

Chapter 4

Putting a Name to Diversity: Taxonomy of the New Zealand Lizard Fauna

Rodney A. Hitchmough, Geoffrey B. Patterson, and David G. Chapple

Abstract The New Zealand lizard fauna is limited to two families, diplodactylid geckos and Eugongylineae skinks. Although its higher-level taxonomic diversity is limited, each family is highly speciose (61 extant skink and 43 extant gecko species). New Zealand lizards are characterised by their ecological, rather than morphological, diversity, which has impeded attempts to delineate and describe species. Numerous species have experienced substantial range reductions following human settlement and the introduction of mammalian predators, whilst others have naturally restricted distributions. Both of these factors have influenced the rate of species discovery and description. However, the implementation of molecular approaches into taxonomic studies has led to an almost threefold increase (38 to 104 extant species) in the number of lizard species recognised. Unfortunately, there remains a large gap between the number of species or taxa recognised in New Zealand and the number that have been formally described (only 55 % of recognised species have been described). Here we provide an overview of the taxonomic history of New Zealand skinks and geckos, outlining the major lineages within each family and providing justification and explanations for the undescribed entities that are recognised. We outline how an integrated morphological and molecular approach can increase the rate of both lizard species discovery and description in New Zealand.

Keywords Gecko • Skink • Taxonomy • Species discovery • Species description • Diplodactylidae • Scincidae

R.A. Hitchmough
Department of Conservation, 10-240, Wellington, New Zealand

G.B. Patterson
149 Mairangi Road, Wilton, Wellington, New Zealand

D.G. Chapple (✉)
School of Biological Sciences, Monash University, 25 Rainforest Walk, Clayton, VIC 3800, Australia
e-mail: David.Chapple@monash.edu

4.1 A Diverse New Zealand Lizard Fauna

New Zealand's lizard fauna combines very low diversity at higher taxonomic levels with extremely high (possibly the highest in the world) species-level diversity for a temperate landmass on a per-area basis (Tables 4.1, 4.2 and 4.3). All of the country's native lizards belong to just two endemic radiations, one of Diplodactylidae geckos and one of Eugongylinae skinks. Both groups have had comprehensive phylogenies published (Chapple et al. 2009; Nielsen et al. 2011) that confirm the monophyly of each.

The lizard fauna of New Zealand is remarkable for its ecological, rather than morphological, diversity. With the notable exception of the diurnal green geckos (genus *Naultinus*), the fauna consists of superficially unremarkable brown, dull green or greyish geckos and skinks. However, both groups are distinguished by pronounced and, in some instances, very extreme K-selection (viviparity of all but one species, low fecundity and great longevity; Cree and Hare 2016). They also use habitats ranging from bare rocks to the canopy and forest floor and from the intertidal zone on the coast to rocky cliffs well above the treeline in mountains where winters are long and snow can fall at any time of the year (Hare et al. 2016).

The taxonomic history of New Zealand's lizards has been strongly influenced by several factors (Shea 2016). Firstly, as a result of mammalian predation (see Towns et al. 2016), lizards were already uncommon on mainland New Zealand when the first European taxonomists and collectors arrived in the country, and they rapidly became even more uncommon due to habitat loss and the introduction of additional mammal species. Collection of specimens was therefore often difficult and serendipitous, and sampling was generally very thin and patchy (Shea 2016). Secondly, many species of both skinks and geckos are superficially very similar to each other, and to confound matters further, there is considerable geographic variation within some species. This made identification of species limits difficult, particularly during the first century of European settlement, when taxonomy tended to be strongly typological in approach. Thirdly, much early work was by visitors to the country or people who never even visited, working on type material deposited by others in Northern Hemisphere museums (Shea 2016). This continued to cause problems well into the twentieth century; for example, McCann (1955), who produced the first comprehensive review of the New Zealand lizard fauna, had no access to the type specimens of many species (S. Bartle pers. comm.), and nomenclatural errors resulted.

The first period of formal taxonomic description of New Zealand's lizards began in the 1830s (Dumeril and Bibron 1836) and continued until the early twentieth century (Boulenger 1906) (Shea 2016). These consisted mostly of descriptions of one or a few species based on one or few specimens, often with very general and limited ('New Zealand' or 'South Sea Islands') and sometimes totally inaccurate, collection locality information. The descriptions were highly variable in quality; some were very brief and did not focus on characters now considered useful to distinguish between closely related species, and some cannot now be associated

Table 4.1 Currently described New Zealand lizard species

Diplodactylidae geckos	Eugongylineae skinks
<i>Dactylocnemis pacificus</i> (Gray, 1842)	<i>Oligosoma acrinasum</i> (Hardy, 1977)
<i>Hoplodactylus delcourti</i> Bauer & Russell, 1986 (extinct)	<i>Oligosoma aeneum</i> (Girard, 1857)
<i>Hoplodactylus duvaucelii</i> (Duméril & Bibron, 1836)	<i>Oligosoma alani</i> (Robb, 1970)
<i>Mokopirirakau cryptozoicus</i> (Jewell & Leschen, 2004)	<i>Oligosoma burganae</i> Chapple et al. 2011
<i>Mokopirirakau granulatus</i> (Gray, 1845)	<i>Oligosoma chloronoton</i> (Hardy, 1977)
<i>Mokopirirakau kahutarae</i> (Whitaker, 1985)	<i>Oligosoma fallai</i> (McCann, 1955)
<i>Mokopirirakau nebulosus</i> (McCann, 1955)	<i>Oligosoma grande</i> (Gray, 1845)
<i>Naultinus elegans</i> Gray, 1842	<i>Oligosoma hardyi</i> (Chapple, Patterson, Bell & Daugherty, 2008)
<i>Naultinus gemmeus</i> (McCann, 1955)	<i>Oligosoma homalonotum</i> (Boulenger, 1906)
<i>Naultinus grayii</i> Bell, 1843	<i>Oligosoma inconspicuum</i> (Patterson & Daugherty, 1990)
<i>Naultinus manukanus</i> (McCann, 1955)	<i>Oligosoma infrapunctatum</i> (Boulenger, 1887)
<i>Naultinus punctatus</i> Gray, 1842	<i>Oligosoma judgei</i> Patterson & Bell, 2009
<i>Naultinus rudis</i> (Fischer, 1882)	<i>Oligosoma levidensum</i> (Chapple, Patterson, Bell & Daugherty, 2008)
<i>Naultinus stellatus</i> Hutton, 1872	<i>Oligosoma lineoocellatum</i> (Duméril & Duméril, 1851)
<i>Naultinus tuberculatus</i> (McCann, 1955)	<i>Oligosoma longipes</i> Patterson, 1997
<i>Toropuku stephensi</i> (Robb, 1980)	<i>Oligosoma maccanni</i> (Patterson & Daugherty, 1990)
<i>Tuketuku rakiurae</i> (Thomas, 1981)	<i>Oligosoma macgregori</i> (Robb, 1975)
<i>Woodworthia chrysoiretica</i> (Robb, 1980)	<i>Oligosoma microlepis</i> (Patterson & Daugherty, 1990)
<i>Woodworthia maculata</i> (Gray, 1845)	<i>Oligosoma moco</i> (Duméril & Bibron, 1839)
	<i>Oligosoma nigriplantare</i> (Peters, 1873)
	<i>Oligosoma northlandi</i> (Worthy, 1991) (extinct)
	<i>Oligosoma notosaurus</i> (Patterson & Daugherty, 1990)
	<i>Oligosoma oliveri</i> (McCann, 1955)
	<i>Oligosoma ornatum</i> (Gray, 1843)
	<i>Oligosoma otagense</i> (McCann, 1955)
	<i>Oligosoma pikitanga</i> Bell & Patterson, 2008
	<i>Oligosoma polychroma</i> (Patterson & Daugherty, 1990)
	<i>Oligosoma repens</i> Chapple et al., 2011
	<i>Oligosoma roimata</i> Patterson, Hitchmough & Chapple, 2013
	<i>Oligosoma smithi</i> (Gray, 1845)
	<i>Oligosoma stenotis</i> (Patterson & Daugherty, 1994)

(continued)

Table 4.1 (continued)

Diplodactylidae geckos	Eugongylinae skinks
	<i>Oligosoma striatum</i> (Buller, 1871)
	<i>Oligosoma suteri</i> (Boulenger, 1906)
	<i>Oligosoma taumakae</i> Chapple & Patterson, 2007
	<i>Oligosoma tekakahu</i> Chapple et al., 2011
	<i>Oligosoma toka</i> Chapple et al., 2011
	<i>Oligosoma townsi</i> (Chapple, Patterson, Gleeson, Daugherty, Ritchie, 2008)
	<i>Oligosoma waimatense</i> (McCann, 1955)
	<i>Oligosoma whitakeri</i> (Hardy, 1977)
	<i>Oligosoma zelandicum</i> (Gray, 1843)

The taxonomic authority for each species is provided

with identifiable type specimens. However, sometimes they were extremely thorough and well illustrated, and some type specimens from that era survive in excellent condition (Shea 2016).

