

The bioinvasion of Guam: inferring geographic origin, pace, pattern and process of an invasive lizard (*Carlia*) in the Pacific using multi-locus genomic data

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Abstract Invasive species often have dramatic negative effects that lead to the deterioration and loss of biodiversity frequently coupled with the burden of expensive biocontrol programs and subversion of socioeconomic stability. The fauna and flora of oceanic islands are particularly susceptible to invasive species and the increase of global movements of humans and their products since WW II has caused numerous anthropogenic translocations and increased the ills of human-mediated invasions. We use a multi-locus genomic dataset to identify geographic origin, pace, pattern and historical process of an invasive scincid lizard (*Carlia*) that has been inadvertently introduced to Guam, the Northern Marianas, and Palau. This lizard is of major importance as its introduction is thought to have assisted in the establishment of the invasive brown treesnake (*Boiga irregularis*) on Guam by providing a food

resource. Our findings demonstrate multiple waves of introductions that appear to be concordant with movements of Allied and Imperial Japanese forces in the Pacific during World War II.

Keywords *Boiga* · Brown Treesnake · Marianas · Micronesia · New Guinea · Palau · World War II

Introduction

Invasive species affect the ecological co-evolutionary cohesion of ecosystems with the potential to cause dramatic declines in biodiversity over short ecological and evolutionary time scales (Rodda et al. 1999). Invasive species can have extreme negative effects on human economic development especially for agriculture and tourism. The economic cost is compounded by the necessity of establishing and maintaining biocontrol programs. The seemingly exponential growth of global movements of humans and their products since World War II has caused numerous anthropogenic translocations and increased the problems of human-mediated invasions (Kraus 2009).

Species introduced to islands often have a greater ecological impact than those introduced to mainland areas (Case and Bolger 1991). Biodiversity loss associated with invasive species is most easily studied on islands, and the oceanic islands in the

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Pacific offer striking examples of ecosystem alterations resulting from biological invasion (Rodda et al. 1991; McKeown 1996; Ota 1999; Urban et al. 2008). Arguably the best-studied island invasive is the brown treesnake, *Boiga irregularis*. This invasive snake has decimated Guam's native wildlife and is responsible for a dramatic decline and extinction of bird species (Rodda et al. 1999).

Boiga irregularis is assumed to have arrived on Guam from the Admiralty Islands following WW II (Rodda et al. 1999). *Boiga irregularis*, however, is not the only species to arrive on Guam post WW II. Other presumed post-WWII species colonizing Guam are: the musk shrew (*Suncus murinus*), the black drongo (*Dicrurus macrocercus*), the green anole (*Anolis carolinensis*), and the Admiralty brown skink (*Carlia ailanpalai*) (Fritts and Rodda 1998). This latter invasive species has received little attention even though it is hypothesized that *C. ailanpalai* indirectly aided the decline and extinction of Guam's native birds by providing a stable food source for juvenile brown treesnakes (Fritts and Rodda 1998). In addition, *Carlia* is invasive on the islands of the Northern Marianas and the Palau archipelago (Crombie and Pregill 1999).

The genus *Carlia* is composed of more than 40 species with a center of diversity in Australia and New Guinea (Zug 2004). The *Carlia fusca* complex is a group of 18 morphologically similar species found mainly on New Guinea and surrounding islands (Zug 2004; Zug and Allison 2006; Donnellan et al. 2009). Although the invasive populations of *Carlia* belong to the *Carlia fusca* complex, the morphological uniformity and taxonomic inattention to this group led to confusion on the specific identity of the invasive populations (Zug 2004). In 2004, Zug delineated species boundaries in the *fusca* complex based on detailed morphological analysis and assigned species identity to the invasive populations. He proposed *Carlia ailanpalai* (native range, Admiralty Islands) as the source for the Guam and Northern Marianas populations and *Carlia tutela* (native range, Halma-hera) as the source for the Palau populations.

In this study, we use a holotypic and topotypic multi-locus genomic dataset to identify the species of introduced *Carlia* (Fig. 1; Appendix). These data reveal the source populations for introduced *Carlia* of Guam, the Northern Marianas, and Palau and allow us to examine and correct the taxonomic confusion of

the introduced and native populations (Fig. 1). In addition to the pattern of invasion, we address the mode and timing of translocations and compare the genetic diversity of various introduced populations with populations from the native range.

Materials and methods

Sampling

A total of 147 individuals of *Carlia* were sampled, including 79 samples from New Guinea and adjacent islands representing potential source populations, and 59 samples from the introduced populations of Guam and the Northern Marianas Islands (including samples from three major islands: Saipan, Tinian and Rota), and 9 from the introduced populations from Palau. Samples were stored in 95% ethanol prior to extraction. Lizards were caught by hand and vouchered and deposited in the Texas Natural History Museum (TNNM), South Australian Museum (SAM), or Louisiana State University Museum of Zoology (LSUMZ). Outgroup sequences of *Carlia rhomboidalis*, *Lygisaurus curtus*, *Menetia timlowi*, and *Lampropholis coggeri* were selected based on previous phylogenetic studies involving *Carlia* skinks (Dolman and Hugall 2008; Donnellan et al. 2009), and were obtained from GenBank (Accession numbers available in Appendix).

DNA isolation, amplification, and sequencing

Whole genomic DNA was extracted from either liver or muscle tissue using an ammonium acetate salt extraction protocol (Fetzner 1999) or a Qiagen DNeasy Tissue Kit (Qiagen, Inc. Valencia, CA) following manufacturer's instructions. Tissues (~100–200 mg) were digested overnight with 20 µl proteinase K, and final extraction concentrations of DNA were stored in AE Buffer at –20°C prior to amplification.

Two mitochondrial gene regions, including cytochrome oxidase b (cyt b) and NADH dehydrogenase subunit 4 (ND4), and one nuclear locus, Beta-globin (B-glob), were selected for sequencing based on the utility of these loci in similar groups (primer sequences and references are available in Table 1). Target gene regions were amplified by PCR on an MJ PTC-200 thermocycler (annealing temperatures

