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Molecular Biogeography of Australian and New Zealand Reptiles and Amphibians

Mitzy Pepper, J. Scott Keogh and David G. Chapple

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Introduction

Reptiles and amphibians are a major and ubiquitous component of the vertebrate fauna of Australia and New Zealand. They are found across all biomes and in environments as diverse as rainforests, snow-capped peaks, arid salt pans and desert dune fields. Despite the proximity of Australia and New Zealand (~1500 km), these adjacent landmasses belong to separate continents (New Zealand is part of the largely submerged subcontinent Zealandia). Thus, the taxonomic composition and evolutionary origins of the herpetofauna are markedly different; Australia is a large, ancient continent with subdued topography and a vast, arid centre, while New Zealand is a comparatively young, geologically active group of oceanic islands, with high altitude peaks and plateaus and extensive alpine habitats. Global tectonic processes, such as the breakup of Gondwana, have shaped the higher-level herpetological composition and diversity of Australia and New Zealand, while recent climatic fluctuations and associated vegetation changes have fuelled adaptive radiations in different groups (Morton and James 1988; Byrne *et al.* 2008; Marin *et al.* 2013).

Compared with current world figures, the number of reptile and amphibian families in Australia is low. Australia has only one of the three major groups of living amphibians – the order Anura, comprising frogs and toads (Table 12.1). The number of squamate (snakes and lizards) families in Australia is also low by world standards, with just 7 of approximately 37 lizard families, and 5 or 6 of 26 snake families (Table 12.1). With the exception of the legless geckos (Pygopodidae), these families are all represented elsewhere in the world (Hutchinson and Donnellan 1993). Of the 12 freshwater turtle families, 2 are found in Australia, while crocodylians are the only represented family of

TABLE 12.1

Summary of Molecular Studies of Australian and New Zealand Reptiles and Amphibians since 1990

Region	Taxon	Genera (*n*)	Species (*n*)	Origin	Origin Reference	Phylogeography Reference
	Iguania					
Australia	Agamidae	15	81	Southeast Asia	Macey *et al.* 2000; Honda *et al.* 2000b; Melville *et al.* 2001; Hugall and Lee 2004; Amer and Kumazawa 2005; Hugall *et al.* 2008; Schulte *et al.* 2003	Scott and Keogh 2000 (*Tympanocryptis*); Melville *et al.* 2001 (*Ctenophorus*), 2008 (*Ctenophorus/Rankinia*), 2011 (*Amphibolurus/Lophognathus*); Shoo *et al.* 2008 (*Tympanocryptis*); Edwards and Melville 2011 (*Diporiphora*); Smith *et al.* 2011 (*Diporiphora*); Ng *et al.* 2013 (*Rankinia*); Pepper *et al.* 2014 (*Amphibolurus*)
	Gekkota				Donnellan *et al.* 1999; Han *et al.* 2004; Gamble *et al.* 2008	
Australia	Gekkonidae	7	47	Southeast Asia	Strasburg and Kearney 2005; Jackman *et al.* 2008; Heinicke *et al.* 2010, 2011; Wood *et al.* 2012	Kearney *et al.* 2003 (*Heteronotia*); Heinicke *et al.* 2010 (*Nactus*); Fujita *et al.* 2010 (*Heteronotia*); Pepper *et al.* 2011b, 2013b (*Heteronotia*); Sistrom *et al.* 2013, 2014 (*Gehyra*)
Australia	Diplodactylidae	17	105	Gondwana	Melville *et al.* 2004; Oliver *et al.* 2007, 2012a,b; Oliver and Sanders 2009; Oliver and Bauer 2011	Hoskin *et al.* 2003 (*Orraya/Phyllurus/Saltuarius*); Melville *et al.* 2004 (*Strophurus*); Pepper *et al.* 2006, 2008 (*Diplodactylus*); Oliver *et al.* 2007 (*Diplodactylus*), 2010, 2013a (*Credadactylus*), 2012a, 2014b (*Oedura*), 2013b (*Pseudothecadactylus*), 2014c (*Diplodactylus*); Couper *et al.* 2008 (*Saltuarius*); Pepper *et al.* 2011a (*Rhynchoedura*); Oliver and Bauer 2011 (*Nephrurus*)
Australia	Pygopodidae	7	43	Gondwana	Jennings *et al.* 2003; Heinicke *et al.* 2011; Lee *et al.* 2009; Oliver and Sanders 2009	
	Scincomorpha				Honda *et al.* 2000a; Reeder 2003	
Australia	Scincidae; Egernia	4	49	Southeast Asia	Rabosky *et al.* 2007; Chapple and Keogh 2004; Skinner *et al.* 2011	Donnellan *et al.* 2002 (*Liopholis*); Adams *et al.* 2003 (*Menetia*); Chapple and Keogh 2004 (*Liopholis*); Chapple *et al.* 2005 (*Liopholis*); Gardner *et al.* 2008 (*Egernia* Group); Doughty *et al.* 2011 (*Egernia*)
Australia	Scincidae; Sphenomorphus	17	273	Southeast Asia	Reeder 2003; Skinner *et al.* 2013	O'Connor and Moritz 2003 (*Eulamprus*); Hodges *et al.* 2007 (*Eulamprus*); Rabosky *et al.* 2007, 2009, 2014 (*Ctenotus*); Kay and Keogh 2012 (*Ctenotus*)

Australia	Scincidae; Eugongylus	19	132	Southeast Asia	Smith *et al.* 2007; Stuart-Fox *et al.* 2002	Moussalli *et al.* 2005 (*Saproscincus*); Horner and Adams 2007 (*Cryptoblepharus*); Dolman and Hugall 2008 (*Carlia*); Dubey and Shine 2010 (*Bassiana*); Bell *et al.* 2010 (*Lampropholis*); Chapple *et al.* 2011a,b (*Lampropholis*); Reeder and Reichert 2011 (*Hemiergis*); Haines *et al.* 2014 (*Pseudomoia*)
	Varanoidea				Vidal *et al.* 2012	
Australia	Varanidae	1	29	Southeast Asia	Fuller *et al.* 1998; Ast 2001; Schulte *et al.* 2003; Jennings and Pianka 2004; Fitch *et al.* 2006; Schuett *et al.* 2009; Vidal *et al.* 2012	Fitch *et al.* 2006 (*Varanus*); Smissen *et al.* 2013 (*Varanus*)
	Scolecophidia					
Australia	Typhlopidae	1	43	Gondwana	Rabosky *et al.* 2004 (*Ramphotyphlops*); Marin *et al.* 2013a,b	Marin *et al.* 2013a,b (*Ramphotyphlops*)
	Booidae					
Australia	Pythonidae	4	13	Southeast Asia	Rawlings and Donnellan 2003; Rawlings *et al.* 2004, 2008	Rawlings and Donnellan 2003 (*Morelia*)
	Colubroidea					
Australia	Acrochordidae	1	2	Southeast Asia	Sanders *et al.* 2010	
Australia	Colubridae	5	7	Southeast Asia		
Australia	Elapidae; Hydrophiinae (terrestrial)	26	99	Southeast Asia	Slowinski *et al.* 1997; Keogh 1998; Keogh *et al.* 1998; Scanlon and Lee 2004; Kuch *et al.* 2005; Wuster *et al.* 2005; Williams *et al.* 2008; Kelly *et al.* 2009	Keogh *et al.* 2003 (*Hoplocephalus*); Skinner *et al.* 2005 (*Pseudonaja*); Kuch *et al.* 2005 (*Pseudechis*); Dubey *et al.* 2010 (*Drysdalia*)
Australia	Elapidae; Hydrophiinae (true sea snakes)	12	33	Southeast Asia	Sanders *et al.* 2008, 2013; Sanders and Lee 2008; Rasmussen *et al.* 2014	Lukoschek and Keogh 2006 (sea snakes); Lukoschek *et al.* 2007 (*Aipysurus*)
Australia	Elapidae; Laticaudinae (sea kraits)	1	2	Southeast Asia	Slowinski *et al.* 1997; Keogh 1998; Keogh *et al.* 1998; Scanlon and Lee 2004; Sanders *et al.* 2008, 2013; Sanders and Lee 2008	
Australia	Homalopsidae	4	5	Southeast Asia	Voris *et al.* 2002; Alfaro *et al.* 2004, 2008	

(*Continued*)

TABLE 12.1 (CONTINUED)

Summary of Molecular Studies of Australian and New Zealand Reptiles and Amphibians since 1990