There was then almost a 50-year hiatus in species descriptions until the monograph of McCann (1955) summarised knowledge at that time (Shea 2016). McCann, in the absence of access to both the type material and much of the historical literature (S. Bartle pers. comm.), did his best to make sense of the reptile collections in the major New Zealand museums. He synonymised many of the earlier-named species, but also proposed 13 new species and subspecies, four of geckos and nine of skinks. In total he recognised ten endemic gecko species and 20 endemic skink taxa (species and subspecies).

Another, shorter hiatus followed, until a burst of new species descriptions began in the 1970s. Biological exploration of seldom-visited offshore islands and other isolated localities led to the discovery and description of several distinctive new species of both skinks and geckos (Robb 1970, 1975, 1980a; Thomas 1981; Whitaker 1984), and some of McCann's more extreme synonymising (Robb and Rowlands 1977; Robb and Hitchmough 1980) and nomenclatural errors began to be corrected (Gill 1976; Robb 1977; Hardy 1977). Robb (1975) was the first to use genetic data in published herpetological taxonomy in New Zealand.

Hardy (1977) published a taxonomic revision of the New Zealand skink fauna, which included more extensive use of limited genetic data. He described four new species and a subspecies and reinstated the genus *Cyclodina* Girard 1857 for a group of heavy-bodied, nocturnal or crepuscular skinks of humid North Island habitats. Subsequently, researchers at Victoria University of Wellington carried out extensive allozyme electrophoresis surveys of almost the entire known New Zealand lizard fauna (Daugherty et al. 1990; Vos 1988; Hitchmough 1997). This work led to several skink species descriptions (Patterson and Daugherty 1990, 1994; Patterson 1997), recognition of the diurnal New Zealand skinks as an endemic genus (Patterson and Daugherty 1995) and the first insights as to the likely age and monophyly of both the skink and gecko faunas (Daugherty et al. 1994;

Table 4.2 Recognised taxonomically indeterminate (unnamed/undescribed) gecko and skink taxa in New Zealand

Diplodactylidae geckos	Eugongylinae skinks
<i>Dactylocnemis</i> ‘Matapia Island’	<i>Oligosoma</i> ‘Whirinaki’ (Barr, Chapple and Hitchmough, unpublished data)
<i>Dactylocnemis</i> ‘Mokohinau’ (see Chong 1999)	<i>Oligosoma</i> aff. <i>chloronoton</i> ‘West Otago’ (Greaves et al. 2007)
<i>Dactylocnemis</i> ‘North Cape’	<i>Oligosoma</i> aff. <i>inconspicuum</i> ‘North Otago’*
<i>Dactylocnemis</i> ‘Poor Knights’ (see Chong 1999)	<i>Oligosoma</i> aff. <i>inconspicuum</i> ‘Okuru’*
<i>Dactylocnemis</i> ‘Three Kings’	<i>Oligosoma</i> aff. <i>infrapunctatum</i> ‘Albom’ (Greaves et al. 2008; Patterson & Melzer unpublished morphological data)
<i>Mokopirirakau</i> ‘Cascades’	<i>Oligosoma</i> aff. <i>infrapunctatum</i> ‘Chesterfield’ (Greaves et al. 2008; Patterson & Melzer unpublished morphological data)
<i>Mokopirirakau</i> ‘Cupola’*	<i>Oligosoma</i> aff. <i>infrapunctatum</i> ‘cobble’ (Greaves et al. 2008; Patterson & Melzer unpublished morphological data)
<i>Mokopirirakau</i> ‘Okarito’	<i>Oligosoma</i> aff. <i>infrapunctatum</i> ‘crenulate’ (Greaves et al. 2008)
<i>Mokopirirakau</i> ‘Open Bay Islands’	<i>Oligosoma</i> aff. <i>infrapunctatum</i> ‘Hokitika’ (Greaves et al. 2008; Patterson & Melzer unpublished morphological data)
<i>Mokopirirakau</i> ‘Roys Peak’	<i>Oligosoma</i> aff. <i>infrapunctatum</i> ‘Southern North Island’ (Greaves et al. 2008)
<i>Mokopirirakau</i> ‘southern forest’	<i>Oligosoma</i> aff. <i>infrapunctatum</i> ‘Westport’ (Greaves et al. 2008)
<i>Mokopirirakau</i> ‘southern North Island’	<i>Oligosoma</i> aff. <i>lineoocellatum</i> ‘Central Canterbury’ (Greaves et al. 2007)
<i>Naultinus</i> ‘North Cape’	<i>Oligosoma</i> aff. <i>lineoocellatum</i> ‘Mackenzie Basin’ (Greaves et al. 2007)
<i>Toropuku</i> ‘Coromandel’	<i>Oligosoma</i> aff. <i>lineoocellatum</i> ‘South Marlborough’ (Greaves et al. 2007)
<i>Woodworthia</i> ‘Central Otago’	<i>Oligosoma</i> aff. <i>longipes</i> ‘Rangitata’ (Chapple et al. 2009)
<i>Woodworthia</i> ‘Cromwell’	<i>Oligosoma</i> aff. <i>longipes</i> ‘southern’ (Chapple et al. 2009)
<i>Woodworthia</i> ‘Kaikouras’*	<i>Oligosoma</i> aff. <i>polychroma</i> Clade 2 (Liggins et al. 2008)
<i>Woodworthia</i> ‘Marlborough mini’	<i>Oligosoma</i> aff. <i>polychroma</i> Clade 3 (Liggins et al. 2008)
<i>Woodworthia</i> ‘Mount Arthur’	<i>Oligosoma</i> aff. <i>polychroma</i> Clade 4 (Liggins et al. 2008)
<i>Woodworthia</i> ‘Otago/Southland large’ (may be further subdivided into four entities)	<i>Oligosoma</i> aff. <i>polychroma</i> Clade 5 (Liggins et al. 2008)
<i>Woodworthia</i> ‘pygmy’	<i>Oligosoma</i> aff. <i>smithi</i> ‘Three Kings, Te Paki, Western Northland’ (Hare et al. 2008)

(continued)

Table 4.2 (continued)

Diplodactylidae geckos	Eugongylinae skinks
<i>Woodworthia</i> ‘Southern Alps’	<i>Oligosoma</i> sp. ‘Homer Tunnel’ (Chapple, Jewell and Hitchmough, unpublished data)
<i>Woodworthia</i> ‘southern mini’	
<i>Woodworthia</i> aff. <i>maculata</i> ‘Muriwai’ (Hitchmough, van Winkel and Nielsen, unpublished data)	
<i>Woodworthia</i> cf. <i>brunnea</i>	

For geckos, most have published phylogenetic support in Nielsen et al. (2011). Exceptions in the genus *Dactylocnemis* were identified in the BSc honours project of Chong (1999). One other recent discovery is supported by unpublished genetic data (Hitchmough, van Winkel and Nielsen, unpublished data), and other exceptions with absent or contradictory genetic information are labelled with an asterisk. For skinks, most have phylogenetic support in Chapple et al. (2009) or other molecular studies (listed below). Exceptions that lack relevant genetic information are labelled with an asterisk.

Table 4.3 Increase in described and recognised New Zealand lizard species/taxa since McCann (1955)

Assessment year	Publication	Geckos	Skinks	Total
1955	McCann (1955)	10	20	30
1980	Newman (1982)	16 + 1 = 17	21	37 + 1 = 38
1994	Daugherty et al. (1994)	16 + 13 = 29	27 + 4 = 31	43 + 17 = 60
2001	Hitchmough (2002)	17 + 25 = 42	28 + 9 = 37	45 + 34 = 79
2005	Hitchmough et al. (2007)	18 + 25 = 43	28 + 16 = 44	46 + 41 = 87
2009	Hitchmough et al. (2010)	18 + 24 = 42	34 + 21 = 55	52 + 45 = 97
2012	Hitchmough et al. (2013)	18 + 24 = 42	38 + 17 = 55	56 + 41 = 97
2015	Hitchmough et al. (2016)	19 + 25 = 44	40 + 22 = 62	59 + 47 = 106

Additional lizard species estimates were produced in 1980 (Newman 1982) and 1994 (Daugherty et al. 1994) and through sequential New Zealand Threat Classification System conservation status assessments in 2001 (Hitchmough 2002), 2005 (Hitchmough et al. 2007), 2009 (Hitchmough et al. 2010), 2012 (Hitchmough et al. 2013) and 2015 (Hitchmough et al. 2016). Figures in each cell refer to taxa that are taxonomically determinate (formally named) and taxonomically indeterminate (unnamed/undescribed).

Chambers et al. 2001). It also facilitated the development of a very comprehensive frozen tissue collection for both groups. This has subsequently been used for DNA sequencing, which has led to robust phylogenies (Chapple et al. 2009; Nielsen et al. 2011).

