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Comparative phylogeography reveals pre-decline population structure of New Zealand *Cyclodina* (Reptilia: Scincidae) species

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We examined the comparative phylogeography of all species within the endemic New Zealand skink genus *Cyclodina* to gain insight into the influence of historical processes on the biogeography of the North Island fauna. Until 1–2 kya, six *Cyclodina* species occurred sympatrically across the North Island of New Zealand. However, most species have undergone dramatic distributional declines subsequent to the introduction of mammals and the arrival of humans. We compare the phylogeographic patterns evident in *Cyclodina* species in three biogeographic categories: widespread species (*Cyclodina aenea*, *Cyclodina ornata*), North Island disjunct relics (*Cyclodina macgregori*, *Cyclodina whitakeri*), and northeastern island relics (*Cyclodina alani*, *Cyclodina oliveri*, *Cyclodina townsi*). Mitochondrial DNA (ND2) sequence data was obtained from across the entire range of each *Cyclodina* species. We used Neighbour-joining, maximum likelihood and Bayesian methods to examine the phylogeographic patterns present in each species. Phylogeographic patterns varied among species in different biogeographic categories. Substantial phylogeographic structure was evident in the two widespread species (*C. aenea*, *C. ornata*), with Pliocene and Pleistocene divergences between clades evident. Divergences among island groups in the three northeastern island relic species (*C. alani*, *C. oliveri*, *C. townsi*) occurred during the late Pliocene–Pleistocene. By contrast, relatively shallow structure, indicative of late Pleistocene divergences, was present in the two North Island disjunct species (*C. macgregori*, *C. whitakeri*). The results strongly suggest that the Poor Knights Islands population of *C. ornata* represents a new species. We suggest that the contrasting phylogeographic patterns exhibited by *Cyclodina* species in different biogeographic categories might be related to body size, ecology, and habitat preferences.

ADDITIONAL KEYWORDS: lizard – mitochondrial DNA – ND2 – Pleistocene glacial cycle – skink – topology tests – volcanic activity.

INTRODUCTION

The New Zealand archipelago has experienced a complex climatic and geological history subsequent to the Pliocene (Cooper & Millener, 1993; Markgraf, McGlone & Hope, 1995; Worthy & Holdaway, 2002). However, the historical processes that have shaped the North Island of New Zealand differed markedly to the processes that have been responsible for shaping the landscape of the South Island (Fig. 1). The Southern Alps that characterize the South Island were formed by tectonic activity along the alpine fault line, which commenced during the Miocene, and intensified during the Pliocene and early Pleistocene (Gage, 1980; King, 2000). The presence of mountainous regions in the South Island has facilitated extensive glaciation since the late Pliocene, created an expansive alpine zone, and fundamentally altered climatic conditions and prevailing weather patterns (Suggate,

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Figure 1. Major geographic regions in New Zealand.

1990; Pillans, 1991; Worthy & Holdaway, 2002). However, the North Island largely escaped the combined impacts of rapid tectonic uplift and glaciation (Suggate, 1990; Pillans, 1991). Instead, volcanic activity and repeated fluctuations in sea level associated with Pleistocene glacial cycles have been the predominant forces that have shaped the North Island landscape. Pleistocene glacial cycles resulted in sea level fluctuations leading to the continual connection and separation of offshore islands to the adjacent mainland (Fleming, 1979; Suggate, 1990). Volcanism has played a dominant role in modifying the landscape of the North Island subsequent to the late Pliocene (McDowall, 1996; Worthy & Holdaway, 2002). For example, the Central Plateau region has experienced substantial volcanic eruptions centred around Lake Taupo (a volcanic lake), which has erupted approximately 28 times over the last 250 kyr (McDowall, 1996; Worthy & Holdaway, 2002).

Although several molecular studies have examined the impact of historical processes, such as Pliocene mountain building, on the biogeographic patterns of the South Island fauna (Buckley, Simon & Chambers, 2001; Trewick, 2001; Chinn & Gemmell, 2004; Trewick & Morgan-Richards, 2005), less attention has been paid to the biogeographic patterns evident in the North Island fauna. In the North Island, two major biogeographic patterns appear to be evident: (1) high levels of species diversity and endemism in the northern half of the island (Northland; Fig. 1) and (2) the presence of a biogeographic barrier in the Central Plateau region. Pleistocene sea level fluctuations are believed to have influenced the evolution of the North Island biota, particularly in the Northland region, which existed as an archipelago of low-lying islands during periods of elevated sea level (Fleming, 1979; Hayward, 1986). The repeated connection and separation of islands in the Northland region during the Pleistocene appears to have resulted in substantial levels of population structuring and speciation in both plant (Gardner *et al.*, 2004) and animal taxa (Morgan-Richards, 1997; Gleeson, Howitt & Ling, 1999; Lloyd, 2003a, b; Morgan-Richards & Wallis, 2003; Berry & Gleeson, 2005; Spencer, Brook & Kennedy, 2006; Hare, Daugherty & Chapple, 2008).

Geological evidence suggests that eruptions from Central Plateau volcanoes over the past 2 Myr resulted in the repeated destruction of forests and vegetation across vast regions of the central North Island (McDowall, 1996; Worthy & Holdaway, 2002). Such eruptions would have potentially created gaps in the distribution of plant and animal taxa across the central North Island (McDowall, 1996), genetically isolating populations on each side of the Central Plateau until revegetation enabled recolonization of the region (Lloyd, 2003a, b). However, other explanations apart from volcanic activity have been suggested for the Central Plateau region (approximately 38–39°S; also called the Taupo line) representing a significant biogeographic barrier for plant (Wardle, 1963; Connor, 2002) and vertebrate taxa (McCann, 1955; Bull & Whitaker, 1975; Towns, Daugherty & Newman, 1985). The depauperate flora of the lower North Island may be the result of the combined effects of Pliocene marine inundation and tectonic activity (Rogers, 1989; Worthy & Holdaway, 2002). However, because the Northland region was dominated by expansive Kauri forests (until the arrival of humans), which were not widespread in the lower North Island (Worthy & Holdaway, 2002), ecological factors might also explain the presence of the Central Plateau biogeographic barrier.

Few studies have investigated the phylogeographic patterns that are evident in species that are widely distributed across the North Island (e.g. weta, *Hemideina thoracica* White: Morgan-Richards, 1997; Morgan-Richards & Wallis, 2003); short-tailed bats, *Mystacina tuberculata* Gray: Lloyd, 2003a, b). In the present study, we examine the comparative phylogeography of all species in the endemic New Zealand skink genus *Cyclodina* to gain insight into the influence of historical processes on the biogeography of the North Island fauna. *Cyclodina* contains nine described species, including three recently described species (Chapple *et al.*, 2008a,b), whose distributions

are restricted to the North Island and outlying islands (Gill & Whitaker, 2001) (Fig. 2, Table 1). Recent molecular studies indicate that *Cyclodina* is not monophyletic (Hickson, Slack & Lockhart, 2000; Smith *et al.*, 2007; our unpublished data). Towns *et al.* (1985) summarized the distributional patterns and biogeographic patterns in the New Zealand skink fauna. The copper skink (*Cyclodina aenea* Girard) and ornate skink (*Cyclodina ornata* Gray) are both widely distributed across the North Island, with their distribution spanning the Central Plateau region (Fig. 2, Table 1). The distribution of the robust skink (*Cyclodina alani* Robb) and marbled skink (*Cyclodina oliveri* McCann) is currently restricted to northeastern offshore Islands, but subfossil evidence (Worthy, 1987, 1991) indicates that until recently (approximately 1–2 kya) they were distributed continuously across the North Island mainland ('northeastern island relics'; Towns *et al.*, 1985) (Fig. 2, Table 1). Whitaker's skink (*Cyclodina whitakeri* Hardy) and McGregor's skink (*Cyclodina macgregori* Robb) both have a disjunct distribution with northeastern island populations and populations in the lower North Island in the Wellington region (Fig. 2), although subfossil evidence (Worthy, 1987, 1991) indicates that both were continually distributed across the south island until recently ('North Island disjunct relics', Towns *et al.*, 1985) (Table 1).

We examine the comparative phylogeography of *Cyclodina* species using mitochondrial (mt)DNA sequence data (ND2) from across the entire distribution of each species. It has been hypothesized that the low levels of genetic variation evident across the range of *Cyclodina* species with relictual distributions (e.g. *C. macgregori*, *C. whitakeri*) are due to the extinction of intervening populations of a previously continuously distributed species, rather than the loss of genetic variation in association with recent population declines (Towns & Daugherty, 1994; Towns, Daugherty & Cree, 2001). Because six *Cyclodina* species were widely distributed across the North Island 1–2 kya (Worthy, 1987, 1991; Towns & Daugherty, 1994; Towns *et al.*, 2001; BioWeb Herpetofauna Database, 2006; Table 1), each species should still possess the genetic imprint of this former distribution. We also complete topology tests to examine several taxonomic issues within *Cyclodina*.

Background to the skink genus *Cyclodina*

There are seven described *Cyclodina* species: six extant (Gill & Whitaker, 2001) and one extinct (*C. northlandi* Worthy, Worthy, 1991). Recent taxonomic work has resulted in the description of three new *Cyclodina* species: *C. townsi* (Chapple *et al.*, 2008a), *C. aenea* 'Poor Knights Islands' and *C. aenea* 'Te Paki' (Chapple *et al.*, 2008b), increasing the number of described species to 10'. Hardy (1977) also suggested that the Poor Knights Islands and Three Kings Islands populations of *C. ornata* were morphologically distinctive, and possibly represent distinct species. Recent molecular studies have suggested that *Cyclodina* is not monophyletic (Hickson *et al.*, 2000; Smith *et al.*, 2007; our unpublished data).

