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ScienceDirect
Molecular Phylogenetics and Evolution 46 (2008) 303–315
MOLECULAR PHYLOGENETICS AND EVOLUTION
www.elsevier.com/locate/ympev

Comparative phylogeography of three skink species (*Oligosoma moco*, *O. smithi*, *O. suteri*; Reptilia: Scincidae) in northeastern New Zealand

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Received 3 May 2007; revised 30 July 2007; accepted 19 August 2007
Available online 31 August 2007

Abstract

Sea-level fluctuations during the Pliocene and Pleistocene have shaped the landscape of the Northland region of New Zealand. We examined the comparative phylogeography of three skink species (*Oligosoma moco*, *O. smithi*, *O. suteri*) in northeastern New Zealand in order to investigate the impact of the historical processes that have prevailed since the Pliocene on the Northland fauna. *O. moco*, *O. smithi* and *O. suteri* have similar distributions across northeastern New Zealand, frequently occurring in sympatry. We obtained sequence data from across the entire range of each species, targeting the *ND2* mitochondrial gene. Using Neighbor-Joining, Maximum likelihood and Bayesian methods, our analysis revealed contrasting phylogeographic patterns in each species. We found substantial phylogeographic structure within *O. moco*, with three distinct clades identified. Similarly, deep phylogeographic divergence was evident within *O. smithi*, with three distinct clades present. Clade 1 included *O. smithi* populations from the Three Kings Islands and the western coastline of Northland, while Clade 2 encompassed the remainder of the range. However, since Clade 3 corresponded to a described species (*O. microlepis*), *O. smithi* might represent a species complex. In both *O. moco* and *O. smithi*, divergences among clades are estimated to have occurred in the Pliocene, with divergences within clades occurring during the Pleistocene. In contrast, genetic divergence among *O. suteri* populations was extremely limited and indicative of more recent divergences during the Pleistocene. The lack of phylogeographic structure in *O. suteri* might be a consequence of its oviparous reproductive mode, which restricted its distribution to warm northern refugia during glacial maxima. Differences in the ecology and biology of each species might have produced contrasting responses to the same historical processes, and ultimately diverse phylogeographic patterns. Our study reveals an absence of consistent and concordant phylogeographic patterns in the Northland biota, even within the same taxonomic group.

Keywords: Biogeography; Glacial cycles; Lizard; Mitochondrial DNA; *ND2*; Northland

1. Introduction

Intense tectonic activity, glacial cycles and dramatic fluctuations in sea-level have shaped both the landscape and evolution of the biota of New Zealand since the Pliocene (Cooper and Millener, 1993; Markgraf et al., 1995; Worthy and Holdaway, 2002). During this period, the North Island of New Zealand largely escaped the combined impacts of rapid tectonic uplift and glaciation that have been instrumental in shaping the current landscape of the South Island (Suggate, 1990; Pillans, 1991). Instead, the coastline of the North Island has been in a continual state of flux due to the inundation of the lower North Island during the Pliocene (Rogers, 1989; Worthy and Holdaway, 2002) and repeated fluctuations in sea-level associated with Pleistocene glacial cycles (Suggate, 1990). This has produced recurring connection and separation of offshore islands to the adjacent mainland and other island groups. The Northland region (Fig. 1) of the North

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1055-7903/$ - see front matter © 2007 Elsevier Inc. All rights reserved.
doi:10.1016/j.ympev.2007.08.012

Island existed as an archipelago of low-lying islands during periods of elevated sea-level (i.e. during interglacial periods; Fleming, 1979; Hayward, 1986, 1991); therefore, the impact of such sea-level fluctuations might have been most pronounced in this region.

The length of time in which different island groups have been isolated has been influenced by both their distance from the North Island mainland and the topography of the intervening sea floor. The Three Kings Islands and Poor Knights Islands have been isolated from the Northland mainland probably for the past 1–2 myr, even though sea-level was approximately 110 m below present at the peak of the last glaciation 18–20 kya (Hayward, 1986, 1991). Most other island groups have been repeatedly connected to the mainland during glacial maxima (Hayward, 1986; Towns et al., 1990). However, since each glacial and interglacial period lasted 10–60 kyr (Hayward, 1991), it is unclear whether this provided sufficient time to enable dispersal of biota among previously isolated island groups or regions. Thus, these processes have shaped the evolution of the Northland biota, driving speciation and substantial levels of population structuring in plants (e.g. *Metrosideros* [Myrtaceae], Gardner et al., 2004), invertebrates (e.g. weta, *Hemideina thoracica*, Morgan-Richards, 1997; Morgan-Richards and Wallis, 2003; kauri snails, Spencer et al., 2006) and vertebrates (e.g. black mudfish, *Neochanna diversus*, Gleeson et al., 1999).

The New Zealand skink genus *Oligosoma* provides an ideal opportunity to adopt a comparative phylogeographic approach within a single taxonomic group to examine how historical processes have influenced the evolution of the Northland biota. Three *Oligosoma* species (moko skink, *Oligosoma moco*; shore skink, *O. smithi*; and egg-laying skink, *O. suteri*) have largely sympatric distributions in northeastern New Zealand (Fig. 2; Table 1). Importantly, none of these three species are each other's closest relatives, and each occurs in a different sub-lineage within the New Zealand skink radiation (DGC, CHD and P. Ritchie, unpublished data). This distributional pattern therefore appears to have arisen independently in each species. *O. smithi* has the widest distribution of the three species, extending further south than *O. moco* or *O. suteri* (Fig. 2). *O. moco* and *O. suteri* occur only at a limited number of localities on the mainland and have a largely relictual distribution on offshore islands (Gill and Whitaker, 1996; Towns et al., 2002; Fig. 2). In contrast, *O. smithi* is widespread both in coastal mainland regions and on offshore islands (Fig. 2).

Although *O. moco*, *O. smithi* and *O. suteri* display similar distributions, substantial differences exist among these three species (Table 1). Both *O. moco* and *O. smithi* are medium-sized skinks (~80 mm snout-vent length, SVL), while *O. suteri* is significantly larger (~108 mm SVL) (Table 1). All three species occur in coastal regions, but inhabit separate ecological niches. *O. suteri* is restricted to rocky beaches and shore platforms, while *O. smithi* occurs further up the beach near the shoreline and adjacent sparsely vegetated areas (Gill and Whitaker, 1996; Towns et al., 2002; Table 1). *O. moco* inhabits open and sparsely vegetated areas beyond the shoreline (Gill and Whitaker, 1996; Towns et al., 2002; Table 1). Perhaps the most important differences among these species are that *O. moco* and *O. smithi* are diurnal and viviparous, while *O. suteri* is nocturnal and oviparous (Table 1). These differences might have influenced how each species responded to the climatic changes and sea-level fluctuations during the Pleistocene. Indeed, the restricted northern distribution of *O. suteri* may result from its oviparous reproductive mode (Hardy, 1977), with the cold climate that prevailed during glacial maxima presumed to have had detrimental impacts on eggs and hatchlings (e.g. Hare et al., 2002, 2004).

Fig. 1. Major geographic regions in New Zealand.

