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ORIGINAL ARTICLE

Biogeographic barriers in south-eastern Australia drive phylogeographic divergence in the garden skink, *Lampropholis guichenoti*

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ABSTRACT

Aim To investigate the impact of climatic oscillations and recognized biogeographic barriers on the evolutionary history of the garden skink (*Lampropholis guichenoti*), a common and widespread vertebrate in south-eastern Australia.

Location South-eastern Australia.

Methods Sequence data were obtained from the ND4 mitochondrial gene for 123 individuals from 64 populations across the entire distribution of the garden skink. A range of phylogenetic (maximum likelihood, Bayesian) and phylogeographic analyses (genetic diversity, Tajima's *D*, Φ_{ST}, mismatch distribution) were conducted to examine the evolutionary history and diversification of the garden skink.

Results A deep phylogeographic break (*c.* 14%), estimated to have occurred in the mid–late Miocene, was found between 'northern' and 'southern' populations across the Hunter Valley in northern New South Wales. Divergences among the geographically structured clades within the 'northern' (five clades) and 'southern' (seven clades) lineages occurred during the Pliocene, with the location of the major breaks corresponding to the recognized biogeographic barriers in south-eastern Australia.

Main conclusions Climatic fluctuations and the presence of several elevational and habitat barriers in south-eastern Australia appear to be responsible for the diversification of the garden skink over the last 10 Myr. Further molecular and morphological work will be required to determine whether the two genetic lineages represent distinct species.

Keywords
Glacial refugia, Hunter Valley, lizard, Miocene, mitochondrial DNA, ND4, phylogeography, Pleistocene, Pliocene, reptile.

INTRODUCTION

Australia is an ancient, eroded and geologically stable continent whose low topographic relief is responsible for it being largely spared from widespread glaciation over the last 2 Myr (Markgraf *et al.*, 1995; Barrows *et al.*, 2002; Byrne, 2008). The mechanisms through which climatic oscillations drive biogeographic and evolutionary patterns in the Australian biota differ compared with those regions that have been subjected to recent tectonic uplift and extensive glaciations (e.g. New Zealand, Wallis & Trewick, 2009; North America, Soltis *et al.*, 2006; Europe, Tribsch & Schonswetter, 2003), and result in divergent genetic signatures of this climatic change (i.e. deep genetic divergence rather than recent or shallow divergences; Dubey & Shine, 2011). The Great Dividing Range (GDR), formed through several periods of tectonic uplift over the past 70 Myr, is the dominant topographic feature in eastern Australia (Keast, 1981; Frakes *et al.*, 1987; Taylor, 1994; Fig. 1). It abuts the east coast in a north–south alignment for *c.* 2500 km, and although only of moderate elevation (*c.* 1000–1300 m, maximum *c.* 2300 m), it provides elevational, climatic and environmental variation in an otherwise

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low-lying landscape (Keast, 1981; Taylor, 1994). The presence of mountainous regions in eastern Australia may influence the ability of species to expand or contract their ranges in response to climatic oscillations (Byrne, 2008).

The mesic regions of eastern Australia are currently dominated by wet forest habitat and sclerophyllous vegetation (Byrne, 2008). However, the extent of each habitat has fluctuated over the past 10 Myr, with a general transition from rain forest towards drier environments and sclerophyllous vegetation (Markgraf *et al.*, 1995; Martin, 2006; Byrne, 2008). The contraction of rain forests between the mid- and late-Miocene coincided with a shift from warm, wet conditions to cooler and drier climates in eastern Australia and the expansion of woodland and open forest vegetation (Bowler, 1982; Gallagher *et al.*, 2001, 2003; Martin, 2006). These climatic conditions led to the retreat of the marine basins in south-eastern Australia (e.g. Gippsland and Murray Basins; Fig. 1), with the expansion of vegetation into these regions (Gallagher *et al.*, 2001, 2003; Martin, 2006). Rain forest habitat expanded during the early Pliocene with the return of warm and wet conditions, but the extent of open woodlands, sclerophyllous forests and grasslands increased as the climate cooled throughout the Pliocene and the frequency of cool-dry to warm-wet climatic fluctuations increased (Bowler, 1982; Frakes *et al.*, 1987; Markgraf *et al.*, 1995; Martin, 2006). The frequency of the climatic oscillations and aridity cycles intensified during the Pleistocene, resulting in the repeated expansion and contraction of the mesic vegetation and habitat and the regular encroachment of the arid zone into eastern Australia (Nix, 1982; Kershaw *et al.*, 1994; Markgraf *et al.*, 1995; Byrne *et al.*, 2008). Sea level changes associated with these climatic cycles led to the periodic flooding of low lying coastal and inland basins across south-eastern Australia and to habitat fragmentation (Frakes *et al.*, 1987; Holdgate *et al.*, 2003; Martin, 2006). At present, sclerophyllous woodlands and open forests are the dominant vegetation within the mesic