Morphological and ecological differences distinguish *Cyclodina* from *Oligosoma*, the other endemic skink genus in New Zealand (Patterson & Daugherty, 1995). *Cyclodina* are crepuscular to nocturnal species that inhabit shaded and forested habitats (Table 1), whereas *Oligosoma* contains diurnal species that inhabit more open habitats (Patterson & Daugherty, 1995; Gill & Whitaker, 2001). *Oligosoma* is more diverse than *Cyclodina*, with 24 described species (23 extant, one extinct species; Gill & Whitaker, 2001; Chapple & Patterson, 2007). Although *Oligosoma* species generally have widespread distributions across the North Island, South Island, and Stewart Island, no species is continuously distributed across the North Island (Gill & Whitaker, 2001).

MATERIAL AND METHODS

Taxonomic sampling

We obtained samples from all described species in the New Zealand skink genus *Cyclodina* (Fig. 2; see also Supporting Information, Table S1). Samples were obtained primarily from the National Frozen Tissue Collection (Victoria University of Wellington, New Zealand) and ethanol preserved specimens housed at Te Papa (National Museum of New Zealand, Wellington). Our sampling encompassed populations from across the entire distribution of each *Cyclodina* species: *C. alani* (seven samples), *C. aenea* (38 samples), *C. aenea* 'Poor Knights' (five samples), *C. aenea* 'Te Paki' (two samples), *C. macgregori* (four samples), *C. oliveri* McCann (three samples), *C. townsi* (three samples), *C. ornata* (24 samples) and *C. whitakeri* (seven samples) (Table S1). Because we examine the taxonomy and phylogeography of the *C. oliveri* species complex in detail elsewhere (Chapple *et al.*, 2008a), we have only included representative samples of *C. oliveri* and *C. oliveri* 'Mokohinau' in the present study. Based on the results of a broader phylogenetic study of the relationships among all members of the New Zealand skink radiation (D. G. Chapple, C. H. Daugherty & P. A. Ritchie, unpubl. data), we included samples from the New Zealand common skink (*Oligosoma nigriplantare polychroma* Patterson & Daugherty), the speckled skink (*Oligosoma infrapunctatum* Boulenger), and the Lord Howe

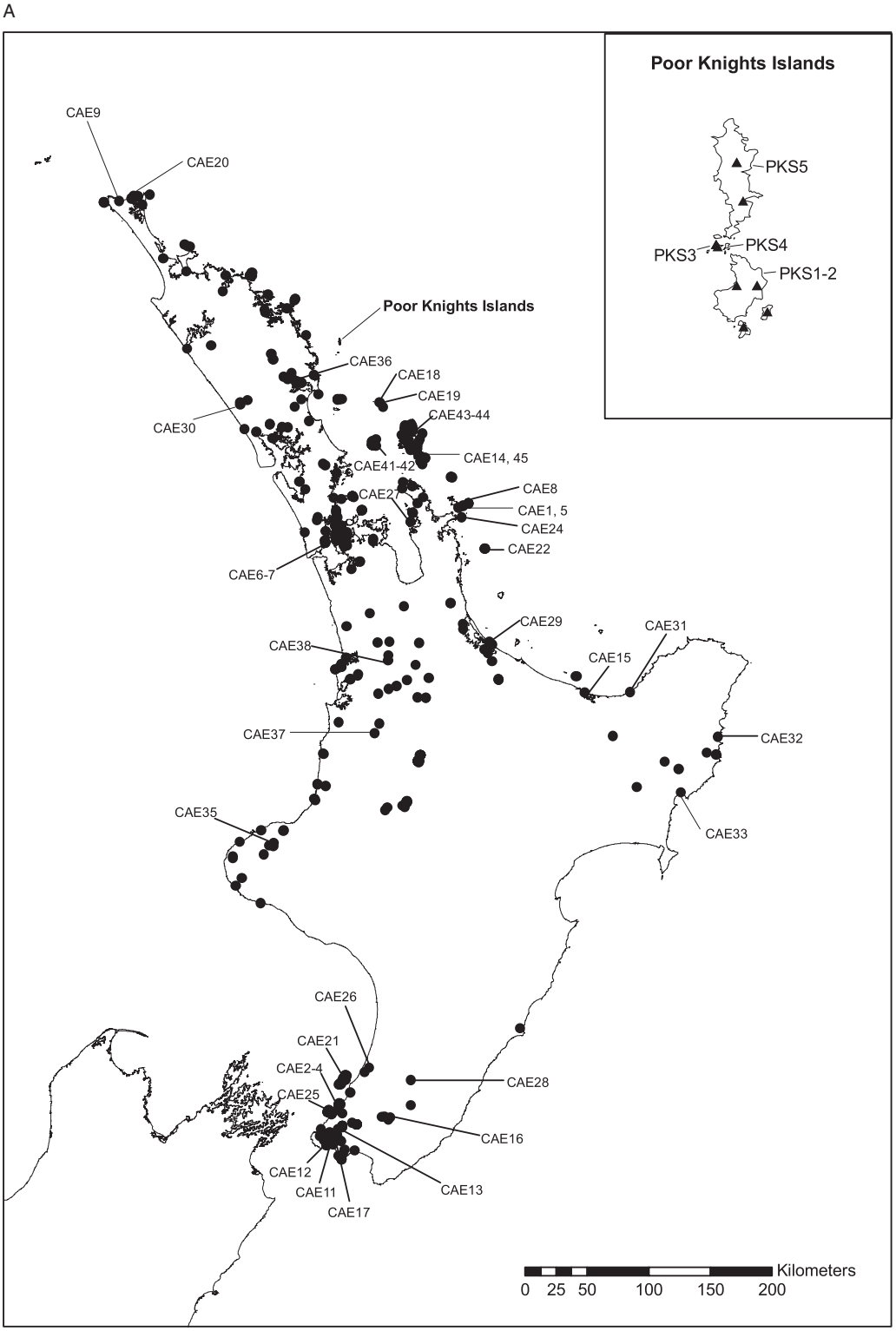

Figure 2. Distribution maps and location of tissue samples used in this study. (A) *Cyclodina aenea* (circles), *Cyclodina aenea* 'Te Paki' (CAE9, CAE20), and *Cyclodina aenea* 'Poor Knights' (triangles in the inset for the Poor Knights Islands); (B) *Cyclodina ornata*; (C) *Cyclodina alani* (black circles), *Cyclodina macgregori* (squares) and *Cyclodina whitakeri* (grey circles); and (D) *Cyclodina oliveri* (circles) and *Cyclodina townsi* (squares). Distributional data were obtained from the New Zealand Department of Conservation's BioWeb Herpetofauna Database (2006).

