*
Gko348	R160062	<i>Lucasium</i>	<i>stenodactylum</i>	-21.29483	121.26394	WA	NE13*
Gko349	R160086	<i>Lucasium</i>	<i>stenodactylum</i>	-21.32558	120.97022	WA	NE08*
Gko350	R160092	<i>Lucasium</i>	<i>stenodactylum</i>	-21.29483	121.26394	WA	NE13*
Gko351	R160123	<i>Lucasium</i>	<i>stenodactylum</i>	-21.32558	120.97022	WA	NE08*
Gko352	R160127	<i>Lucasium</i>	<i>stenodactylum</i>	-21.29483	121.26394	WA	NE13*
Gko353	R160147	<i>Lucasium</i>	<i>stenodactylum</i>	-21.32558	120.97022	WA	NE08*
Gko355	R160151	<i>Lucasium</i>	<i>stenodactylum</i>	-21.33711	120.76950	WA	NE05*
Gko356	R160159	<i>Lucasium</i>	<i>stenodactylum</i>	-21.97964	120.22367	WA	NW01*
Gko357	R160160	<i>Lucasium</i>	<i>stenodactylum</i>	-21.97964	120.22367	WA	NW01*
Gko358	R160161	<i>Lucasium</i>	<i>stenodactylum</i>	-21.39261	120.07228	WA	NW12*
Gko359	R160183	<i>Lucasium</i>	<i>stenodactylum</i>	-21.94806	120.19367	WA	NW02*
Gko360	R160204	<i>Lucasium</i>	<i>stenodactylum</i>	-21.67775	120.15519	WA	NW05*
Gko361	R160212	<i>Lucasium</i>	<i>stenodactylum</i>	-21.39261	120.07228	WA	NW12*
Gko362	R160227	<i>Lucasium</i>	<i>stenodactylum</i>	-21.67775	120.15519	WA	NW05*
Gko363	R160231	<i>Lucasium</i>	<i>stenodactylum</i>	-21.40717	120.07133	WA	NW11*
Gko367	R160931	<i>Lucasium</i>	<i>stenodactylum</i>	-21.06289	116.23331	WA	DRW08*
Gko369	R160979	<i>Lucasium</i>	<i>stenodactylum</i>	-20.87457	116.64864	WA	DRW04*
Gko370	R161022	<i>Lucasium</i>	<i>stenodactylum</i>	-21.05519	116.25144	WA	DRW07*
Gko371	R161050	<i>Lucasium</i>	<i>stenodactylum</i>	-20.87457	116.64864	WA	DRW04*
Gko373	R161064	<i>Lucasium</i>	<i>stenodactylum</i>	-21.05519	116.25144	WA	DRW07*
Gko375	R161075	<i>Lucasium</i>	<i>stenodactylum</i>	-21.07078	116.20625	WA	DRW09*
Gko378	R161992	<i>Lucasium</i>	<i>stenodactylum</i>	-22.17031	115.55942	WA	WYW03*
Gko381	R162055	<i>Lucasium</i>	<i>stenodactylum</i>	-22.43353	115.93000	WA	WYE06*
Gko382	R162123	<i>Lucasium</i>	<i>stenodactylum</i>	-22.77306	116.52203	WA	WYE02*
Gko383	R162205	<i>Lucasium</i>	<i>stenodactylum</i>	-23.31936	119.10142	WA	RHNC02*
Gko386	R162257	<i>Lucasium</i>	<i>stenodactylum</i>	-22.83778	119.27203	WA	RHNC13*
Gko448	SAMAR42516	<i>Lucasium</i>	<i>stenodactylum</i>	-29.05000	133.31667	SA	Tallaringa Well
Gko449	SAMAR29878	<i>Lucasium</i>	<i>stenodactylum</i>	-25.19167	131.61667	NT	Curtin Springs
Gko453	WAMR94617	<i>Lucasium</i>	<i>stenodactylum</i>	-21.58333	117.06666	WA	Millstream
Gko455	SAMAR58047	<i>Lucasium</i>	<i>stenodactylum</i>	-29.83333	133.66667	SA	Dominion Mine
Gko456	CU14283	<i>Lucasium</i>	<i>stenodactylum</i>	-28.09783	123.68633	WA	Yamarna Station

Lab ID	Museum #	Genus	Species	Latitude	Longitude	State	Locality (nearest)
Gko457	SAMAR59337	<i>Lucasium</i>	<i>stenodactylum</i>	-29.89639	131.27917	SA	Maralinga
Gko458	SAMAR59481	<i>Lucasium</i>	<i>stenodactylum</i>	-29.73250	131.08583	SA	Maralinga
Gko460	SAMAR60538	<i>Lucasium</i>	<i>stenodactylum</i>	-26.30222	135.17833	SA	Mt Dare
Gko461	ABTC91358	<i>Lucasium</i>	<i>stenodactylum</i>	-24.7825	128.7789	WA	Mt Ant
Gko462	WAMR166325	<i>Lucasium</i>	<i>stenodactylum</i>	-24.7072	128.7603	WA	Pungkulpirri Waterhole
Gko463	ABTC91566	<i>Lucasium</i>	<i>stenodactylum</i>	-24.7072	128.7603	WA	Pungkulpirri Waterhole
Gko464	ABTC91834	<i>Lucasium</i>	<i>stenodactylum</i>	-25.84618	128.44821	WA	Blackstone
Gko465	WAMR166309	<i>Lucasium</i>	<i>stenodactylum</i>	-25.8572	128.44588	WA	Blackstone
Gko470	SAMAR26536	<i>Lucasium</i>	<i>stenodactylum</i>	-26.95000	133.56667	SA	Granite Downs Homestead
Gko476	SAMAR36111	<i>Lucasium</i>	<i>stenodactylum</i>	-25.23333	131.01667	NT	Yulara
Gko478	SAMAR41864	<i>Lucasium</i>	<i>stenodactylum</i>	-27.19444	132.86861	SA	Blue Hills Bore
Gko479	SAMAR44897	<i>Lucasium</i>	<i>stenodactylum</i>	-28.93500	138.61778	SA	Dulkaninna
Gko480	SAMAR46454	<i>Lucasium</i>	<i>stenodactylum</i>	-29.21639	136.63083	SA	Beresford Rail Station
Gko481	SAMAR46380	<i>Lucasium</i>	<i>stenodactylum</i>	-29.63806	137.80778	SA	Kenneberry Waterhole
Gko482	SAMAR46493	<i>Lucasium</i>	<i>stenodactylum</i>	-29.27139	135.63278	SA	Mungutana Dam
Gko483	SAMAR46431	<i>Lucasium</i>	<i>stenodactylum</i>	-29.28889	135.18333	SA	Baradinna Hill
Gko484	SAMAR46808	<i>Lucasium</i>	<i>stenodactylum</i>	-26.32917	135.70528	SA	Anvil Hole, Native Well
Gko485	SAMAR47229	<i>Lucasium</i>	<i>stenodactylum</i>	-28.95083	136.78194	SA	Nine Dam, Anna Creek Station
Gko486	SAMAR47289	<i>Lucasium</i>	<i>stenodactylum</i>	-28.41556	136.44639	SA	Peake Station
Gko487	SAMAR47317	<i>Lucasium</i>	<i>stenodactylum</i>	-28.14528	136.02806	SA	Peake Station
Gko489	SAMAR48543	<i>Lucasium</i>	<i>stenodactylum</i>	-27.74583	136.69944	SA	Macumba Station
Gko490	SAMAR48940	<i>Lucasium</i>	<i>stenodactylum</i>	-30.74111	137.34111	SA	Andamooka Station
Gko492	SAMAR53061	<i>Lucasium</i>	<i>stenodactylum</i>	-30.46806	138.28083	SA	Leigh Creek
Gko494	SAMAR52779	<i>Lucasium</i>	<i>stenodactylum</i>	-27.02556	135.22111	SA	Mount Sarah Homestead
Gko495	SAMAR52812	<i>Lucasium</i>	<i>stenodactylum</i>	-26.83472	136.07167	SA	Oolgawa WH
Gko496	SAMAR54126	<i>Lucasium</i>	<i>stenodactylum</i>	-29.07861	137.67139	SA	Muloorina Homestead
Gko497	SAMAR46152	<i>Lucasium</i>	<i>stenodactylum</i>	-26.48778	129.17361	SA	Kunytjanu
Gko498	SAMAR47450	<i>Lucasium</i>	<i>stenodactylum</i>	-27.62500	132.91194	SA	Oolarinna East Bore
Gko499	SAMAR50166	<i>Lucasium</i>	<i>stenodactylum</i>	-26.07278	132.41917	SA	Sentinel Hill
Gko500	SAMAR51218	<i>Lucasium</i>	<i>stenodactylum</i>	-26.55444	132.86722	SA	Mundy Dam
Gko501	SAMAR51576	<i>Lucasium</i>	<i>stenodactylum</i>	-26.27694	131.46056	SA	Amata
Gko502	SAMAR51622	<i>Lucasium</i>	<i>stenodactylum</i>	-26.87444	133.02722	SA	Indulkana
Gko503	SAMAR20899	<i>Lucasium</i>	<i>stenodactylum</i>	-30.38333	136.88333	SA	Olympic Dam area
Gko504	SAMAR26234	<i>Lucasium</i>	<i>stenodactylum</i>	-29.35833	134.46667	SA	Lake Phillipson
Gko505	SAMAR31828	<i>Lucasium</i>	<i>stenodactylum</i>	-30.31861	133.21611	SA	Lake Bring
Gko506	SAMAR45122	<i>Lucasium</i>	<i>stenodactylum</i>	-31.54222	136.67639	SA	Yalymboo Station
Gko507	SAMAR45290	<i>Lucasium</i>	<i>stenodactylum</i>	-30.84222	135.74000	SA	Mt Vivian Station
Gko508	SAMAR47641	<i>Lucasium</i>	<i>stenodactylum</i>	-27.06667	134.81667	SA	Todmorden Station
Gko509	SAMAR47644	<i>Lucasium</i>	<i>stenodactylum</i>	-31.06667	137.06667	SA	Arcoona Station
Gko511	SAMAR52477	<i>Lucasium</i>	<i>stenodactylum</i>	-31.69028	137.24417	SA	Pernatty Lagoon
Gko513	ABTC60785	<i>Lucasium</i>	<i>stenodactylum</i>	-21.00890	130.12640	NT	Sangster's Bore
Gko515	SAMAR32310	<i>Lucasium</i>	<i>stenodactylum</i>	-30.63333	133.93333	SA	Lyons Siding
Gko525	156616	<i>Lucasium</i>	<i>stenodactylum</i>	-21.65270	121.21420	WA	Woodie Woodie
Gko230	84540	<i>Rhynchoedura</i>	<i>ornata</i>	-25.05000	128.66667	WA	Giles Creek
Gko231	84541	<i>Rhynchoedura</i>	<i>ornata</i>	-25.05000	128.66667	WA	Giles Creek
Gko232	84592	<i>Rhynchoedura</i>	<i>ornata</i>	-29.06667	121.35000	WA	Leonora
Gko233	100521	<i>Rhynchoedura</i>	<i>ornata</i>	-29.83333	120.91667	WA	Menzies
Gko234	102502	<i>Rhynchoedura</i>	<i>ornata</i>	-23.11306	116.01167	WA	Barlee Range
Gko235	110582	<i>Rhynchoedura</i>	<i>ornata</i>	-19.90278	128.76333	WA	Tanami Desert
Gko236	110583	<i>Rhynchoedura</i>	<i>ornata</i>	-19.90278	128.76333	WA	Tanami Desert
Gko237	112972	<i>Rhynchoedura</i>	<i>ornata</i>	-17.05972	122.71667	WA	Broome
Gko238	112983	<i>Rhynchoedura</i>	<i>ornata</i>	-17.05972	122.71667	WA	Broome
Gko239	132719	<i>Rhynchoedura</i>	<i>ornata</i>	-15.77167	128.28806	WA	Wyndham
Gko240	144746	<i>Rhynchoedura</i>	<i>ornata</i>	-30.46667	119.60000	WA	Bungalbin Hill
Gko241	157554	<i>Rhynchoedura</i>	<i>ornata</i>	-21.67389	115.88917	WA	Pannawonica
Gko242	158315	<i>Rhynchoedura</i>	<i>ornata</i>	-22.63056	114.39250	WA	Giralia
Gko388	R135427	<i>Rhynchoedura</i>	<i>ornata</i>	-29.03333	146.21667	NSW	Morton Plains Station
Gko389	R137630	<i>Rhynchoedura</i>	<i>ornata</i>	-29.66667	144.60000	NSW	Wanaaring
Gko390	R137631	<i>Rhynchoedura</i>	<i>ornata</i>	-29.66667	144.60000	NSW	Wanaaring
Gko391	R138130	<i>Rhynchoedura</i>	<i>ornata</i>	-29.32028	145.84639	NSW	Enngonia
Gko392	R138441	<i>Rhynchoedura</i>	<i>ornata</i>	-29.71667	144.11667	NSW	Wanaaring
Gko393	R138442	<i>Rhynchoedura</i>	<i>ornata</i>	-29.81667	144.58333	NSW	Wanaaring
Gko394	R138443	<i>Rhynchoedura</i>	<i>ornata</i>	-29.98333	145.36667	NSW	Wanaaring
Gko395	R139902	<i>Rhynchoedura</i>	<i>ornata</i>	-16.01861	128.00389	WA	El Questro Station
Gko396	R139903	<i>Rhynchoedura</i>	<i>ornata</i>	-16.01861	128.00389	WA	El Questro Station
Gko397	R139904	<i>Rhynchoedura</i>	<i>ornata</i>	-16.01861	128.00389	WA	El Questro Station
Gko398	R139905	<i>Rhynchoedura</i>	<i>ornata</i>	-16.01861	128.00389	WA	El Questro Station
Gko400	R145587	<i>Rhynchoedura</i>	<i>ornata</i>	-31.28333	142.28333	NSW	Mootwingee National Park
Gko401	R145587	<i>Rhynchoedura</i>	<i>ornata</i>	-31.28333	142.28333	NSW	Mootwingee National Park
Gko402	R145588	<i>Rhynchoedura</i>	<i>ornata</i>	-31.28333	142.28333	NSW	Mootwingee National Park
Gko403	R150159	<i>Rhynchoedura</i>	<i>ornata</i>	-31.20000	142.30000	NSW	Mootwingee National Park
Gko404	R151586	<i>Rhynchoedura</i>	<i>ornata</i>	-31.38167	145.70500	NSW	Cobar
Gko405	R151587	<i>Rhynchoedura</i>	<i>ornata</i>	-31.38167	145.70500	NSW	Cobar
Gko406	R152924	<i>Rhynchoedura</i>	<i>ornata</i>	-29.03333	141.73333	NSW	Sturt National Park
Gko407	R152925	<i>Rhynchoedura</i>	<i>ornata</i>	-29.03333	141.73333	NSW	Sturt National Park
Gko408	R152927	<i>Rhynchoedura</i>	<i>ornata</i>	-29.05583	141.89833	NSW	Sturt National Park
Gko409	R152930	<i>Rhynchoedura</i>	<i>ornata</i>	-29.05417	141.89083	NSW	Sturt National Park
Gko410	R152935	<i>Rhynchoedura</i>	<i>ornata</i>	-29.05583	141.89833	NSW	Sturt National Park

Lab ID	Museum #	Genus	Species	Latitude	Longitude	State	Locality (nearest)
Gko411	R152940	<i>Rhynchoedura</i>	<i>ornata</i>	-29.03333	141.73333	NSW	Sturt National Park
Gko412	R152941	<i>Rhynchoedura</i>	<i>ornata</i>	-29.03333	141.73333	NSW	Sturt National Park
Gko413	R152946	<i>Rhynchoedura</i>	<i>ornata</i>	-29.05583	141.89833	NSW	Sturt National Park
Gko414	R152961	<i>Rhynchoedura</i>	<i>ornata</i>	-29.05417	141.89083	NSW	Sturt National Park
Gko415	R152966	<i>Rhynchoedura</i>	<i>ornata</i>	-29.04944	141.86083	NSW	Sturt National Park
Gko416	R152982	<i>Rhynchoedura</i>	<i>ornata</i>	-29.08333	141.21667	NSW	Sturt National Park
Gko417	R153315	<i>Rhynchoedura</i>	<i>ornata</i>	-33.12444	143.27444	NSW	Spring Hill
Gko418	R153316	<i>Rhynchoedura</i>	<i>ornata</i>	-33.12444	143.27444	NSW	Spring Hill
Gko419	R153317	<i>Rhynchoedura</i>	<i>ornata</i>	-33.12444	143.27444	NSW	Spring Hill
Gko420	R155270	<i>Rhynchoedura</i>	<i>ornata</i>	-29.03111	141.45083	NSW	Sturt National Park
Gko421	R155276	<i>Rhynchoedura</i>	<i>ornata</i>	-29.04444	141.30722	NSW	Sturt National Park
Gko423	R155351	<i>Rhynchoedura</i>	<i>ornata</i>	-29.03111	141.45083	NSW	Sturt National Park
Gko424	R155352	<i>Rhynchoedura</i>	<i>ornata</i>	-29.04444	141.30722	NSW	Sturt National Park
Gko425	R155354	<i>Rhynchoedura</i>	<i>ornata</i>	-29.08333	141.20000	NSW	Sturt National Park
Gko426	R155371	<i>Rhynchoedura</i>	<i>ornata</i>	-29.04444	141.30722	NSW	Sturt National Park
Gko427	R156652	<i>Rhynchoedura</i>	<i>ornata</i>	-32.86500	146.18917	NSW	Yarra Property, Mt Hope
Gko428	R156653	<i>Rhynchoedura</i>	<i>ornata</i>	-32.86500	146.18917	NSW	Yarra Property, Mt Hope
Gko429	R156700	<i>Rhynchoedura</i>	<i>ornata</i>	-32.84889	146.18278	NSW	Yarra Property, Mt Hope
Gko430	R156701	<i>Rhynchoedura</i>	<i>ornata</i>	-32.84889	146.18278	NSW	Yarra Property, Mt Hope
Gko431	R156720	<i>Rhynchoedura</i>	<i>ornata</i>	-32.94417	146.19222	NSW	Yarra Property, Mt Hope
Gko432	R166764/NR9657	<i>Rhynchoedura</i>	<i>ornata</i>	-29.85389	144.13444	NSW	Nocoleche Nature Reserve
Gko433	R166770/NR9656	<i>Rhynchoedura</i>	<i>ornata</i>	-29.84417	144.05417	NSW	Nocoleche Nature Reserve
Gko434	R166799/NR9727	<i>Rhynchoedura</i>	<i>ornata</i>	-29.84417	144.05417	NSW	Nocoleche Nature Reserve
Gko529	SAMAR42576	<i>Rhynchoedura</i>	<i>ornata</i>	-28.21667	133.36667	SA	Tallaringa
Gko530	SAMAR46239	<i>Rhynchoedura</i>	<i>ornata</i>	-27.68750	134.83694	SA	Arckaringa Station
Gko532	NMVD67857	<i>Rhynchoedura</i>	<i>ornata</i>	-24.34590	131.68420	NT	Kathleen Creek, Watarrka
Gko533	SAMAR53747	<i>Rhynchoedura</i>	<i>ornata</i>	-30.13310	139.61070	SA	Mulga Homestead
Gko534	SAMAR38783	<i>Rhynchoedura</i>	<i>ornata</i>	-19.66667	134.23333	NT	Tennant Creek
Gko535	SAMAR40564	<i>Rhynchoedura</i>	<i>ornata</i>	-24.43333	131.81667	NT	Kings Creek Station
Gko536	SAMAR59491	<i>Rhynchoedura</i>	<i>ornata</i>	-29.73250	131.08583	SA	Maralinga
Gko537	SAMAR60328	<i>Rhynchoedura</i>	<i>ornata</i>	-29.50000	129.32917	SA	Oak Valley
Gko538	SAMAR60424	<i>Rhynchoedura</i>	<i>ornata</i>	-29.38361	129.97611	SA	Oak Valley
Gko539	SAMAR60460	<i>Rhynchoedura</i>	<i>ornata</i>	-27.19444	135.65028	SA	Macumba Homestead
Gko540	SAMAR60946	<i>Rhynchoedura</i>	<i>ornata</i>	-32.04639	140.11389	SA	Bimbowrie Station
Gko541	SAMAR49777	<i>Rhynchoedura</i>	<i>ornata</i>	-30.57500	139.47444	SA	Balcanaona Station
Gko543	WAMR166334	<i>Rhynchoedura</i>	<i>ornata</i>	-25.93250	128.44110	WA	Morgan Range
Gko545	SAMAR58950	<i>Rhynchoedura</i>	<i>ornata</i>	-29.13111	130.23500	SA	Oak Valley
Gko546	SAMAR33345	<i>Rhynchoedura</i>	<i>ornata</i>	-32.46667	140.51667	SA	Maldorkey Hill
Gko547	SAMAR32967	<i>Rhynchoedura</i>	<i>ornata</i>	-20.86667	130.26667	NT	Sangster's Bore
Gko548	QMJ48069	<i>Rhynchoedura</i>	<i>ornata</i>	-25.67560	140.54080	QLD	Betoota
Gko549	QMJ48534	<i>Rhynchoedura</i>	<i>ornata</i>	-27.69540	142.20760	QLD	Cooroo
Gko551	WAMR91452	<i>Rhynchoedura</i>	<i>ornata</i>	-29.67270	125.13450	WA	Blue Robin Hill
Gko552	SAMAR43887	<i>Rhynchoedura</i>	<i>ornata</i>	-26.73722	139.52056	SA	Koonchera Waterhole
Gko555	SAMAR30989	<i>Rhynchoedura</i>	<i>ornata</i>	-27.22778	140.19028	SA	Coongie Lakes Area
Gko559	SAMAR26672	<i>Rhynchoedura</i>	<i>ornata</i>	-29.35833	134.46667	SA	Mabel Creek Homestead
Gko560	SAMAR32616	<i>Rhynchoedura</i>	<i>ornata</i>	-28.64889	133.35361	SA	Tallaringa Well
Gko561	SAMAR32621	<i>Rhynchoedura</i>	<i>ornata</i>	-28.94889	133.30417	SA	Tallaringa Well
Gko562	No voucher	<i>Rhynchoedura</i>	<i>ornata</i>	-15.59700	131.10410	NT	Victoria R. Gregory National Park
Gko563	NTMR16429	<i>Rhynchoedura</i>	<i>ornata</i>	-19.49000	132.30000	NT	Green Swamp Well, Tanami
Gko565	NTM	<i>Rhynchoedura</i>	<i>ornata</i>	-19.65000	134.18000	NT	Tennant Creek
Gko566	SAMAR36106	<i>Rhynchoedura</i>	<i>ornata</i>	-25.23333	131.01667	NT	Yulara
Gko567	SAMAR36175	<i>Rhynchoedura</i>	<i>ornata</i>	-25.48333	131.81667	NT	Curtin Springs
Gko568	?QM	<i>Rhynchoedura</i>	<i>ornata</i>	-24.11000	143.18000	QLD	Noonbah Station
Gko570	SAMAR40942	<i>Rhynchoedura</i>	<i>ornata</i>	-28.08472	134.29556	SA	Mt Fumer
Gko571	SAMAR42084	<i>Rhynchoedura</i>	<i>ornata</i>	-26.34972	130.17167	SA	Illinjitija
Gko572	SAMAR44896	<i>Rhynchoedura</i>	<i>ornata</i>	-28.93500	138.61778	SA	Dulkaninna
Gko573	SAMAR44938	<i>Rhynchoedura</i>	<i>ornata</i>	-29.61417	138.68361	SA	Mookawarinna Hill
Gko575	SAMAR45030	<i>Rhynchoedura</i>	<i>ornata</i>	-26.31806	140.33611	SA	Elbow Well
Gko576	SAMAR45060	<i>Rhynchoedura</i>	<i>ornata</i>	-29.46306	138.84444	SA	Toopawarinna Bore
Gko577	SAMAR45099	<i>Rhynchoedura</i>	<i>ornata</i>	-29.79167	139.80194	SA	Moolawatana
Gko578	SAMAR45687	<i>Rhynchoedura</i>	<i>ornata</i>	-27.38778	138.66611	SA	Mt Gason
Gko579	SAMAR45765	<i>Rhynchoedura</i>	<i>ornata</i>	-26.05639	140.06917	SA	Frew Well
Gko580	SAMAR46046	<i>Rhynchoedura</i>	<i>ornata</i>	-28.30000	140.45000	SA	Moomba Gas Field
Gko581	SAMAR46205	<i>Rhynchoedura</i>	<i>ornata</i>	-29.68389	135.81528	SA	Halifax Hill
Gko582	SAMAR46457	<i>Rhynchoedura</i>	<i>ornata</i>	-29.21639	136.63083	SA	Beresford Rail Station
Gko583	SAMAR46488	<i>Rhynchoedura</i>	<i>ornata</i>	-29.27139	135.63278	SA	Mungutana Dam
Gko584	SAMAR46398	<i>Rhynchoedura</i>	<i>ornata</i>	-29.64111	137.88944	SA	Callanna Bore
Gko585	SAMAR46299	<i>Rhynchoedura</i>	<i>ornata</i>	-29.84472	136.87167	SA	White Cliff
Gko586	SAMAR46351	<i>Rhynchoedura</i>	<i>ornata</i>	-29.47111	136.18778	SA	Binda Boudna Hill
Gko587	SAMAR46430	<i>Rhynchoedura</i>	<i>ornata</i>	-29.28889	135.18333	SA	Bacadinna Hill
Gko588	SAMAR46560	<i>Rhynchoedura</i>	<i>ornata</i>	-28.63972	135.94111	SA	Patsy Dam
Gko589	SAMAR46932	<i>Rhynchoedura</i>	<i>ornata</i>	-26.45806	134.89861	SA	Top Camp Well
Gko592	SAMAR47241	<i>Rhynchoedura</i>	<i>ornata</i>	-28.81778	136.73611	SA	Armistice Bore Anna Creek Station
Gko593	SAMAR47256	<i>Rhynchoedura</i>	<i>ornata</i>	-28.43250	136.45333	SA	Four Hills Trig Peake Station
Gko594	SAMAR47324	<i>Rhynchoedura</i>	<i>ornata</i>	-28.13583	136.00167	SA	Peake Station
Gko596	SAMAR48378	<i>Rhynchoedura</i>	<i>ornata</i>	-28.21583	134.58306	SA	Mount Barry Station
Gko597	SAMAR48486	<i>Rhynchoedura</i>	<i>ornata</i>	-27.31944	134.50167	SA	Todmorden Station
Gko598	SAMAR48540	<i>Rhynchoedura</i>	<i>ornata</i>	-27.74583	136.69944	SA	Macumba Station

Lab ID	Museum #	Genus	Species	Latitude	Longitude	State	Locality (nearest)
Gko599	SAMAR50016	<i>Rhynchoedura</i>	<i>ornata</i>	-26.57639	136.94639	SA	Approddinna Attora Knolls
Gko601	SAMAR50374	<i>Rhynchoedura</i>	<i>ornata</i>	-30.50667	138.36889	SA	Mt Aroona
Gko605	SAMAR52795	<i>Rhynchoedura</i>	<i>ornata</i>	-26.75528	135.11944	SA	Hamilton Homestead
Gko606	SAMAR52824	<i>Rhynchoedura</i>	<i>ornata</i>	-26.82333	136.07194	SA	Akoalyerilla Hill Macumba Station
Gko607	SAMAR52847	<i>Rhynchoedura</i>	<i>ornata</i>	-26.69222	134.17222	SA	Lambina Homestead
Gko608	SAMAR52870	<i>Rhynchoedura</i>	<i>ornata</i>	-27.20444	134.99444	SA	Todmorden Homestead
Gko609	SAMAR54162	<i>Rhynchoedura</i>	<i>ornata</i>	-27.77833	138.27583	SA	Kalamurina Homestead
Gko610	SAMAR54230	<i>Rhynchoedura</i>	<i>ornata</i>	-29.02111	138.02278	SA	Clayton Homestead
Gko611	SAMAR54267	<i>Rhynchoedura</i>	<i>ornata</i>	-27.85056	137.86917	SA	Kalamurina Station
Gko612	SAMAR55253	<i>Rhynchoedura</i>	<i>ornata</i>	-33.77667	139.95944	SA	Gluepot Homestead
Gko613	SAMAR41226	<i>Rhynchoedura</i>	<i>ornata</i>	-33.76389	140.43056	SA	Hideaway Hut
Gko614	SAMAR41265	<i>Rhynchoedura</i>	<i>ornata</i>	-33.59722	140.95833	SA	Twenty Three Mile Dam
Gko616	SAMAR41409	<i>Rhynchoedura</i>	<i>ornata</i>	-33.52778	140.65000	SA	Round Dam
Gko617	SAMAR41518	<i>Rhynchoedura</i>	<i>ornata</i>	-33.11944	140.05000	SA	Elmore Dam
Gko618	SAMAR29556	<i>Rhynchoedura</i>	<i>ornata</i>	-26.65000	130.81667	SA	Musgrave Ranges
Gko620	Pianka	<i>Rhynchoedura</i>	<i>ornata</i>	-28.16680	123.66300	WA	Laverton
Gko622	SAMAR46123	<i>Rhynchoedura</i>	<i>ornata</i>	-26.05333	129.40806	SA	Pipalyatjara
Gko623	SAMAR47393	<i>Rhynchoedura</i>	<i>ornata</i>	-27.43028	133.23750	SA	Wallatinna Homestead
Gko624	SAMAR47456	<i>Rhynchoedura</i>	<i>ornata</i>	-27.64528	132.88583	SA	Oolarinna East Bore
Gko625	SAMAR48705	<i>Rhynchoedura</i>	<i>ornata</i>	-27.01417	129.87000	SA	Mt Lindsay
Gko626	SAMAR50122	<i>Rhynchoedura</i>	<i>ornata</i>	-26.06083	132.39917	SA	Sentinel Hill
Gko627	SAMAR51533	<i>Rhynchoedura</i>	<i>ornata</i>	-26.26944	131.47139	SA	Amata
Gko628	SAMAR51617	<i>Rhynchoedura</i>	<i>ornata</i>	-26.85528	133.05250	SA	Indulkana
Gko631	SAMAR22593	<i>Rhynchoedura</i>	<i>ornata</i>	-32.11667	137.58333	SA	Uro Bluff
Gko633	SAMAR25442	<i>Rhynchoedura</i>	<i>ornata</i>	-32.39583	136.16667	SA	Mt Ive Station
Gko634	SAMAR30411	<i>Rhynchoedura</i>	<i>ornata</i>	-28.84444	134.68750	SA	Coober Pedy
Gko635	SAMAR36873	<i>Rhynchoedura</i>	<i>ornata</i>	-31.48333	138.17500	SA	Mem Merna Station
Gko636	SAMAR44780	<i>Rhynchoedura</i>	<i>ornata</i>	-31.58333	136.33333	SA	Mahenewo Station
Gko638	SAMAR45969	<i>Rhynchoedura</i>	<i>ornata</i>	-26.40500	129.12972	SA	Pipalyatjara
Gko639	SAMAR46646	<i>Rhynchoedura</i>	<i>ornata</i>	-29.23333	137.88333	SA	Muloorinna Homestead
Gko640	SAMAR48577	<i>Rhynchoedura</i>	<i>ornata</i>	-27.33694	130.23750	SA	Mt Cheesman
Gko641	SAMAR50245	<i>Rhynchoedura</i>	<i>ornata</i>	-31.58972	136.78611	SA	Oakden Hills Station
Gko642	SAMAR52745	<i>Rhynchoedura</i>	<i>ornata</i>	-32.05000	139.83333	SA	Station
Gko643	SAMAR54101	<i>Rhynchoedura</i>	<i>ornata</i>	-31.11861	134.00722	SA	Yellabinna Reserve
Gko645	AMSR118614	<i>Rhynchoedura</i>	<i>ornata</i>	-31.85310	141.91510	NSW	E Broken Hill
Gko646	AMSR118617	<i>Rhynchoedura</i>	<i>ornata</i>	-33.90110	141.78480	NSW	Wentworth
Gko647	AMSR118619	<i>Rhynchoedura</i>	<i>ornata</i>	-33.00000	141.02170	NSW	Loch Lily
Gko648	AMSR118620	<i>Rhynchoedura</i>	<i>ornata</i>	-32.98333	141.61667	NSW	Coonbah
Gko649	AMSR118621	<i>Rhynchoedura</i>	<i>ornata</i>	-32.90260	144.30130	NSW	Ivanhoe
Gko650	Steve Morton	<i>Rhynchoedura</i>	<i>ornata</i>	-21.00890	130.12640	NT	Sangster's Bore
Gko651	NTMR13652	<i>Rhynchoedura</i>	<i>ornata</i>	-23.18310	132.65480	NT	Yuendumu Road
Gko652	NTMR13666	<i>Rhynchoedura</i>	<i>ornata</i>	-23.28990	132.41700	NT	Yuendumu Road
Gko654	SAMAR32094	<i>Rhynchoedura</i>	<i>ornata</i>	-30.48778	132.05972	SA	Immarna Siding
Gko655	SAMAR32126	<i>Rhynchoedura</i>	<i>ornata</i>	-30.25556	131.55000	SA	Maralinga
Gko657	SAMAR51850	<i>Rhynchoedura</i>	<i>ornata</i>	-29.90972	139.45889	SA	Mt Fitton
Gko658	WAMR166332	<i>Rhynchoedura</i>	<i>ornata</i>	-24.69640	128.76280	WA	Pungkulpirri Waterhole
Gko659	WAMR166340	<i>Rhynchoedura</i>	<i>ornata</i>	-24.59970	128.74470	WA	Pungkulpirri Waterhole
Gko660	SAMAR62132	<i>Rhynchoedura</i>	<i>ornata</i>	-25.93080	128.44940	WA	Blacreekstone
Gko675	102178	<i>Rhynchoedura</i>	<i>ornata</i>	-22.60270	118.45970	WA	Mt Windell
Gko676	102502	<i>Rhynchoedura</i>	<i>ornata</i>	-23.11300	116.01170	WA	Barlee Range
Gko677	104052	<i>Rhynchoedura</i>	<i>ornata</i>	-21.60910	118.97420	WA	Woodstocreek Station
Gko678	110693	<i>Rhynchoedura</i>	<i>ornata</i>	-28.16160	119.52500	WA	Sandstone
Gko679	110753	<i>Rhynchoedura</i>	<i>ornata</i>	-23.37880	120.25640	WA	Newman
Gko680	110788	<i>Rhynchoedura</i>	<i>ornata</i>	-21.94130	116.45390	WA	Pannawonica
Gko682	110903	<i>Rhynchoedura</i>	<i>ornata</i>	-19.88940	128.86000	WA	Tanami Downs
Gko686	110981	<i>Rhynchoedura</i>	<i>ornata</i>	-27.24190	120.69780	WA	Lake Way
Gko687	112022	<i>Rhynchoedura</i>	<i>ornata</i>	-27.02550	116.78140	WA	Booldardy Station
Gko688	112104	<i>Rhynchoedura</i>	<i>ornata</i>	-25.93470	118.84330	WA	Meekatharra
Gko689	119999	<i>Rhynchoedura</i>	<i>ornata</i>	-15.83330	128.03330	WA	Cockburn Range
Gko695	122590	<i>Rhynchoedura</i>	<i>ornata</i>	-25.65380	114.62560	WA	none
Gko696	123804	<i>Rhynchoedura</i>	<i>ornata</i>	-25.08800	115.38000	WA	none
Gko697	125470	<i>Rhynchoedura</i>	<i>ornata</i>	-23.31660	120.03330	WA	Newman
Gko699	126403	<i>Rhynchoedura</i>	<i>ornata</i>	-30.28330	119.75000	WA	Bungalbin Sandplain
Gko700	126566	<i>Rhynchoedura</i>	<i>ornata</i>	-30.45000	120.68330	WA	Kalgoorlie
Gko702	127571	<i>Rhynchoedura</i>	<i>ornata</i>	-30.02000	121.07750	WA	Goongarrie
Gko704	132783	<i>Rhynchoedura</i>	<i>ornata</i>	-16.03220	128.84500	WA	Lake Argyle
Gko705	136253	<i>Rhynchoedura</i>	<i>ornata</i>	-26.79580	115.51690	WA	Muggon
Gko706	137011	<i>Rhynchoedura</i>	<i>ornata</i>	-27.35000	120.76670	WA	Wanjari National Park
Gko707	144557	<i>Rhynchoedura</i>	<i>ornata</i>	-30.25000	119.26670	WA	Mount Jacreekson
Gko708	145610	<i>Rhynchoedura</i>	<i>ornata</i>	-22.39000	119.99000	WA	Port Hedland
Gko709	146721	<i>Rhynchoedura</i>	<i>ornata</i>	-21.32470	118.86330	WA	Port Hedland
Gko019	R96971	<i>Heteronotia</i>	<i>planiceps</i>	-15.71944	125.20694	WA	Kings Cascade
Gko020	R106220	<i>Heteronotia</i>	<i>planiceps</i>	-16.10000	124.63333	WA	Red Cone Hill
Gko021	R113996	<i>Heteronotia</i>	<i>planiceps</i>	-15.35000	126.61667	WA	Carson Escarpment
Gko022	R132761	<i>Heteronotia</i>	<i>planiceps</i>	-15.29111	128.66917	WA	Carlton Hill Station
Gko025	R158015	<i>Heteronotia</i>	<i>planiceps</i>	-16.11417	123.69417	WA	Koolan Island
Gko026	R158024	<i>Heteronotia</i>	<i>planiceps</i>	-16.14583	123.74917	WA	Koolan Island
Gko027	R158033	<i>Heteronotia</i>	<i>planiceps</i>	-16.14722	123.77056	WA	Koolan Island

Lab ID	Museum #	Genus	Species	Latitude	Longitude	State	Locality (nearest)
Gko253	ABTC11740	<i>Heteronotia</i>	<i>planiceps</i>	-23.37300	120.14200	WA	Mt. Newman
Gko254	ABTC29848	<i>Heteronotia</i>	<i>planiceps</i>	-15.76806	129.09000	NT	Jarnarm Escarpment
Gko256	ABTC31418	<i>Heteronotia</i>	<i>spelea_central</i>	-23.69611	134.03556	NT	Undoolya Homestead
Gko257	ABTC31432	<i>Heteronotia</i>	<i>spelea_central</i>	-23.59000	134.47972	NT	Ross River
Gko258	ABTC31433	<i>Heteronotia</i>	<i>spelea_central</i>	-23.69611	134.03556	NT	Undoolya Homestead
Gko259	ABTC31434	<i>Heteronotia</i>	<i>spelea_central</i>	-23.59000	134.47972	NT	Ross River
Gko260	ABTC31435	<i>Heteronotia</i>	<i>spelea_central</i>	-23.69611	134.03556	NT	Undoolya Homestead
Gko261	ABTC32871	<i>Heteronotia</i>	<i>spelea_central</i>	-23.69611	134.03556	NT	Undoolya Homestead
Gko262	ABTC32988	<i>Heteronotia</i>	<i>spelea_central</i>	-23.69611	134.03556	NT	Undoolya Homestead
Gko279	ABTC24118	<i>Heteronotia</i>	<i>spelea_central</i>	-23.89000	133.71972	NT	Mulga Dam MacDonnell Range
Gko280	ABTC31199	<i>Heteronotia</i>	<i>spelea_central</i>	-23.69611	134.03556	NT	Undoolya Homestead
Gko281	ABTC31436	<i>Heteronotia</i>	<i>spelea_central</i>	-23.69611	134.03556	NT	Undoolya Homestead
Gko282	ABTC31437	<i>Heteronotia</i>	<i>spelea_central</i>	-23.69611	134.03556	NT	Undoolya Homestead
Gko283	ABTC31636	<i>Heteronotia</i>	<i>spelea_central</i>	-23.59000	134.47972	NT	Ross River
Gko284	ABTC31659	<i>Heteronotia</i>	<i>spelea_central</i>	-23.59000	134.47972	NT	Ross River
Gko285	ABTC31726	<i>Heteronotia</i>	<i>spelea_central</i>	-23.59000	134.47972	NT	Ross River
Gko286	ABTC31731	<i>Heteronotia</i>	<i>spelea_central</i>	-23.59000	134.47972	NT	Ross River
Gko004	R110056	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-21.03590	117.10658	WA	Roebourne
Gko005	R110075	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-21.03590	117.10658	WA	Roebourne
Gko006	R110076	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-21.03590	117.10658	WA	Roebourne
Gko028	R97258	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-23.36667	120.13333	WA	Wheelarra Hill
Gko029	R102227	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-23.41139	115.89389	WA	Barlee Range
Gko030	R102380	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-23.40000	115.88333	WA	Barlee Range
Gko031	R102436	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-23.13056	115.99444	WA	Goodeman Pool
Gko032	R113545	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-22.83333	119.46667	WA	Capricorn Roadhouse
Gko033	R114561	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-23.08333	119.28333	WA	Newman
Gko034	R115832	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-23.11889	118.78278	WA	The Governor
Gko035	R115833	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-23.11889	118.78278	WA	The Governor
Gko036	R121394	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-22.86667	119.43333	WA	Weeli Wolli
Gko037	R132488	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-23.20000	117.66667	WA	Paraburdoo
Gko038	R132681	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-20.60028	120.29167	WA	Shay Gap
Gko039	R135010	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-23.38611	119.62944	WA	Mount Whaleba Creek
Gko040	R135388	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-22.31056	117.32861	WA	Mount Brockman Station
Gko041	R135446	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-22.31056	117.32194	WA	Mount Brockman Station
Gko042	R135456	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-22.31056	117.32194	WA	Mount Brockman Station
Gko043	R145600	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-20.92860	118.67780	WA	Port Hedland
Gko044	R157546	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-23.19417	118.81500	WA	West Angeles
Gko045	R157719	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-22.94083	118.90500	WA	Newman
Gko278	ABTC11763	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-20.92000	120.20972	WA	Bamboo Creek Mine
Gko287	ABTC32832	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-20.92000	120.20972	WA	Bamboo Creek
Gko288	ABTC32922	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-20.92000	120.20972	WA	Bamboo Creek
Gko436	R111927	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-22.60980	120.72900	WA	BDRN09*
Gko437	R111986	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-22.60980	120.72900	WA	BDRN09*
Gko438	R160085	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-21.32190	121.00200	WA	NE09*
Gko439	R160145	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-21.32190	121.00200	WA	NE09*
Gko440	R161285	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-21.32190	121.00200	WA	NE09*
Gko442	R165152	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-23.05380	119.17700	WA	PW3*
Gko443	R165222	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-21.34130	117.18900	WA	DRC6*
Gko444	R170295	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-21.03640	117.10600	WA	TCMBC05*
Gko445	R170828	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-23.31830	117.87000	WA	MBE06*
Gko446	R170892	<i>Heteronotia</i>	<i>spelea_pilbara</i>	-21.50620	119.41800	WA	MBE1*
31219_CA6	31219	<i>Heteronotia</i>	<i>binoei</i>	-23.60000	134.48333	NT	Ross Ruin
31228_CA6	31228	<i>Heteronotia</i>	<i>binoei</i>	-23.63333	133.88333	NT	Wigley Waterhole
31354_CA6	31354	<i>Heteronotia</i>	<i>binoei</i>	-28.96667	117.11667	WA	Thundelarra Homestead
31355_CA6	31355	<i>Heteronotia</i>	<i>binoei</i>	-25.71670	114.28330	WA	Wooramel
31362_CA6	31362	<i>Heteronotia</i>	<i>binoei</i>	-26.43333	114.16667	WA	Hamelin
31364_CA6	31364	<i>Heteronotia</i>	<i>binoei</i>	-26.53333	118.51667	WA	Yoothapinna Station
31637_CA6	31637	<i>Heteronotia</i>	<i>binoei</i>	-23.70000	134.03333	NT	Undoolya Homestead
31645_CA6	31645	<i>Heteronotia</i>	<i>binoei</i>	-25.83333	133.30000	NT	Kulgera
31660_CA6	31660	<i>Heteronotia</i>	<i>binoei</i>	-23.60000	134.48333	NT	Ross River
31722_CA6	31722	<i>Heteronotia</i>	<i>binoei</i>	-26.20000	114.28333	WA	Carbla Homestead
32337_CA6	32337	<i>Heteronotia</i>	<i>binoei</i>	-25.28333	116.20000	WA	Dalgetty Downs Station
32338_CA6	32338	<i>Heteronotia</i>	<i>binoei</i>	-26.25000	113.81670	WA	Nanga
32344_CA6	32344	<i>Heteronotia</i>	<i>binoei</i>	-26.41670	113.51670	WA	Carrarang
32375_CA6	32375	<i>Heteronotia</i>	<i>binoei</i>	-26.70000	113.75000	WA	Tamala
32383_CA6	32383	<i>Heteronotia</i>	<i>binoei</i>	-26.81667	114.61667	WA	Billabong Roadhouse
32437_CA6	32437	<i>Heteronotia</i>	<i>binoei</i>	-27.00000	133.31700	SA	Chandler
32439_CA6	32439	<i>Heteronotia</i>	<i>binoei</i>	-26.93333	133.50000	SA	Granite Downs
32463_CA6	32463	<i>Heteronotia</i>	<i>binoei</i>	-26.93333	133.50000	SA	Granite Downs Station
32794_CA6	32794	<i>Heteronotia</i>	<i>binoei</i>	-25.03333	115.13333	WA	Jimba Jimba Station
32797_CA6	32797	<i>Heteronotia</i>	<i>binoei</i>	-26.53333	118.51667	WA	Yoothapinna Station
32924_CA6	32924	<i>Heteronotia</i>	<i>binoei</i>	-24.81667	113.78333	WA	Brickhouse Station
52485_CA6	52485	<i>Heteronotia</i>	<i>binoei</i>	-27.05400	132.50600	SA	Victory
52489_CA6	52489	<i>Heteronotia</i>	<i>binoei</i>	-27.02300	132.42400	SA	Betty Well
52498_CA6	52498	<i>Heteronotia</i>	<i>binoei</i>	-27.02300	132.42400	SA	Betty Well
Gko251_CA6	Gko251	<i>Heteronotia</i>	<i>binoei</i>	-26.70000	140.61972	SA	Cordello Downs
MKF299_CA6	MKF299	<i>Heteronotia</i>	<i>binoei</i>	-29.41670	117.30000	WA	Ninghan
MKF383_CA6	MKF383	<i>Heteronotia</i>	<i>binoei</i>	-29.41670	117.30000	WA	Ninghan