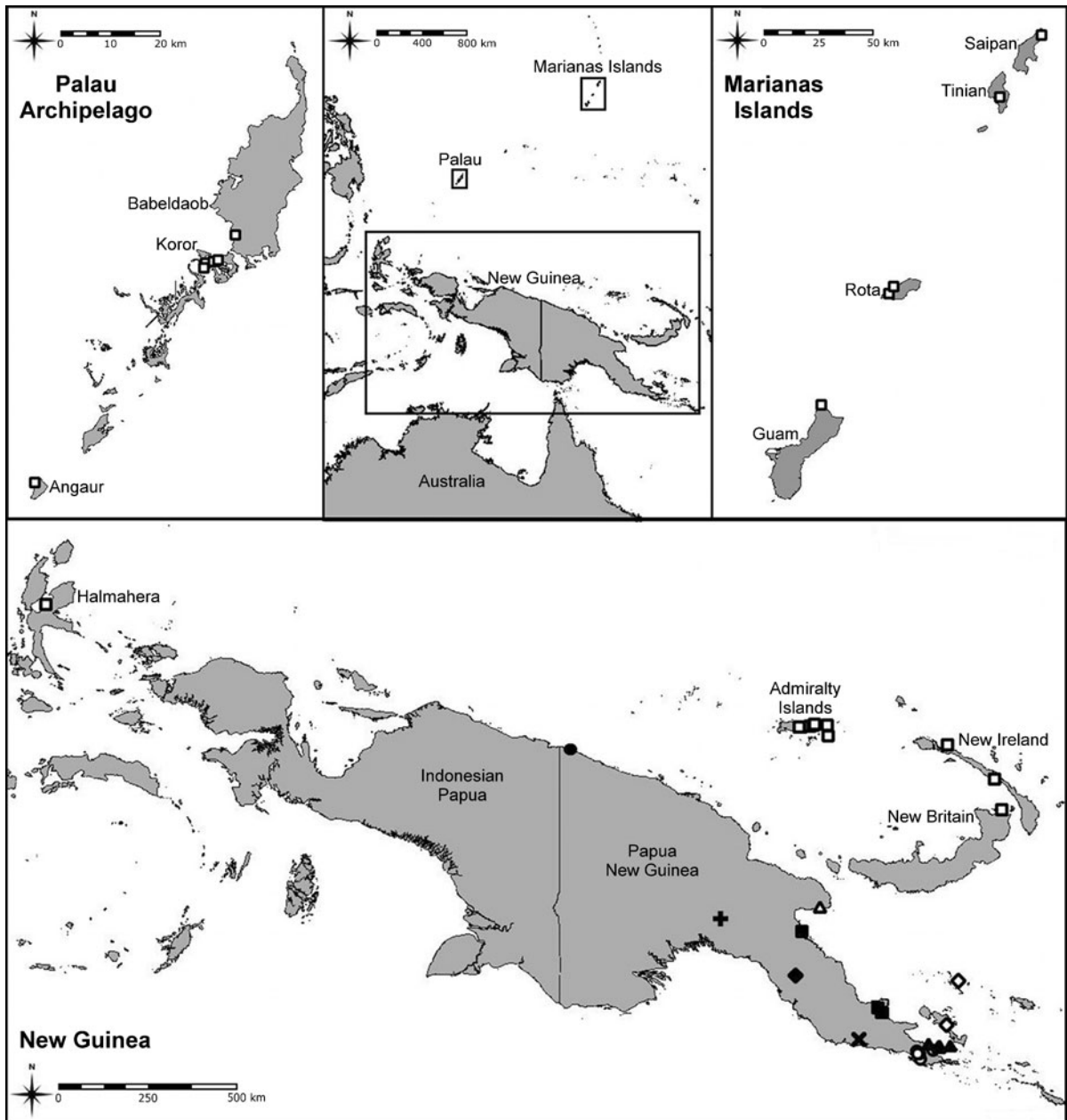


Fig. 1 Sampling localities of *Carlia fusca* group skinks in New Guinea, Palau, and the Marianas Islands. Symbols correspond to clades in Fig. 2: open square, *C. ailanpalai*; closed circle, *C. pulla*; open triangle, *C. mysi*, Huon Peninsula;

closed square, *C. mysi*, Oro, Morobe Provinces; open diamond, *C. eothern*; closed triangle, *C. sp.* Northern Milne Bay; open circle, *C. sp.* Southern Milne Bay; X, *C. sp.* Eastern Central; closed diamond, *C. luctuosa*; +, *C. aenigma*

available in Table 1) using previously published protocols (Austin et al. 2010b). Amplified PCR products were purified with 5 units Exonuclease I and 1.25 units Antarctic Phosphotase (New England Biolabs, Ipswich, MA) as in Austin et al. (2010a), and

sequenced in both directions using BigDye v. 3.1 Terminator Sequencing Kit (Applied Biosystems, Foster City, CA) via previously published protocols (Austin et al. 2010b) on an ABI 3100 automated capillary sequencer.

Table 1 Primers and annealing temperatures used in this study

Locus	Primers	Primer sequence	Temp. (°C)	Reference
Cyt B	H15149	5'-AAA CTG CAG CCC CTC AGA ATG ATA AA-3'	48	Kocher et al. (1989)
	L14841	5'-AAA AAG CTT CCA TCC AAC ATC TCA GC-3'		
ND4	ND4.light	5'-CAC CTA TGA CTA CCA AAA GCT CAT GTA GAA GC-3'	55	Arèvalo et al. (1994)
	Leu3.heavy	5'-GAA TTA GCA GTT CTT TRT G-3'		
β -globin	Bglo1CR	5'-GCG AAC TGC ACT GYG ACA AG-3'	59	Dolman and Phillips (2004)
	Bglo2CR	5'-GCT GCC AAG CGG GTG GTG A-3'		

Phylogenetic analysis

Sequences were visually verified to check for base double-calls or other misreads and complementary strands were assembled into contigs using Sequencher v4.7 (Gene Codes Corp., Ann Arbor, MI, USA) and aligned using ClustalX2 (Larkin et al. 2007) under default settings (Gap opening penalty = 15, Gap extension penalty = 6.66). All protein-coding regions were translated to amino acid sequences using Mesquite v2.73 (Maddison and Maddison 2010) to verify that no premature stop codons disrupted the reading frame. Maximum likelihood and Bayesian inference were used to estimate the phylogeny of *Carlia fusca* group skinks, and to identify the sources of introduced populations. Several partitioning schemes, including partitioning by genome (mitochondrial vs. nuclear), locus, and codon position, were tested and the optimal partitioning scheme was selected by comparing the likelihoods of the resulting topologies using the Akaike information criterion [AIC] (Akaike 1974). The best fit models of nucleotide substitution for each partition were selected using the corrected AIC (Akaike 1974) in jModelTest ver. 0.1.1 (Posada 2008). Maximum Likelihood analyses were implemented in using the partition testing version of GARLI-part v. 0.97 (Zwickl 2006). GARLI analyses were run under default settings with 50 search replicates to ensure the maximum likelihood phylogeny was identified. Maximum likelihood support for the optimal partitioning scheme was estimated using 100 bootstrap pseudoreplicates under default settings with a single search replicate per bootstrap pseudoreplicate. The partitioned Bayesian inference analysis was implemented in Mr. Bayes v. 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). For all models, the prior nucleotide state frequencies,

transition/transversion ratio, and substitution rate priors were set as flat Dirichlet distributions, and the proportion of invariable sites was set as a uniform (0.0–1.0) prior distribution. Rate priors were set to variable to allow the nucleotide substitution rates to vary among partitions. Analyses consisted of two runs, each of 4 chains with default heating and sampling every 1,000 generations for 2,500,000 generations. We discarded the first 15,000 topologies as burn-in, and verified convergence using the program Tracer v1.5 (Rambaut and Drummond 2007) by examining the posterior probability, log likelihood, and all model parameters for stationarity and by examining the effective sample sizes (ESSs), all of which were substantially greater than 200 at run completion. We also used Are We There Yet (AWTY) (Nylander et al. 2008) to compare the posterior probabilities of all splits between runs to further verify convergence. At run completion, the plot comparing posterior probabilities of splits between runs was linear, indicating that the two runs had converged and were sampling the posterior distribution.

To further investigate relationships among introduced *Carlia* populations and source populations identified via phylogenetic analyses, we constructed multilocus haplotype networks for islands containing introduced populations. Individuals for which we could not obtain sequence data for all three loci were excluded from haplotype network analyses. Genetic distance matrices were calculated for each locus using uncorrected *p* distances and maximum likelihood distances in Paup* v4.0b10 (Swofford 2003), and combined to a single genetic distance matrix using Pofad v.1.03 (Joly and Bruneau 2006). Multilocus haplotype networks were then constructed using the NeighborNet algorithm (Bryant and Moulton 2004) in SplitsTree v4.11 (Huson and Bryant 2006).

Genetic diversity

Due to the founder effect associated with introduction, many invasive populations show decreased genetic diversity relative to native populations. To investigate this in *Carlia*, we calculated nucleotide diversity (π) for both native and introduced populations of *Carlia* using the pegas package ver. 0.3-2 (Paradis 2010) in R v. 2.11.0. Populations for the calculation of nucleotide diversity were defined as those samples collected with 5 km of one another. Both mitochondrial loci (cyt b and ND4) were concatenated and samples for which we could not obtain sequence for one mitochondrial locus were excluded; sites with missing data in one or more samples were also excluded from the calculation of nucleotide diversity.

Results

Phylogenetic analyses

The final aligned dataset was a total of 1603 bp. Lengths of each partition, numbers of variable sites, and models of nucleotide substitution (selected using AIC) are provided in Table 2. In both maximum likelihood and Bayesian inference, a scheme of seven partitions was selected as optimal using AIC: B-glob, cyt b 1st, 2nd, and 3rd codon positions, and ND4 1st, 2nd, and 3rd codon positions. Tracer plots of all parameters, posterior probabilities, and likelihood were stationary at similar values after the burnin period for both Bayesian inference analyses, and all ESSs were substantially greater than 200 at run

Table 2 Lengths and number of parsimony informative sites for each partition in the optimal partitioning scheme

Partition	Length (bp)	Parsimony informative sites	Model
cyt b pos. 1	111	25	SYM + G
cyt b pos. 2	111	7	F81 + I
cyt b pos. 3	112	92	GTR + G
ND4 pos. 1	246	79	GTR + I + G
ND4 pos. 2	246	34	HKY + I + G
ND4 pos. 3	246	206	GTR + I + G
B-globin	531	247	GTR + G

completion. Additionally, AWTY plots comparing the posterior probabilities of all splits were linear, indicating that Bayesian inference analyses had reached convergence.