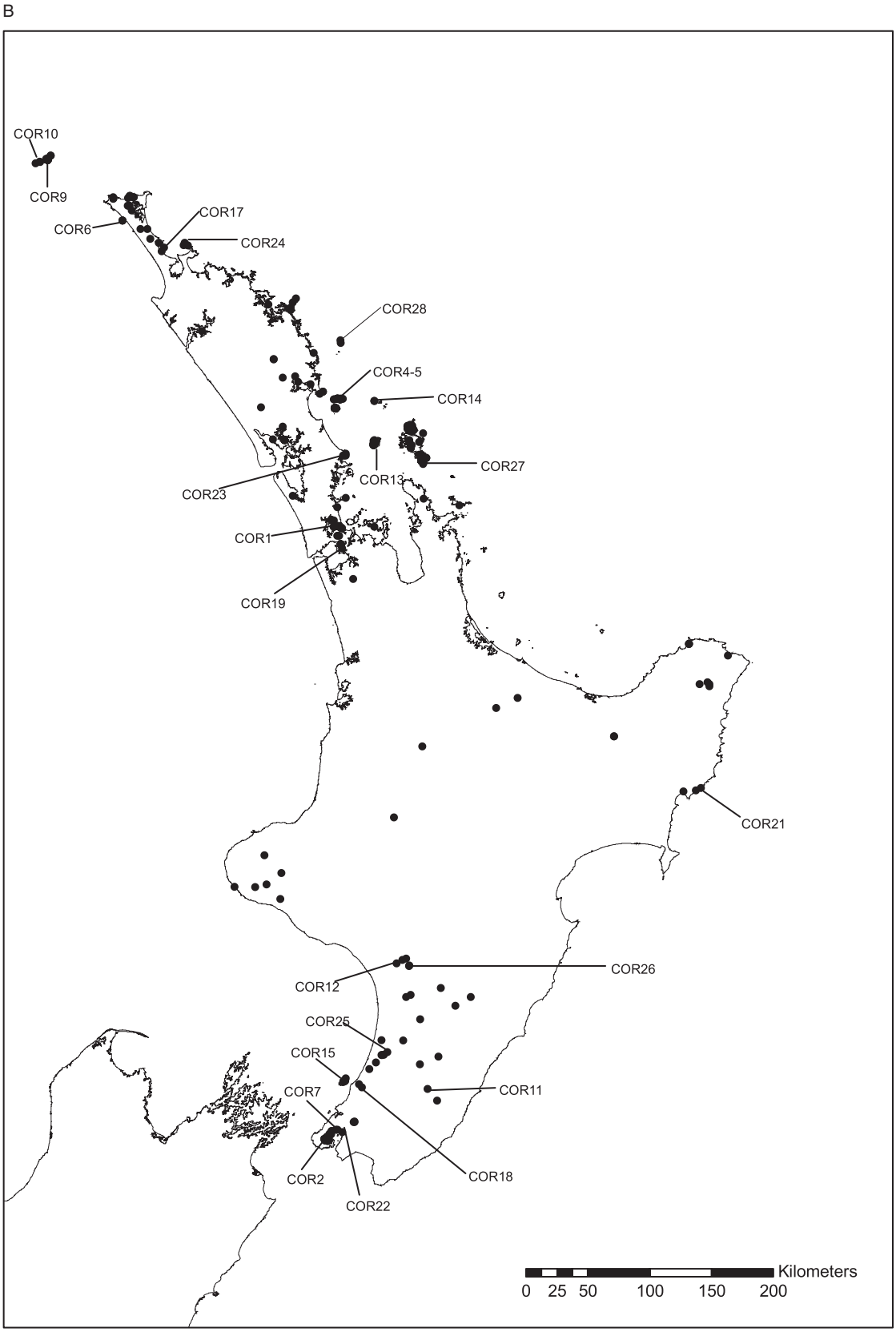

Figure 2. *Continued*

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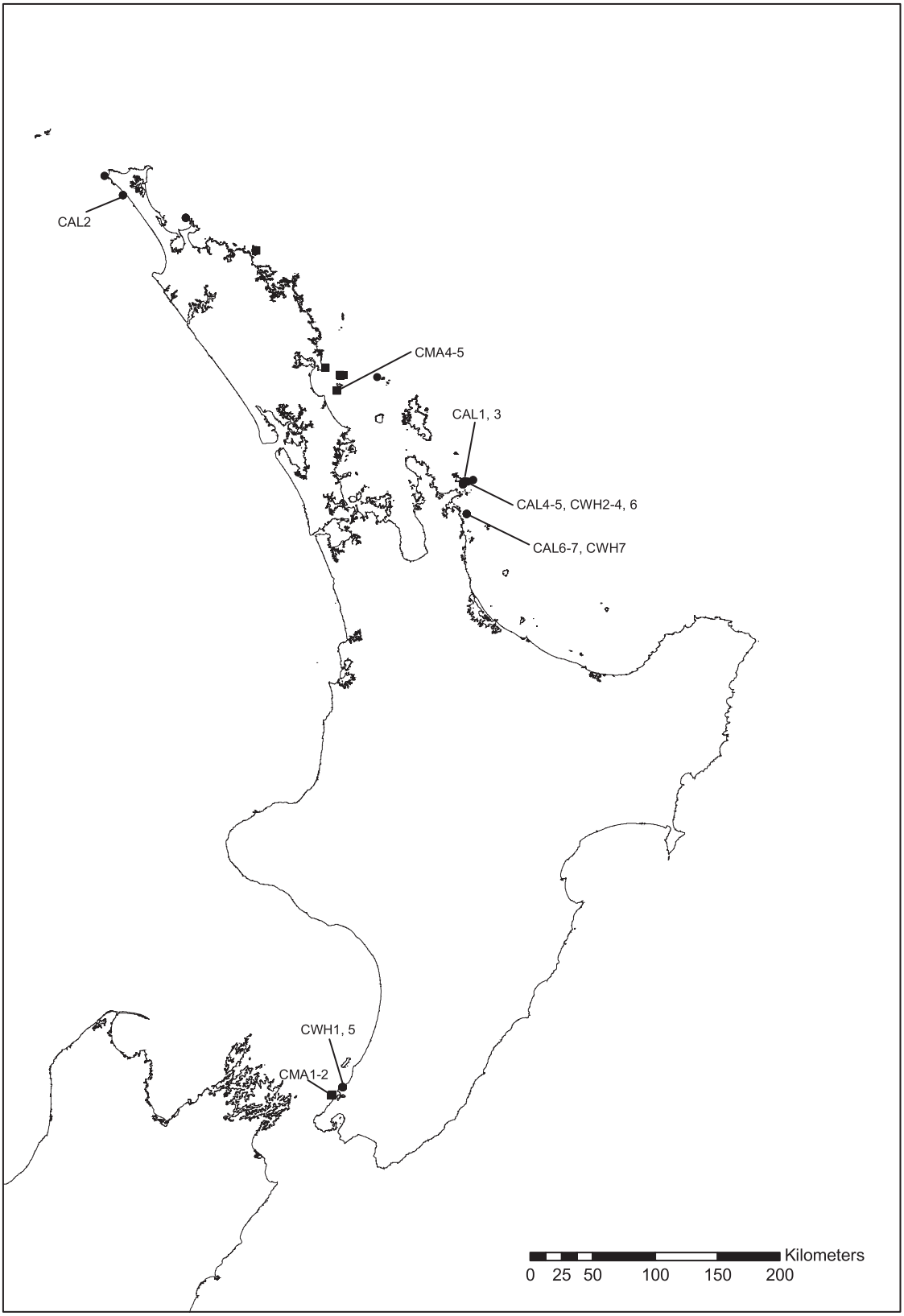

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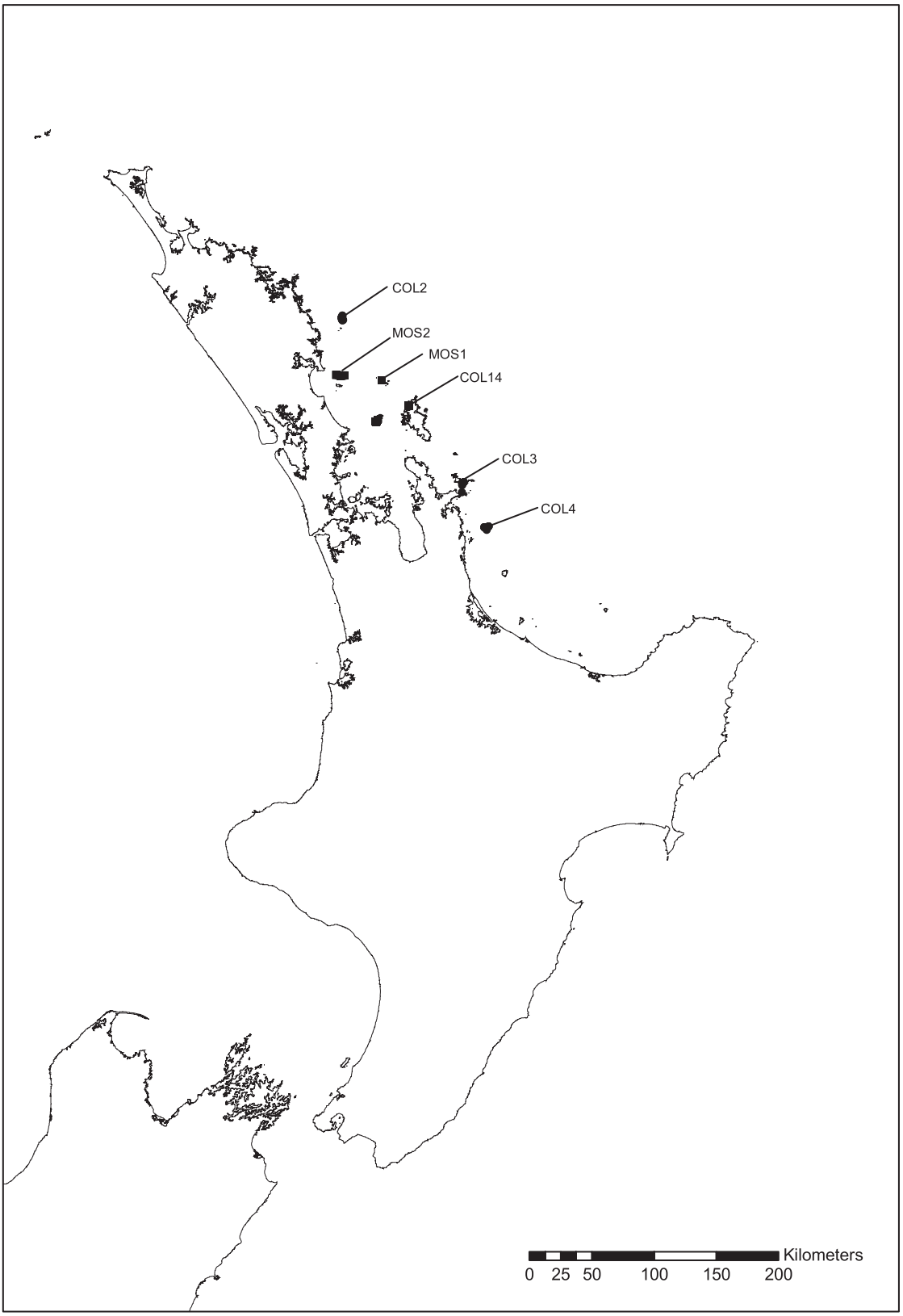

Figure 2. *Continued*

Table 1. Summary of the habitat preferences, body size, present distribution and past distribution of *Cyclodina* species