Lab ID	Museum #	Genus	Species	Latitude	Longitude	State	Locality (nearest)
MKF403_CA6	MKF403	<i>Heteronotia</i>	<i>binoei</i>	-26.66804	113.65450	WA	Tamala
MKF441_CA6	MKF441	<i>Heteronotia</i>	<i>binoei</i>	-26.66804	113.65450	WA	Tamala
MKF495_CA6	MKF495	<i>Heteronotia</i>	<i>binoei</i>	-27.30000	117.96670	WA	Nallan
MKF99_CA6	MKF99	<i>Heteronotia</i>	<i>binoei</i>	-26.93700	133.49500	SA	Granite Downs
31241_CapeYork	31241	<i>Heteronotia</i>	<i>binoei</i>	-11.96670	141.90000	QLD	Mapoon Mission
77126_CapeYork	77126	<i>Heteronotia</i>	<i>binoei</i>	-18.14770	144.31610	QLD	Gulf Developmental Road
SEW7634_CapeYork	SEW763	<i>Heteronotia</i>	<i>binoei</i>	-13.31710	142.95110	QLD	Wolverton
77094_CapeY	77094	<i>Heteronotia</i>	<i>binoei</i>	-18.2945	144.07660	QLD	Einiasleigh
31925_EA6	31925	<i>Heteronotia</i>	<i>binoei</i>	-24.72300	152.00803	QLD	Waterloo Station
31926_EA6	31926	<i>Heteronotia</i>	<i>binoei</i>	-24.72300	152.00803	QLD	Waterloo Station
33017_EA6	33017	<i>Heteronotia</i>	<i>binoei</i>	-22.68679	150.44049	QLD	Shoalwater Bay
33018_EA6	33018	<i>Heteronotia</i>	<i>binoei</i>	-22.68680	150.44049	QLD	Shoalwater Bay
6996_EA6	6996	<i>Heteronotia</i>	<i>binoei</i>	-18.20532	145.95673	QLD	Kennedy
72898_EA6	72898	<i>Heteronotia</i>	<i>binoei</i>	-20.98530	145.01258	QLD	Torrens Creek
72963_EA6	72963	<i>Heteronotia</i>	<i>binoei</i>	-23.35660	144.16654	QLD	Longreach
MKF633_EA6	MKF633	<i>Heteronotia</i>	<i>binoei</i>	-24.10724	143.18576	QLD	Noonbah Station
31181_EA6Desert	31181	<i>Heteronotia</i>	<i>binoei</i>	-29.83333	137.75000	SA	Marree
31372_EA6Desert	31372	<i>Heteronotia</i>	<i>binoei</i>	-31.03333	125.21667	WA	Rawlinna
31375_EA6Desert	31375	<i>Heteronotia</i>	<i>binoei</i>	-31.01670	125.33330	WA	Rawlinna
33059_EA6Desert	33059	<i>Heteronotia</i>	<i>binoei</i>	-30.83333	121.30000	WA	Munari Station
MKF118_EA6Desert	MKF118	<i>Heteronotia</i>	<i>binoei</i>	-27.95000	134.31300	SA	Copper Hills
MKF126_EA6Deser	MKF126	<i>Heteronotia</i>	<i>binoei</i>	-27.95492	134.31931	SA	near Copper Hills
MKF129_EA6Desert	MKF129	<i>Heteronotia</i>	<i>binoei</i>	-28.20470	134.48833	SA	Evelyn Downs
MKF34_EA6Desert	MKF34	<i>Heteronotia</i>	<i>binoei</i>	-34.00000	139.35000	SA	Bower
32941_Gulf	32941	<i>Heteronotia</i>	<i>binoei</i>	-17.45360	138.35750	QLD	Hells Gate
32950_Gulf	32950	<i>Heteronotia</i>	<i>binoei</i>	-17.33330	138.23330	QLD	Westmoreland
70786_Gulf	70786	<i>Heteronotia</i>	<i>binoei</i>	-17.87360	140.83528	QLD	Karumba
72768_Gulf	72768	<i>Heteronotia</i>	<i>binoei</i>	-18.53330	140.66670	QLD	Bang Bang Jumpup
72874_Gulf	72874	<i>Heteronotia</i>	<i>binoei</i>	-19.22750	140.34733	QLD	Burke & Wills Roadhouse Dump
77110_Gulf	77110	<i>Heteronotia</i>	<i>binoei</i>	-18.72180	144.32440	QLD	The Lynd Junction
77115_Gulf	77115	<i>Heteronotia</i>	<i>binoei</i>	-18.88080	144.54710	QLD	The Lynd Roadhouse
MKF563_Gulf	MKF563	<i>Heteronotia</i>	<i>binoei</i>	-20.52900	140.41405	QLD	Lanark Station
MKF577_Gulf	MKF577	<i>Heteronotia</i>	<i>binoei</i>	-18.62850	139.02338	QLD	Yeldham Station
31253_TopEnd	31253	<i>Heteronotia</i>	<i>binoei</i>	-15.70000	126.36667	WA	Drysdale
31377_TopEnd	31377	<i>Heteronotia</i>	<i>binoei</i>	-15.36670	126.30000	WA	Doongan
31424_TopEnd	31424	<i>Heteronotia</i>	<i>binoei</i>	-12.46670	130.83330	NT	Berrimah
31381_TopEnd	31381	<i>Heteronotia</i>	<i>binoei</i>	-15.46670	128.10000	WA	Wyndham
14404_SM6Desert	14404	<i>Heteronotia</i>	<i>binoei</i>	-20.60000	116.50000	WA	Enderby Island
31234_SM6Desert	31234	<i>Heteronotia</i>	<i>binoei</i>	-25.20000	130.70000	NT	Mt. Olga
31248_SM6Desert	31248	<i>Heteronotia</i>	<i>binoei</i>	-19.08333	121.68333	WA	Nita Downs
31254_SM6Desert	31254	<i>Heteronotia</i>	<i>binoei</i>	-25.65700	125.55600	WA	Notabilis Hill
31255_SM6Desert	31255	<i>Heteronotia</i>	<i>binoei</i>	-20.58330	130.35000	NT	The Granites
31350_SM6Desert	31350	<i>Heteronotia</i>	<i>binoei</i>	-25.26667	122.03333	WA	Glenayle Station
31356_SM6Desert	31356	<i>Heteronotia</i>	<i>binoei</i>	-22.55000	115.50000	WA	Nanutarra Station
31368_SM6Desert	31368	<i>Heteronotia</i>	<i>binoei</i>	-19.08333	121.68333	WA	Nita Downs
31404_SM6Desert	31404	<i>Heteronotia</i>	<i>binoei</i>	-17.03333	128.21667	WA	Turkey Creek
31411_SM6Desert	31411	<i>Heteronotia</i>	<i>binoei</i>	-17.03333	128.21667	WA	Turkey Creek
31412_SM6Desert	31412	<i>Heteronotia</i>	<i>binoei</i>	-18.23333	127.66667	WA	Halls Creek
31416_SM6Desert	31416	<i>Heteronotia</i>	<i>binoei</i>	-18.26670	127.76670	WA	Halls Creek
31420_SM6Desert	31420	<i>Heteronotia</i>	<i>binoei</i>	-25.41667	131.96667	NT	Ayers Rock
31446_SM6Desert	31446	<i>Heteronotia</i>	<i>binoei</i>	-20.60000	116.50000	WA	Enderby Island
32406_SM6Desert	32406	<i>Heteronotia</i>	<i>binoei</i>	-25.41670	121.58333	WA	Earahedy
32448_SM6Desert	32448	<i>Heteronotia</i>	<i>binoei</i>	-25.26667	122.03333	WA	Glenayle Station
32775_SM6Desert	32775	<i>Heteronotia</i>	<i>binoei</i>	-22.45000	116.05000	WA	Mt. Stuart Station
32784_SM6Desert	32784	<i>Heteronotia</i>	<i>binoei</i>	-20.63333	119.23333	WA	Carlindi Station
32815_SM6Desert	32815	<i>Heteronotia</i>	<i>binoei</i>	-23.03333	115.03333	WA	Nyang Station
32816_SM6Desert	32816	<i>Heteronotia</i>	<i>binoei</i>	-22.45000	116.05000	WA	Mt. Stuart Station
32827_SM6Desert	32827	<i>Heteronotia</i>	<i>binoei</i>	-21.56667	115.88333	WA	Yarraloola Station
32841_SM6Desert	32841	<i>Heteronotia</i>	<i>binoei</i>	-23.03333	115.03333	WA	Nyang Station
MKF510_SM6Desert	MKF510	<i>Heteronotia</i>	<i>binoei</i>	-20.63300	119.23300	WA	Carlindi
Q262_SM6Desert	Q262	<i>Heteronotia</i>	<i>binoei</i>	-22.55000	115.50000	WA	Nanutarra
31273_SM6	31273	<i>Heteronotia</i>	<i>binoei</i>	-20.91667	120.21667	WA	Bamboo Creek
31347_SM6	31347	<i>Heteronotia</i>	<i>binoei</i>	-22.15000	133.41667	NT	Ti Tree
31385_SM6	31385	<i>Heteronotia</i>	<i>binoei</i>	-20.65000	134.21667	NT	Wauchope
31397_SM6	31397	<i>Heteronotia</i>	<i>binoei</i>	-20.88333	116.66667	WA	Karratha
31400_SM6	31400	<i>Heteronotia</i>	<i>binoei</i>	-20.91667	120.21667	WA	Bamboo Creek
31407_SM6	31407	<i>Heteronotia</i>	<i>binoei</i>	-20.60000	134.25000	NT	Warachope
31657_SM6	31657	<i>Heteronotia</i>	<i>binoei</i>	-21.53333	133.86667	NT	Barrow Creek
32783_SM6	32783	<i>Heteronotia</i>	<i>binoei</i>	-21.33330	120.05000	WA	Mt. Edgar
32786_SM6	32786	<i>Heteronotia</i>	<i>binoei</i>	-21.56667	115.88333	WA	Yarraloola Station
32787_SM6	32787	<i>Heteronotia</i>	<i>binoei</i>	-22.25000	118.33333	WA	Wittenoom
32791_SM6	32791	<i>Heteronotia</i>	<i>binoei</i>	-22.28333	117.68333	WA	Hammersley Station
32951_SM6	32951	<i>Heteronotia</i>	<i>binoei</i>	-21.53333	133.86667	NT	Barrow Creek
32953_SM6	32953	<i>Heteronotia</i>	<i>binoei</i>	-21.55000	133.88330	NT	Barrows Creeks
MKF432_SM6	MKF432	<i>Heteronotia</i>	<i>binoei</i>	-22.37782	118.69105	WA	Munjina
31379_SM6Gulf	31379	<i>Heteronotia</i>	<i>binoei</i>	-15.26667	131.58333	NT	Willeroo
31389_SM6Gulf	31389	<i>Heteronotia</i>	<i>binoei</i>	-16.26667	133.36667	NT	Daly Waters
31410_SM6Gulf	31410	<i>Heteronotia</i>	<i>binoei</i>	-15.28330	131.58330	NT	Willeroo

Lab ID	Museum #	Genus	Species	Latitude	Longitude	State	Locality (nearest)
31724_SM6Gulf	31724	<i>Heteronotia</i>	<i>binoei</i>	-19.91670	138.11670	QLD	Camooweal
31724_SM6Gulf	31724	<i>Heteronotia</i>	<i>binoei</i>	-19.91670	138.11670	QLD	Camooweal
32865_SM6Gulf	32865	<i>Heteronotia</i>	<i>binoei</i>	-16.45000	136.11670	QLD	McArthur R. Station
32943_SM6Gulf	32943	<i>Heteronotia</i>	<i>binoei</i>	-18.70190	138.48455	QLD	Lawn Hill National Park
32952_SM6Gulf	32952	<i>Heteronotia</i>	<i>binoei</i>	-16.45000	134.61667	NT	Tanumbirini Station
82440_SM6Gulf	82440	<i>Heteronotia</i>	<i>binoei</i>	-21.75000	139.90000	QLD	The Monument
MKF547_SM6Gulf	MKF547	<i>Heteronotia</i>	<i>binoei</i>	-20.59740	139.70423	QLD	West Leichhardt
MKF627_SM6Gulf	MKF627	<i>Heteronotia</i>	<i>binoei</i>	-20.21467	138.88350	QLD	Yelvertoft Station
Q313_SM6Gulf	Q313	<i>Heteronotia</i>	<i>binoei</i>	-16.66700	135.85000	NT	none

mitochondrial sequences was first performed automatically using the software MUSCLE (Edgar 2004), then refined by eye in Se-Al (Rambaut 2006). Protein-coding regions were translated into amino acid sequences using the vertebrate mitochondrial genetic code and were checked for internal stop codons and frame-shift mutations.

Maximum-likelihood phylogenetic analysis

Each edited *nd2* alignment was 1038 base pairs long after removing the tRNAs. All sequences could be translated into amino acids with no evidence of pseudogenes. To estimate phylogenetic relationships using maximum likelihood, we used a rapid bootstrap analysis implemented in the program RAxML v7.0.4 (Stamatakis 2006). The datasets were partitioned into 1st+2nd and 3rd codon sites under the general time-reversible substitution model with gamma-distributed rates among sites (GTR+G). Bootstrap support values for the nodes in the maximum-likelihood tree were obtained using 1,000 pseudoreplicate datasets.

To root the maximum-likelihood trees, an outgroup taxon was included in each analysis. *Rhynchoedura ornata*, the sister species to the *Lucasium* species complex (Oliver *et al.* 2007), was used as the outgroup for the *L. stenodactylum* tree. *Lucasium stenodactylum* was used as the outgroup to root the *Rhynchoedura* phylogenetic tree. *Dixonius vietnamensis*, the sister taxon to *Heteronotia* (Jackman *et al.* 2008), was used as the outgroup to root the *Heteronotia* tree.

Diversity and demographic analyses

To infer past demographic patterns in response to aridification, we calculated nucleotide diversity and tested for population size change using the basic population genetic measurements of Tajima's D (Tajima 1989) and Fu's F_s (Fu 1997) as implemented in Arlequin v. 3.1.1. (Excoffier *et al.* 2005). Estimates and tests for significance were calculated for each population, corresponding to the phylogenetically distinct groups based on the mtDNA gene tree.

Bayesian phylogenetic and dating analysis

We used a Bayesian phylogenetic approach to co-estimate the phylogeny, demographic history, and divergence times for each of the study species. Estimation of the time-scale requires some form of calibrating information, which is difficult for our datasets

because of the paucity of reliable fossil data for Gekkota. Therefore, we used a two-step approach to obtain estimates of the time-scale. In the first step, a sample of species of Gekkota was analysed in order to obtain estimates of divergence times. These age estimates were then used as secondary calibrations for the second step, in which analyses of demographic history were conducted.

Step 1: Estimation of divergence times. To estimate divergence times within Gekkota, we downloaded nucleotide sequences for nuclear *rag1* and mitochondrial *nd2* from Genbank for eight species, representing the major lineages within the infraorder (Table 2). We also included new sequences of *Lucasium*, *Rhynchoedura*, and *Heteronotia*. For each of the three species *R. ornata*, *L. stenodactylum*, and *H. binoei*, we randomly selected representatives from the two most divergent lineages in order to ensure the most recent common ancestor (MRCA) of each species was included in the tree. This allowed us to estimate the time to the MRCA (TMRCA) of each species in order to provide calibrating information for the next step of the analysis. To reduce the impact of mutational saturation in the analysis, the third codon sites of *nd2* were excluded from the analysis. The resulting sequence alignment comprised 2784 bp (682 bp from *nd2*, 2102 bp from *rag1*) from 17 taxa.

The lack of multiple, reliable fossils within squamates, particularly geckos, limits the estimation of divergence times. Typically, phylogenetic studies of squamates have been calibrated using a rate of 5.7×10^{-9} substitutions/site/year (error range), originally obtained by Macey *et al.* (1998). However, assuming that a single rate applies to all reptiles and amphibians might be problematic for several reasons. First, there is evidence of substantial rate heterogeneity among reptilian lineages (e.g. Bromham 2002; Eo & DeWoody 2010). Second, this rate applies to species-level comparisons among squamates, whereas it is likely that a higher rate is more appropriate for intraspecific analyses (Ho *et al.* 2005; Ho & Larson 2006).

The phylogeny and divergence times were co-estimated in a Bayesian phylogenetic framework using *BEAST* 1.5.4 (Drummond & Rambaut 2007). The two data partitions, *nd2* and *rag1*, were assigned separate substitution models, selected by comparing values of the Bayesian information criterion as implemented in Modelgenerator (Keane *et al.* 2006). A Yule speciation prior was used for the tree topology and node times. To allow

Table 2. Genbank accession numbers for *rag1* and *nd2* samples representing the major lineages within Gekkota for the dating analysis.

Species	Genbank Accession <i>nd2</i>	Genbank Accession <i>rag1</i>
<i>Delma australis</i>	AY134582	FJ571633
<i>Dixonius vietnamensis</i>	EU054298	EU054282
<i>Eublepharus turkmenicus</i>	AF114248	AY662622
<i>Gekko gekko</i>	AF114249	AY662625
<i>Paradelma orientalis</i>	-	FJ571626
<i>Pseudothecadactylus lindneri</i>	AY369024	AY662626
<i>Pygopus lepidopodus</i>	AY134603	FJ571627
<i>Sphaerodactylus shrevei</i>	AY662547	AY662623

for rate variation among lineages, the phylogenetic analysis was performed using an uncorrelated lognormal relaxed clock (Drummond *et al.* 2006). The analysis was repeated using a strict clock after the posterior distribution of the coefficient of variation of rates, which measures the degree of departure from a strict clock, was found to include a value of zero.

The fossil *Cretaceogekko burmae* (Arnold & Poinar 2008), which is thought to represent the oldest unequivocal gecko and has been dated at 97-110 million years (Ma) old, was used to calibrate the root of the Gekkota tree. To allow for uncertainty in the age of the calibration, the prior age of the root was assumed to be exponentially distributed with a minimum bound of 100 million years (Ma) and with 95% of the prior density between 100 and 150 Ma.

Posterior distributions of parameters, including divergence times, were estimated via Markov chain Monte Carlo (MCMC) sampling. Samples were drawn every 2,000 steps over a total of 20,000,000 steps, with the first 10% discarded as burn-in. Acceptable convergence to the stationary distribution was checked by inspecting the posterior samples using the diagnostic software Tracer v1.5 (Rambaut & Drummond 2007). Effective sample sizes were >2,000 for all parameters, indicating sufficient sampling from the posterior.

Step 2: Estimation of demographic history and divergence times. The second step of our dating analysis utilised our large-scale *nd2* datasets to obtain age estimates for the TMRCA of the major lineages. The total dataset was divided into four subsets which were analysed separately: (i) *Rhynchoedura*, (ii) *Lucasium*, (iii) *H. binoei*, and (iv) *H. spelea* and *H. planiceps*.

It has been suggested that deep, interspecific calibrations are not appropriate for estimating divergence times among conspecific individuals (Ho & Larson 2006). This is because rates appear to be time-dependent, whereby higher rates are observed over smaller phylogenetic depths or shorter time-scales (Ho *et al.* 2005). This effect has been ascribed to a number of potential factors, with incomplete purifying selection suggested as one of the major contributors (Subramanian *et al.* 2009). In support of this hypothesis, third codon sites in vertebrate mtDNA, which are presumably subject to a

lesser degree of selective constraint than the first and second codon sites, have been shown to be relatively clocklike across more recent time-scales (Subramanian *et al.* 2009). For this reason, we used only third codon sites. For the sake of comparison, however, analyses were repeated using all three codon sites.

To estimate the best-fit model of nucleotide substitution for the four subsets of data, we used the Bayesian information criterion as implemented in Modelgenerator (Keane *et al.* 2006). The chosen models were TIM+G (*Rhynchoedura*), TrN+G (*Lucasium*), TIM+G (*H. binoei*) and TIM+G (*H. spelea* and *H. planiceps*). Models incorporating a proportion of invariant sites were disregarded because of the intraspecific nature of most of the datasets.

The date estimates from Step 1 (described above)(Table 3) were used to calibrate the root of the gene tree for each species, with the calibration priors assumed to be normally distributed. For comparison, divergence times were estimated by specifying a normal prior distribution (mean 5.7×10^{-9} subs/site/yr, standard deviation 2.9×10^{-10} subs/site/yr) for the substitution rate based on the estimate by Macey *et al.* (1998).

Results & Discussion

Mountain ranges harbour more diversity than the surrounding deserts

Phylogenetic and population genetic analyses for all three gecko groups strongly support the hypothesis that genetic diversity is greatest in the topographically complex parts of the continent, while clades occupying the low-lying desert interior have substantially less genetic diversity. This pattern is clear from the tree alone, where strong phylogeographic structure is evident within and between clades confined to mountain ranges, while extremely shallow structure characterises desert clades (Figure 2). Levels of nucleotide diversity corroborate this result, showing that saxicolous clades have much higher nucleotide diversity than desert clades (Table 4). When these values are considered in conjunction with geographic distribution, it is clear that clades with high nucleotide diversity occur across small geographic areas, while desert clades that display substantially lower nucleotide diversity are typically distributed over vast geographic areas (Figure 3). This result is exemplified in our data for *Lucasium*, where populations distributed throughout the geographically vast southern and central deserts

Table 3. Posterior root heights for clades based on a relaxed phylogenetic analysis of *nd2* and *rag1*.

Clade	Root height at all sites (subs/site/yr)	Root height at third codon sites (subs/site/yr)
<i>L. stenodactylum</i>	1.61×10^{-7} (9.73×10^{-6} , 2.27×10^{-7})	1.63×10^{-7} (9.86×10^{-6} , 2.25×10^{-7})
<i>R. ornata</i>	1.42×10^{-7} (8.21×10^{-6} , 2.01×10^{-7})	1.42×10^{-7} (8.41×10^{-6} , 2.04×10^{-7})
<i>H. binoei</i>	1.06×10^{-7} (6.46×10^{-6} , 1.47×10^{-7})	1.06×10^{-7} (6.62×10^{-6} , 3.05×10^{-7})
<i>H. spelea/H. planiceps</i>	1.91×10^{-7} (1.49×10^{-7} , 2.36×10^{-7})	1.97×10^{-7} (1.51×10^{-7} , 2.44×10^{-7})

Table 4. Diversity and demographic summary statistics. Bold labels indicate desert clades. *P* values in italics indicate significance.

Clade	Tajima's D	p value	Fu's F _s	p value	Nucleotide diversity	Maximum ML genetic distance (GTR+I+G)
<i>R. ornata</i> NSW desert	-1.16572	0.11500	-5.50464	0.00800	0.004101+/- 0.002364	0.00944
<i>R. ornata</i> NSW desert narrow	-1.41117	0.05500	-8.43479	0.00200	0.006724+/- 0.003637	0.01982
<i>R. ornata</i> Southern desert	-1.74616	0.01600	-24.51409	0.00001	0.010609+/- 0.005428	0.01975
<i>R. ornata</i> Western/Central desert	-1.68004	0.01900	-24.15092	0.00001	0.015753+/- 0.007864	0.04023
<i>R. ornata</i> Kimberley	0.37704	0.68700	-0.94519	0.23100	0.006842+/- 0.004094	0.01141
<i>L. stenodactylum</i> Pilbara	-0.38172	0.40700	-23.98100	<i>0.00200</i>	0.040324+/- 0.019507	0.08217
<i>L. stenodactylum</i> Central desert	-1.75332	0.02100	-17.96309	0.00001	0.007876+/- 0.004153	0.01798
<i>L. stenodactylum</i> Southern desert	-2.54989	0.00001	-26.60136	0.00001	0.002442+/- 0.001494	0.00867
<i>H. planiceps</i>	0.11404	0.55900	1.48798	0.46700	0.15009+/- 0.082259	0.44570
<i>H. spelea</i> Central	0.84724	0.85100	1.30056	0.72400	0.022372+/- 0.011701	0.03873
<i>H. spelea</i> Pilbara	0.89232	0.85200	-0.13347	0.47600	0.079746+/- 0.039113	0.15181
<i>H. binoei</i> CA6	0.31325	0.71800	-1.14687	0.35600	0.046824+/- 0.023180	0.09608
<i>H. binoei</i> EA6 Nullarbor	0.00794	0.52200	2.49120	0.85800	0.020765+/- 0.011701	0.02984
<i>H. binoei</i> EA6	0.02204	0.51400	-0.04408	0.30100	0.034912+/- 0.019421	0.06123
<i>H. binoei</i> SM6	1.24583	0.92500	0.53780	0.52300	0.062205+/- 0.032084	0.11823
<i>H. binoei</i> SM6 West coast	0.58737	0.78100	-1.41948	0.14900	0.016877+/- 0.009022	0.06082
<i>H. binoei</i> SM6 desert	-0.30354	0.42900	-3.70571	0.03700	0.030824+/- 0.016462	0.02386
<i>H. binoei</i> SM6 Gulf	0.70989	0.79000	0.71495	0.54600	0.040476+/- 0.021504	0.08097
<i>H. binoei</i> Top End	0.29321	0.74400	2.46431	0.54000	0.075759+/- 0.049851	0.13204
<i>H. binoei</i> Gulf	0.89029	0.84600	0.22664	0.33600	0.061673+/- 0.033415	0.13995
<i>H. binoei</i> Cape York	0.90317	0.80500	2.65317	0.53800	0.091754+/- 0.060291	0.16914

have between 5 and 18 times less nucleotide diversity than populations in the rocky Pilbara region (Table 4).

The pattern of genetic diversity within and among gecko lineages in our study is consistent with phylogeographic studies of Northern Hemisphere taxa distributed across mountain and lowland regions. High nucleotide diversity within, and strong phylogeographic structure between, gecko clades in isolated mountain ranges is indicative of long-term isolation and diversification in refugia (Hewitt 1999). This result is expected for our data, given the unlikely potential for repeated geographical contact between disjunct refugia in the Australian arid zone following intense aridification of the Plio/Pleistocene and the subsequent development of the intervening sand deserts. The low nucleotide diversity displayed by gecko clades that occupy the desert regions of the continent is indicative of rapid expansion of arid-adapted lineages into large areas of suitable territory (Castoe *et al.* 2007), and is consistent with other studies of Australian arid-zone vertebrates that show little genetic differentiation across the arid zone (Kuch *et al.* 2005; Joseph & Wilke, 2007). This pattern is expected due to the recent nature of severe aridity on the Australian continent and the development of widespread sand deserts < 1 Ma.

Diversity in mountain ranges is older than in deserts

Clades that inhabit rocky ranges are substantially older than desert clades (see Table 5 for posterior estimates of divergence times on the root node of all the major clades), with the exception of Central *H. spelea*. Our TMRCA estimates for the saxicolous clades (Pilbara *H. spelea* and Pilbara *L. stenodactylum*, *H. planiceps* and Kimberley/Top End/Gulf/Cape York *H. binoei*) date to the mid-late Miocene. In contrast, our TMRCA estimates for the desert clades (Central and Southern desert *L. stenodactylum*, and Western/Central desert, Southern desert, NSW desert and NSW desert narrow *Rhynchoedura*) all post-date the Pleistocene. The three arid zone clades of *H. binoei*, CA6, SM6 and EA6 (Fujita *et al.* 2010) have TMRCA estimates in the Pliocene, however individuals of these clades are largely restricted to regions outside the central deserts. The only true desert *H. binoei* clade is SM6 Desert, distributed throughout the Great Sandy, Little Sandy and Tanami deserts, that has a TMRCA of 1.64 Ma (790 Ka – 2.59 Ma, 95% HPD).

Table 5. TMRCA estimates for major clades based on a relaxed phylogenetic analysis of third codon sites of the mtDNA gene nd2. Bold labels indicate desert clades.

Clade	Mean (subs/site/yr)	95% HPD (subs/site/yr)
<i>R. ornata</i> NSW desert	6.85x10⁻⁵	2.63x10⁻⁵ - 1.16x10⁻⁶
<i>R. ornata</i> NSW desert narrow	1.43x10⁻⁶	6.29x10⁻⁸ - 2.33x10⁻⁶
<i>R. ornata</i> Southern desert	1.5x10⁻⁶	7.25x10⁻⁸ - 2.32x10⁻⁶
<i>R. ornata</i> Western/Central desert	2.2x10⁻⁶	1.08x10⁻⁶ - 3.36x10⁻⁶
<i>R. ornata</i> Kimberley	6.80x10 ⁻⁵	2.42x10 ⁻⁵ - 1.20x10 ⁻⁶
<i>L. stenodactylum</i> Pilbara	6.17x10 ⁻⁶	3.45x10 ⁻⁶ - 9.07x10 ⁻⁶
<i>L. stenodactylum</i> Central desert	1.47x10⁻⁶	7.19x10⁻⁸ - 2.33x10⁻⁶
<i>L. stenodactylum</i> Southern desert	8.51x10⁻⁵	3.97x10⁻⁵ - 1.36x10⁻⁶
<i>H. planiceps</i>	1.62x10 ⁻⁷	1.15x10 ⁻⁷ - 2.12x10 ⁻⁷
<i>H. spelea</i> Central	1.15x10 ⁻⁶	6.77x10 ⁻⁵ - 1.74x10 ⁻⁶
<i>H. spelea</i> Pilbara	5.64x10 ⁻⁶	3.63x10 ⁻⁶ - 7.58x10 ⁻⁶
<i>H. binoei</i> CA6	4.26x10 ⁻⁶	2.33x10 ⁻⁶ - 6.44x10 ⁻⁶
<i>H. binoei</i> EA6 Nullarbor	1.42x10 ⁻⁶	5.92x10 ⁻⁵ - 2.33x10 ⁻⁶
<i>H. binoei</i> EA6	2.36x10 ⁻⁶	1.05x10 ⁻⁶ - 3.75x10 ⁻⁶
<i>H. binoei</i> SM6	5.14x10 ⁻⁶	2.90x10 ⁻⁶ - 7.62x10 ⁻⁶
<i>H. binoei</i> SM6 West coast	2.38x10 ⁻⁶	1.10x10 ⁻⁶ - 3.74x10 ⁻⁶
<i>H. binoei</i> SM6 Desert	1.64x10⁻⁶	7.90x10⁻⁸ - 2.59x10⁻⁶
<i>H. binoei</i> SM6 Gulf	3.61x10 ⁻⁶	1.86x10 ⁻⁶ - 5.57x10 ⁻⁶
<i>H. binoei</i> Top End	5.77x10 ⁻⁶	3.19x10 ⁻⁶ - 8.52x10 ⁻⁶
<i>H. binoei</i> Gulf	5.63x10 ⁻⁶	3.07x10 ⁻⁶ - 8.40x10 ⁻⁶
<i>H. binoei</i> Cape York	5.54x10 ⁻⁶	3.13x10 ⁻⁶ - 8.28x10 ⁻⁶

Rocky ranges located on the periphery of the Australian continent, such as the Pilbara, Kimberley, and Top End were protected from climatic extremes due to their close proximity to the coast (Byrne *et al.* 2008). Our phylogenetic and dating analyses support an ancient evolutionary history of saxicolous clades in these regions, consistent with the persistence of these taxa since the onset of aridification in the mid-late Miocene. However, the Central *H. spelea* clade in the rocky ranges of central Australia is estimated to have a much younger MRCA of <1 Ma. Previous studies on the climate and geomorphological history of central Australia have suggested that because this region is completely isolated by deserts, conditions during past glacial cycles were likely to have been more severe, with temperatures much colder than at present (Miller *et al.* 1997). This hyper-arid and unstable climatic history is thought to have repeatedly extinguished narrowly endemic taxa in central Australia, particularly during the punctuated Pleistocene arid cycles (Crisp *et al.* 2001), and offers an explanation for the very young age of this clade relative to the others in the genus (Pepper *et al.* 2011 [Chapter I]).

The opening of desert biomes and the distribution and movement of sand deserts are known to have profoundly influenced diversification patterns and distributions of arid-zone taxa (Scott *et al.* 2004; Melville *et al.* 2009; Fujita *et al.* 2010). In all of our phylogenies, the MRCA estimates of clades distributed throughout the Australian deserts correspond to the initiation of severe aridification across the Australian arid zone. Long-standing debate centres on the timing and pace of diversification in various groups of Northern Hemisphere biota (Avise *et al.* 1998; Lovette 2005) and the role of Pleistocene events in promoting speciation. Our results clearly demonstrate that while species-level divergences substantially pre-date the Pleistocene, the dynamic climate fluctuations of this time period had a marked impact on the genetic architecture of arid-zone desert clades.

Rock and desert populations respond differently to the severe glacial cycles of the Pleistocene

Neutrality statistics of Fu's F_s and Tajima's D suggest no deviation from neutral expectations in saxicolous clades, which can be interpreted demographically as stable populations in mutation-drift equilibrium (Table 4). The only exception is that of the Pilbara *L. stenodactylum* clade which shows a significant and large negative estimate

for Fu's F_s (-23.98 , $p < 0.002$), however this is not reflected in significant estimates of Tajima's D (-0.38 , $p < 0.40$). In contrast, analysis of all desert clades of *Rhynchoedura* and *L. stenodactylum* revealed significant negative estimates of F_s and D (Table 4), consistent with a signature of contiguous range expansion. Fu's F_s in particular returned highly significant and extremely large negative values for the two desert *L. stenodactylum* clades, as well as for the Southern desert and Western/Central desert *Rhynchoedura* clades. In some desert clades the statistical inference of expansion was not significant for Tajima's D (*Rhynchoedura* NSW desert, NSW desert narrow), but moderately large, negative F_s values were significant (Table 4). This is likely due to the greater power of Fu's F_s to detecting population growth (Ramos-Onsins & Rozas 2002).

Historical population expansions over large continental areas following Pleistocene glacial maxima are thought to explain the lack of variation and phylogeographic structure in Northern Hemisphere taxa (Hewitt 1999), with the timing of these expansions often coinciding with the most recent deglaciation event ~ 20 ka ago (eg. Mila *et al.* 2000). A number of studies have documented recent range expansions of widespread and highly vagile organisms in the African dry tropics (Van Hooft *et al.* 2002; Lorenzen *et al.* 2008) and across the Australian arid zone (Joseph & Wilke 2007; Neaves *et al.* 2009) following a peak of Pleistocene aridity and widespread desertification. Our results illustrate the similarity in response of substantially less vagile biota to the severity of Pleistocene arid conditions.

Synthesis

Palynological and geological data demonstrate that aridification was prevalent on most continents from the Miocene (Flower & Kennett 1994), and the initiation and spread of xeric conditions is thought to have had a profound effect on biotic diversification globally (van Dam 2006; Byrne *et al.* 2008; Melville *et al.* 2009). In addition, aridification of desert regions became increasingly severe from the middle Pleistocene in response to major global climatic variations (Clark 2006), but few studies have examined the genetic consequences of this turbulent climatic period for arid-zone taxa. The mtDNA genetic patterns and associated ages of lineages and clades in the geckos examined here are consistent with fragmentation, isolation, and reduction in response to the deepening aridification of the Australian continent. While our interpretation rests on results inferred from a single locus, we have found congruent mtDNA patterns across

three independent gecko radiations, and so have estimates of three independent coalescent histories. Collectively, our data provide novel insights into the evolutionary histories of taxa that evolved in concert with wide-scale aridification and desert formation.

The geographic distributions of *L. stenodactylum*, *Heteronotia* and *Rhynchoedura* span the vast deserts of Australia as well as the rocky ranges in western, northern and central Australia (Cogger 2000). Deep phylogeographic structuring exists in all taxa, reflecting long-term isolation of clades since the Mid-Miocene (~15 Ma). This timing suggests that initial diversification was likely driven by the onset of dry conditions and associated contraction of mesic forest early in the history of aridification on the Australian continent (Martin 2006). Similar divergence estimates have been inferred for arid-zone reptiles in central Asia (Melville *et al.* 2009), Africa (Scott *et al.* 2004) and the southwestern United States (Devitt 2006), corresponding to the initiation of xeric conditions in these regions. Our divergence dates also are consistent with a number of previous studies that included arid and semi-arid reptiles in Australia (reviewed in Byrne *et al.* 2008), as well as the timing of species-level diversification in Australian mesic biomes (Schneider *et al.* 1998). Our data also add to the mounting body of molecular evidence indicating widespread landscape and climate changes associated with the initiation of aridification in the Miocene had a profound influence on the higher-level diversification of the Australian biota (Crisp *et al.* 2004).

The high nucleotide diversity recovered in clades in the mountain ranges can be indicative of larger and more stable historical population size (Avice 2000). If we assume that mesic taxa were unable to move out of refugia following severe aridification of the Plio/Pleistocene, or possibly even earlier depending on the sensitivity and thermal tolerances of the organism, diversity has been sustained in these mountainous pockets for extremely long periods of time. While tectonic uplift and mountain building has been strongly linked to recent biotic diversification on many continents (Trewick & Wallace 2001; Che *et al.* 2010), the mountain ranges of central and Western Australia have been tectonically stable for more than 100 million years (van Kranendonk *et al.* 2002), and cannot account for the generation of such diversity in these regions. However, landscape heterogeneity, such as variation in geology and soil diversity, also is known to be important for promoting genetic diversity and speciation

(Fine *et al.* 2005; Rosenblum 2006). The topographic and spatial diversity of rock types and soil lithologies in the rocky uplands of central, northern and western Australia is linked to the ancient and unique geological history of the Australian craton exposed in these uplifted mountain regions (Wasson 1982). The associated variations in microclimate and vegetation may favour habitat specialisation, and the emergence and maintenance of diversification (Alvarez *et al.* 2009). Much like mesic taxa in the well-studied northeast Queensland rainforest (Schneider *et al.* 1998), our results clearly demonstrate that persistence of biota as aridity oscillated and intensified in the Plio/Pleistocene was maintained in climatically stable mountain refugia in and adjacent to the central arid zone, and that diversity in these regions was sustained through the Pleistocene by topographic and habitat complexity.

For taxa distributed throughout Australia's inland deserts, our results reflect a highly dynamic evolutionary history. While a number of molecular studies support intraspecific diversification during the Pleistocene in the Australian arid zone (reviewed in Byrne *et al.* 2008), our results suggest that the severe climate changes of this time period were responsible for erasing much of the genetic history of desert taxa. On the Australian continent, evidence for a major shift in climate regime 1.4-1.5 Ma has been recorded in sediments from a palaeolake in the southeast (McLaren & Wallace 2010) indicating a major step in the trend towards severe aridification on a local scale. Furthermore, dating of desert dunes in central Australia suggests increasing amplitude of aridity and the formation of major inland sand deserts < 1 Ma (Fujioka *et al.* 2009). The majority of desert clades in our study have MRCA age estimates younger than 1.5 Ma, in line with the timing of these historical climate and landscape changes. The repeated pattern of low mtDNA variation and large, negative F_s values in widespread desert clades is consistent with expectations of recent population expansions in desert-dwelling taxa. While we cannot entirely rule out the possibility of a selective sweep to explain the observed pattern of genetic variation, its recurrence in multiple, co-distributed clades suggest this explanation is less likely. We interpret our results as indicative of a substantial population bottleneck followed by recent expansion of desert clades of *Rhynchoedura* and *L. stenodactylum*, which are likely to have inhabited these arid regions following adaptations to xeric environments since the late Miocene. These desert lineages exhibit a classic broom-shaped tree structure, comprising a long broom-handle lineage abruptly branching into shallow broom-head, which might indicate

survivors of a near-complete extinction (Crisp *et al.* 2004). In contrast, ancestral habitat reconstructions for *Heteronotia* support a mesic origin (Fujita *et al.* 2010). Therefore, it seems more likely that the arid zone *H. binoei* clades expanded their ranges into the arid biome following the spread of xeric habitats in the Pliocene. Diversity in these *H. binoei* clades was probably sustained in refugia outside of the central arid zone, before the SM6 desert clade expanded its distribution across the sand deserts concomitant with the spread of the dunes.

Our molecular data provide robust answers to each of our three questions regarding the genetic consequences of aridification for taxa in arid biomes. The dynamics of biological diversification occur in a myriad of different ways, and often are tied to specific geological and ecological histories of distinct lineages. However, broad-scale climate fluctuations, such as the global glacial cycles of the Pleistocene, leave their signatures on biotic diversification across collections of taxa (Hewitt 1999; Moritz *et al.* 2000; Schneider *et al.* 1998). Despite differences in the actual details of climate and geological changes that occurred within and among regions and biomes, similar patterns emerge. In the Northern Hemisphere, this is evident from glaciations and the movement of continental ice sheets. In Southern Hemisphere arid zones, as demonstrated by the comparative phylogeography in this study, it is driven by aridification.

Chapter III

Ancient river systems divide recent species in Australia's arid zone: Morphological and multi-gene evidence for four new species of Beaked Geckos (*Rhynchoedura*)



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Molecular Phylogenetics and Evolution
(in review)

Abstract

Deserts and other arid zones remain among the least studied biomes on Earth. Emerging genetic patterns of arid distributed biota suggest a strong link between diversification history and both the onset of aridification and more recent cycles of severe aridification. A previous study based on 1 kb of mtDNA of the monotypic gecko genus *Rhynchoedura* identified five allopatric clades across the vast Australian arid zone. We supplemented this data with 2.2 kb from three nuclear loci to test for species level differences. Phylogenetic relationships estimated from the mtDNA data with ML and Bayesian methods were largely concordant with relationships estimated with the nDNA data only, and mtDNA and nDNA data combined. These analyses, and coalescent-based species-tree inference methods implemented with *BEAST, largely resolve the relationships among them. We also carried out an examination of 19 morphological characters for 268 museum specimens from across Australia, including all 197 animals for which we sequenced mtDNA. The mtDNA clades differ in a number of morphological features, and we describe three of them as new species and raise a fourth from synonymy and redescribe it. We also describe a morphologically distinctive new species from Queensland based on very few specimens. The distribution of arid zone clades across what is now relatively homogeneous sand deserts seems to be related to a topographic divide between the western uplands and eastern lowlands, with species' distributions divided by dryland rivers and major drainage lines. The existence of five cryptic species within the formerly monotypic *Rhynchoedura* points to ancient divergences within the arid zone that likely were driven by wet periods as well as dry ones.

Introduction

Arid zones represent some of the most understudied biomes on Earth, largely due to harsh climatic conditions and inaccessibility. They are widely distributed across mid-latitude continental regions and generally have a geologically recent (<20 million years ago [Mya]) history of aridification (Hartley & Chong 2002; Clark *et al.* 2006; Fujioka *et al.* 2009). These features make them exceptional landscape systems to study the consequences of severe and widespread climate change on evolutionary history. Dated molecular studies of arid zone taxa across the globe show deep divergences in line with the onset and development of aridification (*Asia*: Melville *et al.* 2009; *Australia*: reviewed in Byrne *et al.* 2008; *Africa*: Scott *et al.* 2004; Carranza 2008; *North America*: Devitt 2006; *Afro-Arabia*: Fujita & Papenfus 2010), with intensifying aridity and the movement of mobile sand deserts thought to drive phylogenetic divergences and phylogeographic structuring.

The Australian arid zone comprises a vast portion of the landmass, and as such, molecular studies of arid zone biota are essential for our understanding of the unique biotic diversity that has evolved in concert with the progressive drying of the continent since the Miocene (Martin 2006). A growing number of molecular studies are beginning to paint a picture of the impact of climatic and geomorphologic change on the origin and evolutionary history of biota living in the Australian arid zone. For aquatic taxa distributed throughout ephemeral dryland river systems, recent climatic events relating to severe arid cycling of the Pleistocene appear to have been important for diversification, when connectivity of freshwater environments was substantially more restricted (Murphy & Austin 2004; Carini & Hughes 2004; Hughes & Hillyer 2006; Masci *et al.* 2008; Faulks *et al.* 2010). In contrast, genetic studies of terrestrial biota more often show evidence of older diversification of lineages through the Miocene and Pliocene (reviewed in Byrne *et al.* 2008), with a number of small, terrestrial vertebrates displaying complex phylogeographic patterns indicative of habitat specialization (Chapple *et al.* 2004; Pepper *et al.* 2006; Shoo *et al.* 2008; Couper & Hoskin 2008), persistence and diversification within mesic refugia (Blacket *et al.* 2001; Fujita *et al.* 2010; Pepper *et al.* 2011 [Chapter I]), and recent range expansion into the deserts (Jennings *et al.* 2003; Fujita *et al.* 2010; Pepper *et al.* submitted [Chapter II]). Of particular importance for understanding and interpreting the geographic distribution of

genetic diversity in the context of aridification history, widespread arid zone species often are found to comprise substantial cryptic diversity (Rabosky *et al.* 2004; Pepper *et al.* 2006; Oliver *et al.* 2009, 2010; Fujita *et al.* 2010).