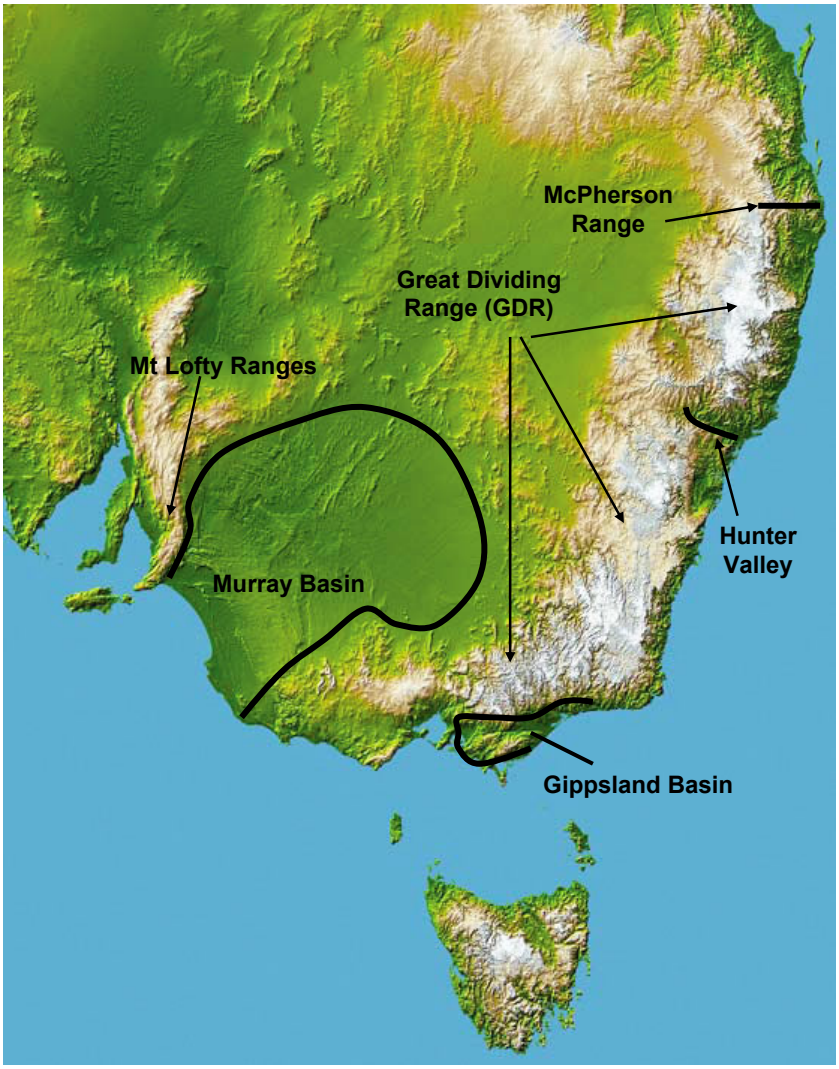


Figure 1 The location of known biogeographic barriers in south-eastern Australia. A description of each barrier is provided in Table 1. The southern New South Wales barrier is not indicated because its exact position and extent are unclear.

region, while the wet forest habitat is restricted to scattered refugia throughout eastern Australia (Byrne, 2008).

Phylogeographic studies investigating the impact of these historical processes on the Australian biota have predominantly focused on the arid (reviewed in Byrne *et al.*, 2008) and wet tropics regions (e.g. Dolman & Moritz, 2006; Bell *et al.*, 2007, 2010; Moritz *et al.*, 2009; Moussalli *et al.*, 2009). Comparatively few studies have examined species inhabiting the wet and sclerophyllous forests and woodlands of south-eastern Australia (Table 1). The high-elevation regions of the GDR would have provided suitable habitat for mesic-adapted species during interglacial periods, but represented a barrier to dispersal during the glacial periods (reviewed in Byrne, 2008). Low elevation dry habitat corridors and basins with frequent marine incursions would have created additional barriers for some species. There are five recognized biogeographic barriers in south-eastern Australia (Fig. 1), although the relative influence of each varies among species and taxonomic groups (Table 1). The biota of this region often exhibit geographically structured divergent genetic lineages, which are indicative of contraction to, and expansion from, multiple localized refugia (Byrne, 2008; Table 1). The heterogeneous environment of south-eastern Australia results in high haplotype diversity, with haplotypes often specific to populations (Byrne, 2008).

Only two phylogeographic studies have examined mesic-adapted species whose distribution span all of the known biogeographic barriers in south-eastern Australia, and even

Table 1 Biogeographic barriers in south-eastern Australia (see Fig. 1) and their impact on vertebrates and plants.

		Amphibians							Reptiles				Birds	Mammals	Plants
Barrier	Explanation of barrier	CS	LimP	LT	LA	LC	LF	LitP	AP	HS	LW	SM	PV	PA	EG
McPherson Range	An east–west spur of the predominately north–south Great Dividing Range (GDR) that runs along the Queensland/New South Wales (NSW) border. A montane block of wet forest that represents a hybrid zone for birds and a barrier for lowland and dry forest plant species[1–3]	–	N	N	–	N	Y	Y	–	Y	S	–	N	N	N
Hunter Valley	A dry, open, lowland river valley that delineates the southern limit of the eastern biogeographic region and the northern limit of the south-east forest region[1–3]	N	Y	S	N	Y	–	–	Y	–	Y	Y	N	S	–
Southern NSW	Transition from the lowland coastal region to the higher elevation southern highlands region of the GDR in NSW[4–5]	Y	S	S	–	Y	–	–	S	–	Y	S	Y	S	–
East Gippsland	Low-lying coastal region that has been subject to repeated marine incursion (i.e. Gippsland Basin), abutted to the north by higher elevation regions of the GDR[5–6]	Y	S	Y	–	–	–	–	–	–	Y	S	N	–	–
Murray Basin	Low lying region that has been subject to repeated marine incursion (i.e. Murray Basin), bordered to the west by the Mt Lofty Ranges, a known refugia[1,6]	Y	–	Y	–	–	–	–	–	–	Y	–	–	–	–

[1]Ford (1987a,b), [2]Cracraft (1991), [3]Crisp *et al.* (1995), [4]reviewed in Nicholls & Austin (2005), [5]reviewed in Chapple *et al.* (2005), [6]Dickinson *et al.* (2002).

Impact codes: Y, genetic break present across barrier; N, no genetic break observed across the barrier; S, insufficient sampling to examine the impact of the barrier; –, species distribution does not span the barrier. Species codes: CS, *Crinia signifera* (Symula *et al.*, 2008); LimP, *Limnodynastes peronii*; LT, *Limnodynastes tasmaniensis* (Schäuble & Moritz, 2001); LA, *Litoria aurea* (Burns *et al.*, 2007); LC, *Litoria citropa* species group (Donnellan *et al.*, 1999); LF, *Litoria fallax* (James & Moritz, 2000); LitP, *Litoria pearsoniana* (McGuigan *et al.*, 1998); AP, *Acritoscincus platynotum* (Dubey & Shine, 2010); HS, *Hoplocephalus stephensi* (Keogh *et al.*, 2003); LW, *Liopholis whitii* (Chapple *et al.*, 2005); SM, *Saproscincus mustelinus* (Moussalli *et al.*, 2005); PV, *Ptilonorhynchus violaceus* (Nicholls & Austin, 2005); PA, *Petaurus australis* (Brown *et al.*, 2006); EG, *Eucalyptus grandis* (Jones *et al.*, 2006).

these studies have often lacked sufficient sampling to adequately assess the impact of some barriers (Table 1). The garden skink, *Lampropholis guichenoti* (Duméril & Bibron, 1839), is one of the most common and widespread terrestrial vertebrates in south-eastern Australia (Wilson & Swan, 2008; Fig. 2). It is a small-sized lizard [adult snout–vent length (SVL) 35–51 mm] whose distribution extends from south-east Queensland (QLD) along the east coast to south-eastern South Australia (SA), with disjunct populations in the Adelaide region and Kangaroo Island (Clarke, 1965; Wilson & Swan, 2008; Fig. 2). The garden skink prefers dry and open habitats, occurs in dry sclerophyll forests and woodlands, and occasionally encroaches on the margins of subtropical rain forests and wet sclerophyll forest (Swan *et al.*, 2004; Wilson & Swan, 2008). It is also extremely abundant in suburban and disturbed habitats (Prosser *et al.*, 2006; Wilson & Swan, 2008). The garden skink therefore represents an ideal species with which to investigate the impact of the major biogeographic barriers in south-eastern Australia.