Species	Habitat	Body size (mm SVL)	Present distribution	Past distribution
Cyclodina aenea	Forested habitats, preferring open or shaded habitats with ground cover[1]	62[1,2]	Widespread throughout NI from Northland to Wellington[1,3]	Widespread throughout NI from Northland to Wellington[1,3]
Cyclodina aenea 'Poor Knights'	Flax and scrub habitats with ground cover[4]	62[4]	Poor Knights Islands[5]	Poor Knights Islands[5]
Cyclodina aenea 'Te Paki'	Unknown[5]	?[5]	Northern tip of Northland[5]	Unknown[5]
Cyclodina alani	Low coastal forest[1]	142[1]	Matapia I, Moturoa I, Mokohinau Islands (Tatapihi [Groper] I), Mercury Islands (Middle I, Green I), Castle I. Translocated to Mercury Islands (Korapuki I, Stanley I, Red Mercury I) & Motuopao I[3,6]	Lowland coastal forest from Northland to the Wellington region, & offshore islands around the northwest, northeast & southwest[3,7–9]
Cyclodina macgregori	Leaf litter under coastal forest and scrub[1]	112[1,2]	Cavalli Islands (Motuharakeke I), Outer Bream Islands (Muitaha I), Hen & Chickens Group (Sail Rock), Mana I near Wellington. Translocated to Hen & Chickens Group (Lady Alice I)[3,6]	NI from Northland to Wellington & many offshore islands[3,7,8]
Cyclodina oliveri	Leaf litter under coastal forest and scrub[1]	116[1,4]	Poor Knights Islands, Ohinau Islands (Old Man Rock), Mercury Islands (Middle I, Green I), Alderman Islands Translocated to Mercury Islands (Korapuki I)[1,3,6]	Northland to the northern Bay of Plenty[6–8]*
Cyclodina townsi	Broadleaf forest and low scrub[10]	87[10]	Mokohinau Islands (Tatapihi [Groper] I, Stack 'H'), Hen & Chickens Group (Muriwhenua I, Wareware I, Pupuha I, One I, Middle stack), Little Barrier I, Great Barrier I. Translocated to Hen & Chickens Group (Lady Alice I, Whatupuke I, Coppermine I)[10]	Northland to the northern Bay of Plenty[6–8]*
Cyclodina ornata	Forest or open areas with stable cover[1]	80[1,2]	Widespread through NI from the Three Kings Islands to Wellington[1,3]	Widespread through NI from the Three Kings Islands to Wellington[1,3]
Cyclodina whitakeri	Coastal forest and scrub[1]	101[1]	Mercury Islands (Middle I), Castle I, Pukerua Bay north of Wellington. Translocated to Mercury Islands (Korapuki I, Stanley I, Red Mercury I)[1,3,6]	lowland forest through the NI from Northland to the Wellington region & islands of the Hauraki Gulf[6–8]

For more detailed information on the current distribution of *Cyclodina* species, see Fig. 2. Body size refers to maximum body size. NI, North Island; SVL, snout–vent length. References (shown as superscripts): 1, Gill & Whitaker (2001); 2, Hardy (1977); 3, BioWeb Herpetofauna Database (2006); 4, Whitaker (1968); 5, Chapple *et al.* (2008b); 6, Towns (1999); 7, Worthy (1987); 8, Worthy (1991); 9, Worthy & Swabey (2002); 10, Chapple *et al.* (2008a).

*It is unknown whether these subfossils relate to *C. oliveri* or *C. townsi* (D. G. Chapple, G. B. Patterson, D. M. Gleeson, C. H. Daugherty & P. A. Ritchie, unpubl. data).

Island skink (*'Oligosoma' lichenigera* O'Shaughnessy; sample from South Australian Museum) (Table S1).

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from liver, toe, or tail samples using a modified phenol-chloroform extraction protocol (Sambrook, Fritsch & Maniatis, 1989). For each sample, we targeted a portion of the mitochondrial gene ND2 (approximately 600 bp). This region was chosen because work at comparable taxonomic levels in other squamate reptile groups has indicated useful levels of variability (Greaves *et al.*, 2007, 2008; Hare *et al.*, 2008).

The primers used to amplify and sequence ND2 were L4437 (Macey *et al.*, 1997) and ND2r102 (Sadlier *et al.*, 2004). However, two internal primers were also used to amplify ND2 for some samples (ND2F-infrapunctatum, 5′-GCATGATTYACCGGAAY ATGAGACAT-3′; ND2R-infrapunctatum, 5′-GGGGC AAGKCCTAGTTTTATGG-3′; Greaves *et al.* (2007). Polymerase chain reaction and sequencing were conducted as described in Greaves *et al.* (2007).

Sequence data were edited using CONTIGEXPRESS, version 9.1.0 (Invitrogen), and aligned using the default parameters of CLUSTAL X (Thompson *et al.*, 1997). The aligned sequences were translated into amino acid sequences using the vertebrate mitochondrial code to check whether the sequences were truly mitochondrial in origin. Because no premature stop codons were observed, we conclude that all sequences obtained are true mitochondrial copies. Sequence data as submitted to GenBank under accession numbers EF033052, EF033050, EF043106, EF-81173, EF081175–EF081177, EF081182–EF081184, EF081187, EF103954, and EF567120–EF567203.

Phylogenetic analyses

Because *Cyclodina* is not monophyletic (our unpublished data; see also Hickson *et al.*, 2000; Smith *et al.*, 2007), we split our dataset into two for all phylogenetic analyses: (1) *Cyclodina aenea* species complex (*C. aenea*, *C. aenea* 'Te Paki', *C. aenea* 'Poor Knights') and (2) other *Cyclodina* (*C. alani*, *C. macgregori*, *C. oliveri*, *C. townsi*, *C. ornata*, *C. whitakeri*).

Neighbour-joining (NJ) analyses, using the Tamura–Nei correction, were conducted in PAUP* v4.0b10 (Swofford, 2002). MODELTEST 3.7 (Posada & Crandall, 1998) was used to determine the most appropriate model of evolution for our dataset, generating log-likelihood scores for the dataset in PAUP* and conducting a hierarchical likelihood ratio test (hRLT). Base frequencies, substitution rates, the proportion of invariant sites (I), and the among-site substitution rate variation were estimated in MODELTEST, with these values implemented in PAUP* to generate a maximum likelihood (ML) tree.

Bayesian analyses were completed using the computer program MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001). We used the default value of four Markov chains per run, and ran the analysis for one million generations. The chain was sampled every 100 generations to obtain 10 000 sampled trees. The first 2500 sampled trees were discarded as the burn-in phase, with the last 7500 trees used to estimate the Bayesian posterior probabilities. We used both bootstrap values and Bayesian posterior probabilities to assess branch support. NJ bootstraps (1000 replicates) were generated in PAUP*. We consider branches supported by bootstraps values greater than or equal to 70% (Hillis & Bull, 1993), and posterior probability values greater than or equal to 95% (Wilcox *et al.*, 2002) to be significantly supported by our data. Uncorrected genetic distances were calculated in MEGA 3.1 (Kumar, Tamura & Nei, 2004).

Estimating divergence times

To estimate the divergence time of lineages, we calibrated the evolutionary rate of ND2 by re-analysing the data from Macey *et al.* (1998) for the agamid genus *Laudakia*. Macey *et al.* (1998) calibrated this rate through geological dating of tectonic events (mountain uplift) on the Iranian Plateau. The ND2 evolutionary rate has been demonstrated to be consistent (approximately 1.2–1.4%) across several vertebrate groups (fish, amphibians, reptiles; Weisrock *et al.* (2001). We recalculated the evolutionary rate for *Laudakia* using only the 550-bp fragment of ND2 used in the present study (Smith *et al.*, 2007). We calculated average between-group nucleotide differences across each of the calibrated nodes from Macey *et al.* (1998) (1.5, 2.5, and 3.5 Mya), plotted them against time and then used the slope of the linear regression to calculate a rate of evolution for our 550-bp fragment of ND2. This resulted in an evolutionary rate of 1.4% per Myr (0.7% per lineage, per Myr) and is slightly faster than the rate of 1.3% per Myr found by Macey *et al.* (1998).

Hypothesis testing

We completed Shimodaira–Hasegawa tests in PAUP* (Shimodaira & Hasegawa, 1999; Goldman, Anderson & Rodrigo, 2000) using full optimization and 1000 replicates to examine several alternative topologies in the genus *Cyclodina*. We tested the significance of the log-likelihood difference between our optimal ML/Bayesian tree (using the ML –ln L) and alternative hypotheses representing three taxonomic hypotheses:

1. Based on evidence from haem compound electrophoresis, Hardy (1977) considered the Great Barrier Island population of *C. aenea* to be closely related to the Poor Knights population that has recently been described as a new species (Chapple *et al.*, 2008b). However, the Great Barrier Island population is not morphologically distinctive from the typical *C. aenea* morphology (Hardy, 1977). We tested the alternative topology that the Great Barrier Island represents a distinct species within the *C. aenea* species complex;
2. Hardy (1977) found that the Three Kings Islands population of *C. ornata* was morphologically distinctive from other *C. ornata* populations, having higher ventral scale counts. We tested the alternative topology that the Three Kings Islands population of *C. ornata* represents a distinct species.
3. Hardy (1977) found that the Poor Knights Islands (Aorangi) population of *C. ornata* had higher lamella counts compared to other *C. ornata* populations. We tested the alternative topology that the morphologically distinctive Poor Knights Islands population of *C. ornata* represents a distinct species.

RESULTS

CYCLODINA AENEA SPECIES COMPLEX

The edited alignment comprised 550 characters, of which 179 (33%) were variable and 128 (23%) were parsimony informative. For the ingroup only, the alignment contained 179 (33%) variable characters, of which 51 (9%) were parsimony-informative. Base frequencies were unequal (A = 0.323, T = 0.215, C = 0.333, G = 0.129), but a chi-square test confirmed the homogeneity of base frequencies among sequences (d.f. = 141, $P = 0.9705$). For one sample (CAE42), only approximately 525 bp of sequence data was obtained, whereas only approximately 325 bp of sequence data was obtained for another sample (CAE41) due to the poor quality of the DNA template.

The hRLT from MODELTEST supported the TrN+G substitution model as the most appropriate for our dataset (–ln L = 2342.5625). Parameters estimated under this model were: relative substitution rates (A ↔ C = 1.0, A ↔ G = 11.32, A ↔ T = 1.0, C ↔ G = 1.0, C ↔ T = 7.64, G ↔ T = 1.00) and gamma shape parameter (0.2758). The topology of the NJ, ML, and Bayesian trees were almost identical, therefore only the optimal ML tree (–ln L = 2427.22515) is shown in Figure 3A, with NJ bootstrap values and Bayesian posterior probabilities indicating branch support. Extremely strong support (100 bootstrap and 0.99–1.0 posterior probability in all cases) exists for the presence of three distinct species within the *C. aenea* species complex: *C. aenea*, *C. aenea* 'Poor Knights Islands', and *C. aenea* 'Te Paki' (Fig. 3A). A substantial level of genetic differentiation is evident between *C. aenea* and the two new taxa: *C. aenea* 'Poor Knights Islands' [mean pairwise genetic distance (PGD) = 14.4%] and *C. aenea* 'Te Paki' (PGD = 14%). A significant level of genetic divergence is also evident between the two undescribed species (PGD = 11.7%).