We examine the comparative phylogeography of *O. moco*, *O. smithi* and *O. suteri* using mitochondrial DNA sequence data (*ND2*) from across the entire distribution of each species. Although the three species have similar distributions in northeastern New Zealand, we predict that each species will exhibit different phylogeographic patterns as a result of their differing ecologies and life-histories. In particular, *O. suteri* is predicted to display a substantially different phylogeographic pattern from *O. moco* and *O. smithi* due to its oviparous reproductive mode and nocturnal activity pattern. Our genetic data provide further insight into how the historical processes that have prevailed in New Zealand since the Pliocene have influenced the phylogeographic patterns in the terrestrial Northland biota.

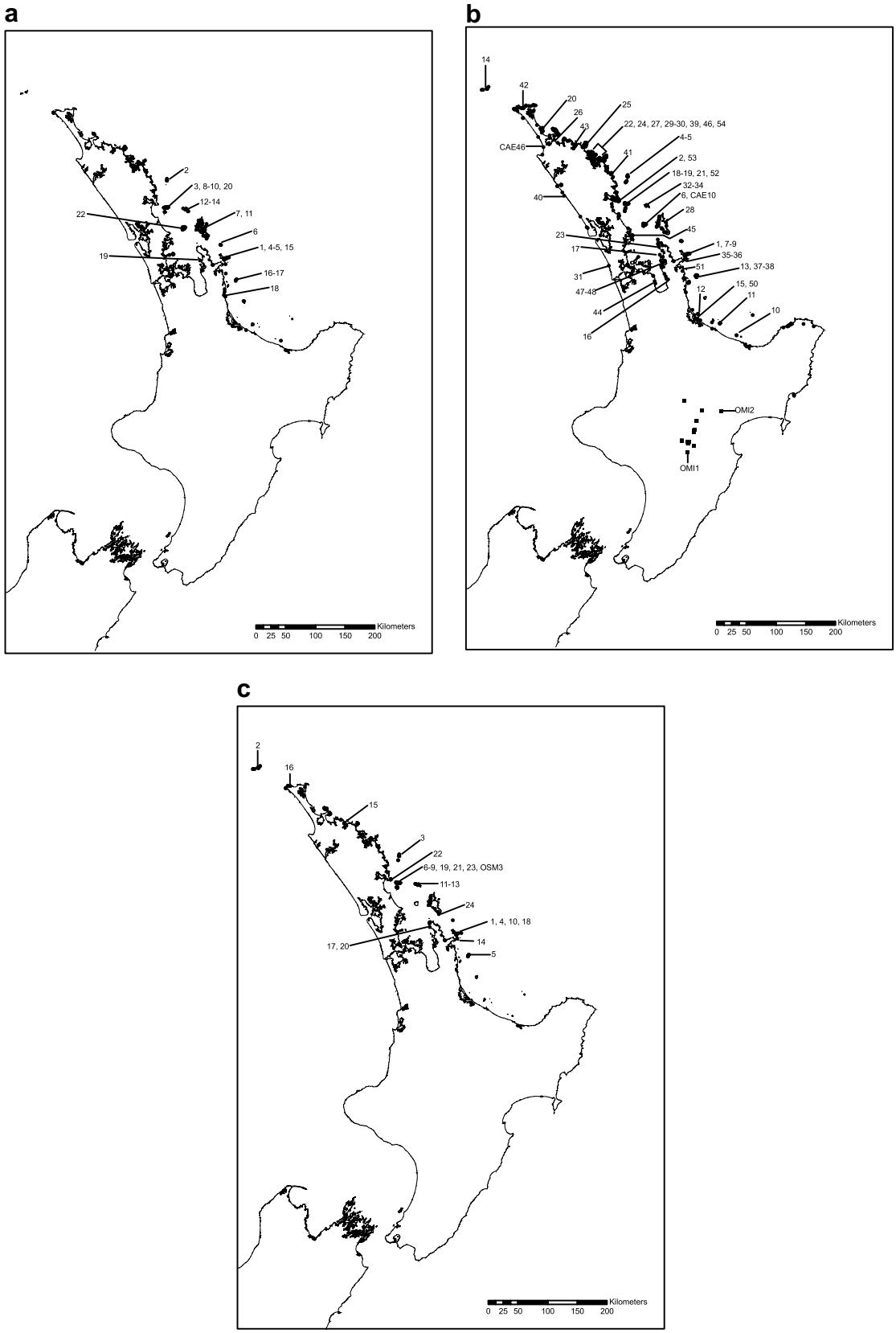

Fig. 2. Distribution maps and location of tissue samples used in this study. (a) *Oligosoma moco* (OMO codes indicated); (b) *Oligosoma smithi* (black circles) (OSM codes indicated) and *O. microlepis* (black squares); and (c) *Oligosoma suteri* (OSU codes indicated). Distributional data were obtained from the New Zealand Department of Conservation's BioWeb Herpetofauna database, 2006.

Table 1
Distribution, activity pattern and life history of *Oligosoma moco*, *O. smithi*, *O. microlepis* and *O. suteri*

Species	*O. moco*	*O. smithi*	*O. microlepis*	*O. suteri*
Distribution	Bay of Plenty region to northern tip of Northland	East Cape region to Three Kings Islands	Central North Island	Northeastern Northland from the Alderman Islands to the Three Kings Islands
Activity pattern	Diurnal[1]	Diurnal[1]	Diurnal[1]	Nocturnal[1]
Habitat preference	Open scrub and grassland in coastal and lowland regions[1]	Coastal. Beach to open grass and shrubland[1,2]	Boulder river beds and rocky areas in grassland[1,2]	Coastal. Boulder beaches and rocky platforms[1]
Maximum SVL (mm)	80[2]	80[2]	70[3]	108[4]
Reproductive mode	Viviparous[1]	Viviparous[1]	Viviparous[1]	Oviparous[1]

References: [1]Gill and Whitaker (1996); [2]Towns et al. (2002); [3]Patterson and Daugherty (1990); [4]Hardy (1977).
The precise distribution of each species is shown in Fig. 2. SVL = snout-vent length.

2. Materials and methods

2.1. Taxonomic sampling

We obtained tissue samples from across the entire distribution of *O. smithi* (54 samples) and *O. suteri* (25 samples), and most of the distribution of *O. moco* (21 samples) (Table 2, Fig. 2). A broader phylogenetic study of the relationships among all members of the New Zealand skink radiation (DGC, CHD and P. Ritchie, unpublished data) indicates that the small-scaled skink (*O. microlepis*) is closely related to *O. smithi*; therefore, we also included two samples of *O. microlepis* in our study (Table 2, Fig. 2). Samples were obtained primarily from the National Frozen Tissue Collection (NFTC; Victoria University of Wellington, New Zealand) and ethanol-preserved specimens housed at Te Papa (National Museum of New Zealand, Wellington). Since *O. moco*, *O. smithi* and *O. suteri* each occur in different subclades within the overall New Zealand skink phylogeny (DGC, CHD and P. Ritchie, unpublished data) we included two Australian *Eugongylus*-lineage skinks (*Lampropholis guichenoti*, *Saproscincus mustelina*) as outgroups in our study (Table 2).