Here we examine the phylogeography of the garden skink using mitochondrial DNA sequence data (ND4) from across the entire range of the species. Due to its continuous distribution across south-eastern Australia, but absence from Tasmania, Rawlinson (1974) hypothesized that the garden skink was a recent invader (i.e. post-glacial intrusive) of southern regions of the country. However, given its presence on Kangaroo Island, Rawlinson (1974) suggested that it had reached the area prior to the separation of the island from the mainland *c.* 10,000 years ago. We conduct a range of phylogenetic analyses to examine Rawlinson's (1974) hypothesis and investigate the impact of historical processes on the evolutionary history of the garden skink.

MATERIALS AND METHODS

Sampling

We obtained tissue samples from 123 specimens of *L. guichenoti*, representing 64 different populations, from across the entire range of the species (Table 2; Fig. 2; Table S1 in the Supporting Information). Samples were primarily obtained from the frozen-tissue collections of several Australian Museums (Australian Museum, South Australian Museum, Museum Victoria, CSIRO Australian National Wildlife Collection), although additional field-collected samples were included (Table S1). We included the closely related *Lampropholis delicata* (Museum Victoria, NMVD73631, NMVZ6229) and an Australian *Eugongylus*-lineage skink, *Niveoscincus pretiosus* (Australian Museum NR391), as outgroups in our study.

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from liver, muscle, toe or tail-tip samples using a Qiagen DNeasy Blood and Tissue Extraction Kit (Qiagen, Hilden, Germany). For each sample we sequenced a portion (*c.* 700 bp) of the ND4 mitochondrial gene, as this region has proven to be extremely informative for phylogeographic studies of squamate reptiles (e.g. Chapple *et al.*, 2004, 2005; Greaves *et al.*, 2008; Liggins *et al.*, 2008a,b; O'Neill *et al.*, 2008). The primers used to amplify and sequence ND4 were ND4I and tRNA-Leu (Forstner *et al.*, 1995). Polymerase chain reaction (PCR) was conducted as outlined in Greaves *et al.* (2007), except on a Corbett Research GC1-960 thermal cycler (Melbourne, Australia). PCR products were purified using ExoSAP-IT (USB Corporation, Cleveland, OH, USA). The purified product was sequenced directly using a BigDye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) and then analysed on an ABI 3730XL capillary sequencer.

Sequence data were edited using ContigExpress in Vector NTI Advance v9.1.0 (Invitrogen, Carlsbad, CA, USA), and aligned using the default parameters of Clustal X v. 1.83 (Thompson *et al.*, 1997). We translated all sequences to confirm that none contained premature stop codons. Sequence data were submitted to GenBank under the accession numbers HQ454789–HQ454913.

Phylogenetic analyses

Maximum likelihood (ML) and Bayesian tree-building methods were used. We used Modeltest v. 3.7 (Posada & Crandall, 1998) and MrModeltest v. 2.3 (Nylander, 2004), for the ML and Bayesian analysis, respectively, to identify the most appropriate model of sequence evolution based on the Akaike information criterion (AIC). Modeltest was also used to estimate base frequencies, substitution rates, the proportion of invariable sites (I) and the among-site substitution rate variation (G). These values were then used as settings in PhyML v. 3.0 (Guindon & Gascuel, 2003) to generate an ML tree with 500 bootstraps.

MrBayes v. 3.1.2 (Ronquist & Huelsenbeck, 2003) was used to complete Bayesian analyses. We ran the full analysis twice, using four Markov chains per run. We ran the chains for five million generations, to ensure sufficient sampling of tree space. The chain was sampled every 100 generations to obtain 50,000 sampled trees. The program Tracer v. 1.4 (Rambaut & Drummond, 2007) was used to check for chain convergence. The first 25% of sampled trees were discarded as the burn-in phase and the last 37,500 trees were used to estimate the

Figure 2 Map showing the collection localities in south-eastern Australia of *Lampropholis guichenoti* samples used in the study. The population numbers from Table 2 are presented next to the sampling localities. The distribution of the 'northern' genetic lineage is indicated with solid black squares, with the distribution of the 'southern' genetic lineage highlighted with solid black circles. The distribution of the clades (dashed lines) identified in Fig. 3 are presented. The approximate distribution (solid line) of *L. guichenoti* is indicated (adapted from Wilson & Swan, 2008).