The level of genetic differentiation evident within *C. aenea* 'Poor Knights Islands' (restricted to the Poor Knights Islands; PGD = 0.6%; 0.43 Mya) and *C. aenea* 'Te Paki' (restricted to northern Northland; PGD = 0.5%; 0.36 Mya) is relatively low, but substantially greater in the more widespread *C. aenea* (PGD = 2.5%; 1.79 Mya). Five clades are evident within *C. aenea*, as well as two divergent clades in the Northland region (CAE30: Dargaville, CAE36: Whangarei; Fig. 3A). Clade 1 (99 bootstrap, 1.0 posterior probability; PGD = 0.8%; 0.57 Mya) contains populations from the Alderman Islands, Mercury Islands (Red Mercury Island), Ohinau Island, and the North Island mainland south of the Waikato/Bay of Plenty region (Fig. 4A). Clade 2 (recovered in the NJ and Bayesian trees with 69 bootstrap and 0.77 posterior probability, but not the ML tree shown in Fig. 3A) contains populations from the Mercury Islands (Korapuki Island), the western side of Coromandel Peninsula, and the Auckland region (PGD = 0.6%; 0.43 Mya). Clade 3 (85 bootstrap, 1.0 posterior probability; PGD = 0.4%; 0.29 Mya) comprises populations from Great Barrier Island (Fig. 4A). The Shimodaira–Hasegawa topology test clearly rejected the hypothesis that the Great Barrier Island population represents a distinct species ($P < 0.001$). Clade 4 (52 bootstrap, 1.0 posterior probability; PGD = 0.6%; 0.43 Mya) contains populations from Little Barrier Island and the Auckland region (Fig. 4A). Clade 5 (96 bootstrap, 1.0 posterior probability) contains populations from the Mokohinau Islands (Fig. 4A). The mean pairwise genetic distances between the five clades and the two divergent Northland samples (CAE30, CAE36) range between 1.2–6.1% (0.86–4.36 Mya) (Table 2).

OTHER *CYCLODINA* SPECIES

The edited alignment comprised 550 characters, of which 203 (37%) were variable and 149 (27%) were parsimony informative. For the ingroup only, the alignment contained 203 (37%) variable characters, of which 54 (10%) were parsimony-informative. Base frequencies were unequal (A = 0.327, T = 0.214, C = 0.345, G = 0.114), but a chi-square test confirmed

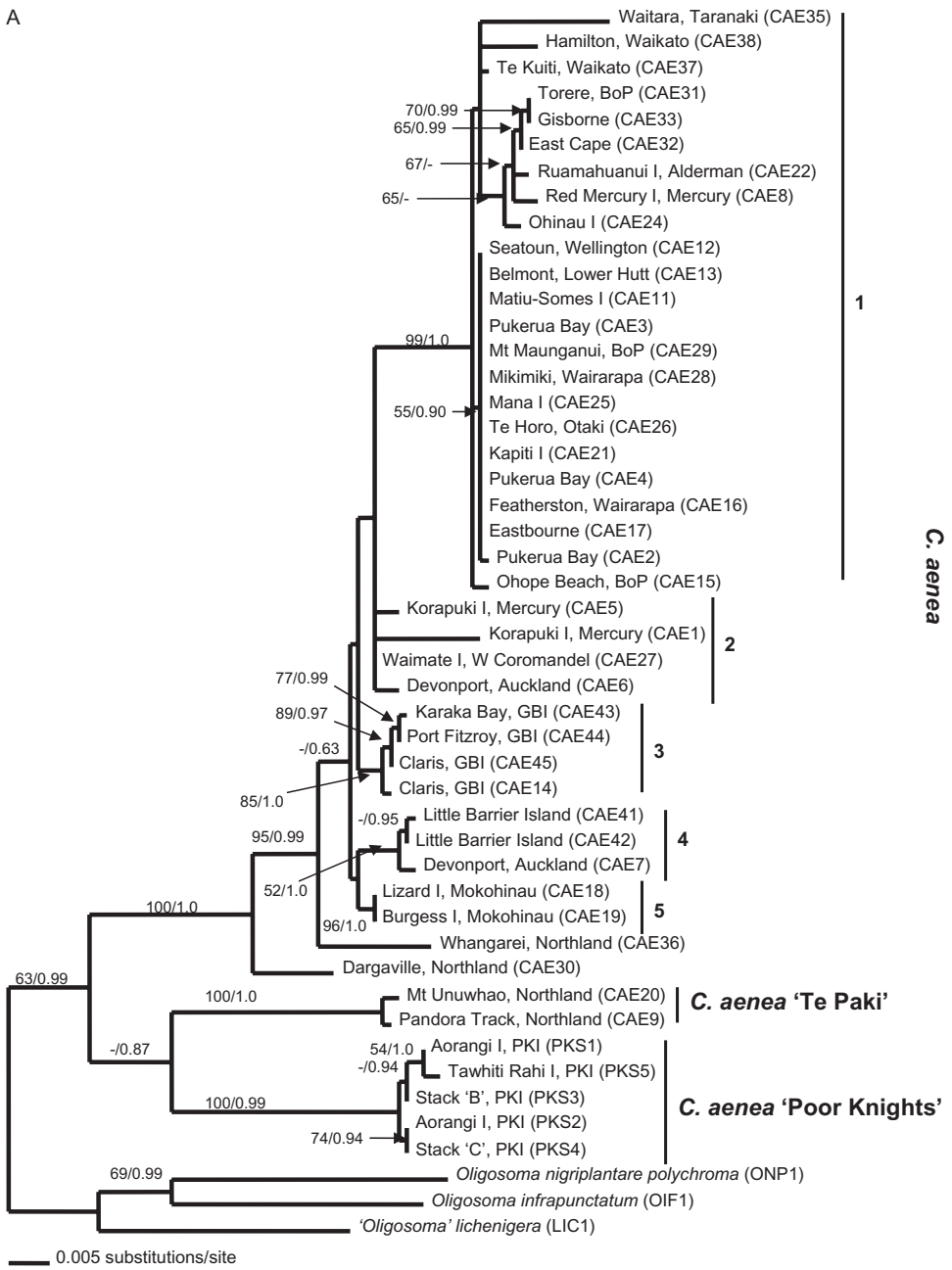

Figure 3. Maximum likelihood (ML) tree for *Cyclodina* based on 550 bp of the ND2 mitochondrial gene. The topology of the Neighbour-joining (NJ) and Bayesian trees were identical to the ML trees shown. Two measures of branch support are indicated with NJ bootstraps shown on the left and Bayesian posterior probabilities shown on the right (only values over 50 and 0.7, respectively, are shown). Because *Cyclodina* is not monophyletic, we split our dataset into two for phylogenetic analyses (see text): (A) *Cyclodina aenea* species complex (nb. clade 2 was recovered in the NJ and Bayesian trees with 69 bootstrap and 0.77 posterior probability, but not the ML tree shown here) and (B) other *Cyclodina* species.

the homogeneity of base frequencies among sequences (d.f. = 150, $P = 0.9999$). For several samples, only approximately 525 bp of sequence data was obtained (COR13, COR15, COR17, COR25–27). In addition, due to the poor quality of the DNA template, a small number of samples had a reduced sequence length of approximately 325 bp (COR9–10, COR18–19, COR21, COR24).

The hRLT from MODELTEST supported the TrN+G substitution model as the most appropriate