This genetic work over the last three decades has led to the identification of a very large number of cryptic species in both groups, more than trebling the size of the known fauna (Tables 4.1, 4.2 and 4.3). Many of these species remain formally unnamed, although work on descriptions is in progress (Hitchmough, unpublished data; Chapple, Patterson and Melzer, unpublished data). Once the taxonomic unit has been delineated by genetic techniques, morphological examination, in almost every case, allows the identification of diagnostic physical characters, although

Table 4.4 Details (identities, discovery dates, taxonomic authors [for subsequently described species] and supporting references) of the novel taxa discovered, since McCann's (1955) monograph that were immediately suspected to be new species

Species and authority or reference	Discovery date
<i>Woodworthia chrysosiretica</i> (Robb 1980)	1960s
<i>Mokopirirakau</i> 'Cupola' (see Newman 1982)	1968
<i>Tukutuku rakiurae</i> (Thomas 1981)	1969
<i>Mokopirirakau kahutarae</i> (Whitaker 1984)	1970
<i>Mokopirirakau</i> 'Open Bay Islands' (see Newman 1982)	1970
<i>Mokopirirakau</i> 'cascades' (see Newman 1982)	1974
<i>Oligosoma inconspicuum</i> (Patterson & Daugherty 1990—later identified as <i>O. burganae</i> (Chapple et al. 2011))	1981
<i>Oligosoma longipes</i> Patterson 1997	1983
<i>Oligosoma microlepis</i> (Patterson and Daugherty 1990)	1985
<i>Dactylocnemis</i> 'Matapia' (see Pickard and Towns 1988—misidentified as <i>W. chrysosiretica</i>)	1986
<i>Oligosoma taumakae</i> (Chapple and Patterson, 2007)	1988
<i>Oligosoma</i> aff. <i>infrapunctatum</i> 'Chesterfield' (see Aviss and Lyall 1995)	1993
<i>Oligosoma</i> aff. <i>infrapunctatum</i> 'Alborn' (see Lettink and Stengs 2014)	1993
<i>Mokopirirakau cryptozoicus</i> (Jewell and Leschen, 2004)	1996
<i>Mokopirirakau</i> 'Roys Peak' (see Tocher and Marshall 2001)	1998
<i>Oligosoma</i> aff. <i>inconspicuum</i> 'Okuru' (Department of Conservation BioWeb Herpetofauna database)	2000
<i>Oligosoma tekakahu</i> Chapple et al. 2011 (M. Tocher pers. comm. to R. Hitchmough; Loh 2003)	2002
<i>Oligosoma</i> 'Whirinaki' (the late A.H. Whitaker pers. comm. to R. Hitchmough)	2003
<i>Oligosoma</i> aff. <i>longipes</i> 'Rangitata' (Department of Conservation BioWeb Herpetofauna database)	2004
<i>Oligosoma pikitanga</i> Bell and Patterson 2008	2004
<i>Oligosoma judgei</i> Patterson and Bell 2009	2005
<i>Oligosoma repens</i> Chapple et al. 2011 (T. Jewell pers. comm. to R. Hitchmough)	2005
<i>Oligosoma</i> aff. <i>infrapunctatum</i> 'cobble' (Jewell 2008)	2006
<i>Oligosoma</i> aff. <i>inconspicuum</i> 'North Otago' (T. Jewell pers. comm. to R. Hitchmough; flickr)	2008
<i>Woodworthia</i> aff. <i>maculata</i> 'Muriwai' (D. van Winkel pers. comm. to R. Hitchmough)	2010
<i>Oligosoma</i> sp. 'Homer Tunnel' (T. Jewell pers. comm. to R. Hitchmough)	2014

substantial geographic variation in body size, colour and morphology within some genetic clades can be confusing.

In addition to the identification of distinct taxa using genetic analysis of already known populations, completely new discoveries of totally novel species continue (T. Jewell, pers. comm.). Novel discoveries which were immediately suspected to be new species, found since publication of the monograph of McCann (1955), are listed in Table 4.4. All but three of these discoveries (*Oligosoma* 'Okuru',

Oligosoma aff. *inconspicuum* ‘North Otago’ and *Mokopirirakau* ‘Cupola’) are now supported as distinct taxa by genetic data. This discovery curve shows no sign of flattening out (Table 4.3), and further discoveries are highly likely.

The regularly revised conservation status lists, generated using the New Zealand Threat Classification System (Townsend et al. 2008), provide a regular update of the size of the known fauna. This system has a precautionary approach and includes taxonomically indeterminate (undescribed) species with a wide range of degree of evidential support for their distinctiveness. Some of these entities are recent discoveries that may not survive the process of formal scientific examination and peer-reviewed publication of a description. However, all have been accepted by a panel of experts as having a reasonable level of evidence for their possible taxonomic distinctiveness, and the majority already have strong genetic support for their separate species status. The number of taxa included in these lists has increased steadily from 2001 to the present (Table 4.3).

4.2 Taxonomic History of New Zealand Skinks (Scincidae, Eugongylinae)

4.2.1 Higher-Level Relationships

Globally, there are seven subfamilies of skinks: Acontinae, Egerniinae, Eugongylinae, Lygosominae, Mabuyinae, Sphenomorphinae and Scincinae (Uetz and Hosek 2015). The Eugongylinae is monophyletic and is distributed throughout Australia, Papua New Guinea, the southwest Pacific (including New Zealand), southeast Asia and Africa (Smith et al. 2007; Skinner et al. 2011; Brandley et al. 2015). All native New Zealand skink species are endemic and members of Eugongylinae (Smith et al. 2007; Chapple et al. 2009). The closest relative of the New Zealand skink radiation is *Oligosoma lichenigerum*, which occurs on Lord Howe Island and Norfolk Island (Smith et al. 2007; Chapple et al. 2009). The sister lineage of New Zealand *Oligosoma* + *O. lichenigerum* is *Lioscincus* from New Caledonia, which suggests that skinks colonised New Zealand from New Caledonia via long-distance overwater dispersal and island-hopping along the Lord Howe Rise and Norfolk Ridge (Smith et al. 2007; Chapple et al. 2009; Chapple and Hitchmough 2016; D.G. Chapple, unpublished data).

4.2.2 Generic Relationships

Prior to the first modern taxonomic revision of New Zealand skinks by McCann (1955), there was substantial instability in the generic assignment of species (Shea 2016). Species were variously placed in *Mocoo*, *Lygosoma*, *Tiliqua*, *Cyclodina* and

several other genera (*Oligosoma*, *Hinulia*, *Euprepes*, *Lygosomella*, *Norbea*, *Hombromia*; see Hardy 1977; Chapple et al. 2009). However, McCann (1955) placed 17 of the 18 species known at the time in *Leiopisma*, with the remaining species placed in *Sphenomorphus* (*S. pseudornatus*). Hardy (1977) subsequently resurrected *Cyclodina* Girard to accommodate *C. alani*, *C. macgregori*, *C. oliveri*, *C. whitakeri*, *C. aenea* and *C. ornata* (the latter two species were previously part of *S. pseudornatus*). Two decades later, Patterson and Daugherty (1995) retained *Cyclodina*, but reinstated *Oligosoma* Girard to accommodate all New Zealand *Leiopisma* species.

Although morphological and ecological differences were evident between *Oligosoma* (shallow pointed heads, long limbs and toes and bodies that are oval in cross section; generally diurnal species that prefer open habitats where they are overt baskers) and *Cyclodina* (deeper and blunter heads, relatively shorter limbs and toes and bodies that are squarish in cross section; nocturnal or crepuscular species that prefer more shaded habitats) (Patterson and Daugherty 1995; Gill and Whitaker 2001), Chapple et al. (2009) demonstrated that each was not reciprocally monophyletic. Instead, the ‘*Cyclodina*’ and ‘*Oligosoma*’ body plans each appear to have evolved on multiple occasions. Whilst eight major genetic clades have been identified within New Zealand skinks, Chapple et al. (2009) were unable to diagnose each on the basis of morphological characters due to the morphological conservatism present, presumably caused by the rapid radiation of skinks following their arrival in New Zealand. Thus, in order to ensure taxonomic stability, Chapple et al. (2009) elected to assign all native New Zealand skink species to a single genus, *Oligosoma*.

The phylogenetic relationships among the eight main clades of New Zealand skinks were poorly resolved (Chapple et al. 2009). The only well-supported relationships were among Clades 1 (*O. longipes* complex, *O. polychroma* complex, *O. lineoocellatum-chloronoton* complex, *O. maccanni*, *O. notosaurus-inconspicuum* complex, *O. grande*, *O. stenotis*) and 2 (*pikitanga*, *judgei*, *otagense*, *waimatense*, *taumakae*, *acrinasum*, *infrapunctatum* complex) (Chapple et al. 2009).