2.2. DNA extraction, amplification and sequencing

Total genomic DNA was extracted from liver, toe or tail samples using a modified phenol–chloroform extraction protocol (Sambrook et al., 1989). For each sample, we targeted a portion of the mitochondrial gene *ND2* (~600 bp). This region was chosen because work at comparable taxonomic levels in other squamate reptile groups has indicated useful levels of variability (e.g. Melville et al., 2004; Keogh et al., 2005).

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′-GCATG ATTYACCGGAAYATGAGACAT-3′; ND2R-infrapunctatum, 5′-GGGGCAAGKCCTAGTTTTATGG-3′; Greaves et al., 2007). PCR and sequencing were conducted as outlined in Greaves et al. (2007).

Sequence data were edited using ContigExpress v9.1.0 (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. As no premature stop codons were observed, we conclude that all sequences obtained are true mitochondrial copies. GenBank accession numbers for all sequences are provided in Table 2.

2.3. Phylogenetic analyses

Neighbor-Joining (NJ) analyses were conducted in PAUP* v4.0b10 (Swofford, 2002). ModelTest 3.7 (Posada and 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 Akaike Information Criterion (AIC) test. Base frequencies, substitution-rates, the proportion of invariant sites (I), gamma distribution (G), and the among-site substitution-rate variation were estimated in ModelTest, with these values implemented in PAUP* to generate a maximum likelihood (ML) tree. Due to the size of the dataset, the ML tree was found by heuristic searching using the subtree-pruning-regrafting algorithm (SPR) with random addition of sequences from the dataset. Ten replicate searches were conducted. Only trees within 2% of the target likelihood score were subject to reiteration.

Bayesian analyses were completed using the computer program MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001). We used the default value of four Markov chains per run, and ran the analysis for one million generations. To ensure that the analyses obtained a sampling of the full tree space rather than becoming trapped in local optima, the analysis was run twice. Chains were sampled every 100 generations to obtain 10,000 sampled trees. The program Tracer 1.3 (Rambaut and Drummond, 2003) was used to check for chain convergence.

Table 2
Locality information and GenBank accession numbers for samples used in this study

Species	Tissue code	Museum code	Locality	Latitude (S)	Longitude (E)	GenBank Accession No.
Oligosoma moco	OMO1	FT156	Stanley Island, Mercury Islands	36.64	175.89	EF567286
O. moco	OMO2	CD1031	Aorangi Island, Poor Knights Islands	35.48	174.74	EF567297
O. moco	OMO3	CD848	Lady Alice Island, Hen and Chickens Islands	35.89	174.73	EF567303
O. moco	OMO4	FT167	Korapuki Island, Mercury Islands	36.66	175.84	EF567283
O. moco	OMO5	FT296	Middle Island, Mercury Islands	36.64	175.86	EF567284
O. moco	OMO6	FT2903	Cuvier Island	36.44	175.77	EF567285
O. moco	OMO7	RE5161 (S1526)	Whangapoua Creek, Great Barrier Island	36.11	175.42	EF567292
O. moco	OMO8	RE5009 (S1372)	West Bay, Marotiri Island, Hen and Chickens Islands	35.89	174.72	EF567300
O. moco	OMO9	RE5008 (S1371)	Araara Island, Hen and Chickens Islands	35.90	174.70	EF567302
O. moco	OMO10	RE5004 (S1367)	Mauitaha Island, Hen and Chickens Islands	35.89	174.69	EF567301
O. moco	OMO11	RE4874 (S1237)	Red Rock, Karaka Bay, Great Barrier Island	36.16	175.34	EF567291
O. moco	OMO12	RE4813 (S1175)	Trig Island, Mokohinau Islands	35.92	175.10	EF567294
O. moco	OMO13	RE4811 (S1173)	Lizard Isle, Mokohinau Islands	35.91	175.11	EF567296
O. moco	OMO14	RE4769 (S1131)	Burgess Island, Mokohinau Islands	35.90	175.11	EF567295
O. moco	OMO15	RE4645 (S1006)	Double Island, Mercury Islands	36.62	175.90	EF567290
O. moco	OMO16	RE4640 (S1001)	Middle Chain Island, Alderman Islands	36.96	176.08	EF567287
O. moco	OMO17	RE4635 (S996)	Ruamahuati Island, Alderman Islands	36.97	176.08	EF567288
O. moco	OMO18	RE4624 (S984)	Whenuakura Island, Whangamata	37.22	175.90	EF567289
O. moco	OMO19	RE4505 (S864)	Motukaramea Island, west of Coromandel Peninsula	36.68	175.39	EF567293
O. moco	OMO20	RE4033 (S391)	Coppermine Island, Hen and Chickens Islands	35.89	174.77	EF567299
O. moco	OMO22	RE1703	Little Barrier Island	36.18	175.08	EF567298
Oligosoma smithi	OSM1	FT166	Middle Island, Mercury Islands	36.64	175.86	EF033055
O. smithi	OSM2	FT193	Ocean Beach, Whangarei	35.84	174.58	EF567220
O. smithi	OSM4	CD1029	Sugarloaf Island, Poor Knights Islands	35.57	174.71	EF567253
O. smithi	OSM5	CD1030	Aorangi Island, Poor Knights Islands	35.48	174.74	EF567254
O. smithi	OSM6	CD1074	Little Barrier Island	36.18	175.08	EF567210
O. smithi	OSM7	FT140	Green Island, Mercury Islands	36.64	175.85	EF567222
O. smithi	OSM8	FT154	Stanley Island, Mercury Islands	36.64	175.89	EF567233
O. smithi	OSM9	FT168	Korapuki Island, Mercury Islands	36.66	175.84	EF567235
O. smithi	OSM10	FT539	Moutoki Island, Bay of Plenty	37.83	176.88	EF567238
O. smithi	OSM11	FT543	Plate Island, Bay of Plenty	37.67	176.56	EF567240
O. smithi	OSM12	FT549	Karewa Island, Bay of Plenty	37.53	176.13	EF567239
O. smithi	OSM13	FT569	Raumahuea-iti, Alderman Islands	36.97	176.08	EF567226
O. smithi	OSM14	FT601	Great Island, Three Kings Islands	34.16	172.14	EF567208
O. smithi	OSM15	FT3021	Matakana Island, Bay of Plenty	37.61	176.13	EF567241
O. smithi	OSM16	FT3299	Waiomu Stream mouth, north of Thames, Coromandel Peninsula	37.02	175.55	EF567214
O. smithi	OSM17	RE5172 (S1537)	Tucks Bay, Coromandel Peninsula	36.74	175.48	EF567217
O. smithi	OSM18	RE5029 (S1392)	Pupuha Island, Hen and Chickens Islands	35.89	174.70	EF567232
O. smithi	OSM19	RE5024 (S1387)	Marotiri Island, Hen and Chickens Islands	35.89	174.73	EF567219
O. smithi	OSM20	RE4965 (S1328)	Mt Camel, Houhora, Northland	34.83	173.14	EF567256
O. smithi	OSM21	RE4942 (S1305)	Sail Rock, Hen and Chickens Islands	36.00	174.70	EF567237
O. smithi	OSM22	RE4921 (S1284)	Brampton Reef, Bay of Islands	35.25	174.07	EF567243
O. smithi	OSM23	RE4920 (S1283)	Waitoitoi Stream, north of Colville Bay, Coromandel Peninsula	36.53	175.36	EF567215
O. smithi	OSM24	RE4919 (S1282)	English Bay, Bay of Islands	35.31	174.11	EF567248
O. smithi	OSM25	RE4915 (S1278)	Matauri Bay, Northland	35.04	173.90	EF567249
O. smithi	OSM26	RE4911 (S1274)	Tokerau Beach, Doubtless Bay, Northland	34.94	173.37	EF567250