The Beaked Geckos (*Rhynchoedura*) comprise a monotypic gecko genus widely distributed throughout the Australian arid zone, with a highly specialized morphology that presumably has evolved to enable efficient feeding on termites (Pianka 1986). The head is narrow and pointed, and at the tip of the snout the rostral (upper) and mental (lower) scales are enlarged and form a beak-like structure. Due to the highly derived ‘beaked’ morphology, all *Rhynchoedura* specimens have been assigned to the species *R. ornata* with no mention of morphological variation in scientific publications or field guides based on examination of specimens (e.g. Storr *et al.* 1990; Cogger 2000). Recently, however, Pepper *et al.* (2006) included several representatives of *R. ornata* from Western Australia as an outgroup for a phylogeographic analysis of *Lucasium* (*Diplodactylus*) *stenodactylum*. A single specimen from the eastern Kimberley region in northern Western Australia was highly divergent from other more southerly-distributed arid zone samples. Examination of this specimen revealed a distinctive morphotype that had not been commented on by previous workers and provided the motivation for the current study. A thorough mtDNA screen of almost all available tissue samples of *Rhynchoedura* throughout the Australian arid zone revealed five divergent clades (Pepper *et al.* submitted [Chapter II]). Here we sequence three additional nuclear genes to further assess genetic diversity within the group and to test the genetic boundaries of the mtDNA clades using both traditional and coalescent-based species tree inference methods. In addition, we carried out morphological examinations of 268 specimens from Australian museum collections to revise the classification of the genus in light of all the available evidence. Our dense sampling permits a detailed examination of the relationship between genetic diversity in a terrestrial vertebrate and regional landscapes across the entire Australian arid zone.

Materials & Methods

Taxonomic sampling

We chose specimen tissues from existing collections of the Western Australian Museum (WAM), the South Australian Museum (SAMA), the Australian Museum (AMS), and the Queensland Museum (QM) to provide the widest geographic sampling possible. The majority of our mtDNA phylogeny was reproduced using previously published material (Pepper *et al.* submitted [Chapter II]); however, we included 10 additional samples to provide a clearer picture of the distribution of genetic diversity across the historically under-represented regions of Queensland and the core of the central sand deserts in Western Australia. In addition to the mtDNA dataset, we present new material from three additional nuclear genes that were sequenced for a subset of individuals in the mtDNA phylogeny. Museum accession numbers and collection localities are given in Table 1.

Abbreviations for regions: NSW, New South Wales; SA, South Australia; WA, Western Australia; NT, Northern Territory; QLD, Queensland.

DNA sequencing and alignment

For all new samples, we followed the protocol of Pepper *et al.* (2006), targeting a ~1200 base pair (bp) fragment of the mitochondrial genome, extending from tRNA^{Met} through the entire protein-coding gene *nd2* (NADH dehydrogenase subunit II) and the genes encoding tRNA^{Trp}, tRNA^{Ala}, and tRNA^{Asn}. For a subset of 43 individuals representing the five mtDNA lineages of Pepper *et al.* (submitted [Chapter II]), we sequenced an additional 838 bp fragment of the recombination activating gene-1 exon (*rag1*). For details of PCR amplification and sequencing, including reactions and primer combinations, see Pepper *et al.* (2006). The utility of nDNA markers for studying closely related groups is limited due to the slower evolution of nuclear loci (Hare 2001). Given non-coding nDNA typically evolves faster than adjacent coding sequence, we also sequenced two recently developed intron markers (developed for another group of Australian geckos), *bzw1* (738 bp) and *snrpd3* (638 bp) for the same 43 individuals, using the PCR, sequencing and primer combinations of Fujita *et al.* (2010). Alignment of sequences was first performed automatically using the software MUSCLE (Edgar 2004), then refined by eye in Se-Al (Rambout 1996). Protein-coding regions were

Table 1. Museum accession numbers and collection locality information for all samples used in this study. Bold indicates the individual was sequenced for three nDNA loci.

Lab ID	Museum #	Genus	species	Latitude	Longitude	State	Locality (nearest)
Gko230	WAMR84540	<i>Rhynchoedura</i>	<i>ornata</i>	-25.05000	128.66667	WA	Giles Creek
Gko231	WAMR84541	<i>Rhynchoedura</i>	<i>ornata</i>	-25.05000	128.66667	WA	Giles Creek
Gko232	WAMR84592	<i>Rhynchoedura</i>	<i>ornata</i>	-29.06667	121.35000	WA	Leonora
Gko233	WAMR100521	<i>Rhynchoedura</i>	<i>ornata</i>	-29.83333	120.91667	WA	Menzies
Gko234	WAMR102502	<i>Rhynchoedura</i>	<i>ornata</i>	-23.11306	116.01167	WA	Barlee Range
Gko235	WAMR110582	<i>Rhynchoedura</i>	<i>ornata</i>	-19.90278	128.76333	WA	Tanami Desert
Gko236	WAMR110583	<i>Rhynchoedura</i>	<i>ornata</i>	-19.90278	128.76333	WA	Tanami Desert
Gko237	WAMR112972	<i>Rhynchoedura</i>	<i>ornata</i>	-17.05972	122.71667	WA	Broome
Gko238	WAMR112983	<i>Rhynchoedura</i>	<i>ornata</i>	-17.05972	122.71667	WA	Broome
Gko239	WAMR132719	<i>Rhynchoedura</i>	<i>sexapora</i> sp. nov.	-15.77167	128.28806	WA	Wyndham
Gko240	WAMR144746	<i>Rhynchoedura</i>	<i>ornata</i>	-30.46667	119.60000	WA	Bungabbin Hill
Gko241	WAMR157554	<i>Rhynchoedura</i>	<i>ornata</i>	-21.67389	115.88917	WA	Pannawonica
Gko242	WAMR158315	<i>Rhynchoedura</i>	<i>ornata</i>	-22.63056	114.39250	WA	Giralia
Gko388	AMSR135427	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-29.03333	146.21667	NSW	Morton Plains Station
Gko389	AMSR137630	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-29.66667	144.60000	NSW	Wanaaring
Gko390	AMSR137631 (holotype)	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-29.66667	144.60000	NSW	Wanaaring
Gko391	AMSR138130	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-29.32028	145.84639	NSW	Enngonia
Gko392	AMSR138441	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-29.71667	144.11667	NSW	Wanaaring
Gko393	AMSR138442	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-29.81667	144.58333	NSW	Wanaaring
Gko394	AMSR138443	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-29.98333	145.36667	NSW	Wanaaring
Gko395	AMSR139902	<i>Rhynchoedura</i>	<i>sexapora</i> sp. nov.	-16.01861	128.00389	WA	El Questro Station
Gko396	AMSR139903	<i>Rhynchoedura</i>	<i>sexapora</i> sp. nov.	-16.01861	128.00389	WA	El Questro Station
Gko397	AMSR139904 (holotype)	<i>Rhynchoedura</i>	<i>sexapora</i> sp. nov.	-16.01861	128.00389	WA	El Questro Station
Gko399	AMSR141041	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-29.35694	146.27111	NSW	Beulah Station
Gko398	AMSR139905	<i>Rhynchoedura</i>	<i>sexapora</i> sp. nov.	-16.01861	128.00389	WA	El Questro Station
Gko400	AMSR145587	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-31.28333	142.28333	NSW	Mootwingee National Park
Gko401	AMSR145587	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-31.28333	142.28333	NSW	Mootwingee National Park
Gko402	AMSR145588	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-31.28333	142.28333	NSW	Mootwingee National Park
Gko403	AMSR150159	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-31.20000	142.30000	NSW	Mootwingee National Park
Gko404	AMSR151586	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-31.38167	145.70500	NSW	Cobar
Gko405	AMSR151587	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-31.38167	145.70500	NSW	Cobar
Gko406	AMSR152924	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-29.03333	141.73333	NSW	Sturt National Park
Gko407	AMSR152925	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-29.03333	141.73333	NSW	Sturt National Park
Gko408	AMSR152927	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-29.05583	141.89833	NSW	Sturt National Park
Gko409	AMSR152930	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-29.05417	141.89083	NSW	Sturt National Park
Gko410	AMSR152935	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-29.05583	141.89833	NSW	Sturt National Park
Gko411	AMSR152940 (holotype)	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-29.03333	141.73333	NSW	Sturt National Park
Gko412	AMSR152941	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-29.03333	141.73333	NSW	Sturt National Park
Gko413	AMSR152946	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-29.05583	141.89833	NSW	Sturt National Park
Gko414	AMSR152961	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-29.05417	141.89083	NSW	Sturt National Park
Gko415	AMSR152966	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-29.04944	141.86083	NSW	Sturt National Park
Gko416	AMSR152982	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.08333	141.21667	NSW	Sturt National Park
Gko417	AMSR153315	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-33.12444	143.27444	NSW	Spring Hill
Gko418	AMSR153316	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-33.12444	143.27444	NSW	Spring Hill
Gko419	AMSR153317	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-33.12444	143.27444	NSW	Spring Hill
Gko420	AMSR155270	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-29.03111	141.45083	NSW	Sturt National Park
Gko421	AMSR155276	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.04444	141.30722	NSW	Sturt National Park
Gko422	AMSR155340	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.04417	141.30417	NSW	Sturt National Park
Gko423	AMSR155351	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.03111	141.45083	NSW	Sturt National Park
Gko424	AMSR155352	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-29.04444	141.30722	NSW	Sturt National Park
Gko425	AMSR155354	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.08333	141.20000	NSW	Sturt National Park
Gko426	AMSR155371	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.04444	141.30722	NSW	Sturt National Park
Gko427	AMSR156652	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-32.86500	146.18917	NSW	Yarra Property, Mt Hope
Gko428	AMSR156653	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-32.86500	146.18917	NSW	Yarra Property, Mt Hope
Gko429	AMSR156700	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-32.84889	146.18278	NSW	Yarra Property, Mt Hope
Gko430	AMSR156701	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-32.84889	146.18278	NSW	Yarra Property, Mt Hope
Gko431	AMSR156720	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-32.94417	146.19222	NSW	Yarra Property, Mt Hope
Gko432	AMSR166764/NR9657	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-29.85389	144.13444	NSW	Nocoleche Nature Reserve
Gko433	AMSR166770/NR9656	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-29.84417	144.05417	NSW	Nocoleche Nature Reserve
Gko434	AMSR166799/NR9727	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-29.84417	144.05417	NSW	Nocoleche Nature Reserve
Gko529	SAMAR42576	<i>Rhynchoedura</i>	<i>ornata</i>	-28.21667	133.36667	SA	Tallaringa
Gko530	SAMAR46239	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-27.68750	134.83694	SA	Arcreekaringa Station
Gko531	SAMAR42833	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-24.10000	143.18333	QLD	Noonbah Station
Gko532	NMVD67857	<i>Rhynchoedura</i>	<i>ornata</i>	-24.34590	131.68420	NT	Kathleen Creek, Watarrka
Gko533	SAMAR53747	<i>Rhynchoedura</i>	<i>ornata</i>	-30.13310	139.61070	SA	Mulga Homestead
Gko534	SAMAR38783	<i>Rhynchoedura</i>	<i>ornata</i>	-19.66667	134.23333	NT	Tennant Creek
Gko535	SAMAR40564	<i>Rhynchoedura</i>	<i>ornata</i>	-24.43333	131.81667	NT	Kings Creek Station
Gko536	SAMAR59491	<i>Rhynchoedura</i>	<i>ornata</i>	-29.73250	131.08583	SA	Maralinga
Gko537	SAMAR60328	<i>Rhynchoedura</i>	<i>ornata</i>	-29.50000	129.32917	SA	Oak Valley
Gko538	SAMAR60424	<i>Rhynchoedura</i>	<i>ornata</i>	-29.38361	129.97611	SA	Oak Valley
Gko539	SAMAR60460	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-27.19444	135.65028	SA	Macumba Homestead
Gko540	SAMAR60946	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-32.04639	140.11389	SA	Bimbowrie Station
Gko541	SAMAR49777	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-30.57500	139.47444	SA	Balcanoona Station

ID#	Museum #	Genus	species	Latitude	Longitude	State	Locality (nearest)
Gko543	WAMR166334	<i>Rhynchoedura</i>	<i>ornata</i>	-25.93250	128.44110	WA	Morgan Range
Gko545	SAMAR58950	<i>Rhynchoedura</i>	<i>ornata</i>	-29.13111	130.23500	SA	Oak Valley
Gko546	SAMAR33345	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-32.46667	140.51667	SA	Maldorkey Hill
Gko547	SAMAR32967	<i>Rhynchoedura</i>	<i>ornata</i>	-20.86667	130.26667	NT	Sangster's Bore
Gko548	QMJ48069	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-25.67560	140.54080	QLD	Betoota
Gko549	QMJ48534	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-27.69540	142.20760	QLD	Cooroo
Gko551	WAMR91452	<i>Rhynchoedura</i>	<i>ornata</i>	-29.67270	125.13450	WA	Blue Robin Hill
Gko552	SAMAR43887	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-26.73722	139.52056	SA	Koonchera Waterhole
Gko555	SAMAR30989	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-27.22778	140.19028	SA	Coongie Lakes Area
Gko559	SAMAR26672	<i>Rhynchoedura</i>	<i>ornata</i>	-29.35833	134.46667	SA	Mabel Creek Homestead
Gko560	SAMAR32616	<i>Rhynchoedura</i>	<i>ornata</i>	-28.64889	133.35361	SA	Tallaringa Well
Gko561	SAMAR32621	<i>Rhynchoedura</i>	<i>ornata</i>	-28.94889	133.30417	SA	Tallaringa Well
Gko562	No voucher	<i>Rhynchoedura</i>	<i>sexapora</i> sp. nov.	-15.59700	131.10410	NT	Victoria R. Gregory National Park
Gko563	NTMR16429	<i>Rhynchoedura</i>	<i>ornata</i>	-19.49000	132.30000	NT	Green Swamp Well, Tanami
Gko566	SAMAR36106	<i>Rhynchoedura</i>	<i>ornata</i>	-25.23333	131.01667	NT	Yulara
Gko567	SAMAR36175	<i>Rhynchoedura</i>	<i>ornata</i>	-25.48333	131.81667	NT	Curtin Springs
Gko570	SAMAR40942	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-28.08472	134.29556	SA	Mt Fumer
Gko571	SAMAR42084	<i>Rhynchoedura</i>	<i>ornata</i>	-26.34972	130.17167	SA	Illintjitja
Gko572	SAMAR44896	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-28.93500	138.61778	SA	Dulkaninna
Gko573	SAMAR44938	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.61417	138.68361	SA	Mookawarinna Hill
Gko575	SAMAR45030	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-26.31806	140.33611	SA	Elbow Well
Gko576	SAMAR45060	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.46306	138.84444	SA	Toopawarinna Bore
Gko577	SAMAR45099	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.79167	139.80194	SA	Moolawatana
Gko578	SAMAR45687	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-27.38778	138.66611	SA	Mt Gason
Gko579	SAMAR45765	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-26.05639	140.06917	SA	Frew Well
Gko580	SAMAR46046	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-28.30000	140.45000	SA	Moomba Gas Field
Gko581	SAMAR46205	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.68389	135.81528	SA	Halifax Hill
Gko582	SAMAR46457	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.21639	136.63083	SA	Beresford Rail Station
Gko583	SAMAR46488	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.27139	135.63278	SA	Mungtana Dam
Gko584	SAMAR46398	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.64111	137.88944	SA	Callanna Bore
Gko585	SAMAR46299	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.84472	136.87167	SA	White Cliff
Gko586	SAMAR46351	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.47111	136.18778	SA	Binda Boudna Hill
Gko587	SAMAR46430	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.28889	135.18333	SA	Bacadinna Hill
Gko588	SAMAR46560	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-28.63972	135.94111	SA	Patsy Dam
Gko589	SAMAR46932	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-26.45806	134.89861	SA	Top Camp Well
Gko592	SAMAR47241	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-28.81778	136.73611	SA	Station
Gko593	SAMAR47256	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-28.43250	136.45333	SA	Four Hills Trig Peake Station
Gko594	SAMAR47324	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-28.13583	136.00167	SA	Peake Station
Gko596	SAMAR48378	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-28.21583	134.58306	SA	Mount Barry Station
Gko597	SAMAR48486	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-27.31944	134.50167	SA	Todmorden Station
Gko598	SAMAR48540	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-27.74583	136.69944	SA	Macumba Station
Gko599	SAMAR50016	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-26.57639	136.94639	SA	Approdinna Attora Knolls
Gko601	SAMAR50374	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-30.50667	138.36889	SA	Mt Aroona
Gko605	SAMAR52795	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-26.75528	135.11944	SA	Hamilton Homestead
Gko606	SAMAR52824	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-26.82333	136.07194	SA	Akoalyerilla Hill Macumba Station
Gko607	SAMAR52847	<i>Rhynchoedura</i>	<i>ornata</i>	-26.69222	134.17222	SA	Lambina Homestead
Gko608	SAMAR52870	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-27.20444	134.99444	SA	Todmorden Homestead
Gko609	SAMAR54162	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-27.77833	138.27583	SA	Kalamurina Homestead
Gko610	SAMAR54230	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.02111	138.02278	SA	Clayton Homestead
Gko611	SAMAR54267 (holotype)	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-27.85056	137.86917	SA	Kalamurina Station
Gko612	SAMAR55253	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-33.77667	139.95944	SA	Gluepot Homestead
Gko613	SAMAR41226	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-33.76389	140.43056	SA	Hideaway Hut
Gko614	SAMAR41265	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-33.59722	140.95833	SA	Twenty Three Mile Dam
Gko616	SAMAR41409	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-33.52778	140.65000	SA	Round Dam
Gko617	SAMAR41518	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-33.11944	140.05000	SA	Elmore Dam
Gko618	SAMAR29556	<i>Rhynchoedura</i>	<i>ornata</i>	-26.65000	130.81667	SA	Musgrave Ranges
Gko620	E. Pianka	<i>Rhynchoedura</i>	<i>ornata</i>	-28.16680	123.66300	WA	Laverton
Gko622	SAMAR46123	<i>Rhynchoedura</i>	<i>ornata</i>	-26.05333	129.40806	SA	Pipalyatjara
Gko623	SAMAR47393	<i>Rhynchoedura</i>	<i>ornata</i>	-27.43028	133.23750	SA	Wallatina Homestead
Gko624	SAMAR47456	<i>Rhynchoedura</i>	<i>ornata</i>	-27.64528	132.88583	SA	Oolarinna East Bore
Gko625	SAMAR48705	<i>Rhynchoedura</i>	<i>ornata</i>	-27.01417	129.87000	SA	Mt Lindsay
Gko626	SAMAR50122	<i>Rhynchoedura</i>	<i>ornata</i>	-26.06083	132.39917	SA	Sentinel Hill
Gko627	SAMAR51533	<i>Rhynchoedura</i>	<i>ornata</i>	-26.26944	131.47139	SA	Amata
Gko628	SAMAR51617	<i>Rhynchoedura</i>	<i>ornata</i>	-26.85528	133.05250	SA	Indulkana
Gko631	SAMAR22593	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-32.11667	137.58333	SA	Uro Bluff
Gko633	SAMAR25442	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-32.39583	136.16667	SA	Mt Ive Station
Gko635	SAMAR36873	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-31.48333	138.17500	SA	Mem Merna Station
Gko636	SAMAR44780	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-31.58333	136.33333	SA	Mahenewo Station
Gko638	SAMAR45969	<i>Rhynchoedura</i>	<i>ornata</i>	-26.40500	129.12972	SA	Pipalyatjara
Gko639	SAMAR46646	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.23333	137.88333	SA	Muloorinna Homestead
Gko640	SAMAR48577	<i>Rhynchoedura</i>	<i>ornata</i>	-27.33694	130.23750	SA	Mt Cheesman
Gko641	SAMAR50245	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-31.58972	136.78611	SA	Oakden Hills Station
Gko642	SAMAR52745	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-32.05000	139.83333	SA	Station
Gko643	SAMAR54101	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-31.11861	134.00722	SA	Yellabinna Reserve
Gko645	AMSR118614	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-31.85310	141.91510	NSW	E Broken Hill
Gko646	AMSR118617	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-33.90110	141.78480	NSW	Wentworth
Gko647	AMSR118619	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-33.00000	141.02170	NSW	Loch Lily

ID#	Museum #	Genus	species	Latitude	Longitude	State	Locality (nearest)
Gko648	AMSR118620	<i>Rhynchoedura</i>	<i>angustus</i> sp. nov.	-32.98333	141.61667	NSW	Coonbah
Gko649	AMSR118621	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-32.90260	144.30130	NSW	Ivanhoe
Gko650	Steve Morton	<i>Rhynchoedura</i>	<i>ornata</i>	-21.00890	130.12640	NT	Sangster's Bore
Gko651	NTMR13652	<i>Rhynchoedura</i>	<i>ornata</i>	-23.18310	132.65480	NT	Yuendumu Road
Gko652	NTMR13666	<i>Rhynchoedura</i>	<i>ornata</i>	-23.28990	132.41700	NT	Yuendumu Road
Gko654	SAMAR32094	<i>Rhynchoedura</i>	<i>ornata</i>	-30.48778	132.05972	SA	Immarna Siding
Gko655	SAMAR32126	<i>Rhynchoedura</i>	<i>ornata</i>	-30.25556	131.55000	SA	Maralinga
Gko657	SAMAR51850	<i>Rhynchoedura</i>	<i>eyrensis</i> sp. nov.	-29.90972	139.45889	SA	Mt Fitton
Gko658	WAMR166332	<i>Rhynchoedura</i>	<i>ornata</i>	-24.69640	128.76280	WA	Pungkulpirri Waterhole
Gko659	WAMR166340	<i>Rhynchoedura</i>	<i>ornata</i>	-24.59970	128.74470	WA	Pungkulpirri Waterhole
Gko660	SAMAR62132	<i>Rhynchoedura</i>	<i>ornata</i>	-25.93080	128.44940	WA	BlaCreekstone
Gko675	WAMR102178	<i>Rhynchoedura</i>	<i>ornata</i>	-22.60270	118.45970	WA	Mt Windell
Gko676	WAMR102502	<i>Rhynchoedura</i>	<i>ornata</i>	-23.11300	116.01170	WA	Barlee Range
Gko677	WAMR104052	<i>Rhynchoedura</i>	<i>ornata</i>	-21.60910	118.97420	WA	Woodstocreek Station
Gko678	WAMR110693	<i>Rhynchoedura</i>	<i>ornata</i>	-28.16160	119.52500	WA	Sandstone
Gko679	WAMR110753	<i>Rhynchoedura</i>	<i>ornata</i>	-23.37880	120.25640	WA	Newman
Gko680	WAMR110788	<i>Rhynchoedura</i>	<i>ornata</i>	-21.94130	116.45390	WA	Pannawonica
Gko682	WAMR110903	<i>Rhynchoedura</i>	<i>ornata</i>	-19.88940	128.86000	WA	Tanami Downs
Gko686	WAMR110981	<i>Rhynchoedura</i>	<i>ornata</i>	-27.24190	120.69780	WA	Lake Way
Gko687	WAMR112022	<i>Rhynchoedura</i>	<i>ornata</i>	-27.02550	116.78140	WA	Boolarly Station
Gko688	WAMR112104	<i>Rhynchoedura</i>	<i>ornata</i>	-25.93470	118.84330	WA	Meekatharra
Gko689	WAMR119999	<i>Rhynchoedura</i>	<i>sexapora</i> sp. nov.	-15.83330	128.03330	WA	Cockburn Range
Gko695	WAMR122590	<i>Rhynchoedura</i>	<i>ornata</i>	-25.65380	114.62560	WA	none
Gko696	WAMR123804	<i>Rhynchoedura</i>	<i>ornata</i>	-25.08800	115.38000	WA	none
Gko697	WAMR125470	<i>Rhynchoedura</i>	<i>ornata</i>	-23.31660	120.03330	WA	Newman
Gko699	WAMR126403	<i>Rhynchoedura</i>	<i>ornata</i>	-30.28330	119.75000	WA	Bungalbin Sandplain
Gko700	WAMR126566	<i>Rhynchoedura</i>	<i>ornata</i>	-30.45000	120.68330	WA	Kalgoorlie
Gko702	WAMR127571	<i>Rhynchoedura</i>	<i>ornata</i>	-30.02000	121.07750	WA	Goongarrie
Gko704	WAMR132783	<i>Rhynchoedura</i>	<i>sexapora</i> sp. nov.	-16.03220	128.84500	WA	Lake Argyle
Gko705	WAMR136253	<i>Rhynchoedura</i>	<i>ornata</i>	-26.79580	115.51690	WA	Muggon
Gko706	WAMR137011	<i>Rhynchoedura</i>	<i>ornata</i>	-27.35000	120.76670	WA	Wanjarri National Park
Gko707	WAMR144557	<i>Rhynchoedura</i>	<i>ornata</i>	-30.25000	119.26670	WA	Mount Jacreekson
Gko708	WAMR145610	<i>Rhynchoedura</i>	<i>ornata</i>	-22.39000	119.99000	WA	Port Hedland
Gko709	WAMR146721	<i>Rhynchoedura</i>	<i>ornata</i>	-21.32470	118.86330	WA	Port Hedland
Gko724	QMA006665/J88379	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-26.09000	145.07000	QLD	Mariala National Park
Gko729	QMA001481/J82497	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-26.20000	147.13000	QLD	Mt Maria
Gko733	QMA006667/J88235	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-25.74806	148.08361	QLD	Womblebank
Gko734	QMA006666/J88378	<i>Rhynchoedura</i>	<i>sulcata</i> sp. nov.	-26.09000	145.07000	QLD	Mariala National Park
Gko782	WAMR84573	<i>Rhynchoedura</i>	<i>ornata</i>	-26.58330	125.00000	WA	Gahnda Rockhole
Gko783	WAMR108808	<i>Rhynchoedura</i>	<i>ornata</i>	-18.15000	122.55000	WA	Thangoo Homestead
Gko784	WAMR142541	<i>Rhynchoedura</i>	<i>ornata</i>	-23.35130	122.66330	WA	Lake Disappointment
Gko785	WAMR164239	<i>Rhynchoedura</i>	<i>ornata</i>	-24.51690	126.21280	WA	Clutterbuck Hills, Gibson Desert
Gko786	WAMR164338	<i>Rhynchoedura</i>	<i>ornata</i>	-24.51690	126.21280	WA	Clutterbuck Hills, Gibson Desert

translated into amino acid sequences using the vertebrate mitochondrial genetic code and were checked for internal stop codons and frame-shift mutations.

Phylogenetic analyses

Phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesian methods. A partitioned ML analysis of our complete *nd2* dataset, totaling 197 taxa, was conducted using RAxML-VI-HPC v7.0.4 (Stamatakis 2006). The analysis implemented the general time-reversible substitution model with gamma-distributed rates among sites (GTR+G), with the data partitioned into 1st + 2nd + 3rd codon sites. We used *Lucasium stenodactylum*, a member of the most likely sister genus to *R. ornata* (Oliver *et al.* 2007a) as the outgroup. Bootstrap support values for the nodes in the maximum-likelihood tree were obtained using 1000 pseudoreplicate datasets.

For each marker we also constructed an un-rooted gene tree under a Bayesian framework in MrBayes version 3.2.1 (Huelsenbeck & Ronquist 2001), partitioning each gene by codon position where applicable. We also conducted a partitioned analysis on our combined mtDNA and nDNA (concatenated) dataset (see below for details on choosing the partition strategy). Again, because we had no appropriate outgroup sample for *bzw1* and *snrpd3*, the outgroup for these sequences was coded as missing data. Each analysis consisted of four independent runs of four chains each. Analyses were run for 20 million generations with samples taken every 2000 generations. Acceptable convergence to the stationary distribution was checked by inspecting the posterior samples using the diagnostic software Tracer v1.5 (Rambaut & Drummond 2007). All runs produced the same topology with very similar posterior probabilities, so we combined runs to generate a single consensus tree.

We used Bayes factors (Kass & Raftery 1995) to determine the best partitioning strategy for our concatenated dataset (Brandley *et al.* 2005). We compared between (1) unpartitioned, (2) partitioned by nDNA and mtDNA, and (3) partitioned by gene and codon partition where applicable, using the best-fit models of molecular evolution determined under the Akaike Information Criterion (AIC) in MrModeltest v2.3 (Nylander 2004) (Table 2). The ratio of the harmonic mean likelihoods for competing partition models were computed using Tracer v1.4 (Rambaut & Drummond 2007).

Table 2. Nucleotide substitution models selected by MrModelTest2 for the gene data partitions based on the Akaike Information Criterion.

Gene data partitions	Nucleotide substitution model
<i>nd2</i>	GTR+I
<i>nd2</i> ; Codon 1	HKY+I
<i>nd2</i> ; Codon 2	HKY+I
<i>nd2</i> ; Codon 3	GTR+G
<i>rag1</i>	HKY
<i>rag1</i> ; Codon 1	HKY
<i>rag1</i> ; Codon 2	F81
<i>rag1</i> ; Codon 3	HKY
<i>bzw1</i>	GTR+I
<i>snrpd3</i>	HKY+G
<i>Concatenated</i> (1 partition)	GTR+I+G
<i>Concatenated</i> (2 partition)	GTR+I+G

Bayesian species tree estimation

The distinction between gene trees and species trees is now widely recognized (Maddison 1997; Dengan & Rosenberg 2006), and a number of multilocus phylogenetic methods are emerging that incorporate information available from incomplete lineage sorting under a coalescent framework in order to infer the species phylogeny (reviewed by Edwards 2009). We used the hierarchical model implemented in *BEAST v. 1.6.0 (Heled & Drummond 2010), that co-estimates the species tree and all gene trees in one Bayesian MCMC analysis, to estimate the species tree phylogeny for *Rhynchoedura*. The *BEAST analysis requires *a priori* designation of species, so we used only those 43 individuals for which we had complete data for each gene, which we divided based on the monophyletic groups identified in the partitioned Bayesian analysis of the concatenated nDNA and mtDNA analysis, giving us five ‘species’ (these five genetic units also were supported by morphological data; see Taxonomy section, below). We partitioned our data by codon position for *nd2* and *rag1*, and by gene for the two introns. Initially we ran the analysis using the same models as the MrBayes analyses, selected under the AIC in MrModeltest. However, many of the parameters failed to converge which we attribute to problems with over-parameterisation. Instead, we used simpler models selected under the BIC in Modelgenerator (Keane 2006) (*bzw1*: HKY+I; *nad2*: TrN+I; *rag1*: HKY; *snrpd3*: HKY+G), but removed the invariant sites parameter from *bzw1* and *nad2*. We used a strict molecular clock, as trial analyses suggested the MCMC had difficulty fitting a relaxed clock to our data. Using the diagnostic software Tracer v.1.5 (Rambaut & Drummond 2007) we were able to determine that the coefficient of variation frequency histograms for all loci abutted against zero, meaning our data could not reject the use of a strict clock (Drummond *et al.* 2007). Using a Speciation: Yule Process tree prior, we conducted four separate runs, with samples drawn every 10,000 steps over a total of 100 million steps, with the first 10% discarded as burn-in. We also ran the same analysis on the nDNA loci only. Acceptable convergence to the stationary distribution was checked by inspecting the posterior samples using Tracer. Effective sample sizes were >600 for all parameters, indicating sufficient sampling from the posterior. All runs produced the same topology with very similar posterior probabilities, so we combined runs to generate a single consensus tree.

Morphology

We examined nearly all specimens of *Rhynchoedura* housed in Australian museum collections, with detailed measurements recorded for a total of 268 specimens, 197 of which also were included in our mtDNA data set. Table 1 gives locality information for all samples used and Table 3 presents the morphological characters measured and their descriptions. Measurements were made with electronic callipers to the nearest 1mm, 0.5 mm or 0.1 mm as appropriate, while fine-scale measurements (i.e. orbit length) were made using a microscope eyepiece. Individuals were sexed by presence (males) of conspicuous bulges posterior to cloaca. We assigned the 197 individuals that we had mtDNA data to the relevant clade, and for the remaining specimens we used morphology and geographic distribution to assign them to clades. Preliminary analyses for *R. ornata*, the lineage for which had the largest sample size (113), did not reveal any evidence for sexual size dimorphism in the morphological characters we examined, so we pooled the sexes in our analyses. We then analyzed the morphological data in two ways. We first tested for significant differences in mean SVL between lineages with a one-way ANOVA. Because SVL was significantly different, we used ANCOVAs to analyze all body size variables with either SVL or HeadL as the covariate, as appropriate. We first tested for homogeneity of slopes and then deleted the interaction term if non-significant to test for differences in the intercepts. If intercepts were different we then used Tukey's post-hoc test ($\alpha = 0.05$) to further examine the differences between clades. We used ANOVAs to test for differences in the remaining continuous variables (AdjMen, IntNar, NarScales). We also analysed the data with Principal Components Analysis (PCA), which does not identify groups *a priori*, to examine the patterns of relationship among all the morphological characters with the statistics software JMP 8.0. We calculated standard principal components (PC) with variance-covariance and did two separate PCAs. The first included only continuous body size variables (the first 12 characters in Table 3) and the second included all variables except for the number of mental scales. In each analysis the first PC was interpreted as largely representing variation in body size and the second PC summarized shape differences among clades. We present these data in terms of the mtDNA clades recovered from the molecular analysis, except for a distinctive morphotype from Queensland for which no tissues were available for analysis.

Table 3. Summaries of characters measured.

Character	Abbreviation	Measurement
Body proportions		
Snout to vent length	SVL	From tip of the snout to cloaca
Trunk length	TrunkL	From axilla to groin
Head length	HeadL	From tip of snout to retroarticular process
Head width	HeadW	At widest point
Foreleg length	ArmL	From elbow to tip of fourth finger
Leg length	LegL	From upper surface of knee to tip of fourth toe
Tail length	TailL	From tip of the tail to cloaca, original tails only
Internarial distance	Inar	Measured at medial edges of nares
Orbit length	OrbL	From anterior to posterior corners of eye
Distance from nostril to eye	NarEye	From nostril to anterior corner of eye
Distance from snout to eye	SnEye	From snout to anterior corner of eye
Distance from eye to ear	EyeEar	From posterior edge of eye to anterior margin of ear
Scale and other characters		
Mental length/width	MenL/W	Ratio of Length/Width of mental scale
Adjacent mental scales	AdjMen	Number of scales in contact with the mental scale
Internarial scales	IntNar	Number of internarial scales
Narial scales	NarScales	Number of scales including main nasal scale surrounding the nostril
Rostral groove	GrooveL%	Proportional length of groove on rostral scale
Groove strength	GrooveS	Strength (0=absent, 1=weak, 2=strong) of the groove on rostral scale
Pre-anal pores	AnPor	Number of pre-anal pores
Mental scales	MenScales	Number of mental scales

Note: Mental scales not used in PCA because not variable enough.

Results

Phylogenetic analyses

The final *nd2* mtDNA alignment consisted of 1035 nucleotide positions. The *rag1* nuclear exon consisted of 838 positions, the *bzw1* intron consisted of 738 positions, and the *snrpd3* intron consisted of 638 positions. The best-fit nucleotide substitution models selected for the mtDNA and nuclear data partitions for each analysis are provided in Table 2.

The ML analysis of the large mtDNA *nd2* dataset recovered the same topology as Pepper *et al.* (submitted [Chapter II]), comprising five well-supported divergent clades; *Kimberley*, *Western/Central desert*, *Southern desert*, *NSW desert*, and *NSW desert narrow*. There is good support for the sister-relationship of *NSW desert* and *NSW desert narrow* and the close relationship of these clades with *Southern desert*. There is little support, however, for the relationship of this trio to either *Kimberley* or *Western/Central desert*. The new mtDNA sequences added to our existing data set all group with the known mtDNA clades, although individuals from the easternmost part of the range in Queensland (represented by Gko 724, 729, 733 and 734) represent an unexpectedly divergent lineage within *NSW desert* given the overall lack of structure in this clade. Figure 1 shows a phylogeny of the full mtDNA data set constrained to summarise the results based on analyses of all the molecular data (see below and Figures. 2 and 3).

The Bayesian analyses of the nuclear data show varying levels of incomplete lineage sorting. The individual nDNA loci were unable to differentiate all of the major mtDNA clades, although the *Kimberley* clade was recovered as monophyletic in both intron loci (shown as un-rooted phylograms in Figure 2). However, when analysed together the concatenated nDNA data clearly discriminate *Kimberley*, *Western/Central desert* and *NSW desert*. When combined with the mtDNA, the concatenated data resolves all taxa into monophyletic groups. For the concatenated analysis, Bayes Factors favoured the gene and codon partition strategies (Table 4). There is some conflict with the phylogenetic relationships inferred from the combined data compared to that of the mtDNA alone, where *Southern desert* and *NSW desert narrow* are sister taxa, albeit with relatively low support (pp. 0.71).

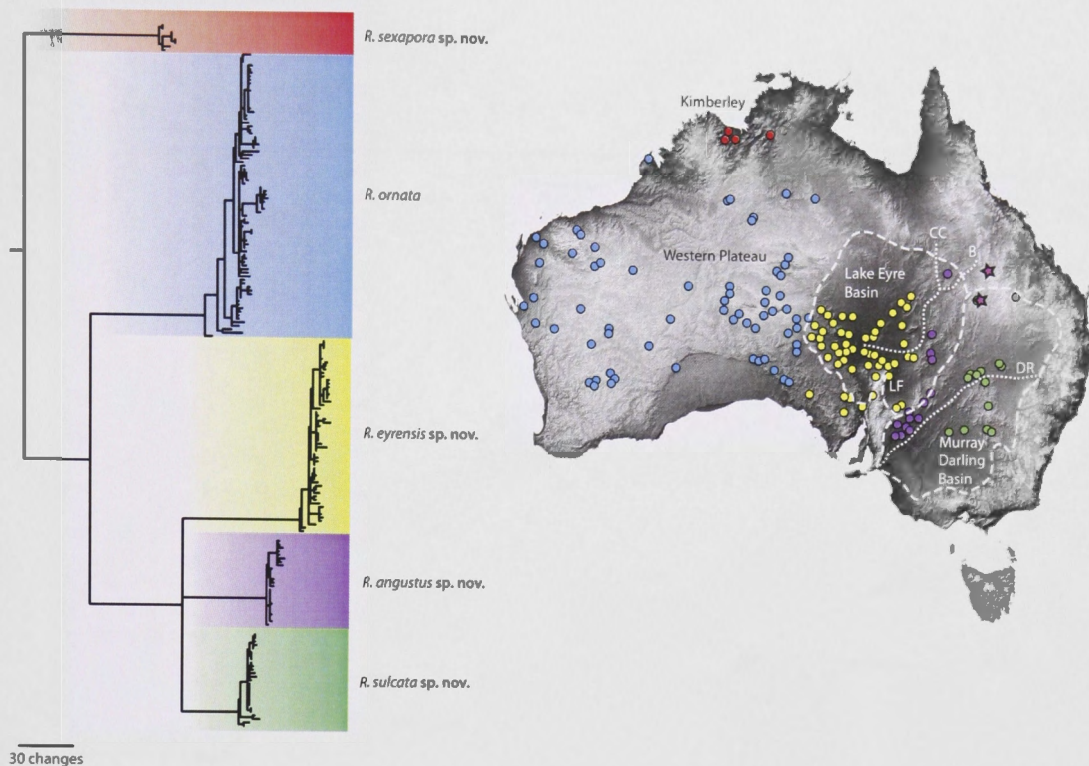


Figure 1. Phylogeny based on 197 mtDNA sequences and their distribution across Australia. These same 197 individuals formed the core material for the morphological data set. The topology of the mtDNA-only data set and additional analyses based on multiple nDNA data sets and nDNA-only data sets are concordant except for the relationships between the three eastern species which we show as a polytomy (see Fig. 3). Dashed lines on the map represent approximate basin boundaries and fine dotted lines represent present-day river courses as follows: CC = Coopers Creek, B = Barcoo, LF = Lake Frome, and DR = Darling River. Colored dots indicate our sampling for each *Rhynchoedura* taxon. *Rhynchoedura mentalis* sp. nov., for which no genetic samples exist, is represented by the pink stars.

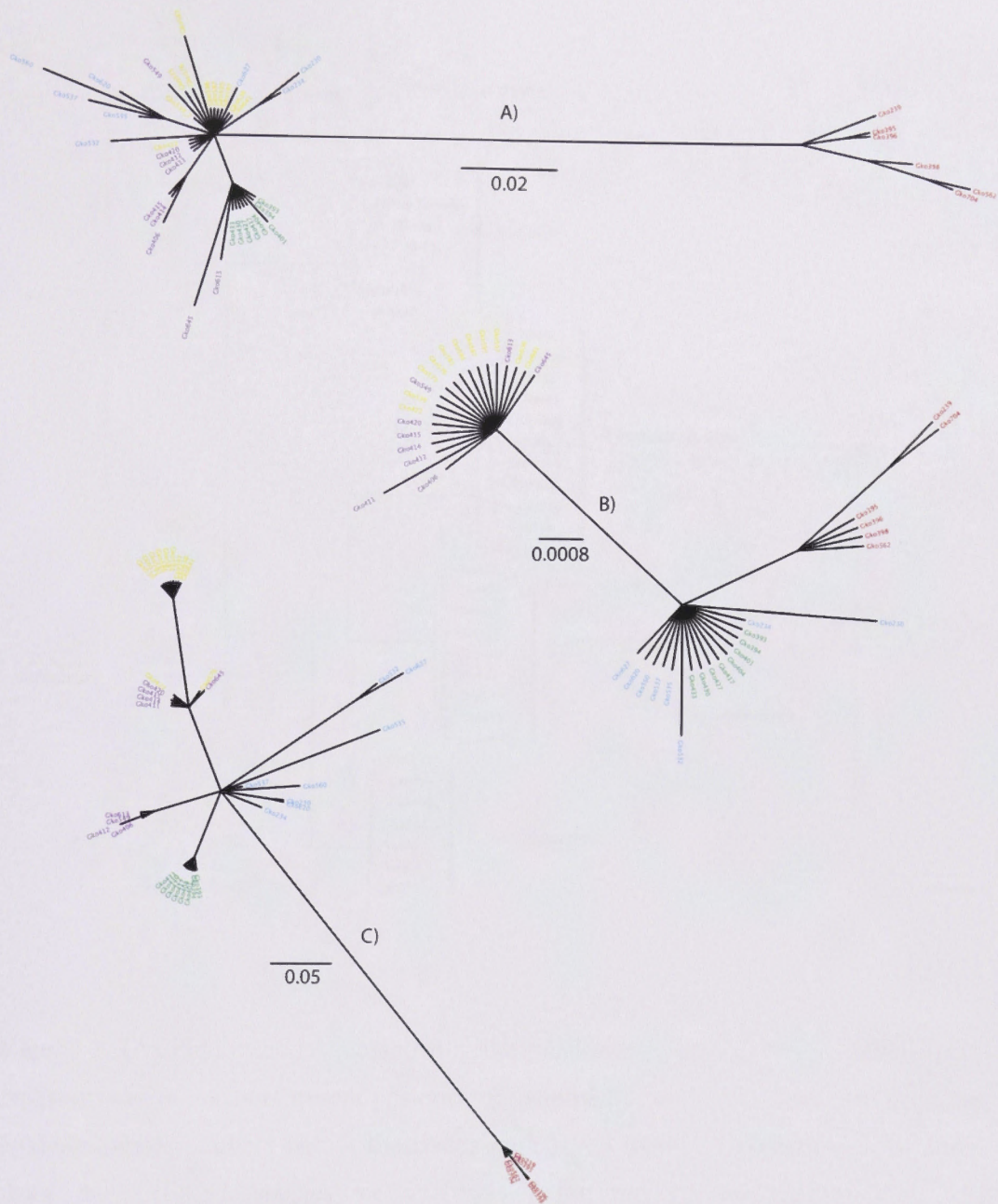


Figure 2. Unrooted Bayesian phylograms of the nDNA loci: A) *snrpd3*, B) *rag1*, and C) *bzw1*. Individuals are colored based on their mtDNA clade: Kimberly = red, Western/Central desert = blue, Southern desert = yellow, NSW desert narrow = purple, NSW desert = green.

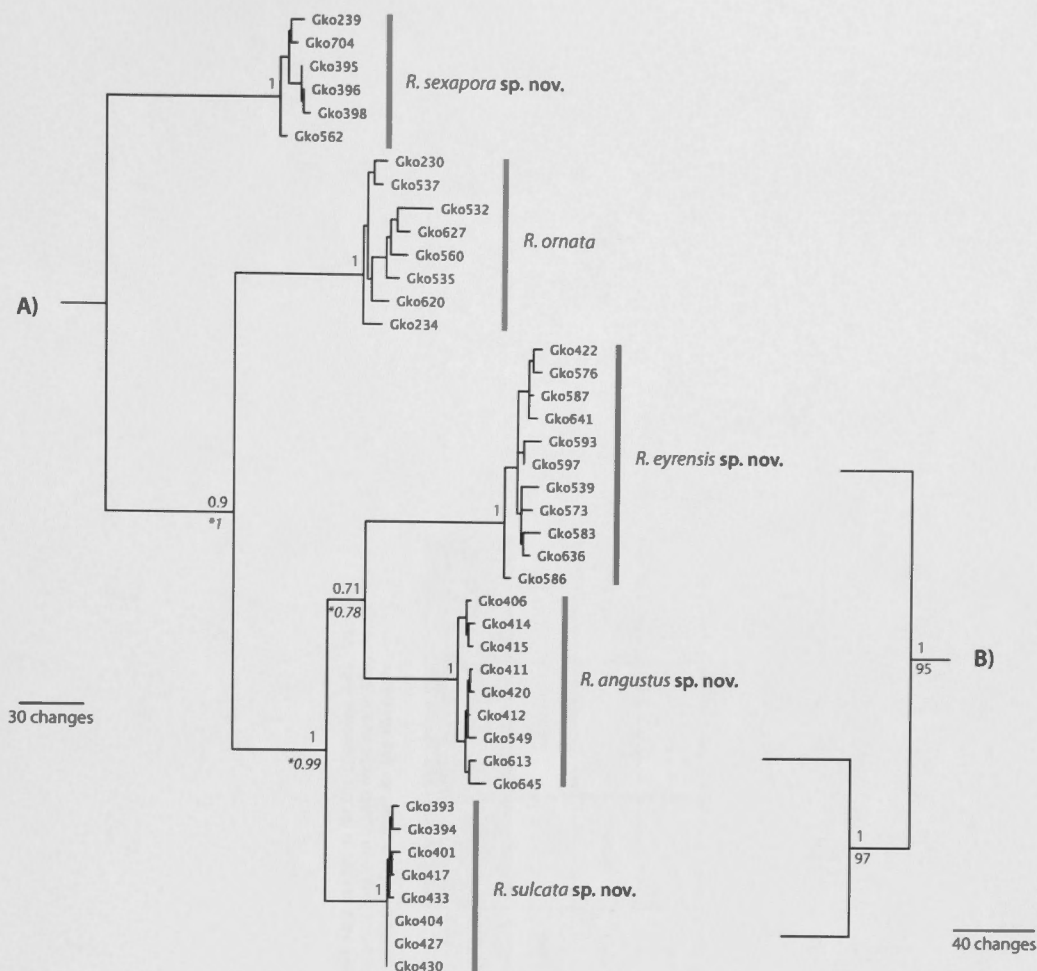


Figure 3. (A) Phylogenetic tree showing the relationships among *Rhynchoedura* taxa. Numbers above nodes represent posterior probabilities from the concatenated Bayesian analysis while numbers below the nodes with a '*' represent posterior probabilities from the *BEAST species-tree analysis of the mtDNA and nDNA data. (B) Phylogenetic relationships of the three eastern taxa inferred using mtDNA only. Numbers above the nodes represent posterior probabilities from the Bayesian analysis and numbers below the nodes represent bootstrap support from the RAxML analysis.

