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Origin, diversification, and systematics of the New Zealand skink fauna (Reptilia: Scincidae)

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ABSTRACT

The diverse scincid lizard fauna of the largely submerged subcontinent of Zealandia (which incorporates New Zealand, New Caledonia, Lord Howe Island, Norfolk Island, and the Chatham Islands) forms a monophyletic lineage within the *Eugongylus* group of skinks. We use 4062 bp of mitochondrial (ND2, ND4, Cytochrome b, 12SrRNA, 16SrRNA) and nuclear (Rag-1) DNA sequence data to recover a molecular phylogeny for the New Zealand skink fauna, and investigate the origin and diversification of skinks in New Zealand. Our phylogeny includes 32 of the 33 extant described New Zealand skink species (*Cyclodina* and *Oligosoma*), the Lord Howe Island skink (*C. lichenigera*), and representatives from several New Caledonian genera. Neighbour-joining, Maximum Parsimony, Maximum Likelihood, and Bayesian phylogenetic analyses are used to demonstrate that the New Zealand skink species form a single monophyletic lineage, with *C. lichenigera* representing a closely related sister lineage to the New Zealand radiation. Our relaxed molecular clock analyses indicate that skinks colonised New Zealand in the early Miocene (16–22.6 mya), shortly after the 'Oligocene drowning' event (~25 mya). We propose that skinks reached New Zealand from New Caledonia via long-distance overwater dispersal, with *C. lichenigera* persisting on volcanic islands along the Lord Howe Rise and Norfolk Ridge. Eight major genetic clades are evident within the New Zealand skink fauna, with the divergences among these clades during the early to mid-Miocene resulting in distinct open habitat, forest, and coastal radiations. Subsequent diversification in the late Miocene–Pliocene appears to coincide with tectonic activity along the Alpine Fault and the uplift of the Southern Alps. We were unable to resolve the phylogenetic affinities of *O. suteri*, New Zealand's only native oviparous skink. We use the phylogeny and topology tests to resolve several taxonomic issues and assess the taxonomic status of several suspected undescribed taxa. We complete a generic revision for the New Zealand skink fauna, placing *C. lichenigera* and all native New Zealand species into a single genus.

1. Introduction

New Zealand is part of the largely submerged subcontinent of Zealandia (Fig. 1), which separated from Gondwana approximately 80 mya (Trewick et al., 2007; Landis et al., 2008; Neall and Trewick, 2008). Zealandia was stretched and thinned as it rifted, resulting in a relatively thin continental crust and the gradual subsidence and marine inundation of the majority of the subcontinent (Trewick et al., 2007; Landis et al., 2008; Neall and Trewick, 2008). Marine inundation reached its peak in the Oligocene ('Oligocene drowning', ~25 mya) when the vast majority of Zealandia was believed to have been submerged (Cooper and Millener, 1993; Waters and Craw, 2006; Trewick et al., 2007; Landis et al., 2008). Even today 93% of Zealandia remains submerged (Mortimer, 2004; Landis et al., 2008; Neall and Trewick, 2008; Goldberg et al., 2008), with the relatively small area of emergent land the result of events such as volcanic eruptions and tectonic activity (Gibbs, 2006).

Zealandia is approximately half the size of the Australian continent, and currently consists of New Zealand, New Caledonia, Norfolk Island, Lord Howe Island, Chatham Islands, numerous subantarctic islands, and several submerged ridges (e.g. Lord Howe Rise, Norfolk Ridge, Chatham Rise, Campbell Plateau) (Fig. 1). New Caledonia emerged during the late Eocene (~33–38 mya) when a region of the Zealandia continental crust collided with the Loyalty Islands Arc (reviewed in Neall and Trewick, 2008; Grandcolas et al., 2008). Lord Howe Island and surrounding islands (including Blackburn Island and Ball's Pyramid) are the remnants of an oceanic volcano that originally emerged 7 mya (McDougall et al., 1981), while Norfolk Island and the nearby Philip Island were formed as a result of volcanic activity 3 mya (Jones and McDougall, 1973). Geological evidence indicates that the Chatham Islands (970 km^2) only recently re-emerged within the last 1–4 myr as a result of volcanic

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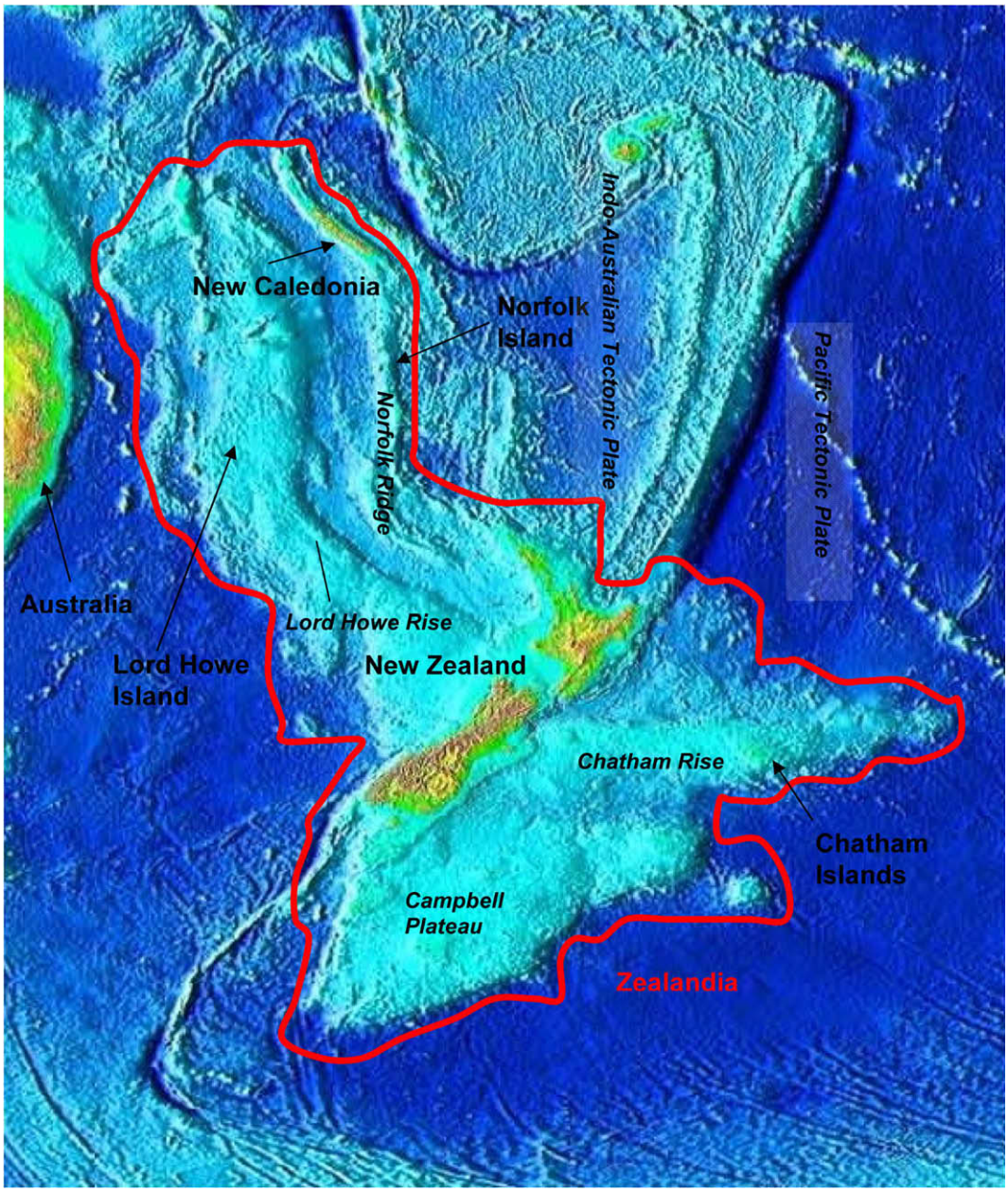

Fig. 1. Map of Zealandia. The red line indicates the approximate extent of the largely submerged continental crust of Zealandia (modified from Trewick et al., 2007). The locations of the Chatham Islands, Chatham Rise, Campbell Plateau, New Zealand, Lord Howe Island, Lord Howe Rise, Norfolk Island, Norfolk Ridge, New Caledonia, and Australia are indicated. New Zealand is located on the boundary of the Indo-Australian and Pacific tectonic plates. The Alpine Fault refers to where this plate boundary diagonally bisects the South Island of New Zealand from the southwest to the northeast. (Base image provided by the National Oceanic and Atmospheric Administration, NOAA).

and tectonic activity at the eastern end of the Chatham Rise (Campbell, 1998; Campbell et al., 2006).

New Zealand is located on the boundary of the Indo-Australian and Pacific plates (Fig. 1), with its current topography the result of continual tectonic activity along the plate boundary over the last 26 myr (Trewick et al., 2007; Landis et al., 2008). The Alpine Fault is where this plate boundary diagonally bisects the South island of New Zealand from the southwest to the northeast (Fig. 1 and 2). The Southern Alps that characterise the South Island were formed by 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). The uplift of the Southern Alps (>3000 m by the early Pleistocene; Chamberlain et al., 1999) transformed the previously low-lying South Island (<1000 m elevation), resulting in increased topographic, climatic and ecological diversity (Lee et al., 2001; Gibbs, 2006). The New Zealand climate cooled during the late Pliocene–Pleistocene (Newnham et al., 1999) and the presence of mountainous regions in the South Island facilitated extensive glaciation during the Pleistocene, created an expansive alpine zone, and fundamentally altered climatic conditions and prevailing weather patterns (Suggate, 1990; Pillans, 1991; Worthy and Holdaway, 2002).

The lower North Island was inundated throughout the Pliocene, with the Manawatu Strait separating present-day Taranaki/Hawkes Bay from the South Island (Lewis et al., 1994; Worthy and Holdaway, 2002; Fig. 2). At this time the southern coastline of the North Island was situated across the present-day Central Plateau region (Worthy and Holdaway, 2002; Fig. 2), a region that cur-

Fig. 2. Major geographic regions of New Zealand. The three main islands are the North Island, South Island, and Stewart Island. The solid line indicates the approximate position of the Taupo Line (approximately 39°S).

rently represents a biogeographic barrier (called the Taupo Line) that delineates the biota of the upper and lower North Island (McCann, 1955, 1956; Wardle, 1963; Towns et al., 1985; Rogers, 1989; Connor, 2002). Tectonic activity in the late-Pliocene and early-Pleistocene resulted in the uplift of the lower North Island and draining of the Manawatu Strait (Lewis et al., 1994; Worthy and Holdaway, 2002). Present-day Cook Strait (separating the North Island and South Island; Fig. 2) was formed during the late-Pleistocene (~0.45 mya; Lewis et al., 1994). Sea-level fluctuations (up to 135 m below present) associated with Pleistocene glacial cycles are believed to have resulted in intermittent landbridges across Cook Strait during glacial maxima of the late-Pleistocene (Lewis et al., 1994; Stevens et al., 1995; Worthy and Holdaway, 2002).

New Zealand spans 13° of latitude (34–47°S) and is currently comprised of two main islands (North Island: 113,729 km^2, South Island: 150,437 km^2), and Stewart Island (1680 km^2) (Fig. 1 and 2; Worthy and Holdaway, 2002; Neall and Trewick, 2008). There are ~650 small islands and islets (250 > 8 ha, 400 < 8 ha) located within 50 km of the two main islands (Worthy and Holdaway, 2002; Neall and Trewick, 2008). Despite its continental (Gondwanan) heritage, in many respects New Zealand's biota resembles that of oceanic islands (Daugherty et al., 1993; Gibbs, 2006; Trewick et al., 2007). The New Zealand biota is characterised by high levels of species richness and endemism, and includes several relictual or archaic forms such as the tuatara (Sphenodontia) and leiopelmatid frogs (Daugherty et al., 1993; Gibbs, 2006). Although some taxa appear to have Gondwanan origins, the majority of the biota has colonised New Zealand since its separation from Gondwana (reviewed in Gibbs, 2006; Waters and Craw, 2006; Trewick et al., 2007; Landis et al., 2008; Goldberg et al., 2008). The source of the colonisers (e.g. Australia, New Caledonia, other Pacific regions), and the timing of their arrival, vary among taxa (reviewed in Goldberg et al., 2008).