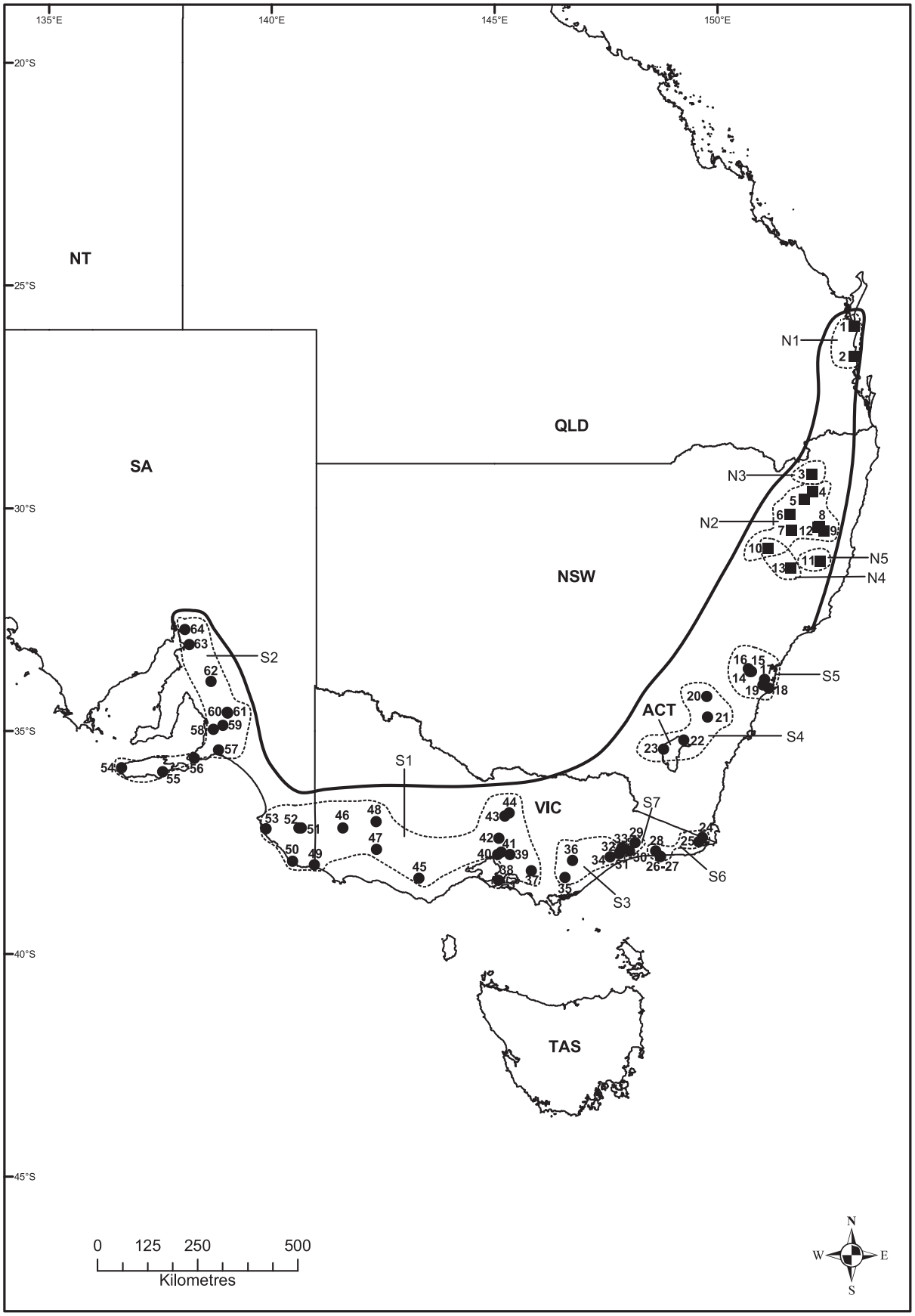


Table 2 Collection localities in south-eastern Australia of *Lampropholis guichenoti* samples used in the study. Population numbers and clades correspond to those listed in Figs 2 & 3. The museum voucher specimen information and GenBank accession numbers are listed in Table S1.

Population	Collection locality	State	No. of samples	Clade
1	3 km W Rainbow Beach	QLD	1	N1
2	Marcoola	QLD	2	N1
3	Forestlands State Forest, Bald Rock	NSW	3	N3
4	45 km E Glen Innes on Glen Innes-Grafton Rd	NSW	3	N2
5	Red Range to Kingsgate Rd	NSW	3	N2
6	Glenshiel Rd, N Guyra	NSW	2	N2
7	Armidale	NSW	2	N2
8	Sandy Creek, 6 km along Ebor-Gyura Road	NSW	3	N2
9	Styx River State Forest, Beech Lookout	NSW	2	N2
10	Poison Swamp Creek, on road to Bendemeer	NSW	3	N2,N4
11	Werrikimbe NP	NSW	2	N5
12	Cathedral Rock NP	NSW	1	N2
13	Riamukka SF, Hell Hole Forest Rd	NSW	1	N4
14	Rickabys Creek, near Londonderry	NSW	3	S5
15	Castlereagh Waste Depot, near Penrith	NSW	3	S5
16	University of Western Sydney, The Driftway	NSW	3	S5
17	Homebush Bay, Cumbungi Wetland	NSW	3	S5
18	Cronulla Sewage Treatment Plant, Kurnell Peninsula	NSW	3	S5
19	Padstow	NSW	1	S5
20	4.6 km S Abercrombie River	NSW	2	S4
21	6 km N Goulbourn	NSW	1	S4
22	Mack's Reef Rd, N of Canberra	NSW	3	S4
23	Piccadilly Circus, Brindabella Ranges	ACT	1	S4
24	Princes Hwy, VIC side VIC-NSW border	VIC	1	S6
25	Parkland near Genoa River Bridge, Genoa	VIC	1	S6
26	Cape Conran	VIC	6	S6
27	Sunset Peak, Cape Conran Nature Trail	VIC	1	S6
28	Murrungowar Picnic Ground, Princes Hwy	VIC	1	S6
29	Buchan Caves Reserve, Moon Hill Walk	VIC	2	S7
30	Lyles Break, Jtn C608 &C620, Bruthen-Nowa Nowa Rd	VIC	1	S7
31	Junction C608 & Duncan Rd, S Bruthen	VIC	1	S3
32	Bruthen Walking Track, Parking Area	VIC	1	S7
33	Princes Downfall, Great Alpine Hwy N Bruthen	VIC	2	S3
34	Bairnsdale, rec centre Wallace St & Victoria St	VIC	1	S3
35	Callignee Sth Rd, 1 km S jtn with Chester Pk Rd	VIC	1	S3
36	Lake Glenmaggie, opp. Glenmaggie Cemetery	VIC	1	S3
37	Drouin Nature Reserve, Pryor Rd, Drouin	VIC	1	S1
38	Buckleys NR Balnarring, Mornington Peninsula	VIC	1	S1
39	Lilydale Lake, Melbourne	VIC	3	S1
40	Main Yarra Trail, Yarra Flats Park, Ivanhoe, Melbourne	VIC	1	S1
41	Eltham	VIC	1	S1
42	Mt. Disappointment	VIC	2	S1
43	Lambing Gully Rd, Avenel	VIC	2	S1
44	Alexandersons Rd (& 1 km S), Locksley	VIC	3	S1
45	5 km W Stonyford	VIC	1	S1
46	Harrow-Balmoral Rd, southern Grampians	VIC	3	S1
47	North Boundary Rd, Dunkeld, southern Grampians	VIC	5	S1
48	Snell's Rd, 2 km S Wartook, Horsham Shire	VIC	2	S1
49	1.9 km N & 0.7 km NE Donovans	SA	2	S1
50	7.3 km E Carpenter Rocks	SA	1	S1
51	Mary Seymour CP	SA	2	S1
52	17.6 km WSW Struan	SA	2	S1
53	10.2 km E & 14.5 km NE Robe	SA	2	S1
54	E of West Bay Rd, 7.5 km E of Cape Borda, Kangaroo I	SA	1	S2

Table 2 Continued

Population	Collection locality	State	No. of samples	Clade
55	1.2 km NE D'Estree's HS, Kangaroo Island	SA	1	S2
56	2.2 km ESE Deep Ck HS, Fleurieu Peninsula	SA	2	S2
57	21–22 km ESE Mt Compass	SA	2	S2
58	2.7 km NNW & 0.7 km SE Mt Lofty	SA	2	S2
59	5 km NE Lobethal	SA	2	S2
60	Pewsey Vale, 6 km SE Tanunda	SA	1	S2
61	Kaiser Stuhl CP	SA	2	S2
62	Seven Hills, Flinders Ranges	SA	1	S2
63	7.2 km E Telowie	SA	2	S2
64	8.1 km SSW Wilmington	SA	2	S2

ACT, Australian Capital Territory; NSW, New South Wales; QLD, Queensland; SA, South Australia; VIC, Victoria; NP, National Park; CP, Conservation Park.

Bayesian posterior probabilities. Bootstrap values (500 ML bootstraps) and Bayesian posterior probabilities were used to assess branch support. We considered branches supported by bootstrap values of 70% or greater (Hillis & Bull, 1993), and/or posterior probability values greater than or equal to 95% (Wilcox *et al.*, 2002) to be supported by our data.