The phylogenetic reconstructions (Fig. 2) strongly support (Bayesian posterior probability, PP = 1.0, maximum likelihood bootstrap support, BS = 100) distinct clades that correspond to species. All of the invasive *Carlia* populations fall within a clade that corresponds to *C. ailanpalai* (holotypic and topotypic material included). Within this *C. ailanpalai* clade, three major clades are recovered: (A) the Northern Marianas Islands (Saipan, Tinian and Rota) and the Admiralty Islands (PP = 0.99, BS = 57), (B) Palau and New Britain (PP = 1.0, BS = 81), and (C) Guam, New Ireland, Halmahera and the Admiralty Islands (PP = 1.0, BS = 77). These subclades are all strongly supported in Bayesian analyses (PP > 0.99), and, with the exception of subclade A, are strongly supported in maximum likelihood analyses (BS = 57, 81, and 77 for clades A, B, and C, respectively). Results of the haplotype networks for native and introduced populations of *C. ailanpalai* were similar between the two methods of genetic distance calculation, and corroborate the results of the phylogenetic analyses. Samples cluster into three clades in the haplotype network, corresponding to the three clades recovered within *C. ailanpalai* in the phylogenetic analyses (Figs. 2, 3). Genetic divergence among these clades (maximum p distance is 0.0153 for cyt b and 0.0346 for ND4) is lower than those among other clades that are currently recognized as good species and indicate at least three introduction events from three genetically identifiable source populations for the introduced Pacific populations of *C. ailanpalai*: New Britain as the source population for Palau, the Admiralty Islands as the source population for the Northern Marianas Islands (Tinian, Saipan and Rota), and the Admiralty Islands, New Ireland, or Halmahera as the source population for Guam.

Genetic diversity

Nucleotide diversity for the concatenated mitochondrial dataset is shown in Fig. 4. Despite the larger sample sizes for the introduced populations relative to the native populations (Appendix), nucleotide diversity within each of the introduced populations

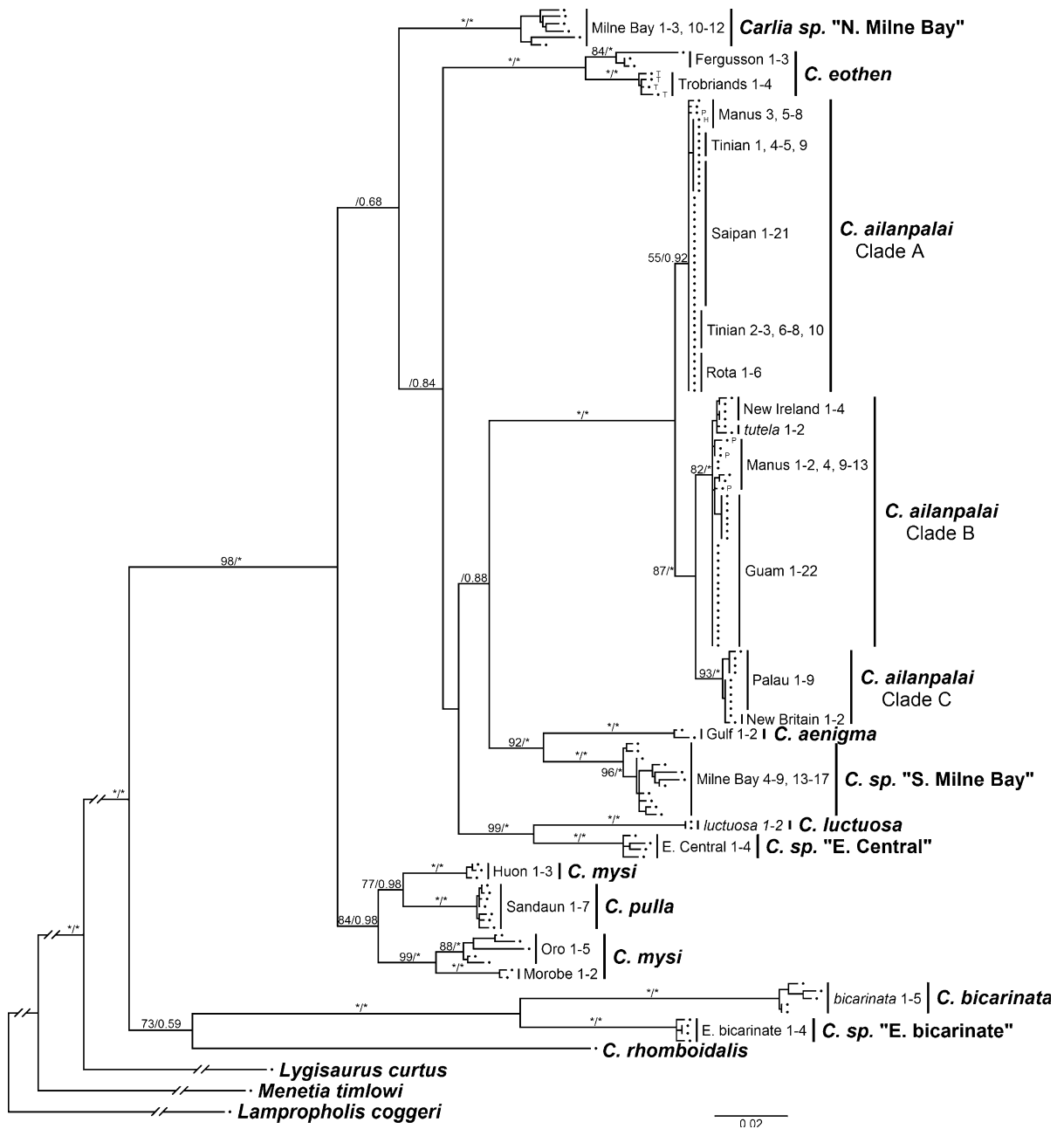


Fig. 2 Maximum likelihood phylogeny of *Carlia fusca* group skinks. Numbers on nodes indicate maximum likelihood bootstrap proportions and Bayesian posterior probabilities, respectively, asterisks indicate bootstrap support of 100 or

posterior probability support of 1.0. The holotype of *C. ailanpalai* is indicated with an H; paratypes of *C. ailanpalai* are indicated with P's; topotype samples are indicated with T's

is zero, with only single haplotypes recovered for each sampled population. In contrast, all of the native populations show expected levels of nucleotide diversity based on previous scincid studies (Smith

et al. 2001; Fuerst and Austin 2004; Austin et al. 2010a; Jackson and Austin 2010). In addition to nucleotide diversity, nucleotide divergence is also high among native populations and species.