All native New Zealand scincid lizards are endemic (Gill and Whitaker, 2001), and belong to the *Eugongylus* lineage of skinks (Smith et al., 2007). Smith et al. (2007) demonstrated that the *Eugongylus* skinks of Zealandia are monophyletic, with skinks colonising New Zealand from New Caledonia. Direct land connections between New Caledonia and New Zealand have not been present since the Oligocene (Lee et al., 2001; Gibbs, 2006; Landis et al., 2008). However, in the early-late Miocene (~10–20 mya) there may have been an island chain connection (i.e. oceanic volcanoes spaced ~50–100 km apart) between New Caledonia and New Zealand along the Lord Howe Rise and Norfolk Ridge (Lee et al., 2001; but see Landis et al., 2008). Colonisation of New Zealand from New Caledonia requires long-distance over-water dispersal (Hickson et al., 2000; Smith et al., 2007). Successful over-water dispersal has been observed in reptiles over contemporary timescales (e.g. Censky, 2006), and inferred over evolutionary timescales (e.g. Rocha et al., 2006), including in several New Zealand skink species (e.g. *Oligosoma acrinasum*, Thomas and Whitaker, 1995; *O. suteri*, Hare et al., 2008a). Indeed, it is clear that the Chatham Islands skink (*O. nigriplantare nigriplantare*) has colonised the Chatham Islands (~800 km east of New Zealand) from New Zealand via long-distance over-water dispersal within the last ~4–6 myr (Liggins et al., 2008a).

Early authors hypothesized multiple Pliocene–Pleistocene colonisations of New Zealand by skinks (McCann, 1955; Towns, 1974; Bull and Whitaker, 1975; Hardy, 1977; Robb, 1973, 1980), but later estimates based on allozymes and mitochondrial DNA indicate a single colonisation in late Oligocene–early Miocene (~20–23 mya; Towns et al., 1985; Hickson et al., 2000). More recently, Smith et al. (2007), using divergence estimates based on mitochondrial and nuclear DNA sequences, suggested a single Miocene (7.9 mya using ND2 molecular clock, 19.9–22.9 mya using ND2 + c-mos molecular clock) origin for the New Zealand skink fauna. However, their favoured age for the New Zealand skink radiation (7.9 myr) is incompatible with the available fossil evidence. Although New Zealand has a relatively poor pre-Quaternary terrestrial fossil record, the St Bathans early Miocene (16–19 mya) fossil deposit in Central Otago clearly indicates the presence of a skink fauna in New Zealand during the early Miocene (Worthy et al., 2006a,b, 2007).

The New Zealand skink fauna has had a complex taxonomic history. The earliest descriptions of New Zealand skink species were made by European (Duméril and Bibron, 1839; Gray, 1843, 1845; Duméril and Duméril, 1851; Peters, 1873) and American (Girard, 1857) taxonomists, describing material that was collected by naturalists on various scientific expeditions (reviewed in McCann, 1955; Robb, 1973; Hardy, 1977). In the late 19th century, New Zealand herpetologists (e.g. Buller, Hutton) started making contributions to the taxonomic literature, with Buller (1871) describing *Mocoa striata* (=*Oligosoma striatum*). Initially, there was substantial instability in the generic assignment of the New Zealand skink species, with species described between 1839–1887 being placed in *Mocoa*, *Lygosoma*, *Tiliqua*, *Cyclodina*, and several other genera (*Oligosoma*, *Hinulia*, *Euprepes*, *Lygosomella*, *Norbea*, *Hombronia*; see Hardy, 1977). Although 10 currently recognised species were originally described during this period, in his *Catalogue of the Lizards in the British Museum* Boulenger (1887) only listed seven New Zealand skink species. Boulenger (1887) included all New Zealand skink species in *Lygosoma* (*grande*, *moco*, *lineoocellatum*, *smithii*, *ornatum*), including *L. infrapunctatum* which he mistakenly considered to be an Australian species. Three new species were described at the start of the 20th century: *L. dendyi* (Chatham Islands, Boulenger, 1902), *L. suteri*, and *L. homalonotum* (Boulenger, 1906).

The early descriptions of New Zealand skinks were inaccurate and largely inadequate, with many of the type specimens subsequently lost or lodged in overseas museums (reviewed in McCann,

1955; Robb, 1973; Hardy, 1977). This ultimately led to multiple descriptions of the same species, a large number of composite species, substantial taxonomic instability, and the proliferation of synonymies (see Hardy, 1977). Taxonomic activity relating to New Zealand skinks all but ceased between 1906 and 1955, apart from a small number of references to the local fauna from authors focused on skinks from other countries and regions (reviewed in McCann, 1955; Hardy, 1977). McCann (1955) provided the first modern taxonomic revision of the New Zealand skink fauna, resolving decades of confused taxonomy and synonymy. He listed 17 species from New Zealand, placing all species in *Leiolopisma* except for *Sphenomorphus pseudornatus*. McCann (1955) considered four of the seven species from Boulenger (1887) to be composite (*grande*, *moco*, *lineoocellatum*, *smithi*), describing two subspecies of *L. smithi* (*smithi*, *numerale*) and three subspecies of *L. grande* (*grande*, *otagense*, *waimatense*). He resurrected *L. zelandica* Gray and *L. aeneum* Girard, also describing several new species (*fallai*, *oliveri*, *festivum*, *latilinearum*), including *L. turbotti* from the Chatham Islands.

The 1970's were an extremely active period for taxonomic research on New Zealand skinks. Joan Robb described *L. alani* (Robb, 1970), *L. pachysomaticum* (for the southern populations of *L. oliveri*) and *L. macgregori* (Robb, 1975). Greer (1974) moved *S. pseudornatus* into *Leiolopisma* with the other New Zealand skink species. A taxonomic study of several skinks from the Manawatu region resulted in the resurrection of *L. zelandicum* Gray (Gill, 1976). Hardy (1977), aided by allozyme and haem compound electrophoresis, completed a comprehensive revision of the New Zealand skink fauna, recognising 22 species in two genera. *Cyclodina* Girard was resurrected to accommodate *alani*, *macgregori*, *oliveri*, *aenea*, and *ornata* (the latter two species were previously part of *S. pseudornatus*), and the newly described *C. whitakeri*. The remaining species were assigned to the widespread genus *Leiolopisma*. Hardy (1977) described three new *Leiolopisma* species: *L. gracilicorpus* (previously part of *L. homalonotum*), *L. chloronoton* (previously part of *L. lineoocellatum*), and *L. acrinasum*. *Leiolopisma nigriplantare* Peters was resurrected, with *L. dendyi* and *L. turbotti* synonymised under *L. nigriplantare nigriplantare* (Chatham Islands subspecies), while *L. n. maccanni* (New Zealand mainland subspecies) was erected for the species described as *L. zelandica* by McCann. Hardy (1977) elevated *L. otagense* to a distinct species, recognising two forms (form *otagense*, form *waimatense*), without providing them with subspecies status. *Leiolopisma latilinearum* was synonymised under the resurrected *L. striatum* Buller, while *L. festivum* was synonymised under *L. lineoocellatum*, and *L. pachysomaticum* synonymised under *C. oliveri*. Hardy (1977) rejected McCann's designation of subspecies (*smithi*, *numerale*) in *L. smithi*, and provided a detailed list of synonymies for all New Zealand skinks species.

In the 1990's, Geoff Patterson and Charles Daugherty used morphological analyses and allozyme electrophoresis to complete a taxonomic revision of the *L. nigriplantare maccanni* species complex (Daugherty et al., 1990; Patterson and Daugherty, 1990). This resulted in the description of five new species (*inconspicuum*, *maccanni*, *microlepis*, *notosaurus*, Patterson and Daugherty, 1990; *stenotis*, Patterson and Daugherty, 1994) and a new subspecies (*L. n. polychroma*) for the New Zealand mainland common skink (Patterson and Daugherty, 1990). Worthy (1991) described a large extinct species of *Cyclodina* from a subfossil deposit in the Northland region of the North Island (*C. northlandi*). Patterson and Daugherty (1995) then reinstated *Oligosoma* Girard to accommodate all New Zealand *Leiolopisma* species, with Patterson (1997) describing a new species from Canterbury (*O. longipes*), and elevating *O. otagense* and *O. waimatense* to distinct species.

More recently, mitochondrial and nuclear DNA sequence data have been pivotal in uncovering cryptic species within several widespread New Zealand skink species. Chapple and Patterson (2007) described *O. taumakae* from the Open Bay Islands, off the coast of Westland. A revision of the *C. oliveri* complex resulted in the description of *C. townsi* and re-affirmed the synonymy of *C. pachysomaticum* under *C. oliveri* (Chapple et al., 2008a). Similarly, a revision of the *C. aenea* complex led to the description of two new species, *C. hardyi* from the Poor Knights Islands and *C. levidensa* from the Northland region (Chapple et al., 2008b). Bell and Patterson (2008) described a recently discovered species (*O. pikitanga*) from the Llawrenny Peaks in Fiordland. Currently, there are 35 described species and subspecies in two genera, *Cyclodina* (9 extant and 1 extinct species) and *Oligosoma* (24 extant species/subspecies and 1 presumed extinct species). However, recent molecular studies have indicated that several recognised species actually constitute species complexes: *O. lineoocellatum*–*O. chloronoton* (Greaves et al., 2007), *O. infrapunctatum* (Greaves et al., 2008), *O. smithi* –*O. microlepis* (Hare et al., 2008a), *O. nigriplantare* (Liggins et al., 2008a,b), *C. ornata* (Chapple et al., 2008c), and *O. inconspicuum*–*O. notosaurus* (DGC, unpublished data). In addition, several presumed new species (e.g. *O. longipes* 'Rangitata', *O. inconspicuum* 'Te Kakahu') continue to be discovered in remote regions of the country (e.g. Patterson, 2002; Jewell, 2008). The authors and collaborators (G. Patterson) are currently in the process of completing morphological revisions and describing these new species. Thus, the actual New Zealand skink fauna may exceed 45 species.

Oligosoma species generally have shallow pointed heads, long limbs and toes, and bodies that are oval in cross-section (Patterson and Daugherty, 1995; Gill and Whitaker, 2001). They are diurnal species (except *O. suteri*) that prefer open habitats where they are overt baskers (Gill and Whitaker, 2001). In contrast, *Cyclodina* species have deeper and blunter heads, relatively shorter limbs and toes, and bodies that are squarish in cross-section (Patterson and Daugherty, 1995; Gill and Whitaker, 2001). They are nocturnal or crepuscular species that prefer more shaded habitats (Gill and Whitaker, 2001). *Oligosoma* species are widespread, occurring throughout the two main islands (North Island, South Island), Stewart Island, and the Chatham Islands, while *Cyclodina* species are restricted entirely to the North Island and surrounding offshore islands. However, several authors have expressed doubts regarding the reciprocal monophyly of *Cyclodina* and *Oligosoma* (Hickson et al., 2000; Smith et al., 2007; Chapple et al., 2008c). In addition, *Cyclodina* currently includes the Lord Howe Island skink (*C. lichenigera*), which occurs on Lord Howe Island (and surrounding islands, including Ball's Pyramid) and Philip Island (6 km south of Norfolk Island) (Wilson and Swan, 2008). Although the Lord Howe Island skink is tentatively placed in either *Cyclodina* (Cogger, 2000; Wilson and Swan, 2008) or *Oligosoma* (Smith et al., 2007), its true taxonomic affinities have proved problematic. However, Smith et al. (2007) recently demonstrated that *C. lichenigera* is a sister species to the entire New Zealand skink radiation.

Cyclodina lichenigera is oviparous, and several authors have suggested that it has a close phylogenetic affinity to *Oligosoma suteri* (restricted to the warmer Northland region), the only native oviparous skink species in New Zealand (Towns, 1974; Bull and Whitaker, 1975; Hardy, 1977). Since cold temperatures have been demonstrated to have a detrimental impact on *O. suteri* egg and hatchling survival (e.g. Hare et al., 2002, 2004, 2008b), its ability to survive glacial maxima (except in warm northern refugia) has been questioned, leading to speculation that *O. suteri* represents a secondary (and more recent) invasion of New Zealand (Towns, 1974; Bull and Whitaker, 1975; Hardy, 1977). However, if *O. suteri* is not a secondary coloniser or a basal member of the New Zealand radiation, it might indicate that there has been a viviparity–oviparity reversal within the lineage. Although there have been 100+ independent origins of viviparity in squamate reptiles, a secondary reversal to oviparity has never been verified in a viviparous squamate lineage (reviewed in Shine, 1985; Blackburn, 1999; Shine and Lee, 1999).

There has only been one published phylogeny for the New Zealand Scincidae (Hickson et al., 2000, based on ~380 bp 12SrRNA), although two unpublished phylogenies have been completed during doctoral studies (Hay, 1998: Cytochrome b and 16SrRNA; Smith, 2001: 12SrRNA and two nuclear introns). These three studies yielded poorly resolved phylogenies with few well-supported relationships among species, presumably due to insufficient taxon sampling (~half of the known species) and sequence data (<1000 bp). However, Hickson et al. (1992) suggested that hybridisation might occur between *O. maccanni* and *O. n. polychroma*. Similarly, captive breeding records have demonstrated the potential for hybridisation between *O. otagense* and *O. waimatense* (D. Keall, unpublished data).