Molecular diversity and population divergence

Estimates of genetic diversity within *L. guichenoti* clades and lineages (number of haplotypes, *h*; haplotype diversity, *Hd*; number of polymorphic sites, *S*; nucleotide diversity, π) were calculated in DnaSP v4.50 (Rozas *et al.*, 2003). Model-corrected genetic distances were calculated in MEGA v. 4 (Tamura *et al.*, 2007). Genetic differentiation among clades and lineages within *L. guichenoti* was estimated in Arlequin v. 3.11 (Excoffier *et al.*, 2005). Pairwise Φ_{ST} values (an analogue of Wright's fixation index F_{ST}) were calculated to estimate among clade/lineage differentiation. We used Tamura–Nei (TrN) genetic distances with gamma correction (using the value calculated from Modeltest). Significance levels of all the estimated values were calculated by 10,000 permutations, and adjusted according to the Bonferroni correction procedure (Rice, 1989) for multiple pairwise comparisons as described by Holm (1979). We estimated the divergence time of *L. guichenoti* clades and lineages using an evolutionary rate of 1.42–1.63% sequence divergence per million years, based on mitochondrial DNA coding region calibrations from other squamate reptile groups (1.42–1.63%, Jennings *et al.*, 2003; 1.55%, Poulakakis *et al.*, 2005; 1.62%, Shoo *et al.*, 2008; 1.63%, Bryson *et al.*, 2008).

We used Tajima's *D* (Tajima, 1989, 1996; calculated in Arlequin) and mismatch distributions to test for signatures of population expansion within *L. guichenoti* clades. Significant and negative Tajima's *D* values are indicative of possible population expansion. Mismatch frequency histograms were plotted in DnaSP to determine whether the clades exhibited evidence of spatial range expansion or a stationary population history (Harpending, 1994). A smooth bell shape signifies either population expansion or spatial range expansion, whereas a multimodal distribution represents a long history *in situ* (Rogers & Harpending, 1992; Ray *et al.*, 2003; Excoffier, 2004). To distinguish between these two types of distribution, a raggedness index (RI, sum of the squared difference between neighbouring peaks) and the sum of squared deviations (SSD) between the observed and expected mismatch were calculated using the methods of Schneider & Excoffier (1999) in Arlequin. The spatial expansion hypothesis (both RI and SSD) was tested using a parametric bootstrap approach (200 replicates).

RESULTS

Molecular diversity and phylogeographic structure

The edited alignment comprised 671 characters, of which 262 (39.0%) were variable and 198 (29.5%) were parsimony-informative. For the ingroup only, the alignment contained 193 (28.8%) variable characters, of which 165 (24.6%) were parsimony-informative (Table 3). Base frequencies were unequal (A = 0.32649, T = 0.25536, C = 0.28872, G = 0.12944), but a chi-square test confirmed the homogeneity of base frequencies among sequences (d.f. = 372, $P = 1.00$).

The AIC from Modeltest and MrModeltest supported the GTR+I+G substitution model as the most appropriate for our dataset. Parameters estimated under this model were: relative substitution rates (A↔C = 0.6445, A↔G = 17.0118, A↔T = 0.4111, C↔G = 0.0001, C↔T = 6.0118, relative to G↔T = 1.00), proportion of invariable sites (0.4911), and gamma distribution shape parameter (0.7944). The topologies of the ML and Bayesian trees were almost identical, therefore we present the optimal ML tree ($-\ln L = 4198.53883$) with ML bootstrap (BS) values and Bayesian posterior probabilities (PP) indicating branch support (Fig. 3). Two separate genetic lineages are present within *L. guichenoti*: (1) a 'northern' lineage (74 BS, 0.51 PP) that comprises populations from QLD and northern New South Wales (NSW), and (2) a 'southern' lineage that encompasses populations from central and southern NSW, the Australian Capital Territory (ACT), Victoria, and SA (Figs 2 & 3).

Table 3 Estimates of genetic diversity for the clades and lineages present within *Lampropholis guichenoti* in south-eastern Australia.

Clade	*n*	*h*	*Hd*	*M*(*S*)	π	Φ_{ST}	Tajima's *D*	RI	SSD
Northern	28	18	0.963	110 (104)	0.035	0.715			
N1	3	2	0.667	11 (11)	0.011	0.882	n/a	n/a	n/a
N2	18	10	0.922	27 (26)	0.010	0.879	−0.422	0.072	0.032
N3	3	2	0.667	3 (3)	0.003	0.889	n/a	n/a	n/a
N4	2	2	1.0	4 (4)	0.006	0.888	n/a	n/a	n/a
N5	2	2	1.0	3 (3)	0.004	0.889	n/a	n/a	n/a
Southern	95	65	0.984	154 (133)	0.047	0.713			
S1	34	23	0.964	51 (48)	0.014	0.874	−0.791	0.022	0.023*
S2	18	14	0.954	31 (31)	0.010	0.878	−0.890	0.030	0.016
S3	6	5	0.933	17 (17)	0.011	0.880	−0.315	0.076	0.047
S4	7	7	1.0	27 (27)	0.013	0.876	−1.017	0.104	0.057
S5	16	5	0.683	4 (4)	0.002	0.889	0.353	0.120	0.021
S6	10	8	0.933	33 (33)	0.014	0.875	−0.954	0.071	0.046
S7	4	3	0.833	3 (3)	0.002	0.889	0.167	0.194	0.039
Southern A	58	42	0.983	94 (88)	0.028	0.587			
Southern B	37	23	0.937	85 (75)	0.027	0.589			
Overall	123	83	0.989	232 (193)	0.074	0.879			

n, sample size; *h*, number of haplotypes; *Hd*, haplotype diversity; *M*, total number of mutations; *S*, number of segregating (polymorphic) sites; π, nucleotide diversity; Φ_{ST}, differentiation within clades/lineages; RI, raggedness index; SSD, sum of squared deviations. Tajima's *D* was non-significant in all instances. Asterisks indicate significant RI and SSD values.