Fig. 3 Network of multilocus data from *Carlia ailanpalai* samples constructed using the NeighborNet algorithm in SplitsTree. Clade names (A, B, C) correspond to those indicated in Fig. 2

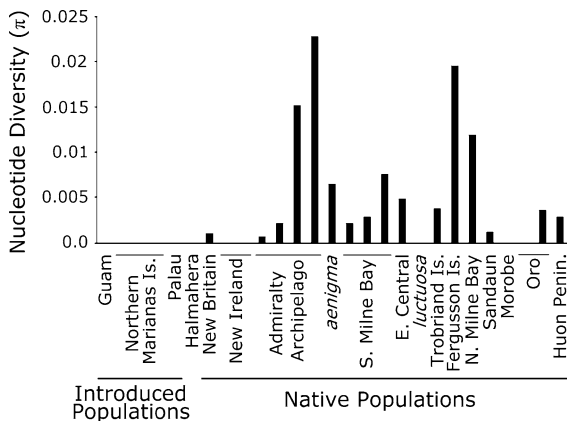
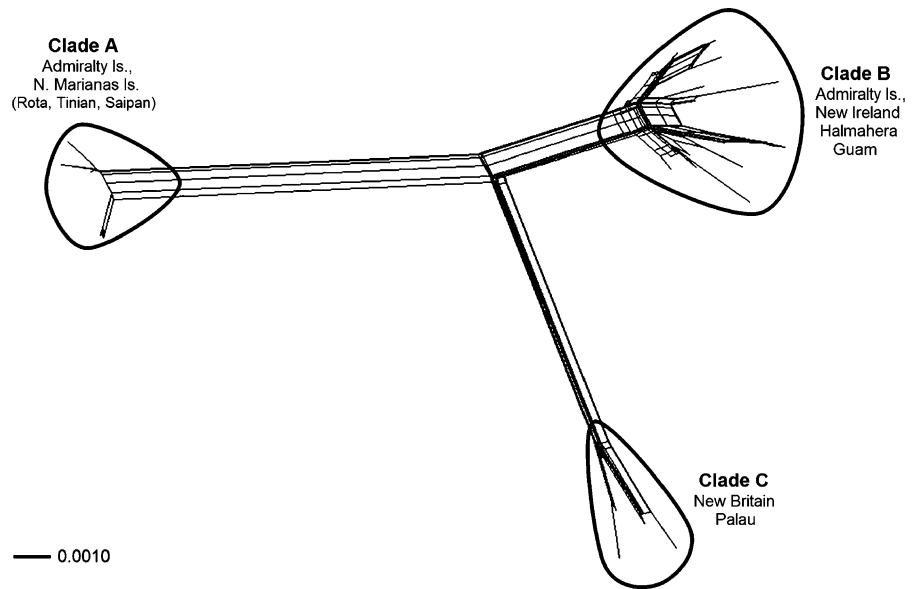


Fig. 4 Histogram of intra-population nucleotide diversity calculated from 1,072 bp of mitochondrial DNA (including both cyt b and ND4) for native and introduced populations of *Carlia fusca* group skinks. Populations with no bars (including all introduced populations and some native populations) indicate that a single mitochondrial haplotype was recovered from that population

Discussion

From a broad taxonomic standpoint, some species delimitations of Zug (2004) conflict with the molecular phylogeographic data presented here. Zug (2004) considered *C. ailanpalai* as restricted to the Admiralty archipelago (Fig. 1); however, our molecular

data demonstrates that *C. ailanpalai* occurs more widely including the Bismarck Archipelago, populations that Zug (2004) assigned to *C. mysi*, a presumed widely occurring species distributed along the north coast of New Guinea. Further, his Halmahera species, *C. tutela*, despite being known from pre-WWII collections (MCZ R-7674, 1907, Patani, Halmahera; RMNH 8659, 3–7 June, 1930 Morotai) appears to be another invasive population of *C. ailanpalai*. Our sampling, however, was limited ($n = 2$); further sampling from Halmahera and re-examination of the type series is needed to better understand the status of the Halmahera population. Our results demonstrate that the uniform morphology of the *C. fusca* species group hides considerable genetic diversity and we are currently investigating the apparent decoupling of morphological and molecular evolution in *Carlia*.

Because of the genetic diversity and divergence within and among populations of *C. ailanpalai* across its native range, it is possible to trace the geographic origins of the invasive populations. Interestingly, the three separate invasions herein identified appear to track the occupation and movements of Allied and Imperial Japanese forces in this region during World War II. First, Palau was invaded by Imperial Japanese forces early in the war as the Japanese forces moved south and eastward culminating with their occupation of northern New Guinea and various Pacific islands.

The natural harbor of Rabaul on the northern end of New Britain was a major Japanese stronghold, and the Allies decided to bypass and isolate it in their campaign to recapture New Guinea and in their movement to retake the Philippines (Gailey 2004). The invasive Palau population is part of a well-supported clade of samples from New Britain suggesting that translocation of military materiel from the Japanese forces on New Britain to Palau could have resulted in the introduction of *C. ailanpalai* from New Britain to Palau. Second, the Guam populations are part of a well-supported clade from New Ireland and the Admiralty archipelago, the later of which was a major base for Allies' operations and support the introduction of *C. ailanpalai* onto Guam via the transport of Allied military materiel (Morison 1953). Finally, the invasive populations from the Northern Marianas islands of Saipan, Tinian and Rota are nested in a clade from the Admiralty archipelago indicating an introduction independent from the Guam introduction. Thus, the Marianas populations show the genetic signature of two separate invasions: one invasion of Guam, and a second invasion of the Northern Marianas Islands of Saipan, Tinian and Rota.

The exact timing of the introductions, however, remains uncertain. The Bismarck-Palau introduction presumably occurred during the latter days of the Japanese occupation of Rabaul and their movement of military materials back to Palau to re-enforce their Palauan base. The general assumption for the introduction of *Carlia* into the Marianas was post-WWII removal of military supplies from New Guinea to permanent bases within the Marianas as there was substantial postwar salvage movement of ships and materiel between Manus and other Pacific islands.

Supporting an hypothesis of WW II era translocations, the first collections of *Carlia* from these regions are: Guam 1968 (USNM 192894, CAS 139825-7), Palau 1968 (MCZ R-104514-6, 104518-24, 111930-73, 113491, 114600-40, 118591), and Northern Marianas (Saipan) 1962 (FMNH 17641-3). Although all these dates are well past the end of WWII, the initial propagules may have needed time to become established to reach sufficient population densities to attract attention and be collected and deposited in museum collections.

The broad geographic distribution of *C. ailanpalai* along with the corresponding phylogeographic structure has allowed us to tease out the genetic signature of the origin, mode and tempo of invasion. The identification of the species and specific source population has the ability to identify potential bio-control methods such as population-specific parasites. Further, if our hypothesized timeline of WWII introductions is correct, this suggests that this species, and possibly other invasive lizards, may require a significant establishment time (~20–30 years) before becoming widely abundant. This lag in establishment, even for species that use secondary growth habitats like *C. ailanpalai*, means that with appropriate long-term sampling programs there may be sufficient time to identify, control and eliminate any future island introductions. Vigilant monitoring and continued museum vouchered collections, therefore, are imperative for sound conservation management. Our data also demonstrates that large movements of military materiel can transport exotic invasive species. Given the large scale transport of military materiel to and from the US and Iraq and Afghanistan appropriate controls should be implemented to preclude transport of invasive species.

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Appendix

See Table 3.

Table 3 Voucher catalog numbers, collection localities, and Genbank accession numbers for specimens included in this study