Here we aim to recover a robust and well-supported molecular phylogeny for the New Zealand Scincidae using mitochondrial (ND2, ND4, Cytochrome b, 12SrRNA, 16SrRNA) and nuclear (Rag-1) DNA sequences. This phylogeny will enable examination of the phylogenetic relationships among the New Zealand skink species, with topology tests used to evaluate taxonomic issues and the phylogenetic placement of *O. suteri*. Our analyses also examine the age of the New Zealand skink radiation and the subsequent diversification across the archipelago. We discuss the taxonomic implications of the molecular phylogeny and use the genetic data to revise the New Zealand skink genera.

2. Materials and methods

2.1. Taxon sampling

We obtained tissue samples from 32 of the 33 extant described species and subspecies of New Zealand skinks (all except *C. levidensa*; Table 1). Samples were also obtained from several putative undescribed species of New Zealand skink: *O. inconspicuum* 'Big Bay' (Jewell, 2008), *O. infrapunctatum* 'Southern North Island' (Greaves et al., 2008), *O. infrapunctatum* 'Chesterfield' (Greaves et al., 2008), and *O. longipes* 'Rangitata' (Jewell, 2008). We also included tissue samples from the Lord Howe Island skink (*C. lichenigera*). For the majority of species, we obtained at least two samples from the National Frozen Tissue Collection (NFTC; Victoria University of Wellington, New Zealand), the ethanol preserved specimens housed at Te Papa Tongarewa (National Museum of New Zealand, Wellington), and the South Australian Museum (Table 1). Based on the phylogeny of Smith et al. (2007), we included representatives from several New Caledonian (*Nannoscincus mariei*, *Marmorosphax tricolor*, *Caledoniscincus austrocaledonicus*, *Lioscincus tillieri*) and Australian (*Lampropholis guichenoti, Niveoscincus pretiosus, Morethia adelaidensis*) *Eugongylus* skink group genera as outgroups (samples obtained from the Australian Museum). Thus, a total of 92 samples (85 ingroup samples, 7 outgroup samples) were used in this study (Table 1).

2.2. DNA extraction, amplification, and sequencing

Total genomic DNA was extracted from liver, muscle, toe or tail samples using a modified phenol–chloroform extraction protocol (Sambrook et al., 1989). For each sample we sequenced portions of five mitochondrial genes: ND2 (~600 bp), ND4 (~700 bp), Cytochrome b (~700 bp), 12SrRNA (~900 bp), and 16SrRNA (~550 bp). We also sequenced a fragment of the protein-coding nuclear gene Rag-1 (~900 bp). These regions were targeted because work across several taxonomic levels in squamate reptiles has indicated useful levels of variability (e.g. Reeder, 2003; Jennings et al., 2003; Townsend et al., 2004; Smith et al., 2007).

The primers used to amplify and sequence the mitochondrial and nuclear genes are provided in Table 2. PCR and sequencing were conducted as outlined in Greaves et al. (2007). Sequence data were edited using ContigExpress in Vector NTI Advance v9.1.0 (Invitrogen), and aligned using the default parameters of Clustal X v1.83 (Thompson et al., 1997). We translated all coding region sequences to confirm that none contained premature stop codons. Sequence data were submitted to GenBank under the accession numbers provided in Table 1.

2.3. Phylogenetic analyses

The number of variable sites, the number of parsimony-informative sites, and the mean nucleotide frequency for each gene region were calculated in MEGA 4 (Tamura et al., 2007). Preliminary analyses for each gene region revealed that there was no substantial incongruence among gene regions. The data was concatenated into a single dataset for all analyses. Neighbour-Joining (NJ), Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian tree building methods were used.

To determine the most appropriate model of sequence evolution for our dataset, we generated log-likelihood scores for the dataset using PAUP* v4.0b10 (Swofford, 2002) and then used those scores to conduct hierarchical likelihood tests (hLRT) and Akaike Information Criterion (AIC) tests in Modeltest 3.7 (Posada and Crandall, 1998). Modeltest was also used to estimate base frequencies, substitution rates, the proportion of invariable sites (I), and the among-site substitution rate variation (G). These values were then used as settings in PhyML 3.0 (Guindon and Gascuel, 2003) to generate a ML tree with 500 bootstraps. A MP tree was generated in PAUP* using the heuristic search option. A NJ tree was generated in PAUP* using the model correction (GTR) selected by Modeltest.

MrModelTest 2.3 (Nylander, 2004) was used to select (using both hLRT and AIC) the most appropriate model of sequence evolution for the Bayesian analyses. MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003) was then used to complete a partitioned Bayesian analysis. Preliminary analysis of each mtDNA coding region revealed congruent tree topologies and similar levels of phylogenetic signal. We therefore employed an analysis with three partitions: mtDNA coding regions (ND2, ND4, Cytochrome b), mtDNA rRNA (12SrRNA, 16SrRNA), and nuclear gene (Rag-1). We ran the full analysis twice, using four Markov chains per run. We ran the chains for five million generations to ensure sufficient sampling of tree space. The chain was sampled every 100 generations to obtain 50,000 sampled trees. The program Tracer 1.4 (Rambaut and Drummond, 2007) was used to check for chain convergence. The first 25% of sampled trees were discarded as the burn-in phase and the last 37,500 trees were used to estimate Bayesian posterior probabilities. Bootstrap values (500 ML bootstraps) and Bayesian posterior probabilities were used to assess branch support. We considered branches supported by bootstrap values of 70 or greater (Hillis and Bull, 1993), and/or posterior probability values greater than or equal to 0.95 (Wilcox et al., 2002) to be supported by our data. Uncorrected genetic distances (for the mtDNA data) among species and clades were calculated in MEGA.

2.4. Testing alternative topologies

We completed Shimodaira–Hasegawa tests in PAUP* (Shimodaira and Hasegawa, 1999; Goldman et al., 2000) using full optimization and 1000 replicates to examine several alternative topologies for the New Zealand skink fauna. We tested the significance of the log-likelihood difference between our optimal ML tree (using the ML $-\ln L$) and several alternative topologies. Specifically, we assessed whether:

(1) *Cyclodina* is monophyletic.
(2) *Oligosoma* is monophyletic.

Table 1
Locality information and GenBank Accession Nos. for samples used in this study. Samples with CD or FT codes were obtained from the National Frozen Tissue Collection (NFTC) housed at Victoria University of Wellington, New Zealand. Samples with RE codes were obtained from ethanol preserved specimens housed at Te Papa Tongarewa, National Museum of New Zealand, Wellington. Samples with ABTC (Australian Biological Tissue Collection) codes were obtained from the South Australian Museum. Samples with NR and EBU codes were obtained from the Australian Museum.

Species	Tissue code	Museum code	Locality	GenBank Accession Nos.					
				ND2	ND4	Cyt b	16SrRNA	12SrRNA	Rag-1
Cyclodina aenea	CAE1	FT171	Korapuki Island, Mercury Islands	EF567130	EU567744	EU567770	EU567865	EU567969	EU568057
C. aenea	CAE2	FT5253	Pukerua Bay	EF567127	EU567745	EU567771	EU567866	EU567970	EU568058
C. alani	CAL1	FT145	Green Island, Mercury Islands	EF043106	EF043169	EU567774	EU567843	EU567971	EU568065
C. alani	CAL2	FT3016	Matapia Island	EF567170	–	EU567775	EU567844	EU567972	EU568070
C. hardyi	PKS1	CD1036	Aorangi Island, Poor Knights Islands	EF567122	EU567746	EU567779	EU567871	EU567991	EU568059
C. hardyi	PKS2	CD1037	Aorangi Island, Poor Knights Islands	EF567125	EU567747	EU567780	EU567872	EU567992	EU568060
C. macgregori	CMA1	FT3	Mana Island	EF567173	EU567730	EU567776	EU567845	EU567973	EU568063
C. macgregori	CMA2	FT1095	Mana Island	EF567174	EU567731	EU567777	EU567846	EU567974	EU568064
C. oliveri	COL1	CD1034	Aorangi Island, Poor Knights Islands	EF033045	EF033069	EF081236	EU567853	EU567977	EU568074
C. oliveri	COL2	CD1035	Aorangi Island, Poor Knights Islands	EF081175	EF081202	EF081237	EU567854	EU567978	EU568076
C. oliveri	COL3	FT137	Green Island, Mercury Islands	EF081176	EF081203	EF081246	EU567855	EU567979	EU568075
C. oliveri	COL4	FT572	Ruamahuanui, Aldermen Islands	EF081177	EF081204	EF081238	EU567856	EU567980	EU568077
C. ornata	COR1	FT188	Devonport, Auckland	EF103954	EF103995	EF104030	EU567863	EU567975	EU568079
C. ornata	COR2	FT3733	Botanic Gardens, Wellington	EF567196	EU567734	EU567778	EU567864	EU567976	EU568078
C. townsi	COL14	–	Ahuriri Stream, Great Barrier Island	EF081173	EF081200	EF081223	EU567857	EU567981	EU568068
C. townsi	COL15	–	Ahuriri Stream, Great Barrier Island	EF081174	EF081201	EF081224	EU567858	EU567982	EU568069
C. townsi	MOS1	FT182	Mokohinau Islands	EF081184	EF081211	EF081228	EU567859	EU567983	EU568080
C. townsi	MOS2	FT617	Pupuha Island, Hen and Chicken Islands	EF081187	EF081214	EF081229	EU567860	EU567984	EU568073
C. whitakeri	CWH1	CD949	Pukerua Bay	EF081182	EF081209	EF081247	EU567861	EU567985	EU568083
C. whitakeri	CWH2	FT294	Middle Island, Mercury Islands	EF081183	EF081210	EF081248	EU567862	EU567986	EU568084
Oligosoma acrinasum	OAC1	CD826	Fiordland	EF033046	EF033060	EF071064	EU567904	EU567993	EU568098
O. acrinasum	OAC3	RE1839	Five Fingers Peninsula, Fiordland	EF033047	EF033061	EU567811	EU567905	EU567994	EU568099
O. chloronoton	OCH1	FT555	Codfish Island, Stewart Island	EF103955	EF103996	EF104031	EU567900	EU567963	EU568051
O. chloronoton	OCH2	CD847	Tara Hills, Omarama	EF103956	EF103997	EF104032	EU567901	EU567964	EU568053
O. fallai	OFA1	FT597	Great Island, Three Kings Islands	EU567722	EU567732	EU567781	EU567847	EU567987	EU568061
O. fallai	OFA2	FT598	Great Island, Three Kings Islands	EU567723	EU567733	EU567782	EU567848	EU567988	EU568062
O. grande	OGR1	CD1055	Central Otago	EU567720	EU567756	EU567807	EU567880	EU567934	EU568031
O. grande	OGR2	FT3017	Lindis Pass	EU567721	EU567757	EU567808	EU567881	EU567935	–
O. homalonotum	OHO1	FT6290	Shoal Bay, Great Barrier Island	EF447146	EF447179	EU567818	EU567839	EU568009	EU568085
O. homalonotum	OHO2	FT6291	Tryphena, Great Barrier Island	EU567724	EU567748	EU567819	EU567840	EU568010	EU568086
O. inconspicuum	OIN1	CD1101	Gorge Burn, Eyre Mountains	EU567708	EU567739	EU567788	EU567875	EU567941	EU568028
O. inconspicuum	OIN2	CD421	Macraes Flat	EU567709	EU567738	EU567787	EU567879	EU567942	EU568048
O. inconspicuum 'Big Bay'	BBS1	FT3783	Awarua Point, Big Bay, Westland	EU567705	EU567735	EU567785	EU567873	EU567938	EU568025
O. inconspicuum 'Big Bay'	BBS2	FT3786	Mackenzie River, Big Bay, Westland	EU567706	EU567736	EU567786	EU567874	EU567939	EU568026
O. inconspicuum 'Big Bay'	BBS17	FT3813	Barn Bay, Westland	EU567707	EU567737	EU567789	EU567878	EU567940	EU568027
O. infrapunctatum	OIF1	CD545	Stephens Island	EF033050	EF033058	EF071066	EU567914	EU568004	EU568104
O. infrapunctatum	OIF2	FT3749	Cobden Beach	EF033051	EF033059	EF071067	EU567913	EU568001	EU568103
O. infrapunctatum 'Chesterfield'	OIF3	FT3214	Chesterfield, Westland	EF070984	EF071024	EF071068	EU567915	EU568006	EU568066
O. infrapunctatum 'Chesterfield'	OIF4	FT3215	Chesterfield, Westland	EF070985	EF071025	EF071069	EU567916	EU568007	EU568067
O. infrapunctatum	OIF5	FT6272	Denniston	EF070986	EF071026	EF071070	EU567911	EU568003	EU568100
O. infrapunctatum 'Southern North Island'	OIF6	FT7649	Waiinu Beach, Wanganui	EF070987	EF071027	EF071071	EU567917	EU568005	EU568101
O. infrapunctatum	PAP1	FT3815	Mt McCawber, Paparoa Ranges	EF071023	EF071063	EF071106	EU567912	EU568002	EU568102
O. lineoocellatum	OLI1	FT302	Ward, South Island	EF103970	EF104011	EF104046	EU567902	EU567957	EU568054
O. lineoocellatum	OLI2	FT3112	Tekapo	EF103971	EF104012	EF104047	EU567903	EU567958	EU568052
O. longipes	OLO1	FT161	Clarence River, Lake Tennyson	EU567717	EU567755	EU567806	EU567899	EU567962	EU568042
O. longipes	OLO2	–	Mt Harper	EU567716	EU567754	EU567805	EU567898	EU567961	EU568043
O. longipes 'Rangitata'	RAN1	–	Mt Harper	EU567714	EU567752	EU567803	EU567896	EU567959	EU568044
O. longipes 'Rangitata'	RAN2	–	Mt Harper	EU567715	EU567753	EU567804	EU567897	EU567960	EU568045
O. maccanni	OMA1	CD930	Nevis Range, Central Otago	EF081195	EF081222	EF081249	EU567882	EU567945	EU568032
O. maccanni	OMA2	CD1261	Puketoi	EF447115	EF447148	EU567794	EU567885	EU567948	EU568033
O. maccanni	OMA3	FT3213	Garston	EF447116	EF447149	EU567793	EU567884	EU567946	EU568034