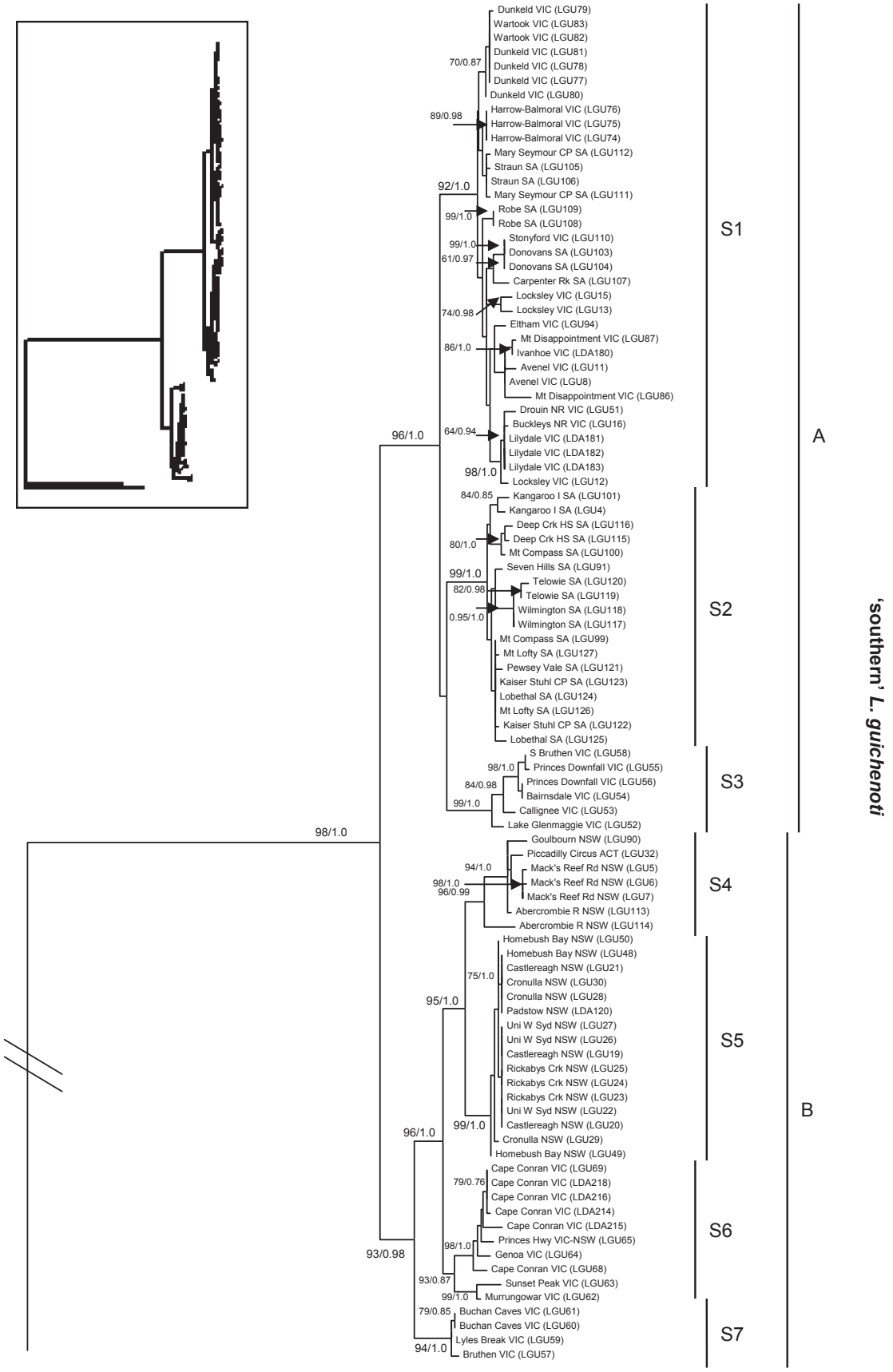
Five distinct clades are evident within the 'northern' lineage of *L. guichenoti* (Figs 2 & 3; Table 2). Both haplotypic and nucleotide diversity are high within the lineage and each clade (Table 3). Clade N1 comprises the QLD populations, while Clade N2 (96 BS, 0.77 PP) encompasses populations from northern NSW, with the exception of isolated populations from Forestlands State Forest (Clade N3), Riamukka State Forest (Clade N4) and Werrikimbe National Park (Clade N5) (Figs 2 & 3; Table 2). Two samples collected from Poison Swamp Creek grouped out within Clade N2 (LGU45-46), while a third sample was contained within Clade N4 (LGU47) (Figs 2 & 3; Table 2).

Seven distinct clades are evident within the 'southern' lineage of *L. guichenoti* (Figs 2 & 3; Table 2), with high levels of both haplotype and nucleotide diversity within the lineage and each clade (Table 3). There was no overlap in the geographic distribution of each clade (Figs 2 & 3). Clade S1 encompasses populations from central and western Victoria and south-eastern SA, with Clade S2 comprising populations from the remainder of the species distribution in SA (Figs 2 & 3; Table 2). Clade S3 occurs in the West, South and East Gippsland region of Victoria, with Clade S6 (93 BS, 0.87 PP) and Clade S7 present in the East Gippsland region (Figs 2 & 3; Table 2). Clade S4 encompasses populations from the ACT and surrounding region of NSW, while Clade S5 is restricted to the Sydney and central NSW coast region (Figs 2 & 3; Table 2). There is strong support for a close relationship between Clade S4 and S5, and more generally among Clades S4–S6 (Fig. 3). Two well-supported genetic sublineages are present within 'southern' *L. guichenoti*, sublineage A (Clades S1–S3) and sublineage B (Clades S4–S7) (Fig. 3). The mean pairwise genetic divergence between the two sublineages is 7.1%, with the phylogeographic break located in the East Gippsland region of Victoria (Figs 2 & 3). This region potentially represents a narrow secondary contact zone between to the two main southern sublineages.

Genetic differentiation among clades and lineages

Substantial genetic differentiation was evident among the clades, sublineages and lineages within *L. guichenoti*. Pairwise Φ_{ST} values among each clade were extremely high and generally statistically significant, except for comparisons involving clades with low sample sizes (e.g. N1, N3–N5; Table 4). There is substantial genetic divergence between the 'northern' and 'southern' lineages within *L. guichenoti* (12.9–16.5%, 7.91–11.62 Ma; Table 3). Despite the relatively limited geographic distribution of the 'northern' lineage, the mean genetic distance among clades (3.5–8.2%, 2.15–5.77 Ma) is equivalent to the more widespread 'southern' lineage (mean

Figure 3 Maximum likelihood (ML) phylogram for *Lampropholis guichenoti* in south-eastern Australia based on 671 bp of ND4. The overall tree topology is indicated in the inset. Two major genetic lineages are identified within *L. guichenoti*: a 'northern' lineage and a 'southern' lineage. Five genetic clades are present within the 'northern' lineage, while seven clades are evident within the 'southern' lineage. Two measures of branch support are indicated with ML bootstraps (500 replicates) on the left and Bayesian posterior probabilities on the right (only values over 50 and 0.7, respectively, are shown). The scale bar indicates branch length.