Species	Catalogue no.	ID	Locality	Latitude	Longitude	GenBank accession numbers		
						cyt b	ND4	B-glob
<i>Carlia aenigma</i>	LSUMZ 94741	Sobo 1	PNG: Gulf Prov.: Wabo Village	-6.979736	145.069213	HQ173045	HQ173187	HQ173330
<i>Carlia aenigma</i>	LSUMZ 94747	Sobo 2	PNG: Gulf Prov.: Wabo Village	-6.979736	145.069213	HQ172980	HQ173122	HQ173267
<i>Carlia aitanpalai</i>	LSUMZ 92042	Guam 1	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172907	HQ173046	-
<i>Carlia aitanpalai</i>	LSUMZ 92043	Guam 2	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172908	HQ173047	HQ173188
<i>Carlia aitanpalai</i>	LSUMZ 92044	Guam 3	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172909	-	HQ173189
<i>Carlia aitanpalai</i>	LSUMZ 92045	Guam 4	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172910	HQ173048	HQ173190
<i>Carlia aitanpalai</i>	LSUMZ 92046	Guam 5	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172911	HQ173049	HQ173191
<i>Carlia aitanpalai</i>	LSUMZ 92047	Guam 6	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172912	HQ173050	HQ173192
<i>Carlia aitanpalai</i>	LSUMZ 92048	Guam 7	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172913	HQ173051	HQ173193
<i>Carlia aitanpalai</i>	LSUMZ 92049	Guam 8	Guam: Guam National Wildlife Refuge	13.653367	144.861983	-	HQ173052	HQ173194
<i>Carlia aitanpalai</i>	LSUMZ 92050	Guam 9	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172914	HQ173053	HQ173195
<i>Carlia aitanpalai</i>	LSUMZ 92051	Guam 10	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172915	HQ173054	HQ173196
<i>Carlia aitanpalai</i>	LSUMZ 93369	Guam 11	Guam: Guam National Wildlife Refuge	13.653367	144.861983	-	HQ173092	HQ173233
<i>Carlia aitanpalai</i>	LSUMZ 93370	Guam 12	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172949	HQ173093	-
<i>Carlia aitanpalai</i>	LSUMZ 93371	Guam 13	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172950	HQ173094	HQ173234
<i>Carlia aitanpalai</i>	LSUMZ 93372	Guam 14	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172951	HQ173095	HQ173235
<i>Carlia aitanpalai</i>	LSUMZ 93373	Guam 15	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172952	HQ173096	HQ173236
<i>Carlia aitanpalai</i>	LSUMZ 93374	Guam 16	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172953	HQ173097	HQ173237
<i>Carlia aitanpalai</i>	LSUMZ 93375	Guam 17	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172954	HQ173098	HQ173238
<i>Carlia aitanpalai</i>	LSUMZ 93376	Guam 18	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172955	HQ173099	HQ173239
<i>Carlia aitanpalai</i>	LSUMZ 93377	Guam 19	Guam: Guam National Wildlife Refuge	13.653367	144.861983	-	HQ173100	HQ173240
<i>Carlia aitanpalai</i>	LSUMZ 93378	Guam 20	Guam: Guam National Wildlife Refuge	13.653367	144.861983	-	HQ173101	HQ173241
<i>Carlia aitanpalai</i>	LSUMZ 93379	Guam 21	Guam: Guam National Wildlife Refuge	13.653367	144.861983	-	HQ173102	HQ173242
<i>Carlia aitanpalai</i>	LSUMZ 93380	Guam 22	Guam: Guam National Wildlife Refuge	13.653367	144.861983	HQ172956	HQ173103	HQ173243
<i>Carlia aitanpalai</i>	BJE 1146	tutela 1	Indonesia: Halmahera:	1.0025	128.002222	HQ172957	HQ173104	HQ173244
<i>Carlia aitanpalai</i>	BJE 1156	tutela 2	Indonesia: Halmahera:	1.0025	128.002222	HQ172958	HQ173105	HQ173245
<i>Carlia aitanpalai</i>	LSUMZ 92052	Saipan 1	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172916	HQ173055	HQ173197
<i>Carlia aitanpalai</i>	LSUMZ 92053	Saipan 2	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	-	HQ173056	HQ173198
<i>Carlia aitanpalai</i>	LSUMZ 92054	Saipan 3	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172917	HQ173057	HQ173199

Table 3 continued

Species	Catalogue no.	ID	Locality	Latitude	Longitude	GenBank accession numbers		
						cyt b	ND4	B-glob
<i>Carlia aitanpalai</i>	LSUMZ 92055	Saipan 4	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	–	HQ173058	HQ173200
<i>Carlia aitanpalai</i>	LSUMZ 92056	Saipan 5	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	–	HQ173059	HQ173201
<i>Carlia aitanpalai</i>	LSUMZ 92057	Saipan 6	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172918	HQ173060	HQ173202
<i>Carlia aitanpalai</i>	LSUMZ 92058	Saipan 7	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172919	HQ173061	HQ173203
<i>Carlia aitanpalai</i>	LSUMZ 92059	Saipan 8	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172920	HQ173062	HQ173204
<i>Carlia aitanpalai</i>	LSUMZ 92060	Saipan 9	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172921	HQ173063	HQ173205
<i>Carlia aitanpalai</i>	LSUMZ 92062	Saipan 10	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172922	HQ173064	–
<i>Carlia aitanpalai</i>	LSUMZ 92064	Saipan 11	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172923	HQ173065	HQ173206
<i>Carlia aitanpalai</i>	LSUMZ 92065	Saipan 12	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172924	HQ173066	HQ173207
<i>Carlia aitanpalai</i>	LSUMZ 92066	Saipan 13	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172925	HQ173067	HQ173208
<i>Carlia aitanpalai</i>	LSUMZ 92067	Saipan 14	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172926	HQ173068	HQ173209
<i>Carlia aitanpalai</i>	LSUMZ 92068	Saipan 15	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172927	HQ173069	HQ173210
<i>Carlia aitanpalai</i>	LSUMZ 92069	Saipan 16	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172928	HQ173070	HQ173211
<i>Carlia aitanpalai</i>	LSUMZ 92070	Saipan 17	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172929	HQ173071	HQ173212
<i>Carlia aitanpalai</i>	LSUMZ 92071	Saipan 18	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172930	HQ173072	HQ173213
<i>Carlia aitanpalai</i>	LSUMZ 92072	Saipan 19	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172931	HQ173073	HQ173214
<i>Carlia aitanpalai</i>	LSUMZ 92073	Saipan 20	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172932	HQ173074	HQ173215

Table 3 continued

Species	Catalogue no.	ID	Locality	Latitude	Longitude	GenBank accession numbers		
						cyt b	ND4	
							B-glob	
<i>Carlia aitanpalai</i>	LSUMZ 92074	Saipan 21	Northern Mariana Is.: Saipan: Bird Island Trail Head	15.262278	145.81508	HQ172933	HQ173075	HQ173216
<i>Carlia aitanpalai</i>	SAMR 48002	Palau 9	Palau: Angaur	6.916667	134.124167	HQ172979	HQ173121	HQ173266
<i>Carlia aitanpalai</i>	SAMR 47707	Palau 1	Palau: Babeldaob	7.391	134.511433	HQ172971	-	HQ173258
<i>Carlia aitanpalai</i>	SAMR 47708	Palau 2	Palau: Babeldaob	7.391	134.511433	HQ172972	-	HQ173259
<i>Carlia aitanpalai</i>	SAMR 47754	Palau 5	Palau: Koror	7.333333	134.47	HQ172975	HQ173120	HQ173262
<i>Carlia aitanpalai</i>	SAMR 47900	Palau 6	Palau: Koror	7.3375	134.473333	HQ172976	-	HQ173263
<i>Carlia aitanpalai</i>	SAMR 47901	Palau 7	Palau: Koror	7.3375	134.473333	HQ172977	-	HQ173264
<i>Carlia aitanpalai</i>	SAMR 47975	Palau 8	Palau: Koror	7.3375	134.473333	HQ172978	-	HQ173265
<i>Carlia aitanpalai</i>	SAMR 47733	Palau 4	Palau: Malakal	7.321833	134.441667	HQ172974	HQ173119	HQ173261
<i>Carlia aitanpalai</i>	SAMR 47729	Palau 3	Palau: Ngermalik	7.336667	134.455	HQ172973	HQ173118	HQ173260
<i>Carlia aitanpalai</i>	THNM 51388	New Britain 1	PNG: East New Britain Prov.: Rabaul	-4.195914	152.172903	HQ172959	HQ173106	HQ173246
<i>Carlia aitanpalai</i>	THNM 51389	New Britain 2	PNG: East New Britain Prov.: Rabaul	-4.195914	152.172903	HQ172960	HQ173107	HQ173247
<i>Carlia aitanpalai</i>	LSUMZ 93933*	Manus 4	PNG: Manus Prov.: Los Negros Is.: Loniu Village	-2.070167	147.340833	HQ172988	HQ173130	HQ173275
<i>Carlia aitanpalai</i>	LSUMZ 93934*	Manus 5	PNG: Manus Prov.: Los Negros Is.: Loniu Village	-2.070167	147.340833	HQ172989	HQ173131	HQ173276
<i>Carlia aitanpalai</i>	USNM 560085***	Manus 8	PNG: Manus Prov.: Los Negros Is.: Peyon Village	-2.032667	147.434167	HQ172992	HQ173134	HQ173279
<i>Carlia aitanpalai</i>	USNM 560087**	Manus 6	PNG: Manus Prov.: Los Negros Is.: Rio Rio Village	-2.049167	147.418667	HQ172990	HQ173132	HQ173277
<i>Carlia aitanpalai</i>	LSUMZ 93941	Manus 7	PNG: Manus Prov.: Los Negros Is.: Rio Rio Village	-2.049167	147.418667	HQ172991	HQ173133	HQ173278
<i>Carlia aitanpalai</i>	LSUMZ 93925	Manus 1	PNG: Manus Prov.: Manus Is.: Kawaliap Village	-2.11	147.067667	HQ172981	HQ173123	HQ173268
<i>Carlia aitanpalai</i>	LSUMZ 93926	Manus 2	PNG: Manus Prov.: Manus Is.: Kawaliap Village	-2.11	147.067667	HQ172982	HQ173124	HQ173269
<i>Carlia aitanpalai</i>	LSUMZ 93927	Manus 3	PNG: Manus Prov.: Manus Is.: Kawaliap Village	-2.11	147.067667	HQ172983	HQ173125	HQ173270
<i>Carlia aitanpalai</i>	USNM 560088**	Manus 9	PNG: Manus Prov.: Manus Is.: Tingau Village	-2.096	147.1055	HQ172993	HQ173135	HQ173280
<i>Carlia aitanpalai</i>	USNM 560089**	Manus 10	PNG: Manus Prov.: Manus Is.: Tingau Village	-2.096	147.1055	HQ172994	HQ173136	HQ173281