Region	Taxon	Genera (*n*)	Species (*n*)	Origin	Origin Reference	Phylogeography Reference
	Anura					
Australia	Bufonidae	1	1	Introduced	Slade and Moritz 1998	Estoup *et al.* 2004
Australia	Hylidae	2	85	?		McGuigan *et al.* 1998 (*Litoria*); James and Moritz 2000 (*Litoria*); Bell *et al.* 2012 (*Litoria*)
Australia	Microhylidae	2	24	?		Hoskin *et al.* 2011 (*Cophixalus*)
Australia	Myobatrachidae	14	87	Gondwana	Read *et al.* 2001; Edwards 2007	Schauble and Moritz 2001 (*Limnodynastes*); Morgan *et al.* 2007 (*Heleioporus*); Catullo *et al.* 2011, 2014; Catullo and Keogh 2014 (*Uperoleia*)
Australia	Ranidae	1	1	Southeast Asia	Bossuyt *et al.* 2006	
Australia	Limnodynastidae	8	40	Gondwana		
	Testudines				Crawford *et al.* 2014	
Australia	Chelidae	7	24	Gondwana	Le *et al.* 2013; Georges *et al.* 2014; Todd *et al.* 2014a	Todd *et al.* 2013, 2014a (*Elseya*); Todd *et al.* 2014b (*Emydura*); Hodges *et al.* 2014 (*Chelodina*); Georges *et al.* 2014 (*Elseya*)
	Carettochelyidae	1	1	?		
	Crocodilia					
Australia	Crocodylus	1	2	?	Oaks 2011; Brochu and Storrs 2012	

	Anura					
New Zealand	Hylidae	1	3	Introduced (Australia)	Voros *et al.* 2008	
New Zealand	Leiopelmatidae	1	4	Gondwana	Holyoake *et al.* 2001; Roelants and Bossuyt 2005; Irisarri *et al.* 2010; Pyron and Wiens 2011	Fouquet *et al.* 2010
	Rhynchocephalia					
New Zealand	Sphenodontidae	1	1	Gondwana	Rest *et al.* 2003; Hugall *et al.* 2007; Cree 2014	Hay *et al.* 2010
	Gekkota					
New Zealand	Diplodactylidae	7	43	Australia	Nielsen *et al.* 2011	Nielsen *et al.* 2011
	Scincomorpha					
New Zealand	Scincidae; Eugongylus (native)	1	61	New Caledonia	Hickson *et al.* 2000; Smith *et al.* 2007; Chapple *et al.* 2009	Berry and Gleeson 2005; Greaves *et al.* 2007, 2008; Chapple and Patterson 2007; Bell and Patterson 2008; Hare *et al.* 2008; O'Neill *et al.* 2008; Liggins *et al.* 2008a,b; Chapple *et al.* 2008a,b,c, 2011c, 2012; Miller *et al.* 2009; Patterson *et al.* 2013
New Zealand	Scincidae; Eugongylus (introduced)	1	1	Australia (1960s)	Chapple *et al.* 2013	

Note: This table does not include sea turtles or sea snakes that are occasional visitors or vagrants in New Zealand. Nor does it include the red-eared slider. It also does not include new species description papers despite the fact that they often now contain molecular data as part of the description.

crocodiles (Uetz *et al.* 2016). In contrast, at the species level, several widespread groups including skinks (Scincidae), blindsnakes (Typhlopidae), terrestrial elapids and sea snakes (Elapidae), dragons (Agamidae) and goannas (Varanidae) have radiated extensively, with the former three reaching their greatest diversity in Australia (Hutchinson and Donnellan 1993) (Table 12.1). The higher-level herpetological diversity of New Zealand is considerably more depauperate than Australia, comprising just four families. There is a single lineage of frog (with four species), the last remaining species of the reptile order Rhynchocephalia (the tuatara, *Sphenodon punctatus*), one genus of skinks (*Oligosoma*, ~61 species) and seven genera of geckos (~43 species) (Table 12.1). Terrestrial snakes, freshwater turtles and crocodiles are absent. Like Australia, while diversity at higher taxonomic levels is low, species-level diversity in the few lineages of herpetofauna is exceptionally high in New Zealand (Table 12.1).

In the past two decades, the description of new species has increased rapidly worldwide (Bickford *et al.* 2007; Padial *et al.* 2010; Goldstein and DeSalle 2011; Blackwell 2011; Costello *et al.* 2013), fuelled largely by the increasing availability and use of DNA sequence data. While this phenomenon is particularly evident in poorly studied organisms (i.e. fungi; Buee *et al.* 2009) or regions (i.e. New Guinea; Riedel *et al.* 2013), even groups that have received thorough taxonomic assessment continue to herald new discoveries (i.e. mammals, Ceballos and Ehrlich 2009; birds, Lohman *et al.* 2010). In Australia, the number of currently recognised reptile and amphibian species has nearly doubled in the past 40 years, from 664 recognised species in 1975 to more than 1218 species in the most recent catalogue of the Australian herpetofauna (Cogger 2014). While some of this new biodiversity represents morphologically well-differentiated taxa uncovered by fieldwork in unexplored regions (e.g. Hoskin 2013; Hoskin and Couper 2013; Hoskin 2014, from an expedition to the remote Cape Melville), a major consequence of recent molecular assessments is that many previously unrecognised species have been detected within morphologically similar forms that comprise *species complexes* of a larger number of cryptic taxa (Oliver *et al.* 2013a, 2014c). In the Australian herpetofauna, such complexes are particularly well documented in geckos (Oliver *et al.* 2007, 2009, 2010, 2014a,b; Fujita *et al.* 2010; Pepper *et al.* 2011a, 2013a,b; Shea *et al.* 2011; Sistrom *et al.* 2013), but also have been detected in blindsnakes (Marin *et al.* 2013b), skinks (Rabosky *et al.* 2004; Horner and Adams 2007; Smith and Adams 2007; Dolman and Hugall 2008), dragons (Smith *et al.* 2011) and frogs (Catullo *et al.* 2011, 2014). A similar story has unfolded in New Zealand, first with allozyme electrophoresis data and later mitochondrial and nuclear DNA sequence data uncovering cryptic species within several widespread New Zealand skinks (Daugherty *et al.* 1990; Patterson and Daugherty 1990; Greaves *et al.* 2007, 2008; Chapple *et al.* 2008a,b, 2009, 2011; Bell and Patterson 2008; Chapple and Ritchie 2013; Patterson *et al.* 2013) and geckos (Nielsen *et al.* 2011). However, much of the recognised lizard biodiversity (~45%) in New Zealand remains to be formally described (Hitchmough *et al.* 2013).

Data from molecular genetics can play a major role in our understanding of patterns of species richness on global, regional and local scales. The herpetofauna in particular provide an excellent system for exploring evolutionary and biogeographic hypotheses (Vitt *et al.* 2003), due to their age (an overwhelming proportion of the anuran and chelonian faunas are Gondwanan), extreme diversity, near-worldwide distribution and the dispersal ability of many taxa across oceanic basins (Vences *et al.* 2003; Rocha *et al.* 2006). The broad-level biogeography of the Australian and New Zealand herpetofauna has been addressed previously in several important publications (i.e. Storr 1964; Cogger and Heatwole 1981; Cracraft 1991; Hutchinson and Donnellan 1993; Merrick *et al.* 2006 and references within). However, as molecular approaches have driven our recent enhanced understanding of the diversity and distribution of the Australian and New Zealand herpetofauna, it is timely to reconsider their biogeographic patterns. In this chapter, we summarise our current understanding of the biogeography of Australian and New Zealand herpetofauna based on molecular data and new analytical methods, with an emphasis on intracontinental distributional and phylogeographic patterns. We focus on regions rather than biogeographical accounts by families in order to showcase the contribution of reptiles and amphibians to improving our understanding of broader evolutionary patterns and processes emerging in these regions. We begin with an overview of the geophysical and climatic history of Australia and New Zealand to provide important context within which to interpret modern biogeographical patterns of the herpetofauna.

Major Geologic and Climatic Determinants Underlying Patterns in Herpetological Biodiversity

An understanding of earth history is crucial to any discussion of biogeographic patterns and undoubtedly goes a long way towards explaining present species richness and evolutionary history. For example, the large-scale movement of continents over geologic time has been the principal explanation for global distribution patterns of organisms (Craw *et al.* 1999). At the regional scale, it also is well known that geology and geophysical processes play a major role in shaping the evolutionary dynamics of organisms. Tectonic uplift can drive diversification both by creating new habitats and isolating populations on either side of mountain ranges (Hughes and Eastwood 2006). Similarly, vicariance processes involving river barriers (Hall and Harvey 2002) or the intermittent connection of land bridges (Riddle *et al.* 2000) also impact on evolutionary dynamics. At the local scale, the importance of geological heterogeneity in shaping plant diversification and distribution patterns via edaphic specialisation is widely recognised (Kruckeberg 2002; Fine *et al.* 2005), with colour variations in animals also related to variations in geological substrates (Rosenblum and Harmon 2011). As a general rule, geological diversity (and therefore habitat heterogeneity) is positively correlated to species richness (Anderson and Feree 2010).