4.2.3 Species Recognition

Of the eight major genetic clades within *Oligosoma* skinks (Chapple et al. 2009), Clade 1 is the most widespread, with species within this clade distributed across the southern North Island, South Island and Stewart Island. It is also the most speciose clade (14 described species, 12 undescribed taxa; Tables 4.1 and 4.2), comprising members of the *O. longipes* species complex (*O. longipes*, *O. aff. longipes* ‘Rangitata’, *O. aff. longipes* ‘southern’; Chapple et al. 2009), *O. nigriplantare*, members of the *O. polychroma* species complex (*O. polychroma*, *O. aff. polychroma* Clade 2, *O. aff. polychroma* Clade 3, *O. aff. polychroma* Clade 4, *O. aff. polychroma* Clade 5; Liggins et al. 2008), members of the *O. chloronoton-lineoocellatum* species complex (*O. chloronoton*, *O. aff. chloronoton* ‘West Otago’,

O. lineocellatum, *O. aff. lineocellatum* ‘Central Canterbury’, *O. aff. lineocellatum* ‘Mackenzie Basin’, *O. aff. lineocellatum* ‘South Marlborough’; Greaves et al. 2007), *O. maccanni*, members of the *O. inconspicuum*–*O. notosaurus* species complex (*O. burganae*, *O. inconspicuum*, *O. aff. inconspicuum* ‘North Otago’, *O. aff. inconspicuum* ‘Okuru’, *O. notosaurus*, *O. repens*, *O. tekakahu*, *O. toka*; Chapple et al. 2011), *O. grande* and *O. stenotis*. The undescribed taxonomic diversity in the *O. polychroma* (Liggins et al. 2008) and *O. chloronoton-lineocellatum* complexes (Greaves et al. 2007) is due to molecular studies identifying deep genetic splits within these widespread species (though a recent morphological study suggests the presence of an additional taxon within *O. lineocellatum*; Patterson and Melzer, unpublished data). In contrast, the taxonomic diversity within the *O. inconspicuum*–*notosaurus* complex is the result of the discovery of several morphologically distinct taxa in remote regions of the South Island, as well as molecular studies identifying deep genetic splits within *O. inconspicuum* (Chapple et al. 2011). The undescribed taxa within the *O. longipes* complex reflect both genetic substructure within *O. longipes* (*O. aff. longipes* ‘southern’; Chapple et al. 2009) and the discovery of a morphologically distinct, sympatric population (*O. aff. longipes* ‘Rangitata’; Tables 4.2 and 4.4).

Clade 2 is predominately a South Island radiation (all apart from two members of the *O. infrapunctatum* complex). It includes seven described species and eight undescribed taxa: *O. pikitanga*, *O. judgei*, *O. sp.* ‘Homer Tunnel’, *O. otagense*, *O. waimatense*, *O. taumakae*, *O. acrinasum* and members of the *O. infrapunctatum* species complex (*O. infrapunctatum*, *O. aff. infrapunctatum* ‘Alborn’, *O. aff. infrapunctatum* ‘Chesterfield’, *O. aff. infrapunctatum* ‘cobble’, *O. aff. infrapunctatum* ‘crenulate’, *O. aff. infrapunctatum* ‘Hokitika’, *O. aff. infrapunctatum* ‘Southern North Island’, *O. aff. infrapunctatum* ‘Westport’; Greaves et al. 2008; Hitchmough et al. 2016; Tables 4.1 and 4.2). The undescribed species diversity within the *O. infrapunctatum* species group is concentrated (for all but ‘Southern North Island’ and *O. aff. infrapunctatum* ‘crenulate’) along the north-west coast of the South Island (Westland), with the putative species having restricted, isolated distributions (Chapple and Hitchmough 2016; Table 4.2). A recent morphological study indicates that an additional *O. infrapunctatum* taxon may exist in the Heaphy Track region (Patterson and Melzer, unpublished data).

Clade 3 contains three species that were formally part of *Cyclodina*: *O. aeneum*, *O. hardyi* and *O. levidensum*. *Oligosoma aeneum* is widely distributed throughout the North Island (and several offshore islands), whilst *O. hardyi* is restricted to the Poor Knights Islands and *O. levidensum*, the smallest native New Zealand skink species, to the Te Pahi region at the northern tip of Northland (Chapple and Hitchmough 2016). A detailed taxonomic revision of the former *C. aenea* species complex was completed recently (Chapple et al. 2008a), and therefore there are unlikely to be any additional species present within this clade.

Clade 4 comprises the majority of the species previously assigned to *Cyclodina* (*O. ornatum*, *O. roimata*, *O. townsi*, *O. oliveri*, *O. whitakeri*, *O. macgregori*, *O. alani*), along with the Three Kings Islands skink (*O. fallai*). All species occur in the North Island, with several endemic to offshore islands (*O. roimata*, *O. townsi*,

O. oliveri, *O. fallai*). Given the recent taxonomic activity within this clade (Chapple et al. 2008b; Patterson et al. 2013), no additional species are expected.

Clade 5 contains three forest-dwelling species with arboreal tendencies (*O. zelandicum*, *O. striatum* and *O. homalonotum*; Neilson 2002; Neilson et al. 2004) and the recently discovered ‘Whirinaki’ skink, which appears to be a sister species to *O. zelandicum*. The distribution of *O. zelandicum* ranges from the Taranaki region in the North Island, across Cook Strait to the Westland region of the South Island (O’Neill et al. 2008). In contrast, *O. striatum* occurs in the central-northern North Island, whilst *O. homalonotum* is restricted to Great Barrier and Little Barrier Islands. The synonymy of *O. gracilicarpus* with *O. homalonotum* (Chapple et al. 2009) suggests that *O. homalonotum* was also formerly found on the Northland mainland. The ‘Whirinaki’ skink is known (from video footage) from the Whirinaki forest in the central North Island and (from specimens) from Bream Head near Whangarei (B. Barr, D.G. Chapple, R.A. Hitchmough, unpublished data; Tables 4.2 and 4.4).

The egg-laying skink, *O. suteri*, is the sole member of Clade 6. *Oligosoma suteri* is restricted mainly to islands off the coast of the northeastern North Island and exhibits extremely low levels of intraspecific genetic divergence across its range (Hare et al. 2008).

Oligosoma moco is the only member of Clade 7 (Chapple et al. 2009). It occurs on the east coast of the North Island, northwards from the Bay of Plenty and throughout the islands off the northeastern coast of the North Island. A recent molecular study showed substantial genetic structuring within *O. moco*, with a mean pairwise genetic distance (GD) of 2.7% and three clades identified, but this was interpreted as intraspecific geographic population structuring (Hare et al. 2008). The northernmost and southernmost populations were not included in this study.

The final clade, Clade 8, contains members of the *O. smithi-microlepis* species complex (*O. microlepis*, *O. smithi*, *O. aff. smithi* ‘Three Kings, Te Pahi, Western Northland’). *O. smithi* occurs on beaches and islands along the northeast of the North Island, whilst *O. aff. smithi* ‘Three Kings, Te Pahi, Western Northland’ occurs on the Three Kings Islands and along the west coast of Northland (Hare et al. 2008). *O. microlepis* has a patchy distribution in the central North Island (Hare et al. 2008). Morphological investigations remain to be conducted to ascertain whether the three taxa within the species complex represent distinct species.

In total, therefore, there are 39 named extant (and 1 extinct) species of New Zealand skinks and 22 taxonomically indeterminate entities.

4.3 Taxonomic History of New Zealand Geckos (Diplodactylidae)

4.3.1 Higher-Level Relationships

The history of family-level taxonomy of the group including the New Zealand geckos was extremely confused, until resolved by Han et al. (2004). The

New Zealand geckos are now considered to belong to the family Diplodactylidae, along with three other distinct groups: the New Caledonian gecko radiation (genera *Bavayia*, *Correlophus*, *Dierogecko*, *Eurydactylodes*, *Mniarogecko*, *Oedodera*, *Paniegecko*, *Rhacodactylus*) and two distinct clades in Australia, *Pseudothecadactylus* which is a sister clade to the New Caledonian radiation and a larger clade (*Amalosia*, *Crenadactylus*, *Diplodactylus*, *Hesperoedura*, *Lucasium*, *Nebulifera*, *Oedura*, *Rhynchoedura*, *Strophurus*) which is a sister clade to the New Zealand clade (Nielsen et al. 2011). The Diplodactylidae are part of an Australasian radiation of three gekkotan families and are the sister group of the Carphodactylidae plus the legless Pygopodidae (Han et al. 2004; Nielsen et al. 2011).

4.3.2 Generic Relationships

Within New Zealand, McCann (1955), in the first modern taxonomic review of the New Zealand lizard fauna, recognised ten endemic gecko species divided into three genera: *Hoplodactylus* Fitzinger 1843 ('brown geckos'), *Naultinus* Gray 1842 (North Island 'green geckos') and *Heteropholis* Fischer 1882 (South Island 'green geckos'). *Heteropholis* was subsequently synonymised with *Naultinus* (Bauer 1990), and a diversity of new species, chiefly *Hoplodactylus*, was described, resulting in 20 currently recognised, named species (Daugherty et al. 1994; Jewell and Leschen 2004). However, cryptic diversity revealed by allozyme (Daugherty et al. 1994; Hitchmough 1997) and preliminary mitochondrial DNA sequence data (Chambers et al. 2001) suggested that many additional, unnamed taxa exist.