(*continued on next page*)

Table 1 (*continued*)

Species	Tissue code	Museum code	Locality	GenBank Accession Nos.					
				ND2	ND4	Cyt b	16SrRNA	12SrRNA	Rag-1
O. maccanni	OMA4	FT3039	Garston	EF447117	EF447150	EU567792	EU567883	EU567947	EU568035
O. microlepis	OMI1	CD1299	Taihape	EF043107	EF043170	EU567824	EU567849	EU568015	EU568087
O. microlepis	OMI2	FT3730	Mokimokonui River, Southern Urewera	EF567257	EU567760	EU567825	EU567850	EU568016	EU568088
O. moco	OMO1	FT156	Stanley Island, Mercury Islands	EF567286	EU567764	EU567783	EU567920	EU567989	EU568071
O. moco	OMO2	CD1031	Aorangi Island, Poor Knights Islands	EF567297	EU567765	EU567784	EU567921	EU567990	EU568072
O. nigriplantare nigriplantare	ONN1	CD1061	South East Island, Chatham Islands	EF043108	EF043171	EU567801	EU567891	EU567955	EU568029
O. n. nigriplantare	ONN2	FT3615	Mangere Island, Chatham Islands	EF043119	EF043182	EU567802	EU567892	EU567956	EU568030
O. n. polychroma	ONP1	FT5252	Pukerua Bay	EF033052	EF033068	EU567797	EU567890	EU567951	EU568038
O. n. polychroma	ONP2	CD618	Birdlings Flat	EU074693	EU077444	EU567800	EU567895	EU567954	EU568039
O. n. polychroma	ONP4	FT3219	Tiwai Point	EU074694	EU077445	EU567798	EU567893	EU567952	EU568040
O. n. polychroma	ONP5	FT3041	Tiwai Point	EU074695	EU077446	EU567799	EU567894	EU567953	EU568041
O. n. polychroma	GVS1	FT3796	Kangaroo Crk, Nelson Ck, Grey Valley	EU074762	EU077433	EU567795	EU567888	EU567949	EU568036
O. n. polychroma	GVS2	FT3804	Blaketown Beach	EU074763	EU077434	EU567796	EU567889	EU567950	EU568037
O. notosaurus	ONT1	FT575	Magog, Stewart Island	EU567710	–	EU567790	EU567876	EU567943	EU568049
O. notosaurus	ONT2	CD1089	Arena Ridge, Stewart Island	EU567711	–	EU567791	EU567877	EU567944	EU568050
O. otagense	OOT1	CD1053	Central Otago	EF033053	EF033064	EF071065	EU567908	EU568000	EU568096
O. otagense	OOT2	CD349	Macraes Flat	EF033054	EF033065	EU567814	EU567909	EU567998	EU568093
O. smithi	OSM1	FT166	Middle Island, Mercury Islands	EF033055	EF033067	EU567826	EU567851	EU568017	EU568089
O. smithi	OSM2	FT193	Ocean Beach, Whangarei	EF567220	EU567761	EU567827	EU567852	EU568018	EU568090
O. stenotis	OST1	FT2	Mt Anglem, Stewart Island	EU567718	EU567758	EU567809	EU567886	EU567936	EU568046
O. stenotis	OST2	FT289	Table Hill, Stewart Island	EU567719	EU567759	EU567810	EU567887	EU567937	EU568047
O. striatum	OSR1	FT3301	Waipuku, Taranaki	EF447147	EF447180	EU567820	EU567867	EU568011	EU568055
O. striatum	OSR2	FT3296	Little Barrier Island	EU567725	EU567749	EU567821	EU567868	EU568012	EU568056
O. suteri	OSU1	FT148	Green Island, Mercury Islands	EF567261	EU567750	EU567772	EU567837	EU567967	EU568105
O. suteri	OSU2	FT602	Great Island, Three Kings Islands	EF567282	EU567751	EU567773	EU567838	EU567968	EU568106
O. taumakae	OBI2	RE5237	Taumaka, Open Bay Islands	EF033048	EF033062	EU567812	EU567906	EU567996	EU568091
O. taumakae	OBI3	FT311	Taumaka, Open Bay Islands	EF033049	EF033063	EU567813	EU567907	EU567997	EU568092
O. waimatense	OWA1	CD1207	Mt Ida	EU567712	EU567742	EU567815	EU567910	EU567999	EU568094
O. waimatense	OWA2	CD1209	Wairau River, Marlborough	EF033056	EF033066	EU567816	EU567918	EU567995	EU568095
O. zelandicum	OZE2	FT6516	Pukerua Bay	EF447181	EF447201	EU567822	EU567841	EU568013	EU568081
O. zelandicum	OZE3	FT3814	Mokihinui River Mouth	EF033057	EF033070	EU567823	EU567842	EU568014	EU568082
O. pikitanga	SVS1	RE5315 (FT7648)	Sinbad Gully, Llawrenny Peaks, Fiordland	EU567713	EU567743	EU567817	EU567919	EU568008	EU568097
'Cyclodina' lichenigera	LIC1	ABTC68934 (SAMAR52030)	Blackburn Island, Lord Howe Island	EF567203	EU567762	EU567828	EU567869	EU567965	EU568107
'Cyclodina' lichenigera	LIC2	ABTC58889 (SAMAR52161)	Blackburn Island, Lord Howe Island	EU567704	EU567763	EU567829	EU567870	EU567966	EU568108
Nannoscincus mariei	EUG1	NR9808	New Caledonia	EU423132	EU423130	EU567832	EU567924	EU567933	EU568021
Marmorosphax tricolor	EUG2	NR9800	New Caledonia	EU423133	EU423131	EU567831	EU567925	EU567932	EU568023
Caledoniscincus austrocaledonicus	EUG3	EBU3522	New Caledonia	EU567727	EU567766	EU567835	EU567922	EU567931	EU568024
Lioscincus tillieri	EUG5	NR3617	Mt Mou, New Caledonia	–	EU567729	EU567833	EU567923	EU567929	EU568022
Lampropholis guichenoti	EUG7	NR2639	Australia	EF567304	EU567769	EU567836	EU567928	EU568020	EU568111
Niveoscincus pretiosus	EUG9	NR391	Tasmania, Australia	EU567726	EU567768	EU567834	EU567927	EU568019	EU568110
Morethia adelaidensis	EUG10	NR8560	Australia	EU567728	EU567767	EU567830	EU567926	EU567930	EU568109

Table 2
Oligonucleotide primers used in this study. The letters L and H refer to the light and heavy strands. Values in '5' position' refer to the position of the 5' position in the complete *Eumeces egregius* mtDNA sequence (Kumazawa and Nishida, 1999).

Gene	Primer name	Sequence (5′–3′)	5′ Position	Source
ND2	L4221	AAGGATTACTTTGATAGAGT	3691	Macey et al. (1997)
	L4437	AAGCTTTCGGGCCCATACC	3833	Macey et al. (1997)
	H4980	ATTTTTCGTAGTTGGGTTTGRTT	4396	Macey et al. (1997)
	ND2r102	CAGCCTAGGTGGGCGATTG	4432	Sadlier et al. (2004)
	H5540	TTTAGGGCTTTGAAGGC	4947	Macey et al. (1997)
	H5617	AAAATRTCTGRGTTGCATTCAG	5019	Macey et al. (1997)
ND4	ND4I	TGACTACCAAAAGCTCATGTAGAAGC	10,771	Forstner et al. (1995)
	ND4R-NZ	CCAAGRGTTTTGGTGCCTAAGACC	11,670	Greaves et al. (2007)
	tRNA-Leu	TACTTTTACTTGGATTTGCACCA	11,691	Forstner et al. (1995)
Cytochrome b	mtD-25	CCATCCAACATCTCAGCATGATGAAA	14,202	Kocher et al. (1989)
	SkCytBR	TAGGCAAANARRAAGTAYCAYTCTGG	14,940	Greaves et al. (2007)
12SrRNA	tPhe	AAAGCACRGCACTGAAGATGC	23	Reeder (2003)
	12e	GTRCGCTTACCWTGTTACGACT	982	Reeder (2003)
16SrRNA	L2510	CGCCTGTTTATCAAAAACAT	1907	Palumbi (1996)
	H3056	CTCCGGTCTGAACTCAGATCACGTAGG	2452	Modified from Palumbi (1996)
Rag-1 (nuclear)	G396(F)	TCTGAATGGAAATTCAAGCTGTT	NA	Smith (2001) (R13 in Groth and Barrowclough, 1999)
	G440(F)	CATGATAAAGGGAGAGTRGAAGA	NA	Smith (2001)
	G425(R)	AAAGCAAGGATAGCGACAAGAG	NA	Smith (2001)

(3) *O. suteri* is not a basal member of the New Zealand skink radiation.
(4) *Oligosoma* 'Rangitata' is genetically distinct from sympatric *O. longipes*.
(5) previously reported sister species relationships are supported: (a) *O. infrapunctatum* and *Lampropholis guichenoti* (Hickson et al., 2000), (b) *O. grande* and *O. stenotis* (Hickson et al., 2000), (c) *O. zelandicum* and *C. hardyi* (Hickson et al., 2000), (d) *O. fallai* and *Cyclodina* (Hickson et al., 2000), (e) *O. striatum* and *O. zelandicum* (Hardy, 1977), and (f) *C. ornata* and *C. aenea* (Hardy, 1977).

2.5. Estimating divergence times and the age of the New Zealand skink fauna

The relaxed molecular clock method of Drummond et al. (2006), implemented in BEAST v1.4.8 (Drummond and Rambaut, 2007), was used to estimate the age of the New Zealand skink fauna and the divergence times among clades and species. A reduced tree containing a single representative of each species, subspecies and distinct genetic lineage was used for the analysis. Two calibration points were used, based on: (i) the emergence of New Caledonia 37 mya (Grandcolas et al., 2008), and (ii) the St Bathans Miocene fossil deposit that demonstrates that a skink fauna was present in the Otago region of New Zealand 16–19 mya (Worthy et al., 2006a,b, 2007). We used this information to calibrate the divergence of the skink fauna of Zealandia (uniform distribution, upper bound: 37 mya, lower bound: 16 mya), and the divergence of the New Zealand skink fauna (uniform distribution, lower bound: 16 mya). A GTR + I + G model of evolution was employed, using an uncorrelated lognormal relaxed molecular clock with a Speciation: Yule Process tree prior. The analysis was completed twice, with 10 million generations per run. The output was viewed in Tracer v1.4 to check that stationarity had been reached, ensure that the effective sample size (ESS) for each parameter exceeded 200, and examine the coefficient of variation and covariance (see Drummond et al., 2007). The two separate runs were then combined using LogCombiner, with a maximum clade credibility tree generated in TreeAnnotator and visualised in FigTree v1.1.2.

3. Results

3.1. Phylogenetic relationships

Prior to concatenation, several short un-alignable regions of 12SrRNA and 16SrRNA were excluded. Following concatenation, the edited alignment comprised 4062 bp of sequence data for 92 individuals (85 ingroup, 7 outgroups). The aligned length of each gene region, number of variable sites, number of parsimony-informative sites, and nucleotide frequencies are provided in Table 3. The alignment has been submitted to TreeBase (Accession No. S2337, M4442). A χ^2 test executed in PAUP* confirmed the homogeneity of base frequencies across all taxa (df = 273, $P = 1.0$). No indels were present in any of the mitochondrial DNA coding regions (i.e. ND2, ND4, Cytochrome b), but a 3 bp insertion was present in Rag-1 in *O. n. polychroma* (ONP1-2, ONP4-5, GVS1-2). For several samples (CAE1, CAL1-2, COL2-3, COR2, OFA1, OHO1-2, OIN1, ONN1-2, OSR2, BBS17, SVS1), only ~800 bp of Rag-1 sequence data was obtained. For a limited number of individuals were for unable to amplify all six gene regions (missing data: EUG5, ND2; CAL2, ND4; ONT1-2, ND4; OGR2, Rag-1) (Table 1).