Table 3 continued

Species	Catalogue no.	ID	Locality	Latitude	Longitude	GenBank accession numbers		
						cyt b	ND4	B-glob
<i>Carlia aitanpalai</i>	USNM 560090**	Manus 11	PNG: Manus Prov.: Manus Is.: Tingau' Village	-2.096	147.1055	HQ172995	HQ173137	HQ173282
<i>Carlia aitanpalai</i>	LSUMZ 93942	Manus 12	PNG: Manus Prov.: Rambutyo Is.: Penchal Village	-2.3405	147.7945	HQ172996	HQ173138	HQ173283
<i>Carlia aitanpalai</i>	USNM 560137	Manus 13	PNG: Manus Prov.: Tong Is.	-2.058333	147.758333	HQ172997	HQ173139	HQ173284
<i>Carlia aitanpalai</i>	THNM 51468	New Ireland 3	PNG: New Ireland Prov.: Kavieng	-2.566496	150.798547	HQ172963	HQ173110	HQ173250
<i>Carlia aitanpalai</i>	THNM 51469	New Ireland 4	PNG: New Ireland Prov.: Kavieng	-2.566496	150.798547	HQ172964	HQ173111	HQ173251
<i>Carlia aitanpalai</i>	THNM 51406	New Ireland 1	PNG: New Ireland Prov.: Lelet Plateau	-3.430352	151.998138	HQ172961	HQ173108	HQ173248
<i>Carlia aitanpalai</i>	THNM 51411	New Ireland 2	PNG: New Ireland Prov.: Lelet Plateau	-3.430352	151.998138	HQ172962	HQ173109	HQ173249
<i>Carlia aitanpalai</i>	LSUMZ 93363	Rota 1	Rota: Tenetu	14.137019	145.154436	HQ172943	HQ173086	HQ173227
<i>Carlia aitanpalai</i>	LSUMZ 93364	Rota 2	Rota: Tenetu	14.137019	145.154436	HQ172944	HQ173087	HQ173228
<i>Carlia aitanpalai</i>	LSUMZ 93365	Rota 3	Rota: Veteran's Memorial Park	14.167714	145.175692	HQ172945	HQ173088	HQ173229
<i>Carlia aitanpalai</i>	LSUMZ 93366	Rota 4	Rota: Veteran's Memorial Park	14.167714	145.175692	HQ172946	HQ173089	HQ173230
<i>Carlia aitanpalai</i>	LSUMZ 93367	Rota 5	Rota: Veteran's Memorial Park	14.167714	145.175692	HQ172947	HQ173090	HQ173231
<i>Carlia aitanpalai</i>	LSUMZ 93368	Rota 6	Rota: Veteran's Memorial Park	14.167714	145.175692	HQ172948	HQ173091	HQ173232
<i>Carlia aitanpalai</i>	LSUMZ 92724	Tinian 1	Tinian	14.993603	145.633328	HQ172934	HQ173076	HQ173217
<i>Carlia aitanpalai</i>	LSUMZ 92725	Tinian 2	Tinian	14.993603	145.633328	HQ172935	HQ173077	HQ173218
<i>Carlia aitanpalai</i>	LSUMZ 92726	Tinian 3	Tinian	14.993603	145.633328	HQ172936	HQ173078	HQ173219
<i>Carlia aitanpalai</i>	LSUMZ 92727	Tinian 4	Tinian	14.993603	145.633328	-	HQ173079	HQ173220
<i>Carlia aitanpalai</i>	LSUMZ 92728	Tinian 5	Tinian	14.993603	145.633328	HQ172937	HQ173080	HQ173221
<i>Carlia aitanpalai</i>	LSUMZ 92729	Tinian 6	Tinian	14.993603	145.633328	HQ172938	HQ173081	HQ173222
<i>Carlia aitanpalai</i>	LSUMZ 92732	Tinian 7	Tinian	14.993603	145.633328	HQ172939	HQ173082	HQ173223
<i>Carlia aitanpalai</i>	LSUMZ 92733	Tinian 8	Tinian	14.993603	145.633328	HQ172940	HQ173083	HQ173224
<i>Carlia aitanpalai</i>	LSUMZ 92734	Tinian 9	Tinian	14.993603	145.633328	HQ172941	HQ173084	HQ173225
<i>Carlia aitanpalai</i>	LSUMZ 92735	Tinian 10	Tinian	14.993603	145.633328	HQ172942	HQ173085	HQ173226
<i>Carlia eothen</i>	THNM 51496	Fergusson 1	PNG: Milne Bay Prov.: D'Entrecasteaux Arch.: Fergusson Is.	-9.664622	150.792103	HQ172968	HQ173115	HQ173255
<i>Carlia eothen</i>	THNM 51497	Fergusson 2	PNG: Milne Bay Prov.: D'Entrecasteaux Arch.: Fergusson Is.	-9.664622	150.792103	HQ172969	HQ173116	HQ173256
<i>Carlia eothen</i>	THNM 51501	Fergusson 3	PNG: Milne Bay Prov.: D'Entrecasteaux Arch.: Fergusson Is.	-9.664622	150.792103	HQ172970	HQ173117	HQ173257