In addition to geological processes, historical climate change also drives speciation and biotic diversification (Hewitt 1996, 2000). Global climate has fluctuated greatly through the Cenozoic, particularly from the mid-Neogene (23.0–2.5 mya) and throughout the Quaternary (2.5 mya–present), when rapid global cooling led to diminishing precipitation and the instigation of sharply oscillating temperatures of the glacial and interglacial cycles of the Pleistocene. The expansion and contraction of different habitats during these climatic oscillations led to great changes in species distributions (Hewitt 2000), with the persistence and diversification of some lineages in refugia allowing populations to evolve independently with limited gene flow, facilitating biotic diversification and speciation. This phenomenon has been well documented in herpetofauna (and other taxa) across all biomes, including in boreal (i.e. Ursenbacher *et al.* 2006), tropical (i.e. Schauble and Moritz 2001), temperate (i.e. Chapple *et al.* 2011a,b) and arid systems (i.e. Pepper *et al.* 2011b).

Australia and New Zealand both have a long tectonic history following the breakup of Gondwana, and more than 80 Ma of subsequent geographic isolation. However, given they are characterised by strikingly different modern-day environments and palaeogeological histories, they are addressed separately in the following sections.

Australia: An Old and Stable Continent

The Australian continent possesses the oldest known materials on earth, as well as the oldest landforms (Gale 1992). Many features of the landscape have been geologically stable for tens of millions of years (Gale 1992; Twidale 2000), and as a result Australia's 'mountainous' regions are considerably more subdued than those of other continents, and these have been progressively eroding, with little in the way of modern tectonic uplift. Recent tectonic events have been confined largely to the leading edge of the Australia–New Guinea Plate (Hill and Hall 2002).

Modern surface landforms across Australia are directly influenced by the underlying geology. For example, the western two-thirds of Australia is situated on higher-elevation regions associated with the Western Plateau (Mabbutt 1988) and comprises a number of inland ranges, including the Pilbara, Kimberley and central Australian ranges (Wasson 1982). These regions are ancient, uplifted exposures of the underlying Australian craton, characterised by rugged landscapes of razor-back ridges, scarps and scattered mesas. In contrast, much of eastern Australia is situated on the desert floodplains of the Interior or Central Lowlands (Wasson 1982; Mabbutt 1988). This landscape is low-lying with little topographic variation, and is dominated by the extensive Lake Eyre and Murray–Darling Basins. The main topographic feature of eastern Australia is the Great Dividing Range (GDR), stretching more than 3500 km down the entire eastern coast. While the timing of the uplift of these eastern highlands is contentious, with various hypotheses ranging from the Palaeozoic to the Cenozoic (Van der Beek *et al.*

1999), substantial uplift along this mountain chain is almost certainly related to the Cretaceous rifting of the Tasman Sea ~94 mya (O'Sullivan *et al.* 2000).

Despite the apparent antiquity of the landscapes, the Australian continent has had a dynamic tectonic history during the Cenozoic, having migrated more than 3000 km to the north-northeast over the past 45 Ma as part of the Indo-Australian Plate (Quigley *et al.* 2010). This greatly increased convergence between the Australian and Pacific Plates lead to the immigration of lineages with Southeast Asian origins, to an Australian biota that had previously evolved in isolation since separation from Antarctica (discussed in more detail later in the chapter).

The biggest change in more recent Australian history has undoubtedly been the aridification of the continental interior, with vast inland seas and tropical ecosystems replaced over the last 15 Ma by increasingly arid landscapes and ecosystems (Frakes *et al.* 1987; Fujioka and Chappell 2010). The height of arid conditions in Australia appears to correlate with the transition from high-frequency, low-amplitude glaciations (every 40 ka) that characterised 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 and dune systems (Bowler 1976; Frakes *et al.* 1987; Mabbutt 1988; Martin 2006; Fujioka *et al.* 2009; McLaren and Wallace 2010) as recently as 1 mya (Fujioka *et al.* 2009). The mesic fringes of Australia were not immune to the influence of aridification, with palaeoenvironmental evidence suggesting much drier conditions in the tropical north of Australia during Pleistocene glacial cycles, in conjunction with cooler temperatures, especially in lowland regions (Reeves *et al.* 2013a). Evidence of extensive sand dune activity also has been discovered beneath presently forested regions along the humid margins of eastern Australia, indicating substantially drier conditions during the Last Glacial Maximum (LGM) (Thom *et al.* 1994; Hesse *et al.* 2004). While on many continents glacial cycles of the Pleistocene promoted widespread glaciation, in Australia the Koskiuszko Massif in the Snowy Mountains of New South Wales and the Tasmanian Highlands are thought to be the only regions affected by glacial activity during this period (Barrows *et al.* 2002).

New Zealand: A Gondwanan Fragment with a Post-Oligocene Makeover

In contrast to Australia, New Zealand has had a complex and tumultuous geological and climatic history. Due to the quirks of its evolutionary history, New Zealand displays the blended characteristics of both a continental fragment, with Gondwanan heritage, and an isolated oceanic archipelago (Daugherty *et al.* 1993; Gibbs 2006; reviewed in Wallis and Trewick 2009). Zealandia separated from Gondwana ~82 mya, with the formation of the Tasman Sea by ~65 mya resulting in the 1500 km isolation of New Zealand from Australia, which has been maintained through to the present day (Cooper and Millener 1993; Gibbs 2006; Campbell and Hutching 2007; Wallis and Trewick 2009). Over 40 Ma (64–24 mya) Zealandia was slowly stretched and thinned, which resulted in the substantial thinning of the continental crust and the gradual subsidence and marine inundation of New Zealand (Gibbs 2006; Trewick *et al.* 2007; Landis *et al.* 2008; Neall and Trewick 2008; Wallis and Trewick 2009). While there is consensus that this marine inundation reached its peak in the Oligocene with the Oligocene transgression (or *Oligocene drowning*; Suggate *et al.* 1978; Cooper and Millener 1993; Gibbs 2006; Wallis and Trewick 2009), there is considerable debate as to whether New Zealand was completely submerged (e.g. Trewick *et al.* 2007; Landis *et al.* 2008) or simply reduced to a series of low-lying islands (e.g. Cooper and Cooper 1995; Lee *et al.* 2009).

The rebirth of New Zealand following the Oligocene drowning has been driven by tectonic and volcanic activity. New Zealand is situated at the boundary of the Pacific and Indo-Australian Plates, and continual uplift along the Alpine Fault (running southwest–northeast along the majority of the South Island) since the Late Oligocene (~25–23 mya) has led to the formation of modern New Zealand (Gibbs 2006; Trewick *et al.* 2007; Landis *et al.* 2008). Volcanic activity associated with this tectonism occurred until 13 mya in the South Island and until the present day in the North Island (Wallis and Trewick 2009). The Southern Alps that currently characterise the South Island are the result of tectonic activity along the Alpine Fault that commenced during the Miocene and intensified during the Pliocene (Gage 1980; Suggate 1982; Stevens *et al.* 1995; Landis *et al.* 2008). During this time, severe tectonic uplift (up to

16 km, 2–11 mm/year; Wellman 1979) has been countered by high rates of erosion (up to 12 km; Craw 1995), but has still resulted in the formation of prominent, high-elevation regions (>3000 m) within the Southern Alps (Chamberlain *et al.* 1999; Lee *et al.* 2001; Gibbs 2006; Wallis and Trewick 2009). The stable warm-/cool-temperate climate that had prevailed since the Oligocene (Fleming 1975; Cooper and Millener 1993; Lee *et al.* 2001) eventually gave way in the Late Pliocene to rapid cooling that continued through to Pleistocene glacial cycles (Cooper and Millener 1993; Newnham *et al.* 1999). While large areas of the South Island (up to 30%) were covered by glaciers during the Pleistocene, the North Island was not subjected to any extensive glaciation (Newnham *et al.* 1999; Carter 2005). Despite the post-Oligocene topographic makeover of New Zealand, episodes of regional marine inundation have still occurred during the Pliocene (Manawatu Strait [the inundation of the lower North Island]) and Pleistocene (Northland, Cook Strait [separating the North Island and South Island]; Foveaux Strait [separating the South Island and Stewart Island]) (Lewis *et al.* 1994; Worthy and Holdaway 2002).

Recapitulating Biogeographical Origins with Molecular Data

A number of authors have previously reviewed the age, origin and regional affinities of the Australian and New Zealand herpetofauna (e.g. Storr 1964; Cogger and Heatwole 1981; Cracraft 1991; Hutchinson and Donnellan 1993; Table 12.1). These evolutionary hypotheses have been based largely on species distribution/area relationships and fossils, in combination with geological and climate history. More than two decades of subsequent research, in particular ever-increasing amounts of molecular data as well as increased taxonomic effort, has seen many of these ideas tested in a phylogenetic framework (Table 12.1).