Both the hLRT and AIC from Modeltest supported the GTR + I + G substitution model as the most appropriate for our dataset ($-\ln L = 44732.3359$). Parameters estimated under this model were: relative substitution rates ($A \leftrightarrow C = 1.56$, $A \leftrightarrow G = 18.23$, $A \leftrightarrow T = 1.22$, $C \leftrightarrow G = 0.95$, $C \leftrightarrow T = 14.39$, relative to $G \leftrightarrow T = 1.00$), proportion of invariable sites (0.5289), and gamma distribution shape parameter (0.6552). For the partitioned Bayesian analysis, MrModeltest selected the GTR + I + G model for both the mtDNA coding regions ($-\ln L = 31292.7344$, $I = 0.4507$, $G = 0.9875$) and mtDNA rRNA regions ($-\ln L = 9360.6650$, $I = 0.5614$, $G = 0.5988$), while the HKY + G model was selected for Rag-1 ($-\ln L = 3044.5820$, $G = 0.4490$).

All analysis methods recovered very similar tree topologies, with the same major clades and lineages identified. Each method found *C. lichenigera* to be the sister lineage to the entire New Zealand skink radiation. The NJ and MP methods were unable to resolve the basal relationships among the major lineages within the New Zealand skink fauna. However, the ML and Bayesian tree topologies have several well-supported basal nodes, resolving the relationships among some of the major clades. The main difference between the four analysis methods related to the placement of *O.*

Table 3
Summary table of descriptive statistics for each gene and the combined dataset. PI, parsimony informative.

	Mitochondrial DNA					Nuclear DNA	Overall
	ND2	ND4	Cytb	16SrRNA	12SrRNA	Rag-1	
Sequence length (bp)	550	671	699	469	819	854	4062
No. variable sites (%)							
All taxa	307 (55.8)	361 (53.8)	326 (46.6)	123 (26.2)	280 (34.2)	197 (23.1)	1594 (39.2)
Ingroup only	291 (52.9)	332 (49.5)	309 (44.2)	95 (20.3)	230 (28.1)	121 (14.2)	1384 (34.1)
No. PI sites (%)							
All taxa	272 (49.5)	322 (48.0)	300 (42.9)	92 (19.6)	236 (28.8)	98 (11.5)	1314 (32.3)
Ingroup only	266 (48.4)	309 (46.1)	291 (41.6)	81 (17.3)	210 (25.6)	83 (9.7)	1240 (30.5)
Mean nucleotide freq.							
A	0.319	0.327	0.268	0.330	0.351	0.305	0.316
C	0.316	0.298	0.305	0.239	0.260	0.214	0.269
G	0.135	0.123	0.146	0.201	0.185	0.262	0.179
T	0.230	0.252	0.281	0.229	0.204	0.219	0.235

suteri and *O. moco*. In the Bayesian tree, *O. suteri* was most closely related to the clade comprising *C. aenea* and *C. hardyi* (clade 3), but it formed a separate basal lineage in the NJ, MP and ML trees. Similarly, in the Bayesian tree *O. moco* was a member of the main *Cyclodina* clade (clade 4), but formed a separate basal lineage in the NJ, MP and ML trees. The optimal ML tree ($-\ln L = 44756.71482$) is shown in Fig. 3, with 500 ML bootstraps and Bayesian posterior probabilities indicating branch support.

There is extremely strong support for the monophyly of the New Zealand skink radiation (96 bootstrap [BS], 1.0 posterior probability [PP]). The Lord Howe Island skink (*C. lichenigera*) represents a closely related sister lineage (100 BS, 1.0 PP) to the New Zealand skink radiation, with the mean mtDNA genetic distance between *C. lichenigera* and the New Zealand skink lineage (9.7–10.8%; Table 4) overlapping with that found among the major clades within the New Zealand skink fauna (8.7–11%; Table 4). In contrast, the New Zealand skink radiation is more distantly related to both the New Caledonian (13.5%) and Australian outgroups (15%) (Fig. 3).

The New Zealand skink fauna comprises eight well-supported clades (Fig. 3). The basal relationships among these clades are not well-resolved, with the short basal nodes and long internodes/tips indicative of a rapid diversification. The only well-supported relationship (66 BS, 0.99 PP) was for clades 1 and 2, which comprise the majority of *Oligosoma* species. However, the S–H topology tests strongly rejected the monophyly of *Oligosoma* (as presently defined), although the monophyly of *Cyclodina* could not be rejected (Table 5). Although the basal relationships among clades are uncertain, the phylogenetic relationships among species within each major clade are resolved and extremely well-supported (Fig. 3).

Clade 1 (95 BS, 1.0 PP) comprises ten recognised *Oligosoma* species and subspecies, and the recently discovered *O. longipes* 'Rangitata' (Fig. 3). Within this clade, the *O. longipes* species complex and *O. nigriplantare* exhibit a strong phylogenetic affinity (97 BS, 1.0 PP). *Oligosoma longipes* 'Rangitata' is genetically divergent (7.1%) from sympatric *O. longipes* at Mt Harper (Table 5), supporting its recognition as a distinct species. However, the *O. longipes* populations from Mt Harper (OLO2) and Clarence River, Lake Tennyson (OLO1) are not monophyletic (8.2% genetic divergence), suggesting that further cryptic species might be present within *O. longipes*. There is strong support for a close relationship between *O. chloronoton* and *O. lineoocellatum* (100 BS, 1.0 PP), between *O. grande* and *O. stenotis* (85 BS, 1.0 PP; Table 5), and among *O. maccanni*, *O. notosaurus* and *O. inconspicuum* (76 BS, 1.0 PP) (Fig. 3). A strong phylogenetic affinity is also evident between *O. notosaurus* and *O. inconspicuum* (100 BS, 1.0 PP; Fig. 3). There was no support for the Big Bay skink (BBS1, BBS2, BBS17) being genetically distinct from *O. inconspicuum* (Fig. 3). The level of genetic divergence between the two subspecies of *O. nigriplantare* is 7.6%.

Clade 2 (95 BS, 1.0 PP) comprises six recognised *Oligosoma* species (*O. pikitanga*, *O. waimatense*, *O. otagense*, *O. taumakae*, *O. acrinasum*, and *O. infrapunctatum*) and two undescribed species: *O. infrapunctatum* 'Southern North Island' and *O. infrapunctatum* 'Chesterfield' (Fig. 3). *Oligosoma pikitanga* represents a sister lineage to the unresolved clade 2 (98BS, 1.0 PP). The Mt Ida population of *O. waimatense* (OWA1) grouped with *O. otagense*, possibly as a result of hybridisation with *O. otagense* at the southern extreme of the distribution of *O. waimatense*. Hickson et al.'s (2000) hypothesized relationship between *O. infrapunctatum* and *Lampropholis guichenoti* was strongly rejected (Table 5). The level of genetic divergence between the *L. guichenoti* sample (AF194112; which grouped with our *O. infrapunctatum* samples) contained in Hickson et al. (2000) and that sequenced in this study was 13.1% (12S data only), with 13.6% divergence in 12S between our *L. guichenoti* and *O. infrapunctatum* samples.

Clade 3 (98 BS, 1.0 PP) comprises the *Cyclodina aenea* species complex: *C. aenea* and *C. hardyi* (Fig. 3). The hypothesized relationship (Hickson et al., 2000) between *C. hardyi* and *O. zelandicum* was rejected (Table 5). The remaining *Cyclodina* species are contained in clade 4 (52 BS, 0.99 PP), which also includes *O. fallai* as a basal member of the clade (72 BS, 0.99 PP; Table 5). *Cyclodina alani* and *C. macgregori* are the most basal of the *Cyclodina* species in clade 4 (Fig. 3). There is strong support (100 BS, 1.0 PP) for a relationship between *C. ornata* and the members of the *C. oliveri* species group (*C. townsi*, *C. whitakeri*, *C. oliveri*). The hypothesized relationship between *C. aenea* and *C. ornata* was strongly rejected (Table 5).

Clade 5 (100 BS, 1.0 PP) comprises three *Oligosoma* species (*O. zelandicum*, *O. striatum*, *O. homalonotum*), with *O. striatum* and *O. homalonotum* exhibiting a close affinity (100 BS, 1.0 PP; Fig. 3; Table 5). *Oligosoma suteri* is the sole member of clade 6 (100 BS, 1.0 PP); however, an alternative topology where *O. suteri* was closely aligned to the main *Oligosoma* group (clades 1 and 2) could not be rejected (Table 5). *Oligosoma moco* is the sole member of clade 7 (100 BS, 1.0 PP), although in some analyses *O. moco* groups with members of clade 4 (Fig. 3). Clade 8 (100 BS, 1.0 PP) is comprised of *O. smithi* and *O. microlepis* (Fig. 3).

3.2. Divergence time estimates and age of the New Zealand skink fauna

The relaxed molecular clock analysis produced an almost identical tree topology to that obtained with the partitioned Bayesian analysis (Fig. 4). The mean covariance was positive (0.032), indicating a slight correlation in the parent to child branches, but since the 95% highest posterior density (HPD) interval (−0.179–0.242) included zero this autocorrelation was not considered to be significant (e.g. Drummond et al., 2006). The dataset was not found to be strictly clock-like (coefficient of variation 0.269, 95% HPD: 0.210–

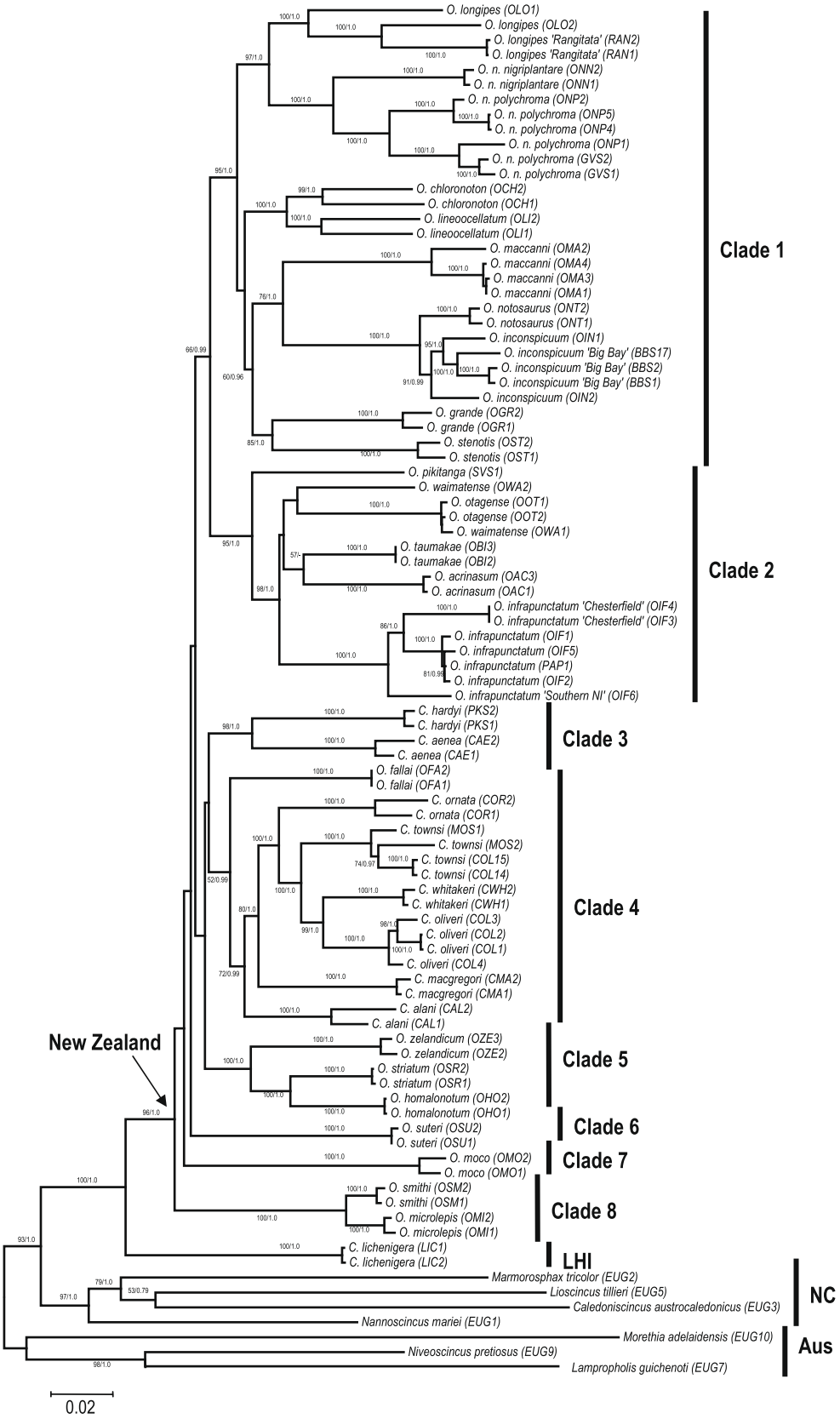

Fig. 3. Maximum Likelihood (ML) phylogram for the New Zealand skink fauna based on five mitochondrial genes (ND2, ND4, Cytochrome b, 12SrRNA, 16SrRNA) and one nuclear gene (Rag-1) (Total 4062 bp). Eight clades are identified within the New Zealand skink radiation. Two measures of branch support are indicated with ML bootstraps (500 replicates) on the left and Bayesian posterior probabilities on the right (only values over 50 and 0.7, respectively, are shown).