(*continued on next page*)

Table 2 (*continued*)

Species	Tissue code	Museum code	Locality	Latitude (S)	Longitude (E)	GenBank Accession No.
O. smithi	OSM27	RE4910 (S1273)	Paihia Beach, Bay of Islands	35.29	174.09	EF567245
O. smithi	OSM28	RE4877 (S1240)	Red Rock, Karaka Bay, Great Barrier Island	36.16	175.34	EF567218
O. smithi	OSM29	RE4842 (S1204)	Waihihi Bay, Bay of Islands	35.26	174.12	EF567246
O. smithi	OSM30	RE4841 (S1203)	Moturoa Island, Bay of Islands	35.22	174.19	EF567247
O. smithi	OSM31	RE4833 (S1195)	Muriwai Beach, 30 km NW of Auckland	36.84	174.42	EF567206
O. smithi	OSM32	RE4822 (S1184)	Lizard Isle, Mokohinau Islands	35.91	175.11	EF567231
O. smithi	OSM33	RE4818 (S1180)	Trig Island, Mokohinau Islands	35.92	175.10	EF567216
O. smithi	OSM34	RE4807 (S1169)	Burgess Island, Mokohinau Islands	35.90	175.11	EF567227
O. smithi	OSM35	RE4722 (S1083)	Ohinau Island, E of Coromandel Peninsula	36.71	175.87	EF567228
O. smithi	OSM36	RE4719 (S1080)	Little Ohinau Island, E of Coromandel Peninsula	36.72	175.88	EF567229
O. smithi	OSM37	RE4694 (S1055)	Hongiora, Alderman Islands	36.96	176.06	EF567230
O. smithi	OSM38	RE4651 (S1012)	Half Island, Alderman Islands	36.97	176.08	EF567224
O. smithi	OSM39	RE4592 (S952)	Deep Water Cove, Bay of Islands	35.20	174.30	EF567251
O. smithi	OSM40	RE4591 (S951)	Aranga Beach, NW of Dargaville, Northland	35.78	173.57	EF567207
O. smithi	OSM41	RE4590 (S950)	Oakura Beach, Whangaruru Harbour	35.40	174.33	EF567255
O. smithi	OSM42	RE4588 (S948)	Spirits Bay, Northland	34.43	172.85	EF567205
O. smithi	OSM43	RE4573 (S933)	Taupo Bay, Whangaroa Bay, Northland	35.00	173.71	EF567225
O. smithi	OSM44	RE4571 (S931)	6.4 km north of Wakatiwai, Firth of Thames	37.09	175.31	EF567213
O. smithi	OMS45	RE4568 (S928)	Waikauri Beach, 16 km E of Warkworth	36.38	174.81	EF567236
O. smithi	OSM46	RE4557 (S917)	Taranaki Island, Kerikeri Inlet, Northland	35.21	174.01	EF567244
O. smithi	OSM47	RE4527 (S886)	Motuoruhi Island, western side of Coromandel Peninsula	36.74	175.40	EF567211
O. smithi	OSM48	RE4521 (S880)	Calf Island, western side of Coromandel Peninsula	36.81	175.40	EF567212
O. smithi	OSM50	RE4166 (S524)	Moturiki Island, Tauranga, Bay of Plenty	37.63	176.18	EF567242
O. smithi	OSM51	RE4181 (S519)	Hot Water Beach, Coromandel Peninsula	36.89	175.81	EF567234
O. smithi	OSM52	RE4029 (S387)	Coppermine Island, Hen and Chickens Islands	35.89	174.77	EF567223
O. smithi	OSM53	RE3964 (S322)	Bream Island, off Bream Head, Northland	35.84	174.54	EF567221
O. smithi	OSM54	RE3806 (S164)	Waewaetorea Island, Bay of Islands	35.22	174.21	EF567252
O. smithi	CAE10	CD1075	Little Barrier Island	36.18	175.08	EF567209
O. smithi	CAE46	RE5321	Waipapakauri, Northland	35.04	173.18	EF567204
Oligosoma microlepis	OMI1	CD1299	Taihape	39.63	176.02	EF043107
O. microlepis	OMI2	FT3730	Wakemans clearing, Mokimokonui River, Southern Urewera	38.99	176.64	EF567257
Oligosoma suteri	OSU1	FT148	Green Island, Mercury Islands	36.64	175.85	EF567261
O. suteri	OSU2	FT602	Great Island, Three Kings Islands	34.16	172.14	EF567282
O. suteri	OSU3	CD1027	Aorangi Island, Poor Knights Islands	35.48	174.74	EF567276
O. suteri	OSU4	FT158	Middle Island, Mercury Islands	36.64	175.86	EF567277
O. suteri	OSU5	FT570	Rumamahuea-iti, Alderman Islands	36.97	176.08	EF567278
O. suteri	OSU6	FT578	Hen Island, Hen and Chickens Islands	35.92	174.73	EF567279
O. suteri	OSU7	FT624	One, NW Hen and Chickens Islands	35.92	174.73	EF567280
O. suteri	OSU8	FT2493	Ware Ware Island, NW Hen and Chickens Islands	35.88	174.70	EF567259
O. suteri	OSU9	FT2496	Muriwhenua Island, Hen and Chickens Islands	35.88	174.70	EF567260
O. suteri	OSU10	FT5494	Green Island, Mercury Islands	36.64	175.85	EF567263
O. suteri	OSU11	RE4819 (S1181)	Burgess Island, Mokohinau Islands	35.90	175.11	EF567266