For example, it has long been considered that the Australian squamate fauna consists predominantly of Indo-Malay lineages, with major adaptive radiations within Australia of elapid snakes and diplodactyline geckos, as well as major lizard groups of the agamids, varanids and skinks thought to be derived from ancestors that arrived no later than the mid-Tertiary (Cogger and Heatwole 1981; Figure 12.1). Recent genetic data from agamids (Hugall *et al.* 2008) confirmed this using mitochondrial and nuclear loci, suggesting agamids immigrated into Australia from Southeast Asia via northern mesic forest biomes within the last 30 Ma, with diversification initially within mesic habitats followed by radiations of xeric taxa into the emerging arid zone. Scincid lizards in the clade Lygosominae also are thought to have dispersed on multiple occasions to Australia from Southeast Asia within the last 25 Ma, subsequent to the rifting of Australia and Antarctica (Skinner *et al.* 2011). Similarly, varanids appear to have dispersed to Australia from Southeast Asia in the Late Eocene/Oligocene around 32 mya (Vidal *et al.* 2012), while the venomous elapid snakes may have arrived from Southeast Asia as recently as 10 mya, and then radiated extensively in both the terrestrial and marine environments (Keogh 1998; Keogh *et al.* 1998, 2001; Lukoscheck and Keogh 2006; Sanders *et al.* 2008). In contrast, the limbless Pygopodidae have long been thought to have a Gondwanan history, owing to their endemicity in the Australian–Papuan region, and fossil evidence that establishes their presence in Australia well before the time when other biotic elements of Asian origin invaded Australia (Hutchinson 1997; Jennings *et al.* 2003). Recent molecular evidence has not only confirmed that pygopodids and diplodactytline geckos are sister groups (Donnellan *et al.* 1999), but in addition indicates much of the Australian gekkonid fauna (carphodactyalids, diplodactylids and pygopodids) comprises ancient Gondwanan lineages estimated to have arisen 70 mya (Oliver and Sanders 2009). Myobatrachid frogs also are a Gondwanan group (Littlejohn *et al.* 1993; Pyron 2014), while the evolutionary history of the Australian hylid frogs is less clear, with some authors suggesting they arrived via long-distance rafting from South America during the Palaeocene/Eocene (Pyron 2014).

The strong affinity between the herpetofauna of Australia and New Guinea has been emphasised (Cogger and Heatwole 1981), with these regions sharing a diverse array of taxa, especially at the generic level (Allison 2006; Menzies 2006; Todd *et al.* 2014a). More detailed examination using phylogenetic data has shed light on the patterns and directions of dispersal between these regions, highlighting differences between herpetofaunal lineages. For example, freshwater turtles in the family Chelidae appear to have dispersed from Australia to New Guinea on multiple occasions during the Miocene and Pliocene

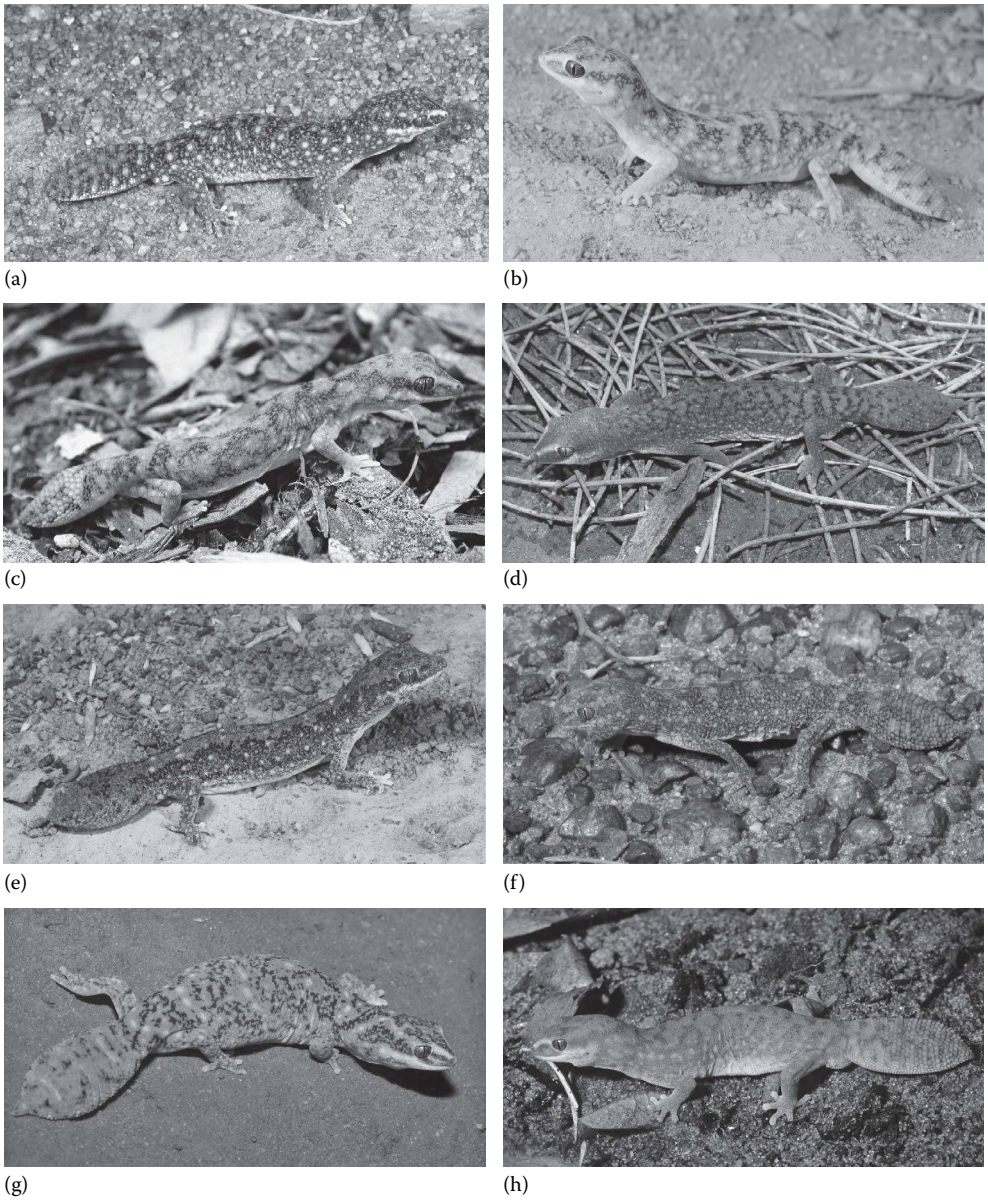

FIGURE 12.1 (See colour insert.) A recently delineated species complex of gecko, formerly *Diplodactylus conspicillatus*. (From Oliver, P. M., *et al.*, *PLoS One*, 2014.) Species of the *D. conspicillatus* complex in life: (a) *D. conspicillatus* from 10 km north of Barkley Hwy on Ranken to Alexander Station Road, northeastern Northern Territory (image: Ross Sadlier); (b) *D. conspicillatus* Alice Springs, Northern Territory (image: Eric Vanderduys); (c) *D. hillii*, Dorat Road, Northern Territory (Image: Paul Horner); (d) *D. laevis* in life from Morgan Range, Western Australia (Image: Mark Hutchinson); (e) *D. platyurus*, Brooklyn Station, north Queensland (Image: Eric Vanderduys); (f) *D. platyurus* Myendetta Stn., Charleville, Queensland (image: Steve Wilson); (g) *D. bilybara* sp. nov. Onslow, Western Australia (image: Ryan Ellis); (h) *D. custos* sp. nov. Gibb River Road turnoff via Wyndham, Western Australia (image: Steve Wilson).

(Le *et al.* 2013; Todd *et al.* 2014), with Papuan members of rainbow skinks (Stuart-Fox *et al.* 2002), elapid snakes (Wuster *et al.* 2005; Williams *et al.* 2008) and forest dragons (Hugall *et al.* 2008) also appearing to be derived from Australian ancestors. In contrast, genetic examples are emerging that also clearly demonstrate Australian lineages that have been derived from New Guinean taxa, such as in the geckos *Cyrtodactylus* (Oliver *et al.* 2012b) and *Nactus* (Heinicke *et al.* 2010).

The New Zealand herpetofauna have played a pivotal role in our understanding of the biogeographic significance of the Oligocene drowning. In the absence of strong geological evidence for the continuous presence of land throughout the Oligocene (reviewed in Landis *et al.* 2008), some authors have suggested that New Zealand was completely submerged (Waters and Craw 2006; Trewick *et al.* 2007; Goldberg *et al.* 2008; reviewed in Wallis and Trewick 2009). However, the presence of Leiopelmatid frogs and the tuatara in New Zealand, two lineages with strong evidence (including molecular data) for Gondwanan origins (Table 12.1) and a limited capacity for long-distance over-water dispersal (Rest *et al.* 2003; Roelants and Bossuyt 2005; Hugall *et al.* 2007; Cree 2014), has formed a central pillar of the evidence for the continued presence of land throughout the Oligocene (Daugherty *et al.* 1993; Wallis and Trewick 2009; Sharma and Wheeler 2013). In contrast, recent molecular studies have indicated diplodactylid geckos colonised New Zealand from Australia during the Oligocene (between 40.2–24.4 mya; Nielsen *et al.* 2011), with Eugongylus group skinks reaching New Zealand from New Caledonia (via the Lord Howe Rise and Norfolk Ridge) during the Early Miocene (24.4 mya, range 16–22.6 mya; Chapple *et al.* 2009) (Table 12.1).