Table 4
Uncorrected genetic distances (mtDNA dataset only) among the major clades identified in Fig. 3. Genetic distances are shown below the diagonal, with standard errors (1000 replicates) shown above the diagonal. LHI, Lord Howe Island skink, *Cyclodina lichenigera*.

	Clade 1	Clade 2	Clade 3	Clade 4	Clade 5	Clade 6	Clade 7	Clade 8	LHI
Clade 1	–	0.003	0.003	0.003	0.003	0.004	0.004	0.004	0.004
Clade 2	0.102	–	0.004	0.004	0.004	0.004	0.005	0.005	0.004
Clade 3	0.102	0.102	–	0.004	0.003	0.005	0.005	0.004	0.005
Clade 4	0.100	0.097	0.091	–	0.003	0.004	0.004	0.005	0.005
Clade 5	0.100	0.097	0.091	0.087	–	0.004	0.004	0.004	0.004
Clade 6	0.101	0.100	0.094	0.090	0.095	–	0.006	0.005	0.005
Clade 7	0.110	0.107	0.102	0.097	0.100	0.104	–	0.005	0.005
Clade 8	0.104	0.102	0.101	0.098	0.095	0.101	0.106	–	0.005
LHI	0.108	0.106	0.101	0.098	0.097	0.099	0.108	0.107	–

Table 5
Results of the S–H tests (Shimodaira and Hasegawa, 1999) of alternative topologies for the New Zealand skink fauna. A significant *P*-value (<0.05) indicates that the alternative topology is significantly different from the optimal Maximum Likelihood (ML) tree.

Hypothesis	S–H Test	
	Diff. −ln *L*	*P*-value
(1) *Cyclodina* is monophyletic	22.05	0.397
(2) *Oligosoma* is monophyletic	111.92	<0.001
(3) *Oligosoma suteri* is not basal and is closely related to *Oligosoma*	1.58	0.949
(4) *Oligosoma longipes* 'Rangitata' is genetically distinct from sympatric *O. longipes*	Supported by optimal tree	NA
(5) Sister species relationship between:		
(a) *Oligosoma infrapunctatum* & *Lampropholis guichenoti*	111.47	<0.001
(b) *Oligosoma grande* & *O. stenotis*	supported by optimal tree	NA
(c) *Oligosoma zelandicum* & *Cyclodina hardyi*	66.25	0.019
(d) *Oligosoma fallai* & *Cyclodina*	Supported by optimal tree	NA
(e) *Oligosoma striatum* & *O. zelandicum*	Supported by optimal tree	NA
(f) *Cyclodina ornata* & *C. aenea*	97.98	<0.001

0.332), indicating that our use of a relaxed lognormal molecular clock was appropriate.

The skink fauna of Zealandia appears to have originated in the Oligocene (mean divergence date 30.58 mya, 95% HPD: 25.11–37.0 mya; Fig. 4). Our analyses indicate that skinks colonised New Zealand in the early Miocene (mean: 18.34 mya, 95% HPD: 16.0–22.64 mya; Fig. 4), shortly after the 'Oligocene drowning'. Skinks appear to have rapidly radiated across New Zealand, with the divergences among the major clades occurring in the early to mid-Miocene (Fig. 4). Divergences among the members of the *O. lineoocellatum*–*O. chloronoton* species complex, the *O. longipes* complex, and the *O. nigriplantare* complex, are estimated to have occurred during the late Miocene (Fig. 4). More recent speciation during the Pliocene appears to be evident in the *O. infrapunctatum* species complex, the *O. inconspicuum*–*O. notosaurus* species complex, and the *O. smithi*–*O. microlepis* species complex (Fig. 4).

4. Discussion

4.1. Origin and diversification of the New Zealand skink fauna

Our analyses indicate that skinks colonised New Zealand in the early Miocene (16–22.6 mya), relatively soon after the near-complete marine inundation of the archipelago during the 'Oligocene drowning' (~25 mya; Cooper and Millener, 1993; Trewick et al., 2007; Landis et al., 2008). The increasing land area in the early Miocene (Lee et al., 2001) might provide an explanation for the rapid radiation of skinks across New Zealand following their arrival, with diversification among all of the major clades occurring at this time. The skink fauna that is evident in the St Bathans Miocene fossil deposit in Otago (Worthy et al., 2006a, Worthy et al., 2006b; Worthy et al., 2007) captures evidence of this early diversification of skinks in New Zealand. An early Miocene origin for the New Zealand skink fauna is consistent with several previous estimates (~20 mya, Towns et al., 1985; ~23 mya, Hickson et al., 2000; 19.9–22.9 mya, based on a ND2 + c-mos calibration, Smith et al., 2007), but not with the late Miocene (7.9 mya) origin favoured by Smith et al. (2007). It is therefore necessary to re-assess the proposed scenario for how skinks colonised New Zealand from New Caledonia.

Smith et al. (2007) proposed that skinks dispersed via long-distance overwater dispersal from New Caledonia to Lord Howe Island, reaching New Zealand by ~7.9 mya. This scenario was favoured as it was consistent with the known geological age of Lord Howe Island (~7 myr, McDougall et al., 1981; *C. lichenigera* was suggested to have reached Philip Island/Norfolk Island, from Lord Howe Island, shortly after its formation ~3 mya; Jones and McDougall, 1973). However, this scenario is inconsistent with our analyses that were based on the available fossil evidence. Since *C. lichenigera* is a closely related sister lineage to the New Zealand skink fauna, we propose that following the divergence from the New Caledonian fauna, *C. lichenigera* persisted on volcanic islands, now submerged (Mortimer et al., 1998), along the Lord Howe Rise and/or Norfolk Ridge (Lee et al., 2001; Gibbs, 2006; Fig. 1), prior to reaching Lord Howe Island (~7 mya) and the Norfolk Island group (~3 mya). Indeed the high level of genetic divergence among *C. lichenigera* populations (S. Smith and G. Shea, unpublished data) might indicate that it represents the remnants of a once more diverse skink fauna that inhabited the volcanic islands along the Lord Howe Rise and Norfolk Ridge between New Caledonia and New Zealand.

Our scenario requires *C. lichenigera* and the ancestor of the New Zealand skink fauna to both have a high propensity for long-distance overwater dispersal. Indeed, *C. lichenigera* inhabits the littoral and supra-littoral zone (Cogger, 1971, 2000; Wilson and Swan, 2008), and lives amongst vegetation and material that is regularly swept out to sea during severe storms. Interestingly, three of the most genetically divergent lineages of New Zealand skinks (clades 6–8) comprise coastal species that are restricted to the Northland region of the North Island (see Hare et al., 2008a) (Table 6). At least

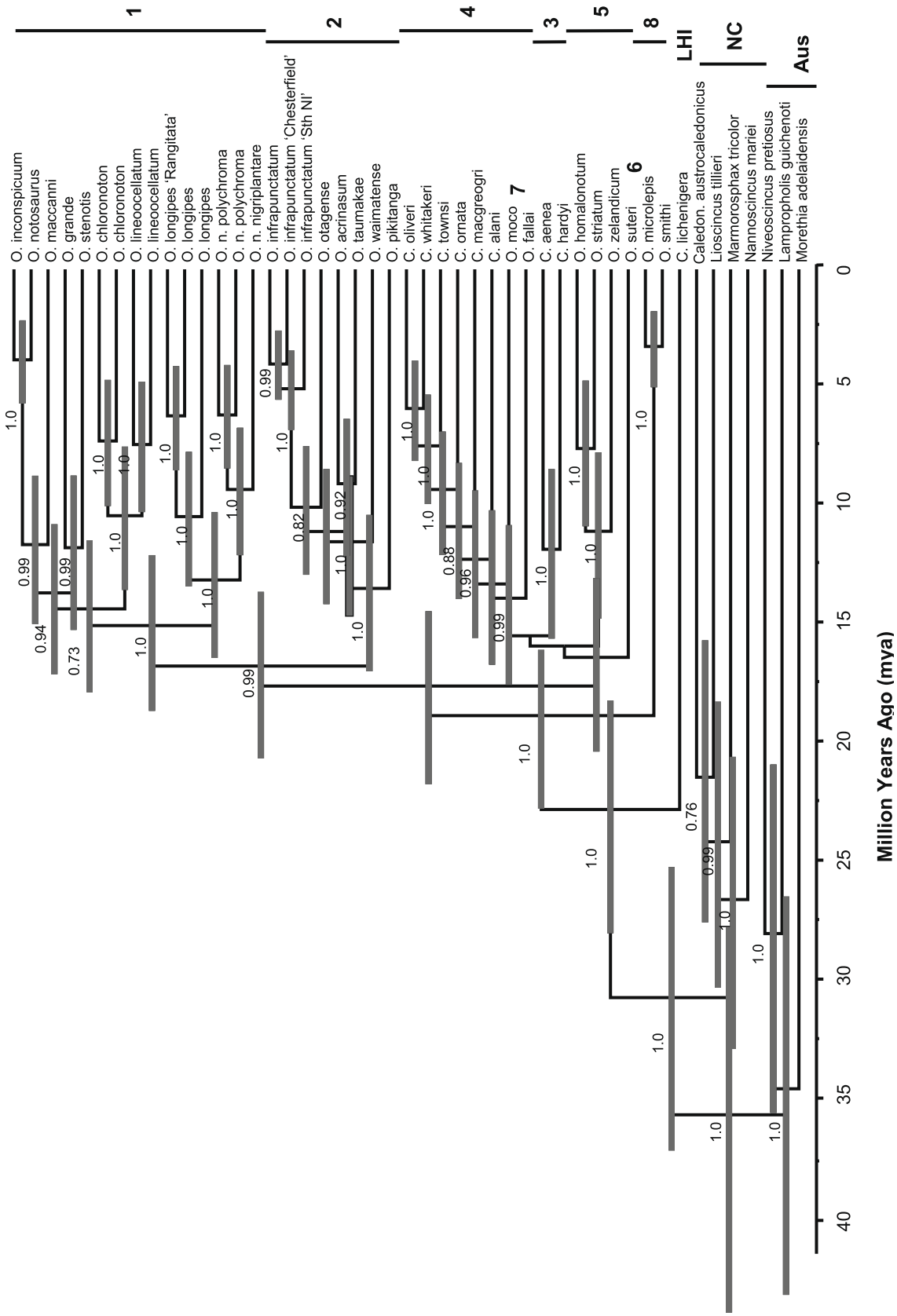

Fig. 4. BEAST maximum clade credibility tree for the New Zealand skink fauna. The divergence times correspond to the mean posterior estimate of their age in millions of years. The grey bars indicate the 95% HPD interval for the divergence time estimates. Each node with a posterior probability >0.7 is labelled. The eight major clades identified in Fig. 3 are identified.

Table 6
Current distribution of skink species in New Zealand (adapted from Gill and Whitaker, 2001). The geographic regions of New Zealand are presented in Fig. 2. The genetic clade (see Fig. 3) to which each species belongs is indicated. Key to geographic regions: 1, Northland (including Three Kings Islands, Poor Knights Islands, other offshore islands); 2, Waikato (including Coromandel Peninsula and offshore islands); 3, Bay of Plenty; 4,Taranaki; 5, Hawkes Bay; 6, Manawatu; 7, Wellington; 8, Nelson/Marlborough (including Cook Strait Islands); 9, West Coast; 10, Canterbury; 11, Otago; 12, Southland; 13, Stewart Island; 14, Chatham Islands.