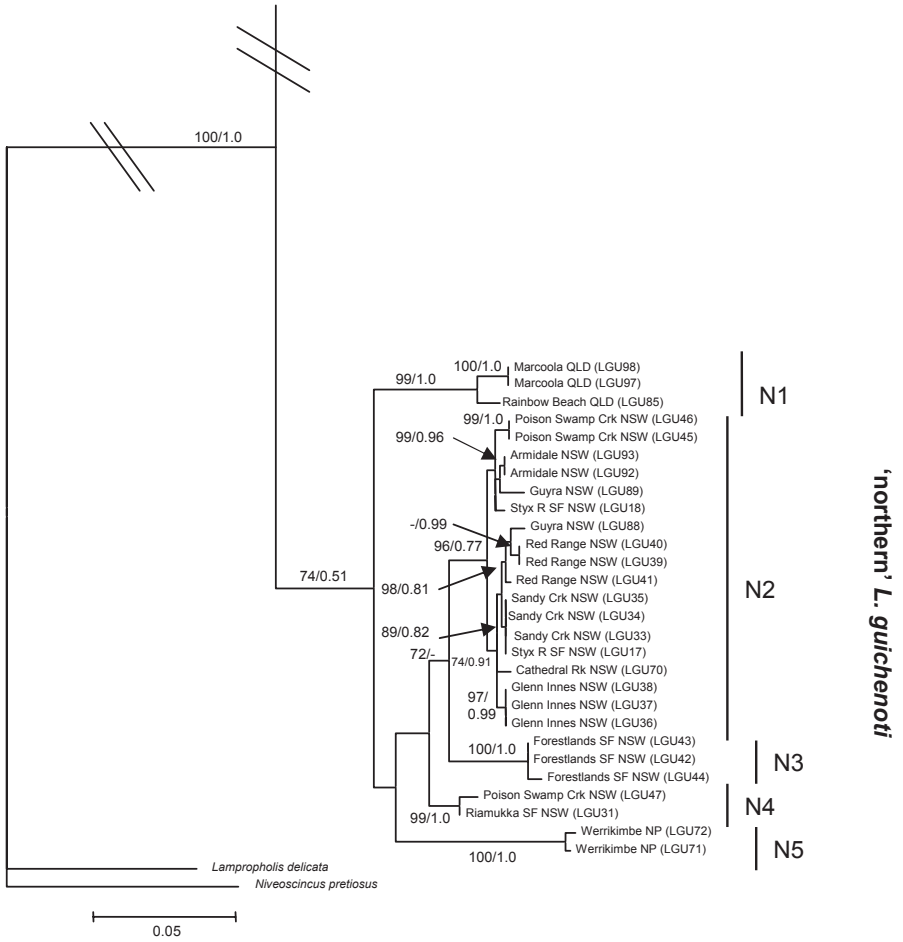


Figure 3 Continued

genetic distance among clades 3.2–8.2%, 1.96–5.77 Ma) (Table 4). The mean genetic distance among the two sublineages within 'southern' *L. guichenoti* is 5.9–8.2% (3.62–5.77 Ma) (Table 4). There are equivalent levels of differentiation among clades within each sublineage (southern A: 4.0–4.5%, 2.45–3.17 Ma; southern B: 3.2–4.8%, 1.96–3.38 Ma; Table 4). Intra-clade genetic divergences in *L. guichenoti* have occurred during the mid- to late Pleistocene (0.2–1.4%, 0.12–0.99 Ma; Table 3).

There is no conclusive support for the model of spatial expansion in *L. guichenoti* clades. None of the clades deviated significantly from the expectations of neutrality (Tajima's *D*),

Table 4 Mean model-corrected ND4 genetic distances (below diagonal) and pairwise Φ_{ST} (above diagonal) among the major clades of *Lampropholis guichenoti* in south-eastern Australia identified in Fig. 3. Asterisks denote statistical significance following Bonferroni correction.

	N1	N2	N3	N4	N5	S1	S2	S3	S4	S5	S6	S7
N1	–	0.843*	0.900	0.838	0.885	0.896*	0.917*	0.918	0.891	0.974*	0.887*	0.950
N2	0.070	–	0.770*	0.717	0.866*	0.902*	0.917*	0.920*	0.903*	0.951*	0.906*	0.932*
N3	0.075	0.041	–	0.904	0.951	0.896*	0.923*	0.933	0.915	0.984*	0.908*	0.981
N4	0.060	0.035	0.044	–	0.914	0.893*	0.913*	0.921	0.897	0.983	0.895	0.973
N5	0.082	0.077	0.077	0.065	–	0.900*	0.924*	0.928	0.908	0.985	0.904	0.977
S1	0.149	0.145	0.140	0.141	0.152	–	0.674*	0.696*	0.807*	0.853*	0.801*	0.784*
S2	0.144	0.140	0.142	0.131	0.152	0.040	–	0.752*	0.850*	0.899*	0.824*	0.846*
S3	0.148	0.146	0.141	0.139	0.150	0.045	0.044	–	0.841*	0.940*	0.821*	0.882
S4	0.133	0.129	0.144	0.136	0.149	0.076	0.081	0.082	–	0.821*	0.637*	0.789*
S5	0.138	0.146	0.156	0.152	0.165	0.070	0.068	0.075	0.032	–	0.805*	0.943*
S6	0.134	0.138	0.146	0.142	0.153	0.074	0.071	0.076	0.040	0.036	–	0.735*
S7	0.132	0.149	0.162	0.143	0.150	0.059	0.062	0.067	0.048	0.038	0.042	–

although a low sample size precluded analyses for several clades within the 'northern' lineage (N1, N3–5) (Table 3). While none of the mismatch distributions for N2 and the southern clades (S1–S7) were strictly unimodal, they exhibited relatively smooth frequency histograms consistent with that expected under the model of spatial expansion. The RI and SSD values indicated that a model of population expansion could only be conclusively rejected for Clade S1 (Table 3).

DISCUSSION

Our phylogeographic analyses indicate that *L. guichenoti* comprises two genetically divergent lineages. The 'northern' lineage occurs to the north of the Hunter Valley in south-eastern QLD and the New England tableland region of NSW, while the 'southern' lineage is distributed throughout southern NSW, the ACT, Victoria and south-eastern SA. The mid–late Miocene divergence of these two lineages is consistent with the timing of diversification within other vertebrates in south-eastern Australia (e.g. Chapple *et al.*, 2005; Moussalli *et al.*, 2005; Symula *et al.*, 2008; Dubey & Shine, 2010). Although the garden skink is a common and abundant species with a continuous distribution throughout south-eastern Australia, substantial phylogeographic substructure (i.e. Φ_{ST}) was evident within both the 'northern' and 'southern' lineages. The main genetic breaks within each lineage are concordant with the recognized biogeographic barriers (i.e. McPherson Range, southern NSW, East Gippsland, Murray Basin) within south-eastern Australia. The clades within each *L. guichenoti* lineage exhibit high haplotypic diversity and are geographically structured and non-overlapping (apart from clades N2 and N4 at Poison Creek Swamp in northern NSW), a pattern observed previously in other species in southern Australia (reviewed in Byrne, 2008). However, further sampling in the East Gippsland region might reveal the presence of a secondary contact zone between the two sublineages of 'southern' *L. guichenoti*. Here we discuss the historical processes and biogeographic barriers that have influenced the evolutionary history of the garden skink, and the taxonomic implications of our study.