O. suteri	OSU12	RE4770 (S1132)	Groper Rock, Mokohinau Islands	35.90	175.05	EF567267
O. suteri	OSU13	RE4759 (S1121)	Lizard Isle, Mokohinau Islands	35.91	175.11	EF567268
O. suteri	OSU14	RE4716 (S1077)	Flat Island, off Ohinau Island, Coromandel Peninsula	36.71	175.87	EF567269
O. suteri	OSU15	RE4587 (S947)	Taupo Bay, Whangaroa Bay, Northland	35.00	173.71	EF567264
O. suteri	OSU16	RE4583 (S943)	Tapotupotu Bay, Northland	34.44	172.71	EF567270
O. suteri	OSU17	RE4451 (S809)	Waitoitoi Bay, north of Colville Bay, Coromandel Peninsula	36.53	175.36	EF567271
O. suteri	OSU18	RE4356 (S714)	Red Mercury Island, Mercury Islands	36.63	175.94	EF567272
O. suteri	OSU19	RE4302 (S660)	Coppermine Island, Hen and Chickens Islands	35.89	174.77	EF567273
O. suteri	OSU20	RE4069 (S427)	Cape Colville, Coromandel Peninsula	36.47	175.35	EF567265
O. suteri	OSU21	RE4012 (S370)	Whatupuke Island, Hen and Chickens Islands	35.89	174.75	EF567274
O. suteri	OSU22	RE3998 (S356)	Bream Island, off Bream Head, Northland	35.84	174.54	EF567275
O. suteri	OSU23	RE3876 (S234)	Hen Island, Hen and Chickens Islands	35.92	174.73	EF567262
O. suteri	OSU24	RE1877	Island Bay, Tryphena, Great Barrier Island	36.31	175.49	EF567281
O. suteri	OSM3	CD850	Muriwhenua Island, Hen and Chickens Islands	35.88	174.70	EF567258
Lampropholis guichenoti	EUG7	NR2639	Australia	—	—	EF567304
Saproscincus mustelina	EUG8	NR3782	Australia	—	—	EF567305

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, National Museum of New Zealand, Wellington (S codes refer to specimens from the former Ecology Division collection, now housed at Te Papa). Latitude and Longitude is presented in decimal format [from BioWeb Herpetofauna database (2006)].

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. Neighbor-Joining bootstraps (1000 replicates) were generated in PAUP*. We consider branches supported by bootstrap values greater than or equal to 70% (Hillis and Bull, 1993), and posterior probability values greater than or equal to 95% (Wilcox et al., 2002) significantly supported by our data. Pairwise uncorrected genetic distances were calculated in MEGA 3.1 (Kumar et al., 2004).

2.4. 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*. Specifically, we re-calculated the evolutionary rate for *Laudakia* using only the 550-bp fragment of *ND2* used in the present study (e.g. 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, 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).

3. Results

The edited alignment comprised 550 characters, of which 208 (38%) were variable and 152 (28%) were parsimony-informative. For the ingroup only, the alignment contained 166 (30%) variable characters, of which 141 (26%) were parsimony-informative. Base frequencies were unequal ($A = 0.3450$, $T = 0.2042$, $C = 0.3323$, $G = 0.1184$), but a χ^2 test confirmed the homogeneity of base frequencies among sequences ($df = 309$, $p = 1.00$). For several samples, only ~525 bp of sequence data were obtained (OSM20, OSM38, OSM46, OSM52-53, OSU23). In addition, due to the poor quality of the DNA template, a small number of samples had a reduced sequence length of ~325 bp (OSM22, OSM25, OMO17-20).

The AIC from ModelTest supported the TrN + I + G substitution model as the most appropriate for our dataset ($-\ln L = 2800.5190$). Parameters estimated under this model were: relative substitution-rates ($A \leftrightarrow C = 1.0$, $A \leftrightarrow G = 18.82$, $A \leftrightarrow T = 1.0$, $C \leftrightarrow G = 1.0$, $C \leftrightarrow T = 8.86$, $G \leftrightarrow T = 1.00$), gamma-shape parameter (1.5316) and proportion of invariable sites (0.5240). The topologies of the NJ, ML (single optimal tree, $-\ln L = 2795.77429$) and Bayesian trees were very similar, except that the ML tree placed *O. microlepis* as the sister lineage to *O. smithi*, whereas the NJ and Bayesian trees indicated that *O. microlepis* was a well-supported clade within *O. smithi* (Fig. 3). We

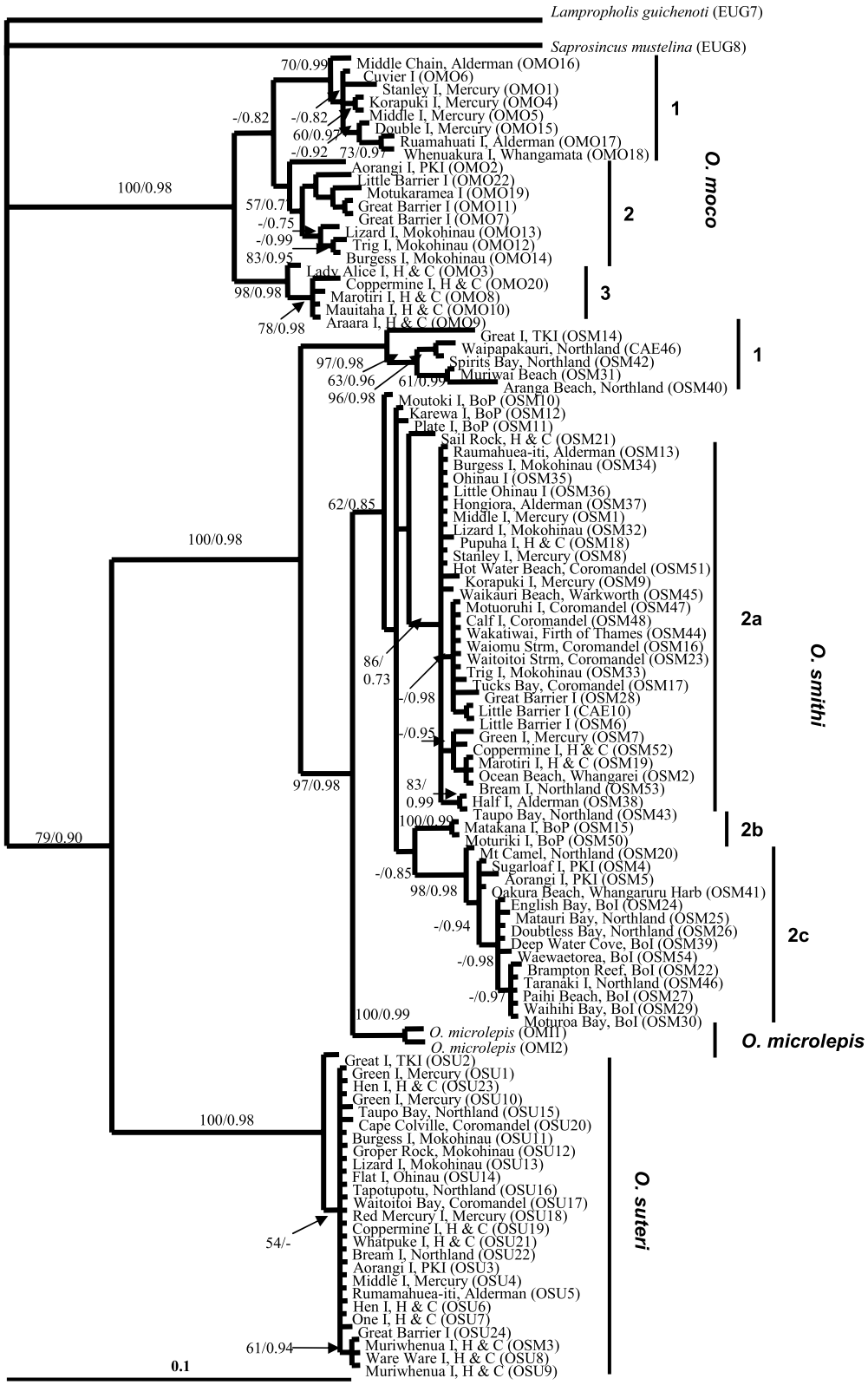

Fig. 3. Bayesian tree for *Oligosoma moco*, *O. smithi* (including *O. microlepis*) and *O. suteri* based on 550 bp of the *ND2* mitochondrial gene. The topology of the Neighbor-Joining (NJ) tree was the same as for the Bayesian tree, but the Maximum likelihood tree differed in the position of *O. microlepis* (see text). Two measures of branch support are indicated with NJ bootstraps shown on the left and Bayesian posterior probabilities on the right (only values over 50 and 0.7, respectively, are shown). The three main clades within *O. moco* are indicated, as are the three main clades within *O. smithi* (includes *O. microlepis*).