Bauer (1990) regarded *Naultinus* as monophyletic and a sister to remaining members of the clade, but intra-generic relationships could not be resolved. *Hoplodactylus* was paraphyletic with respect to the New Caledonian forms, but was also poorly resolved. Based on allozyme data, Hitchmough (1997) concluded that New Zealand geckos were monophyletic and sister to the New Caledonian clade. He recognised three complexes within *Hoplodactylus*: the *Hoplodactylus maculatus* complex, the *Hoplodactylus pacificus* complex and the *Hoplodactylus granulatus* complex. These complexes, as well as *Naultinus*, corresponded to two general, morphological groupings: a broad-toed clade, including only the *H. maculatus* group; and a narrow-toed clade, comprising remaining *Hoplodactylus* plus *Naultinus*. Although some nodes received high support, on the whole, relationships within the different groups were poorly resolved and/or weakly supported. Hitchmough (1997) considered this poor support to be a result of short branch lengths, which could signify a rapid radiation of these species.

A subsequent analysis of 16S mtDNA, conducted by Chambers et al. (2001), found New Zealand and New Caledonian diplodactylids to be reciprocally monophyletic and largely supported Hitchmough's (1997) within-group relationships. Chambers et al. (2001) recognised the necessity to erect at least two new genera to maintain the monophyly of *Hoplodactylus* whilst preserving the name, *Naultinus*,

for the distinctive and long-recognised green geckos, but they did not complete a generic revision themselves.

Nielsen et al. (2011) used both mitochondrial and nuclear DNA sequences to answer many long-standing questions about the evolution and systematics of New Zealand's geckos. Seven genera are now recognised as a result of their work: *Dactylocnemis*, *Hoplodactylus*, *Mokopirirakau*, *Naultinus*, *Toropuku*, *Tuketuku* and *Woodworthia*. *Hoplodactylus*, which formerly included all the New Zealand geckos, except the diurnal, brightly coloured *Naultinus*, was rendered paraphyletic by the confirmation that *Naultinus*, rather than being the sister group to the remainder of the New Zealand radiation (as had been thought prior to the work of Chambers et al. 2001), was nested deep within the radiation. To retain generic monophyly, either the highly distinctive *Naultinus* would have to have been included in *Hoplodactylus*, or splitting of *Hoplodactylus* was required. Unlike the New Zealand skinks, which show a very bushy pattern of evolution, with many branching events in very quick succession near the base of the clade, the geckos show strong structure with seven clear groups separated by long branches. The decision was therefore made by Nielsen et al. (2011) to name each of these groups as a genus. Each is also readily diagnosable by morphology (again unlike most possible subgroups of skinks).

Within the New Zealand radiation, there was an initial split between a group with broadly expanded toe pads, v-shaped or strongly curved distal lamellae and flesh-coloured, unpigmented mouth lining (*Hoplodactylus* and *Woodworthia*) and the remaining genera, three of which (*Mokopirirakau*, *Naultinus* and *Tuketuku*) have narrow toes, straight to only slightly curved lamellae and intense yellow and/or blue to black pigment in the mouth. *Dactylocnemis* and *Toropuku* are morphologically anomalous. In particular, *Dactylocnemis* most closely matches *Hoplodactylus* and *Woodworthia* in external morphology, to the extent that all *Dactylocnemis*, *Toropuku* and *Woodworthia* were considered to be a single variable species (*Hoplodactylus pacificus*) between 1955 (McCann 1955) and 1977 (Robb and Rowlands 1977). *Toropuku* is closer to *Mokopirirakau*, *Naultinus* and *Tuketuku* in some aspects of morphology, but appears morphologically intermediate between them and *Dactylocnemis*. *Toropuku* was briefly considered conspecific with *Dactylocnemis* to the exclusion of *Woodworthia* under the name *Hoplodactylus pacificus* by Robb and Rowlands (1977), but this was quickly reversed by the naming of *T. stephensi* (as *Hoplodactylus stephensi*) by Robb (1980a). Morphology therefore strongly suggests *Dactylocnemis*, and then *Toropuku*, to be the most basal members of the narrow-toed clade, but they are nested among the other narrow-toed genera in the DNA-based phylogeny of Nielsen et al. (2011). However, the meta-analysis of Pyron et al. (2013) placed *Dactylocnemis* and *Toropuku* as the sister group to *Mokopirirakau*, *Naultinus* and *Tuketuku*.

The narrow-toed genera, *Mokopirirakau*, *Naultinus* and *Tuketuku*, are strongly arboreal (particularly the first two), avid baskers (R. Hitchmough, pers. obs.) and often confine their use of retreats to periods of adverse weather, relying on camouflage whilst inactive at other times (Romijn et al. 2013; Hare et al. 2007; L. Moran, New Zealand Department of Conservation, pers. comm. to R. Hitchmough).

Naultinus is diurnal (Hare et al. 2007), and the other two can be active both by day and by night (Romijn et al. 2013; L. Moran, New Zealand Department of Conservation, pers. comm. to R. Hitchmough). The other genera are more strictly nocturnal (although they will emerge to bask near their retreats). They consistently use daytime retreats (Gibson et al. 2015) and are generally considered more terrestrial, though all forage, generally use crevice retreats on the ground, but also use crevice retreats in shrubs and trees if these occur in their habitat (Jewell and McFarlane 1997; Hoare et al. 2007, Barry et al. 2014).

4.3.3 Species Recognition

The genus *Tukutuku*, erected by Nielsen et al. (2011), contains only a single species, *T. rakiurae* (Thomas 1981). This species has a restricted distribution in southern Stewart Island, so barring new discoveries elsewhere, this is unlikely to change (Tables 4.1 and 4.2).

Toropuku, another genus erected by Nielsen et al. (2011), has a single described species, *T. stephensi* (Robb 1980a), which is found on two islands in Cook Strait (Table 4.1). However, in 1997, not long after the second of these Cook Strait populations was found (in 1990; Whitaker 1991), specimens of *Toropuku* began to be discovered at Coromandel, 500 km to the north (Whitaker et al. 1999; Table 4.2). They have now been found over a large part of the Coromandel Peninsula, although never by deliberate searching, and only in small numbers at each site. Preliminary investigations suggested that these populations were genetically distinct from but conspecific with *T. stephensi*. However, after comparing genetic and morphological divergence of the two regional populations, with the divergence between species within *Naultinus* and *Mokopirirakau* (the sister clades to *Toropuku*; Nielsen et al. 2011; Hitchmough et al. unpublished data), both are now considered to be distinct species. A description is in preparation.

In contrast to all other New Zealand lizard genera, and reflecting its strikingly bright and often polymorphic colours and colour patterns, *Naultinus* Gray 1842 has historically been over-split (Tables 4.1 and 4.2). This includes a history of synonymies of names based on colour morphs, and including generic synonymy; the generic name *Heteropholis* Fischer, 1882 was used for the South Island species between 1955 (McCann 1955) and 1990 (Bauer 1990). Most recently *N. poecilochlorus* (Robb 1980a, b) has been synonymised with *N. tuberculatus* by Nielsen et al. (2011). Only one undescribed species was identified by Nielsen et al. (2011). Currently recognised species are *N. gemmeus* (McCann, 1955); *N. tuberculatus* (McCann, 1955); *N. stellatus* Hutton, 1872; *N. rudis* (Fischer, 1882); *N. manukanus* (McCann, 1955); *N. punctatus* Gray, 1842; *N. elegans* Gray, 1842, and *N. grayii* Bell, 1843. An additional species from the Te Pahi area is morphologically and genetically distinct, and a description is in preparation.

Mokopirirakau was erected by Nielsen et al. (2011) for forest and alpine geckos (Tables 4.1 and 4.2). The forest gecko, *M. granulatus* (Gray, 1845), is one of the

longer-recognised species in the fauna and was previously regarded as occurring in forests and shrublands throughout most of the country, except the lower-rainfall eastern parts of the South Island and the northern part of Northland. However, McCann (1955) separated the Stewart Island population as *M. nebulosus* (McCann, 1955) (although he originally placed it incorrectly in *Heteropholis*, which is now part of *Naultinus*). *Mokopirirakau kahutarae* (Whitaker 1984), the first alpine member of the genus to be discovered, was found accidentally by an ornithological expedition in the Kaikoura Ranges in 1970. *Mokopirirakau cryptozoicus* (Jewell and Leschen 2004) was discovered in somewhat similar, high-altitude rocky habitat in the Takitimu Range in 1996, and an additional two alpine species, one from northern Fiordland and the other from western Otago, have had their distinctiveness confirmed by genetic (Nielsen et al. 2011) and morphological analysis, and descriptions are in preparation (Hitchmough, Neilsen, Bauer, unpublished data). Another possible alpine species from the Nelson Lakes area is far more poorly known, and its genetics have not yet been examined. In addition, two new lowland species from south Westland, one species from the southern North Island and one species from the Catlins and Southland, await splitting from *M. granulatus* following confirmation of their genetic and morphological distinctiveness (Nielsen et al. 2011). This makes a total of four named species, six with descriptions in preparation and one more awaiting further work to confirm its distinctiveness.

