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Phylogeography of the prehensile-tailed skink *Corucia zebrata* on the Solomon Archipelago

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Abstract

The biogeography of islands is often strongly influenced by prior geological events. *Corucia zebrata* (Squamata: Scincidae) is endemic to the geologically complex Solomon Archipelago in Northern Melanesia. We examined the level of divergence for different island populations of *C. zebrata* and discussed these patterns in light of Pleistocene land bridges, island isolation, and island age. *Corucia zebrata* was sampled from 14 locations across the Solomon Archipelago and sequenced at two mitochondrial genes (*ND2* and *ND4*; 1697 bp in total) and four nuclear loci (*rhodopsin*, an unknown intron, *AKAP9*, and *PTPN12*). Measures of genetic divergence, analyses of genetic variation, and Bayesian phylogenetic inference were used and the data assessed in light of geological information. Populations of *C. zebrata* on separate islands were found to be genetically different from each other, with reciprocal monophyly on mitochondrial DNA. Populations on islands previously connected by Pleistocene land bridges were marginally less divergent from each other than from populations on other nearby but isolated islands. There are indications that *C. zebrata* has radiated across the eastern islands of the archipelago within the last 1–4 million years. Nuclear loci were not sufficiently informative to yield further information about the phylogeography of *C. zebrata* on the Solomon Archipelago. Analyses of the mitochondrial data suggest that dispersal between islands has been very limited and that there are barriers to gene flow within the major islands. Islands that have been isolated during the Pleistocene glacial cycles are somewhat divergent in their mitochondrial genotypes, however, isolation by distance (IBD) and recent colonization of isolated but geologically younger islands appear to have had stronger effects on the phylogeography of *C. zebrata* than the Pleistocene glacial cycles. This contrasts with patterns reported for avian taxa, and highlights the fact that biogeographic regions for island species cannot be directly extrapolated among taxa of differing dispersal ability.

Introduction

Islands represent natural laboratories that allow for simpler examination of evolution and ecology than is possible on large continental landmasses. Long periods of geographic isolation, with subsequent genetic drift and differing selection pressures lead to genetic divergence (Balloux and Lugon–Moulin 2002; Vanderwerf et al. 2010) that may result in allopatric speciation on separate islands (Orr and Smith 1998; Glor et al. 2004). The geological histories of archipelagos play an important role in shaping the biogeography of islands. Island colonization often moves in the direction from older to younger islands, as seen on Hawaii (Hormiga et al. 2003; Rubinoff 2008) and the Galapagos (Parent et al. 2008; Benavides et al. 2009). The last glacial maximum (LGM) 18,000 years ago, when the sea level was 120 m or more lower than today (Fairbanks 1989) has also affected the biogeography of many islands. The lowered sea level exposed land bridges and eliminated or decreased the over-water distance between landmasses, which facilitated dispersal between

islands. Consequently, current populations of species on islands that were connected by Pleistocene land bridges often show decreased genetic distance compared to those on islands that have remained isolated, and this pattern can be detected for both volant and nonvolant species (Heaney et al. 2005).

The Melanesian Solomon Archipelago is situated in the South West Pacific and spans two countries, Papua New Guinea (PNG), which has political claim on the island of Bougainville, and the Solomon Islands, to which the remaining islands belong (Fig. 1). The islands have complex geological histories that create excellent conditions for assessment of biogeography, ecology, and evolution. The islands of the Solomon Archipelago have never been connected to neighboring continents, but emerged from the ocean as a consequence of a collision between the Indian and Pacific Plates (Hall 2002). All of the endemic biota on the archipelago has therefore originated from speciation through founder events rather than vicariance. The various islands of the archipelago have different geological compositions, origins, and emergence times. The Western Province is the youngest part of the archipelago and is a result of volcanic activity during the Pliocene and Pleistocene (Petterson et al. 1999; Cowley et al. 2004). The islands of the Western Province are therefore likely to have emerged less than 5 million years ago (MYA) (Petterson et al. 1999). The earlier emergence times of the remaining islands are largely uncertain, but are estimated to range from 30 to 90 MYA (Petterson et al. 1999; Hall 2002). Several islands of the archipelago were connected to each other during the LGM (Fig. 1). Bougainville, Choiseul, Isabel, and Ngela were joined in the Great Bukida landmass and Guadalcanal would have been either connected to the same landmass or separated from it by a narrow channel. At the same time, the Western Province was represented probably by two major islands (Mayr and Diamond 1976, 2001). Makira and Malaita are separated from each other and from the rest of the archipelago by deeper channels and probably have been isolated for a substantial geological time (Mayr and Diamond 2001; Fig. 1). The historical colonization patterns of the archipelago are important in order to understand the origins of the Pacific biota and are now being explored with molecular genetic methods on a number of taxonomic groups, such as birds (Filardi and Smith 2005; Smith and Filardi 2007), bats (Pulvers and Colgan 2007), and reptiles (Austin et al. 2010). Pulvers and Colgan (2007) described a close association between genetic lineages of bats on the