Regional Biogeography: Species Richness and Endemism

At the continental scale, Australia and New Zealand have markedly contrasting biogeographic patterns; Australia generally has large-scale, biome-level patterns, which may be a reflection of widespread climate-driven diversification. In contrast, patterns in the New Zealand herpetofauna exhibit continental-level biogeographic patterns (e.g. deep genetic splits) over short geographic distances, likely influenced by regional and local tectonic or eustatic processes (e.g. the Alpine Fault, Cook Strait, Taupo Line).

Various authors have used ever-increasing database records to identify geographic patterns of endemism and species richness in the herpetofauna of Australia (Pianka and Schall 1981; Cogger and Heatwole 1981; Gambold and Woinarski 1993; Williams and Pearson 1997; Williams and Hero 2001; Slatyer *et al.* 2007; Rosauer *et al.* 2009; Powney *et al.* 2010) and New Zealand (Gibbs 2006; Chapple *et al.* 2009; Nielsen *et al.* 2011; Di Virgilio *et al.* 2014; Cree 2014). As physiological constraints (e.g. the permeable skin of amphibians) strongly influence the biomes and geographic distributions where different taxa are concentrated, centres of species diversity are different between reptiles and amphibians, and even within major groups (Cogger and Heatwole 1981). For example, the greatest amphibian species richness in Australia exists along the humid east and southeast coasts, with major centres of diversity in the Wet Tropics of Queensland, and the coastal region near the Queensland/New South Wales border (Slatyer *et al.* 2007; Powney *et al.* 2010). In contrast, for reptiles, a group thought to be generally preadapted physiologically and behaviourally to xeric conditions (Pianka and Schall 1981), species diversity across many lineages is especially high in the arid zone, particularly geckos and agamids (Cogger and Heatwole 1981; Powney *et al.* 2010). Indeed, the Great Victoria Desert of Western Australia contains the highest diversity of lizards anywhere on earth (Mittermeier *et al.* 1999). In contrast, elapid snakes and scincid lizards have their greatest species diversity along the mesic east coast, while varanid lizards reach their highest species diversity in the Monsoon Tropics of northern Australia (Cogger and Heatwole 1981; Powney *et al.* 2010). In New Zealand, despite some differences between skinks and geckos, species richness and endemism is highest in Northland, Nelson/Marlborough and Otago/Southland (Chapple *et al.* 2009; Nielsen *et al.* 2011; Di Virgilio *et al.* 2014).

Knowledge on the evolutionary history of the herpetofauna of Australia and New Zealand is patchy and variable within and between taxonomic groups and geographic areas. For example, in Australia, considerable molecular systematic research has been focused on the herpetofauna of the mesic areas of the east coast (e.g. McGuigan *et al.* 1998; Schneider *et al.* 1998; James and Moritz 2000; Schauble and Moritz 2001; Stuart-Fox *et al.* 2001; Moussalli *et al.* 2005; Symula *et al.* 2008; Edwards 2010; Bell *et al.* 2011; Chapple *et al.* 2011a,b; Pepper *et al.* 2014) and in the arid zone (Kearney *et al.* 2003; Chapple and Keogh 2004; Chapple *et al.* 2004; Strasburg and Kearney 2005; Pepper *et al.* 2006, 2008, 2011a,b, 2014; Rabosky *et al.* 2014; Oliver and Bauer 2011; Oliver *et al.* 2007). However, some regions of Australia

still remain vastly underexplored in a molecular sense, and it is thought that significant evolutionary diversity is not reflected in current taxonomy (Oliver *et al.* in press). For example, increased taxonomic effort in the remote Monsoon Tropics region of northern Australia is revealing this region to be much more diverse and complex than previously thought, with remarkably high endemism over restricted geographic ranges in a number of lizard genera (reviewed later in this chapter) (Fujita *et al.* 2010; Oliver *et al.* 2010, 2013a, 2014a; Pepper *et al.* 2011b; Smith *et al.* 2011; Marin *et al.* 2013b) as well as in amphibians (Doughty and Anstis 2007; Doughty and Roberts 2008; Doughty *et al.* 2009; Anstis *et al.* 2010; Catullo *et al.* 2014; Oliver and Parkin 2014).

In New Zealand, the biogeographic and phylogeographic patterns have been explored most extensively in skinks (Berry and Gleeson 2005; Chapple and Patterson 2007; Greaves *et al.* 2007, 2008; Hare *et al.* 2008; Liggins *et al.* 2008a,b; O'Neill *et al.* 2008; Chapple *et al.* 2008a,b,c, 2009, 2011c, 2012; Miller *et al.* 2009; Patterson *et al.* 2013; Di Virgilio *et al.* 2014) and the tuatara (Hay *et al.* 2010; Cree 2014), with relatively less attention on the frogs (Holyoake *et al.* 2001; Fouquet *et al.* 2010) and geckos (Towns *et al.* 1985; Nielsen *et al.* 2011; Di Virgilio *et al.* 2014). However, many regions of New Zealand are yet to be explored in detail to assess their herpetological diversity. Recent expeditions to some remote regions (e.g. Jewell and Tocher 2005; Jewell 2007) have uncovered new lizard species (Chapple and Patterson 2007; Bell and Patterson 2008; Patterson and Bell 2009; Chapple *et al.* 2011c), and thus the true herpetological diversity of New Zealand is likely higher than currently recognised.

Patterns within Local Regions of Endemism

Because fossil and geological records are often poor, and palaeoclimate reconstructions for one area are regularly extrapolated and applied to distant geographic regions, phylogenetic data provide an important means to develop and refine hypotheses about when, and how, organisms adapted to and diversified within biomes or regions of endemism. For example, despite the sedimentary hiatus that typically characterises the geological records of xeric landforms, dated molecular studies of arid-zone taxa across the globe show deep divergences in line with the postulated onset and development of aridification, with intensifying aridity, persistence in localised mesic refugia and the movement of mobile sand deserts thought to drive phylogenetic divergences and phylogeographic structuring. Similarly, biogeographic studies in New Zealand have been used in concert with geological evidence to gain a better understanding of the Oligocene drowning (reviewed in Wallis and Trewick 2009), the uplift of the Southern Alps (Liggins *et al.* 2008a; Wallis and Trewick 2009) and the formation of the Chatham Islands (Liggins *et al.* 2008b; Wallis and Trewick 2009). Largely due to their extreme diversity, distribution across multiple biomes and habitats and low vagility, the herpetofauna are an ideal system in which to explore phylogeographic patterns, and as such they are well represented in the phylogeographic literature. In particular, the regular use of common molecular markers (e.g. the mitochondrial loci ND2, ND4 and 16SrRNA, as well as the nuclear loci RAG1 and Cmos) have made it possible to compare the levels and timing of divergences across lineages. In the following sections, we consider the major biomes within both Australia and New Zealand, and use molecular studies of the herpetofauna to characterise shared patterns in order to better understand biome origins, assembly and maintenance.

Australia

Broadly speaking, the Australian continent can be classified into a number of different biogeographical units corresponding to major biome types (i.e. Crisp and Cook 2007). For simplicity, we consider the following four broad regions: the vast central arid zone, the northern Monsoon Tropics, the Eastern Mesic Biome (EMB) and the Southwestern Mesic Biome (SMB) (Catullo and Keogh 2014; Figure 12.2a). Within these broadly defined regions, several authors have identified areas of endemism based on congruent biogeographic patterns of flora and fauna (e.g. Cracraft 1991; Crisp and Cook 2007). However, the relationships between areas of endemism within a given biome have been rather obscure, particularly