Dactylocnemis was erected as a new genus by Fitzinger (1861) for his *Dactylocnemis wüllerstorfi* (now regarded as a nomen nudum). Steindachner (1869) used this generic name for *D. pacificus*, making it available when the former *Hoplodactylus pacificus* complex was elevated to genus level by Nielsen et al. (2011). The phylogenetics of this group was investigated by Chong (1999), and her work, together with additional information from Nielsen et al. (2011), provides very strong evidence that *D. pacificus* should be split into six deeply divergent, congeneric species (Tables 4.1 and 4.2). Three of these species are endemics of single island groups (the Three Kings, Poor Knights and Mokohinaus/Pokohinaus), and two occur in sympatry in Te Pahi and on surrounding small islands, with the distribution of one of these species also extending to the Karikari Peninsula. *D. pacificus* itself occupies the balance of that species' range as formerly understood (Robb and Rowlands 1977; Robb 1980a, b). However, the identity of populations between the Bay of Islands and Kaitaia requires confirmation.

Hoplodactylus Fitzinger 1843 now contains only a single extant species, the large *H. duvaucelii* (Dumeril and Bibron 1836) (Tables 4.1 and 4.2). The genus also contains the giant, extinct *H. delcourti* Bauer and Russell, 1986, which, anomalously is known only from a single stuffed museum specimen with no locality data; strangely there are no known fossil remains of this species (see Shea 2016; Worthy 2016). *H. duvaucelii* contains two quite distinct groups of extant populations; one population occurs on islands in Cook Strait, and the other occurs off the northeastern North Island. These form distinct, reciprocally monophyletic genetic subclades, which differ in body size, scalation and colour pattern, and may thus potentially have been regarded as distinct species. However, the current distribution is a result

of range contractions due to extinction elsewhere as a result of predation by invasive mammals; bones of *H. duvaucelii* have been found in caves and pre-European-era predator middens across most of both major islands of New Zealand (Worthy 1987; Worthy and Holdaway 2002, Worthy 2016). In 2010, decades after the most recent mainland record, a survivor was accidentally collected in a mainland sanctuary in the Waikato region (Morgan-Richards et al. 2016). Genetic and morphological analysis of this specimen showed that it had a mix of genetic alleles and morphological characters otherwise confined to the northern or Cook Strait subclades (Morgan-Richards et al. 2016). This was interpreted as evidence that these subclades are conspecific and were previously connected by mainland gene flow.

The final genus, *Woodworthia* Garman, 1901, contains two described species, *W. maculata* (Gray, 1845) and *W. chrysoiretica* (Robb 1980a, b) (Tables 4.1 and 4.2). The generic name is feminine, so the endings of the specific names changed from—*us* to—*a* to match it in gender. *Woodworthia* also has nine new species with descriptions in preparation (although one of these probably has an available existing name, *W. brunnea* (Cope 1869)). In addition, one of these nine species (*W.* ‘Otago/Southland large’) has four very distinct subgroups, which might each warrant separate description. The inclusion of an additional taxon in *Woodworthia* (*W.* ‘Kaikouras’) was very strongly supported by the allozyme study of Hitchmough (1997). This taxon is readily distinguishable by morphology, but it was not recovered as a distinct mitochondrial DNA clade by Nielsen et al. (2011); instead each population clustered closely with the adjacent or sympatric population of *W.* ‘Marlborough mini’. This probably indicates a hybrid origin, but as the two sampled populations are quite widely separated geographically but share allozyme and morphological characters, indicating evolutionary cohesiveness, it may still justify formal description as a species. A very recent discovery (2010) was a population of *Woodworthia* on the Auckland west coast (Muriwai). This is the close genetic sister group to *W. maculata* sensu stricto, but has much shorter distal phalanges and a distinctive colour pattern (D. van Winkel pers. comm.); this may represent another undescribed species. *Woodworthia* therefore has two named species, nine with descriptions in preparation and up to five additional candidates for species status.

In total, therefore, there are 18 named extant (and one extinct) species of New Zealand gecko; 22 well-known, unnamed species with descriptions in preparation; and up to six additional possible new species (Tables 4.1 and 4.2).

4.4 Enhancing the Rate of Species Discovery and Description

To identify new species, it is necessary to have a clear definition of what constitutes a species (Coyne and Orr 2003). At a single place and time, it will be obvious that some groups of organisms exchange genes by breeding with each other and are therefore obviously the same species, whereas others never do so and are therefore clearly different species. However, when the same organisms are examined across a broad landscape or over geological time frames, that simple dichotomy becomes blurred; species vary in size and appearance across the landscape; some pairs of related species never interbreed, even when they are in contact; some produce rare, non-viable or sterile hybrids; some meet at narrow hybrid zones where frequent hybridisation, but little gene flow, occurs between the parental species; and others occur in broader zones where the species or populations merge. Other pairs of closely related populations are never found in contact with each other, so natural reproductive isolation cannot be used to assess species status. To define species, we use an evolutionary species concept (Wiley 1981), where either evidence of reproductive isolation or, if they are not in contact, of long-term independent evolutionary trajectories indicates separate species status. Evidence for independent trajectories includes very deep genetic divergence, consistent variation of multiple genetically independent characters, strong morphological divergence of sister clades indicating very different ecological adaptations and major differences in reproductive timing.

The existence of robust and almost completely comprehensive phylogenies for both geckos (Nielsen et al. 2011) and skinks (Chapple et al. 2009) means that it is now easy to genetically assess the identity of new specimens and the taxonomic position of those that do not match existing known species (named or unnamed). However, expert judgement and consideration of a range of contextual information are also necessary for decisions about whether new discoveries represent new species. For those, such as the recently discovered Homer skink, which are the sister taxon to a clade of several existing species, the answer is immediately obvious. However, for many others, it is not. The DNA barcoding approach, where all genetic distances above a certain threshold for that group are considered to represent distinct species, has not been found to work easily for New Zealand lizards (Chapple and Ritchie 2013). There is a very broad ‘grey zone’ of genetic distances, within which some pairs of sister taxa appear to meet the biological criteria for separate species status whilst others do not. For example, many of the long-recognised species of *Naultinus* are separated by genetic distances similar to those found among conspecific populations of other New Zealand geckos (Nielsen et al. 2011). However, the evidence for their species status is quite strong; they differ substantially in secondary sexual colouration of the males (in contrast there is no sexual colour dimorphism in the other New Zealand gecko genera), in timing of reproductive events and in body size, and based on the few examples remaining in the wild, they appear to meet at narrow contact zones where there may be some

introgressive hybridisation without a loss of distinct identities between species. An example has been found recently at the Denniston and Stockton Plateaus, where *N. tuberculatus* and *N. stellatus* are both present (M. Lettink pers. comm.). It does not help that we are now making inferences from very fragmented populations, so the contact zones between them often no longer exist.

There is currently no paid full-time taxonomic herpetologist in New Zealand (and there has not been one since Charles McCann; McCann 1955), and species descriptions are either being prepared by unpaid enthusiasts or by people who have to fit this task around a very busy schedule of other work. Although a great deal of progress has been made on the taxonomy of both geckos and skinks, many unanswered questions remain for both groups, and the high likelihood of new discoveries means that the expertise of herpetological taxonomists will be required in New Zealand for a long time to come. New genetic approaches, such as the assessment of large numbers of single nucleotide polymorphisms (SNPs), are rapidly becoming more affordable and could, in future, be very useful for addressing the remaining questions, and any new questions that may arise as additional species are recognised.

Taxonomic research requires access to specimens, and the requirements of formal taxonomic description and naming usually require that a type specimen or specimens are lodged in one of the major museums. High-quality digital photographs and the ability to extract DNA from tiny skin or tail-tip biopsies mean that large-scale collecting is no longer as important for preliminary assessment of taxonomic status. However, if a new species is to be described, a type specimen or, more usually, a series of specimens must be collected. Since all New Zealand native lizards have been protected under the Wildlife Act since 1996, this requires a permit from the Department of Conservation.

Acknowledgements We thank C. Daugherty and P. Ritchie for the advice and assistance during this project. DGC's New Zealand lizard taxonomic work was funded by a postdoctoral fellowship from the Allan Wilson Centre for Molecular Ecology and Evolution. The Marsden Fund provided financial support for preliminary gecko work by RAH. and C. Daugherty.