Phylogeographic structure in the garden skink corresponds to recognized barriers

The substantial phylogeographic break (*c.* 14%) between the 'northern' and 'southern' lineages of the garden skink occurs across the Hunter Valley region and accounts for over 70% of the genetic variation within the species. Genetic divergences across the Hunter Valley have been observed in several open forest/woodland frogs (*Litoria citropa*, Donnellan *et al.*, 1999; *Limnodynastes peronii*, Schäuble & Moritz, 2001) and lizards (*Liopholis whitii*, Chapple *et al.*, 2005; *Acritoscincus platynotum*, Dubey & Shine, 2010; *Saproscincus mustelinus*, Moussalli *et al.*, 2005), but not others (Table 1). Where present, divergence either side of the Hunter Valley has generally been placed in the Pliocene during the expansion of open woodlands and sclerophyllous forests in eastern Australia. However, the split between the two lineages of the garden skink appears to have occurred earlier during the Miocene, suggesting that the Hunter Valley has been a persistent habitat and elevational barrier in eastern Australia over the past 10 Myr.

A small distributional gap may exist between the two lineages through the Hunter Valley region (Swan *et al.*, 2004; Wilson & Swan, 2008). Populations within the 'northern' lineage occur predominantly in the elevated New England tableland region of northern NSW, with relatively deep (3.5–7.7%) phylogeographic structure evident among clades in the area (N2–N5). This might indicate that garden skink populations have retreated to multiple refugia within this mountainous region during climatic oscillations, a pattern that has been observed in other lizard species in New England tablelands region (Colgan *et al.*, 2009). However, the most substantial genetic break (*c.* 7%) within the 'northern' lineage occurs between the QLD and NSW populations, either side of the McPherson Range. The montane wet forest on the McPherson Range (Table 1) appears to be a barrier to dispersal in the garden skink, which prefers open woodlands and dry sclerophyll forests (Wilson & Swan, 2008). The Pliocene divergence observed across the McPherson Range in the garden skink is intermediate between the Miocene split evident in two frog species (*Litoria pearoniana*, McGuigan *et al.*, 1998; *Litoria fallax*, James & Moritz, 2000) and the Pleistocene break found in Stephens' banded snake (*Hoplocephalus stephensi*, Keogh *et al.*, 2003). Intriguingly, the McPherson Range appears not to be a substantial barrier to dispersal in several other frogs, birds, mammals and plants that have been examined (Table 1).

Several substantial phylogeographic breaks are evident within the 'southern' lineage of the garden skink, three of which correspond to recognized biogeographic barriers (e.g. southern NSW, East Gippsland, Murray Basin; Table 1). The low-lying coastal regions of East Gippsland are bordered to the north by high-elevation regions of the Australian Alps and have experienced repeated marine incursions since the Miocene (Gallagher *et al.*, 2001, 2003; Dickinson *et al.*, 2002; Table 1). Deep genetic breaks, estimated to have occurred in the late Miocene–Pliocene, are evident in this region in White's skink (*Liopholis whitii*, Chapple *et al.*, 2005), the common froglet (*Crinia signifera*, Symula *et al.*, 2008) and the spotted grass frog (*Limnodynastes tasmaniensis*, Schäuble & Moritz, 2001). The two main sublineages (southern A, southern B) of the 'southern' garden skink lineage diverged in the early–mid Miocene, with the break located in the East Gippsland region. Three clades (southern A: S3, southern B: S6 and S7) separated by up to 7.6% sequence divergence occur within 30–75 km of each other in the Buchan and Bruthen region north of Lakes Entrance in East Gippsland (Fig. 2; Table 2). These three clades may have moved back into this region following the retreat of the marine basin (i.e. Gippsland Basin) in a recent interglacial period; S3 from the west, S6 from the east, and S7 from the north-east (Fig. 2). It is unclear whether these three clades have come back into secondary contact in East

Gippsland. A late Pliocene genetic break is evident between clades S1 and S3 in West Gippsland, which may also be a consequence of marine inundation and habitat fragmentation in the region. As the current study has only employed mitochondrial DNA, to rule out the possibility of the patterns being the result of ancestral polymorphism, future studies in the potential contact zones will need to use multiple nuclear loci.

All four phylogeographic studies (Donnellan *et al.*, 1999; Chapple *et al.*, 2005; Nicholls & Austin, 2005; Symula *et al.*, 2008) that have had sufficient sampling in southern NSW have identified a genetic break between coastal populations and those further inland along the GDR (Table 1). In the garden skink, genetic divergence between the coastal and inland populations in southern NSW appears to have occurred in the early Pleistocene. Nicholls & Austin (2005) hypothesized that this break may be due to a sharp elevational transition from lowland coastal vegetation to the sclerophyllous woodlands, forests and grasslands of the southern highlands. Similarly, a consistent genetic break has been observed across the Murray Basin region in south-eastern SA in two frog species (Schäuble & Moritz, 2001; Symula *et al.*, 2008) and a lizard species (Chapple *et al.*, 2005) (Table 1). In the garden skink, there is a distributional gap across the Murray Basin region (Wilson & Swan, 2008), with clades S1 and S2 on either side separated since the onset of increased climatic and sea level fluctuations in the late Pliocene. Frequent marine incursions, along with the unsuitable mallee vegetation in this area, may have prevented the recent expansion of garden skinks across the Murray Basin area.

Contrary to the hypothesis of Rawlinson (1974), garden skinks have had a long evolutionary history in southern Australia rather than representing a recent arrival in the region. Seven divergent phylogeographic clades occur in the region, indicating that the garden skink might have persisted periodically in several isolated refugia areas (e.g. Mt Lofty Ranges, regions of the GDR; Ford, 1987a,b), with subsequent range expansion during suitable climatic conditions (e.g. Byrne, 2008). Indeed, there was some evidence for the recent range or population expansion of the seven clades of the garden skink in southern Australia. However, it is not clear why the garden skink was not able to extend its range into Tasmania along the land bridges that were repeatedly present across Bass Strait during Pleistocene glacial maxima (e.g. Lambeck & Chappell, 2001).

Two genetically divergent lineages within the garden skink: taxonomic implications

The 'northern' and 'southern' lineages of the garden skink diverged in the mid–late Miocene. Given this substantial level of genetic divergence, further molecular (i.e. nuclear loci) and morphological analyses and taxonomic investigations might indicate that each lineage represents a distinct species. Analyses of differences in morphology and nuclear loci are currently being conducted to test whether the two lineages should be recognized as separate species (C.J. Hoskin & D.G. Chapple, in prep.). Should these analyses confirm the taxonomic distinctiveness of each lineage, then a new name will need to be applied to the 'northern' lineage of the garden skink, as the type specimen for *Lampropholis guichenoti* is from Kangaroo Island, SA (Cogger *et al.*, 1983), which is part of the 'southern' lineage.

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SUPPORTING INFORMATION

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

Table S1 Locality data, museum voucher specimen information, and GenBank accession numbers for the *Lampropholis guichenoti* samples used in this study.

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