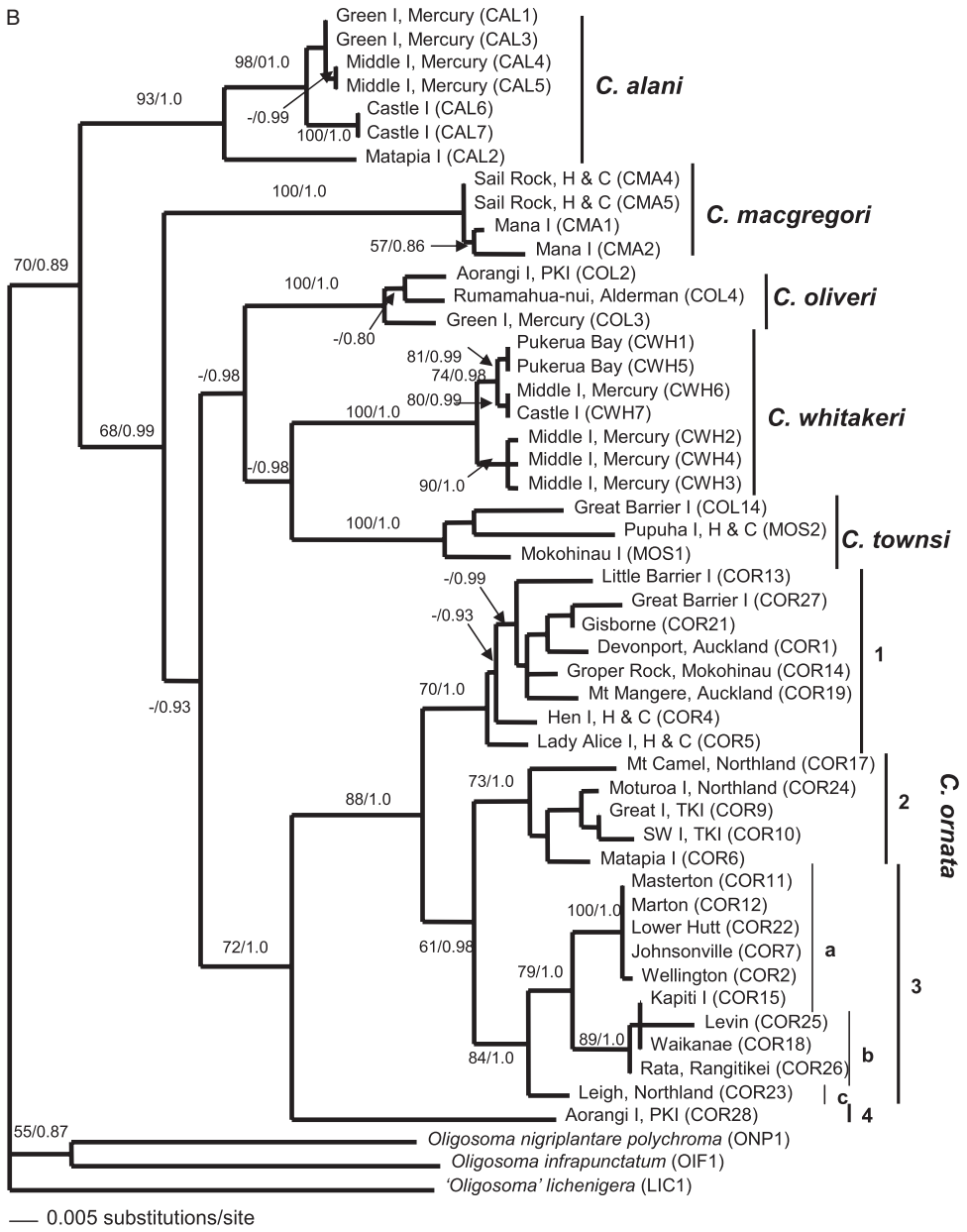

Figure 3. *Continued*

Table 2. Uncorrected genetic distance matrix for *Cyclodina aenea* clades based on 550 bp of the ND2 mitochondrial gene

Clade	Clade 1	Clade 2	Clade 3	Clade 4	Clade 5	CAE30	CAE36
Clade 1	NA						
Clade 2	0.030	NA					
Clade 3	0.036	0.017	NA				
Clade 4	0.042	0.040	0.020	NA			
Clade 5	0.032	0.014	0.013	0.015	NA		
CAE30	0.060	0.052	0.049	0.058	0.047	NA	
CAE36	0.051	0.042	0.041	0.033	0.039	0.061	NA

NA, not applicable.

A

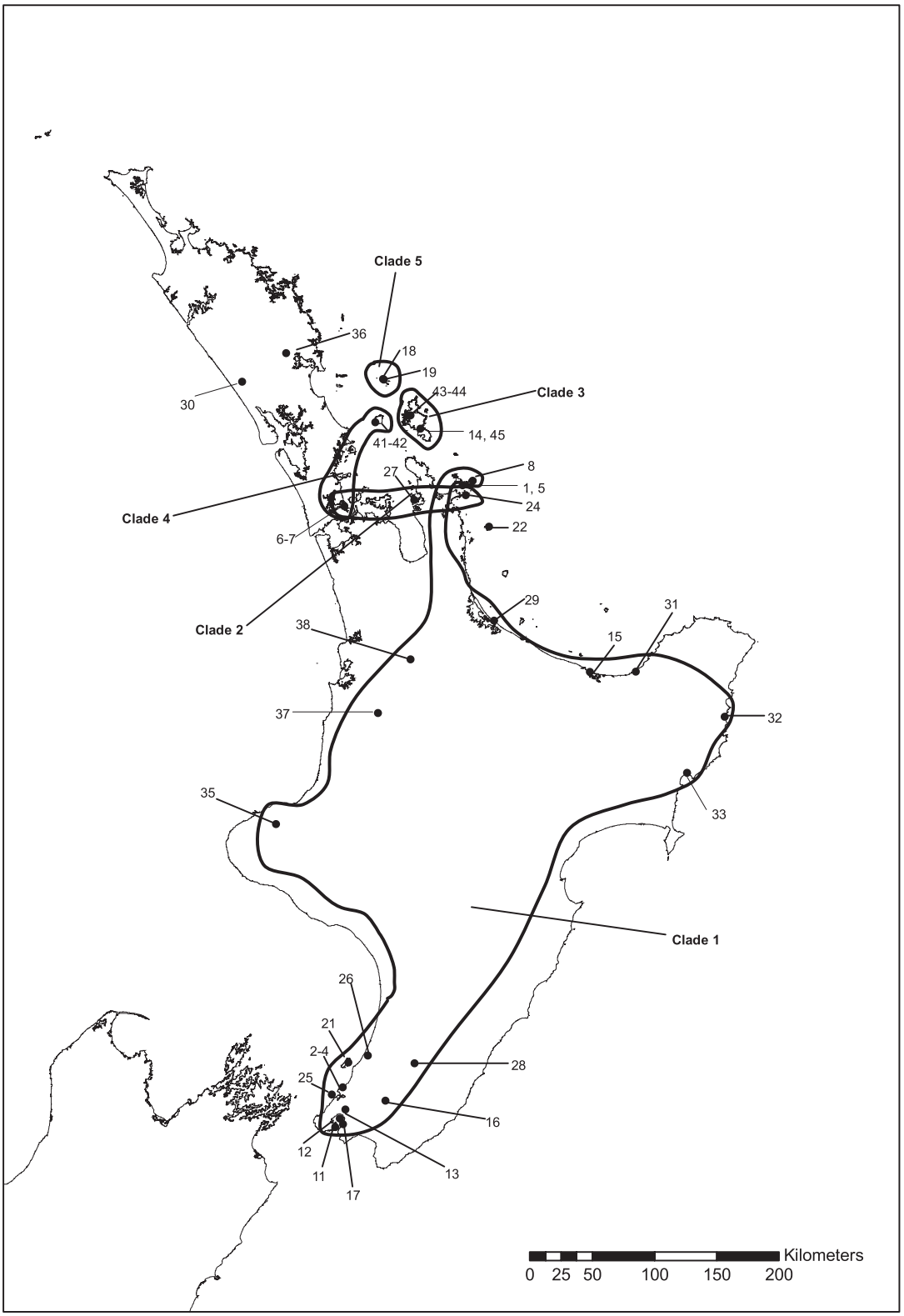

Figure 4. Distribution of clades within (A) *Cyclodina aenea* and (B) *Cyclodina ornata* identified in Fig. 3.

B

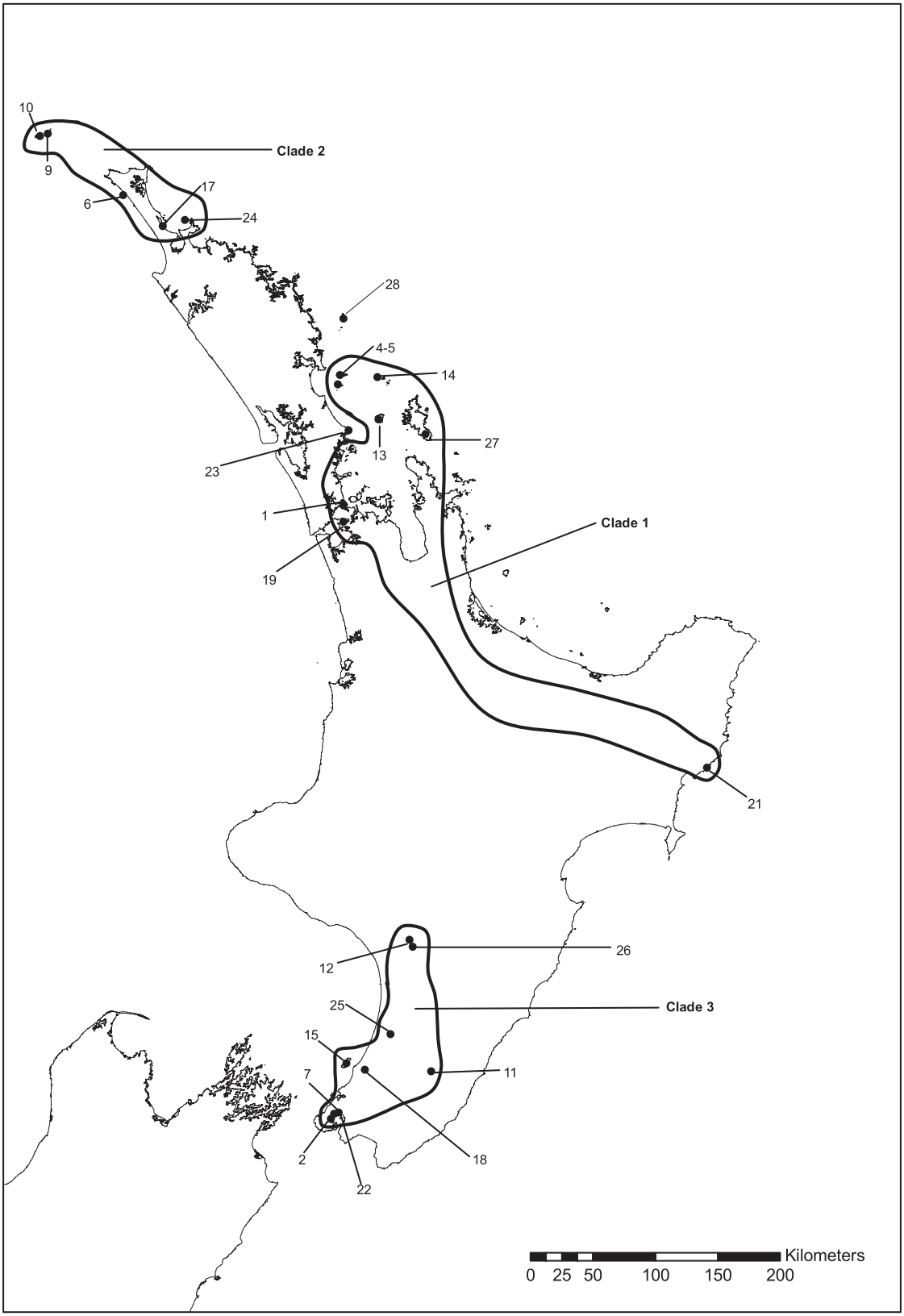

Figure 4. *Continued*

Table 3. Uncorrected genetic distance matrix for *Cyclodina* based on 550 bp of the ND2 mitochondrial gene