References

- Awiss M, Lyall J (1995) Survey for the "Chesterfield" skink (*Leiopisma* sp.) near Hokitika on the West Coast, 7–9 March 1995. Threatened Species Occasional Publication No. 8. Department of Conservation, 8p + figures
- Barry M, Shanas U, Brunton DH (2014) Year-round mixed-age shelter aggregations in Duvaucel's geckos (*Hoplodactylus duvaucelii*). *Herpetologica* 70:395–406
- Bauer AM (1990) Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). *Bonn Zool Monogr* 30:1–218
- Bell TP, Patterson GB (2008) A rare alpine skink *Oligosoma pikitanga* n. sp. (Reptilia: Scincidae) from Llawrenny Peaks, Fiordland, New Zealand. *Zootaxa* 1882:57–68
- Boulenger GA (1906) Descriptions of two new lizards from New Zealand. *Ann Mag Nat Hist* 7 (17):369–371 + plate

- Brandley MC, Bragg JG, Singhal S, Chapple DG, Jennings CK, Lemmon AR, Moriarty Lemmon E, Thompson MB, Moritz C (2015) Evaluating the performance of anchored hybrid enrichment at the tips of the tree of life: a phylogenetic analysis of Australian *Eugongylus* group scincid lizards. *BMC Evol Biol* 15:62. doi:10.1186/s12862-015-0318-0
- Chambers GK, Boon WM, Buckley TR, Hitchmough RA (2001) Using molecular methods to understand the Gondwanan affinities of the New Zealand biota: three case studies. *Aust J Bot* 49:377–387
- Chapple DG, Hitchmough RA (2016) Biogeography of New Zealand lizards. Chap. 5. In: Chapple DG (ed) *New Zealand lizards*. Springer, Cham
- Chapple DG, Patterson GB (2007) A new skink species (*Oligosoma taumakae* sp. nov.; Reptilia: Scincidae) from the Open Bay Islands, New Zealand. *N Z J Zool* 34:347–357
- Chapple DG, Ritchie PA (2013) A retrospective approach to testing the DNA barcoding method. *PLoS One* 8:e77882. doi:10.1371/journal.pone.0077882
- Chapple DG, Patterson GB, Bell T, Daugherty CH (2008a) Taxonomic revision of the New Zealand Copper Skink (*Cyclodina aenea*: Squamata: Scincidae) species complex, with descriptions of two new species. *J Herpetol* 42:437–452
- Chapple DG, Patterson GB, Gleeson DM, Daugherty CH, Ritchie PA (2008b) Taxonomic revision of the marbled skink (*Cyclodina oliveri*, Reptilia: Scincidae) species complex, with a description of a new species. *N Z J Zool* 35:129–146
- Chapple DG, Ritchie PA, Daugherty CH (2009) Origin, diversification and systematics of the New Zealand skink fauna (Reptilia: Scincidae). *Mol Phylogenet Evol* 52:470–487
- Chapple DG, Bell T, Chapple SNJ, Miller KA, Daugherty CH, Patterson GB (2011) Phylogeography and taxonomic revision of the New Zealand cryptic skink (*Oligosoma inconspicuum*; Reptilia: Scincidae) species complex. *Zootaxa* 2782:1–33
- Chong NL (1999) Phylogenetic analysis of the endemic New Zealand gecko species complex *Hoplodactylus pacificus* using DNA sequences of the 16S rRNA gene. Unpublished BSc (Hons) thesis, Victoria University of Wellington, Wellington
- Cope ED (1869) Observations on reptiles of the old world. *Proc Acad Nat Sci Phila* 20(1868):316–323
- Coyne JA, Orr HA (2003) *Speciation*. Sinauer Associates, Sunderland, MA
- Cree A, Hare KM (2016) Reproduction and life history of New Zealand lizards. Chap. 7. In: Chapple DG (ed) *New Zealand lizards*. Springer, Cham
- Daugherty CH, Patterson GB, Thorn CJ, French DC (1990) Differentiation of the members of the New Zealand *Leiopisma nigriplantare* species complex (Lacertilia: Scinidae). *Herpetol Monogr* 4:61–76
- Daugherty CH, Patterson GB, Hitchmough RA (1994) Taxonomic and conservation review of the New Zealand herpetofauna. *N Z J Zool* 21:317–323
- Dumeril AMC, Bibron G (1836) *Erpetologie generale ou histoire naturelle complete des reptiles*, Vol 3. Roret, Paris, iv + 517p
- Fitzinger LJ [FJ] (1861) Die ausbeute der oesterreichischen naturforscher an saugethieren und reptilien waehrend der weltumsegelung Sr. Majestat Fregatte Novara Oesterreichische Akademie der Wissenschaften Mathematische- naturwissenschaftliche Klasse 42:383–416
- Gibson S, Penniket S, Cree A (2015) Are viviparous lizards from cool climates ever exclusively nocturnal? Evidence for extensive basking in a New Zealand gecko. *Biol J Linn Soc* 115:882–895
- Gill BJ (1976) Aspects of the ecology, morphology and taxonomy of two skinks (Reptilia: Lacertilia) in the coastal Manawatu area of New Zealand. *N Z J Zool* 3:141–157
- Gill B, Whitaker T (2001) *New Zealand frogs and reptiles*. David Bateman, Auckland
- Girard C (1857) Descriptions of some new reptiles, collected by the United States Exploring Expedition, under the command of Capt. Charles Wilkes, U.S.N. Part 4: Including the species of saurians, exotic to North America. *Proc Acad Nat Sci Philadelphia* 1857:195–199
- Greaves SNJ, Chapple DG, Gleeson DM, Daugherty CH, Ritchie PA (2007) Phylogeography of the spotted skink (*Oligosoma lineocellatum*) and green skink (*O. chloronoton*) species

- complex (Lacertilia: Scincidae) in New Zealand reveals pre-Pleistocene divergence. *Mol Phylogenet Evol* 45:729–739
- Greaves SNJ, Chapple DG, Daugherty CH, Gleeson DM, Ritchie PA (2008) Genetic divergences pre-date Pleistocene glacial cycles in the New Zealand speckled skink, *Oligosoma infrapunctatum*. *J Biogeogr* 35:853–864
- Han D, Zhou K, Bauer AM (2004) Phylogenetic relationships among gekkotan lizards inferred from C-mos nuclear DNA sequences and a new classification of the Gekkota. *Biol J Linn Soc* 83:353–368
- Hardy GS (1977) The New Zealand Scincidae (Reptilia : Lacertilia); a taxonomic and zoogeographic study. *N Z J Zool* 4:221–325
- Hare KM, Hoare JM, Hitchmough RA (2007) Investigating natural population dynamics of *Naultinus manukanus* to inform conservation management of New Zealand’s cryptic diurnal geckos. *J Herpetol* 41:81–93
- Hare KM, Daugherty CH, Chapple DG (2008) Comparative phylogeography of three skink species (*Oligosoma moco*, *O. smithi*, *O. suteri*; Reptilia: Scincidae) in northeastern New Zealand. *Mol Phylogenet Evol* 46:303–315
- Hare KM, Chapple DG, Towns DR, van Winkel D (2016) The ecology of New Zealand’s lizards. Chap. 6. In: Chapple DG (ed) *New Zealand lizards*. Springer, Cham
- Hitchmough RA (1997) A systematic review of the New Zealand Gekkonidae PhD. Victoria University of Wellington, Wellington
- Hitchmough RA (compiler) (2002) New Zealand threat classification system lists 2002. Threatened Species Occasional Publication 23. Department of Conservation, Wellington, 210p
- Hitchmough RA, Bull L, Cromarty P (compilers) (2007) New Zealand threat classification system lists 2005. Department of Conservation, Wellington, 194p
- Hitchmough RA, Hoare JM, Jamieson H, Newman D, Tocher MD, Anderson PJ, Lettink M, Whitaker AH (2010) Conservation status of New Zealand reptiles, 2009. *N Z J Zool* 37:203–224
- Hitchmough R, Anderson P, Barr B, Monks J, Lettink M, Reardon J, Tocher M, Whitaker T (2013) Conservation status of New Zealand reptiles, 2012. *New Zealand Threat Classification Series* 2. Department of Conservation, Wellington, 16p
- Hitchmough R, Barr B, Monks J, Lettink M, Reardon J, Tocher M, van Winkel, D, Rolfe, J (2016) Conservation status of New Zealand reptiles, 2015. *New Zealand Threat Classification Series*. Department of Conservation, Wellington
- Hoare JM, Pledger S, Nelson NJ, Daugherty CH (2007) Avoiding aliens: behavioural plasticity in habitat use enables large, nocturnal geckos to survive Pacific rat invasions. *Biol Conserv* 136:510–519
- Jewell T (2008) A photographic guide to reptiles and amphibians of New Zealand (Photographs by R. Morris). New Holland, Auckland
- Jewell T, Leschen RAB (2004) A new species of *Hoplodactylus* (Reptilia: Pygopodidae) from the Takitimu Mountains, South Island, New Zealand. *Zootaxa* 792:1–11
- Jewell T, McFarlane L (1997) Research on grey geckos (genus *Hoplodactylus* Fitzinger, 1843) in the Hawea–Wanaka district, 5–9 May 1997. Unpublished report, Otago Conservancy, Department of Conservation, Dunedin, 73p
- Lettink M, Stengs H (2014) Survey for Chesterfield skink (*Oligosoma* aff. *infrapunctatum* ‘Chesterfield’) in the Reefton area and Grey Valley, West Coast. Unpublished Report prepared for the Department of Conservation National Office, Wellington, 12p
- Liggins L, Chapple DG, Daugherty CH, Ritchie PA (2008) A SINE of restricted gene flow across the Alpine Fault: phylogeography of the New Zealand common skink (*Oligosoma nigripantare polychroma*). *Mol Ecol* 17:3668–3683
- Loh G (2003) Te Kakahu skink hunt (Unpublished). Otago Conservancy, Department of Conservation, Dunedin, 4p