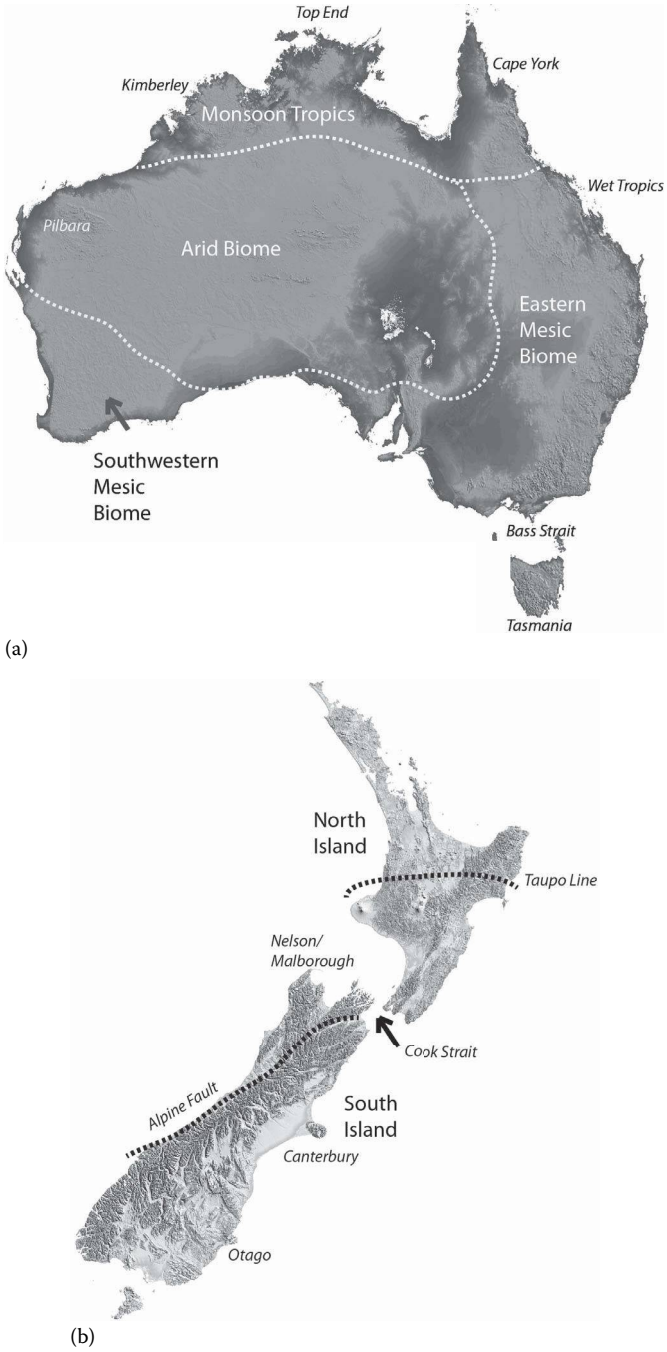

FIGURE 12.2 The location of areas of endemism and biogeographic barriers in (a) Australia and (b) New Zealand mentioned in the text.

for vast areas such as the arid zone (Cracraft 1991). Molecular data based on the sampling of widespread taxa are revealing that biogeographic barriers identifiable at higher taxonomic levels also act at the intraspecific level to restrict gene flow, leading to congruent phylogeographic patterns at finer genetic scales. As such, we are beginning to better understand how genetic diversity is structured within biomes, and the relationships among areas of endemism.

Arid Zone

The Australian arid zone comprises more than 70% of the continent and is one of the largest arid systems in the world. While often portrayed in the literature as a homogeneous region in the centre of Australia, the landscape is considerably more complex and comprises a matrix of different desert systems. While the topography of the region is generally subdued, ancient and isolated rocky uplands occur in the Pilbara, the central Australian ranges and the Flinders ranges. In stark contrast, the vast intervening lowlands comprise stony and sandy deserts, the latter of which are thought to have formed less than a million years ago at the height of the Pleistocene (Fujioka and Chappell 2010). A major geomorphic division separates the western desert systems (the Great Sandy, Little Sandy, Great Victoria, Gibson and Tanami Deserts) formed on the tablelands of the Great Western Plateau, from the eastern desert systems (the Strzelecki, Simpson and Sturts Stony Deserts) and floodplains of the Central-Eastern Lowlands. Importantly for desert organisms, watercourses in the western deserts are thought to have ceased flowing in the Late Miocene (Quilty 1994), while palaeochannels (and indeed current riparian systems and floodplains) in the eastern arid zone indicate the large volume of water that continued to drain from the uplands of the Monsoon Tropics during wet periods.

Cracraft (1991) identified four centres of endemism in the arid zone: the Pilbara, the Western Desert, the Eastern Desert and the Northern Desert, noting that the Western Desert and the Northern Desert were particularly ill-defined. Molecular data from a number of reptile species generally support this cohesion, with distinct lineages in the Pilbara, as well as the topographically differentiated Western and Eastern Deserts (Pepper *et al.* 2011a; Oliver *et al.* 2014c). While sampling is particularly sparse in the Northern Desert, this region also is emerging genetically as a distinct area of endemism (Smith *et al.* 2011; Catullo *et al.* 2014). In addition, genetic data sets accumulating for arid-zone reptiles suggest that range shifts due to climate fluctuations had diverse impacts on genetic structure, with complex phylogeographic patterns indicative of habitat specialisation (Chapple and Keogh 2004; Pepper *et al.* 2006, 2008; Couper and Hoskin 2008; Shoo *et al.* 2008), persistence and diversification within mesic refugia (Fujita *et al.* 2010; Pepper *et al.* 2011a,b), and recent range expansion into the deserts (Jennings *et al.* 2003; Fujita *et al.* 2010; Oliver and Bauer 2011; Pepper *et al.* 2011a,b; Oliver *et al.* 2014c).

Divergence dates estimated for numerous arid-zone herpetofauna suggest the majority of taxa are much older than the age of the desert systems they now live in. Recent research has focused on the role of the rocky uplands as ancient centres of persistence and diversification for mesic-adapted reptiles as the surrounding landscapes dried out (Pepper *et al.*, 2008, 2011a,b, 2013b, 2014; Fujita *et al.* 2010). These mesic refugia typically are characterised by elevated levels of genetic diversity, with Miocene-aged crown nodes reflecting long-term persistence and the repeated movement in and out of refugia (Pepper *et al.* 2011b). However, the desert lowlands also are home to a remarkably diverse assemblage of arid-adapted lineages that have evolved in the absence of topographic and other physical barriers to dispersal. In stark contrast to saxicolous taxa, the genetic signatures of a number of desert lizards are characterised by exceptionally low genetic diversity over large geographic areas (Pepper *et al.* 2011c). While deeper divergences within these lineages are inferred to be Miocene in age, this pattern is indicative of the rapid expansion of arid-adapted lineages into large areas of suitable territory (Castoe *et al.* 2007), concomitant with the development of the widespread sand deserts less than 1 mya.

To date, few data sets include comprehensive sampling across the arid zone (but see Fujita *et al.* 2010; Pepper *et al.* 2011a,c; Oliver *et al.* 2014c), and our understanding of processes that may be responsible for diversification within true deserts is limited. Identifying whether common patterns can be found across the arid zone and whether they relate to different desert systems (i.e. stony vs. sandy, eastern vs. western), and whether and where arid refugia (i.e. centres of persistence for xeric-adapted taxa) existed, will be a fruitful area of future research in an area still very much unknown.

Eastern Mesic Biome

The eastern coastline of Australia encompasses a steep climatic gradient, ranging from tropical in the north, warm temperate in the central coast, to cool temperate in the southeast and Tasmania. Spanning more than 23° in latitude, the GDR mountain system runs the entire length of the coast from northern

Queensland to southern Victoria. Cracraft (1991) considered four areas of endemism along the east coast: the Atherton Plateau, eastern Queensland, the Southeastern Forest and Tasmania, with boundaries between the mainland areas corresponding to major breaks in the uplands (e.g. the Burdekin Gap, Hunter Valley, etc.). In a study on *Lampropholis* skinks, Chapple *et al.* (2011a) summarised major biogeographic barriers in eastern Australia, as well as a number of additional barriers repeatedly identified in the genetic signatures of numerous vertebrate and plant taxa.

The formation of the GDR during the Cretaceous undoubtedly had a profound influence on the evolution of taxa on the east coast of Australia (Dubey *et al.* 2010). In addition, the nonuniform relief along its great length of more than 3500 km, and width of over 300 km in some sections, would have provided multiple microclimatic refuges during Plio-Pleistocene cycles of aridification, dividing formerly continuous distributions and allowing the development of genetically distinct local populations. Indeed, genetic studies of numerous herpetological taxa along the GDR show congruent phylogenetic patterns indicative of persistence in higher-elevation mesic refugia during arid phases, with deep genetic breaks across lowland areas inferred to be historically dry biogeographic barriers to dispersal (e.g. Horton 1972; Schäuble and Moritz 2001; Chapple *et al.* 2005, 2011a,b; Symula *et al.* 2008; Bell *et al.* 2010; Pepper *et al.* 2014). The genetic impacts of repeated forest expansion and contraction has been particularly well studied in the herpetofauna of the Queensland Wet Tropics (Schneider *et al.* 1998; McGuigan *et al.* 1998; Schauble and Moritz 2001; Stuart-Fox *et al.* 2001; Couper and Hoskin 2008; Moussalli *et al.* 2009; Moritz *et al.* 2009; Edwards and Melville 2010; Bell *et al.* 2010). Using extensive data based on palaeoclimate surfaces to predict rainforest distribution since the last glacial cycle, the size and location of refugia have been reconstructed and compared with species distribution models and phylogeographic patterns of extant populations. As well as evaluating refugia, detailed phylogeographic data sets for diverse herpetofauna in the Wet Tropics have been used to explore a broad range of evolutionary questions, including the location of suture zones (Moritz *et al.* 2009), reproductive isolation at contact zones (Singhal and Moritz 2013), differences in thermal physiological parameters (Moritz *et al.* 2012) and divergent selection in phenotypic traits (Hoskin *et al.* 2011).