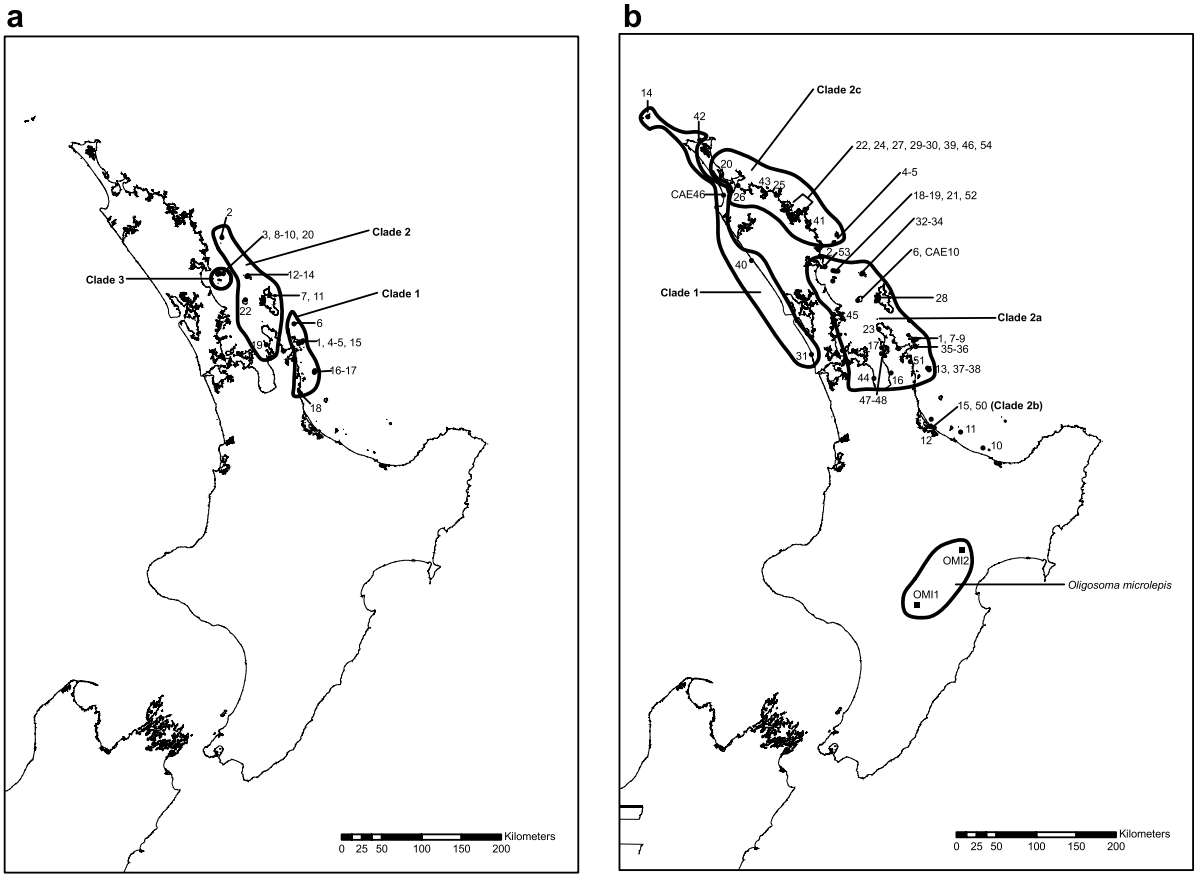

Fig. 4. Distribution of clades within (a) *Oligosoma moco* and (b) *O. smithi* (including *O. microlepis*) identified in Fig. 3.

present the Bayesian tree with bootstrap values and posterior probabilities indicating branch support (Fig. 3). The Bayesian tree strongly supports the monophyly of both *O. moco* and *O. suteri* (100 bootstrap and 0.98 posterior probability in both cases).

3.1. Oligosoma moco

Substantial genetic structuring was evident within *O. moco*, with a mean pairwise genetic distance (GD) of 2.7% and three clades identified (Fig. 3). Clade 1 (70 bootstrap, 0.99 posterior probability) encompassed populations from the eastern side of the Coromandel Penninsula, Alderman Islands, Mercury Islands and Cuvier Island (Fig. 4a). Clade 2 is a weakly supported clade (57 bootstrap, 0.77 posterior probability) that incorporates populations from the Hauraki Gulf region from the western side of the Coromandel Peninsula to the Poor Knights Islands, excluding the Hen and Chickens Islands (Fig. 4a). Strong support (98 bootstrap, 0.98 posterior probability) exists for the Hen and Chickens Islands populations forming a distinct clade (Clade 3) (Fig. 4a). The level of genetic differentiation within clades (Clade 1 GD = 0.7%, 0.5 mya; Clade 2 GD = 1.4%, 1.0 mya; Clade 3 GD = 0.5%, 0.36 mya) was relatively minor compared to that observed among the three clades (Clade 1 versus 2 GD = 2.8%, 2.0 mya; Clade 1 versus 3 GD = 4.1%, 2.93 mya; Clade 2 versus 3 GD = 3.8%, 2.71 mya).

3.2. Oligosoma smithi complex

Significant phylogeographic structuring was evident within the *O. smithi* complex (GD = 2.6%), with three clades identified (Fig. 3). Clade 1 (97 bootstrap, 0.98 posterior probability) encompassed populations from the Three Kings Islands, North Cape, and along the western coast of Northland to Muriwai Beach (Fig. 4b). Clade 2 (62 bootstrap, 0.85 posterior probability) contains three well-supported subclades (Fig. 3). Clade 2a (86 bootstrap, 0.73 posterior probability, GD = 0.4%, 0.29 mya) comprises populations from the Coromandel Penninsula, Firth of Thames, Alderman Islands, Mercury Islands, Islands of the Hauraki Gulf (Great Barrier Island, Little Barrier Island, Mokohinau Islands, Hen and Chickens Group) and the Whangarei region (Fig. 4b). Clade 2b (100 bootstrap, 0.99 posterior probability) contains populations from two islands near Tauranga in the Bay of Plenty (Fig. 4b). Clade 2c (98 bootstrap, 0.98 posterior probability, GD = 0.4%, 0.29 mya) is represented by populations along the east coast of Northland from Poor Knights

Islands to Cape Reinga (Fig. 4b). Three populations in the Bay of Plenty (OSM10-12) and the population on Sail Rock near the Hen and Chickens Group (OSM21) were not assigned to a subclade within Clade 2. *O. microlepis* (100 bootstrap, 0.99 posterior probability) forms the final clade within the *O. smithi* complex (Figs. 3 and 4b). Genetic differentiation within clades was relatively low (Clade 1 GD = 2.4%, 1.71 mya; Clade 2 GD = 1.8%, 1.29 mya; *O. microlepis* GD = 0.7%, 0.50 mya) compared to the substantial genetic divergences evident among clades in the *O. smithi* complex (Clade 1 v 2 GD = 6.0%, 4.29 mya; Clade 1 v *O. microlepis* GD = 6.0%, 4.29 mya; Clade 2 v *O. microlepis* GD = 3.6%, 2.57 mya).