Table 4. Bayes factors comparisons of different data partitions for the combined data. Standard errors (S.E.) were estimated using a bootstrap procedure with 1,000 replicates in Tracer v.1.4 (Rambaut and Drummond, 2007). Negative values indicate support for the alternative model.

Concatenated Data	Ln P(model data) (harmonic mean)	S.E.	Alternative Model		
			Unpartitioned	2-Partitions (nDNA & mtDNA)	8-Partitions (by genes & codons)
Unpartitioned	-9214.974	+/- 0.288	—	-62.296	-237.167
2-Partitions (nDNA & mtDNA)	-9071.533	+/- 0.263	62.296	—	-174.871
8-Partitions (by genes & codons)	-8668.876	+/- 0.435	237.167	174.871	—

Bayesian species tree estimation

Our *BEAST analyses utilizing the combined mtDNA and nDNA data, as well as the nDNA data alone, produced the same species-level topology as the partitioned Bayesian analysis of the concatenated data. The *Kimberley* clade is strongly supported as the most divergent lineage (posterior probability [pp] 1.00), with *Western/Central* inferred to be the sister lineage to the three eastern lineages (pp 1.00). While there is good support for *NSW desert* being the sister lineage to *Southern desert* and *NSW desert narrow* (combined data: pp. 0.99, nDNA only: pp. 0.89), the posterior probability for the sister relationship of *Southern desert* and *NSW desert narrow* is not strongly supported in the combined data analysis (0.78) (Figure 3).

Morphology

Table 5 summarizes the morphological measurement and the results of the statistical tests. The ANCOVAs on body size variables and one-way ANOVAs on mean values of scale characters all show statistically significant differences across the clades in all variables except TrunkL, although differences in TrunkL approached significance. We summarize the results of our PCA analyses in Figure 4 where we show mean PC scores and standard deviations for the two PCA analyses. For the PCA based on 12 body size variables, PC1 explains 62.0% of the variation, PC2 explains 8.3% of the variation and the mean PC scores varied significantly (PC1: $F_{5,267} = 3.48$, $P = 0.0046$; PC2: $F_{5,267} = 10.51$, $P = 0.0001$). For the PCA based on all variables, except for the number of mental scales, PC1 explains 39.8% of the variation, PC2 explains 11.8% of the variation and the mean PC scores varied significantly (PC1: $F_{5,267} = 4.75$, $P = 0.0004$; PC2: $F_{5,267} = 43.75$, $P = 0.0001$). While there is considerable overlap among clades in most of the variables measured, our analyses show that most of the variables show significant differences in at least one clade and our PCA analyses show consistent differences in body size (PC1) and shape (PC2). Additional qualitative differences in scalation and coloration also were apparent among clades, which we describe below as a series of new species. Due to their relatively conservative morphology, we provide a generic diagnosis and description for *Rhynchoedura*, before focusing on characters that vary among species for the redescription and descriptions of species. We adopt an explicitly phylogenetic species concept based on multiple lines of independent data.

Table 5. Summaries of characters and ratios measured for members of *Rhynchoedura*. Mean±SD (range). See Supplementary Table 3 for abbreviations of characters used. As SVL differed among taxa we used ANCOVAs with either SVL or HeadL as the covariate, as appropriate, for body size characters. ANOVAs were used for other characters. *Rhynchoedura mentalis* sp. nov. was excluded from these analyses due to small sample sizes.

Character	<i>R. ornata</i>	<i>R. sexapora</i> sp. nov.	<i>R. eyrensis</i> sp. nov.	<i>R. angustus</i> sp. nov.	<i>R. sulcata</i> sp. nov.	<i>R. mentalis</i> sp. nov.	Statistics
Sample Size	N = 113	N = 50	N = 48	N = 22	N = 32	N = 2	
SVL	45.2±5.0 (32.0–57.0)	41.8±3.7 (32.0–48.5)	43.6±5.0 (33.0–51.0)	44.2±3.5 (39.0–51.0)	44.5±3.8 (33.5–50.0)	46.0±5.7 (42.0–50.0)	ANOVA: $F_{4,266}=4.732$, $P=0.0011$
TrunkL	21.8±3.3 (14.5–29.6)	20.5±2.4 (16.1–27.2)	20.7±3.4 (14.2–26.6)	21.3±2.8 (14.5–26.2)	21.8±2.7 (14.9–26.3)	23.0±1.8 (21.8–24.2)	ANCOVA slopes: $F_{4,256}=1.227$, $P=0.2997$; ANCOVA intercepts: $F_{4,260}=2.164$, $P=0.0734$; Covariate: SVL
HeadL	8.2±0.7 (6.6–9.8)	8.0±0.6 (6.3–9.0)	7.9±0.7 (6.3–9.5)	7.8±0.5 (6.8–8.9)	7.8±0.5 (6.8–8.5)	8.2±0.4 (8.0–8.5)	ANCOVA slopes: $F_{4,256}=0.511$, $P=0.7279$; ANCOVA intercepts: $F_{4,260}=8.717$, $P<0.0001$; Covariate: SVL
HeadW	6.5±0.6 (4.7–8.0)	6.6±0.5 (5.4–7.6)	6.2±0.7 (4.7–7.3)	6.4±0.5 (5.3–7.6)	6.4±0.5 (5.2–7.6)	7.3±0.1 (7.2–7.3)	ANCOVA slopes: $F_{4,256}=1.057$, $P=0.3784$; ANCOVA intercepts: $F_{4,260}=11.264$, $P<0.0001$; Covariate: SVL
ArmL	9.3±0.9 (7.0–11.0)	9.0±0.8 (8.0–10.0)	9.0±1.1 (7.0–11.0)	9.5±0.9 (7.0–11.0)	9.5±0.8 (8.0–11.0)	10.3±0.4 (10.0–10.5)	ANCOVA slopes: $F_{4,256}=1.777$, $P=0.1338$; ANCOVA intercepts: $F_{4,260}=2.666$, $P=0.0329$; Covariate: SVL
LegL	12.3±1.1 (9.0–15.0)	11.9±0.8 (10.0–13.5)	11.7±1.2 (9.0–14.0)	12.2±1.2 (10.0–14.0)	12.9±1.0 (10.0–14.0)	13.8±1.1 (13.0–14.5)	ANCOVA slopes: $F_{4,256}=1.024$, $P=0.3956$; ANCOVA intercepts: $F_{4,260}=7.532$, $P<0.0001$; Covariate: SVL
TailL	32.3±3.3 (24.0–38.5) N = 65	28.9±3.1 (23.5–36.0) N = 26	30.1±4.5 (20.5–37.0) N = 25	29.9±2.3 (26.0–34.5) N = 18	31.0±2.5 (23.0–34.0) N = 18	-	ANCOVA slopes: $F_{4,143}=0.280$, $P=0.8907$; ANCOVA intercepts: $F_{4,147}=2.870$, $P=0.0252$; Covariate: SVL
Inar	1.19±0.12 (0.88–1.50)	1.16±0.12 (0.94–1.40)	1.07±0.12 (0.76–1.24)	1.07±0.07 (0.88–1.20)	1.15±0.09 (0.99–1.38)	1.21±0.09 (1.15–1.27)	ANCOVA slopes: $F_{4,256}=0.742$, $P=0.5641$; ANCOVA intercepts: $F_{4,260}=12.420$, $P<0.0001$; Covariate: HeadL
OrbL	2.69±0.26 (1.92–3.40)	2.51±0.30 (1.93–3.25)	2.48±0.26 (2.00–3.00)	2.39±0.19 (2.09–2.86)	2.45±0.21 (1.98–2.80)	2.68±0.12 (2.60–2.75)	ANCOVA slopes: $F_{4,256}=0.929$, $P=0.4478$; ANCOVA intercepts: $F_{4,260}=8.344$, $P<0.0001$; Covariate: HeadL
NarEye	3.09±0.26 (2.50–3.68)	2.93±0.21 (2.48–3.25)	3.04±0.24 (2.48–3.44)	2.91±0.20 (2.48–3.30)	2.95±0.23 (2.26–3.30)	2.96±0.06 (2.92–3.00)	ANCOVA slopes: $F_{4,256}=0.883$, $P=0.4746$; ANCOVA intercepts: $F_{4,260}=5.811$, $P=0.0002$; Covariate: HeadL
SnEye	3.69±0.36 (2.74–4.47)	3.61±0.30 (2.95–4.04)	3.63±0.34 (3.01–4.46)	3.55±0.24 (2.96–3.99)	3.68±0.27 (2.90–4.18)	3.90±0.11 (3.82–3.98)	ANCOVA slopes: $F_{4,256}=1.426$, $P=0.2258$; ANCOVA intercepts: $F_{4,260}=4.667$, $P=0.0012$; Covariate: HeadL
EyeEar	2.14±0.23 (1.56–2.65)	2.24±0.23 (1.75–2.75)	2.07±0.25 (1.60–2.80)	2.12±0.19 (1.71–2.48)	2.10±0.23 (1.65–2.65)	2.15±0.08 (2.09–2.20)	ANCOVA slopes: $F_{4,256}=0.813$, $P=0.5178$; ANCOVA intercepts: $F_{4,260}=6.428$, $P<0.0001$; Covariate: HeadL
MenL/W	1.54±0.26 (1.09–2.50)	1.40±0.26 (1.00–2.20)	1.78±0.36 (0.77–3.00)	1.60±0.34 (1.00–2.17)	1.26±0.23 (0.82–1.78)	-	-
AdjMen	4.9±0.6 (3–8)	4.6±0.7 (4–6)	4.8±0.8 (3–7)	4.7±0.5 (4–5)	4.1±0.4 (4–5)	-	ANOVA: $F_{4,265}=8.077$, $P<0.0001$

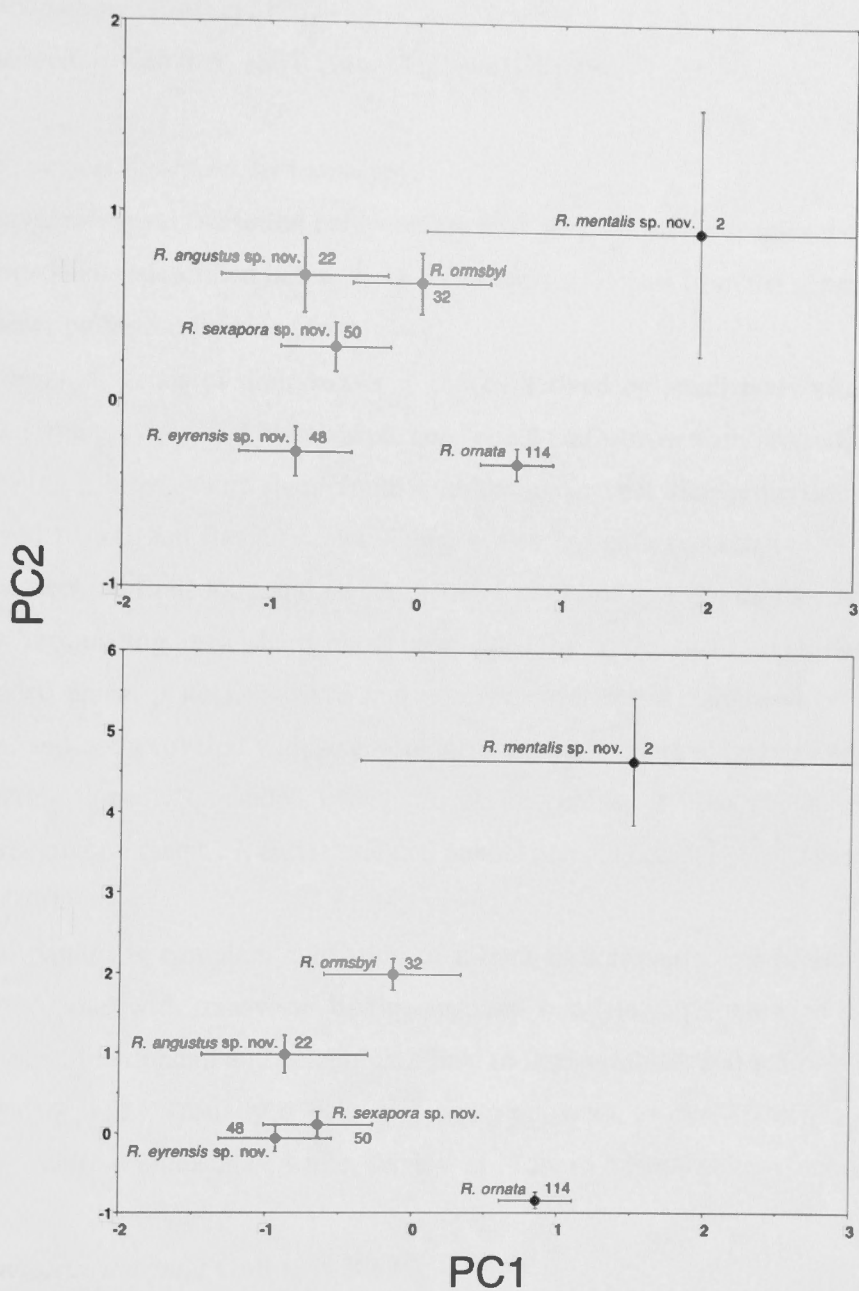


Figure 4. Summary of results for the principle component analyses (PCAs) of the morphological data for 268 *Rhynchoedura* specimens. Mean principal component scores and standard deviations are shown with sample sizes noted.

*Taxonomy****Rhynchoedura* Günther, 1867**

Rhynchoedura Günther, 1867, Ann. Mag. Nat. Hist., Ser. 2, 20: 50.

Type species: *R. ornata*, by monotypy.

The diagnosis and description below embrace all *Rhynchoedura* species. For the species described and redescribed below, only characters that depart from the generic diagnoses and descriptions are provided for brevity.

Diagnosis. A genus of diplodactyloid geckos defined by small body size (to 57 mm SVL), slender cylindrical body shape, head small and narrow with protruding eyes with overhanging brow, short sharp snout terminating in beak-like projections formed by enlarged rostral and mental scales, labial scales not enlarged relative to neighboring scales, neck and tail long and slender; limbs short and gracile, digits covered in fine scales terminating in a sharp claw surrounded by a sheath of modified scales (no expanded apical plates), 2–6 pre-anal pores, cloacal spurs comprised of 1–3 pointed scales, and body covered with fine homogeneous scales. Internal morphology: lacrimal contacting dorsally expanded lateral process of prefrontal, four phalanges on fourth finger, vertebral count 27, and lateral and medial pairs of cloacal bones absent (Oliver *et al.* 2007a).

Dorsal pattern is complex, consisting of a dark background color often with a light vertebral zone with transverse barring; usually small to large white to yellow spots covering entire dorsum and head or confined to flanks; labials and scales bordering eye whitish to yellow; usually a pale spot dorso-posterior to eye; transition to ventrum abrupt; ventrum immaculate white; original tail pattern mirrors pattern on body.

***Rhynchoedura ornata* Günther, 1867**

Rhynchoedura ornata Günther, 1867, Ann. Mag. Nat. Hist., Ser. 2, 20: 51.

Western Beaked Gecko (lineage *Western/Central desert*)

Holotype. BMNH 1946.8.20.50, from Nickol Bay, WA.

Diagnosis. Unique lineage based on multiple molecular sequence data sets (Figures 1 & 3). Morphologically distinguished from congeners by relatively large body size (to 57.0 mm SVL), a single enlarged mental scale (Figure 5a), rostral ungrooved, two oblong

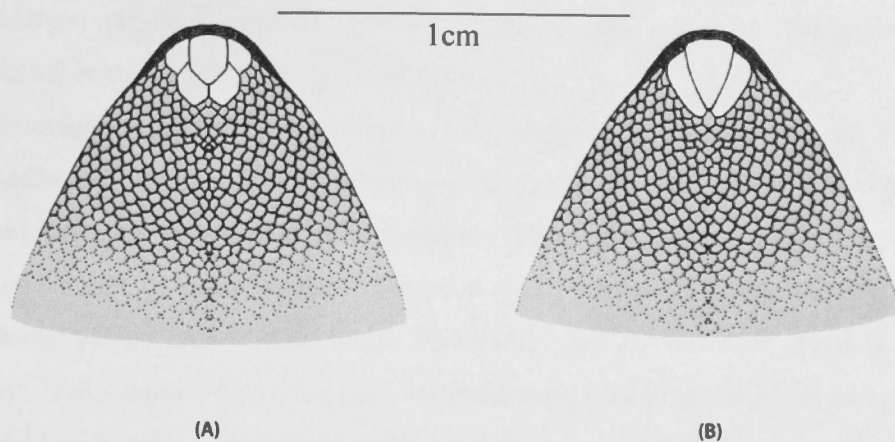


Figure 5. Ventral view of chin showing arrangement of the mental scales in *Rhynchoedura* species: A) typical *Rhynchoedura* configuration, B) *R. mentalis* sp. nov.

enlarged pre-anal pores (Figure 6a), single cloacal spurs, relatively flat dorsal and ventral scales approximately equal in size.

Description. As for genus, except as follows. Body size relatively large; rostral without medial groove; two oblong enlarged (4–6 typical scales long) pre-anal pores in contact and medial edge angled slightly anteriorly (Figure 6a); cloacal spurs in males comprised of a single enlarged scale, often ringed at the base by slightly larger scales.

Dorsal pattern complex and highly variable (Figure 7), consisting of a dark ground color with a discernible pale amoeboid vertebral zone with irregular edges and often forming wide transverse bars; the entire dorsal surface including the top of the head is overlain with medium to large pale white to sulphur spots with brown borders, often giving the appearance of a dark reticulum; labial and scales bordering eye pale to yellow; usually a pale spot dorso-posterior to eye; ventral surface immaculate to a pale off-white; canthal stripes present and often extend to above eye; often a diffuse streak behind eye, sometimes connecting with dark nuchal band; transition from dorsal to ventral pattern abrupt; limb pattern as for dorsum except more subdued; tail as for body.

Habitat. Widely distributed in the western arid zone, including sandy deserts, spinifex grasslands, and mulga woodlands.

Distribution. This species occurs in the western arid zone of Australia, including north to the Great Sandy Desert, south to the edge of the arid zone (excluding the wheatbelt), and east to the western portions of the NT and SA (Figure 1).

***Rhynchoedura sexapora* sp. nov.**

Northern Beaked Gecko (lineage *Kimberley*)

Holotype. WAM R170241 (formerly AMS R139904) (male), collected from El Questro Station, WA (-16.01861°S, 128.00389°E), on 1 September 1992 by H. Cogger *et al.* (Figure 8)

Paratypes. WAM R164785 (female), 35 km W Kununurra, WA (-15.8486°S, 128.4244°E); WAM R132755 (female), Carlton Hill Station, WA (-15.0400°S, 128.8914°E); AMS R117265 (male), track to Hann Yards, Barnett River, WA (-16.7833°S, 125.8500°E); AMS R139902 (male), AMS R139905 (female), AMS R139903 (female), El Questro Station, WA (-16.0186°S, 128.0039°E).

Diagnosis. Unique lineage based on multiple molecular sequence data sets (Figures 1 & 3). Morphologically distinguished from congeners by six (occasionally four) slightly

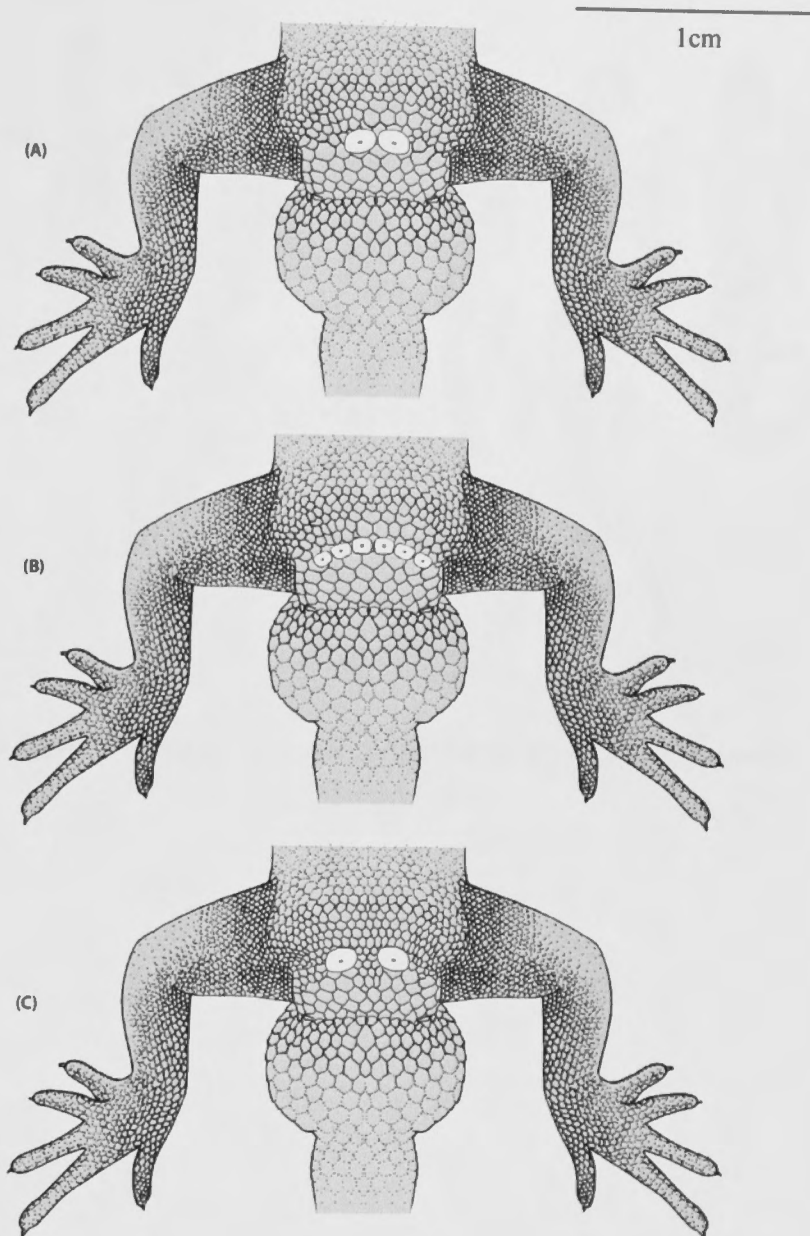


Figure 6. Arrangement of the pre-anal pores in *Rhynchoedura* species: A) typical *Rhynchoedura* arrangement (*ornata*, *angustus* sp. nov., *eyrensis* sp. nov., *ormsbyi*), B) *R. sexapora* sp. nov., C) *R. mentalis* sp. nov.



Figure 7. Variation of dorsal pattern within *Rhynchoedura ornata*.



Figure 8. *Rhynchoedura sexapora* sp. nov. (holotype, WAM R170241, formerly AMS R139904).



Figure 9. Variation of dorsal pattern within *Rhynchoedura sexapora* sp. nov.

enlarged round pre-anal pores in a shallow 'V' pointing anteriorly (Figure 6b). Further distinguished by a combination of a single enlarged mental scale (Figure 5a), rostral with a groove, single cloacal spurs, small body size with relatively short limbs, dorsal scales moderately gabled, ventrals slightly larger than dorsal scales, fingers surrounded by slightly larger small scales. Dorsal pattern dark brown with lighter tan vertebral zone with short transverse processes extending to top of flanks and covered with small pale spots, but less dense on head and vertebral zone (Figure 9).

Description. As for genus, except as follows. Body size relatively small (to 48.5 mm SVL) with small limbs; projecting rostral and a single enlarged mental scale surrounded by only slightly enlarged scales; rostral with median groove; limbs relatively short; dorsal scales moderately gabled with apex directed posteriorly; ventral scales flatter than dorsals and slightly larger; six (occasionally four) pre-anal pores that are only slightly enlarged and round (Figure 6b); pores in close contact forming a weak chevron directed anteriorly, cloacal spurs in males comprised of a single enlarged scale, often ringed at the base by slightly larger scales.

Dorsal pattern complex and variable (Figure 9); dark brown ground color with lighter tan vertebral zone with short transverse processes or connected blotches that extend to flanks; covered with small pale spots, especially towards flanks and less dense and smaller in vertebral zone; head pale without conspicuous spotting; eye rimmed with white to yellow; canthal stripe poorly defined or absent; diffuse streak behind and above eye diffuse, rarely connecting to a nuchal band; labials pale; a pale spot or blotch behind and below eye; pattern on limbs similar but subdued and tips of digits pale; tail as for body.

Habitat. Occurs on many different soil types within subtropical forests of northern Australia. Collector's notes indicate occurring on many surfaces, such as laterite, sandplains, stony soils, basalt flats, 'hard red brown clay', reddish sand or soil and sandy loams. Known to shelter in spider burrows during the day.

Distribution. This species occurs in a band from the Kimberley region in WA and extends east to below the NT's Top End region (Figure 1).

Etymology. *sexapora* is derived from the Latin *sex* (six) and *porus* (pore), referring to the condition of the pre-anal pores. Used as an adjective: 'six-pored'.

Rhynchoedura mentalis

Brigalow Beaked Gecko

Holotype. AMS R60283 (female), collected 54 km north of Blackall, QLD (-17.6167°S, 123.6000°E), on 30 December 1977 by P. Rankin and G. Husband.

Paratypes. QM J88376 (male), collected from Mariala National Park, QLD (-26.09°S, 145.07°E).

Diagnosis. Distinguished all other *Rhynchoedura* by possession of three large mental scales (Figure 5b), two round pre-anal pores separated by two to three smaller scales (Figure 6c), rostral ungrooved, cloacal spurs comprised of two to three enlarged scales, and dorsal coloration with strong vertebral stripe and not densely covered in spots (Figure 10).

Description. As for genus, except as follows. SVL to 50.0 mm; snout terminating in a beak-like structure formed by a projecting rostral and three enlarged mental scales; rostral without medial groove; two round slightly enlarged pre-anal pores separated by 2–3 scales; cloacal spurs in males comprised of 2–3 enlarged scales, often ringed at the base by slightly larger scales.

Dark brown to black ground color; tan vertebral stripe with straight edges (AMS R60283) to pale vertebral stripe formed by irregularly-shaped interconnected blotches (QM J74892 and J88376); top of head pale, not covered in spots; flanks with small fine spots, not occurring in vertebral zone; AMS R60283 (holotype) has short transverse blotches connected to the vertebral stripe (Figure 10).

Habitat. All specimens have been collected from near mulga (*Acacia aneura*) sites with clay soils.

Distribution. *Rhynchoedura mentalis* sp. nov. is only known from three specimens in QLD. Two specimens were collected from Mariala National Park and the other specimen from between Blackall and Longreach. It is thus the most restricted species of *Rhynchoedura*, although further surveys from the region may expand its distribution in the mulga woodlands of inland QLD and possibly to NSW.

Etymology. *mentalis* refers to this species' unique mental scale configuration within *Rhynchoedura*. Used as a noun in apposition.

Remarks. We recommend the conservation status of *R. mentalis* sp. nov. is listed as 'data deficient'. Its known geographic range is very small (Figure 1) and it is only known from three individuals in museum collections (all Australian museum specimens



Figure 10. *Rhynchoedura mentalis* sp. nov. (holotype AMS R60283, paratype QMJ88376).

have been examined, thus it is unlikely there are further unidentified specimens). Two specimens come from Mariala National Park, where the species is likely secure.

No tissue samples exist to test the genetic affinities of *R. mentalis* sp. nov. with other *Rhynchoedura*. The pre-anal pore configuration appears to be intermediate between the presumably ancestral multiple-pore arrangement in *R. sexapora* sp. nov. and the unique highly derived arrangement in the other species.

***Rhynchoedura ormsbyi* Wells & Wellington, 1985**

Rhynchoedura ormsbyi Wells & Wellington, 1985, Aust. J. Herpetol., Suppl. Ser. 1: 15.
Eastern Beaked-Faced Gecko (lineage *NSW desert*)

Holotype. AMS R116979, formerly AM Field series no 16781, from Round Hill Nature Reserve, NSW.

Diagnosis. Unique lineage based on multiple molecular sequence data sets (Figures 1 & 3). Morphologically distinguished from *R. ornata*, *R. sexapora* and *R. mentalis* by a combination of relatively small body size (to 50.00 mm SVL), a single enlarged mental scale (Figure 5a), rostral with a strong medial groove, two oblong enlarged pre-anal pores in contact (Figure 6a), single cloacal spurs, and dorsum covered with small to medium pale white to sulphur spots. *Rhynchoedura ormsbyi*, *R. eyrensis* and *R. angustus* can be difficult to distinguish based on morphology (see 3.4.8 *Distinguishing among species*).

Description. As for genus, except as follows. SVL to 50 mm; snout terminating in a beak-like structure formed by a projecting rostral and a single enlarged mental scale (Figure 5a); rostral usually with a strong medial groove that typically extends down more than 50% (and up to 100%) of the scale; digits surrounded by fine scales; two enlarged oblong pre-anal pores in contact and angled slightly anteriorly (Figure 6a); cloacal spurs in males comprised of a single enlarged scale, often ringed at the base by slightly larger scales.

Dorsal pattern complex and variable (Figure 11), consisting of a dark ground color with a discernible pale vertebral zone with wavy edges, but not tending to form transverse bars; the entire dorsal surface including the top of the head is overlain with numerous small pale white to sulphur spots with brown borders, with spots tending to be larger on the flanks and occur on top of darker lateral markings; labial and scales bordering eye pale to yellow; canthal stripe and streak posterior to eye poorly defined, if connecting to



Figure 11. Variation of dorsal pattern within *Rhynchoedura ormsbyi*.

a nuchal band there is usually a medial gap; white spot behind lower corner of eye conspicuous; upper labials pale white to yellow, especially posteriorly; ventral surface immaculate to a pale off-white; transition from dorsal to ventral pattern abrupt, although outlines of spots sometimes discernible on venter below transition; limb pattern as for dorsum except more subdued; tail as for body.

Habitat. Distributed in the low-lying eastern arid zone, comprising alluvial floodplains and mulga and eucalypt woodlands.

Distribution. Distributed in the eastern lowlands (Figure 1), in the northern part of the Murray-Darling basin throughout the Cobar Peneplain and Mulga Lands bioregions.

Remarks. In their self-published catalogue, Wells and Wellington (1985) proposed the name *R. ormsbyi* for populations from “New South Wales”, but in the absence of any sort of analysis of geographic variation in morphology. Their holotype is from Round Hill Nature Reserve near Euabalong, NSW, which is in the distributional range of our lineage “NSW desert”.

***Rhynchoedura eyrensis* sp. nov.**

Eyre Basin Beaked Gecko (lineage *Southern desert*)

Holotype. SAMA R54267 (male), collected 2.8 km northwest of Kannakaninna waterhole, Kalamurina Station, SA (-27.85056°S, 137.86917°E) on 12 November 2000 by Jeff Foulkes (Figure 12).

Paratypes. SAMA R46205 (male) collected from Halifax Hill, SA (-29.68389°S, 135.81528°E); SAMA R52745 (female) collected from Plumbago Station, SA (-32.05000°S, 139.83333°E); SAMA R52795 (female) collected from Hamilton Homestead, SA (-26.75528°S, 135.11944°E); SAMA R52824 (male) collected from Macumba Station, SA (-26.82333°S, 136.07194°E); SAMA R52870 (female) collected from Todmorden Station, SA (-27.20444°S, 134.99444°E).

Diagnosis. Unique lineage based on multiple molecular sequence data sets (Figures 1 & 3). Morphological diagnosis as for *R. ormsbyi*, except that some *R. eyrensis* tend to have larger pale spots that often merge to form elongated splodges. *Rhynchoedura ormsbyi*, *R. eyrensis* and *R. angustus* can be difficult to distinguish based on morphology (see 3.4.8 *Distinguishing among species*).

Description. As for genus except as follows. Body size relatively small; snout terminating in a beak-like structure formed by a projecting rostral and a single enlarged

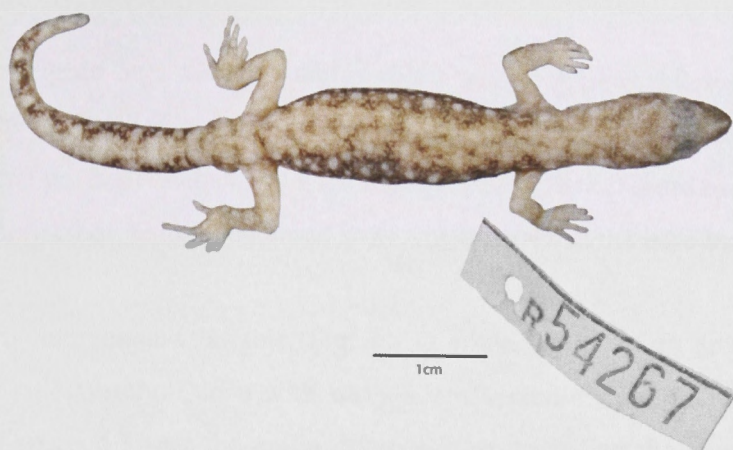


Figure 12. *Rhynchoedura eyrensis* sp. nov. (holotype SAMA R54267).



Figure 13. Variation of dorsal pattern within *Rhynchoedura eyrensis* sp. nov.

mental scale (Figure 5a); rostral usually with a medial groove that typically extends down 30% (but up to 70%) of the scale; digits surrounded by fine scales; two enlarged oblong pre-anal pores in contact and angled slightly anteriorly (Figure 6a); cloacal spurs in males comprised of a single enlarged scale, often ringed at the base by slightly larger scales.

Dorsal pattern complex and variable (Figure 13), consisting of a dark ground color with a discernible pale vertebral zone with wavy edges sometimes forming transverse bars comprised of merged spots; the entire dorsal surface including the top of the head is overlain with small to medium pale white to sulphur spots with brown borders, with spots tending to be larger on the flanks and occur on top of darker lateral markings; labial and scales bordering eye pale to yellow; canthal stripe and streak posterior to eye poorly defined, if connecting to a nuchal band there is usually a medial gap; white spot behind lower corner of eye conspicuous; upper labials pale white to yellow, especially posteriorly; ventral surface immaculate to a pale off-white; transition from dorsal to ventral pattern abrupt, although outlines of spots sometimes discernible on venter below transition; limb pattern as for dorsum except more subdued; tail as for body.

Habitat. Occurs on many different soil types within the eastern arid zone, including floodplains, and sandy and stony desert terrains.

Distribution. This species is widely distributed throughout the eastern half of SA, extending into the southern NT and SW QLD, including in the Simpson, Strzelecki, and Sturt Stony Deserts and the Channel Country.

Etymology. *eyrensis* refers to the distributional area of this species across the Lake Eyre Basin in central/southern Australia.

***Rhynchoedura angustus* sp. nov.**

Angus' Beaked Gecko (lineage *NSW desert narrow*)

Holotype. AMS R152940, an adult male collected 5 km south of Millers Tank on Miller Road, Sturt National Park, NSW (-29.03333°S, 141.73333°E) on 30 September 1998 by G. Swan *et al.* (Figure 14).

Paratypes. AMS R150161 (female), collected from Mootwingee National Park, NSW (-31.28333°S, 142.25°E); AMS R152927 (male) (-29.05583°S, 141.89833°E); AMS R155270 (female) (-29.03111°S, 141.45083°E); AMS R152966 (male) (-29.04944°S,



Figure 14. *Rhynchoedura angustus* sp. nov. (holotype, AMS R152940).



Figure 15. Variation of dorsal pattern within *Rhynchoedura angustus* sp. nov.

141.86083°E); AMS R152941 (male) (-29.03333°S, 141.73333°E) all collected from Sturt National Park, NSW.

Diagnosis. Unique lineage based on multiple molecular sequence data sets (Figures 1 & 3). Morphological diagnosis as for *R. ormsbyi* except that some *R. angustus* tend to have fewer small, well defined spots. *Rhynchoedura ormsbyi*, *R. eyrensis* and *R. angustus* can be difficult to distinguish based on morphology (*Distinguishing among species* below).

Description. As for genus except as follows. Body size relatively small; snout terminating in a beak-like structure formed by a projecting rostral and a single enlarged mental scale (Figure 5a); rostral usually with a medial groove that typically extends down 30% (but up to 55%) of the scale; digits surrounded by fine scales; two enlarged oblong pre-anal pores in contact and angled slightly anteriorly (Figure 6a); cloacal spurs in males comprised of a single enlarged scale, often ringed at the base by slightly larger scales.

Dorsal pattern complex and variable (Figure 15), consisting of a dark ground color with a discernible pale vertebral zone with wavy edges tending to form transverse bars comprised of merged spots; the entire dorsal surface including the top of the head is overlain with small to medium pale white to sulphur spots with brown borders, with spots tending to be of similar size across the dorsum and occur on top of darker lateral markings; labial and scales bordering eye pale to yellow; canthal stripe and streak posterior to eye poorly defined, if connecting to a nuchal band there is usually a medial gap; white spot behind lower corner of eye conspicuous; upper labials pale white to yellow, especially posteriorly; ventral surface immaculate to a pale off-white; transition from dorsal to ventral pattern abrupt, although outlines of spots sometimes discernible on venter below transition; limb pattern as for dorsum except more subdued; tail as for body.

Habitat. Distributed in the Murray Darling Depression bioregion, in mallee shrublands and open woodlands, and on the alluvial and flood plains of the Channel Country on Mitchell grass and spinifex grasslands.

Distribution. This species has a narrow north-south trending distribution extending north of Renmark, SA to Longreach in central Queensland (Figure 1).

Etymology. *angustus* is Latin for narrow/constricted, in reference to the narrow north-south distribution of this species. Used as a noun in apposition. Also in reference to

Angus Emmott for his contribution to herpetology, and the collection locality of the northernmost extent of this species on his Noonbah Station property in Queensland.

Distinguishing among species

Rhynchoedura sexapora sp. nov. is the only species to possess more than two pre-anal pores – usually six (occasionally four). *Rhynchoedura mentalis* sp. nov. is the only species with three enlarged mental scales (all other species have one mental scale which is smaller). *Rhynchoedura ornata* can be differentiated from the eastern species, *R. eyrensis* sp. nov., *R. angustus* sp. nov., and *R. ormsbyi* by larger maximum body size and rostral usually ungrooved. The three eastern species *R. eyrensis* sp. nov., *R. angustus* sp. nov. and *R. ormsbyi* are morphologically very similar but population samples can be differentiated as follows. *Rhynchoedura eyrensis* sp. nov. tends to have shorter arms and legs (relative to SVL) and more NarScales than both *R. angustus* sp. nov. and *R. ormsbyi*. *Rhynchoedura ormsbyi* has a longer Inar (relative to HeadL), round rather than long mental scale (lower MenL/W ratio), fewer AdjMen scales, more IntNar scales and longer mental groove than both *R. angustus* sp. nov. and *R. eyrensis* sp. nov. *Rhynchoedura angustus* sp. nov. tends to have longer arms (relative to SVL), smaller NarEye (relative to HeadL), and fewer NarScales than *R. eyrensis* sp. nov. Importantly, the three eastern species appear to be allopatric based on our extensive sampling and so geographic location will help in identification. *Rhynchoedura mentalis* sp. nov. appears to be sympatric with *R. ormsbyi* but these are easily distinguished based on the number of mental scales.

Discussion

Our study based on mitochondrial DNA, three nuclear DNA genes, and a comprehensive assessment of morphological variation, with dense sampling from across the vast arid zone range of *Rhynchoedura*, provides multiple lines of evidence for six species within the traditionally recognized monotypic genus. The mtDNA data alone provides strong support for five genetic groups (no genetic information is available for *R. mentalis*). Corrected (GTR+I+G) ML genetic distances between these lineages range from 10.5% (*angustus* and *ormsbyi*) to 36% (*angustus* and *sexapora*) for the mtDNA data. When comparing nuclear versus mtDNA-based topologies for the *Rhynchoedura* lineages, there is conflict regarding the relationships of the three south-eastern taxa.

This explains the lower support of these relationships in the *BEAST analysis of all the molecular data compared to the *BEAST analysis of the nDNA loci alone, but each individual data set and the combined data provide clear evidence for species-level differences among these clades, as well as a robust, though not fully resolved, hypothesis of the relationships among them (Figures 1 & 3). Our molecular data also provide one of the most comprehensive assessments of genetic variation across the Australian arid zone, with important implications for our understanding of arid zone diversity and biogeography.

Systematics

We interpret and revise the taxonomy of *Rhynchoedura* using the information from our collective analyses of the multi-gene data, including species tree reconstruction with *BEAST, in conjunction with detailed morphological and distributional data. Our results corroborate what is intuitively expected based on morphological differences and the geographic distribution of populations. Our detailed measurements of 268 individuals confirmed the morphological conservatism across *Rhynchoedura*. When examined in light of the genetic clades, despite substantial intra-clade variation in scale counts and color patterns, each species is diagnosable based on a number of characters. The endemic Queensland species, *R. mentalis*, for which only three specimens exist and none with tissue samples taken, has a unique configuration of mental scales, pre-anal pores, and an unusual dorsal pattern featuring a wide, vertebral stripe. The northern clade, *R. sexapora*, is most obviously distinguished from all other *Rhynchoedura* by six (occasionally four) pre-anal pores instead of two. Discrimination of the arid zone lineages based on morphology alone is less obvious because there are no simple binary characters that consistently differ between them, but morphometric analyses are able to distinguish them easily. The Western/Central clade *R. ornata* is consistently larger in body size, often possesses larger and more striking dorsal spots, and unlike the eastern species, rarely has a groove in the rostral scale. The three eastern species, *R. eyrensis*, *R. angustus*, and *R. ormsbyi*, can be distinguished from each other using a combination of differences in body proportions and dorsal patterning.

The Australian arid zone has long been recognized for its extraordinarily rich and diverse lizard communities (Pianka 1969, 1981, 1986, 1989; Cogger 1984; James & Shine 2000). However, a number of recent molecular studies have highlighted the

extraordinary underestimation of species diversity within the arid zone, with many ‘species’ actually comprising species complexes of multiple, morphologically similar, yet genetically distinctive taxa (Rabosky *et al.* 2004; Chapple & Keogh 2004; Pepper *et al.* 2006; Oliver *et al.* 2007b, 2009, 2010; Shoo *et al.* 2008; Fujita *et al.* 2010; Doughty *et al.* 2010; Pepper *et al.* 2011 [Chapter I], submitted [Chapter II]). Our study of *Rhychoedura* adds to this growing body of literature, and demonstrates how genetic data can be essential for species delimitation in morphologically conservative groups, especially geckos (Aplin and Adams 1998; Pepper *et al.* 2006; Oliver *et al.* 2007b; Doughty *et al.* 2010).

Biogeography

Our dense sampling of *Rhynchoedura* across the arid zone allows a detailed assessment of the geographic structure of mtDNA clades in relation to landscape features. Genetic studies of widespread taxa in the Australian arid zone are scarce (a notable exception being freshwater organisms for which a rich literature exists), and while our biogeographic inference of *Rhynchoedura* is largely descriptive and must therefore be interpreted with caution (Crisp *et al.* 2011), there is potential for broad patterns to emerge, and as studies accumulate these biogeographic boundaries can be tested with unrelated taxa.

All taxa for which we have genetic material are well sampled throughout their range and apparently have allopatric distributions based on our sampling. *Rhynchoedura sexapora* is the most divergent species genetically and it also is the most geographically disjunct. This species has a distribution in the Kimberley region that extends east to the Top End of the NT (Figure 1), adding to the growing body of evidence that this isolated region harbours a unique and diverse biota (Bowman *et al.* 2010). The contacts between each of the arid zone taxa are extremely sharp (Figure 1). At the broadest geographic scale, the strong influence of topography is immediately apparent. The distribution of *R. ornata* appears to be limited to the geographic extent of the uplands of the Australian Craton, a vast and ancient geological structure representing the foundations of the Australian continent (Wasson 1982) (Figure 1, where high elevation is expressed in pale shades). In contrast, the three eastern *Rhynchoedura* lineages are distributed throughout the basins of the central lowlands (Figure 1, where low elevation is expressed in dark grey). A small number of samples belonging to *R. ormsbyi* were collected from the

tablelands of Central QLD. Interestingly, these individuals are the most genetically divergent from the lowland populations. To our knowledge, the broad topographic distinction between the western uplands and central lowlands has not been commented on in previous molecular studies. Examination of the published literature, however, reveals coincident geographic patterns of divergence across other arid zone taxa. In particular, the detailed study of Shoo *et al.* (2008) of the pebble-mimic dragons shows a similar east/west division and the distribution of major clades is likely related to this topographic divide. Given the substantial environmental and climatic differences between these upland and lowland regions, further molecular studies across this landscape juncture are needed to test the generality of this biogeographic pattern. *Rhynchoedura mentalis* appears to be found in sympatry with *R. ormsbyi*, at least in part of their range in Mariala National Park in southern QLD (Figure 1). However, a lack of genetic material and only three specimens from geographically close collection localities precludes us from commenting on the phylogeographic patterns of *R. mentalis*.