In addition to the expansion and contraction of forest habitats, topographic barriers such as mountain ranges, river valleys and lava fields also are thought to have played an important role in shaping the evolutionary history of modern herpetofauna in eastern Australia (Chapple *et al.* 2011a,b; Haines *et al.* 2014; Smissen *et al.* 2013; Ng *et al.* 2014). Furthermore, while significant glaciation during the Plio-Pleistocene only occurred in Tasmania and had little impact on mainland taxa (Barrows *et al.* 2001), the intermittent land connection (and current isolation of Tasmania) across the Bass Strait during times of low sea level was also important in historical lineage divergence within a number of reptile and amphibian species (reviewed in Ng *et al.* 2014; cf. Chapple *et al.* 2005; Symula *et al.* 2008; Dubey *et al.* 2010).

Monsoon Tropics

The Monsoon Tropics biome of northern Australia lies within the seasonally dry tropics, and presently has a summer (November–April) rainfall regime originating from tropical depressions, thunderstorms and the northern Australian monsoon trough (Wende 1997). Temperatures are high year round, with monthly averages between 25°C and 35°C (Waples 2007). The landscapes are dominated by ranges and dissected escarpments of Proterozoic sandstone, with extensive savannah woodland habitats as well as rainforest, heath and shrublands, mangroves and salt marsh flats (Woinarski *et al.* 2007; Bowman *et al.* 2010).

The Monsoon Tropics can be broadly divided into three areas of endemism, each comprising major sandstone regions: the Kimberley Plateau, Arnhem Land and the Cape York Peninsula (Cracraft 1991). A number of well-known biogeographic barriers have been identified across these regions (reviewed in Bowman *et al.* 2010; Eldridge *et al.* 2011; Catullo *et al.* 2014), largely associated with breaks in the ranges and arid lowlands surrounding major ephemeral river systems. Recently, the Monsoon Tropics have become the focus of increased phylogeographic research (Bowman *et al.* 2010; Fujita *et al.* 2010; Toon *et al.* 2010; Melville *et al.* 2011; Potter *et al.* 2012; Moritz *et al.* 2013; Catullo *et al.* 2014; Catullo and Keogh 2014), with fine-scale molecular data shedding light on the taxonomic composition and distribution of cryptic species complexes, as well as landform attributes that may have contributed to these

genetic patterns (i.e. Pepper and Keogh 2014). In addition, these molecular data are helping to unravel the complex evolutionary relationships between the broader arid zone to the south, and New Guinea and other islands to the north. In particular, the herpetofauna are playing a central role in understanding the complex biogeographic history of the region, with large research programs focused on comprehensive sampling and generating large molecular data sets for a number of lizard species complexes such as *Carlia*, *Cryptoblepharus*, *Gehyra* and *Heteronotia*.

The most striking pattern to come out of recent studies of the herpetofauna of the Monsoon Tropics is the extreme level of highly localised endemism (Fujita *et al.* 2010; Pepper *et al.* 2011b; Smith *et al.* 2011; Oliver *et al.* 2010, in press; Catullo *et al.* 2014; C. Moritz *et al.*, unpublished data). Sampling from Arnhem Land and Cape York remains sparse due to inaccessibility and restricted access to private indigenous land; however, concentrated effort in the Kimberley region in the northwest continues to reveal cryptic diversity in the herpetofauna at a scale not seen anywhere else on the continent (e.g. Pepper *et al.* 2011b; Pepper and Keogh 2014; Oliver *et al.* 2010, 2013a,b; C. Moritz *et al.*, unpublished data). For example, the gecko species *Heteronotia planiceps* comprises lineage diversity in the Kimberley on par with the diversity found across the entire continental range of *H. binoei* (Fujita *et al.* 2010; Pepper *et al.* 2011b), with an additional nine deeply diverged lineages uncovered in the Kimberley since the publication of the latter (C. Moritz *et al.*, unpublished data). Similarly, another gecko in the genus *Crenadactylus* currently consisting of two subspecies in the Kimberley was recently found to comprise multiple highly divergent and allopatric lineages, including seven candidate new taxa (Oliver *et al.* 2010, 2013a). This kind of extreme short-range endemism 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 nonvagile organisms (Phillips *et al.* 2009). The uplands of the Kimberley Plateau would also provide a more thermally buffered environment than that of the surrounding lowlands, and species diversity would therefore be expected to be high in this region. Indeed, the rugged and deeply dissected uplands in the high-rainfall area of northwest Kimberley has particularly high species diversity and levels of endemism compared with more topographically subdued parts of the region (Slatyer *et al.* 2007; Doughty 2011; Gonzalez-Orozco *et al.* 2011; Maslin *et al.* 2013).

Southwestern Mesic Biome

The SMB has been identified as a global 'biodiversity hotspot'; based largely on plant species richness and endemism, it is the only Australian region in the top 25 (Myers *et al.* 2000). The SMB is surrounded by xeric regions to the north and east, and oceans to the south and west, and is geographically isolated from other temperate mesic zones in Australia. The landscapes are ancient and highly weathered, with little in the way of mountainous topography, and the region has been tectonically stable since the Carboniferous/Permian (Hopper and Gioia 2004).

Considerable research attention has been focused on the high diversity and endemism of southwestern plant taxa (reviewed in Hopper and Gioia 2004; Rix *et al.* 2014), with molecular phylogenies suggesting multiple dispersal events both into, out of and within the SMB throughout the Cretaceous and the Cenozoic (Hopper and Gioia 2004). A significant number of the herpetofauna species also are endemic, including 26% of the reptiles and over 80% of the amphibians (Myers *et al.* 2000; Morgan *et al.* 2007). Two alternative hypotheses have featured prominently in trying to understand the origin of southwestern Australian herpetological diversity (Morgan *et al.* 2007); a historical relationship between the SMB and other regions of Australia has long been suggested to explain the number of genera or related genera found in both the SMB and the EMB (the *multiple invasion hypothesis*), with this hypothesis extensively tested using higher-level frog systematics and distributional data (i.e. Main *et al.* 1958; Lee 1967; Main 1968; Littlejohn 1981). However, in situ diversification within the SMB (the *endemic speciation hypothesis*) has also been proposed, with a number of recent phylogenetic studies supporting high intraspecific genetic divergence between populations in the southwest, rather than repeated migrations across Australia (Read *et al.* 2001; Jennings *et al.* 2003; Morgan *et al.* 2007; Rix *et al.* 2014).

Within the SMB, major climatic gradients and physical features across the landscape are thought to have been important in shaping phylogeographic patterns (Kay and Keogh 2012). For example, strong rainfall and temperature gradients between the High Rainfall Zone of the southwest coast and the inland

Transitional Rainfall Zone (Hopper 1979) appear to have been significant barriers to frogs (Wardell-Johnson and Roberts 1993; Edwards *et al.* 2007, 2008) and skinks (Kay and Keogh 2012). In addition, physical barriers such as the Darling Scarp (Kay and Keogh 2012) and the waterlogged Pingerup Plains (Wardell-Johnson and Roberts 1993; Edwards *et al.* 2008) as well as sea-level fluctuations in coastal areas (Edwards *et al.* 2008; Kay and Keogh 2012) also appear to have been important in the regional diversification of herpetofauna in the SMB.

New Zealand

The introduction of a diverse suite of mammals into New Zealand, which was previously largely devoid of native terrestrial mammals (Worthy and Holdaway 2002; Worthy *et al.* 2006), has resulted in widespread range contractions of many native herpetofauna species (Towns *et al.* 1985; Hitchmough *et al.* 2013; Tingley *et al.* 2013; Nelson *et al.* 2015). This has acted to disrupt and obscure many biogeographic patterns within New Zealand, with molecular or fossil data sometimes required to reconstruct the patterns and processes that have driven the diversity of the native herpetofauna (Worthy and Holdaway 2002; Chapple *et al.* 2008a; Lee *et al.* 2009a). In addition, the New Zealand herpetofauna includes two relictual lineages (Leiopelmatid frogs, tuatara) that are the last remnants of ancient, previously more diverse groups (Holyoake *et al.* 2001; Cree 2014; Table 12.1). This leaves their biogeographic history to be pieced together using the fossil record and the current distribution of the remaining members of the lineages (e.g. *Leiopelma hochstetteri*; Fouquet *et al.* 2010). For instance, the tuatara was previously distributed throughout the North Island, South Island and Stewart Island, but now has a relictual distribution on several Cook Strait Islands and on several island groups off the northeast of the North Island (Cree 2014). The only substantial genetic breaks evident within the tuatara are between the Cook Strait and northeastern island regions (Hay *et al.* 2010).