3.3. Oligosoma suteri

Virtually no geographic structuring was evident across the entire range of *O. suteri* (Fig. 3). This was exemplified by the extremely low level of genetic differentiation among *O. suteri* populations (GD = 0.1%, 0.07 mya).

4. Discussion

Our study reveals contrasting phylogeographic patterns in *O. moco*, *O. smithi* and *O. suteri* despite their similar distributions in northeastern New Zealand. Substantial phylogeographic structuring is evident in both *O. moco* and *O. smithi*, while virtually no genetic structuring occurs across the entire range of *O. suteri*. This difference might be a consequence of the oviparous reproductive mode and/or nocturnal activity pattern of *O. suteri*. We examine how historical processes might have produced the phylogeographic patterns evident in these three species. In addition, our data also suggest that *O. smithi* represents a species complex that incorporates *O. microlepis*, with future taxonomic work required.

4.1. Substantial phylogeographic structuring within O. moco

Although our sampling did not encompass the entire distribution of *O. moco*, our study revealed substantial phylogeographic structuring within this species. *O. moco* is currently restricted to a limited number (<10) of localities on the North Island mainland, but subfossil deposits indicate that it was previously more widespread across the mainland throughout most of the Pleistocene (Towns and Daugherty, 1994; Towns et al., 2002). The three clades within *O. moco* appear to have diverged during the late Pliocene (2.93–2.0 mya). The repeated connection and separation of mainland and offshore island populations during the Pleistocene might have acted to restrict gene flow among *O. moco* populations, maintaining this substantial geographic structuring.

Previous phylogeographic studies in the Northland region have revealed deep genetic structuring, but the extent of structuring and the location of breaks have rarely been concordant among animal taxa (e.g. Gleeson et al., 1999; Morgan-Richards and Wallis, 2003; Spencer et al., 2006). Relatively few consistent patterns have been observed, apart from deep divergence among island groups (Morgan-Richards, 1997) and populations on the Poor Knights Islands showing evidence of genetic divergence or speciation (Hitchmough, 1997) due to its estimated 1–2 myr isolation (Hayward, 1986, 1991). While the Poor Knights Islands population of *O. moco* does not exhibit the substantial divergence evident within other skink species (*Cyclodina aenea* and *C. ornata*; DGC, CHD, P. Ritchie, unpublished data), significant structuring is present among different island groups. In particular there is substantial divergence among the Hauraki Gulf islands (Poor Knights Islands, Mokohinau Islands, Little Barrier Island, Great Barrier Island) and the islands off the eastern coastline of Coromandel Peninsula (Cuvier Island, Mercury Islands, Alderman Islands). More surprisingly, the Hen and Chicken Islands population forms its own clade within *O. moco*. Similar deep phylogeographic structure (i.e. Pliocene divergences) among the Hen and Chickens Islands and other islands in the Hauraki Gulf is evident in the marbled skink (*C. oliveri*) species complex (DGC, G. Patterson, D. Gleeson, CHD and P. Ritchie, unpublished data), and might indicate that the islands in the Hen and Chickens group have been isolated for longer than previously believed.

4.2. Phylogeography of the O. smithi species complex and taxonomic implications

Oligosoma smithi is the most common and widespread skink species in coastal regions in the northeastern North Island of New Zealand (Gill and Whitaker, 1996). Considerable variation in colour and colour pattern is evident both within and among populations of *O. smithi*, with individuals varying in colour from grey/green to jet black (Hardy, 1977). Substantial variation in body size (SVL) is also present among populations (Hardy, 1977). Such morphological variation within *O. smithi* led McCann (1955) to describe two subspecies (*smithi*, *numerale*), although both were later synonymised by Hardy (1977). Although our genetic data revealed three distinct clades within *O. smithi*, none of these clades corresponded to the distribution of these former subspecies.

Our genetic data indicate that *O. microlepis* forms a distinct clade within *O. smithi*, suggesting that *O. smithi* constitutes a species complex. All previous genetic studies using both allozymes (CHD, unpublished data) and DNA sequence data (16SrRNA and Cytochrome b, Hay, 1998; 12SrRNA, Hickson et al., 2000; *ND2*, c-mos and Rag-1, Smith et al., 2007) have indicated that *O. smithi* and *O. microlepis* are each other's closest relatives. However, none of these studies sampled across the entire range of *O. smithi*. *O. microlepis* occurs in rocky and grassy areas near rivers and lakes in the Central Plateau region of the North Island (Gill and Whitaker, 1996; Fig. 2b). *O. microlepis* was considered part of the New Zealand common

skink (*O. nigriplantare*) species complex until 1990, when it was recognised as a distinct species (Daugherty et al., 1990; Patterson and Daugherty, 1990). Due to its relatively recent description, little is known about the ecology and biology of *O. microlepis*.

Although *O. smithi* is occasionally observed several hundred metres inland, it usually occurs within 20 m of the high tide mark (Hardy, 1977; Gill and Whitaker, 1996; Parrish and Gill, 2003). Therefore, it is surprising that an inland species such as *O. microlepis* appears to be part of the *O. smithi* species complex. However, the North Island coastline has been modified by several processes such as tectonic activity, volcanic activity and marine transgressions (Worthy and Holdaway, 2002). In particular, geological evidence indicates that the lower North Island was submerged during the Pliocene, with the southern coastline of the North Island occurring between the present-day Hawkes Bay and Taranaki regions (Bull and Whitaker, 1975; Rogers, 1989; Worthy and Holdaway, 2002; Fig. 1). Thus, during the Pliocene a continuous coastline would have been present between the Central Plateau region and the present-day Bay of Plenty (Fig. 1). Thus, *O. microlepis* might represent a remnant, but genetically divergent, inland '*O. smithi*' population that persists in suitable habitats surrounding lakes and rivers. This scenario is supported by our divergence time estimates that indicate that *O. microlepis* diverged from *O. smithi* populations in the Bay of Plenty region in the late Pliocene.