In a recent study of Australian arid zone biogeography using a number of gecko taxa, Pepper *et al.* (submitted [Chapter II]) dated the age of lineage diversification in *Rhynchoedura* as well as the time to most recent common ancestor (TMRCA) of each of the mtDNA clades. While deep lineage divergences were inferred to be of mid-Miocene age (10-15 Mya), the lack of genetic variation within clades was attributed to substantial population bottlenecks following the onset of Pleistocene aridification in the Australian arid zone, with the eastern lineages (*Southern desert*, *NSW desert narrow* and *NSW desert*) inferred to have TMRCA's of < 1.5 Mya. This arid history offers a plausible explanation for the genetic architecture of *Rhynchoedura* lineages (reviewed in Pepper *et al.* [submitted {Chapter II}]), however the present day geographic distributions of the eastern *Rhynchoedura* lineages show an intriguing correlation to the distribution of drainages and river catchments (Figure 1). For example, the distribution of *R. eyrensis* conforms to the extent of the Lake Eyre basin, one of the largest internally draining systems in the world (Alexandre *et al.* 2004). The adjacent *R. angustus* has a distribution that straddles the boundary between the Lake Eyre basin and Murray Darling basin, an immense drainage division incorporating a number of Australia's longest rivers. The sharp boundary between *R. eyrensis* and *R. angustus* also conforms to the path of Coopers Creek and other major drainages into Lake Frome,

which, despite their present ephemeral existence, appear as large scars across the landscape on satellite imagery (e.g. Google Earth), indicating their immense presence under historically wetter climates. *Rhynchoedura ormsbyi*, the easternmost lineage, is almost entirely distributed throughout the lowlands of the Murray Darling Basin and is separated from *R. angustus* by the lower reaches of the Darling River.

The combination of genetic history and fine-scale present day distribution data suggests that both dry and wet phases may have been important in the diversification of *Rhynchoedura*. The middle Miocene corresponds to the initiation of arid conditions on the Australian continent, and a number of molecular studies report divergences during this timeframe and attribute them to aridification (reviewed in Byrne *et al.* 2008). Certainly this time period saw drainages across large parts of central WA cease their regular flow regime (Martin 2006) and arid-intolerant taxa presumably would have begun to retract their distribution to more mesic refugia (Pepper *et al.* 2011 [Chapter I], submitted [Chapter II]). The ancestors of major river systems in Eastern Australia such as the Murray and the Darling are ancient, and these drainages are known to have existed during the late Cretaceous (Quilty 1994). Despite the overarching trend towards permanent aridification of the arid zone from the mid-Miocene, where particularly dry phases would likely have led to population contractions such as during the Pleistocene (Pepper *et al.* submitted [Chapter II]), discharge from Eastern river systems is thought to have been substantially greater during intermittent wet intervals of the Miocene and Pliocene (Kershaw *et al.* 2003; Martin, 2006), and may have been both temporally and spatially great enough to create barriers to dispersal for expanding *Rhynchoedura* populations, allowing them to diverge in allopatry. The ongoing cyclical nature of wet and dry phases, particularly during the Pleistocene where regular cycling between glacial and interglacial climates corresponded to periods of severe aridity and intervening wet interglacial periods in Australia, presumably could have reinforced this biogeographic pattern until the present time.

The structuring of genetic lineages by rivers and drainage divides in Eastern Australia is well documented in arid and semi-arid freshwater biota (Unmack 2001; Nguyen *et al.* 2004; Murphy & Austin 2004; Carini & Hughes 2004; Hughes & Hillyer 2006; Thacker *et al.* 2007; Masci *et al.* 2008). Because freshwater fauna are biogeographically constrained by spatially and temporally disconnected drainages, they are considered

more likely to reflect historical hydrological connections than terrestrial species (Avice 2000). However, the biogeographic patterns observed in *Rhynchoedura* offer a unique perspective on terrestrial arid zone biogeography, one where deep genetic patterns may have been shaped not only by aridification, but also by river systems during extreme wet periods. This result contrasts to studies of mesic-adapted arid zone reptiles that, as would be expected, show diversification between major lineages that is likely linked to extreme dry phases and divergence in refugia (Fujita *et al.* 2010; Pepper *et al.* 2011 [Chapter I]). In addition, differences in habitat across the vast arid zone are likely to be important in unravelling the evolutionary history of *Rhynchoedura*, and a better understanding of the spatial distribution of sand dune systems, soils and vegetation would be beneficial in a more complete understanding of genetic differentiation within the Beaked Geckos and other widely distributed arid zone taxa.

Conclusions

Our study provides some of the most detailed work to have been carried out across the Australian arid zone, with dense genetic sampling spanning a wide range of desert landforms. We combine data from mtDNA, nDNA, and morphology, and interpret our results in light of the landscape and climatic history of the Australian continent. Despite vastly different ecologies, we have uncovered biogeographic patterns remarkably concordant with freshwater taxa, indicating the profound influence of palaeo and modern rivers and drainage divides on the evolutionary histories of both terrestrial and aquatic biota. These broad patterns will likely be reflected in other arid-adapted terrestrial vertebrates as molecular studies across this region accumulate. Indeed, examination of the published literature reveals the Lake Eyre and Murray Darling Basin regions are likely reflected in a number of other small arid zone vertebrates, including two Dasyurid marsupials (Blacket *et al.* 2000, 2001), a scincid lizard (Chapple *et al.* 2004) and a dragon lizard (Shoo *et al.* 2008). As the current work demonstrates, using genetic information in conjunction with landscape history can offer insights into the historical biogeography of desert regions, in spite of the inherently poor records of palaeolandscapes and palaeoclimate in the arid zone. With the addition of more fine-scale phylogeographic and phylogenetic studies, along with the development of sophisticated biogeographic models, a much better understanding of the complex history of the Australia arid zone may be possible.

Echoes in the gecko jars



MITZY PEPPER

In 1967, a young man, Arnold Kluge was busy at his desk in a museum at the University of Michigan. He had a microscope, some callipers, tweezers, rulers and trays. The smell of formaldehyde lingered. Next to him were big glass jars, with scientific names written on them.

The jars were packed full of preserved Australian geckos, pickled in formalin and each with a special identification tag attached to one of their toes. The formalin had erased most of the colours from their skin, and their eyes were glassy and grey.

Kluge had finished his PhD in southern California a few years before and had been lucky enough to find a permanent position at the Museum of Zoology where, among other things, he could follow his passion of studying and describing Australian geckos.

There is much more to museums than the exhibits on display. Special rooms away from the public eye are full of preserved specimens, stored in jars, and representing the biodiversity firstly of the state, the country, and sometimes further abroad. These collections are often called the "spirit house" of the museum.

On this particular day, Kluge was looking at a group (or genus) of geckos that contained five species. The group was *Diplodactylus*, meaning "double-digit" and referring to the two pads at the end of each of their toes. The species were thought to be closely related, as they had lots of similarities: similar arrangements of scales, similar shaped skeletons, toes and tails, and they all had tiny preanal pores (special scent glands) on the inside of their thighs.

In Kluge's day, those were the only sorts of things you could look at to describe a species. Minute scales had to be counted, toes, tails and heads had to be measured, skeletons had to be uncovered so the number of vertebrae could be verified. It wasn't until you had looked at and measured hundreds of specimens, and were sure you could tell them apart, that you



Preserved Australian geckos – just right for Arnold Kluge's studies at the University of Michigan and later ones as well.

could publish your results and formally describe the species.

One of the jars on Kluge's desk contained a peculiar looking gecko. Examining one closely, he noticed it had many of the same characteristics as the other species in *Diplodactylus*, but two things perplexed him. Firstly, it had a bird-like "beak", formed by one big scale on the end of its snout. Secondly, instead of tiny preanal pores, this guy had two really big ones (and so did all the girls). Because of the differences, this little beak-faced gecko wasn't put in the same group as the others. It was to be all on its own, in a unique genus called *Rhynchoedura*.

Forty years later, in 2007, I was sitting at my desk at the Australian National University, working on my own PhD on Australian geckos. Things have changed a lot since Kluge's day, most obviously with genetic techniques. While Kluge counted scales and measured body parts, I count the number of bits in certain strings of DNA and measure how many bits are stuck together to make up individual genes of the geckos.

Different species have variation in the arrangement of their genetic code; sometimes the code reads a little differently, sometimes there are extra bits and other times there are bits missing. And when you

spatially compare the same genes across different geckos (using special computer programs), those in the same species will generally cluster together, while those in a different species will be clustered further away.

As part of my research, I was using modern methods to see whether Kluge had been correct in assuming the five species he had looked at were closely related, and whether the beak-faced gecko deserved to be in its own genus. After all, there aren't too many lizards in Australia that were special enough to be the sole member of their genus. The thorny devil is one, and the bizarre chameleon gecko is another.

But, to my surprise, even though I thought that my techniques were far superior to Kluge's old-school method of taxonomy, he had it spot-on. The five species in *Diplodactylus* were each other's closest relatives, and *Rhynchoedura* was indeed in its own group. I was beaten to it. My project told me nothing science didn't already know. That was, until I looked more closely at what the genes in the little beak-faced gecko were telling me.

When I analysed the genes of a number of specimens of *Rhynchoedura*, instead of clustering together, there were two separate clusters. The beak-faced

gecko had some major variation in its genetic make-up – a big clue that there might be a second species.

The cluster I was interested in contained samples that were collected from a remote part of the Kimberley in Western Australia. I flew to the Museum of Western Australia and to the Australian Museum in Sydney to have a look at some of these specimens to see if they looked the same as the *Rhynchoedura* Kluge had examined.

And what did I find? Instead of big spots, they had little spots. Instead of two big pores they had six small ones. Subtle, if you didn't know what you were looking for, but the genes had given me an advantage that Kluge never had. I still have to do what Kluge did, but this time it's my turn to hit the jars, with my own rulers and callipers, so that I can describe a second beak-faced gecko.

And like most scientific discoveries, it doesn't end here. There's far more to this cryptic little lizard than meets the eye.

Mitzy Pepper is a second-year PhD student in the School of Botany and Zoology at the Australian National University, studying the evolution of geckos in the Australian deserts.



A stone gecko.

Riddle of gecko trek

In my last column, my genetic research had just confirmed a new beak-faced gecko only found in the isolated, rugged ranges of the Kimberley in far north-western Australia.

To formally describe a new species, scientists need to detail by writing and illustrations how the species differs from its closest relatives, so researchers in the field can readily identify them. This requires meticulous examination of preserved specimens housed in museum collections.

While visiting the Australian Museum in Sydney, I was sorting my way through their collection of beak-faced geckos, about 60 pickled specimens preserved in formaldehyde. I was looking for subtle differences in the number and arrangement of scales between different individuals, and in the colours and patterns on their velvety skin. My priority was to pinpoint the differences between beak-faced geckos from the Kimberley, and those found in the rest of the country. But in doing so, I made an unexpected discovery.

One of the geckos in the jar I was working from was very peculiar. The scales under his chin, rather than being tiny and bead-like, were large and elongate, and instead of spots this gecko had a pale stripe meandering down his back. Every now and again a lizard is put in the wrong jar, and a unique looking individual is nothing more than a misidentified rogue. But this specimen was in the right jar, because it still had a very pointy snout. Could this be a third species of beak-faced gecko? I checked the rest of the specimens to find others with these unusual scales. Because of the natural variation that exists between individuals of any species, I needed more than a single specimen to prove that



MITZY PEPPER

this little gecko wasn't simply a freak of nature. Unfortunately, it was the only specimen of its type in the Australian Museum.

Every specimen lodged in a museum has an identification tag which is linked to information in the museum database. This animal had been collected in 1999 on the side of the Landsborough Highway in western Queensland, 50km out of Blackall. It is far less common these days to find a new species based purely on morphology (what it looks like) with no genetic corroboration. An unfortunate characteristic of formalin is that it breaks down DNA over time, so formaldehyde-preserved specimens cannot provide DNA for genetic analyses. I needed a tissue sample (tail tip) to see if beak-faced geckos from this part of Australia were genetically unique as well.

Pooling some resources, I took a team of researchers to Brisbane, where we hired a 4WD and headed west. The lush green hues of the landscape trickled into browns and yellows, and the progressively cultivated land became texturally monotonous except for those sadly invaluable reminders of vanished landscapes that line our country roads like comic strips. It was in these pockets of remnant vegetation where we concentrated our efforts as we drove south from Barcaldine.

Geckos are nocturnal, so to find them you have to search during the night. This is best done from the comfort of a car seat, with a hot cup of coffee to

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1. How many hearts does an earthworm have?
2. Where is digested food absorbed into the bloodstream?
3. What types of frequencies are too high to be heard by humans?
4. Which bird has the largest wingspan of 11 feet?
5. True or false? Cholesterol is an essential type of fat that is carried in the blood. It is needed to produce some hormones and for other functions.

Answers: 1. 5. 2. The small intestine. 3. Ultrasonic. 4. Wandering albatross. 5. True. The body generally makes all the cholesterol it needs. However eating too much saturated fat leads to excess cholesterol in the blood stream. CSIRO is carrying out research to develop strategies for reducing cholesterol levels, the risk of heart disease and other conditions that are food-related and correctable through modifying our diet.

on foot, using our head torches to scour the surface of the ground. The air was dry, and the clay soil crumbled under our shoes.

The brilliant green eye-shine of spiders covered the landscape like a myriad shimmering stars. Geckos have red eye-shine, and there was far less of that for us to see.

After two nights of searching, we had found two common variegated geckos, and the large and beautiful marbled gecko. While this was beak-faced gecko territory, we had not found a single one!

Back in Brisbane with a pile of field gear, unused calico gecko bags and empty, optimistically labelled sample vials, I had two hours to kill before my flight back to Canberra. I decided to call in at the Queensland Museum to look at their modest collection of specimens. From a jar with 25 representatives of the beak-faced gecko from all over Queensland, I took them out one by one, looking at their chins under a microscope. All their scales looked the same. Racing against the clock, I was down to the last two individuals. And there it was. I rubbed my eyes to make sure I wasn't hallucinating on the formaldehyde, but it was still there. Three long scales under its chin, and a stripe down its back. I had found another one, this time collected from a locality not too far away from Blackall in 2002.

I'm pretty sure I have a new species on my hands now, but I still need the genetics to prove it. The mystery of the little beak-faced gecko is not yet entirely solved.

■ Mitzy Pepper is a third-year PhD student in the School of Botany and Zoology at the Australian National University, studying the evolution of geckos in the Australian deserts.

keep you awake. Driving slowly along the deserted roads, in the beam of the headlights you can pick up almost every animal crossing the road, from the little ones (such as the suspiciously gecko-like caterpillars and locusts) to the many big ones likely to do some damage to a vehicle. Sadly for us, the only geckos we found were spiny-tailed tree geckos and the curiously abundant stone gecko. There were no beak-faced geckos to be seen.

When we reached the exact collection locality of the museum specimen, we searched

Chapter IV

Endemism and genetic diversity in the iconic Australian Pilbara region: A review of landscape evolution and biotic responses in an ancient, heterogeneous refugium



Hamersley Range, Pilbara, Western Australia

Manuscript

Abstract

The remote Pilbara region is a topographic refuge in Australia's low-lying arid zone. A growing amount of molecular evidence suggests high endemism and a complex evolutionary history of resident biota. We review the physical and biological history of the Pilbara and highlight emerging patterns in the distribution of a variety of organisms. In particular, we draw on detailed information from geology, topography, and phytogeography to examine genetic structure in light of three different biogeographic delimitations of the Pilbara. We test predictions arising from our hypotheses using comparative phylogenetic datasets of seven Pilbara gecko lizards, including both endemic and more widespread taxa. Our maximum likelihood phylogenetic analyses confirm that the Pilbara is an area of high species diversity and endemism. We found mixed support for the relationships between the Pilbara, the adjacent desert regions, and the Kimberley. Our data clearly show that the Pilbara harbors taxa genetically distinct from their non-Pilbara relatives, despite the often close geographic proximity of individuals. Shimodaira-Hasegawa topology tests rejected the hypothesis that phylogeographic structure within the Pilbara is concordant with any of the three biogeographic divisions at a broad scale, however the large amount of intra-specific diversity uncovered in each taxon suggests that finer-scale sampling may show a different pattern. While diversification patterns are idiosyncratic and reflect species-specific ecological differences, the partitioning of genetic diversity across the Pilbara reflects a north/south division, broadly in line with major geological differences and the opposite sides of the Fortescue River. This pattern is consistent with species richness compositional patterns of invertebrates across the region. Together these concordant results across different taxa and at different levels of the genealogical hierarchy highlight the important role of geology and habitat in shaping evolutionary processes and current species distributions in the Pilbara. Understanding the biogeography of the Pilbara and the partitioning of genetic diversity across the heterogeneous landscape is of paramount importance in the face of expanding economic and developmental pressures.

Introduction

Australia is an old and weathered continent, with subdued topography and few major physical barriers. The landmass is dominated by a relatively homogeneous central arid zone surrounded by a periphery of wetter biomes that often are separated by relatively arid corridors. The historical fragmentation and isolation of these regions has had important consequences for the evolution of the Australian biota, and recognition of distinctive fauna and flora has led to the delimitation of a number of areas of endemism (Cracraft 1991; Boden & Given 1995; Crisp *et al.* 1995, 2001; Unmack 2001; Laffan & Crisp 2003; Ladiges *et al.* 2005; Slatyer *et al.* 2007). While fine-scale patterns of diversity and evolutionary history have been well studied in areas such as the rainforests of Eastern Queensland (eg. Schneider *et al.* 1998; Hugall *et al.* 2002; Dolman & Moritz, 2006; Bell *et al.* 2010) and the temperate forests of the southwest (eg. Beard *et al.* 2000; Berry 2001; Hopper & Goia 2004; Gouws *et al.* 2006; Edwards *et al.* 2007; Kay *et al.* in prep) and southeast (eg. Beavis *et al.* 2004; Garrick *et al.* 2004; Chapple *et al.* 2005; Sunnucks *et al.* 2006; Hodges *et al.* 2007), other regions, particularly in the arid parts of the continent, have received comparatively little attention (Byrne *et al.* 2008).

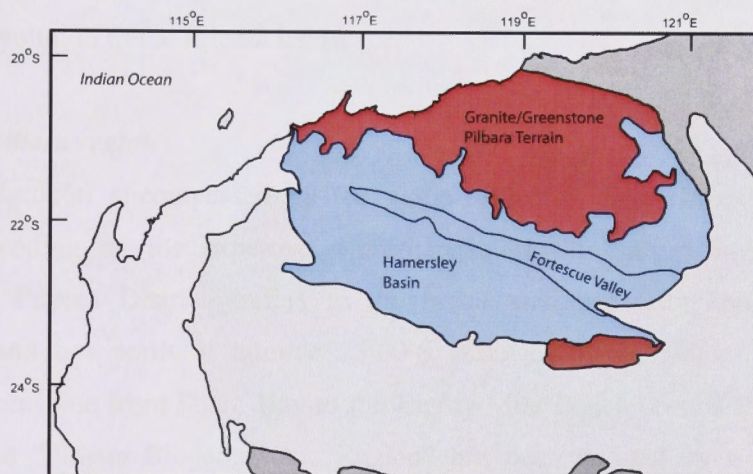
The Pilbara region in remote northwest Western Australia is one of the oldest land surfaces on Earth (Pillans 2007). It has long been regarded as one of Australia's centers of biological endemism (Cracraft 1991), and has a landscape so unique from surrounding regions it can be seen from space (Figure 1a). Situated in what is presently part of Australia's vast arid zone, the Pilbara has preserved in its unique and ancient sediments a rich and complex history: marine structures in the form of a 3.43 billion-year-old stromatolite reef (Allwood *et al.* 2007), immense glacial scarring from the Permo-Carboniferous ice age (Gale 1992), numerous palaeochannels reflecting past, wetter hydrological regimes (Macphail & Stone 2004), and the richest concentration of indigenous rock art in the world (EPA 1995).

While the Pilbara is well known to harbor a unique biota, little is known of the evolutionary history of flora and fauna that inhabit the region. Existing studies typically only have used the broader Pilbara region in context of other areas of endemism, largely due to inadequate fine-scale sampling across the remote region. However, a recent comprehensive survey of biodiversity has collected and catalogued a wealth of

A)



B)



C)

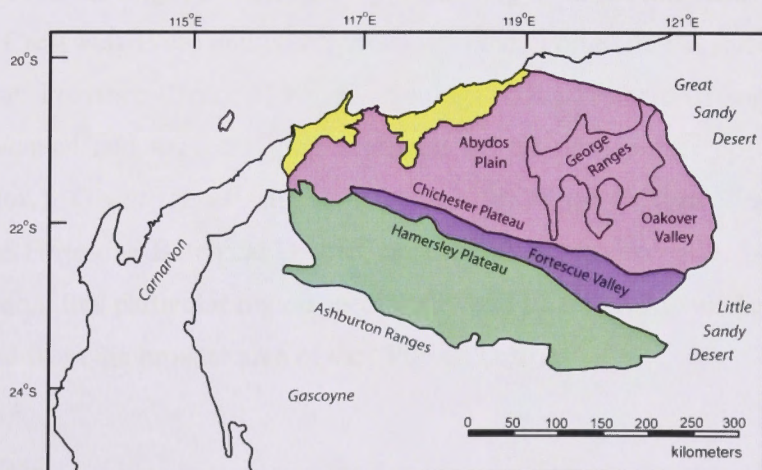


Figure 1. A) True-color Aqua MODIS image (NASA) showing the Pilbara Craton and surrounds. B) Simplified geologic basement map of the Pilbara showing component features discussed in the text. The geology is adapted from the 1978 BMR Geological Map of Australia. C) Boundaries of the four IBRA subregions: Chichester (pink), Hamersley (green), Fortescue Plains (purple) and Roebourne (yellow), overlain with Beard's (1975) physiographic units. Surrounding the Pilbara are other bioregions discussed in the text.

biological material, along with detailed records of habitat and physical landscape for samples across the region (McKenzie et al. 2009). The enormous potential of the availability of these data warrants an assessment of what is currently known about the Pilbara. Here we review the geophysical and climate history of the region, to lay the foundations upon which hypotheses regarding the evolution of the unique Pilbara fauna can be outlined, refined and tested. We then evaluate patterns emerging from studies of Pilbara biota, both in the broader context of the arid zone, and also how they relate to the distribution of major geo and biophysical units across the Pilbara itself. We test alternate biogeographic scenarios using a phylogenetic approach based on multiple gecko taxa, in order to shed light on the relationship between biotic diversification and the historical evolution of the Pilbara landscape.

Defining the Pilbara region

The precise region(s) encompassed by the name “Pilbara” differ in extent and/or definition depending on the expertise and interests of the authors involved. For example, the “Pilbara District” refers to the broad area generally known as the “Northwest”, and lies north of latitude 25°00’S and west of longitude 121°30’ E, including the coastline from Shark Bay to the Eighty-Mile Beach (Beard 1975). More specifically, the “Pilbara Biogeographic Region” has been defined by a number of major attributes including climate, geology, lithology, landform, and vegetation (Thackway & Cresswell 1995) and corresponds with the “Fortescue Botanical District” of the Eremaean Province (Beard 1990). For geologists, the “Pilbara Craton” refers to the ovoid, plateaued and rugged region distinguished by surface outcrops of ancient rocks (see below). Given the classification boundaries of the Pilbara Biogeographic Region and the Fortescue Botanical District closely follow the geological boundary of the Pilbara Craton, this particular region specifically will be referred to as the “Pilbara”, as differentiated from the broader area of the “Pilbara District”.

Geological setting

The Pilbara is a unique geological entity, so distinctive from surrounding regions that it is visible in satellite imagery. The region is defined by underlying sedimentary and igneous rocks of the Pilbara **Craton** ranging up to 3.72 billion years (Ga) in age, and is overlain by one of the most ancient erosion surfaces on Earth (Geological Survey of Western Australia 1990; Myers & Hocking 1998). The Craton can be divided into two

parts; heavily weathered Archaean (3.72 to 2.85 Ga) granites and metamorphosed volcanic rocks (“greenstones”) forming undulating hills and plains in the north, and stratigraphically overlying these rocks in the south is a group of younger (2.77 to 2.40 Ga) Archaean to Proterozoic basalts, and iron-rich sedimentary rocks deposited in the Hamersley Basin (van Kranendonk *et al.* 2002) (formally named the Mt Bruce **Supergroup** [Trendall 1995]) (Figure 1b). Much younger **terrains** of unmetamorphosed sedimentary rocks surround the Pilbara Craton, and these are overlain by topographically homogeneous sand deserts that dominate the arid interior of Australia. A comprehensive summary of the different geological formations and their landform expression can be found in Beard’s (1975) description of the Pilbara’s natural regions. For more detailed information on the structure and **tectonic** development of the craton see Myers (1993), Trendall (1995), and Van Kranendonk *et al.* (2002).

Physiography

The Pilbara landscape is topographically variable and largely determined by the underlying geological structure. The rugged ranges of the Pilbara comprise ridges and mountains that generally are associated with the rocks of the Hamersley Basin in the southern part of the craton. The most noticeable topographic elements of this region are the plateaus of the iron-rich Hamersley and basaltic Chichester Ranges that traverse the craton roughly east to west, and reach elevations of around 900 (and up to 1250) and 600 meters above sea level, respectively. In addition, the Fortescue River valley dissects the Hamersley Basin east to west, and consists of alluvial plains in the east, and deeply incised gorge systems in the western part of the drainage. The northern part of the craton is much more topographically subdued, due to the highly weathered nature of the granite/greenstone terrains. This region is characterized by low hills and **alluvial plains**, which are traversed by numerous flood channels of the Oakover, DeGrey, Coonan, Shaw, Yule and Turner rivers (see Reeves *et al.* 2007). The northern part of the craton can be divided into a number of distinct landforms represented in the ‘natural regions’ of Beard (1975), and these appear to correlate to distinct structural elements of the underlying geology (see Van Kranendonk *et al.* 2006, and Allwood *et al.* 2007). For example, there is a strong east/west division separating the Abydos Plain of Beard (1975) (correlating to the underlying De Grey Superbasin [Van Kranendonk *et al.* 2006]), and the Oakover Valley (and associated underlying East Pilbara Terrain). A gently sloping coastal plain has developed along the northwest Pilbara. For a detailed

review of the physiography of the region, see Beard (1975) and Johnson (2004).

Vegetation and bioregions

The richness of regional habitats and vegetation types often is a measure of geological diversity (Kruckeberg 2004), and this is exemplified in the Pilbara. The extensive river systems and deeply excised gorges, aquifer-fed springs and wetlands, flat coastal plains and razor-backed ridges all contribute to the heterogeneous nature of the Pilbara landscape that, as mentioned above, is shaped to a large degree by underlying geological substrate. At the regional scale, biogeographic patterns can be seen across the Pilbara that broadly reflect the geologic and physiographic units of the craton. Using information from a combination of geology, landform, climate, vegetation and animal communities, the Pilbara has been formally divided into four geographically distinct subregions (Interim Biogeographic Regionalisation for Australia [IBRA], Environment Australia 2008) (Figure 1c). The Hamersley subregion comprises the southernmost portion of the Hamersley Basin and encompasses the Hamersley Range. This region is characterized by skeletal soils developed on the iron-rich sedimentary rocks, and generally consists of spinifex grassland with mulga and snappy gum associations (tree steppe) (Beard 1975). The Chichester subregion encompasses the granite/greenstone terrains of northern craton but also includes the Chichester Plateau of the Hamersley Basin. Beard (1975) defined a number of subdivisions within the northern craton (see above), reflecting substantial landscape heterogeneity across this broad area. While the broader Chichester subregion is characterized by deeply weathered **regolith** and is dominated by spinifex (*Triodia*) grassland with irregularly scattered shrubs (shrub steppe), the Chichester Plateau more closely reflects the soil landscape and vegetation of the Hamersley Plateau (Tille 2006). The Fortescue Plains subregion is delineated by the extent of the Fortescue river valley, that cuts through the sedimentary rocks of the Hamersley Basin. This region consists of salt marshes, mulga-bunch and short grass communities, along with *Eucalyptus* woodlands along the permanent springs. Finally, the Roebourne subregion encompasses the mudflats and low dunes of the coastal plain and is comprised largely of alluvial and aeolian sediments, often with a cover of grasses and soft spinifex. Detailed descriptions of the subregions can be found in McKenzie *et al.* (2009) and are summarized nicely in Guthrie *et al.* (2010). In addition, the soil landscapes of the Pilbara have been mapped and described in detail by Tille (2006). The districts surrounding the Pilbara (i.e., Carnarvon to the southeast, Gascoyne to the

south, and the Great and Little Sandy Deserts to the west) differ in climate, landform, geology and soil, and therefore comprise different vegetation associations (Beard 1969, 1975, 1990).

A stable refuge amidst changing climates

The landscapes of the Pilbara have been subaerially exposed since the Pre-Cambrian (>540 Ma) (Pillans 2007). During this time, vastly different climatic regimes have come and gone, and the region has been greatly modified, with extensive glaciers during the Permo-Carboniferous ice age carving valleys into the Pilbara plateau, and aiding the erosion of more than 700 meters from the mountains (Taylor 1994). During its more recent history, and the timeframe of relevance to studies of the modern biota, vast changes have occurred across areas surrounding the Pilbara, but the climate of the region itself is thought to have remained remarkably stable, largely due to its elevation, proximity to the coast, and the topographic complexity of its landforms (Byrne *et al.* 2008).

Excellent descriptions of the palaeohistory of landforms in Australia, including the Pilbara, can be found in Wasson (1982) and Taylor (1994), so the following includes only a brief summary of events that have contributed to the isolation of the Pilbara in more recent timescales. The mid-Cretaceous (~ 100 Mya) saw the chain of basins to the east of the Pilbara inundated by shallow oceans, separating the Archaean rocks of the Pilbara Craton from their exposures in the Kimberley and Central Australia. Sea-level transgressions and regressions during the Cretaceous saw the basins oscillate between non-marine and open-water conditions, and would have had a significant impact on spatial and habitat diversity in the area (Wasson 1982). Changes in sea level along the continental shelf also periodically connected offshore islands such as those in the Dampier Archipelago, most recently during the Last Glacial Maximum (Yokoyama *et al.* 2001). As well as encompassing physical changes to the environment, global oscillations in sea level reflect large-scale variations in climate regimes. Global cooling of sea surface temperatures during the Cenozoic had a profound affect on atmospheric pressure systems and circulation. On the Australian continent the effect of these changes was the aridification of the continental interior (Frakes *et al.* 1987), with widespread arid conditions thought to be prevalent by the late Miocene (Flower & Kennett 1994). A detailed chronology of aridification history in Australia can be found in Martin (2006),

Byrne *et al.* (2008), and Fujioka and Chappell (2010). Largely due to its topographic heterogeneity and proximity to the coast, the Pilbara would likely have sustained more thermally buffered environments compared to the lower-lying, homogeneous landscapes that comprise much of the arid zone, and allowed the persistence of mesic-adapted taxa (Pepper *et al.* 2011 [Chapter I], Pepper *et al.* submitted [Chapter II]). The height of arid conditions in Australia appears to be correlated to the transition from high-frequency, low-amplitude glaciations (every 40 thousand years (ka)) that characterized the late Pliocene/early Pleistocene, to the low-frequency, high-amplitude glaciations (every 100 ka) that became established in the middle Pleistocene (Huybers 2007). This led to increasingly severe aridification and the development of the vast inland sand deserts (Fujioka *et al.* 2009; McLaren & Wallace 2010). While a lack of chronological data from Western Australia precludes an accurate estimate of the age of the Great Sandy, Gibson, and Great Victoria deserts, dated **playas** and dunes in Central Australia indicate they likely formed < 1 Mya (Fujioka *et al.* 2009; Fujioka & Chappell, 2010). The recent development of these vast sand deserts entirely isolated the Pilbara from rocky exposures in central and northern Australia with hundreds of kilometers of dune fields and sand plains.

Biotic elements of the Pilbara

The antiquity and complex geological and climatic history of the Pilbara and surrounds has undoubtedly had a profound influence on the evolutionary history of the flora and fauna that inhabit the area. Indeed, the distinctive biota has led to recognition of the Pilbara as one of Australia's regional centers of endemism (Cracraft 1991; Crisp *et al.* 1995; Unmack 2001; Ladiges *et al.* 2006). A number of studies have attempted to put the Pilbara in context with other areas of endemism, in particular that of Cracraft (1991), who used species area relationships of a number of groups of vertebrates to conclude that, although the precise affinity of the Pilbara to other regions of endemism was uncertain, a close association with the Western and Eastern deserts was evident. This relationship has been supported by a number of subsequent molecular studies on both plants and animals (Edwards 2003; Pepper *et al.* 2006, 2011 [Chapter I], submitted [Chapter II & III]; Ladiges *et al.* 2006, 2011; Melville *et al.* in press; Catullo *et al.* in press).

While detailed studies of Pilbara biota are in their infancy, the Pilbara appears to be a

region of high species diversity, due in part to its long history as a mesic refugium (Pepper *et al.* 2011 [Chapter I]). In particular, a growing literature is emerging on subterranean invertebrate fauna (Humphreys 1999, 2001; Halse *et al.* 2002; Finston & Johnson 2004; Eberhard *et al.* 2005a, 2005b; Finston *et al.* 2007, 2009; Karanovic 2007; Edward & Harvey 2008; Harvey *et al.* 2008). These studies suggest vicariant isolation and divergence due to surface aridification, coupled with underlying geological complexity, have generated astonishing levels of extremely localized diversity, highlighting the Pilbara as a region of global significance (Eberhard *et al.* 2005a, 2005b). High diversity also has been found in snails (Johnson *et al.* 2004, 2006), and preliminary results from the Pilbara Biological Survey indicate a substantial undescribed flora and terrestrial invertebrate taxa (eg. Guthrie *et al.* 2010 who reported 68% of beetles collected could not be assigned to currently recognized species).

The Pilbara is known to harbor a suite of endemic vertebrates (Morton *et al.* 1995; How & Cooper 2002; How & Dell 2004), with studies of widespread taxa typically revealing morphologically and genetically divergent Pilbara populations (eg. Baverstock *et al.* 1983, Painter *et al.* 1995; Aplin & Adams 1998; Blacket *et al.* 2000; Pepper *et al.* 2006; Ford & Johnson 2007; Melville *et al.* in press). Emerging results from fine-scale molecular studies of terrestrial vertebrates suggest substantial cryptic diversity and complex genetic patterns across the Pilbara landscape (Pepper *et al.* 2008, 2011 [Chapter I]; Shoo *et al.* 2008; Doughty *et al.* 2010; Melville *et al.* in press).

Biogeographic Hypotheses

The spatial heterogeneity within the Pilbara, as well as that of the surrounding deserts, suggests numerous potential physiographic and habitat barriers that may have influenced the evolutionary history of terrestrial biota that inhabit the region. Using a hypothesis testing phylogenetic approach, it is possible to assess patterns of genetic structuring and test alternative hypotheses concerning the distribution of major landscape types, and their importance as barriers to dispersal and factors in diversification (Crisp *et al.* 2011).

Hypothesis 1. Pilbara populations are monophyletic with respect to closely related populations or species outside the Pilbara. The vastly dissimilar climate and landforms of the extensive sand deserts surrounding the Pilbara is likely to have isolated habitat-specialized fauna. For example, the distributions of saxicolous taxa in western

and northern Australia often are disjunct, reflecting the presence of vast, intervening sand dunes (Ford & Johnson 2007, Shoo *et al.* 2008; Pepper *et al.* 2011 [Chapter I]). However, the Pilbara is thought to have provided a mesic refugium following Miocene aridification (Pepper *et al.* 2011 [Chapter I]), and a genetic study of the gecko *L. stenodactylum* (Pepper *et al.* 2006) revealed closely related taxa in the adjacent deserts also are genetically distinct with respect to Pilbara populations. Further sampling of widespread taxa that occur both in the Pilbara and surrounds provides the opportunity to test whether habitat specificity and/or vicariance has played a role in the differentiation of Pilbara biota. If this is true, taxa should exhibit genetic breaks concordant with the boundary of the Pilbara craton. The level of differentiation across this boundary can provide a broad indication of the length of time of isolation.

Hypothesis 2. The phylogeographic structure of populations/species within the Pilbara is distributed in recognized geographic subdivisions. We are interested in fine-scale genetic structure across the Pilbara, and whether congruence across taxa can illuminate general biogeographic patterns. Variation in geology, topography and phytogeography is expected, either individually or in conjunction, and to varying degrees depending on the taxon, to influence the partitioning of genetic diversity across the region. Because little is known of intra-specific structure of Pilbara terrestrial vertebrates, it is important to assess concordance to broad geographic subdivisions within the Pilbara in order to lay foundations for future phylogeographic studies. Based on existing knowledge of geology and vegetation structure that is widely used in biodiversity assessment of the Pilbara, three simple biogeographic subdivisions are relevant to test:

(A) the major geologic divide separating the northern Granite/Greenstone terrain from the southern Hamersley Basin (Figure 1b). The results of Pepper *et al.* (2008), suggested a possible correlation between genetic patterns and variation in underlying geological substrate.

(B) the four IBRA subregions, Chichester, Hamersley, Roebourne and Fortescue (Figure 1c), delimited based on differences in vegetation communities and landsystems across the Pilbara. Importantly, the Chichester range (a major mountain range in the Pilbara), closely aligned with the southern geological unit of the Hamersley Basin, is considered part of the broad northern Chichester subregion in the IBRA regionalization.

A number of recent studies have examined species compositional patterns in light of these subregions (Guthrie *et al.* 2010; Durrant *et al.* 2010; Pinder *et al.* 2010).

C) north and south of the Fortescue river. The Fortescue river valley is known to harbour a unique assemblage of invertebrate taxa (eg. Durrant *et al.* 2010), however there is potential for this substantial topographic discontinuity to act as a barrier to dispersal for small terrestrial vertebrates.

If local adaptation to distinct regions within the Pilbara, and the subsequent diversification of taxa within each region (hypotheses A or B), or vicariance (hypothesis C) are responsible for the diversification of Pilbara biota, then taxa should exhibit phylogeographic structuring concordant with major geo and/or biophysical units. Furthermore, adaptation to distinct habitats should act to reduce gene flow between habitat types resulting in greater genetic divergence between rather than within habitat types.

To test the above predictions, we build on previous results with new and published molecular datasets to generate phylogenies for seven co-distributed gecko taxa. Specifically, we address the following questions: (1) What is the relationship of the Pilbara to other known areas of endemism, and do taxa exhibit genetically differentiated populations across the Pilbara craton boundary? (2) Within the Pilbara, is genetic diversity concordant with previously hypothesized regions (A, B or C, above), and is there congruence across taxa?

The timing of our study is significant. The Pilbara also has unique geological resources, endowed with rich deposits of minerals, oil and gas. The large-scale exploitation of these natural resources across the Pilbara presents an ever-increasing challenge for conserving biodiversity in the region (Lloyd *et al.* 2002), and this has been publicly acknowledged for short-range endemic invertebrate fauna in particular (Majer 2009; Moya & Boulton 2010). With so little known about the distribution and partitioning of genetic diversity of low-vagility terrestrial vertebrates across the region, the potential for short-range endemism, particularly of habitat specialists, requires immediate scientific attention.

Materials & Methods

Taxonomic sampling

We chose taxa representing both Pilbara endemics, as well as more widespread species, to assess the Pilbara in a broader biogeographic context. *Diplodactylus conspicillatus* is a habitat generalist widespread through arid and tropical northern Australia. Previous genetic work on this species in other parts of its range across central/southern Australia has identified multiple cryptic species (Oliver *et al.* 2009). *Lucasium stenodactylum* also is widespread throughout the arid zone, although previous work has identified substantial genetic diversity across its distribution (Pepper *et al.* 2006, 2008). *Gehyra pilbara* is distributed throughout the northwestern and central arid zone and inhabits termite mounds, while *G. punctata* is a rock-adapted specialist distributed throughout rocky hills of central and north Western Australia (Wilson & Swan 2003). The genus *Gehyra* is known to represent a taxonomic predicament, with substantial cryptic diversity and a high misidentification rate hampering efforts to resolve the species complexes (Sistrom, *pers. com.*). *Heteonotia spelea*, *Lucasium wombeyi*, and *Diplodactylus savagei* are rock/stony-soil specialists and are endemic to the Pilbara (but see Pepper *et al.* 2011 [Chapter I] for a detailed assessment of *H. spelea*).

Our sampling for *D. conspicillatus*, *L. wombeyi*, *G. pilbara* and *G. punctata* represents new material. We use previously published material for *L. stenodactylum* (Pepper *et al.* 2006; Pepper *et al.* 2008), *D. savagei* and the closely related *D. galaxius* (Doughty *et al.* 2010) and *H. spelea* (Pepper *et al.* 2011 [Chapter I]). Museum accession numbers and collection localities are given in Table 1.

DNA sequencing and alignment

For all new samples we followed the protocol of Pepper *et al.* (2006), targeting a ~1200 base pair fragment of the mitochondrial genome, extending from tRNA^{Met} through the entire protein-coding gene *nd2* (NADH dehydrogenase subunit II) and the genes encoding tRNA^{Trp}, tRNA^{Ala}, and tRNA^{Asn}. Sequence data were edited using Sequencher 4.1 (Gene Codes Corporation). Alignment of sequences was first performed automatically using the software MUSCLE (Edgar 2004), then refined by eye in Se-Al (Rambaut 1996). Protein-coding regions were translated into amino acid sequences using the vertebrate mitochondrial genetic code and were checked for internal stop codons and frame-shift mutations.

Phylogenetic analyses and hypothesis testing

Each edited alignment comprised 1053 characters. Maximum likelihood (ML) estimation of the phylogeny of each dataset was performed in RAxML, v.7.0.4 (Stamatakis *et al.* 2008, Stamatakis, 2006). The data were partitioned by codon position, and analyzed under the Generalized Time Reversible model of sequence evolution (variable base frequencies, and a symmetrical substitution matrix) (Rodríguez *et al.* 1990), and with across site rate variation modeled to a Gamma distribution (GTR+ Γ). Ten runs with different starting trees were performed, and the most likely tree chosen from this set. Support values were estimated from 100 bootstrap replicates using the *-f i* search function. For geckos in the subfamily Diplodactylinae, appropriate outgroups were chosen based on higher-level phylogenetic studies of Pepper *et al.* (2006) and Oliver *et al.* (2007). For *D. conspicillatus*, the geckos *D. klugei*, *D. pulcher* and *D. savagei* were used as the outgroups. For *D. savagei* and *D. galaxius*, the geckos *D. klugei*, *D. pulcher* and *D. conspicillatus* were used as the outgroups. For *L. wombeyi*, the geckos *L. squarrosus*, and *L. stenodactylum* were used as the outgroups. For *L. stenodactylum*, the geckos *L. squarrosus* and *L. wombeyi* were used as the outgroups. For the Gekkonine geckos *G. pilbara* and *G. punctata*, the gecko *Cyrtodactylus marmoratus* was used as the outgroup. We chose to combine our datasets for *G. pilbara* and *G. punctata* because initial analyses suggested a high degree of paraphyly. For *H. spelea*, *Dixonius vietnamensis*, the sister taxon to *Heteronotia* (Jackman *et al.* 2008), and the other members of the genus *Heteronotia* (*H. binoei*, *H. planiceps* and Central *H. spelea* [Pepper *et al.* 2011 {Chapter I}]) were used as the outgroups.

To address our hypotheses we tested the statistical significance of log-likelihood differences between the optimal ML tree in each phylogenetic analysis outlined above and a series of constraint trees that were consistent with the various alternative hypotheses outlined in the introduction. For each constraint tree we created the simplest possible topology that was consistent with the alternative hypotheses and then used the Shimodaira-Hasegawa test in PAUP* (Shimodaira & Hasegawa 1999; Goldman *et al.* 2000) to produce the test statistic. For ease of analysis, presentation and discussion we have divided both the *Gehyra* and *D. conspicillatus* phylogenies into two clades.

Results and Discussion

Table 1. Locality information for all individuals sampled in Chapter IV. Samples in bold indicate new sequences in this study.