Table 3 continued

Species	Catalogue no.	ID	Locality	Latitude	Longitude	GenBank accession numbers	
						cyt b	ND4
<i>Carlia eothen</i>	LSUMZ 94750*	Trobriands 1	PNG: Milne Bay Prov.: Trobriand Is.: Kiriwina Is.	-8.542208	151.079164	HQ172984	HQ173126
<i>Carlia eothen</i>	LSUMZ 94248*	Trobriands 2	PNG: Milne Bay Prov.: Trobriand Is.: Kiriwina Is.	-8.542208	151.079164	HQ172985	HQ173127
<i>Carlia eothen</i>	LSUMZ 94249*	Trobriands 3	PNG: Milne Bay Prov.: Trobriand Is.: Kiriwina Is.	-8.542208	151.079164	HQ172986	HQ173128
<i>Carlia eothen</i>	LSUMZ 94250*	Trobriands 4	PNG: Milne Bay Prov.: Trobriand Is.: Kiriwina Is.	-8.542208	151.079164	HQ172987	HQ173129
<i>Carlia luctuosa</i>	LSUMZ 93564	luctuosa 1	PNG: Central Prov.: Kone Village	-8.415183	146.95865	HQ173015	HQ173157
<i>Carlia luctuosa</i>	LSUMZ 93565	luctuosa 2	PNG: Central Prov.: Kone Village	-8.415183	146.95865	HQ173016	HQ173158
<i>Carlia mysi</i>	THNM 51301	Huon 1	PNG: Morobe Prov.: Huon Peninsula: near Oligadu	-6.709008	147.572558	HQ172965	HQ173112
<i>Carlia mysi</i>	THNM 51336	Huon 2	PNG: Morobe Prov.: Huon Peninsula: near Oligadu	-6.709008	147.572558	HQ172966	HQ173113
<i>Carlia mysi</i>	THNM 51338	Huon 3	PNG: Morobe Prov.: Huon Peninsula: near Oligadu	-6.709008	147.572558	HQ172967	HQ173114
<i>Carlia mysi</i>	LSUMZ 93547	Morobe 1	PNG: Morobe Prov.: Kamiali Village	-7.3005	147.133667	HQ173006	HQ173148
<i>Carlia mysi</i>	LSUMZ 93549	Morobe 2	PNG: Morobe Prov.: Kamiali Village	-7.3005	147.133667	HQ173007	HQ173149
<i>Carlia mysi</i>	LSUMZ 93552	Oro 3	PNG: Oro Prov.: Base of Mt. Victory	-9.239067	149.0543	HQ173009	HQ173151
<i>Carlia mysi</i>	LSUMZ 93553	Oro 4	PNG: Oro Prov.: Base of Mt. Victory	-9.239067	149.0543	HQ173010	HQ173152
<i>Carlia mysi</i>	CCA 2157	Oro 1	PNG: Oro Prov.: Koreaf Village, near Wanigela	-9.337667	149.14	HQ172999	HQ173141
<i>Carlia mysi</i>	LSUMZ 93551	Oro 2	PNG: Oro Prov.: Koreaf Village, near Wanigela	-9.337667	149.14	HQ173000	HQ173142
<i>Carlia mysi</i>	LSUMZ 93554	Oro 5	PNG: Oro Prov.: Sarad Mission, Wanigela	-9.339	149.158833	HQ173011	HQ173153
<i>Carlia pulla</i>	LSUMZ 93556	Sandaun 2	PNG: Sandaun Prov.: near Waromo Village	-2.666283	141.238783	HQ173013	HQ173155
<i>Carlia pulla</i>	LSUMZ 93557	Sandaun 3	PNG: Sandaun Prov.: near Waromo Village	-2.666283	141.238783	HQ173014	HQ173156
<i>Carlia pulla</i>	LSUMZ 93117	Sandaun 4	PNG: Sandaun Prov.: Vanimo	-2.684433	141.304883	HQ173019	HQ173161
<i>Carlia pulla</i>	LSUMZ 92712	Sandaun 5	PNG: Sandaun Prov.: Vanimo	-2.684433	141.304883	HQ173020	HQ173162
<i>Carlia pulla</i>	LSUMZ 92713	Sandaun 6	PNG: Sandaun Prov.: Vanimo	-2.684433	141.304883	HQ173021	HQ173163
<i>Carlia pulla</i>	LSUMZ 93118	Sandaun 7	PNG: Sandaun Prov.: Vanimo	-2.684433	141.304883	HQ173022	HQ173164
<i>Carlia pulla</i>	LSUMZ 93555	Sandaun 1	PNG: Sandaun Prov.: Waromo Village	-2.6682	141.2442	HQ173012	HQ173154

Table 3 continued

Species	Catalogue no.	ID	Locality	Latitude	Longitude	GenBank accession numbers		
						cyt b	ND4	B-glob
<i>Carlia</i> sp. "Amau fusca group"	LSUMZ 94695	Amau 1	PNG: Central Prov.: Amau Village	-10.0368	148.564633	HQ173037	HQ173179	HQ173323
<i>Carlia</i> sp. "Amau fusca group"	LSUMZ 94696	Amau 2	PNG: Central Prov.: Amau Village	-10.0368	148.564633	HQ173038	HQ173180	HQ173324
<i>Carlia</i> sp. "Amau fusca group"	LSUMZ 94697	Amau 3	PNG: Central Prov.: Amau Village	-10.0368	148.564633	HQ173039	HQ173181	HQ173325
<i>Carlia</i> sp. "Amau fusca group"	LSUMZ 94719	Amau 4	PNG: Central Prov.: Amau Village	-10.0368	148.564633	HQ173040	HQ173182	HQ173326
<i>Carlia</i> sp. "Milne Bay North Coast"	LSUMZ 93156	MB 12	PNG: Milne Bay Prov.: Eastern Cape	-10.230083	150.8745	HQ173031	HQ173173	HQ173317
<i>Carlia</i> sp. "Milne Bay North Coast"	LSUMZ 92880	MB 11	PNG: Milne Bay Prov.: Huhuna Village	-10.284817	150.60105	HQ173030	HQ173172	HQ173316
<i>Carlia</i> sp. "Milne Bay North Coast"	USNM 560107	MB 1	PNG: Milne Bay Prov.: Iapoa #2 Village	-10.258667	150.5735	HQ173001	HQ173143	HQ173287
<i>Carlia</i> sp. "Milne Bay North Coast"	USNM 560108	MB 2	PNG: Milne Bay Prov.: Iapoa #2 Village	-10.258667	150.5735	HQ173002	HQ173144	HQ173288
<i>Carlia</i> sp. "Milne Bay North Coast"	USNM 560099	MB 3	PNG: Milne Bay Prov.: Netuli Is.	-10.234333	150.597667	HQ173003	HQ173145	HQ173289
<i>Carlia</i> sp. "Milne Bay North Coast"	LSUMZ 92877	MB 10	PNG: Milne Bay Prov.: Topura Village	-10.1933	150.33705	HQ173029	HQ173171	HQ173315
<i>Carlia</i> sp. "Milne Bay South"	LSUMZ 93128	MB 6	PNG: Milne Bay Prov.: Napatana Lodge grounds, Alotau	-10.305867	150.437183	HQ173025	HQ173167	HQ173311
<i>Carlia</i> sp. "Milne Bay South"	LSUMZ 93129	MB 7	PNG: Milne Bay Prov.: Napatana Lodge grounds, Alotau	-10.305867	150.437183	HQ173026	HQ173168	HQ173312
<i>Carlia</i> sp. "Milne Bay South"	LSUMZ 92874	MB 8	PNG: Milne Bay Prov.: Napatana Lodge grounds, Alotau	-10.305867	150.437183	HQ173027	HQ173169	HQ173313
<i>Carlia</i> sp. "Milne Bay South"	LSUMZ 92875	MB 9	PNG: Milne Bay Prov.: Napatana Lodge grounds, Alotau	-10.305867	150.437183	HQ173028	HQ173170	HQ173314
<i>Carlia</i> sp. "Milne Bay South"	LSUMZ 93102	MB 13	PNG: Milne Bay Prov.: Oil palm plantation, west of Alotau	-10.399283	150.091617	HQ173032	HQ173174	HQ173318
<i>Carlia</i> sp. "Milne Bay South"	LSUMZ 93103	MB 14	PNG: Milne Bay Prov.: Oil palm plantation, west of Alotau	-10.399283	150.091617	HQ173033	HQ173175	HQ173319
<i>Carlia</i> sp. "Milne Bay South"	CCA 4802	MB 16	PNG: Milne Bay Prov.: Padi Village	-10.4021	150.062717	HQ173035	HQ173177	HQ173321