Apart from *O. microlepis*, two additional clades are evident within the *O. smithi* species complex. Members of Clade 1 occur on the Three Kings Island, North Cape region, and along the western coastline of Northland, while Clade 2 encompasses populations across the remainder of the distributional range of *O. smithi*. The Three Kings Islands are believed to have been isolated from the North Island mainland for 1–2 myr (Hayward, 1986). Our divergence time estimates indicate a much older divergence between Clade 1 and Clade 2 (late Pliocene, ~4.3 mya). The close affinity of the Three Kings Islands *O. smithi* population to those on the west coast of Northland may indicate recent over-water dispersal. The presence of distinct clades along the eastern and western coastline of Northland might indicate that *O. smithi* does not move far from the shoreline and is therefore unlikely to disperse over land between the two coastlines, despite their close proximity in some regions. Instead, *O. smithi* might disperse from north to south along the coastline using the prevailing ocean currents (Heath, 1985). Interestingly, a similar east-west split in the Northland region has been documented in some species of kauri snails (*Paryphanta busbyi*), but not others (*Amborhytida* spp.) (Spencer et al., 2006).

Three subclades are evident within Clade 2, a northern subclade (far northern coastline of Northland from the Poor Knights Islands region, Clade 2c), a southern subclade (Hauraki Gulf and Coromandel Peninsula region, Clade 2a) and a subclade in the Bay of Plenty (Clade 2b) (Fig. 4b). The genetic substructuring evident in *O. smithi* in the northeastern North Island is similar to that observed in *O. moco*. However, only relatively shallow divergence among populations is evident within each of the subclades in Clade 2 (late Pleistocene divergences). This pattern might indicate that there has been continual geneflow among populations in these regions, by repeated connection of mainland and island groups during glacial cycles and/or frequent over-water dispersal between islands. Geological evidence exists for the repeated connection of most offshore islands to the Northland mainland during the Pleistocene (Hayward, 1986; Towns et al., 1990), but also the potential for over-water dispersal. *Oligosoma smithi* is a coastal species that forages in the intertidal zone, is a strong swimmer, readily enters the water, and can hold its breath underwater for ~7 min (Gill and Whitaker, 1996; K. Miller and KMH, unpublished data).

The presence of three divergent clades within the *O. smithi* species complex, one of which corresponds to a described species (*O. microlepis*), highlights the need for future taxonomic and morphological work. Although the level of genetic divergence between Clade 2 and *O. microlepis* is minor (GD = 3.6%), the genetic divergence evident between Clade 1 and Clade 2 (GD = 6.0%) is more substantial and equivalent to that observed between Clade 1 and *O. microlepis* (GD = 6.0%). Further work is required to assess the taxonomic significance of these clades within the *O. smithi* species complex.

4.3. Limited phylogeographic structure in O. suteri

The present distribution of *O. suteri*, which is restricted to ~3 mainland localities, is considered relictual, having previously been more widespread across coastal mainland regions of the northeastern North Island (Towns et al., 2002). Despite this formerly more widespread distribution, several authors have questioned the ability of the oviparous *O. suteri* to survive Pleistocene glacial maxima (Towns, 1974; Bull and Whitaker, 1975; Hardy, 1977). Consequently, *O. suteri* has been suggested to represent a relatively recent colonisation (during the Pleistocene) of New Zealand that survived glacial maxima in warmer northern refugia (Towns, 1974; Bull and Whitaker, 1975; Hardy, 1977). However, recent molecular studies clearly reject recent colonisation. Molecular data strongly support the monophyly of the New Zealand skink fauna and a single colonisation of New Zealand (Hickson et al., 2000; DGC, CHD and P. Ritchie, unpublished data). Since skinks appear to have colonised New Zealand ~8–25 mya (Hickson et al., 2000; Smith et al., 2007), *O. suteri* and its ancestors have a long evolutionary history in New Zealand.

The level of genetic divergence across the range of *O. suteri* was extremely low, with gene flow among most populations as recently as the late Pleistocene. This phylogeographic pattern could be the result of several factors, including rapid expansion following a recent population bottleneck and high levels of gene flow among populations. Cold incubation temperatures are detrimental to the sur-

vival and fitness of *O. suteri* eggs and hatchlings (Hare et al., 2002, 2004). Since temperatures during glacial maxima were 3–6 °C below present (Fleming, 1979; Markgraf et al., 1995; Elliot et al., 2005), climatic conditions might have had a pivotal influence on the distribution of *O. suteri* during the Pleistocene. Thus, the low genetic divergence evident in *O. suteri* might be a result of range contractions to warmer northern regions (i.e. refugia) during glacial maxima, followed by rapid range expansions during interglacials.

Under the glacial refugia scenario, *O. suteri* would need to be able to disperse among island groups. Lizards are generally considered excellent transoceanic disperses (e.g. Censky, 2006; Rocha et al., 2006), and there is strong evidence to suspect that *O. suteri* is capable of dispersing over-water. *O. suteri* is a strictly coastal species that lives on rocky beaches, often with abundant driftwood (Gill and Whitaker, 1996). It can tolerate saltwater, is a strong swimmer that readily enters rock pools and the surf zone, and can hold its breath underwater for up to 20 min (Whitaker, 1968; Robb, 1980; Gill and Whitaker, 1996; K. Miller, unpublished data). These factors not only place *O. suteri* in a position where it is likely transported between islands (on driftwood, etc.), but also increase its likelihood of surviving long distance over-water travel. Frequent over-water dispersal might also act to maintain gene flow among geographically isolated island groups, further limiting genetic divergence. Since the prevailing current off northeastern New Zealand (East Auckland current) flows north to south (Heath, 1985), northern glacial refugia might facilitate southward expansion across island groups during interglacial periods.

4.4. Comparative phylogeography of *O. moco, O. smithi* and *O. suteri*

Although *O. moco*, *O. smithi* and *O. suteri* have similar distributions and appear to have been exposed to the same historical processes since the Pliocene, each species shows a different response to these processes, resulting in different phylogeographic patterns. Presumably, the divergent responses result from differences among the three species in terms of ecology, habitat use, behaviour and life-history. Since, *O. smithi* and *O. suteri* occur in similar habitats and both have high likelihoods of successful over-water dispersal, the oviparous reproductive mode of *O. suteri* may be partly responsible for the different phylogeographic patterns evident in these two species. However, while temperature apparently limits the current and/or past distribution of *O. suteri*, the factors that limit *O. moco* and *O. smithi* are unclear. The presence of *O. microlepis* within the *O. smithi* species complex might suggest that *O. smithi* was once distributed further south or in inland regions (e.g. rivers). The comparative phylogeography of *O. moco*, *O. smithi* and *O. suteri* highlights that, due to the influence of ecology and biology on the response to historical processes, it is difficult to identify common phylogeographic patterns in the Northland region, even within the same taxonomic group.

Acknowledgments

We thank Benno Kappers and Andrew Townsend for providing access to the Department of Conservation's Herpetofauna database, Stephanie Greaves and Peter Ritchie for assistance with the phylogenetic analyses, and Jen Moore for providing assistance in preparing the distributional maps. Karen Britton, Sue Keall, Raymond Coory, Stephanie Greaves and Libby Liggins assisted in obtaining tissue samples from the NFTC and Te Papa. We especially thank Lorraine Berry at the Allan Wilson Centre Genome Service. Funding for this project was provided by the Allan Wilson Centre for Molecular Ecology and Evolution, the Society for Research on Amphibians and Reptiles in New Zealand (SRARNZ), and the Victoria University of Wellington University Research Fund (VUW URF).

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