Species	Clade	Geographic regions													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cyclodina aenea	3	X	X	X	X	X	X	X							
C. alani	4	X	X												
C. hardyi	3	X													
C. levidensa	3[a]	X													
C. macgregori	4	X						X							
C. oliveri	4	X	X												
C. ornata	4	X	X	X	X	X	X	X							
C. townsi	4	X													
C. whitakeri	4		X					X							
Oligosoma acrinasum	2												X		
O. chloronoton	1											X	X	X	
O. fallai	4	X													
O. grande	1											X			
O. homalonotum	5	X													
O. inconspicuum	1									X		X	X		
O. infrapunctatum	2		X	X			X	X	X	X					
O. lineoocellatum	1					X		X	X		X				
O. longipes	1								X		X				
O. longipes 'Rangitata'	1										X				
O. maccanni	1										X	X	X		
O. microlepis	8			X			X								
O. moco	7	X	X												
O. nigriplantare nigriplantare	1														X
O. n. polychroma	1				X	X	X	X	X	X	X	X	X	X	
O. notosaurus	1													X	
O. otagense	2											X			
O. pikitanga	2												X		
O. smithi	8	X	X	X											
O. stenotis	1													X	
O. striatum	5	X	X	X	X										
O. suteri	6	X	X												
O. taumakae	2									X					
O. waimatense	2								X		X	X			
O. zelandicum	5				X		X	X	X	X					

[a] *Oligosoma pikitanga* is presumed to be part of Clade 3 (see Chapple et al., 2008b).

two of these species (*O. suteri*, *O. smithi*) live on rocky beaches (often with abundant driftwood), are strong swimmers that can tolerate seawater, readily enter rock pools and the surf zone, and can hold their breath underwater for up to 20 min (reviewed in Miller, 2007; Hare et al., 2008a). These factors not only place these two species in a habitat from which they are likely to be transported on driftwood and vegetation, but also increase their likelihood of surviving long-distance overwater travel. The extremely low level of genetic divergence found across the range of *O. suteri* might indicate that it is particularly adept at overwater dispersal (Hare et al., 2008a).

Due to the ecological, behavioural and morphological similarities between *C. lichenigera* and *O. suteri* (Cogger, 1971; Towns, 1974; Hardy, 1977), it is possible that New Zealand was colonised by an *O. suteri*-like ancestor. Both species are nocturnal, oviparous, forage in the littoral zone, and have similar morphological features (Cogger, 1971; Towns, 1974; Hardy, 1977). Importantly, both *C. lichenigera* (Lord Howe group: Blackburn Island and Ball's Pyramid; Norfolk group: Philip Island) and *O. suteri* (offshore islands & islets in the Northland region) are capable of living on the small volcanic islands, islets and rock stacks that would have been present along the Lord Howe Rise and Norfolk Ridge between New Caledonia and New Zealand. However, the basal relationships among New Zealand skinks were not well resolved and we were unable to rule out the possibility that *O. suteri* is a member of the main *Oligosoma* lineage (Table 5). As a consequence, we were not able to determine the phylogenetic affinities of *O. suteri*, nor whether viviparity has evolved on a single occasion or whether a viviparity–oviparity reversal has occurred in New Zealand skinks.

Our tree topology and divergence time estimates indicate that there was a rapid diversification across New Zealand following the initial colonisation. New Zealand would have been comparatively warm and flat when skinks first reached the archipelago (Lee et al., 2001; Gibbs, 2006). Habitat and climatic factors appear to have been responsible for the initial speciation and diversification of New Zealand skinks, with subsequent diversification into predominately open habitat (clades 1–2), forest (clades 3–5), and coastal (clades 6–8) radiations. Clades 6–8 comprise coastal *Oligosoma* species (except *O. microlepis*) that are restricted to the Northland region of the North Island, above the Taupo Line (Gill and Whitaker, 2001; Jewell, 2008) (Table 6, Fig. 2). The two lineages of *Cyclodina* (clades 3–4, including *O. fallai*) are restricted to predominately forest habitat in the North Island (Gill and Whitaker, 2001; Jewell, 2008) (Table 6). In contrast, the main *Oligosoma* lineage (clades 1–2) appears to represent a predominately South Island diversification of open habitat skinks (with *O. n. nigriplantare* on the Chatham Islands), and interestingly, no member of this lineage has a distribution that extends north of the Taupo Line (Gill and Whitaker, 2001; Jewell, 2008) (Table 6, Fig. 2). The three species whose distributions currently span Cook Strait (*O. n. polychroma*, *O. lineoocellatum*, *O. infrapunctatum*) might have reached the North Island more recently via landbridges during the Pliocene and/or Pleistocene (Greaves et al., 2007, 2008; Liggins et al., 2008b) (Table 6). The three species in clade 5 are cryptic forest-dwelling

species (Neilson, 2002; Neilson et al., 2004), with *O. striatum* occurring across the northern and central North Island, *O. homalonotum* on Great Barrier and Little Barrier Island, while *O. zelandicum* occurs in the lower North Island and upper South Island (Gill and Whitaker, 2001; Jewell, 2008) (Table 6). O'Neill et al. (2008) proposed that *O. zelandicum* dispersed across a Cook Strait landbridge during the late Pleistocene from the South Island to the North Island.

It appears that six of the eight New Zealand skink clades originated in the North Island (clades 3–8), with clades 1 and 2 representing a single South Island radiation (Table 6). This might suggest that the New Zealand skink ancestor initially colonised the North Island. Our phylogenetic analyses highlight the historical importance of the Manawatu Strait in determining species distributions. The Taupo Line, which delineates the boundary between the upper North Island (i.e. Northland) and lower North Island biogeographic regions (Wardle, 1963; Rogers, 1989; Connor, 2002; Gibbs, 2006; Fig. 2), appears to constitute a major barrier to dispersal in skinks and geckos (McCann, 1955, 1956; Towns et al., 1985). For instance, no *Oligosoma* species is continuously distributed across the Taupo Line (McCann, 1955, 1956; Bull and Whitaker, 1975; Gill and Whitaker, 2001; Jewell, 2008) (Table 6, Fig. 2). In contrast, several *Cyclodina* species are currently have (*C. aenea*, *C. ornata*), or historically had (*C. macgregori*, *C. whitakeri*), distributions across the entire North Island, spanning the Taupo Line (reviewed in Chapple et al., 2008c; Miller et al., 2009) (Table 6). The mechanisms underlying this biogeographic pattern are largely unstudied, but it might be due to the relatively recent uplift, and thus colonisation, of the lower North Island (Worthy and Holdaway, 2002), a region known to have a depauperate biota (Wardle, 1963; Rogers, 1989; Connor, 2002), and *Oligosoma* and *Cyclodina* differing in their habitat preferences and dispersal abilities (Gill and Whitaker, 2001). For example, three *Oligosoma* species might have recently colonised the North Island from the South Island (*O. n. polychroma*, *O. lineoocellatum*, *O. infrapunctatum*), but *Cyclodina* species have never been recorded in the South Island (reviewed in Chapple et al., 2008c).

Although most speciation within the New Zealand skink fauna might have occurred in the early to mid-Miocene, more recent diversification is evident in several lineages. Divergences among the members of the *O. lineoocellatum*–*O. chloronoton* species complex (see Greaves et al., 2007), the *O. longipes* complex, and the *O. nigriplantare* species complex (see Liggins et al., 2008b) appear to have originated in the late Miocene to early Pliocene. Pliocene diversification is evident among the members of the *O. infrapunctatum* species complex (see Greaves et al., 2008), *O. inconspicuum* complex, and *O. smithi*–*O. microlepis* complex (see Hare et al., 2008a). Apart from the *O. smithi*–*O. microlepis* complex and some *Cyclodina* species, this more recent speciation has been restricted to the South Island and may be a consequence of the rapid tectonic uplift that has occurred since the late Miocene associated with the formation of the Southern Alps (Lee et al., 2001; Gibbs, 2006; Landis et al., 2008). In contrast, the divergence between *O. smithi* and *O. microlepis* appears to be the result of *O. microlepis* being isolated in the Central Plateau region following the uplift of the lower North Island and draining of the Manawatu Strait in the late Pliocene (reviewed in Hare et al., 2008a).

4.2. Phylogenetic relationships among New Zealand skink species

Our phylogenetic analyses provide substantial insight into the phylogenetic relationships among New Zealand skink species. Although the basal relationships among the major clades are not resolved, the relationships among species within clades are well resolved. Several hypothesized sister species relationships (e.g. *O. grande* & *O. stenotis*, *O. fallai* & *Cyclodina*, *O. striatum* & *O. zelandicum*) were supported by our analyses, but several other proposed relationships were not supported (e.g. *O. zelandicum* & *C. hardyi*, *C. ornata* & *C. aenea*). In particular, the proposed close relationship between *O. infrapunctatum* and *Lampropholis guichenoti* (Hickson et al., 2000) was strongly rejected. This purported relationship appears to stem from an identification, labelling, or sequencing error. The level of genetic divergence between the *L. guichenoti* sample (AF194112) sequenced by Hickson et al. (2000) and that in this study was 13.1% (12S data only), with 13.6% divergence in 12S between our *L. guichenoti* and *O. infrapunctatum* samples. Our data thus corroborates previous evidence that the *L. guichenoti* sequence contained in Hickson et al. (2000) is substantially divergent from 'real' *L. guichenoti* sequences (Hay, 1998; Smith, 2001).

Our analyses supported the distinctiveness of several putative undescribed species (*O. infrapunctatum* 'Southern North Island', *O. infrapunctatum* 'Chesterfield', *O. longipes* 'Rangitata'), but not others (*O. inconspicuum* 'Big Bay'). The presence of undescribed taxa within the *O. infrapunctatum* species complex has been discussed in detail in Greaves et al. (2008). *Oligosoma longipes* 'Rangitata' was found to be substantially divergent (7.1%) from sympatric *O. longipes* at Mt Harper, supporting its recognition as a distinct species. However, more surprising was the 8.2% divergence between the two populations of *O. longipes* (Clarence River, Lake Tennyson and Mt Harper) included in our study. This indicates that there might be at least two undescribed taxa within the *O. longipes* complex, and that further morphological and genetic work is required to resolve these taxonomic issues.

Captive breeding programs have highlighted the potential for successful hybridisation (i.e. hybrids are fertile) between *O. otagense* and *O. waimatense* (D. Keall, unpublished data; Jewell, 2008). Also, a detailed phylogeographic study suggests that hybridisation (current and/or historic) has occurred between the two species in the southern populations of *O. waimatense* (DGC, unpublished data). The close affinity of the Mt Ida population of *O. waimatense* (OWA1) with *O. otagense* in this study reflects such hybridisation. However, the suggestion of hybridisation between *O. n. polychroma* and *O. maccanni* (Hickson et al., 1992) appears to be erroneous. Hickson et al. (1992) reported that *O. n. polychroma* (CD1110–CD1112) and *O. maccanni* (CD1106–CD1108) from the Eyre Mountains (Gorge Burn) had identical 12SrRNA haplotypes, but different allozyme profiles, and suggested that this might represent an instance of hybridisation. However, CD1106–CD1112 are clearly labelled as *O. maccanni* from the Eyre Mountains (Gorge Burn), and these specimens were examined in the original description of this species (as *Leiolopisma maccanni*; Patterson and Daugherty, 1990), although several *O. n. polychroma* specimens (CD1113–1115) were collected from the same locality (Patterson and Daugherty, 1990). We therefore conclude that the suggestion of Hickson et al. (1992) was based on a labelling or species identification error and that there is no evidence for hybridisation between *O. maccanni* and *O. n. polychroma*.

5. Taxonomic implications, nomenclature, and revised generic diagnoses

Our phylogenetic analyses have demonstrated that *Cyclodina* and *Oligosoma*, as currently defined, are not reciprocally monophyletic and that a generic revision is therefore required. This implies that the '*Cyclodina*' and '*Oligosoma*' body plans have evolved on multiple occasions. However, generic assignment of New Zealand skink species is particularly troublesome given: (i) difficulties in resolving the affinities of *O. moco* and *O. suteri*, (ii) confusion regarding the type species for *Oligosoma*, (iii) lack of resolution among the eight major clades (Fig. 3), possibly due to the rapid

radiation that occurred following the arrival of skinks in New Zealand, and (iv) morphological conservatism, which makes it difficult to provide reliable morphological diagnoses for the clades within the New Zealand skink radiation.

Although there is substantial ecological and behavioural diversity within the New Zealand skink fauna (Jewell, 2008; see Chapple and Hitchmough, 2009), we are unable to reliably diagnose the major genetic clades identified in this study on the basis of morphological characters. However, even if the major genetic clades could be reliably diagnosed it would result in substantial taxonomic changes to the New Zealand skink fauna. For example, the type species for *Oligosoma* (*O. zelandicum*; see below) does not belong to either of the two clades (clades 1 and 2) that contain the majority of the *Oligosoma* species. Rather, *O. zelandicum* is part of a clade (clade 5) that also includes *O. striatum* and *O. homalonotum* (Fig. 3). Thus, any generic subdivision would result in all species currently assigned to *Oligosoma* (apart from the three species in clade 5) being assigned to a new genus.