Species	*Cyclodina alani*	*Cyclodina macgregori*	*Cyclodina oliveri*	*Cyclodina whitakeri*	*Cyclodina ornata*	*Cyclodina ornata* 'PKI'	*Cyclodina townsi*
Cyclodina alani	NA						
Cyclodina macgregori	0.111	NA					
Cyclodina oliveri	0.103	0.095	NA				
Cyclodina whitakeri	0.092	0.092	0.075	NA			
Cyclodina ornata	0.104	0.111	0.097	0.096	NA		
Cyclodina ornata 'PKI'	0.112	0.108	0.104	0.119	0.094	NA	
Cyclodina 'Mokohinau'	0.112	0.106	0.085	0.086	0.103	0.116	NA

The Poor Knights Islands population of *C. ornata* (*C. ornata* 'PKI') is considered as a distinct taxa (see text).
NA, not applicable.

for our dataset (–ln L = 3065.2251). Parameters estimated under this model were: relative substitution rates (A ↔ C = 1.0, A ↔ G = 24.81, A ↔ T = 1.0, C ↔ G = 1.0, C ↔ T = 9.65, G ↔ T = 1.00) and gamma shape parameter (0.2464). The topology of the NJ, ML, and Bayesian trees were identical, therefore only the optimal ML tree (–ln L = 3302.01234) is shown in Figure 3B, with NJ bootstrap values and Bayesian posterior probabilities indicating branch support. There is extremely strong support for the monophyly of all described species (*C. alani*, 93 bootstrap, 1.0 posterior probability; *C. macgregori*, 100 bootstrap, 1.0 posterior probability; *C. oliveri*, 100 bootstrap, 1.0 posterior probability; *C. ornata*, 72 boostrap, 1.0 posterior probability), as well as the recently described Towns' skink (*C. townsi*, 100 bootstrap, 1.0 posterior probability). The mean pairwise genetic distance between recognized species ranges between 7.5–11.9% (Table 3).

Geographic structure is present within *C. alani* (PGD = 1.8%; 1.29 Mya), with the Matapia Island population (CAL2) clearly divergent from the Castle Island and Mercury Islands populations (PGD Matapia I versus other *C. alani* = 4.4%; 3.14 Mya) (Fig. 3). Relatively less genetic differentiation was evident between the Castle Island and Mercury Islands populations (PGD = 1.4%; 1 Mya). By contrast, no substantial phylogeographic structure was evident within *C. macgregori* (PGD = 0.7%; 0.5 Mya), with low levels of genetic divergence between the populations on Mana Island (lower North Island) and Sail Rock in the Hen and Chickens Islands (northeastern North Island) (PGD = 0.7%; 0.5 Mya). Likewise, geographic structuring within *C. whitakeri* was relatively minor (PGD = 0.9%; 0.64 Mya). Although the Pukerua Bay population forms a well-supported clade (81 bootstrap, 0.99 posterior probability), the level of genetic differentiation between the Pukerua Bay population and the two northeastern island populations (Castle Island PGD = 0.4%, 0.29 Mya; Mercury Islands PGD = 1.1%; 0.79 Mya) populations was not greater than that observed between the Castle Island and Mercury Islands populations (PGD = 1%; 0.71 Mya). A relatively high level of genetic differentiation was evident within both *C. oliveri* (PGD = 1.9%; 1.36 Mya) and *C. townsi* (PGD = 3.9%; 2.79 Mya).

Substantial geographic structuring is present within *C. ornata* (PGD = 4.1%; 2.93 Mya), with four well-supported clades evident (Fig. 3B). Clade 1 (70 bootstrap, 1.0 posterior probability; PGD = 1.9%; 1.36 Mya) contains populations from the Auckland region, the islands in the Hauraki Gulf (Mokohinau Islands, Hen and Chickens Islands, Little Barrier Island, Great Barrier Island), and Gisborne (Fig. 4B). Clade 2 (73 bootstrap, 1.0 posterior probability; PGD = 1.7%; 1.21 Mya) comprises populations from the Three Kings Islands and northern Northland (Fig. 4B). The Shimodaira–Hasegawa topology test clearly rejected the hypothesis that the Three Kings Islands population represents a distinct species ($P = 0.002$). Clade 3 (84 bootstrap, 1.0 posterior probability; PGD = 1.5%; 1.07 Mya) contains populations from across the lower North Island and a single population from Leigh, north of Auckland (Fig. 4B). Three subclades were evident within clade 3 (Fig. 3B), with the mean pairwise genetic distances between these subclades in the range 2.5–2.8% (1.79–2 Mya). The Poor Knights Islands (Aorangi) population represents the final clade (Clade 4) within *C. ornata* (Fig. 4B). The mean pairwise genetic distances between clades 1–3 ranges between 4.3–4.9% (3.07–3.50 Mya), but is significantly higher between clade 4 and the other three clades (PGD 8.7–9.8%; 6.21–7 Mya). It was not possible to conduct a topology test to examine the taxonomic status of the Poor Knights Islands *C. ornata* population since the genetic distinctiveness of this population was supported by the optimal ML tree (Fig. 3B).

DISCUSSION

Several contrasting phylogeographic patterns appear to exist within the genus *Cyclodina*. Subfossil evidence indicates that at least six *Cyclodina* species occurred sympatrically across the majority of the North Island during the Pleistocene (Worthy, 1987, 1991; Towns & Daugherty, 1994; Towns *et al.*, 2001; BioWeb Herpetofauna Database, 2006). However, over the past 1–2 kyr, introduced mammals and anthropogenic impacts have modified reptile assemblages and resulted in dramatic declines in some species (Towns & Daugherty, 1994; Towns *et al.*, 2001). Phylogeographic studies provide insight into how these disjunct and isolated distributional patterns were derived, and enable the level of population structuring in each species prior to decline to be inferred (Towns *et al.*, 2001). *Cyclodina* species that remain widespread (*C. aenea*, *C. ornata*) display deep phylogeographic structure whereas, in northeastern island relic species (*C. alani*, *C. oliveri*, *C. townsi*), substantial divergence exists between populations on different island groups. By contrast, relatively shallow genetic divergences are evident between disjunct populations in both *C. macgregori* and *C. whitakeri* (North Island disjunct relics; Towns *et al.*, 1985). We discuss the significance of these phylogeographic patterns, and examine the taxonomic implications of these findings.

WIDESPREAD SPECIES: *CYCLODINA AENEA* AND *C. ORNATA*

Cyclodina aenea and *C. ornata* are the two most widespread skink species in the North Island of New Zealand (Gill & Whitaker, 2001; Fig. 2A, B), with neither species exhibiting evidence of substantial recent range reduction (Towns *et al.*, 1985; Towns & Daugherty, 1994; Towns *et al.*, 2001). The two species occur sympatrically across the majority of their range, and display similar population structure, reproductive ecology, activity patterns (crepuscular), and habitat preferences (forest and scrub habitat) (Porter, 1987). However, *C. aenea* and *C. ornata* differ in morphology [e.g. *C. ornata* has a longer snout–vent length (SVL); Table 1] and some aspects of their behaviour and diet (Porter, 1987). *Cyclodina aenea* and *C. ornata* do not represent closely related sister species, with molecular evidence indicating that these two species diverged during the Miocene (our unpubl. data). Thus, it appears that *C. aenea* and *C. ornata* have independently converged on similar biology, ecology, and distributional patterns, providing an ideal opportunity to compare the phylogeography of these two species.

Although similar phylogeographic patterns are evident in both the *C. aenea* species complex and *C. ornata*, the depth and estimated timing of the divergences differs in each species (Fig. 3A, B). There are several patterns shared by both species: (1) relatively minor levels of phylogeographic structuring across the lower North Island; (2) substantial phylogeographic structure (i.e. multiple clades) in the Northland region; and (3) the significant divergence of the Poor Knights Islands populations.

Substantial phylogeographic structure is present in *C. aenea*, with one clade (clade 1) present in the lower North Island and four clades (clades 2–5) and two divergent populations (Dargaville, Whangarei) present in the Northland region (Fig. 4A). We found no evidence for the taxonomic distinctiveness of the Great Barrier Island populations as suggested by Hardy (1977). Phylogeographic structure and recent speciation in the Northland region has been documented in several taxa (Gleeson *et al.*, 1999; Gardner *et al.*, 2004; Spencer *et al.*, 2006), including other skink species (Hare *et al.*, 2008) and has usually been associated with the repeated connection and separation of populations as a result of sea level fluctuations during Pleistocene glacial cycles. However, no consistent patterns have emerged in regard to the location of these breaks. Our divergence time estimates indicate that phylogeographic structure within clades occurred during the Pleistocene, while those among clades originated in the late Pliocene–Pleistocene (Table 2). *Cyclodina* 'Te Paki', the new species at the northern tip of Northland (Chapple *et al.*, 2008b), appears to have diverged from *C. aenea* during the Miocene. Interestingly, more recent genetic divergence and speciation in this region of Northland has been documented in Kauri snails (Spencer *et al.*, 2006).