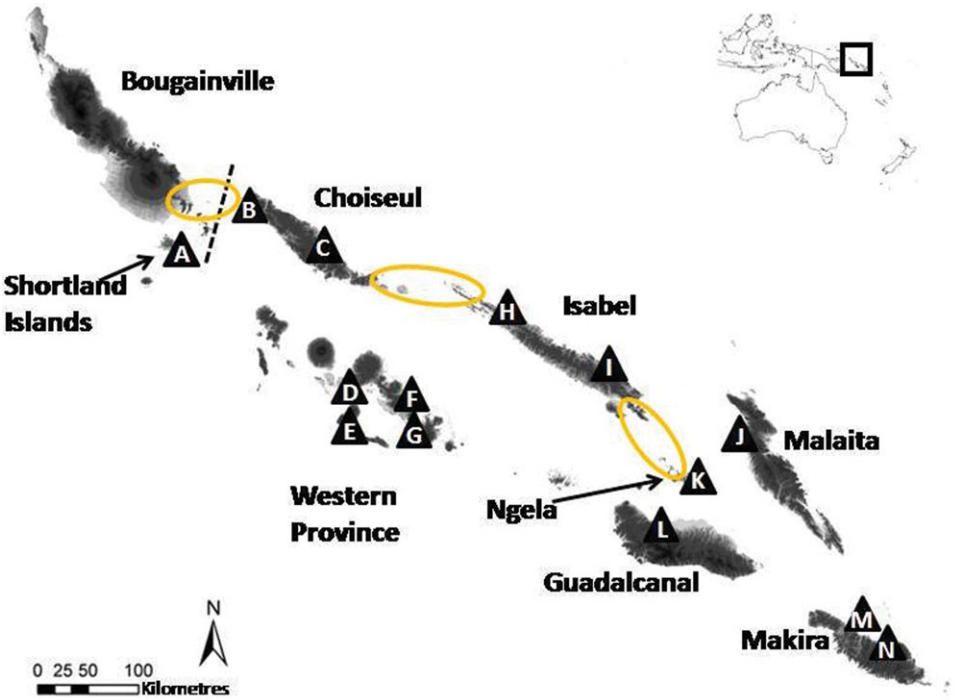

Figure 1. The Solomon Archipelago. The broken line represents the subspecies boundary according to McCoy (2006). Sample locations are indicated by black triangles with letters for reference in the text. Yellow ovals indicate the Pleistocene land bridges of the Great Bukida landmass, which included Bougainville, Choiseul, Isabel, and Ngela. The Western Province was separated into two larger islands. Malaita and Makira have been isolated throughout the glacial cycles, while Guadalcanal may have been separated from Ngela by a narrow channel.

Figure 2. *Corucia zebrata* from Rendova Island in the Western Province.

Solomon Archipelago and phylogenetic relationships predicted from presumed Pleistocene landmass conformations. A similar pattern was found for birds (Smith and Filardi 2007; Uy et al. 2009). Nonvolant animals such as reptiles and amphibians generally have slower dispersal rates than avian taxa, which could result in smaller scale genetic structure and higher local population differentiation (Hughes et al. 1997). Currently, no extensive biogeographic study that is based on molecular phylogenetics and that includes samples of a single species from all major islands has been conducted on the reptiles (or amphibians) of the Solomon Archipelago.

The genus *Corucia*

The prehensile tailed skink, *Corucia zebrata* (Gray 1855) is an ecologically and evolutionary unique reptile endemic to the archipelago (Fig. 2). Belonging to the *Egernia* group (Gardner et al. 2008), a largely Australian lineage of skinks, *C. zebrata* is the sister lineage to the remainder of the group and molecular clock estimates suggest that it has been separated from the other seven genera in the group for about 26 MYA (Skinner et al. 2011); a divergence that postdates the period when the Solomon Archipelago is believed to have emerged (Hall 2002). *Corucia* has traditionally been considered monotypic, with its single species represented by two geographically separated subspecies, *C. z. zebrata* to the east and *C. z. alfredschmidti* to the west (Kőhler 1997). The exact geographic location of the subspecies boundary is uncertain, but is likely to lie between the Shortlands/Bougainville and Choiseul (Kőhler 1997; McCoy 2006) (Fig. 1).