Lab ID	Museum #	Genus	Species	Latitude (decimal)	Longitude (decimal)	State	Location (nearest)
DC06	R129957	<i>Diplodactylus</i>	<i>conspicillatus</i>	-27.29861	121.05417	WA	Mt Joel
DC07	R126769	<i>Diplodactylus</i>	<i>conspicillatus</i>	-24.51139	114.63667	WA	Mardathuna Homestead
DC08	R126770	<i>Diplodactylus</i>	<i>conspicillatus</i>	-24.41306	113.66306	WA	Boolathana Homestead
DC09	R126821	<i>Diplodactylus</i>	<i>conspicillatus</i>	-25.12583	113.82278	WA	Bush Bay
DC10	R126827	<i>Diplodactylus</i>	<i>conspicillatus</i>	-24.41306	113.70667	WA	Boolathana Homestead
DC11	R126859	<i>Diplodactylus</i>	<i>conspicillatus</i>	-25.12583	113.82278	WA	Bush Bay
DC13	R113039	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.28333	118.89444	WA	Lesley Salt Works
DC14	R114921	<i>Diplodactylus</i>	<i>conspicillatus</i>	-23.71667	119.71667	WA	Capricorn Roadhouse
DC15	R102637	<i>Diplodactylus</i>	<i>conspicillatus</i>	-24.07528	120.36056	WA	Little Sandy Desert
DC16	R102477	<i>Diplodactylus</i>	<i>conspicillatus</i>	-23.04472	115.78722	WA	Barlee Range Nature Reserve
DC17	R102478	<i>Diplodactylus</i>	<i>conspicillatus</i>	-23.04472	115.78722	WA	Barlee Range Nature Reserve
DC19	R102480	<i>Diplodactylus</i>	<i>conspicillatus</i>	-23.04472	115.78722	WA	Barlee Range Nature Reserve
DC20	R102503	<i>Diplodactylus</i>	<i>conspicillatus</i>	-23.10167	116.00778	WA	Barlee Range Nature Reserve
DC21	R123119	<i>Diplodactylus</i>	<i>conspicillatus</i>	-25.12583	113.82278	WA	Bush Bay
DC22	R122888	<i>Diplodactylus</i>	<i>conspicillatus</i>	-24.40694	114.47306	WA	Mardathuna Homestead
DC23	R119206	<i>Diplodactylus</i>	<i>conspicillatus</i>	-25.53333	115.46667	WA	Carey Downs Homestead
DC24	R127498	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.73333	115.08333	WA	Onslow
DC25	R127520	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.73333	115.08333	WA	Onslow
DC26	R119777	<i>Diplodactylus</i>	<i>conspicillatus</i>	-27.03333	124.78333	WA	Tehan Rockface
DC27	R120700	<i>Diplodactylus</i>	<i>conspicillatus</i>	-24.41306	113.70667	WA	Boolathana Homestead
DC28	R119956	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.66667	121.58333	WA	Woodie Woodie Mine
DC29	R157395	<i>Diplodactylus</i>	<i>conspicillatus</i>	-19.66472	128.88583	WA	Tanami Desert
DC30	R162453	<i>Diplodactylus</i>	<i>conspicillatus</i>	0.00000	0.00000	WA	West Kununurra
DC31	R120671	<i>Diplodactylus</i>	<i>conspicillatus</i>	-24.40694	114.47306	WA	Mardathuna Homestead
DC32	R127701	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.81111	117.76750	WA	Mount Tom Price Mine
DC33	R90895	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.61167	118.95556	WA	Woodstock
DC34	R94956	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.78333	125.65000	WA	Well 39, Canning Stock Route
DC35	R97324	<i>Diplodactylus</i>	<i>conspicillatus</i>	-28.45833	122.24167	WA	Mount Windarra
DC36	R99143	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.60972	118.96222	WA	Woodstock Station
DC37	R102048	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.36667	119.01667	WA	Strelley Homestead
DC38	R102054	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.75000	118.25000	WA	Mundabullangana
DC39	R104021	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.61167	118.95556	WA	Woodstock
DC40	R104047	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.61167	118.95556	WA	Woodstock
DC41	R104050	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.60917	118.97417	WA	Woodstock
DC42	R104051	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.60917	118.97417	WA	Woodstock
DC43	R104056	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.67056	119.04167	WA	Woodstock
DC45	R104061	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.60917	118.97417	WA	Woodstock
DC46	R104158	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.60917	118.97417	WA	Woodstock
DC47	R108856	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.78333	118.11667	WA	Mount Spinifex
DC48	R113068	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.31944	118.90000	WA	Lesley Salt Works
DC49	R104059	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.60944	118.96194	WA	Woodstock
DC50	R132529	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.68028	116.74361	WA	Burrup Peninsula
DC51	R132531	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.67667	116.75222	WA	Burrup Peninsula
DC52	R132532	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.67667	116.75222	WA	Burrup Peninsula
DC53	R132546	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.28028	119.20194	WA	Degrey River Station
DC54	R132175	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.66667	121.58333	WA	Nifty Mine
DC55	R132176	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.66667	121.58333	WA	Nifty Mine
DC56	R132177	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.66667	121.58333	WA	Nifty Mine
DC57	R132178	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.66667	121.58333	WA	Nifty Mine
DC58	R132689	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.57778	120.33306	WA	Shay Gap
DC59	R132713	<i>Diplodactylus</i>	<i>conspicillatus</i>	-15.71194	128.26556	WA	Wyndham
DC60	R135321	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.75444	117.08111	WA	Cape Lambert
DC61	R135378	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.41972	117.43000	WA	Mt Brockman
DC62	R135406	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.35000	117.35000	WA	Mt Brockman
DC63	R135408	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.41972	117.43000	WA	Mt Brockman
DC64	R135431	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.41972	117.43000	WA	Mt Brockman
DC65	R135455	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.46667	117.30000	WA	Mount Brockman Area
DC66	R113612	<i>Diplodactylus</i>	<i>conspicillatus</i>	-23.01750	119.89056	WA	Newman
DC67	R113620	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.41667	115.61667	WA	Nanutarra
DC68	R113621	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.41667	115.61667	WA	Nanutarra
DC69	R113635	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.41667	115.61667	WA	Nanutarra
DC70	R137010	<i>Diplodactylus</i>	<i>conspicillatus</i>	-27.35000	120.76667	WA	Wanjari Nature Reserve
DC71	R138110	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.66667	121.58333	WA	Nifty Copper Mine
DC72	R102917	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.19917	115.54861	WA	Cane River
DC73	R102945	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.19917	115.54861	WA	Cane River
DC74	R102946	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.19917	115.54861	WA	Cane River
DC75	R140334	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.46194	117.16250	WA	Millstream-Chichester Range National Park
DC76	R140708	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.73278	119.40861	WA	Hope Downs
DC77	R140712	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.83694	119.37583	WA	Hope Downs
DC78	R140980	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.77667	114.87194	WA	Urala Station
DC79	R139020	<i>Diplodactylus</i>	<i>conspicillatus</i>	-19.81222	121.47361	WA	Mandora
DC80	R141359	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.01639	116.19556	WA	Cape Preston Area
DC81	R139168	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.65000	116.76667	WA	Burrup Peninsula
DC82	R139264	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.28694	120.45944	WA	Meentheena
DC83	R139283	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.29000	120.46639	WA	Meentheena
DC84	R144640	<i>Diplodactylus</i>	<i>conspicillatus</i>	-30.20139	120.97417	WA	Kalgoorlie
DC85	R145193	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.24306	114.03472	WA	Learmonth Airstrip

Lab ID	Museum #	Genus	Species	Latitude (decimal)	Longitude (decimal)	State	Location (nearest)
DC86	R145516	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.06000	118.75000	WA	Port Hedland
DC88	R112197	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.67583	115.14583	WA	Onslow Area
DC91	R157003	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.41444	119.00667	WA	Fortescue Marsh
DC92	R157018	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.45917	119.03639	WA	Fortescue Marsh
DC93	R157024	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.45917	119.03639	WA	Fortescue Marsh
DC94	R157500	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.45917	119.03639	WA	Fortescue Marsh
DC95	R157533	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.74778	116.07528	WA	Robe River
DC97	R158325	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.69389	114.39111	WA	Giralia Homestead
DC98	R158327	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.69389	114.39111	WA	Giralia Homestead
DC99	R158330	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.69389	114.39111	WA	Giralia Homestead
DC100	R158331	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.69389	114.39111	WA	Giralia Homestead
DC101	R158333	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.69389	114.39111	WA	Giralia Homestead
DC102	R158335	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.69389	114.39111	WA	Giralia Homestead
DC103	R158349	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.78444	114.27917	WA	Giralia Station
DC104	R157131	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.65417	120.40972	WA	Roy Hill
DC106	R157275	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.26750	114.52278	WA	Yanrey Station
DC107	R157276	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.29972	114.59306	WA	Yanrey Station
DC108	R157302	<i>Diplodactylus</i>	<i>conspicillatus</i>	-22.15778	114.52861	WA	Yanrey Station
DC110	R110626	<i>Diplodactylus</i>	<i>conspicillatus</i>	-19.89444	128.83389	WA	Tanami Desert
DC111	R110758	<i>Diplodactylus</i>	<i>conspicillatus</i>	-23.36556	120.33028	WA	Jimblebar East
DC112	R110769	<i>Diplodactylus</i>	<i>conspicillatus</i>	-23.36556	120.32111	WA	Jimblebar East
DC113	R110770	<i>Diplodactylus</i>	<i>conspicillatus</i>	-23.44056	120.33333	WA	Jimblebar East
DC114	R156243	<i>Diplodactylus</i>	<i>conspicillatus</i>	-21.68861	115.09250	WA	Onslow Area
DC115	R110762	<i>Diplodactylus</i>	<i>conspicillatus</i>	-23.39472	120.30972	WA	Jimblebar East
DC116	R110767	<i>Diplodactylus</i>	<i>conspicillatus</i>	-23.39611	120.31000	WA	Jimblebar East
DC117	R151061	<i>Diplodactylus</i>	<i>conspicillatus</i>	-24.88333	113.76667	WA	Camarvon
DC119	R165713	<i>Diplodactylus</i>	<i>conspicillatus</i>	-26.05667	117.21611	WA	Jack Hills
DC120	R166625	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.86639	117.82194	WA	Mons Cupri Mine
DC121	R166479	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.36972	119.63333	WA	Port Hedland
DC122	R166480	<i>Diplodactylus</i>	<i>conspicillatus</i>	-20.36972	119.63333	WA	Port Hedland
GPII01	R127509	<i>Gehyra</i>	<i>pilbara</i>	-21.73333	115.08333	WA	Onslow
GPII02	R129337	<i>Gehyra</i>	<i>pilbara</i>	-21.68333	114.81667	WA	Griffin
GPII03	R129338	<i>Gehyra</i>	<i>pilbara</i>	-21.68333	114.81667	WA	Griffin
GPII04	R129655	<i>Gehyra</i>	<i>pilbara</i>	-22.99583	119.09167	WA	Newman
GPII05	R129336	<i>Gehyra</i>	<i>pilbara</i>	-21.68333	114.81667	WA	Griffin
GPII06	R129339	<i>Gehyra</i>	<i>pilbara</i>	-21.68333	114.81667	WA	Griffin
GPII07	R129420	<i>Gehyra</i>	<i>pilbara</i>	-21.68333	114.81667	WA	Griffin
GPII08	R114212	<i>Gehyra</i>	<i>pilbara</i>	-16.40000	122.93333	WA	Cape Leveque
GPII09	R114923	<i>Gehyra</i>	<i>pilbara</i>	-20.45000	118.90000	WA	Marble Bar Road
GPII11	R125413	<i>Gehyra</i>	<i>pilbara</i>	-20.76667	115.40000	WA	Barrow Island
GPII12	R125472	<i>Gehyra</i>	<i>pilbara</i>	-23.31667	120.03333	WA	Newman
GPII13	R102506	<i>Gehyra</i>	<i>pilbara</i>	-23.10583	116.99778	WA	Barlee Range Nature Reserve
GPII14	R119934	<i>Gehyra</i>	<i>pilbara</i>	-22.46667	117.30000	WA	Mt Brockman
GPII15	R119943	<i>Gehyra</i>	<i>pilbara</i>	-21.55000	121.68333	WA	Nifty Mine Site
GPII17	R162914	<i>Gehyra</i>	<i>pilbara</i>	-17.73306	123.56556	WA	
GPII18	R100985	<i>Gehyra</i>	<i>pilbara</i>	-18.11667	125.58333	WA	Fitzroy Crossing
GPII19	R108603	<i>Gehyra</i>	<i>pilbara</i>	-21.80000	116.23333	WA	Pannawonica
GPII21	R108771	<i>Gehyra</i>	<i>pilbara</i>	-18.91667	125.26667	WA	Supplejack Bore
GPII23	R108947	<i>Gehyra</i>	<i>pilbara</i>	-21.88333	122.36667	WA	Telfer
GPII24	R108948	<i>Gehyra</i>	<i>pilbara</i>	-21.88333	122.36667	WA	Telfer
GPII25	R132553	<i>Gehyra</i>	<i>pilbara</i>	-20.28028	119.20194	WA	Degrey River Station
GPII26	R131070	<i>Gehyra</i>	<i>pilbara</i>	-22.81667	127.65000	WA	Kiwirrkurra
GPII27	R131748	<i>Gehyra</i>	<i>pilbara</i>	-22.33333	117.86667	WA	Hamersley Station
GPII28	R135348	<i>Gehyra</i>	<i>pilbara</i>	-22.29194	117.29889	WA	Mt Brockman
GPII29	R90606	<i>Gehyra</i>	<i>pilbara</i>	-21.61667	119.02333	WA	Woodstock
GPII30	R90767	<i>Gehyra</i>	<i>pilbara</i>	-21.61167	118.95556	WA	Woodstock
GPII31	R90826	<i>Gehyra</i>	<i>pilbara</i>	-21.61667	118.95000	WA	Woodstock
GPII32	R90903	<i>Gehyra</i>	<i>pilbara</i>	-21.61667	118.95000	WA	Woodstock
GPII36	R102167	<i>Gehyra</i>	<i>pilbara</i>	-22.60222	118.52083	WA	Mt Windell
GPII37	R104135	<i>Gehyra</i>	<i>pilbara</i>	-21.61167	118.95556	WA	Woodstock
GPII38	R108633	<i>Gehyra</i>	<i>pilbara</i>	-21.80000	116.23333	WA	Pannawonica
GPII39	R108744	<i>Gehyra</i>	<i>pilbara</i>	-18.68333	128.58333	WA	Gordon Downs Homestead
GPII40	R113241	<i>Gehyra</i>	<i>pilbara</i>	-21.73333	116.25000	WA	Jimmawurrada Creek/Robe River junction
GPII41	R140311	<i>Gehyra</i>	<i>pilbara</i>	-21.41167	117.15611	WA	Millstream-Chichester Range National Park
GPII42	R140312	<i>Gehyra</i>	<i>pilbara</i>	-21.41167	117.15611	WA	Millstream-Chichester Range National Park
GPII43	R141314	<i>Gehyra</i>	<i>pilbara</i>	-20.90528	116.21694	WA	Cape Preston Area
GPII44	R139203	<i>Gehyra</i>	<i>pilbara</i>	-21.96667	115.18333	WA	Mount Minnie Homestead
GPII46	R139383	<i>Gehyra</i>	<i>pilbara</i>	-21.23000	120.31278	WA	Meentheena
GPII47	R112645	<i>Gehyra</i>	<i>pilbara</i>	-20.79806	115.34917	WA	Barrow Island
GPII48	R112678	<i>Gehyra</i>	<i>pilbara</i>	-21.70389	115.12778	WA	Onslow
GPII49	R112705	<i>Gehyra</i>	<i>pilbara</i>	-21.70389	115.12778	WA	Onslow
GPII52	R139440	<i>Gehyra</i>	<i>pilbara</i>	-21.37333	115.37333	WA	Mount Minnie
GPII53	R139441	<i>Gehyra</i>	<i>pilbara</i>	-21.37333	115.37333	WA	Mount Minnie
GPII54	R112946	<i>Gehyra</i>	<i>pilbara</i>	-17.07306	122.71222	WA	Beagle Bay Aboriginal Community
GPII55	R112967	<i>Gehyra</i>	<i>pilbara</i>	-17.07806	122.71111	WA	Beagle Bay Aboriginal Community
GPII56	R112970	<i>Gehyra</i>	<i>pilbara</i>	-17.08361	122.65972	WA	Beagle Bay Aboriginal Community
GPII57	R158313	<i>Gehyra</i>	<i>pilbara</i>	-22.60361	114.39306	WA	Giralia Homestead

Lab ID	Museum #	Genus	Species	Latitude (decimal)	Longitude (decimal)	State	Location (nearest)
GPII58	R158434	<i>Gehyra</i>	<i>pilbara</i>	-22.68333	114.36667	WA	Giralia Homestead
GPII59	R158435	<i>Gehyra</i>	<i>pilbara</i>	-22.58694	114.38722	WA	Giralia Homestead
GPII61	R158437	<i>Gehyra</i>	<i>pilbara</i>	-22.58694	114.38722	WA	Giralia Homestead
GPII62	R158438	<i>Gehyra</i>	<i>pilbara</i>	-22.58694	114.38722	WA	Giralia Homestead
GPII63	R158439	<i>Gehyra</i>	<i>pilbara</i>	-22.58694	114.38722	WA	Giralia Homestead
GPII64	R157285	<i>Gehyra</i>	<i>pilbara</i>	-22.29972	114.59306	WA	Yanrey Station
GPII68	R156584	<i>Gehyra</i>	<i>pilbara</i>	-20.55778	120.18194	WA	Cundaline Gap
GPII69	R156590	<i>Gehyra</i>	<i>pilbara</i>	-20.57444	120.19667	WA	Cundaline Gap
GPII70	R165739	<i>Gehyra</i>	<i>pilbara</i>	-20.85000	115.40000	WA	Barrow Island
GPII71	R165741	<i>Gehyra</i>	<i>pilbara</i>	-20.85000	115.40000	WA	Barrow Island
GPII72	R165743	<i>Gehyra</i>	<i>pilbara</i>	-20.80000	115.38333	WA	Barrow Island
GPII73	R165744	<i>Gehyra</i>	<i>pilbara</i>	-20.76667	115.45000	WA	Barrow Island
GPII75	R165746	<i>Gehyra</i>	<i>pilbara</i>	-20.76667	115.45000	WA	Barrow Island
GPII78	R165752	<i>Gehyra</i>	<i>pilbara</i>	-20.71667	115.46667	WA	Barrow Island
GPII79	R165753	<i>Gehyra</i>	<i>pilbara</i>	-20.71667	115.46667	WA	Barrow Island
GPII80	R165971	<i>Gehyra</i>	<i>pilbara</i>	-20.38667	115.55111	WA	Trimouille Island
GPII81	R165972	<i>Gehyra</i>	<i>pilbara</i>	-20.38667	115.55111	WA	Trimouille Island
GPII82	R165973	<i>Gehyra</i>	<i>pilbara</i>	-20.42278	115.53167	WA	Hermite Island
GPII83	R165974	<i>Gehyra</i>	<i>pilbara</i>	-20.42278	115.53167	WA	Hermite Island
GPII84	R165975	<i>Gehyra</i>	<i>pilbara</i>	-20.42278	115.53167	WA	Hermite Island
GPunc01	R164116	<i>Gehyra</i>	<i>punctata</i>	-22.22306	118.95528	WA	Newman
GPunc03	R127645	<i>Gehyra</i>	<i>punctata</i>	-21.66667	121.58333	WA	Nifty Mine
GPunc04	R129925	<i>Gehyra</i>	<i>punctata</i>	-23.25000	118.66667	WA	West Angelas
GPunc05	R129926	<i>Gehyra</i>	<i>punctata</i>	-23.25000	118.66667	WA	West Angelas
GPunc07	R129949	<i>Gehyra</i>	<i>punctata</i>	-21.33000	117.18889	WA	Mount Herbert Area
GPunc09	R117114	<i>Gehyra</i>	<i>punctata</i>	-22.70000	116.71667	WA	Wyloo Homestead
GPunc13	R114251	<i>Gehyra</i>	<i>punctata</i>	-25.58333	118.36667	WA	Mount Fraser
GPunc14	R114290	<i>Gehyra</i>	<i>punctata</i>	-20.85000	116.60000	WA	Myaree Pool
GPunc15	R114291	<i>Gehyra</i>	<i>punctata</i>	-20.85000	116.60000	WA	Myaree Pool
GPunc16	R114292	<i>Gehyra</i>	<i>punctata</i>	-20.85000	116.60000	WA	Myaree Pool
GPunc19	R114301	<i>Gehyra</i>	<i>punctata</i>	-24.00000	119.56667	WA	Bulloo Downs Homestead
GPunc20	R114308	<i>Gehyra</i>	<i>punctata</i>	-24.46667	118.56667	WA	Ethel Creek.
GPunc22	R114315	<i>Gehyra</i>	<i>punctata</i>	-25.81667	115.38333	WA	Lallytharra Springs Homestead
GPunc23	R114316	<i>Gehyra</i>	<i>punctata</i>	-25.81667	115.38333	WA	Lallytharra Springs Homestead
GPunc25	R114329	<i>Gehyra</i>	<i>punctata</i>	-20.85000	116.60000	WA	Myaree Pool
GPunc26	R114330	<i>Gehyra</i>	<i>punctata</i>	-20.85000	116.60000	WA	Myaree Pool
GPunc28	R114335	<i>Gehyra</i>	<i>punctata</i>	-23.71667	119.43333	WA	Prairie Downs
GPunc29	R114336	<i>Gehyra</i>	<i>punctata</i>	-23.71667	119.43333	WA	Prairie Downs
GPunc30	R114337	<i>Gehyra</i>	<i>punctata</i>	-23.71667	119.43333	WA	Prairie Downs
GPunc31	R114343	<i>Gehyra</i>	<i>punctata</i>	-20.73333	117.00000	WA	Cleaverville.
GPunc32	R114370	<i>Gehyra</i>	<i>punctata</i>	-18.33333	125.75000	WA	Gogo Homestead
GPunc33	R114540	<i>Gehyra</i>	<i>punctata</i>	-21.71667	116.50000	WA	Yangadee Gorge near Pannawonica
GPunc35	R114571	<i>Gehyra</i>	<i>punctata</i>	-20.78333	118.71667	WA	Poonthune Pool, Turner River
GPunc37	R114917	<i>Gehyra</i>	<i>punctata</i>	-21.65000	120.08333	WA	Nullagine
GPunc38	R114926	<i>Gehyra</i>	<i>punctata</i>	-20.40000	118.95000	WA	Port Hedland
GPunc39	R116893	<i>Gehyra</i>	<i>punctata</i>	-22.78944	116.54611	WA	Kooline Homestead
GPunc40	R116894	<i>Gehyra</i>	<i>punctata</i>	-22.78944	116.54611	WA	Kooline Homestead
GPunc41	R116895	<i>Gehyra</i>	<i>punctata</i>	-24.76667	116.21667	WA	Mt Phillip Homestead
GPunc42	R116896	<i>Gehyra</i>	<i>punctata</i>	-24.76667	116.21667	WA	Mt Phillip Homestead
GPunc43	R116897	<i>Gehyra</i>	<i>punctata</i>	-24.76667	116.21667	WA	Mt Phillip Homestead
GPunc44	R116898	<i>Gehyra</i>	<i>punctata</i>	-24.76667	116.21667	WA	Mt Phillip Homestead
GPunc45	R117399	<i>Gehyra</i>	<i>punctata</i>	-22.71667	119.01667	WA	Yandicoogina
GPunc46	R117008	<i>Gehyra</i>	<i>punctata</i>	-24.00000	118.53333	WA	Yilbrinna Pool
GPunc47	R117011	<i>Gehyra</i>	<i>punctata</i>	-23.26667	116.85000	WA	Ashburton Downs Homestead
GPunc48	R117027	<i>Gehyra</i>	<i>punctata</i>	-23.13333	117.56667	WA	Paraburdoo
GPunc50	R131002	<i>Gehyra</i>	<i>punctata</i>	-21.13833	117.11583	WA	Mount Herbert Area
GPunc52	R131008	<i>Gehyra</i>	<i>punctata</i>	-21.31278	117.23389	WA	Mount Herbert Area
GPunc53	R127414	<i>Gehyra</i>	<i>punctata</i>	-24.72028	116.11972	WA	Yinnietharra Homestead
GPunc54	R127415	<i>Gehyra</i>	<i>punctata</i>	-24.72028	116.11972	WA	Yinnietharra Homestead
GPunc55	R127475	<i>Gehyra</i>	<i>punctata</i>	-23.65000	119.71667	WA	Newman
GPunc56	R125459	<i>Gehyra</i>	<i>punctata</i>	-23.31667	120.03333	WA	Newman
GPunc58	R125480	<i>Gehyra</i>	<i>punctata</i>	-23.31667	120.03333	WA	Newman
GPunc61	R117009	<i>Gehyra</i>	<i>punctata</i>	-24.00000	118.53333	WA	Yilbrinna Pool
GPunc64	R117036	<i>Gehyra</i>	<i>punctata</i>	-24.30000	116.35000	WA	Cobra Homestead
GPunc67	R117039	<i>Gehyra</i>	<i>punctata</i>	-22.43333	115.88333	WA	Mt Stuart Homestead
GPunc70	R117070	<i>Gehyra</i>	<i>punctata</i>	-24.36667	116.31667	WA	Yinnetharra Homestead
GPunc73	R123764	<i>Gehyra</i>	<i>punctata</i>	-25.21000	115.51417	WA	Pells Creek
GPunc74	R123769	<i>Gehyra</i>	<i>punctata</i>	-25.21000	115.51417	WA	Pells Creek
GPunc75	R123770	<i>Gehyra</i>	<i>punctata</i>	-25.21000	115.51417	WA	Pells Creek
GPunc79	R125083	<i>Gehyra</i>	<i>punctata</i>	-23.36667	119.90000	WA	Newman
GPunc82	R125086	<i>Gehyra</i>	<i>punctata</i>	-23.36667	119.90000	WA	Newman
GPunc83	R119278	<i>Gehyra</i>	<i>punctata</i>	-26.43333	117.15000	WA	Mt Levrá Station Pells Creek
GPunc86	R120703	<i>Gehyra</i>	<i>punctata</i>	-20.40000	118.46667	WA	Boodarie Station
GPunc88	R162915	<i>Gehyra</i>	<i>punctata</i>	-20.84556	117.79583	WA	
GPunc89	R162916	<i>Gehyra</i>	<i>punctata</i>	-20.84556	117.79556	WA	
GPunc90	R162917	<i>Gehyra</i>	<i>punctata</i>	-18.55556	127.22333	WA	
GPunc91	R120534	<i>Gehyra</i>	<i>punctata</i>	-25.21000	115.51417	WA	Pells Creek
GPunc92	R120738	<i>Gehyra</i>	<i>punctata</i>	-20.40000	118.51667	WA	Boodarie Hill

Lab ID	Museum #	Genus	Species	Latitude (decimal)	Longitude (decimal)	State	Location (nearest)
GPunc96	R106164	<i>Gehyra</i>	<i>punctata</i>	-25.63333	118.38333	WA	Mt Frazer
GPunc103	R106156	<i>Gehyra</i>	<i>punctata</i>	-23.86667	118.56667	WA	Turee Creek Homestead
GPunc104	R129932	<i>Gehyra</i>	<i>punctata</i>	-23.25000	118.66667	WA	Newman
GPunc105	R132523	<i>Gehyra</i>	<i>punctata</i>	-20.67056	116.75611	WA	Burrup Peninsula
GPunc107	R132563	<i>Gehyra</i>	<i>punctata</i>	-20.61611	116.78500	WA	Burrup Peninsula
GPunc110	R135009	<i>Gehyra</i>	<i>punctata</i>	-23.40667	119.62417	WA	Mt Whaleback
GPunc111	R135013	<i>Gehyra</i>	<i>punctata</i>	-23.40306	119.69611	WA	Mt Whaleback
GPunc112	R135018	<i>Gehyra</i>	<i>punctata</i>	-23.33472	119.66944	WA	Mt Whaleback
GPunc114	R131758	<i>Gehyra</i>	<i>punctata</i>	-21.32361	117.12528	WA	Millstream-Chichester Range National Park
GPunc115	R131769	<i>Gehyra</i>	<i>punctata</i>	-26.61667	115.53333	WA	Muggon Station
GPunc116	R132679	<i>Gehyra</i>	<i>punctata</i>	-20.57889	120.31861	WA	Shay Gap
GPunc117	R132716	<i>Gehyra</i>	<i>punctata</i>	-17.08889	128.18472	WA	Warmun
GPunc119	R132736	<i>Gehyra</i>	<i>punctata</i>	-21.40139	118.70611	WA	Abydos
GPunc120	R132856	<i>Gehyra</i>	<i>punctata</i>	-16.96639	128.23278	WA	Bow River Sation
GPunc123	R108729	<i>Gehyra</i>	<i>punctata</i>	-17.28333	128.18333	WA	Mabel Downs Station
GPunc124	R108850	<i>Gehyra</i>	<i>punctata</i>	-21.03333	116.81667	WA	Cherralta Homestead
GPunc125	R108851	<i>Gehyra</i>	<i>punctata</i>	-21.03333	116.81667	WA	Cherralta Homestead
GPunc126	R113239	<i>Gehyra</i>	<i>punctata</i>	-21.73333	116.25000	WA	Jimmawurrada Creek/Robe River junction
GPunc130	R138946	<i>Gehyra</i>	<i>punctata</i>	-23.19472	118.59639	WA	West Angelas
GPunc131	R140014	<i>Gehyra</i>	<i>punctata</i>	-21.26583	117.07417	WA	Millstream-Chichester Range National Park
GPunc132	R140307	<i>Gehyra</i>	<i>punctata</i>	-21.26583	117.07417	WA	Millstream-Chichester Range National Park
GPunc134	R141312	<i>Gehyra</i>	<i>punctata</i>	-20.90528	116.21694	WA	Cape Preston Area
GPunc135	R141332	<i>Gehyra</i>	<i>punctata</i>	-20.90528	116.21694	WA	Cape Preston Area
GPunc136	R141333	<i>Gehyra</i>	<i>punctata</i>	-20.90528	116.21694	WA	Cape Preston Area
GPunc137	R141338	<i>Gehyra</i>	<i>punctata</i>	-21.04389	116.18722	WA	Cape Preston Area
GPunc139	R141352	<i>Gehyra</i>	<i>punctata</i>	-20.90528	116.21694	WA	Cape Preston Area
GPunc143	R145251	<i>Gehyra</i>	<i>punctata</i>	-22.80722	117.75000	WA	Mount Tom Price Mine
GPunc152	R145755	<i>Gehyra</i>	<i>punctata</i>	-21.94389	118.96278	WA	Chichester Range
GPunc153	R136281	<i>Gehyra</i>	<i>punctata</i>	-26.81694	115.54778	WA	Muggon Station
GPunc154	R154306	<i>Gehyra</i>	<i>punctata</i>	-22.05194	118.98778	WA	Chichester Range
GPunc157	R154311	<i>Gehyra</i>	<i>punctata</i>	-22.95778	119.17889	WA	Weeli Wolli Creek
GPunc159	R154517	<i>Gehyra</i>	<i>punctata</i>	-20.54778	120.24528	WA	Yarri Mining Camp
GPunc160	R154776	<i>Gehyra</i>	<i>punctata</i>	-23.32111	119.93778	WA	Brockman Ridge
GPunc164	R157722	<i>Gehyra</i>	<i>punctata</i>	-22.94083	118.90500	WA	Packsaddle Range
GPunc165	R158267	<i>Gehyra</i>	<i>punctata</i>	-22.63333	120.41111	WA	Roy Hill
GPunc167	R156588	<i>Gehyra</i>	<i>punctata</i>	-20.54889	120.16806	WA	Cundaline Gap
GPunc168	R156587	<i>Gehyra</i>	<i>punctata</i>	-20.54889	120.16806	WA	Cundaline Gap
GPunc171	R165249	<i>Gehyra</i>	<i>punctata</i>	-20.75889	116.68528	WA	Karratha
GPunc172	R165250	<i>Gehyra</i>	<i>punctata</i>	-20.75889	116.68528	WA	Karratha
GPunc175	R165253	<i>Gehyra</i>	<i>punctata</i>	-20.75889	116.68528	WA	Karratha
GPunc176	R165508	<i>Gehyra</i>	<i>punctata</i>	-20.70000	116.58333	WA	West Intercourse Island
GPunc180	R165518	<i>Gehyra</i>	<i>punctata</i>	-20.70000	116.58333	WA	West Intercourse Island
GPunc181	R165527	<i>Gehyra</i>	<i>punctata</i>	-20.68528	116.63000	WA	West Intercourse Island
GPunc182	R165534	<i>Gehyra</i>	<i>punctata</i>	-20.68583	116.63056	WA	West Intercourse Island
GPunc183	R165601	<i>Gehyra</i>	<i>punctata</i>	-20.67444	116.71556	WA	Dampier Area
DS01	R129589	<i>Diplodactylus</i>	<i>savagei</i>	-22.93333	118.93333	WA	Newman
DS02	R108597	<i>Diplodactylus</i>	<i>savagei</i>	-21.80000	116.23333	WA	Pannawonica
DS03	R120023	<i>Diplodactylus</i>	<i>savagei</i>	-22.97500	119.07500	WA	Hope Downs
DS04	R102495	<i>Diplodactylus</i>	<i>savagei</i>	-23.37917	115.88056	WA	Barlee Range Nature Reserve
DS05	R119932	<i>Diplodactylus</i>	<i>savagei</i>	-22.46667	117.30000	WA	Mt Brockman
DS06	R108605	<i>Diplodactylus</i>	<i>savagei</i>	-21.78333	116.25000	WA	Mount Dempster
DS07	R108636	<i>Diplodactylus</i>	<i>savagei</i>	-21.80000	116.23333	WA	Pannawonica
DS08	R132581	<i>Diplodactylus</i>	<i>savagei</i>	-20.61611	116.78500	WA	Burrup Peninsula
DS09	R132637	<i>Diplodactylus</i>	<i>savagei</i>	-20.59278	116.79944	WA	Burrup Peninsula
DS10	R135017	<i>Diplodactylus</i>	<i>savagei</i>	-23.35139	119.65139	WA	Mt Whaleback
DS11	R127751	<i>Diplodactylus</i>	<i>savagei</i>	-22.79611	117.79000	WA	Mount Tom Price Mine
DS12	R127812	<i>Diplodactylus</i>	<i>savagei</i>	-22.80722	117.75000	WA	Mount Tom Price Mine
DS13	R113623	<i>Diplodactylus</i>	<i>savagei</i>	-21.98333	118.83333	WA	Auski Roadhouse
DS14	R140703	<i>Diplodactylus</i>	<i>savagei</i>	-22.88333	119.25278	WA	Hope Downs
DS15	R140719	<i>Diplodactylus</i>	<i>savagei</i>	-22.83694	119.37528	WA	Hope Downs
DS16	R140771	<i>Diplodactylus</i>	<i>savagei</i>	-23.28333	119.73333	WA	Newman
DS17	R141346	<i>Diplodactylus</i>	<i>savagei</i>	-20.93806	116.20083	WA	Cape Preston Area
DS18	R139367	<i>Diplodactylus</i>	<i>savagei</i>	-21.28889	120.47194	WA	Meentheena
DS19	R146616	<i>Diplodactylus</i>	<i>savagei</i>	-22.15167	119.01611	WA	Port Hedland
DS20	R146622	<i>Diplodactylus</i>	<i>savagei</i>	-21.90083	118.90306	WA	Port Hedland
DS21	R151171	<i>Diplodactylus</i>	<i>savagei</i>	-22.48806	117.72917	WA	Tom Price Area
DS22	R145734	<i>Diplodactylus</i>	<i>savagei</i>	-22.87778	119.24000	WA	Weeli Wolli Creek
DS23	R151741	<i>Diplodactylus</i>	<i>savagei</i>	-22.01694	118.98194	WA	Chichester Range
DS24	R151742	<i>Diplodactylus</i>	<i>savagei</i>	-22.01694	118.98194	WA	Chichester Range
DS25	R145735	<i>Diplodactylus</i>	<i>savagei</i>	-22.95778	119.17889	WA	Weeli Wolli Creek
DS26	R157619	<i>Diplodactylus</i>	<i>savagei</i>	-23.31528	119.80639	WA	Newman
DS27	R156178	<i>Diplodactylus</i>	<i>savagei</i>	-24.59000	117.25250	WA	Waldburg Station
DS28	R110736	<i>Diplodactylus</i>	<i>savagei</i>	-22.51806	117.23639	WA	Brockman Mine
DS29	R110737	<i>Diplodactylus</i>	<i>savagei</i>	-22.51806	117.23639	WA	Brockman Mine
DS30	R110743	<i>Diplodactylus</i>	<i>savagei</i>	-22.61750	117.18139	WA	Brockman Mine
DS31	R110819	<i>Diplodactylus</i>	<i>savagei</i>	-21.66667	115.83528	WA	Pannawonica
DS32	R156589	<i>Diplodactylus</i>	<i>savagei</i>	-20.56833	120.18972	WA	Cundaline Gap
DS33	R156617	<i>Diplodactylus</i>	<i>savagei</i>	-21.65583	121.22139	WA	Woodie Woodie Minesite

Lab ID	Museum #	Genus	Species	Latitude (decimal)	Longitude (decimal)	State	Location (nearest)
DS34	R156682	<i>Diplodactylus</i>	<i>savagei</i>	-20.63944	114.30500	WA	Yarrie Minesite
DS35	R110933	<i>Diplodactylus</i>	<i>savagei</i>	-21.67111	115.96222	WA	Pannawonica
DS36	R110934	<i>Diplodactylus</i>	<i>savagei</i>	-21.74611	116.22000	WA	Pannawonica
DS37	R165502	<i>Diplodactylus</i>	<i>savagei</i>	-20.68694	116.63278	WA	West Intercourse Island
DS38	R165516	<i>Diplodactylus</i>	<i>savagei</i>	-20.68528	116.63000	WA	West Intercourse Island
DS39	R165532	<i>Diplodactylus</i>	<i>savagei</i>	-20.68694	116.63250	WA	West Intercourse Island
DS40	R166181	<i>Diplodactylus</i>	<i>savagei</i>	-21.96472	120.12667	WA	Nullagine
DS41	R166639	<i>Diplodactylus</i>	<i>savagei</i>	-20.84917	117.83028	WA	Mons Cupri Mine
DW01	R164118	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.26806	119.18917	WA	Newman
DW02	R164119	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.26806	119.18917	WA	Newman
DW06	R102489	<i>Diplodactylus</i>	<i>wombeyi</i>	-23.07944	115.79083	WA	Barlee Range Nature Reserve
DW07	R102493	<i>Diplodactylus</i>	<i>wombeyi</i>	-23.38917	115.88667	WA	Barlee Range Nature Reserve
DW08	R110894	<i>Diplodactylus</i>	<i>wombeyi</i>	-21.77083	116.22833	WA	Pannawonica
DW11	R139411	<i>Diplodactylus</i>	<i>wombeyi</i>	-21.28528	120.41528	WA	Meentheena
DW12	R146600	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.39000	119.99000	WA	Port Hedland
DW13	R139429	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.13528	115.68889	WA	Cane River
DW14	R151294	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.55000	118.01667	WA	Mount Bruce
DW15	R154651	<i>Diplodactylus</i>	<i>wombeyi</i>	-23.37917	120.10528	WA	Wheelarra Hill
DW16	R154653	<i>Diplodactylus</i>	<i>wombeyi</i>	-23.37917	120.10528	WA	Wheelarra Hill
DW17	R157026	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.06750	118.99528	WA	Fortescue Marsh
DW18	R157118	<i>Diplodactylus</i>	<i>wombeyi</i>	-23.19056	118.82611	WA	West Angelas
DW19	R157637	<i>Diplodactylus</i>	<i>wombeyi</i>	-23.30694	119.75500	WA	Newman
DW20	R157787	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.40250	119.86111	WA	Roy Hill
DW21	R157133	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.40250	119.86111	WA	Roy Hill
DW22	R157134	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.40250	119.86111	WA	Roy Hill
DW25	R158272	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.40250	119.86111	WA	Roy Hill
DW26	R158279	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.40250	119.86111	WA	Roy Hill
DW27	R110722	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.43778	117.28444	WA	Brockman Mine
DW28	R110729	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.60361	117.19333	WA	Brockman Mine
DW29	R110730	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.60361	117.19333	WA	Brockman Mine
DW30	R110742	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.51806	117.23639	WA	Brockman Mine
DW31	R156229	<i>Diplodactylus</i>	<i>wombeyi</i>	-20.57167	120.24917	WA	Cattle Gorge
DW32	R156583	<i>Diplodactylus</i>	<i>wombeyi</i>	-20.55778	120.18194	WA	Cundaline Gap
DW33	R166180	<i>Diplodactylus</i>	<i>wombeyi</i>	-21.95917	120.13278	WA	Nullagine
DW34	R166195	<i>Diplodactylus</i>	<i>wombeyi</i>	-21.95194	120.13111	WA	Nullagine
Gko218	R102488	<i>Diplodactylus</i>	<i>wombeyi</i>	-23.07972	115.79028	WA	Barlee Range Nature Reser
Gko219	R102489	<i>Diplodactylus</i>	<i>wombeyi</i>	-23.07944	115.79083	WA	Barlee Range Nature Reser
Gko220	R113382	<i>Diplodactylus</i>	<i>wombeyi</i>	-21.85000	118.75000	WA	East Mulga Downs
Gko221	R114916	<i>Diplodactylus</i>	<i>wombeyi</i>	-23.25000	119.88333	WA	Newman
Gko222	R139370	<i>Diplodactylus</i>	<i>wombeyi</i>	-21.22528	120.35556	WA	Meentheena
Gko223	R139399	<i>Diplodactylus</i>	<i>wombeyi</i>	-21.22528	120.35556	WA	Meentheena
Gko226	R139429	<i>Diplodactylus</i>	<i>wombeyi</i>	-22.13528	115.68889	WA	Cane River
Gko227	R154653	<i>Diplodactylus</i>	<i>wombeyi</i>	-23.37917	120.10528	WA	Newman
Gko101	R90635	<i>Lucasium</i>	<i>stenodactylum</i>	-21.60944	118.97444	WA	Woodstock Station
Gko102	R90671	<i>Lucasium</i>	<i>stenodactylum</i>	-21.60944	118.97444	WA	Woodstock Station
Gko103	R90702	<i>Lucasium</i>	<i>stenodactylum</i>	-21.60972	119.02139	WA	Woodstock Station
Gko104	R97256	<i>Lucasium</i>	<i>stenodactylum</i>	-23.38333	120.15000	WA	Wheelarra Hill
Gko105	R97257	<i>Lucasium</i>	<i>stenodactylum</i>	-23.38333	120.15000	WA	Wheelarra Hill
Gko106	R102053	<i>Lucasium</i>	<i>stenodactylum</i>	-20.31667	119.25000	WA	Degray River
Gko107	R102181	<i>Lucasium</i>	<i>stenodactylum</i>	-22.60000	118.51194	WA	Mt Windell
Gko108	R102185	<i>Lucasium</i>	<i>stenodactylum</i>	-22.60000	118.51194	WA	Mt Windell
Gko109	R102481	<i>Lucasium</i>	<i>stenodactylum</i>	-23.04472	115.78722	WA	Barlee Range Nature Reserve
Gko112	R104001	<i>Lucasium</i>	<i>stenodactylum</i>	-21.61167	118.95556	WA	Woodstock Station
Gko113	R106155	<i>Lucasium</i>	<i>stenodactylum</i>	-23.86667	118.56667	WA	Turee Creek Homestead
Gko114	R108799	<i>Lucasium</i>	<i>stenodactylum</i>	-18.94056	128.78444	WA	Banana Springs
Gko115	R108800	<i>Lucasium</i>	<i>stenodactylum</i>	-17.25000	128.30000	WA	Bream Gorge
Gko117	R108807	<i>Lucasium</i>	<i>stenodactylum</i>	-18.15000	122.55000	WA	Thangoo Homestead
Gko118	R108835	<i>Lucasium</i>	<i>stenodactylum</i>	-24.70000	119.60000	WA	Kumarina
Gko119	R108846	<i>Lucasium</i>	<i>stenodactylum</i>	-21.03333	116.81667	WA	Cherralta Homestead
Gko120	R108847	<i>Lucasium</i>	<i>stenodactylum</i>	-21.03333	116.81667	WA	Cherralta Homestead
Gko121	R110584	<i>Lucasium</i>	<i>stenodactylum</i>	-19.88917	128.86000	WA	Tanami Desert
Gko122	R110588	<i>Lucasium</i>	<i>stenodactylum</i>	-19.85694	128.84806	WA	Tanami Desert
Gko125	R110592	<i>Lucasium</i>	<i>stenodactylum</i>	-19.59333	128.86111	WA	Tanami Desert
Gko126	R110593	<i>Lucasium</i>	<i>stenodactylum</i>	-19.89972	128.82694	WA	Tanami Desert
Gko127	R110706	<i>Lucasium</i>	<i>stenodactylum</i>	-22.58861	117.23639	WA	Mount Brocreekman
Gko128	R110710	<i>Lucasium</i>	<i>stenodactylum</i>	-22.61750	117.18139	WA	Mount Brocreekman
Gko129	R110723	<i>Lucasium</i>	<i>stenodactylum</i>	-22.43778	117.28444	WA	Mount Brocreekman
Gko130	R110741	<i>Lucasium</i>	<i>stenodactylum</i>	-22.51806	117.28444	WA	Mount Brocreekman
Gko131	R112692	<i>Lucasium</i>	<i>stenodactylum</i>	-21.68778	115.09194	WA	Onslow
Gko132	R112964	<i>Lucasium</i>	<i>stenodactylum</i>	-17.05972	122.71667	WA	Broome
Gko133	R112974	<i>Lucasium</i>	<i>stenodactylum</i>	-17.08361	122.65972	WA	Broome
Gko134	R113026	<i>Lucasium</i>	<i>stenodactylum</i>	-20.28056	118.88056	WA	Lesley Salt Works
Gko135	R113031	<i>Lucasium</i>	<i>stenodactylum</i>	-20.24722	118.84722	WA	Lesley Salt Works
Gko136	R113181	<i>Lucasium</i>	<i>stenodactylum</i>	-24.70000	119.58333	WA	Kumarina
Gko137	R113194	<i>Lucasium</i>	<i>stenodactylum</i>	-23.33333	119.86667	WA	Newman
Gko138	R113229	<i>Lucasium</i>	<i>stenodactylum</i>	-21.70000	116.16667	WA	Deepdale
Gko140	R113591	<i>Lucasium</i>	<i>stenodactylum</i>	-21.98333	118.83333	WA	Auski Roadhouse
Gko141	R113601	<i>Lucasium</i>	<i>stenodactylum</i>	-21.98333	118.83333	WA	Auski Roadhouse