Table 3 continued

Species	Catalogue no.	ID	Locality	Latitude	Longitude	GenBank accession numbers			
						cyt b	ND4	B-glob	
<i>Carlia</i> sp. "Milne Bay South"	LSUMZ 92583	MB 17	PNG: Milne Bay Prov.: Padi Padi Village	-10.4021	150.062717	HQ173036	HQ173178	HQ173322	
<i>Carlia</i> sp. "Milne Bay South"	USNM 560136	MB 4	PNG: Milne Bay Prov.: Saga AHO River	-10.544167	150.115167	HQ173004	HQ173146	HQ173290	
<i>Carlia</i> sp. "Milne Bay South"	USNM 560101	MB 5	PNG: Milne Bay Prov.: Saga AHO River	-10.544167	150.115167	HQ173005	HQ173147	HQ173291	
<i>Carlia</i> sp. "Milne Bay South"	LSUMZ 95752	MB 15	PNG: Milne Bay Prov.: Takwatakawai Village	-10.325617	150.03765	HQ173034	HQ173176	HQ173320	
<i>Outgroups:</i>									
<i>Carlia bicarinata</i>	LSUMZ 93542	bicarinata 1	PNG: NCD: Port Moresby, National Museum grounds	-9.425565	147.190129	HQ173008	HQ173150	HQ173294	
<i>Carlia bicarinata</i>	LSUMZ 93545	bicarinata 2	PNG: NCD: Port Moresby, 2 Mile	-9.473283	147.1776	HQ173017	HQ173159	HQ173303	
<i>Carlia bicarinata</i>	LSUMZ 93546	bicarinata 3	PNG: NCD: Port Moresby, 2 Mile	-9.473283	147.1776	HQ173018	HQ173160	HQ173304	
<i>Carlia bicarinata</i>	LSUMZ 92680	bicarinata 4	PNG: Central Prov.: Bootless Bay	-9.509333	147.290183	HQ173023	HQ173165	HQ173309	
<i>Carlia bicarinata</i>	LSUMZ 92681	bicarinata 5	PNG: Central Prov.: Bootless Bay	-9.509333	147.290183	HQ173024	HQ173166	HQ173310	
<i>Carlia</i> sp. "Amau bicarinate"	LSUMZ 94724	Amau bicarinate 1	PNG: Central Prov.: Amau Village	-10.0368	148.564633	HQ173041	HQ173183	HQ173327	
<i>Carlia</i> sp. "Amau bicarinate"	LSUMZ 94731	Amau bicarinate 2	PNG: Central Prov.: Amau Village	-10.0368	148.564633	HQ173042	HQ173184	HQ173328	
<i>Carlia</i> sp. "Amau bicarinate"	LSUMZ 94732	Amau bicarinate 3	PNG: Central Prov.: Amau Village	-10.0368	148.564633	HQ173043	HQ173185	HQ173329	
<i>Carlia</i> sp. "Amau bicarinate"	LSUMZ 94526	Amau bicarinate 4	PNG: Central Prov.: Amau Village	-10.0368	148.564633	HQ173044	HQ173186	-	
<i>Carlia rhonboidalis</i>						AJ406203	DQ350070	DQ349566	
<i>Lygisaurus curtus</i>						HQ172998	HQ173140	HQ173285	
<i>Menetia timlowi</i>						-	AJ290552	AY508895	
<i>Lampropholis coggeri</i>						-	FJ379463	AY508900	

* Indicates topotypes

** Indicates paratypes

*** Indicates holotypes

References

- Akaike H (1974) A new look at the statistical model identification. *IEEE Trans Autom Control* 19:716–723
- Arèvalo E, Davis SK, Sites JW Jr (1994) Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in Central Mexico. *Syst Biol* 43:387–418
- Austin CC, Rittmeyer EN, Richards SJ, et al (2010a) Phylogeny, historical biogeography and body size evolution in Pacific Island Crocodile skinks *Tribolonotus* (Squamata; Scincidae). *Mol Phylogenet Evol* 57:227–236
- Austin CC, Spataro M, Peterson S, et al (2010b) Conservation genetics of Boelen's python (*Morelia boeleni*) from New Guinea: reduced genetic diversity and divergence of captive and wild animals. *Conserv Genet* 11:889–896
- Bryant D, Moulton V (2004) Neighbor-Net: an agglomerative method for the construction of phylogenetic networks. *Mol Biol Evol* 21:255–265
- Case TJ, Bolger DT (1991) The role of introduced species in shaping the distribution and abundance of island reptiles. *Evol Ecol* 5:272–290
- Crombie RI, Pregill GK (1999) A checklist of the herpetofauna of the Palau islands (Republic of Belau), Oceania. *Herpetol Monogr* 13:29–80
- Dolman G, Hugall AF (2008) Combined mitochondrial and nuclear data enhance resolution of a rapid radiation of Australian rainbow skinks (Scincidae: *Carlia*). *Mol Phylogenet Evol* 49:782–794
- Dolman G, Phillips BP (2004) Single copy nuclear DNA markers characterized for comparative phylogeography in Australian wet tropics rainforest skinks. *Mol Ecol Notes* 4:185–187
- Donnellan SC, Couper PJ, Saint KM, et al (2009) Systematics of the *Carlia 'fusca'* complex (Reptilia: Scincidae) from northern Australia. *Zootaxa* 2227:1–31
- Fetzner FWJ (1999) Extracting high-quality DNA from shed reptile skins: a simplified method. *BioTechniques* 26:1052–1054
- Fritts TH, Rodda GH (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annu Rev Ecol Syst* 29:113–140
- Fuerst GS, Austin CC (2004) Population genetic structure of the prairie Skink (*Eumeces septentrionalis*): nested clade analysis of post Pleistocene populations. *J Herpetol* 38:257–268
- Gailey HA (2004) MacArthur's victory: the war in New Guinea, 1943–1944. Presidio Press, New York
- Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17:754–755
- Huson DH, Bryant D (2006) Application of phylogenetic networks in evolutionary studies. *Mol Biol Evol* 23:254–267
- Jackson ND, Austin CC (2010) The combined effects of rivers and refugia generate extreme cryptic fragmentation within the common ground skink (*Scincella lateralis*). *Evolution* 64:409–428
- Joly S, Bruneau A (2006) Incorporating allelic variation for reconstructing the evolutionary history of organisms from multiple genes: an example from *Rosa* in North America. *Syst Biol* 55:623–636
- Kocher TD, Thomas WK, Meyer A, et al (1989) Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences of the United States of America* 86:6196–6200
- Kraus F (2009) Alien reptiles and amphibians: a scientific compendium and analysis. Springer Science, New York
- Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, Thompson JD, Gibson TJ, Higgins DG (2007) Clustal W and Clustal X version 2.0. *Bioinformatics* 23:2947–2948
- Maddison WP, Maddison DR (2010) Mesquite: a modular system for evolutionary analysis. Version 2.73 <http://mesquiteproject.org>
- McKeown S (1996) A field guide to reptiles and amphibians of the Hawaiian islands. Diamond Head Publishing, Los Osos
- Morison SE (1953) History of United States naval operations in world war II volume 8: New Guinea and the Marianas, March 1944–August 1944. University of Illinois Press, Urbana
- Nylander JAA, Wilgenbusch JC, Warren DL, Swofford DL (2008) AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics* 24:581–583
- Ota H (1999) Introduced amphibians and reptiles of the Ryukyu Archipelago, Japan. In: Rodda GH, Sawai Y, Chiszar D, Tanaka H (eds) Problem snake management: the Habu an the brown treesnake. Comstock Publishing Associates, Ithaca, pp 439–452
- Paradis E (2010) pegas: an R package for population genetics with an integrated-modular approach. *Bioinformatics* 26:419–420
- Posada D (2008) jModelTest: phylogenetic model averaging. *Mol Biol Evol* 25:1253–1256
- Rambaut A, Drummond AJ (2007) Tracer v1.4. Available from <http://beast.bio.ed.ac.uk/Tracer>
- Rodda GH, Fritts TH, Reichel JD (1991) Distributional patterns of reptiles and amphibians in the Mariana Islands. *Micronesica* 24:195–210
- Rodda GH, Sawai Y, Chiszar D, Tanaka H (1999) Problem snake management: the Habu an the brown treesnake. Comstock Publishing Associates, Ithaca
- Ronquist F, Huelsenbeck JP (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574
- Smith SA, Austin CC, Shine R (2001) A phylogenetic analysis of variation in reproductive mode within an Australian lizard (*Saiphos equalis*, Scincidae). *Biol J Linn Soc* 74:131–139
- Stuart-Fox DM, Hugall AF, Moritz C (2002) A molecular phylogeny of rainbow skinks (Scincidae: *Carlia*): taxonomic and biogeographic implications. *Aust J Zool* 50:39–51
- Swofford DL (2003) PAUP*. Phylogenetic analysis using parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland

- Urban MC, Phillips BL, Skelly DK, Shine R (2008) A toad more traveled: the heterogeneous invasion dynamics of cane toads in Australia. *Am Nat* 171:134–148
- Zug GR (2004) Systematics of the *Carlia* “fusca” lizards of New Guinea and nearby islands. Bishop Museum Press, Honolulu
- Zug GR, Allison A (2006) New *Carlia fusca* complex lizards (Reptilia: Squamata: Scincidae) from New Guinea, Papua-Indonesia. *Zootaxa* 1237:27–44
- Zwickl DJ (2006) Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. dissertation, The University of Texas, Austin. Available from: <http://www.bio.utexas.edu/faculty/antisense/garli/Garli.html>