Four clades are evident within *C. ornata*, with one clade (clade 4) representing a deeply divergent clade from the Poor Knights Islands (Fig. 3B). One *C. ornata* clade (clade 3) is present in the lower North Island, whereas another (clade 1) is distributed from the Hauraki Gulf region to East Cape (Fig. 4B). Although the Three Kings Islands populations were part of a clade (clade 2) that incorporated populations from the northern tip of Northland, there was no support for the taxonomic distinctiveness of these populations. Phylogeographic structure within *C. ornata* is deeper than that observed in *C. aenea*. The estimated divergences within clades appear to have occurred during the late Pliocene and Pleistocene, whereas the divergences among clades occurred during the Pliocene.

Volcanic activity in the Central Plateau region of the North Island during the Pleistocene (McDowall, 1996; Worthy & Holdaway, 2002) does not appear to have resulted in genetic breaks in *C. aenea*. However, there is a genetic break between *C. ornata* popula-

tions from either side of the Central Plateau (Fig. 4B). Thus, although the extensive deforestation that is believed to have resulted from volcanic eruptions (McDowall, 1996) might have restricted gene flow across the Central Plateau region in forest-dwelling taxa such as *Cyclodina*, evidence consistent with such events is only present in *C. ornata*. Indeed, it has been inferred from molecular data that volcanic eruptions resulted in repeated fragmentation of New Zealand short-tailed bat (*Mystacina tuberculata*) populations, with gene flow restored following reforestation (Lloyd, 2003a, b).

The Poor Knights Islands populations of both *C. aenea* and *C. ornata* represent deeply divergent lineages that potentially represent distinct species. *Cyclodina aenea* 'Poor Knights' has recently been described as a new species (Chapple *et al.*, 2008b), having diverged from *C. aenea* during the Miocene. Similarly, we estimate that the Poor Knights Islands population of '*C. ornata*' diverged from *C. ornata* in the Miocene, providing strong support for this population representing a distinct species. Hardy (1977) suggested that the Poor Knights Islands '*C. ornata*' was morphologically distinctive, and therefore further morphological work is required to assess its taxonomic status. The high incidence of endemic species on the Poor Knights Islands (Hitchmough, 1997; de Lange & Cameron, 1999) has generally been explained by the prolonged isolation (1–2 Myr) of this island group from the North Island mainland (Hayward, 1986, 1991). However, the estimated Miocene divergence of *C. aenea* 'Poor Knights' and *C. ornata* 'Poor Knights' indicates deeper divergences that pre-date the most recent land connection to the Poor Knights Islands.

North Island disjunct relics: *Cyclodina macgregori* and *C. whitakeri*

The relatively minor level of phylogeographic structure present in *C. macgregori* and *C. whitakeri* provides an insight into the population structuring of these species prior to their recent declines. The shallow divergences present within both species indicates that gene flow was present between the disjunct populations until the late Pleistocene. This result supports the inference from subfossil evidence that both *C. macgregori* and *C. whitakeri* were continuously distributed across the North Island mainland prior to the arrival of humans and introduced mammals 1–2 kya (Worthy, 1987, 1991; BioWeb Herpetofauna Database, 2006). However, both species now have disjunct distributions with a limited number of populations on northeastern offshore islands and a single population in the Wellington region of the lower North Island (Fig. 2C, Table 1). There is strong evidence indicating that both species are unable to coexist with rats and/or mice (*C. macgregori*: Newman, 1994; *C. whitakeri*: Hoare *et al.*, 2007), suggesting that introduced mammals are a likely cause for the declines (Towns & Daugherty, 1994; Towns, 1999; Towns *et al.*, 2001). Both *C. macgregori* and *C. whitakeri* share similar activity patterns (nocturnal), habitat preferences (coastal forest and scrub), body size (SVL of approximately 100–110 mm), and have experienced similar declines (Table 1). Indeed, it has been noted previously that large nocturnal reptile species have been the most susceptible to introduced mammals, displaying the most dramatic declines (Towns & Daugherty, 1994; Towns *et al.*, 2001).

Northeastern Island relics: *Cyclodina alani*, *C. oliveri*, and *C. townsi*

Subfossil evidence indicates that *C. alani*, *C. oliveri*, and *C. townsi* were widely distributed across the northern half of the North Island until 1–2 kya (Worthy, 1987, 1991; BioWeb Herpetofauna Database, 2006). None of these species remain on the North Island mainland, with their distributions restricted to northeastern offshore islands (Fig. 2C, D, Table 1). Although *C. alani* (SVL of approximately 142 mm) is considerably larger than *C. oliveri* and *C. townsi* (SVL of approximately 87–116 mm), the three species have similar activity patterns (nocturnal) and habitat preferences (coastal forest and scrub) (Table 1). All three species appear to be unable to coexist with introduced mammals (Towns, 1999). The phylogeographic patterns evident in *C. oliveri* and *C. townsi* are examined in detail elsewhere (Chapple *et al.*, 2008a) but, in both species, divergences between populations on different island groups are estimated to have occurred during the late Pliocene and Pleistocene. Although only a limited number of samples were available for *C. alani*, there is evidence for similar deep divergences between populations on different island groups (Fig. 3B). The divergence between populations on the Mercury Islands and the Castle Island population is estimated to have occurred in the mid-Pleistocene, whereas the Matapia Island population appears to have diverged from both the Mercury Islands and Castle Island populations during the late Pliocene. Thus, it appears that the deep divergences between island groups were present in *C. alani*, *C. oliveri*, and *C. townsi* prior to their recent distributional declines.

Comparative phylogeography of the genus *Cyclodina*

The phylogeographic patterns evident in *Cyclodina* species in the same biogeographic catergory (i.e. widespread species, North Island disjunct relics, northeast-

ern island relics) are relatively consistent at a broad scale, but the patterns of genetic structuring appear to differ considerably between species in different biogeographic categories. This might be partly due to *Cyclodina* species within categories having more similar body size and habitat preferences compared to species in different biogeographic categories (Table 1). This result is intriguing because six *Cyclodina* species occurred sympatrically across the majority of the North Island until 1–2 kya (Towns & Daugherty, 1994; Towns *et al.*, 2001). However, it is clear from our divergence time estimates that these phylogeographic patterns were created in the late Pliocene to mid-Pleistocene and significantly pre-date the impacts of humans and introduced mammals that have occurred over the past 1–2 kyr. Recent molecular studies of other New Zealand taxa have revealed deep divergences (i.e. Pliocene, Miocene) (Buckley *et al.*, 2001; Arensburger, Simon & Holsinger, 2004; Chinn & Gemmell, 2004; Baker *et al.*, 2005; Berry & Gleeson, 2005; Trewick & Morgan-Richards, 2005; Apte, Smith & Wallis, 2007; Hare *et al.*, 2008), indicating that pre-Pleistocene processes have had a strong influence in shaping the evolution of the New Zealand biota.

Subfossil and genetic evidence indicates that every *Cyclodina* species (except the undescribed species within the *C. aenea* and *C. ornata* species complexes) is currently, or was previously (1–2 kya), continuously distributed across the Central Plateau region (Worthy, 1987, 1991; Towns & Daugherty, 1994; Towns *et al.*, 2001; BioWeb Herpetofauna Database, 2006). By contrast, the distributions of *Oligosoma* species are restricted entirely to the north or entirely to the south of this region, with no species continuously distributed across the North Island (McCann, 1955; Bull & Whitaker, 1975; Towns *et al.*, 1985; Gill & Whitaker, 2001). This is surprising because there is no evidence of phylogeographic structure across the Central Plateau region in any *Cyclodina* species apart from *C. ornata* (Fig. 4B). Interestingly, the Central Plateau region forms the boundary between two floristic biogeographic regions (Wardle, 1963; Connor, 2002) and therefore differences in the habitat requirements of *Cyclodina* and *Oligosoma* (Gill & Whitaker, 2001) might result in this region representing a major biogeographic barrier to *Oligosoma*. However, this pattern might also be a consequence of *Cyclodina* and *Oligosoma* differing in their response to the marine inundation of the lower North Island during the Pliocene (Rogers, 1989; King, 2000; Worthy & Holdaway, 2002).

Another interesting biogeographic contrast exists between *Cyclodina* and *Oligosoma*. Despite the presence of *Cyclodina* on the North Island since at least the Miocene, no evidence exists (current distributional data or fossil evidence) to indicate that any *Cyclodina* species occurs on the South Island (Gill & Whitaker, 2001; BioWeb Herpetofauna Database, 2006). However, the distribution of several *Oligosoma* species spans Cook Strait (*O. infrapunctatum* Boulenger, *Oligosoma lineoocellatum* Dumeril & Dumeril, *Oligosoma nigriplantare polychroma*, *Oligosoma zelandicum* Gray; Gill & Whitaker, 2001). Due to the repeated presence of a Cook Strait landbridge subsequent to the Pliocene (Worthy & Holdaway, 2002), there is evidence for recent (i.e. during the late Pleistocene) geneflow between populations either side of Cook Strait in *O. zelandicum* (O'Neill *et al*., 2008). The apparent inability of *Cyclodina* species to use such landbridges (or earlier Pliocene landbridges; Worthy & Holdaway, 2002) remains a largely unexplored biogeographic phenomenon.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Locality information and GenBank accession numbers for samples used in this study. Samples with CD or FT codes were obtained from the National Frozen Tissue Collection housed at Victoria University of Wellington, New Zealand. Samples with RE codes were obtained from ethanol preserved specimens housed at Te Papa, National Museum of New Zealand, Wellington (S codes refer to specimens from the former Ecology Division collection, now housed at Te Papa). The sample with the ABTC (Australian Biological Tissue Collection) code is from the South Australian Museum.

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