Lab ID	Museum #	Genus	Species	Latitude (decimal)	Longitude (decimal)	State	Location (nearest)
Gko142	R114210	<i>Lucasium</i>	<i>stenodactylum</i>	-16.40000	122.93333	WA	Cape Leveque
Gko143	R114211	<i>Lucasium</i>	<i>stenodactylum</i>	-16.40000	122.93333	WA	Cape Leveque
Gko144	R114234	<i>Lucasium</i>	<i>stenodactylum</i>	-17.36667	122.15000	WA	Coulomb Point Nature Reserve
Gko145	R114918	<i>Lucasium</i>	<i>stenodactylum</i>	-21.16667	119.81667	WA	Marble Bar
Gko146	R114919	<i>Lucasium</i>	<i>stenodactylum</i>	-21.16667	119.81667	WA	Marble Bar
Gko147	R114920	<i>Lucasium</i>	<i>stenodactylum</i>	-21.16667	119.81667	WA	Marble Bar
Gko148	R115245	<i>Lucasium</i>	<i>stenodactylum</i>	-21.63333	114.38333	WA	South Muiron Island
Gko149	R119277	<i>Lucasium</i>	<i>stenodactylum</i>	-26.43333	117.15000	WA	Mt Levrá Station Homestead
Gko152	R122758	<i>Lucasium</i>	<i>stenodactylum</i>	-24.40556	114.44417	WA	Mardathuna Homestead
Gko153	R123831	<i>Lucasium</i>	<i>stenodactylum</i>	-25.08806	115.38000	WA	Gascoyne Junction
Gko154	R125017	<i>Lucasium</i>	<i>stenodactylum</i>	-22.70972	118.98194	WA	Yandicoogina
Gko155	R125031	<i>Lucasium</i>	<i>stenodactylum</i>	-22.70972	118.98194	WA	Yandicoogina
Gko156	R125037	<i>Lucasium</i>	<i>stenodactylum</i>	-22.72056	118.99056	WA	Yandicoogina
Gko158	R126773	<i>Lucasium</i>	<i>stenodactylum</i>	-24.44306	114.51167	WA	Mardathuna Homestead
Gko159	R127444	<i>Lucasium</i>	<i>stenodactylum</i>	-21.75000	115.08333	WA	Onslow
Gko160	R127493	<i>Lucasium</i>	<i>stenodactylum</i>	-21.73333	115.08333	WA	Onslow
Gko161	R127515	<i>Lucasium</i>	<i>stenodactylum</i>	-21.73333	115.08333	WA	Onslow
Gko162	R127518	<i>Lucasium</i>	<i>stenodactylum</i>	-21.73333	115.08333	WA	Onslow
Gko163	R127703	<i>Lucasium</i>	<i>stenodactylum</i>	-22.79917	117.77639	WA	Mount Tom Price Mine
Gko164	R127776	<i>Lucasium</i>	<i>stenodactylum</i>	-22.79917	117.77639	WA	Mount Tom Price Mine
Gko165	R129656	<i>Lucasium</i>	<i>stenodactylum</i>	-22.99583	119.09167	WA	Newman
Gko166	R131012	<i>Lucasium</i>	<i>stenodactylum</i>	-21.13833	117.11583	WA	Millstream-Chichester
Gko167	R131487	<i>Lucasium</i>	<i>stenodactylum</i>	-23.37167	119.62889	WA	Mount Whaleback Creek
Gko168	R132239	<i>Lucasium</i>	<i>stenodactylum</i>	-21.77778	114.87056	WA	Urala Station
Gko169	R132240	<i>Lucasium</i>	<i>stenodactylum</i>	-21.76167	114.85278	WA	Urala Station
Gko170	R132528	<i>Lucasium</i>	<i>stenodactylum</i>	-20.67222	116.75611	WA	Burrup Peninsula
Gko171	R132533	<i>Lucasium</i>	<i>stenodactylum</i>	-20.67222	116.75611	WA	Burrup Peninsula
Gko172	R132556	<i>Lucasium</i>	<i>stenodactylum</i>	-20.62611	116.78972	WA	Burrup Peninsula
Gko174	R132759	<i>Lucasium</i>	<i>stenodactylum</i>	-16.02250	128.86861	WA	Lake Argyle
Gko175	R135006	<i>Lucasium</i>	<i>stenodactylum</i>	-23.33750	119.69667	WA	Mount Whaleback Creek
Gko176	R135007	<i>Lucasium</i>	<i>stenodactylum</i>	-23.40306	119.69611	WA	Mount Whaleback Creek
Gko178	R139043	<i>Lucasium</i>	<i>stenodactylum</i>	-19.81222	121.47361	WA	Mandora
Gko179	R139232	<i>Lucasium</i>	<i>stenodactylum</i>	-21.26639	120.45528	WA	Meentheana Homestead
Gko180	R140755	<i>Lucasium</i>	<i>stenodactylum</i>	-15.71667	128.73333	WA	Kununurra
Gko182	R145077	<i>Lucasium</i>	<i>stenodactylum</i>	-27.05194	125.15861	WA	Officer Basin
Gko183	R145195	<i>Lucasium</i>	<i>stenodactylum</i>	-22.24306	114.03472	WA	Learmonth Airstrip
Gko184	R145196	<i>Lucasium</i>	<i>stenodactylum</i>	-22.24306	114.03472	WA	Learmonth Airstrip
Gko185	R145449	<i>Lucasium</i>	<i>stenodactylum</i>	-26.26250	121.51083	WA	Lorna Glen Station
Gko186	R145566	<i>Lucasium</i>	<i>stenodactylum</i>	-20.70000	118.64000	WA	Port Hedland
Gko187	R145592	<i>Lucasium</i>	<i>stenodactylum</i>	-20.78000	118.64000	WA	Port Hedland
Gko188	R145703	<i>Lucasium</i>	<i>stenodactylum</i>	-22.82083	119.28694	WA	Weeli Wolli Creek
Gko189	R145704	<i>Lucasium</i>	<i>stenodactylum</i>	-22.83389	119.27278	WA	Weeli Wolli Creek
Gko190	R145742a	<i>Lucasium</i>	<i>stenodactylum</i>	-21.94000	118.96083	WA	Chichester Range
Gko191	R145742b	<i>Lucasium</i>	<i>stenodactylum</i>	-21.94000	118.96083	WA	Chichester Range
Gko192	R151021	<i>Lucasium</i>	<i>stenodactylum</i>	-15.93333	128.90000	WA	Kununurra
Gko195	R151440a	<i>Lucasium</i>	<i>stenodactylum</i>	-26.20083	121.30361	WA	Lorna Glen Station
Gko197	R151484a	<i>Lucasium</i>	<i>stenodactylum</i>	-26.26250	121.51083	WA	Lorna Glen Station
Gko198	R151484b	<i>Lucasium</i>	<i>stenodactylum</i>	-26.26250	121.51083	WA	Lorna Glen Station
Gko199	R151743	<i>Lucasium</i>	<i>stenodactylum</i>	-21.94000	118.96083	WA	Chichester Range
Gko200	R154249	<i>Lucasium</i>	<i>stenodactylum</i>	-22.29917	119.02278	WA	Munjina Roadhouse
Gko201	R154560	<i>Lucasium</i>	<i>stenodactylum</i>	-23.37917	120.10528	WA	Newman
Gko202	R157145	<i>Lucasium</i>	<i>stenodactylum</i>	-22.70583	120.53806	WA	Roy Hill
Gko203	R157156	<i>Lucasium</i>	<i>stenodactylum</i>	-22.78389	120.50056	WA	Roy Hill
Gko204	R157189	<i>Lucasium</i>	<i>stenodactylum</i>	-22.16417	114.58972	WA	Yanrey
Gko205	R157273	<i>Lucasium</i>	<i>stenodactylum</i>	-22.25750	114.60000	WA	Yanrey
Gko206	R157539	<i>Lucasium</i>	<i>stenodactylum</i>	-21.74778	116.07528	WA	Pannawonica
Gko207	R157573	<i>Lucasium</i>	<i>stenodactylum</i>	-21.74778	116.07528	WA	Pannawonica
Gko208	R157732	<i>Lucasium</i>	<i>stenodactylum</i>	-19.57944	128.86806	WA	Larranganni Bluff
Gko209	R157733	<i>Lucasium</i>	<i>stenodactylum</i>	-19.57944	128.86806	WA	Larranganni Bluff
Gko214	R157949	<i>Lucasium</i>	<i>stenodactylum</i>	-23.35194	122.66667	WA	Savory Creek Mouth
Gko215	R157950	<i>Lucasium</i>	<i>stenodactylum</i>	-23.35194	122.66667	WA	Savory Creek Mouth
Gko216	R158319	<i>Lucasium</i>	<i>stenodactylum</i>	-22.65778	114.39194	WA	Giralia
Gko217	R158320	<i>Lucasium</i>	<i>stenodactylum</i>	-22.62167	114.39250	WA	Giralia
Gko300	R140585	<i>Lucasium</i>	<i>stenodactylum</i>	-18.08333	122.28333	WA	Roebuck Bay, Broome Bird Observatory
Gko300	R140585	<i>Lucasium</i>	<i>stenodactylum</i>	-18.08333	122.28333	WA	Roebuck Bay, Broome Bird Observatory
Gko307	R139897	<i>Lucasium</i>	<i>stenodactylum</i>	-16.00000	127.96667	WA	El Questro Station
Gko313	R110130	<i>Lucasium</i>	<i>stenodactylum</i>	-21.88230	117.79436	WA	PE02°
Gko314	R110195	<i>Lucasium</i>	<i>stenodactylum</i>	-21.38408	117.06078	WA	PW12°
Gko315	R110251	<i>Lucasium</i>	<i>stenodactylum</i>	-22.67519	119.84078	WA	RHNE05°
Gko316	R110270	<i>Lucasium</i>	<i>stenodactylum</i>	-22.11789	119.87647	WA	RHNE10°
Gko317	R110294	<i>Lucasium</i>	<i>stenodactylum</i>	-22.67519	119.84078	WA	RHNE05°
Gko318	R110298	<i>Lucasium</i>	<i>stenodactylum</i>	-22.76608	119.63069	WA	RHNE02°
Gko319	R110305	<i>Lucasium</i>	<i>stenodactylum</i>	-22.81983	119.61389	WA	RHNE01°
Gko320	R110310	<i>Lucasium</i>	<i>stenodactylum</i>	-22.67519	119.84078	WA	RHNE05°
Gko321	R158064	<i>Lucasium</i>	<i>stenodactylum</i>	-21.31010	117.27561	WA	PW13°
Gko322	R158067	<i>Lucasium</i>	<i>stenodactylum</i>	-21.67752	116.97497	WA	PW06°
Gko323	R158092	<i>Lucasium</i>	<i>stenodactylum</i>	-21.38408	117.06078	WA	PW12°
Gko324	R158093	<i>Lucasium</i>	<i>stenodactylum</i>	-21.38408	117.06078	WA	PW12°

Lab ID	Museum #	Genus	Species	Latitude (decimal)	Longitude (decimal)	State	Location (nearest)
Gko325	R158186	Lucasium	stenodactylum	-22.29453	119.06136	WA	RHNW11*
Gko327	R159841	Lucasium	stenodactylum	-20.94990	117.85017	WA	DRE11*
Gko328	R159850	Lucasium	stenodactylum	-20.60730	118.15700	WA	DRE07*
Gko329	R159851	Lucasium	stenodactylum	-20.52552	118.07728	WA	DRE06*
Gko331	R159884	Lucasium	stenodactylum	-20.91968	117.86092	WA	DRE10*
Gko332	R159891	Lucasium	stenodactylum	-20.86988	117.85847	WA	DRE09*
Gko333	R159895	Lucasium	stenodactylum	-20.94990	117.85017	WA	DRE11*
Gko334	R159906	Lucasium	stenodactylum	-20.96942	118.04792	WA	DRE13*
Gko338	R159919	Lucasium	stenodactylum	-20.86988	117.85847	WA	DRE09*
Gko339	R159920	Lucasium	stenodactylum	-20.86988	117.85847	WA	DRE09*
Gko342	R159941	Lucasium	stenodactylum	-20.91968	117.86092	WA	DRE10*
Gko343	R159942	Lucasium	stenodactylum	-20.91968	117.86092	WA	DRE10*
Gko346	R160024	Lucasium	stenodactylum	-20.52552	118.07728	WA	DRE06*
Gko347	R160061	Lucasium	stenodactylum	-21.28844	121.23761	WA	NE12*
Gko348	R160062	Lucasium	stenodactylum	-21.29483	121.26394	WA	NE13*
Gko349	R160086	Lucasium	stenodactylum	-21.32558	120.97022	WA	NE08*
Gko350	R160092	Lucasium	stenodactylum	-21.29483	121.26394	WA	NE13*
Gko351	R160123	Lucasium	stenodactylum	-21.32558	120.97022	WA	NE08*
Gko353	R160147	Lucasium	stenodactylum	-21.32558	120.97022	WA	NE08*
Gko355	R160151	Lucasium	stenodactylum	-21.33711	120.76950	WA	NE05*
Gko356	R160159	Lucasium	stenodactylum	-21.97964	120.22367	WA	NW01*
Gko357	R160160	Lucasium	stenodactylum	-21.97964	120.22367	WA	NW01*
Gko358	R160161	Lucasium	stenodactylum	-21.39261	120.07228	WA	NW12*
Gko359	R160183	Lucasium	stenodactylum	-21.94806	120.19367	WA	NW02*
Gko360	R160204	Lucasium	stenodactylum	-21.67775	120.15519	WA	NW05*
Gko361	R160212	Lucasium	stenodactylum	-21.39261	120.07228	WA	NW12*
Gko362	R160227	Lucasium	stenodactylum	-21.67775	120.15519	WA	NW05*
Gko363	R160231	Lucasium	stenodactylum	-21.40717	120.07133	WA	NW11*
Gko367	R160931	Lucasium	stenodactylum	-21.06289	116.23331	WA	DRW08*
Gko369	R160979	Lucasium	stenodactylum	-20.87457	116.64864	WA	DRW04*
Gko370	R161022	Lucasium	stenodactylum	-21.05519	116.25144	WA	DRW07*
Gko371	R161050	Lucasium	stenodactylum	-20.87457	116.64864	WA	DRW04*
Gko373	R161064	Lucasium	stenodactylum	-21.05519	116.25144	WA	DRW07*
Gko375	R161075	Lucasium	stenodactylum	-21.07078	116.20625	WA	DRW09*
Gko378	R161992	Lucasium	stenodactylum	-22.17031	115.55942	WA	WYW03*
Gko381	R162055	Lucasium	stenodactylum	-22.43353	115.93000	WA	WYE06*
Gko382	R162123	Lucasium	stenodactylum	-22.77306	116.52203	WA	WYE02*
Gko383	R162205	Lucasium	stenodactylum	-23.31936	119.10142	WA	RHNC02*
Gko386	R162257	Lucasium	stenodactylum	-22.83778	119.27203	WA	RHNC13*
Gko449	SAMAR29878	Lucasium	stenodactylum	-25.19167	131.61667	NT	Curtin Springs
Gko453	R94617	Lucasium	stenodactylum	-21.58333	117.06666	WA	Millstream
Gko456	CU14283	Lucasium	stenodactylum	-28.09783	123.68633	WA	Yamama Station
Gko476	SAMAR36111	Lucasium	stenodactylum	-25.23333	131.01667	NT	Yulara
Gko525	R156616	Lucasium	stenodactylum	-21.65270	121.21420	WA	Woodie Woodie
Gko004	R110056	Heteronotia	spelea pilbara	-21.03590	117.10658	WA	Roebourne
Gko005	R110075	Heteronotia	spelea pilbara	-21.03590	117.10658	WA	Roebourne
Gko006	R110076	Heteronotia	spelea pilbara	-21.03590	117.10658	WA	Roebourne
Gko028	R97258	Heteronotia	spelea pilbara	-23.36667	120.13333	WA	Wheelarra Hill
Gko029	R102227	Heteronotia	spelea pilbara	-23.41139	115.89389	WA	Barlee Range
Gko030	R102380	Heteronotia	spelea pilbara	-23.40000	115.88333	WA	Barlee Range
Gko031	R102436	Heteronotia	spelea pilbara	-23.13056	115.99444	WA	Goodeman Pool
Gko032	R113545	Heteronotia	spelea pilbara	-22.83333	119.46667	WA	Capricorn Roadhouse
Gko033	R114561	Heteronotia	spelea pilbara	-23.08333	119.28333	WA	Newman
Gko034	R115832	Heteronotia	spelea pilbara	-23.11889	118.78278	WA	The Governor
Gko035	R115833	Heteronotia	spelea pilbara	-23.11889	118.78278	WA	The Governor
Gko036	R121394	Heteronotia	spelea pilbara	-22.86667	119.43333	WA	Weeli Wolli
Gko037	R132488	Heteronotia	spelea pilbara	-23.20000	117.66667	WA	Paraburdoo
Gko038	R132681	Heteronotia	spelea pilbara	-20.60028	120.29167	WA	Shay Gap
Gko039	R135010	Heteronotia	spelea pilbara	-23.38611	119.62944	WA	Mount Whaleba Creek
Gko040	R135388	Heteronotia	spelea pilbara	-22.31056	117.32861	WA	Mount Brockman Station
Gko041	R135446	Heteronotia	spelea pilbara	-22.31056	117.32194	WA	Mount Brockman Station
Gko042	R135456	Heteronotia	spelea pilbara	-22.31056	117.32194	WA	Mount Brockman Station
Gko043	R145600	Heteronotia	spelea pilbara	-20.92860	118.67780	WA	Port Hedland
Gko044	R157546	Heteronotia	spelea pilbara	-23.19417	118.81500	WA	West Angeles
Gko045	R157719	Heteronotia	spelea pilbara	-22.94083	118.90500	WA	Newman
Gko278	ABTC11763	Heteronotia	spelea pilbara	-20.92000	120.20972	WA	Bamboo Creek Mine
Gko287	ABTC32832	Heteronotia	spelea pilbara	-20.92000	120.20972	WA	Bamboo Creek
Gko288	ABTC32922	Heteronotia	spelea pilbara	-20.92000	120.20972	WA	Bamboo Creek
Gko436	R111927	Heteronotia	spelea pilbara	-22.60980	120.72900	WA	BDRN09*
Gko437	R111986	Heteronotia	spelea pilbara	-22.60980	120.72900	WA	BDRN09*
Gko438	R160085	Heteronotia	spelea pilbara	-21.32190	121.00200	WA	NE09*
Gko439	R160145	Heteronotia	spelea pilbara	-21.32190	121.00200	WA	NE09*
Gko440	R161285	Heteronotia	spelea pilbara	-21.32190	121.00200	WA	NE09*
Gko442	R165152	Heteronotia	spelea pilbara	-23.05380	119.17700	WA	PW3*
Gko443	R165222	Heteronotia	spelea pilbara	-21.34130	117.18900	WA	DRC6*
Gko444	R170295	Heteronotia	spelea pilbara	-21.03640	117.10600	WA	TCMBC05*
Gko445	R170828	Heteronotia	spelea pilbara	-23.31830	117.87000	WA	MBE06*
Gko446	R170892	Heteronotia	spelea pilbara	-21.50620	119.41800	WA	MBE1*

We have produced the first detailed mtDNA phylogenies that clarify phylogenetic structure among Pilbara populations in *C. conspicillatus*, *L. wombeyi*, *G. pilbara* and *G. punctata*. Together with previously published material, we use these phylogenetic datasets to place the Pilbara in context with other arid zone regions, and to test three intra-regional biogeographic hypotheses.

Our phylogenies are characterized by generally well-supported clades at the tips of the trees, and for *L. stenodactylum* and *H. spelea*, this genetic structure is supported by a number of additional nDNA loci (Pepper *et al.* 2006, 2011 [Chapter 1]). For each newly sequenced taxon, a substantial amount of intra-specific diversity was uncovered, that in many instances is equal to or exceeds species-level differences in closely related taxa (Oliver *et al.* 2009). This is particularly evident in the two *Gehyra* species where deep genetic structure and paraphyly of currently recognized species is clearly indicative of multiple species complexes. The taxonomic assessment of the taxa represented here is beyond the scope of this paper, (and in the case of *Gehyra* is being prepared elsewhere [Sistrom *et al.* in prep]), and for our purposes is irrelevant. We proceed by assigning the genetic groups to their appropriate geographic regions independent of potential species boundaries, and use this information to address our hypotheses below.

What is the relationship of the Pilbara to other known areas of endemism, and do taxa exhibit genetically differentiated populations across the Pilbara craton boundary?

Our datasets for *Diplodactylus conspicillatus*, *G. pilbara*, *G. punctata* and *L. stenodactylum* include populations sampled in the Kimberley, as well as the Pilbara and central deserts, providing insights into the relationship between these areas of endemism. The phylogeny for *L. stenodactylum* strongly supports the Kimberley to be more closely related to the central deserts than to the Pilbara. For *D. conspicillatus*, the central deserts are most closely associated with the Pilbara, whereas the Kimberley individuals are much more divergent. While weak support of the deepest divergences within our *Gehyra* phylogeny precludes any comment on the relationships between major clades, Kimberley individuals of *G. pilbara* and *G. punctata* also are highly divergent, and are more closely related to each other than either is to the remaining *Gehyra*. In addition, all taxa examined have populations found outside the Pilbara craton, including the Pilbara “endemics”, *L. wombeyi*, *D. savagei* and *H. spelea* that also comprise samples from ranges in the Ashburton subregion of the Gascoyne bioregion to the south of the craton (Figure 1c). Topology tests provided mixed support for the monophyly of Pilbara populations to the exclusion of their non-Pilbara counterparts (Table 2). There is no support for the monophyly of Pilbara *D. conspicillatus* Clade 2, but results were equivocal in regard to Clade 1. There is no support for the monophyly of Pilbara *Gehyra* Clade 2, however results were equivocal regarding Clade 1. Topology tests provided no support for the monophyly of Pilbara *L. stenodactylum* or *L. wombeyi*, but were equivocal regarding the monophyly of *H. spelea* and *D. savagei*. Despite this general lack of support for monophyly of the Pilbara at the broad scale, there is a clear genetic distinction between Pilbara and non-Pilbara populations in all taxa except *L. wombeyi*.

Like previous studies on the area relationships between the Kimberley, Pilbara and Western/Central deserts (ie. Cracraft 1991; Unmack 2001), our study of seven taxa does not clearly support a single pattern. Our phylogenetic analyses of *Diplodactylus conspicillatus*, *G. pilbara*, *G. punctata* and *L. stenodactylum* infer different relationships between these regions, and it is clear that the genetic patterns are idiosyncratic and reflect a diversity of historical processes within the arid zone.

Table 2. Results of Shimodaira-Hasegawa tests of alternative topologies regarding the monophyly of Pilbara populations (Hypothesis 1) and the three biogeographic subdivisions (Hypothesis 2A, 2B and 2C).

Taxon	-ln L	Hypothesis 1		Hypothesis 2A		Hypothesis 2B		Hypothesis 2C	
		Difference in -ln L score	P value	Difference in -ln L score	P value	Difference in -ln L score	P value	Difference in -ln L score	P value
<i>D. conspicillatus 1</i>	7651.7054	58.8845	0.1900	150.0466	0.0020*	215.2325	0.0001*	147.4095	0.0020*
<i>D. conspicillatus 2</i>	7651.7054	109.2301	0.0060*	116.2485	0.0050*	310.1976	0.0001*	64.6634	0.1100
<i>Gehyra 1</i>	18678.6736	23.9554	0.7860	366.1766	0.0001*	332.0545	0.0001*	303.2597	0.0001*
<i>Gehyra 2</i>	18678.6736	1120.3828	0.0001*	1448.8026	0.0001*	950.5416	0.0001*	1315.7260	0.0001*
<i>D. savagei/D. galaxius</i>	5181.9350	25.9971	0.1440	60.6349	0.0060*	26.1847	0.0770	59.7769	0.0100*
<i>H. spelea</i>	7677.1444	11.7708	0.5480	208.2569	0.0001*	536.1885	0.0001*	536.1885	0.0001*
<i>L. stenodactylum</i>	7179.1850	334.7031	0.0010*	250.5980	0.0330*	1515.7597	0.0001*	411.4958	0.0001*
<i>L. wombeyi</i>	3888.9753	177.7329	0.0001*	n/a		n/a		n/a	

Significant *P* values (<0.05) shown with a "*" indicate that the alternative topology is significantly different from the maximum likelihood (ML) tree

However, our results support earlier suggestions of an endemic and highly divergent Kimberley biota (Bowman *et al.* 2010; Melville *et al.* 2010; Pepper *et al.* 2011 [Chapter 1]). Despite the geological similarities of the Kimberley to the Pilbara, the climate is substantially different, largely due to the dominating influence of the summer monsoon (Wyrwoll & Miller 2001). Although palaeontological evidence is limited, the monsoonal climatic regime is thought to have originated between the late Eocene and early Oligocene (reviewed in Bowman *et al.* 2010). Accordingly, habitat in the Kimberley also is very different from the Pilbara, with large areas dominated by tropical high-grass and woodland savanna (Beard 1979). The historical distribution of savanna-type habitat is thought to have extended to the Pilbara in the past (Ford & Blaire 2005), but presumably the transition to an arid climate in the Pilbara since the mid-Miocene substantially altered the environment and associated vegetation in the region. Furthermore, intensifying aridification in the intervening central desert regions likely forced taxa to periodically contract their ranges to mesic refuges in topographically complex areas such as the Kimberley and Pilbara (Pepper *et al.* 2011 [Chapter II]). While we have not attempted to date lineages in our study due to the limited power of a single mtDNA locus (Edwards & Beerli 2000), the high level of divergence of Kimberley populations suggest it is unlikely that divergence was the result of the recent isolation of the Pilbara and Kimberley by the development of the sand deserts < 1 Mya. Indeed, Pepper *et al.* (2011 [Chapter II]) inferred the split between Kimberley *Heteronotia* geckos and Pilbara/Central Australian *Heteronotia* geckos occurred at least 4 million years ago, while divergence of Pilbara and Kimberley *Livistona* plants was estimated to have occurred between 5 and 7 Mya (Crisp *et al.* 2010).

In a study of the widespread arid zone gecko *L. stenodactylum*, Pepper *et al.* (2006) found strong genetic differentiation between individuals in the general Pilbara district and those in the remaining arid zone. Certainly the number of lineages within each taxa found in the Pilbara in our current broader study suggests multiple invasions either into or out of the region. In addition, substantial diversification within the Pilbara craton supports previous conjectures of Pilbara mountain ranges providing important refugia following Miocene aridification (Byrne *et al.* 2008; Pepper *et al.* 2008, 2011 [Chapter 1]). Pepper *et al.* (2008) also found that within the Pilbara “group” of *L. stenodactylum*, populations south and east of the Pilbara craton were genetically divergent across the craton boundary, despite extremely close geographic proximity to individuals within the

craton. Our results across multiple taxa broadly corroborate this finding. With the exception of *L. wombeyi* (where no apparent differentiation between Pilbara and Ashburton individuals is apparent), all taxa exhibit highly differentiated populations outside the craton, particularly along the southern craton margin at the boundary with the Carnarvon and Gascoyne bioregions, and the eastern margin bordering the central deserts. An emerging pattern in our data is that those taxa distributed in the low-lying Carnarvon and southern Gascoyne tend not to occur in the northern Gascoyne (ie. the Ashburton subregion) or the Pilbara craton. Similarly the rocky Pilbara “endemics”, *L. wombeyi*, *D. savagei* and *H. spelea*, are limited by the distribution of the topographically complex Pilbara craton and adjacent Ashburton ranges. This pattern, repeated across taxa, suggests an important role of habitat specialization and/or climate-induced vicariance. Certainly major differences in vegetation, topography and substrate exist in the Carnarvon and the southern Gascoyne (Beard 1975; Environment Australia 2008), and while topographic differences are less pronounced between the Pilbara Craton and the Ashburton subregion, the vegetation and substrates are distinct (Tille 2006). Similarly, the topographic, substrate and vegetation differences between the eastern Pilbara craton boundary and the adjacent dunes of the Great and Little Sandy Deserts are pronounced in this area. In addition to the habitat gradient across the Pilbara craton boundary, the northern, eastern, and southern margins of the craton are traversed by river channels and tributaries of the De Grey and Ashburton rivers. Despite the present ephemeral existence of these arid zone rivers, the size of their channels and floodplains appear as large scars across the landscape on satellite imagery (GoogleEarth), indicating their immense presence under historically wetter climates (Martin 2006), and would have periodically isolated the Pilbara from surrounding regions.

Within the Pilbara, does genetic diversity correlate to previously hypothesized biogeographic regions, and is there congruence across taxa?

We found a substantial amount of genetic diversity within populations of *D. conspicillatus*, *G. pilbara*, *G. punctata* and *L. wombeyi* distributed across the Pilbara craton. Added to the genetic patterns in *H. spelea*, *D. savagei* and *L. stenodactylum*, it is clear that the Pilbara has had a dynamic evolutionary history resulting in high species diversity and endemism. Because little is known about the partitioning of genetic

diversity across the Pilbara landscape for terrestrial vertebrates, we tested three simple biogeographic hypotheses based on the delimitation of the Pilbara into sub-bioregions, and also the distribution of major geological units and landforms (Figures 2-7). Below we outline the phylogenetic support for each hypothesis.

(A) The major geologic divide separating the northern Granite/Greenstone terrain from the southern Hamersley Basin

Topology tests reject the hypothesis of monophyly of populations distributed on these broadly defined geological units (Table 2). However, some patterns are apparent that suggest a broad distinction between these two geological domains. This is most obvious in the phylogenies for *L. stenodactylum* and *D. conspicillatus* Clade 2. *Lucasium wombeyi*, *D. savagei* and *H. spelea* are almost entirely restricted in their range by the distribution of the rocks of the Hamersley Basin (Figures 2a, 3a and 4a). Examination of patterns in other taxa reveals this same geological unit harbors the majority of genetic diversity. In *Gehyra* in particular, many of the genetic lineages found in this region comprise numerous geographically overlapping clades, and may reflect narrow range endemism.

(B) The four IBRA biogeographic subregions

With the exception of *D. galaxius*, topology tests reject the hypothesis of monophyly of populations distributed on the IBRA subregions (Table 2). However, depending on the taxon, and at what level of the genealogical hierarchy patterns are examined, there are varying degrees of support for the subregions. For example, the phylogenies of *L. wombeyi*, *D. savagei* and *H. spelea* broadly reflect the Hamersley, Chichester and Roebourne subregions (Figures 2b, 3b and 4b), while *L. stenodactylum* shows no clear pattern (Figure 5b). Only two of the taxa examined comprise individuals collected from within the Fortescue subregion. Our phylogeny for *D. conspicillatus* revealed a highly divergent Fortescue clade distributed in the wider, eastern extent of the valley (Figure 6b and c). In contrast, individuals of *L. stenodactylum* from throughout the Fortescue subregion show no genetic association (Figure 5b). There appears to be a close association between the two northern subregions, the Roebourne and the Chichester. In particular, *D. conspicillatus*, *G. punctata*, and *L. stenodactylum* each comprise clades confined to the Roebourne and western Chichester, while *D. savagei* and *L. wombeyi* have clades restricted to the eastern Chichester.

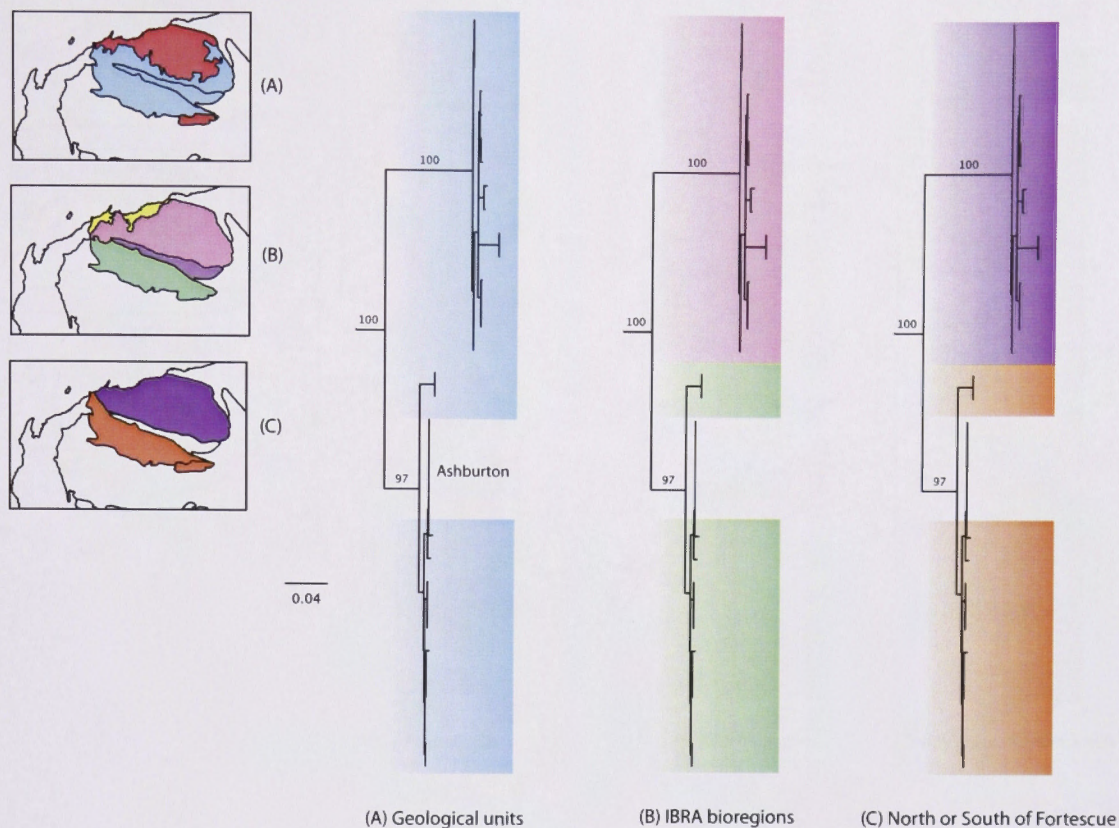


Figure 2. Phylogenetic results of *Lucasium wombeyi*, based on maximum likelihood analyses. Values on the tree refer to bootstrap support obtained using the ‘-f i’ function in RAxML. Only individuals that are found within the boundaries of the Pilbara craton are coloured on the trees. Clades are colour-coded according to their distribution in relation to three biogeographic hypotheses.

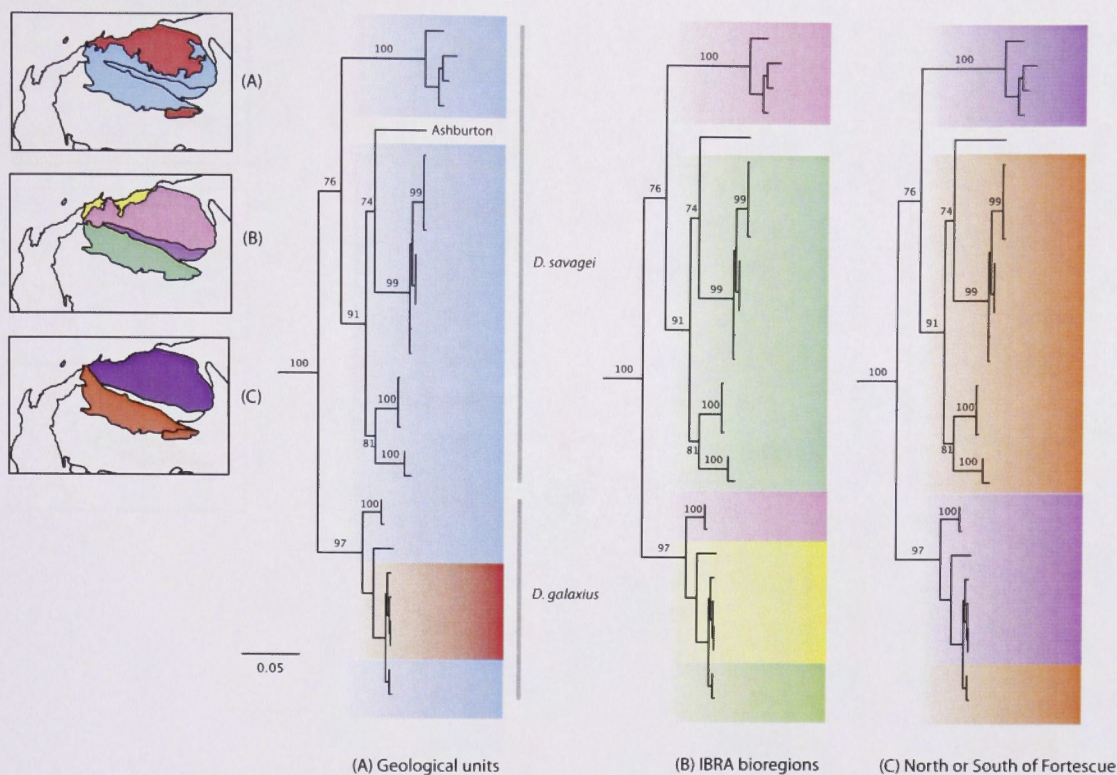


Figure 3. Phylogenetic results of *Diplodactylus savagei* and *D. galaxius*, based on maximum likelihood analyses. Values on the tree refer to bootstrap support obtained using the ‘-f i’ function in RAxML. Only individuals that are found within the boundaries of the Pilbara craton are coloured on the trees. Clades are colour-coded according to their distribution in relation to three biogeographic hypotheses.

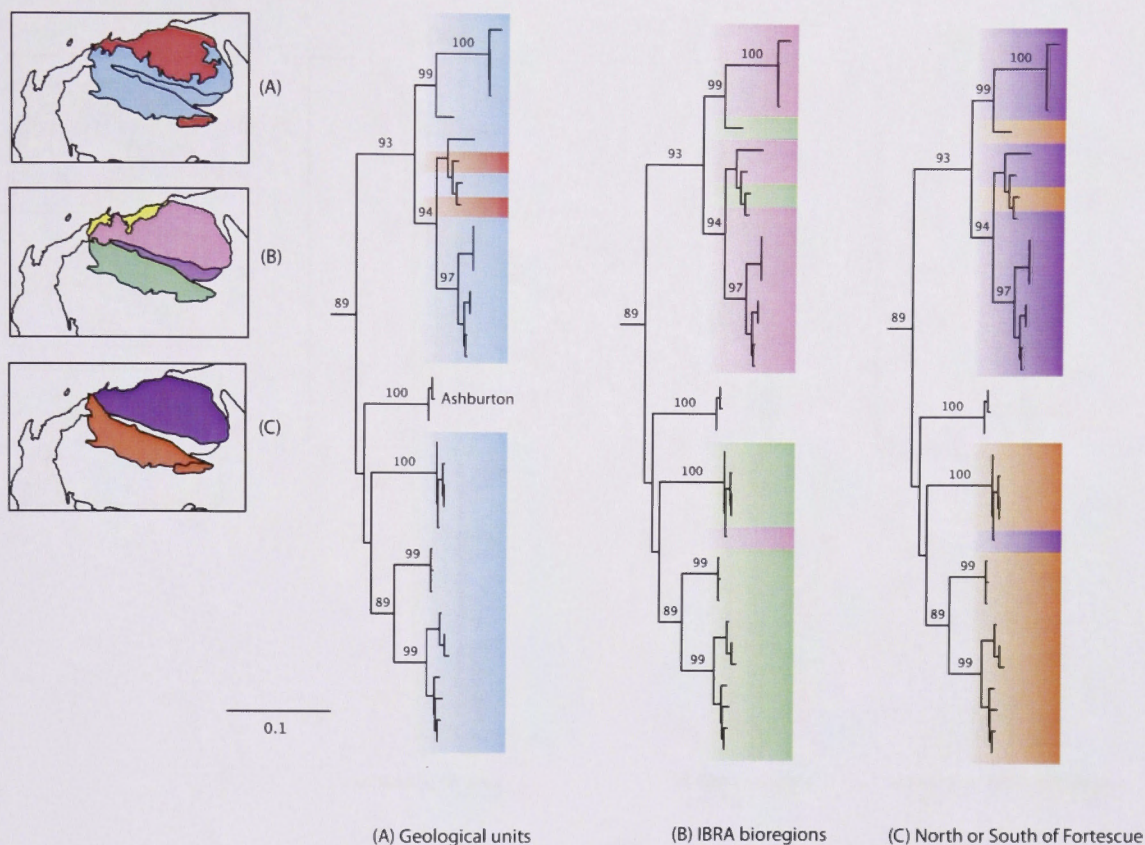


Figure 4. Phylogenetic results of *Heteronotia spelea*, based on maximum likelihood analyses. Values on the tree refer to bootstrap support obtained using the ‘-f i’ function in RAXML. Only individuals that are found within the boundaries of the Pilbara craton are coloured on the trees. Clades are colour-coded according to their distribution in relation to three biogeographic hypotheses.

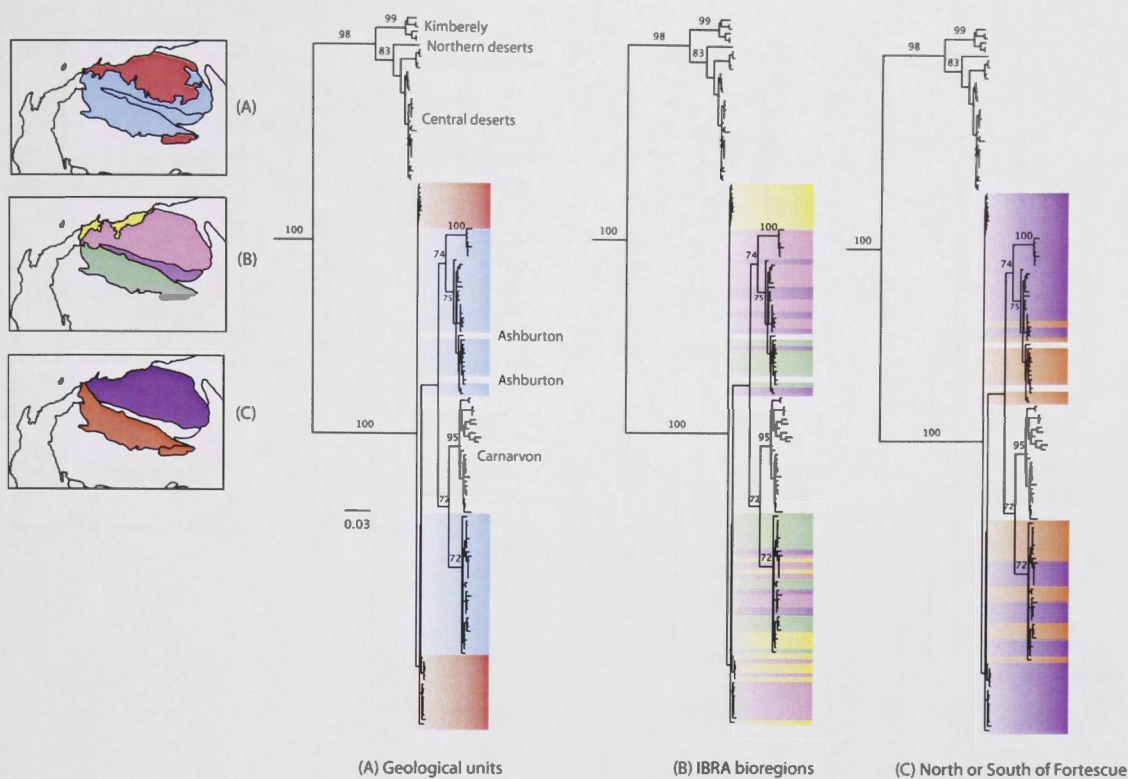


Figure 5. Phylogenetic results of *Lucasium stenodactylum*, based on maximum likelihood analyses. Values on the tree refer to bootstrap support obtained using the ‘-f i’ function in RAxML. Only individuals that are found within the boundaries of the Pilbara craton are coloured on the trees. Clades are colour-coded according to their distribution in relation to three biogeographic hypotheses.