Similarly, the type species for *Cyclodina* (*C. aenea*; clade 3) is genetically divergent from the lineage comprising the majority of species currently assigned to *Cyclodina* (clade 4). Thus, any generic revision that recognised the major genetic clades as distinct genera would restrict the name *Cyclodina* to clade 3 (containing three species: *C. aenea*, *C. hardyi* and presumably *C. levidensa*; see Chapple et al., 2008b). The members of clade 4 would then be moved to a different genus. Indeed, if the generic revision was completed according to the major genetic clades identified in this study: (i) *Lygosomella* Girard, 1857 would represent the name available for clade 8, (ii) *Robbisaurus* Wells and Wellington, 1984 might be available for clade 6, and (iii) *Girardiscincus* Wells and Wellington, 1985 might be available for clade 2 (or a genus comprising the members of clades 1 and 2). In addition, *Vaderscincus* Wells and Wellington, 1984 would be available to accommodate the Lord Howe Island skink, *C. lichenigera*. Such a generic revision would result in all but six (*O. zelandicum*, *O. striatum*, *O. homalonotum*, *C. aenea*, *C. hardyi*, *C. levidensa*) of the 35 recognised species being assigned to a new genus, with the erection (or resurrection) of at least six new genera with a correspondingly complex number of generic synonymies. While such a generic revision might be valid, we have instead opted for an equally valid alternative by assigning *C. lichenigera* and all native New Zealand skink species to a single genus. Our generic revision provides the most taxonomic stability for the New Zealand skink fauna.

This single genus therefore represents a classical monophyletic rapid island radiation of skinks (34 extant species and 10+ undescribed species from the New Zealand archipelago, Chatham Islands, Lord Howe Island, Philip Island). Although *C. lichenigera* was a sister lineage to the entire New Zealand skink radiation in all our analyses, it is more closely related to the New Zealand skink fauna than to the *Eugongylus* group skinks from New Caledonia or Australia. Indeed, the genetic distance between *C. lichenigera* and New Zealand skink species (9.7–10.8%) overlaps with that found among the major genetic clades in New Zealand (8.7–11%; Table 4). A molecular phylogeny for the *Eugongylus* group skinks of the Zealandia region demonstrated that the lineage containing *C. lichenigera* and the New Zealand skinks is at an equivalent level to generic level splits within the New Caledonian skink fauna (Smith et al., 2007; see Fig. 4). Strong evidence therefore exists to support *C. lichenigera* as being congeneric with the members of the New Zealand skink radiation.

Four names (*Cyclodina*, *Oligosoma*, *Lygosomella*, and *Hombronia*), all contained in the same publication (Girard, 1857), are simultaneously the oldest available for this single genus, although only *Cyclodina* and *Oligosoma* have been subsequently used for part of it. *Lygosomella* and *Hombronia* have been previously treated as junior synonyms of *Oligosoma* (by Patterson and Daugherty, 1995). Since no previous publication has treated *Cyclodina* and *Oligosoma* as synonymous with one having priority over the other (Principle of the First Reviser, ICZN Article 24.2), both names are available. Although the name *Cyclodina* has been in use for longer (resurrected by Hardy, 1977; versus Patterson and Daugherty, 1995 for *Oligosoma*), we have opted to retain *Oligosoma* in order to maximise taxonomic stability (i.e. move the 10 *Cyclodina* species into *Oligosoma* rather than 24 *Oligosoma* species into *Cyclodina*). In addition, all but one of the putative undescribed species (*C. ornata* 'Poor Knights Islands') are contained in species complexes currently assigned to *Oligosoma*.

There has been some confusion regarding the type species for *Oligosoma* (Hardy, 1977; Patterson and Daugherty, 1995). Girard (1857) defined *Oligosoma* based on a range of morphological characters, and assigned the type species as *Mocoa zelandica* Gray. No date was provided, but this appears to be *Mocoa zelandica* Gray, 1845, a subsequent redescription of *Tiliqua zelandica* Gray, 1843. It appears that Girard (1857) examined one or more specimens that he ascribed to *M. zelandica*, as there are some features of the definition of *Oligosoma* that could not have been obtained simply from the account contained in Gray (1845). However, Hardy (1977) considered *M. zelandica* to be a composite species: "The description given by Gray (1843) for *Tiliqua zelandica* differs considerably from that given by him 2 years later for *Mocoa zelandica*, the synonymy of which included the former name. Clearly, Gray had confused 2 species in his account of *M. zelandica*. His description of *T. zelandica*, although meagre, appears to correspond to the holotype (BMNH RR1946.8.16.19), whereas the description under *M. zelandica* is suggestive of *Leiolopisma moco* [= *O. moco*]". Hence, Hardy (1977) suggested that *M. zelandica* was a composite of *T. zelandica* and a second species, which *may* have been *O. moco*. Patterson and Daugherty (1995) nominated *O. moco* as the type species when reinstating *Oligosoma*. Although it is possible that Girard was working from a misidentification of *Tiliqua zelandica* when erecting *Oligosoma*, there is no conclusive evidence that *O. moco* was part of the redescription of *zelandica* or was one of the species examined by Girard (1857) when describing *Oligosoma*, nor is there any evidence that Girard was deliberately using a misapplication or misidentification of Gray's *Tiliqua zelandica* in nominating *Mocoa zelandica* Gray as the type species. Hence, Patterson and Daugherty's (1995) nomination of *O. moco* as type species of *Oligosoma*, presumably (though not explicity) invoking the provisions of the Code of Zoological Nomenclature regarding misidentified type species, is invalid. We therefore treat *Tiliqua zelandica* Gray, 1843 (= *O. zelandicum*), which was the only explicit basis for *Mocoa zelandica* Gray, 1845, as the type species for *Oligosoma*, invoking Article 70.3 of the Code.

Our findings in the present study, along with the results of several recent molecular studies, have taxonomic implications for several New Zealand skink species. We hereby elevate the two subspecies of *O. nigriplantare* (*O. n. nigriplantare* and *O. n. polychroma*) to species status based on substantial genetic divergence (7.6%; also see Liggins et al., 2008a,b) and morphological differentiation (a detailed morphological description of *O. nigriplantare* is provided in Hardy (1977), with a morphological description for *O. polychroma* contained in Patterson and Daugherty (1990)). Jewell (2008) recently resurrected *C. pachysomaticum* Robb (Mercury Islands, Alderman Islands, and Ohinau Islands populations of *C. oliveri*) from synonymy with *C. oliveri* McCann despite morphological and molecular evidence to the contrary (see Chapple et al., 2008a). Since the present study confirms that no substantial genetic divergence exists between the Poor Knights Islands (COL1, 2) and Mercury Islands (COL3)/Alderman Islands (COL4) populations of *C. oliveri*, we re-synonymise *C. pachysomaticum* under *C. oliveri*. We also synonymise *O. gracilicorpus* (Hardy, 1977) under *O. homalonotum* (Boulenger, 1906). Hardy (1977) described

O. gracilicorpus from one faded museum specimen collected in the Hokianga area of Northland prior to 1955, believing it to be a juvenile 'kawekaweau' (a large lizard reported by Maori and early European explorers). However, examination of this specimen has shown it to be a sexually mature male (Towns and Daugherty, 1994; Daugherty et al., 1994). McCann (1955) originally believed this specimen to be *O. homalonotum*, and given that the specimen falls within the size range of *O. homalonotum* (Towns and Daugherty, 1994; Daugherty et al., 1994), we consider *O. gracilicorpus* to represent an extinct mainland population of *O. homalonotum*.

5.1. Eugongylus group of skinks

Greer (1979) characterised the *Eugongylus* group of scincid lizards by the following suite of characters: premaxillary teeth 11 or more; Meckel's groove completely obliterated by the overlapping and fusion of dentary; parietals meet behind interparietal; parietal bordered along its posterior edge by upper secondary temporal and transversely enlarged nuchal; medial pair of preanal scales more or less equal in size to more lateral preanals; scales on dorsal surface of fourth toe in single row throughout length of digit; iris lighter than pupil; hemipenis consisting of short columnar base and bulbous cap. The endemic skinks of Zealandia belong to the *Eugongylus* subgroup (alpha palate), in which the palatal rami of the pterygoids diverge smoothly along their medial edges (see Greer, 1979).

5.2. Oligosoma Girard, 1857

Type species. Tiliqua zelandica (Gray, 1843) (= *O. zelandicum*) by subsequent designation.

Cyclodina Girard, 1857. Type species *Cyclodina aenea* Girard, 1857, by monotypy.

Hombronia Girard, 1857. Type species *Hombronia fasciolaris* Girard, 1857, by subsequent designation.

Lygosomella Girard, 1857. Type species *Lygosomella aestuosa* Girard, 1857 (= *O. smithi*), by monotypy.

Vaderscincus Wells and Wellington, 1984. Type species *Mocoa lichenigera* O'Shaughnessy, 1874 (= *O. lichenigerum*), by monotypy.

Girardiscincus Wells and Wellington, 1985. Type species *Leiolopisma grande otagense* McCann,1955 (= *O. otagense*), by original designation.

Robbisaurus Wells and Wellington, 1985. Type species *Lygosoma suteri* Boulenger, 1906 (= *O. suteri*), by monotypy.

Definition. The clade comprising *Oligosoma zelandicum* (Gray, 1843), and all species that share a more recent common ancestor with *O. zelandicum* than with the *Eugongylus* group skinks of New Caledonia (specifically *Nannoscincus mariei*, *Marmorosphax tricolor*, *Caledoniscincus austrocaledonicus*, *Lioscincus tillieri*) and Australia (specifically *Lampropholis guichenoti, Niveoscincus pretiosus, Morethia adelaidensis*) (also see Smith et al., 2007). This genus includes all native skinks from New Zealand (including the Chatham Islands), the Lord Howe Island group, and Philip Island (6 km south of Norfolk Island). Members of this genus can be distinguished from the introduced delicate skink (*Lampropholis delicata* De Vis, 1888), which has its frontoparietals fused to form a single shield, by the presence of paired frontoparietals (Wilson and Swan, 2008; Jewell, 2008).

Description. A genus of *Eugongylus* group skinks, comprising small to large sized (50–145 mm adult SVL) terrestrial species lacking supranasals, with a movable lower eyelid and well-developed prefrontals. Frontoparietals paired. External ear opening well-developed. Midbody scales in 24–72 rows. Limbs well-developed, pentadactyl. Subdigital lamellae smooth. Viviparous, except for *O. suteri* and *O. lichenigerum* which are oviparous.

Included species. New Zealand (& Chatham Islands) – *O. acrinasum* (Hardy, 1977), *O. aeneum* (Girard, 1857), *O. alani* (Robb, 1970), *O. chloronoton* (Hardy, 1977), *O. fallai* (McCann, 1955), *O. grande* (Gray, 1845), *O. hardyi* (Chapple, Patterson, Bell & Daugherty, 2008), *O. homalonotum* (Boulenger, 1906), *O. levidensum* (Chapple, Patterson, Bell & Daugherty, 2008), *O. inconspicuum* (Patterson and Daugherty, 1990), *O. infrapunctatum* (Boulenger, 1887), *O. lineoocellatum* (Duméril and Duméril, 1851), *O. longipes* Patterson, 1997, *O. maccanni* (Patterson and Daugherty, 1990), *O. macgregori* (Robb, 1975), *O. microlepis* (Patterson and Daugherty, 1990), *O. moco* (Duméril and Bibron, 1839), *O. nigriplantare* (Peters, 1873), *O. northlandi* [extinct] (Worthy, 1991), *O. notosaurus* (Patterson and Daugherty, 1990), *O. oliveri* (McCann, 1955), *O. ornatum* (Gray, 1843), *O. otagense* (McCann, 1955), *O. pikitanga* Bell and Patterson, 2008, *O. polychroma* (Patterson and Daugherty, 1990), *O. smithi* (Gray, 1845), *O. stenotis* (Patterson and Daugherty, 1994), *O. striatum* (Buller, 1871), *O. suteri* (Boulenger, 1906), *O. taumakae* Chapple and Patterson, 2007, *O. townsi* (Chapple, Patterson, Gleeson, Daugherty, Ritchie, 2008), *O. waimatense* (McCann, 1955), *O. whitakeri* (Hardy, 1977), *O. zelandicum* (Gray, 1843); Lord Howe Island group (including Ball's Pyramid) & Philip Island (6 km south of Norfolk Island) – *O. lichenigerum* (O'Shaughnessy, 1874).

This genus also includes numerous undescribed species, including *O. ornatum* 'Poor Knights Islands' (Chapple et al., 2008c) and members of the: (i) *O. longipes* species complex (e.g. *O. longipes* 'Rangitata'), (ii) *O. lineoocellatum–O. chloronoton* species complex (see Greaves et al., 2007), (iii) *O. infrapunctatum* species complex (see Greaves et al., 2008), (iv) *O. polychroma* species complex (see Liggins et al., 2008b), (v) *O. inconspicuum* species complex (e.g. *O. inconspicuum* 'Te Kakahu'), and (vi) *O. smithi–O. microlepis* species complex (see Hare et al., 2008a). If found to represent a distinct taxon the Whirinaki skink (*Oligosoma* 'Whirinaki'; Jewell, 2008) will also belong to this genus.

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