Previous detailed investigations of the biogeography of New Zealand skinks and geckos (e.g. Towns *et al.* 1985) are now considerably out of date due to the extensive taxonomic revisions that have occurred in both lineages over the last two decades (e.g. Chapple *et al.* 2009; Nielsen *et al.* 2011; Chapple and Ritchie 2013). Recent molecular phylogenetic studies for both skinks (Chapple *et al.* 2009) and geckos (Nielsen *et al.* 2011) have shed light on interspecific biogeographic patterns, while extensive phylogeographic studies of New Zealand skinks also enable the examination of intraspecific patterns. Here we outline six main biogeographic patterns that are present in New Zealand lizards (Figure 12.2b).

1. *Northland diversification*: The extent of landmass in the Northland region, and the degree of connection between the North Island and offshore islands, has been in continual flux since the Pliocene, particularly due to sea-level changes associated with Pleistocene glacial cycles (Rogers 1989; King 2000; Worthy and Holdaway 2002). In particular, some island groups (e.g. Poor Knights Islands, Three Kings Islands) have been isolated from the North Island mainland for 1–2 Ma (Hayward 1986, 1991). While the repeated connection and separation of landmasses and islands in the Northland region appears to have driven substantial diversification in *Oligosoma* skinks (Chapple *et al.* 2008a,b,c, 2009; Hare *et al.* 2008; Patterson *et al.* 2013) and geckos (*Dactylocnemis* and *Naultinus*; Nielsen *et al.* 2011), no consistent patterns have emerged regarding their placement or timing (Wallis and Trewick 2009).
2. *Taupo Line biogeographic barrier*: The Manawatu Strait, which inundated the lower North Island during the Pliocene (Bull and Whitaker 1975; Rogers 1989; Worthy and Holdaway 2002), appears to have had a long-lasting influence on the distribution of lizards (Chapple *et al.* 2009). The Taupo Line, which runs between the present-day Hawkes Bay and Taranaki regions, corresponds to the northern boundary of the Manawatu Strait and represents a major species turnover zone in *Oligosoma* skinks (Hare *et al.* 2008; Liggins *et al.* 2008a; Chapple *et al.* 2009) and geckos (McCann 1955, 1956; Nielsen *et al.* 2011).
3. *Cook Strait*: The North and South Islands of New Zealand are separated by the Cook Strait, a narrow and shallow waterway (Lewis *et al.* 1994). Land bridges formed intermittently during glacial maxima during the Pleistocene that provided the potential for the faunal interchange of taxa between the two islands (Lewis *et al.* 1994; Worthy and Holdaway 2002). Genetic

studies inferred recent dispersal or connection across the Cook Strait in several skinks species (*Oligosoma maccanni*, *O. infrapunctatum*, *O. lineoocellatum*, *O. polychroma*; Greaves *et al.* 2007, 2008; O'Neill *et al.* 2008; Liggins *et al.* 2008a). In addition, several gecko species have distributions that span the Cook Strait (e.g. *Mokopirirakau granulatus*, *Woodworthia maculatus*; Nielsen *et al.* 2011). However, the Cook Strait represents a distributional barrier for several *Oligosoma* skinks (e.g. *O. aeneum*, *O. ornatum*, *O. whitakeri*; Chapple *et al.* 2008a, 2009; Miller *et al.* 2009) and geckos (Nielsen *et al.* 2011). Interestingly, lizard species whose distributions fail to span the Cook Strait are more likely to be continuously distributed across the Taupo Line (reviewed in Chapple *et al.* 2009).

4. *Alpine Fault*: The Alpine Fault has been responsible for the uplift of the Southern Alps since the Miocene. The presence of the Southern Alps is believed to be responsible for the east–west biogeographic breaks (of Miocene–Pliocene origin), or distributional limits, of several South Island lizard species, including *O. polychroma* (Liggins *et al.* 2008a), *O. lineoocellatum* (Greaves *et al.* 2007), *O. infrapunctatum* (Greaves *et al.* 2008) and several gecko species (*Dactylocnemis*, *Mokopirirakau*, *Naultinus*; Nielsen *et al.* 2011). As a result, many lizard species have distributions that are restricted entirely to either the east or west of the Southern Alps (Chapple *et al.* 2009; Nielsen *et al.* 2011).
5. *North–south splits in the South Island*: On the eastern side of the Southern Alps, a combination of tectonic activity and climatic process (mostly Pleistocene glacial cycles) have resulted in alternating extremes of endemism from north to south: Nelson–Marlborough (high), Canterbury (low), Otago-Southland (high) (Wardle *et al.* 1988, Wardle 1991; Craw 1989; Gibbs 2006). As a result, north–south biogeographic breaks in the South Island are common at both the intra- and interspecific level in both skinks (e.g. *O. polychroma*, *O. maccanni*, *O. chloronoton-lineoocellatum*, *O. otagense-waimatense*; Greaves *et al.* 2007; O'Neill *et al.* 2008; Liggins *et al.* 2008a; Chapple *et al.* 2012) and geckos (*Naultinus*, *Woodworthia*; Nielsen *et al.* 2011).
6. *East–west splits in Otago*: The Nevis–Cardrona fault system, which is delineated by the Cardrona and Nevis rivers, has been active since the Late Miocene and constitutes the boundary between eastern and western Otago (reviewed in Waters *et al.* 2001). Several skink species (*O. grande*, *O. maccanni*, *O. otagense*; Berry and Gleeson 2005; O'Neill *et al.* 2008; Chapple *et al.* 2012) exhibit deep genetic breaks across this region, with species breaks also evident in geckos (*Woodworthia*; Nielsen *et al.* 2011). Similarly, tectonic activity in the southern South Island appears to have resulted in several isolated or disjunct species of Miocene–Pliocene origin in mountainous regions (Bell and Patterson 2008; Patterson and Bell 2009; Chapple *et al.* 2011c; Nielsen *et al.* 2011).

Future Research

Our ability to understand the complex biogeographic history of the Australian and New Zealand herpetofauna is rapidly gaining momentum. The application of next-generation sequencing technologies and the availability of phylogenomic data, combined with powerful inferential tools of statistical phylogeography, have made it possible to robustly estimate population connectivity and gene flow, test shared biogeographic barriers and detect underlying mechanisms of diversification in a statistical framework. In particular, emerging model-based analytical methods to infer parameters and compare models (reviewed in Hickerson *et al.* 2010) provide a powerful means for statistically testing complex and competing biogeographical hypotheses, including vicariance versus ecological scenarios, while methods for model-based comparative phylogeographical inference such as approximate Bayesian computation (ABC) can test for simultaneous divergence times (Leache *et al.* 2007) or congruence in biogeographical scenarios across co-distributed taxa (Carnaval *et al.* 2009).

In addition, the increasing availability of online species distribution databases (e.g. the *Atlas of Living Australia* [ALA] website, www.ala.org.au, and BioWeb Herpetofauna Database 2016) allows digital access to point- and museum-based records, expert range maps and checklists, with ever-improving model-based infrastructure (Jetz *et al.* 2012), including the ability to integrate biodiversity data with

phylogenies (i.e. Phylojive). While Australian-based museums now routinely collect and store tissue for genetic analyses, this is not common practice in New Zealand. However, new methods for extracting genetic material from formalin-preserved material or dried skins are overcoming the challenges associated with working with highly degraded DNA from historic samples (Bi *et al*. 2013). Access to all these types of data, along with ever-improving analytical techniques, are allowing researchers to get a better handle on true species diversity and distributions, which in turn improves our understanding of biogeographic patterns and processes. Targeted sampling in poorly studied regions (such as the Australian Monsoon Tropics) will be particularly fruitful in this regard.

The delimitation and description of new species, especially those belonging to cryptic species complexes, is being improved through an increasingly utilised *integrative taxonomy* framework (Padial *et al*. 2010; Miralles and Vences 2013). With an emphasis on the demographic and evolutionary processes responsible for lineage diversification, the advantage of coalescent-based approaches is that they have clear and objective underpinnings. When such approaches are combined with more traditional phylogenetic inference methods, as well as with detailed morphological, geographical and ecological data, they provide more complete and robust information on species distributions and boundaries.

Finally, advances in GIS, remote sensing and biodiversity spatial modelling are revolutionising our ability to visualise and analyse biogeography. Not only is access to quality global environmental data layers continuously improving, but the increase in data-sampling points combined with sophisticated ecological niche modelling (e.g. Laffan *et al*. 2010; Rosauer *et al*. 2013) is enhancing our ability to predict not only current species distributions but also to estimate palaeodistributions to understand biogeographic history. The next decade of molecular biogeography and phylogenomics will undoubtedly continue to see reptiles and amphibians playing a central role in the exploration of questions related to a broad range of evolutionary applications in biogeography and ecology.

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