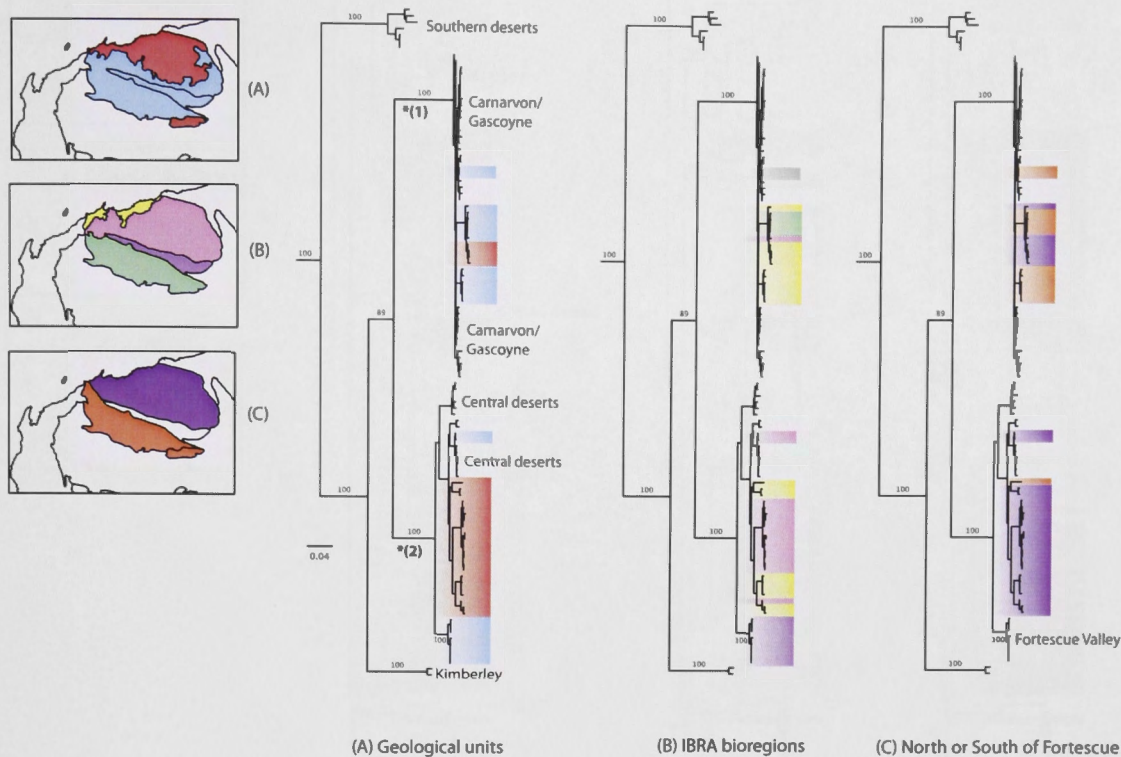


Figure 6. Phylogenetic results of *Diplodactylus conspicillatus*, based on maximum likelihood analyses. *(1) and *(2) indicate Clades 1 and 2 as referred to in the text. Values on the tree refer to bootstrap support obtained using the ‘-f i’ function in RAxML. Only individuals that are found within the boundaries of the Pilbara craton are coloured on the trees. Clades are colour-coded according to their distribution in relation to three biogeographic hypotheses.

(C) *North and South of the Fortescue river valley.*

Lucasium wombeyi and *D. savagei* comprise major clades distributed on opposite sides of the Fortescue River. For remaining taxa, topology tests reject the hypothesis of monophyly of populations distributed north and south of the Fortescue River, with the exception of *D. conspicillatus* Clade 2 (Table 2). However, as is the case with the previous hypotheses, at finer scales of genetic subdivision, broad patterns emerge that suggest some level of distinction between clades north and south of the valley.

Our phylogenies of multiple, co-distributed gecko taxa reveal that genetic patterns in the Pilbara are complex, and likely reflect a diversity of historical processes. None of our biogeographic hypotheses clearly reflect the genetic partitions observed in our datasets, but the high degree of intra-specific diversity and unclear taxonomic boundaries, species-specific ecological differences, and difficulties in assigning individuals to specific geographic regions, particularly at boundary edges, complicate the observed patterns. Despite this, broad biogeographic patterns are emerging that appear to be repeated across taxonomic groups. The most consistent feature of the phylogeographies is a north/south differentiation across the Pilbara craton. However, determining which of the three biogeographic scenarios above best reflects the genetic patterns is difficult, because they all are based to some extent on a north/south division.

Our data illustrate that interpreting patterns in the western Pilbara is particularly vexing. In this region, individuals show little correlation with the IBRA subregions, and while not apparent in the level of detail shown in our phylogenetic results, individuals from the southwestern Chichester subregion show closer affinities to the broader Hamersley subregion than to the northern Chichester. In this same area, individuals also show little, if any differentiation across the Fortescue River. This pattern is better explained by the distribution of the Hamersley Basin geologic unit, which encompasses a portion of the Chichester subregion and both sides of the Fortescue River valley in this part of the Pilbara. While the Fortescue river may have played a role in the vicariant diversification of Pilbara taxa some time in the past, the distribution of closely related individuals on either side of the river valley suggests recent connectivity across this topographic divide. This connectivity appears to be associated with the eastern and western bounds of the river valley, where topographic variation is less pronounced. The

ephemeral nature of this arid zone river could potentially lead to a weakening of this geographic barrier over time.

Finer-scale sampling, particularly where the different geographic units overlap will help tease apart and refine the boundaries of biogeographic zones. The patterns identified in our study are largely consistent with previous work. In particular, a signal of regional north/south differentiation across the Pilbara has been found in patterns of species composition of spiders (Durrant *et al.* 2010), beetles (Guthrie *et al.* 2010) and ostracods (Reeves *et al.* 2007). Examination of the published literature reveals similar genetic patterns across the Pilbara reflected in a number of other reptiles, including Pebble-mimic dragons (Shoo *et al.* 2008), and Spiny-tailed skinks (Doughty *et al.* in prep).

There also appears to be an east/west pattern emerging across the northern Pilbara. In particular, the genetic distinctiveness of taxa in the northwest Pilbara (Beard's [1975] Abydos Plain) compared to the northeast Pilbara (Beard's [1975] Oakover Valley) is apparent (Figure 1c). Based on our results, we agree with Guthrie *et al.* (2010) and conclude that the classification of the Chichester subregion into a single unit is too simplistic, and Beard's (1975) physio-geographic subdivisions within this subregion better explain genetic variation across the northern Pilbara.

Future directions

Little is known about the biogeographic history of the Pilbara and the evolution of its biota. However, this likely will change in the near future following a recent (2002-2009) comprehensive systematic survey lead by the Western Australian Department of Environment and Conservation, through access to comprehensive biological collections across the plant and animal kingdoms, coupled with detailed geo/biophysical data associated with collection localities. The availability of these data, along with ever-improving analytical techniques, will facilitate detailed tests of diversification history in this arid region, and provide much needed insights into the evolutionary consequences of the most severe climate change in recent geological history in Australia. While the evolutionary distinctiveness of Pilbara biota appears to be well established (Baverstock *et al.* 1983; Painter *et al.* 1995; Cracraft 1991; Humphreys 1999, 2001; Blacket *et al.* 2000; Unmack 2001; Finston & Johnson 2004; Ladiges 2006; Pepper *et al.* 2006, 2011

[Chapter I]; Ford & Johnson 2007; Shoo *et al.* 2008; Doughty *et al.* 2010; Melville *et al.* in press), further studies involving widespread taxa will be required to shed more light on the area relationships of the Pilbara to other arid zone regions.

Our results suggest that habitat specificity as well as vicariant processes have played an important role in the evolutionary history and genetic cohesiveness of the Pilbara biota. The challenge for future studies of Pilbara phylogeography will be to incorporate more detailed sampling in order to delineate centers of diversity with greater precision, and to further test the biogeographic scenarios outlined above at a finer scale. In addition, the high level of diversity and potential short-range endemism associated with the geological unit of the Hamersley Basin (including the Hamersley subregion) suggests future work also should consider the influence of finer-scale geologic and habitat divisions within this broad region. Furthermore, while our sampling allowed insights into genetic differentiation on the southern and eastern margins of the Pilbara craton, we had insufficient data to examine genetic patterns at the interface of the north Pilbara craton and the northern deserts. The highly weathered nature of the Granite/Greenstone terrain in the north Pilbara and the sandy substrates that characterize this region means the boundary between the craton and the deserts to the north is much less pronounced than in the south or east Pilbara. While we found some level of genetic differentiation in *D. conspicillatus* across this northern boundary, two *G. pilbara* individuals within the Kimberley clade were collected from the northern Pilbara, suggesting a very recent range expansion across the northern deserts. Testing the strength of this potential habitat barrier in other taxa would be a fruitful area for further study. Finally, our phylogeny for *D. conspicillatus* identified a second highly divergent lineage comprising two clades; one containing individuals from the southwest arid zone and another clustering around the southwestern boundary of the Pilbara craton. Interestingly, a highly divergent lineage of *G. punctata* also was found to contain a cluster of individuals from this same general area of the craton boundary. The geology in this region is distinctive, as outcrops of the Granite/Greenstone terrains that characterize the northern Pilbara are exposed in a small area (Figure 1b). Further sampling is required to assess the distributional extent of these clades in order to determine the geographic level of endemism.

Conservation implications

The information emerging from fine-scale molecular studies such as ours have significant implications for diversity assessment and conservation management in a region heavily impacted by human development. It is now well known that short-range endemic invertebrates are particularly vulnerable to the impacts of mining and industrial development in the Pilbara, and have received considerable attention from conservation agencies and mining companies (Johnson 2004; Majer 2009; Eberhard *et al.* 2009). While the degree of short-range endemism in many of the subterranean invertebrate fauna is of a much finer scale than for terrestrial vertebrates, an alarming discovery from our study concerns the number of evolutionarily distinct gecko lineages that appear to have extremely restricted distributions, particularly in the Hamersley Plateau, the region comprising the unique iron-rich rocks at the core of Australia's iron-ore mining industry. While further sampling may extend the known distributions of these lineages in the Pilbara, the low-dispersal capability of small terrestrial vertebrates suggests there may be potential consequences for failing to recognize the partitioning of genetic diversity across the region. Emerging views of the Pilbara as an historic and ancient center of refugia (Pepper *et al.* 2011 [Chapter I], submitted [Chapter II]) warrants high priority from Government and conservation agencies with the ability to protect and conserve its unique biota.

Glossary of geological terms (as defined by the Collins Dictionary of Geology, 2003 edition).

Craton

A major structural unit of the Earth's crust, consisting of a large stable mass of rock, generally igneous and/or metamorphic, sometimes with a thin veneer of sediment; craton is practically synonymous with "shield".

Terrain

A fault-bounded portion of the Earth's crust that has a distinct geology differing sharply from the areas adjacent to it.

Tectonics

A branch of geology that is closely related to, but not synonymous with, 'structural geology'. Whereas structural geology is concerned primarily with the geometry of rocks, tectonics deals not only with larger features of the Earth but also with the forces and movements that produced them.

Supergroup

The formal 'stratigraphic unit' next in order above 'formation'; it includes two or more geographically associated formations with notable features in common. A differentiated assemblage of formations is a *subgroup*, and an assemblage of related groups or formations and groups is called a *supergroup*.

Alluvial plains

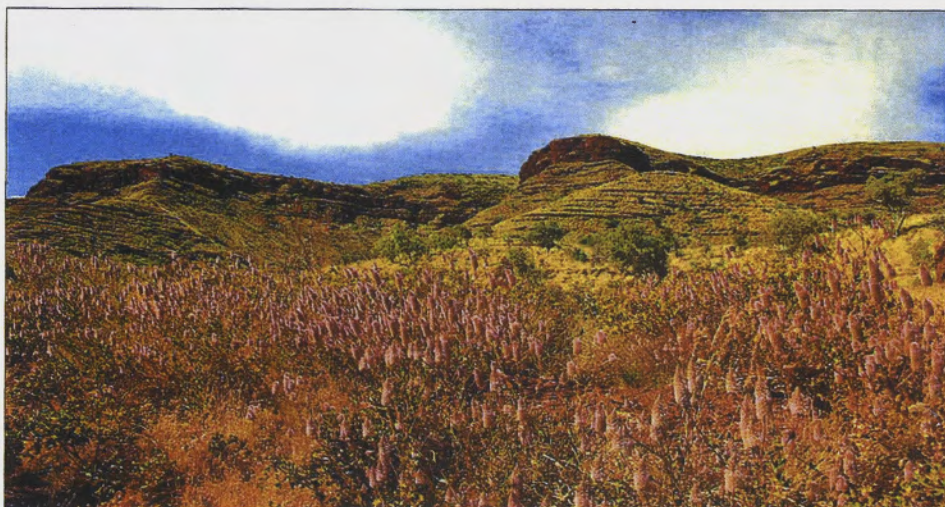
The general name for a plain produced by the deposition of alluvium by rivers, e.g. floodplain, delta plain, alluvial flat.

Regolith

Unconsolidated rock material and weathered products thereof, resting on bedrock, found at and near the surface of the Earth, including soils, alluvium, and dune sand.

Playa

A flat dry barren plain at the bottom of a desert basin. It is often the bed of an ephemeral lake and may be covered with white salts.



Prize patch of Pilbara

I first went to the Pilbara in 2004, as a volunteer for the Western Australian Museum and the Department of Environment and Conservation. I have been back many times since, drawn mainly by research, but also a keen sense of exploration. It is a rugged, ancient landscape, where billion-year-old rocks stand crumbling at the surface, slowly weathering away the remains of the world's oldest fossilised algae communities.

Rounded hummocks of spinifex grass creep over almost everything, leaving the air heavy with the sickly sweet aroma of their spines baking under the blistering sun. Pale ghost gums offer little shade, and contrast starkly against the rusty ironstone rocks. It is a harsh, but awesomely beautiful place.

Despite its remote location, most people have probably heard of the Pilbara, and many will even have some idea of where it is. Nestled in the north-western bulge of the Australian continent, the name "Pilbara" often conjures up unpleasant imagery of big iron-ore mining companies, searing summer temperatures, and a yearly battering of tropical cyclones.

For biologists, however, the Pilbara recently has put its name on the map for entirely different reasons.

Locals and researchers have long been aware that the Pilbara is home to a unique group of plants and animals. But the truth is that it is a difficult place to get to, and even harder to lug



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scientific equipment around. So for science, the Pilbara has, for a long time, been very much the unknown.

The Pilbara Biological Survey was set up to discover and document as many species of living organism as could be found there. Starting in 2004, this was done over four years with a series of sites set up across the entire region, and surveyed for plants, birds, mammals, lizards, snakes, frogs and invertebrates. For the many small and often elusive animals, this can only be achieved using specially designed "pit traps", dug into the ground to catch the animals as they move through the landscape.

Although inherently random this method works surprisingly well, and on a successful trapping night you can expect to find all sorts of unique and wonderful animals, waiting quietly in the pits dug into the cool of the earth: the tiny, feisty marsupial Ningau weighing only 5g; the elegant Notomys hopping mouse, with long ears and a feather-duster tail; velvet-skinned geckos with spectacularly coloured, unblinking eyes; striped skinks with scarlet red or cobalt blue tails; pygmy goannas the length

of a pencil; pebble-mimic dragons, specially camouflaged to look like two dusty rocks with a stick tail; and termite-eating blind snakes, with an odour so pungent no amount of Dettol could possibly remove.

These are just some of the remarkable animals that can be found in the Pilbara. Hundreds of species new to science were documented in the survey. To put this in mind-boggling perspective, 600 species of terrestrial invertebrates were recorded, and more than 20 per cent of them had never been seen before. And this is likely to be just the tip of the iceberg, as scientists begin genetic screening of these organisms to place them in their family trees.

The sheer number of species unique to the Pilbara makes it an evolutionary biologist's playground to throw around ideas as to how they came to be. What processes in the landscape history were responsible for this diversity of plants and animals? Some of the most important clues to this biological enigma can be found in the communities of tiny underground invertebrates that live in caves and water bodies below the Pilbara's surface. The number of species is so spectacularly prolific that a single cave can have its own suite of unique species.

Scientists believe that millions of years ago, when inland Australia was covered in rainforest, these invertebrates lived among the leaf litter on the forest floor, as they still do today in the tropical rainforests of Queensland. The huge change in

climate as the deserts were formed in Central Australia made the surface an inhospitable place for the moist-loving invertebrates, and to avoid extinction they had no choice but to move underground to the subterranean refuge where it was cooler. The rocks in the Pilbara have a special structure, and are full of tiny cavities and caves. Over time, the rocks weathered and shifted, water moved in and out of the underground caves, and populations of the invertebrates were cut off from one another. Unable to mix their genes any more, they continued to evolve separately, with myriad new species arising.

Scientists (including this one) want to know if the rocks in the Pilbara have had the same effect on the evolution of animals that live on the surface. In figuring out how past climate change has affected the evolution of species, we can try to predict what might happen to them under future climate scenarios.

Without the significant changes of climate that have occurred in the past, the huge number of species that exist today may never have evolved. But will these species be able to keep up with the rapid climate change of our generations? And importantly for some, where else can they go?

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Appendix

Popular Science article: *Wee frog causes a stir*

Popular Science article: *Special breed of gecko has twists in the tale*

Popular Science article: *The cost of casual sex*

Popular Science article: *The little Aussie gecko*

Popular Science article: *Where biologists dare*

Popular Science article: *Spare a thought for lizards*



Wee frog causes a stir

The rain fell steadily through the sticky air. Beneath my soaking boots, shallow pools were forming on the rocks that were still baking from the heat of the day. In the striated darkness ahead of me I could see the wandering glow of other head torches, illuminating the vast rock flats that stretched ahead. Unnervingly, I knew that to my right this plateau sharply dropped away into an enormous sinkhole filled with lush vine thickets, hiding their last retreat deep in the gorges that dissected this immense landscape. My eyelids felt heavy, and my weary steps became less deliberate with the passing hours. Suddenly the torch beams disappeared and our late-night natter hushed, leaving only the sound of rain splattering the sandstone. I stood motionless, with my head tilted slightly, hoping and straining to hear what we had all been waiting for.

He started, tentatively at first, a few high-pitched pulses which quickly turned into a manic din, then spurred on by the rival calls of conspecific (same species) competitors. Gathered around a huge clump of spinifex grass, the three of us pointed through the blackness to where we thought the creature was; a process of triangulation to more accurately pinpoint where the sound was coming from. Under the low orange glow of a head torch, we peered down through the spiky blades.

I was part of a team of biologists sent to the Prince Regent Nature Reserve in the remote wilderness of the north-western Kimberley. One of a number of expeditions set up to record and collect the biodiversity of this ancient and isolated corner of Australia, our emphasis was on discovering new species, of which there were plenty. The frog fauna was of particular importance to survey before the anticipated arrival of



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the cane toad. On this trip, the "Holy Grail" for the herpetologists such as myself was to bring back a call recording of a new species of frog that had just been described by the curator of herpetology at the Western Australian Museum. He had collected some specimens the previous year, and an analysis of morphology – what the animal looks like – and DNA had confirmed their distinctiveness from other Kimberley frogs. What we needed now was information on the call, only emitted by males to attract females, because frog calls are hugely important for telling species apart, both for the humans who study them and the animals themselves.

Being the middle of the wet season, the only way to get our team of biologists there was by helicopter. Our supplies had been driven in months before the monsoon started. We had two weeks to try to locate this new frog, at night, by its unique call, which none of us had ever heard before. It was a tough gig. So this is how I came to be on an exposed rock face, hundreds of kilometres from anywhere, late at night in the pouring rain, leaning over a clump of spinifex grass where a little frog was causing a big stir.

We carefully unpacked the recording equipment and set up the microphone, pushing the end into the frog's grassy studio. All our lights were turned out again and we held our breaths. As the minutes ticked over on the recorder, the pulse of his call lighting up on the screen, we beamed in the darkness. This was it. We had the call of the new

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1. What is an ephemeral wetland?
2. Do babies have more or less bones than adults?
3. How do vultures keep their legs cool?
4. How many orbits does the International Space Station complete per day? a) One. b) none, it is stationary. c) Less than 10. d) More than 10.
5. Which of the seven continents has the oldest rocks?

1. A wetland that only appears when it rains. 2. The song, *Don't Stop Believin'*, goes for a lot longer as a baby because they have about 90 more bones. A number of them fuse together to leave the 206 bones that the average adult has. 3. By urinating on them. They also projectile vomit their stomach acid to defend themselves against predators. Charming. 4. d. The ISS travels about 27,724 km/h, completing about 157 orbits per day. That's one fast spacewalk! 5. Australia. About 45 per cent of Australian land and more than 90 per cent of its marine area have never been comprehensively studied by scientists. A new initiative called Bush Blitz aims to tackle these understudied areas and is expected to discover hundreds of new species of flora and fauna.

species. It was necessary to collect the frog, as the specimen was to be lodged in the museum along with its call to aid in future scientific research on this species. Just as we were preparing to put the animal in a bag, the curator paused. A look of horror set across his face. It had just dawned on him that in this northern part of Australia this might be the black-shinned rocket frog and not the new species. Gingerly, he held on to

its foot, and extended the little frog's leg out behind him. It had a black shin.

My excitement was shattered, and my body exhausted. It was going to be a rough night sleeping on the rocks. I crawled into my tent and tossed my field clothes into the corner, dried from the rain but drenched in sweat, knowing I would have to put the same ones on again in a few hours' time. The life of a field biologist is far from glamorous. And we didn't even have the new species to make up for it.

I had to fly out of Prince Regent early, to make room for another biologist interested in crocodiles. The last time I saw my colleagues, we had been flying through the building winds of an oncoming cyclone, the rain pelting into the convex windshield. We dropped them off on a drenched rocky platform, to spend another wet night searching for the frog. I waved goodbye through the misty window, while they covered beneath a tiny overhang, waiting for the rain to ease. They never did get the call recording they needed.

I received a phone call a few weeks ago. On returning to the Western Australian Museum, the curator had located some old call recordings of the black-shinned rocket frog and compared them to the calls we had collected near the sinkhole. The pitch and pulse rate were different. The body size of the new specimens was smaller, and the markings were dissimilar. I was chuffed. It wasn't the frog we had been looking for, but we had a new species after all.

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Special breed of gecko has twists in the tale

A short drive down the rutted, bumpy track and we come to the next destination of the day. Scouring the remains of generations of garbage, kitchen sinks, ovens, rusty drum barrels and truck tyres, our gaze falls on a neat pile of sheet iron, radiating and glimmering in the midday sun.

This is prime gecko real estate, and exactly what we have been driving around stations in outback north-western Queensland to find. A quick sigh and a "here we go again" and we grab our hats, lizard bags and gloves and jump out of the truck. The tropical air hits you like a swag full of cane toads. Within seconds of opening the door the air-conditioned sanctuary disappears, engulfed by sticky heat and a layer of flies.

There is a trick to catching these geckos, and Professor Craig Moritz along with his student Matt Fujita from the University of California,



Berkeley, are old hands at it. They have been travelling around Australia to some of the finest rubbish tips in the country to find the gecko they're after—*Heteronotia binoei*, or the Bynoe's gecko. These little lizards tell an intriguing story through their genetic history, and it's a story that Moritz has been following for decades.

Common, and with a distribution that covers almost all of Australia, Bynoe's geckos are one of the few geckos you might be lucky enough to see just outside of Canberra. And while some species of gecko are specialised to live in particular habitats, such as on

rocks, up trees, or on sand dunes, the Bynoe's gecko is a habitat generalist, and loves just about anything. But it particularly likes man-made habitats such as rubbish dumps.

The reason the Bynoe's gecko has caused such a stir in the scientific community is because Moritz discovered during his PhD at the Australian National University almost 30 years ago that some populations of Bynoe's gecko consist entirely of females; identical, genetic clones of one another reproducing without the help of males. The phenomenon is called "parthenogenesis" and comes from the Greek *parthenos*, "virgin" and *genesis*, "creation".

While not uncommon in the biological world (lots of plants do it, some insects do it, and some fish do it too), Bynoe's gecko is the only Australian reptile known to do this. The parthenogenetic geckos evolved when two genetically distinct groups of

Bynoe's gecko came into contact and bred, and through a twist of genetic fate ended up with three sets of chromosomes (we only have two).

Geckos are cold-blooded animals and on a cool day they come up through the tin pile to the top layers where they can warm their blood, enabling them to stay active at night so they can go out and hunt for food.

But this day is hot, almost 43 degrees, and this means the geckos move down the pile to be closer to the ground where it's cooler. Our hot day is about to get even hotter, because the closer the geckos are to the bottom of the pile the more tin we have to flip to get to them.

Things start to get serious when we get close to the last piece of tin. Two of us stand on guard, ready to pounce as the bottom sheet is upturned and thrown aside. The geckos are warm, and therefore very, very quick. It only takes them



Heteronotia binoei, or Bynoe's gecko.

Photo: Matthew Fujita

a second to realise they have been discovered, before they make a dash to the nearest cover. The trick is to be fast, but with a gentle hand so you don't crush them in the panic of the moment. If you are quick enough, you can feel their soft, velvety bodies wriggling

beneath your palm, trying to move up between the cracks in your fingers. Too slow and all you may be left with is a tiny squirming tail, like a fish out of water, flapping in the dust.

We don't know how long the parthenogenetic geckos will exist,

and research has shown that in evolutionary time, parthenogenetic organisms don't last long. Their "fleeting existence" relates to the fact that they all are genetically identical. Without the genetic variation and recombination that occurs through the mixing of DNA of the parents through sexual reproduction, the female clones will be far less able to cope with random changes in climate and the environment.

While Bynoe's gecko as a broad species group should persist for millions of years, the premature extinction of the parthenogenetic groups is a far more likely scenario. At least there are some cases where humans may not be entirely to blame.

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The cost of casual sex

Parasites could be responsible for monogamous behaviour in sleepy lizards. You may have recently driven along a country road on a warm day and noticed the odd shadowy slug-like creature slinking across the bitumen. If you look hard enough along the roadside verges, you would also see their crumpled black carcasses, reminiscent of pieces of blown-out tyre, or the silhouette of dried scales flattened against the tar. This is a tragically common end for one of Australia's most recognisable yet socially enigmatic lizards.

The number of common names used to describe these animals is a testament to our familiarity with them. *Tiliqua rugosa*, also called the sleepy lizard, shingleback, stumpy-tail, boggi, two-headed lizard, bobtail or pinecone lizard, is one of the biggest skinks in the world. They have large, robust bodies, short, stumpy legs and can grow to lengths of more than 30cm (not including their bulbous tail, which biologists don't include when measuring lizards). While their evolutionary cousins, the blue-tongues, and most other skinks have smooth, shiny skin, sleepy lizards are distinguished by their extremely large protruding scales that armour their bodies like pointed shingles.

Sleepy lizards share a number of common traits with blue-tongues (both are in the same genus, *Tiliqua*); they are ponderously slow (experiments of running these lizards on a treadmill have identified an average maximum running speed of 2.7km/h) and when threatened or harassed they will inflate their bodies, hiss, gape at the mouth and protrude their flat, purply-blue tongue. While sleepy lizards are variable in colour, in the ACT they are usually black, which makes them difficult to spot on the road, particularly with tree shadows



and mirages in the middle of a glary, hot day. In western areas they tend to be browner in colour, with some individuals in Western Australia displaying bright orange scales, particularly on their heads.

Unlike many other lizards, sleepy lizards are viviparous which means they give birth to live young. This is common in cooler parts of Australia where the incubation of eggs is hindered by low temperatures.

Litters can vary in size from one to three, and the young are so large at birth they can measure up to 20cm long and weigh almost two-thirds of their mother's body weight. While this might seem alarming (particularly to any female readers), the advantage of live bearing is that a mother lizard can warm the embryos within her body as she basks in the sun. By putting a greater amount of effort into producing fewer offspring, she can ensure that her young are better equipped for survival on their own.

Incredibly, the lifespan of a sleepy lizard is thought to be up to 50 years. While this seems amazing in itself, there is another more anthropocentric reason that these reptiles have caused such a stir in the scientific community. Long-lasting, monogamous pairings are uncommon in reptiles, but have been the subject of much research in sleepy lizards, particularly in Professor Michael Bull's laboratory at Flinders University.

It is common in many animal species for both sexes to mate promiscuously with multiple partners (called polygynandry). For males, the advantage of such behaviour is the ability to sire a large quantity of offspring, while

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1. Where would you find the hadley and ferrel cells?
2. How many chromosomes do human cells have?
3. Who or what is the Gaia hypothesis?
4. When you eat hot foods such as chilli peppers you excite your tongue's a) nociceptors, b) leptons or c) prototista.
5. What is a PHEV?

Answers: 1. In the Earth's atmosphere. They are terms used to describe specific weather patterns. 2. Forty-six chromosomes: 22 matching pairs plus the male and female sex chromosomes. 3. Gaia is the term, coined by James Lovelock, to describe the theory that everything on Earth is part of a single, interacting, living system. 4. a) nociceptors. 5. A PHEV is a plug-in hybrid electric vehicle, a car that could one day end up in every Australian driveway. CSIRO engineers have modified PHEVs to carry a 30 amp-hour NiMH battery which is capable of holding a 6kW charge, and a battery charger, to allow the cars to plug into and charge with electricity from the grid or from on-site renewable energy sources.

for females it allows them to be "choosy" and ensure the highest quality of offspring possible. What makes sleepy lizards so intriguing (envious even) is that studies have shown a high proportion of lizards retain the same partner each year, with some pairs recording more than 21 years of continuous partnership. While male and female sleepy lizards spend most of the year apart, they meet up in the same location each spring for six to eight weeks before mating in early November.

Little progress has been made in understanding why sleepy

lizards consistently choose the same partner every year, but one hypothesis is that it may have to do with reducing the opportunity for the transmission of ticks. A number of parasitic tick species commonly infect these lizards, and can have a detrimental effect on both their running speed and their general levels of activity.

Rather like a sexually transmitted disease in humans, the more sexual partners a sleepy lizard has, the greater the risk of higher levels of tick infection. Studies have shown that if a male developed a higher tick load, females were more likely to change partners, and males that had been abandoned by their partners had significantly higher tick loads than those that retained the same partner every year. Maintaining long-term partnerships is clearly advantageous for the health and wellbeing of these charismatic lizards.

The strength of their pair bonds has been illustrated by the repeated observation of sleepy lizards attending the bodies of their recently killed partners (who had died either on the road or in fence wire) for up to two days, tongue-flicking and nudging the dead animal in partner-specific cues.

This is the time of year that these lizards are most active. Sadly, the number of adult lizards killed on the roads every day in summer can have potentially devastating consequences for these socially complex creatures. The next time you drive out on a warm day, look a little harder at the shadows on the road. It might just be a sleepy lizard on its way to reunite with its life-long partner.

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The little Aussie gecko

Hundreds of millions of years ago, when all the continents were fused into a single supercontinent called Pangaea, the ancestors of squamate reptiles (lizards, snakes and worm-like reptiles called amphisbaenids) were evolving. Unlike the dinosaurs that became extinct in the following epochs, squamates diversified into more than 8000 species and today represent a major component of the world's terrestrial biodiversity. Gecko lizards are one of the oldest groups of squamates and have an extremely ancient evolutionary history that spans more than 150 million years.

As Australia eased itself away from its Gondwanan neighbours, with it went a group of geckos that evolved in isolation and radiated into a diverse and spectacular range of species. Australia is a biological "hot spot" for geckos with more than 150 described species, most of which are found nowhere else.

The morphological diversity and evolutionary adaptations of Australian geckos are staggering. You need only flip through a field guide of Australian reptiles to appreciate what 100 million years of evolution can achieve: there are desert geckos with vibrating knobs on the end of their tails; long-limbed rainforest geckos whose tails, when dropped, can audibly squeak as they wriggle around to distract predators; geckos with bright blue mouths and glands in their tails capable of projecting a sticky, white, spider-like web; giant cave-dwelling geckos; geckos that can slough off huge pieces of their skin under your fingertips and escape looking like a chicken fillet; geckos that can reproduce asexually without the need of males; and geckos that look more like snakes, with no trace of front legs and small scaly flaps in place of their hind legs. Understanding what led to this extraordinary diversity is what drives evolutionary biologists such as myself.

My interest in geckos revolves around trying to understand



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how historical changes in the landscape and climate in Australia have shaped their evolution and distribution across the continent. Why do we have so many species? Which parts of Australia have the highest levels of genetic diversity? Has the distribution of this diversity been influenced by mountain ranges or the development of sand deserts?

These sorts of questions can be addressed by identifying the make-up and distribution of genetic variation within geckos. My research has highlighted regions in Australia that have been extremely important for harbouring and maintaining genetic diversity. We know this because both the number of species and the genetic variation within species is much higher in these regions than elsewhere.

Mountainous regions like the Pilbara, Kimberley and Central Ranges have provided habitats for species to take refuge when the climate in central Australia became drier and more hostile over the last 15 million years or so, eventually leading to the establishment of the inland sand deserts. This drastic environmental change must have had a profound effect on the distribution and evolution of geckos in central Australia and my research is helping to understand how.

The demographic history of a species leaves a signature in the genetic make-up of its modern representatives. This means that by looking at the genes of living geckos, scientists can essentially look backwards through time and figure out how big historical populations were, what their genetic make-up was, whether they suffered (and recovered) from large population extinctions and where their ancestors most likely originated. One would expect that because

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2. When viewing the night sky, the stars appear to rotate around what points?
3. Prosopagnosia is the inability to recognise what?
4. What substance should you use to treat a box jellyfish sting?
5. The rate at which the Earth gets hotter with depth (geothermal gradient) in degrees Celsius per kilometre is approximately: a) 5-10, b) 25-30, c) 50-100, d) 150+

Answers 1. Its belly. Thankfully, its intestines are not transparent because they are known to eat their own young. **2.** The celestial poles. **3.** Faces. **4.** Vinegar. The acetic acid inactivates the box jellyfish's nematocytes (needle-like stingers). This prevents the stingers from discharging their poison into the bloodstream. **5.** b. CSIRO researchers have been working on improving drilling into the Earth to use the heat emanating from the core for geothermal energy.

the sand deserts in Australia are geologically very young and have existed for less than one million years, desert geckos will have less genetic diversity because they have not had enough time to accrue as many changes in their DNA.

Proving this hypothesis is relatively straightforward, and a comparison of the DNA from geckos in mountain regions versus deserts shows that this is indeed true. It is also reasonable to expect that the genetic signature of desert geckos should show evidence of population growth around the time the deserts were formed, as species expanded their ranges with the opening of a new environmental niche.

This second hypothesis is not so easy to test, because in order to figure out the timing of past

genetic events ideally you need some sort of fossil with a known age with which to "calibrate" your genetic species tree. What I mean by this is, because we know that some genes evolve at a relatively constant rate over time, if we know the age when one ancestor split from another (which can be determined to some degree with fossils) we can work out how long it takes for a certain amount of genetic change to occur. This "molecular clock" can then be extrapolated to date any part of the species' genetic family tree.

The oldest unequivocal gecko fossil was excavated in 2001 from Burma. The fossil consists of a leg, a foot and a partial tail preserved in amber, and is thought to be about 100 million years old. The scientific value of this fossil is immense. Not only does it provide concrete evidence that geckos were in Asia by the middle Cretaceous, the immaculately preserved toes show that the sophisticated adhesive toe-pads of many modern geckos had already evolved by this time. Perhaps most importantly for my research however, is that this fossil provides a calibration for my molecular clock, so I can figure out whether the desert geckos are the same age as the deserts themselves.

Unfortunately the life of a PhD student doesn't always involve field trips to remote parts of Australia. Currently I am office-bound, passing the days editing strings of genetic data on my computer screen and analysing it using complicated algorithms that attempt to mathematically model the fantastic intricacy of biological reality. In a few days my computer will finish running these analyses, and I should know how my molecular clock has kept the time.

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Where biologists dare



MITZY PEPPER

As an evolutionary and field biologist, my research takes me all over the country looking for gecko lizards. From the dunes of the great inland deserts, to the rugged plateaus of the Pilbara and Kimberley and drenched forests of the far north coast, I catch geckos to get samples of their DNA for genetic studies. This research reveals how many different species there are, how they are related, and what sort of forces (for example climatic or biological) drove them down their unique evolutionary pathways.

The study is not only interesting, but is crucial for assessing the conservation status of vulnerable species, and predicting how populations might respond to future changes in climate and fragmentation of their habitat by comparing the present with the past.

Geckos make up just a fraction of the biodiversity we have in this country. Scientists estimate Australia has more than one million plant and animal species, many of which are so far undescribed or yet to be discovered. All over the continent, there are biologists devoting their lives to identify, categorise and describe this plethora of organisms, no matter how insignificant some might initially appear.

To the non-biologist, these scientists may seem to have personalities as eccentric and colourful as the organisms they study, but their understanding of the biology of their study species is often unheralded, sometimes backed by decades of research and experience. Spending time in the field with these biologists is mind-blowing, particularly because knowledge leads to understanding things we didn't even see.

Vince Kessner is a snail man. He knows more about snails than almost any other person in the country. A medic as well as a scientist, Kessner has worked with the world expert on snails, the late Alan Solem, and has spent the last 30 years of his life collecting and studying these peculiar molluscs. Australia has an extraordinary radiation of native land snails with an estimated 2000 species, from small, desert-dwelling varieties to giant forest snails with shells the size of tennis balls.

I met Kessner in the remote north-west Kimberley, and decided to spend a night out with him to see exactly what it is that someone interested in snails gets up to after dark. What I discovered was nothing short of amazing. We flew by helicopter to a remote gorge filled with overgrown vine thickets late in the afternoon, and were dropped off on a sandstone pavement where the rock-faces were decorated with ghostly silhouettes from ancient indigenous artists. As the sun disappeared, we set out with head-torches and calico bags, squeezing our way through the



A rare fungus - *Gloeophyllum concentricum* - found only in tropical Australia. Photo: Matthew Barrett

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1. What feature of a daddy long-leg's web traps its prey - its structure or its stickiness?
2. The haemoglobin in our blood contains iron for capturing oxygen. Which metal does this job for the haemocyanin in insect blood?
3. Is the Tasmanian devil's vision more suited to the day or night?
4. If you see a bolt of lightning and

tangled forest. We were looking for a species of Hadra snail that has never been seen alive. The species was described almost 30 years ago from a number of faded, brittle shells, and Kessner has been searching for them ever since.

Long after dark, the humidity in the gorge was nearly 100 per cent. The webs of gigantic orb-weaving spiders wisped across

hear thunder nine seconds later, how far away is the storm?

5. Immediately after feeding, the vampire bat excretes which part of its meal before take-off?

Answers: 1. Its structure. Their web contains no adhesive properties but has an irregular structure that tangles insects. 2. Copper. Haemocyanin carries the oxygen in the "blood" (hemolymph) of some arthropods. It gives the blood a blue (cyan) colour. 3. Night. Their vision is strongest in black and white, which aids in the detection of movement. 4. About 3km. It takes about three seconds for sound to travel 1km through the atmosphere. 5. Plasma (it has little nutritional value). Within two minutes of sucking the blood of its victims, it excretes plasma-rich urine in order to become light enough to take-off again. Otherwise, it would be a wee-bit heavy.

my face and heavy flying insects, attracted by the light of my head torch, pelted into my forehead. As we picked our way up the gorge, oversized millipedes and hairy, bird-sized tarantulas scurried over the leaf litter.

After three uncomfortable hours of searching, and with only snails common to the area in our bags, I was beginning to wonder if the Hadra would

remain a scientific mystery. Well, it turned out that they liked to come out last. Deep in the gorge, creeping across the moist rocks, they finally appeared. It is impossible to convey the elation in the vine thicket that night. In our torchlight, the Hadra's robust shells glowed like gold. And to Kessner, they were just as precious.

Meanwhile, Dr Matthew Barrett is a botanist and evolutionary biologist. He and his brother were raised on a cattle station in the Kimberley that forged a life-long biological obsession with the ancient landscape. During the time I spent with Barrett in the Kimberley, there was barely a plant he wasn't able to immediately identify, before rattling off the evolutionary and taxonomic history, close relatives, and medicinal uses.

In the right company, the surrounding landscapes can be unbelievably interesting, and the plant life told a story of ancient connections with Gondwana, and recent immigrants from the collision of the Australian plate with Asia. The only plants Barrett was unable to identify inevitably turned out to be one of the 15 or so new species he and his brother discovered during our two weeks in the remote Prince Regent Nature Reserve. Over the course of 15 years, this extraordinary young duo have discovered more than 150 species new to science in some of the most remote parts of the Kimberley.

Barrett's other passion is studying fungi. I spent a day helping him collect the fan, ball, club, and cap shaped fruit bodies that fungi send up after rain. Most people will be familiar with mushrooms. The fungi itself is actually a network of microscopically thin fibres that spread through the soil making up more than 90 per cent of the organism, while the mushroom is just the fruit structure that produces and disperses spores.

The fungi in the Kimberley are incredibly diverse, and during the wet season they put on a magical show of colours and textures, if you're prepared to search for them. We spent more than seven hours on our hands and knees in a patch of vine thicket no more than 50m long, and found more than 50 different species. I even found a species that had never been seen in Australia before. Not bad for a gecko biologist!

The lengths Kessner and Barrett go for scientific advancement is hugely admirable. This type of scientific fieldwork is definitely not for everyone. But it's a very good thing people like them are happy to do it. Just last week, a United Nations report on the global biodiversity outlook painted a dire picture of the accelerating extinction rates of plants and animals around the world. Unfortunately, these are only the ones we know about already.

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Burton's legless lizard, *Lialis burtonis*, one of four species of legless lizard found in the ACT. Two other species, the striped legless lizard and the pink-tailed legless lizard, are considered threatened species.

Spare a thought for lizards

I was crouched in the red dust, squinting down the hole in the ground to the murky bottom of the pit trap. In among pieces of crumbly earth I could just make out the shapes of some of last night's visitors circling the bottom of the plastic pit. I reached into my pockets to retrieve a number of calico animal bags and diligently scribbled the number of the pit trap on the bottom corner.

Working with the Western Australian Museum, I was lending a hand to the Department of Environment on a biological survey of the Pilbara region in the remote wilderness of north-western Australia.

These traps were set up to capture all sorts of ground-dwelling animals in the Pilbara so that biologists could try to get a first grasp on the levels of biodiversity that existed in this mysterious and ancient landscape.

There are many reasons why it pays to be prudent before thrusting a naked hand down the bottom of a pit trap. For starters, arthropods (like insects and spiders) seem to quadruple in size in the desert, and many have adopted a fiery attitude to match: colossal orange and black scolopendrid centipedes the width of your index finger, with 21 pairs of thick, pointed yellow legs and two huge black fangs to top off the "scary" effect, and giant scorpions and hairy black spiders the size of small rodents, with sharp tail spikes or pointed fangs that clink against my field tweezers as if they too were made of metal.



MITZY PEPPER

Even the humble crickets look like they're on steroids and are capable of inflicting a painful bite.

As well as the odd beetle trampling awkwardly in circles, in this particular pit trap there was something long, thin and shiny coiled on the bottom. In the middle of the desert, a bite from one of Australia's many venomous snakes could be unpleasant, at best, or potentially deadly.

With a small pocket mirror I reflected the sunlight down towards the animal to get a better look. And then I saw the strange creature shoot out its tongue and wipe its eyeball. Relieved, I tore off my glove and stuck my eager hand into the pit, knowing this animal would cause me no harm.

Australia is home to a group of "legless" lizards called the *Pygopodidae*. Over evolutionary time, these lizards have lost all traces of front legs, and each hind leg has been reduced to a toothless, scaly flap that is almost invisible in some species. They were first described in 1804 after a French expedition led by Nicolas Baudin was sent to map the coastline of Australia from 1800 to 1803 and brought back six specimens. Today there are 38 described species, with 36 of those found only in Australia.

Because of their limblessness

and long slender bodies, these lizards superficially look like small snakes, but there are a number of key differences that set them apart. Most obviously, almost all *Pygopods* have two visible external ear openings, whereas snakes completely lack these features. Secondly, rather than having a slender, forked tongue, *Pygopods* have a short, thick tongue which they use like windshield wipers to clean their transparent, fixed eyelids. And lastly, while snakes have very short tails compared to their overall length, *Pygopods* have much longer tails, that can sometimes be as much as 400 per cent longer than their bodies.

Interestingly, genetic research on Australian reptiles has revealed that *Pygopods* are most closely related to gecko lizards. Furthermore, it appears that one particular group of Australian geckos is more closely related to *Pygopods* than to other geckos elsewhere in the world.

Perhaps because *Pygopods* are inconspicuous and seemingly uncharismatic, biologists know very little about their life history. We do know that they lay two leathery eggs and can live up to seven years in captivity. While most *Pygopods* eat arthropods, some feed almost exclusively on small lizards, while others are specialised to eat only scorpions or only spiders.

The ACT is home to four species of *Pygopod*. Two of these, Burton's legless lizard (*Lialis burtonis*) and the common delma (*Delma inornata*) are seen regularly, and can generally be encountered by

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2. Prions are a a) type of virus b) type of protein c) type of car.
3. If the Sun became a black hole of equal mass, what would happen to Earth?
4. If you injured your L3 vertebra, what might your doctor take an X-ray of?
5. When was the first camel brought to Australia?

Answers: 1. The same colour as any other full moon – a blue moon refers to the second full moon in a month. 2. b) a type of protein. 3. Aside from growing cold, absolutely nothing. As long as the Sun has the same mass it will still have the same amount of gravity (just concentrated into a very small space). 4. The small of your back. Vertebrae are your backbones; L stands for "lumbar", and there are five lumbar vertebrae boxes. 5. "Hairy" the dromedary was brought to Australia in 1840, but it would be another 20 years before they were imported in large numbers. Today, Australia has the world's largest feral population of dromedary camels, which are considered to be a major pest.

parapulchella), are considered threatened species in the ACT under the Environment Protection and Biodiversity Conservation Act. Sadly, much of their open grassland habitat has either degraded under the hooves of livestock or disappeared beneath the vast footprints of commercial and other land-hungry developments with their associated bitumen surfaces. With only 0.5 per cent of temperate lowland grasslands in south-eastern Australia remaining in semi-natural condition, the story is much the same for another lizard, the grassland earless dragon (*Tympanocryptis pinguicolla*), now considered endangered in the ACT.

The ACT is running out of land and what undeveloped portions remain will come under ever-increasing pressure for uses that are incompatible with the specialised habitat of these unique creatures.

As much as people are concerned about the plight of the un-endangered and highly mobile kangaroo, spare a thought for the legless lizards that have nowhere else to go. History demonstrates that scientific knowledge without informed public support is insufficient to ensure the survival of a species.

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scratching around in the leaf litter beneath logs and grasses. Two other species, the striped legless lizard (*Delma impar*) and the pink-tailed legless lizard (*Aprasia*

"Make them like me adorers of the good science of rock-breaking." □

- Charles Darwin (giving advice to Charles Lyell)