- McCann [YM] C (1955) The lizards of New Zealand. Gekkonidae and Scincidae. Dominion Mus Bull 17:1–127
- Morgan-Richards M, Rheyda Hinlo M, Smuts-Kennedy C, Innes J, Ji W, Barry M, Brunton D, Hitchmough RA (2016) Identification of a rare gecko from North Island New Zealand, and genetic assessment of its probable origin: a novel mainland conservation priority? J Herpetol 50:77–86
- Neilson KA (2002) Evaporative water loss as a restriction on habitat use in endangered New Zealand endemic skinks. J Herpetol 36:342–348
- Neilson KA, Duganzich D, Goetz B, Waas JR (2004) Improving search strategies for the cryptic New Zealand striped skink (*Oligosoma striatum*) through behavioural contrasts with the brown skink (*Oligosoma zelandicum*). N Z J Ecol 28:267–278
- Newman DG (1982) New Zealand herpetology. In: Proceedings of a symposium held at the Victoria University of Wellington, 29–31 Jan 1980. New Zealand Wildlife Service occasional publication No. 2, 495p
- Nielsen SV, Bauer AM, Jackman TR, Hitchmough RA, Daugherty CH (2011) New Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. Mol Phylogenet Evol 59:1–22
- O'Neill SB, Chapple DG, Daugherty CH, Ritchie PA (2008) Phylogeography of two New Zealand lizards: McCann's skink (*Oligosoma maccanni*) and the brown skink (*O. zelandicum*). Mol Phylogenet Evol 48:1168–1177
- Patterson GB (1997) South Island skinks of the genus *Oligosoma*: description of *O. longipes* n. sp. with redescription of *O. otagense* (McCann) and *O. waimatense* (McCann). J R Soc N Z 27:439–450
- Patterson G, Bell T (2009) The Barrier skink *Oligosoma judgei* n.sp. (Reptilia: Scincidae) from the Darran and Takitimu Mountains, South Island, New Zealand. Zootaxa 2271:43–56
- Patterson GB, Daugherty CH (1990) Four new species and one new subspecies of skinks, genus *Leiolopisma* (Reptilia: Lacertilia: Scincidae) from New Zealand. J R Soc N Z 20:65–84
- Patterson GB, Daugherty CH (1994) *Leiolopisma stenotis* n. sp., (Reptilia: Lacertilia: Scincidae) from Stewart Island. J R Soc N Z 24:125–132
- Patterson GB, Daugherty CH (1995) Reinstatement of the genus *Oligosoma* (Reptilia: Lacertilia: Scincidae). J R Soc N Z 25:327–331
- Patterson GB, Hitchmough RA, Chapple DG (2013) Taxonomic revision of the ornate skink (*Oligosoma ornatum*; Reptilia: Scincidae) species complex from northern New Zealand. Zootaxa 3736:54–68
- Pickard CR, Towns DR (1988) Atlas of the amphibians and reptiles of New Zealand. Conservation Sciences Publication No. 1, Department of Conservation, Wellington
- Pyron RA, Burbrink FT, Wiens JJ (2013) A phylogeny and updated classification of Squamata, including 4161 species of lizards and snakes. BMC Evol Biol 13:93
- Robb J (1970) A new skink of the genus *Leiolopisma* from New Zealand. Proceedings of the Section of Sciences, Koninklijke Nederlandse Akademie van Wetenschappen C73(2):228–229
- Robb J (1975) Two new skinks of the genus *Leiolopisma* from New Zealand. Proceedings of the Section of Sciences, Koninklijke Nederlandse Akademie van Wetenschappen C78(5):477–484
- Robb J (1977) A revision of the synonymy of three species of Leiolopismid skinks from New Zealand. Br Mus Nat Hist 31(6):303–310
- Robb J (1980a) Three new species of gekkonid lizards, genera *Hoplodactylus* Fitzinger and *Heteropholis* Fischer, from New Zealand. Natl Mus N Z Rec 1:305–310
- Robb J (1980b) New Zealand amphibians and reptiles in colour. Collins, Auckland, 128p
- Robb J, Hitchmough RA (1980) Review of the genus *Naultinus* Gray (Reptilia: Gekkonidae). Rec Auckland Inst Mus 16:189–200
- Robb J, Rowlands RPV (1977) Reinstatement of *Hoplodactylus maculatus* (Boulenger) with redescription of *H. pacificus* (Gray) (Reptilia: Squamata : Gekkonidae). Rec Auckland Inst Mus 14:133–142

- Romijn RL, Nelson NJ, Monks JM (2013) Forest geckos (*Mokopirirakau* 'Southern North Island') display diurno-nocturnal activity and are not reliant on retreats. *N Z J Zool* 41:103–113
- Shea GM (2016) History of discovery of the New Zealand lizard fauna. Chap. 2. In: Chapple DG (ed) *New Zealand lizards*. Springer, Cham
- Skinner A, Hugall AF, Hutchinson MN (2011) Lygosomine phylogeny and the origins of Australian scincid lizards. *J Biogeogr* 38:1044–1058
- Smith SA, Sadlier RA, Bauer AM, Austin CC, Jackman T (2007) Molecular phylogeny for the scincid lizards of New Caledonia and adjacent areas: evidence for a single origin of the endemic skinks of Tasmantis. *Mol Phylogenet Evol* 43:1151–1166
- Steindachner F (1869) Reptilien. In: Wullerstorff-Urbair B von (ed) *Reise der Oesterreichischen Fregatte Novara um die Erde, in den Jahren 1857, 1857, 1859*. 1(3) Staatsdruckerei, Wien
- Thomas BW (1981) *Hoplodactylus rakiuræ* n. sp. (Reptilia : Gekkonidae) from Stewart Island, New Zealand, and comments on the taxonomic status of *Heteropholis nebulosus* McCann. *N Z J Zool* 8:33–47
- Tocher MD, Marshall LJ (2001) Surveys for *Hoplodactylus* aff. *granulatus*, Roys Peak and Mt Alpha, Wanaka. Conservation advisory science notes No. 344. Department of Conservation
- Towns DR, Hitchmough RA, Perrott J (2016) Conservation of New Zealand lizards: a fauna not forgotten but undervalued? Chap. 11. In: Chapple DG (ed) *New Zealand lizards*. Springer, Cham
- Townsend AJ, de Lange PJ, Duffy CAJ, Miskelly CM, Molloy J, Norton D (2008) *New Zealand threat classification system manual*. Department of Conservation, Wellington, 35p
- Uetz P, Hosek J (eds) (2015) *The reptile database*. <http://www.reptile-database.org>. Accessed 13 Aug 2015
- Vos ME (1988) A biochemical, morphological and phylogenetic review of the genus *Cyclodina*. Unpublished Honours Thesis, Victoria University of Wellington, Wellington
- Whitaker AH (1984) *Hoplodactylus kahutaræ* n.sp. (Reptilia: Gekkonidae) from the Seaward Kaikoura Range, Marlborough, New Zealand. *N Z J Zool* 11:259–270
- Whitaker AH (1991) Research on the striped gecko, *Hoplodactylus stephensi*, on Maud Island, Pelorus Sound, Marlborough, 6–12 March, 1991. N.Z. Dept. of Conservation, Nelson/Marlborough Conservancy, Nelson
- Whitaker T, Hitchmough RA, Chappell R (1999) A striped gecko (*Hoplodactylus stephensi*) at Coromandel. Conservation Advisory Science Notes No. 2, 32. Department of Conservation, Wellington
- Wiley EO (1981) *Phylogenetics. The theory and practice of phylogenetic systematics*. Wiley-Interscience, New York
- Worthy TH (1987) Osteological observations on the larger species of the skink *Cyclodina* and the subfossil occurrence of these and the gecko *Hoplodactylus duvaucelii* in the North Island, New Zealand. *N Z J Zool* 14:219–229
- Worthy TH (2016) A review of the fossil record of New Zealand lizards. Chap. 3. In: Chapple DG (ed) *New Zealand lizards*. Springer, Cham
- Worthy TH, Holdaway RN (2002) *The lost world of the Moa. Prehistoric life of New Zealand*. Indiana University Press, Bloomington, IN