Corucia gives birth to live young and may reach a weight of over 1000 g. The combination of large size, a prehensile tail and a nocturnal, herbivorous, and arboreal nature makes it ecologically unique among the Scincidae (McCoy 2006; Hagen and Bull 2011). The species has been subject to poaching for the international pet market, a process that is believed to have put severe pressure on some populations (McCoy 2006). Although the conservation status for *C. zebrata* is unknown, the species' forest habitat is under threat, due to forest fragmentation and destruction as a result of intense logging (Dauvergne 1998).

We used molecular genetic tools to elucidate the phylogeography of *Corucia* under the hypothesis that the geographic distance between islands and the sea level changes during the LGM have affected the phylogeography of the species. Specifically, the following predictions were made: (1) The genetic divergences will be lower between populations on islands that were connected by Pleistocene land bridges than between those on islands that have remained isolated. (2) The genetic distance between populations will increase with geographic distance between islands (Isolation by distance [IBD] [Wright 1943]), reflecting that gene flow decreases with increasing distance between populations and that selection and genetic drift due to environmental conditions differ increasingly with increasing geographic distance between populations.

Additionally, we aimed to make inferences on the geographical origin and dispersal pattern of *Corucia* within the Solomon Archipelago and to use molecular clock calibrations and knowledge of the geological history to estimate the dates of the colonization events for the different islands across the archipelago.

Materials and Methods

We collected samples from 46 *C. zebrata* caught in the Solomon Islands between July 2007 and May 2008. The sample locations are indicated on Figure 1. The lizards were

captured by hand and their GPS locations were recorded. Scale clips were collected and preserved in 70% ethanol (no *Corucia* was killed and no vouchers were taken for conservation and permitting reasons). Tissue samples from another 17 individuals from the frozen tissue collections of the Australian and South Australian Museums were also included. The sample locations for all 63 samples are listed in Appendix 1. The 63 samples included representatives from all major island groups with the exception of Bougainville, as permits to enter Bougainville for sampling purposes were not obtained during the study period. The sample sizes from the respective locations are as follows, with the letters in brackets referring to the locations on Figure 1 and Appendix 1: Shortland Islands (A) = 2, Choiseul West (B) = 6, Choiseul East (C) = 11, Western Province (D, E, F, G) = 9, Isabel West (H) = 4, Isabel East (I) = 5, Ngela (K) = 1, Malaita (J) = 2, Guadalcanal (L) = 6, and Makira Province (M, N) = 17. Three other species of the *Egernia* group (*Egernia depressa, E. saxatilis,* and *Lissolepis coventryi*) were used as outgroups for the analyses of the mitochondrial data. Outgroup details are listed in Appendix 1.

DNA extraction, PCR amplification, and sequencing

DNA was extracted from scales or liver using a Puregene™ DNA Isolation Tissue Kit, D–7000A (Gentra Systems, Minneapolis, MN), following the manufacturer's instructions. We amplified two sections of the mitochondrial genome (*ND2* and *ND4*) and four nuclear loci (*rhodopsin* intron 4, an unknown intron, *AKAP9* coding for amino acid positions 482–688 in the human gene, and *PTPN12* coding for amino acid positions 298–497 in the human gene). See Table 1 for primer sequences and PCR conditions for each locus. The two mitochondrial markers have been informative for previous phylogeographic studies in reptiles (e.g., Gardner et al. 2008). The noncoding nuclear locus *rhodopsin* (Bossuyt and Milinkovitch 2000; Page 2000; Austin et al. 2010) is known to show intraspecific variation in a number of taxa. The two nuclear protein encoding genes were reported by Townsend (2008) to be among the most variable nuclear genes screened across a range of squamate reptile species, and therefore likely to be informative in phylogeographic studies.

The PCR reaction mixtures were prepared using AmpliTaq Gold (Applied Biosystems, Foster City, CA) following the manufacturer's recommendations, with approximately 100 ng template DNA, 10mM total of each dNTP, 0.2 μM of each primer, 0.5 μg/μL BSA, and 4 mM MgCl, in a final volume of 25 μl. The following PCR cycle was used: 94°C, 5 min; (94°C, 45 sec; T_a, 45 sec; 72°C, 1 min) × 38 cycles; 72°C, 10 min. The PCR reactions were purified using a MultiScreen vacuum manifold (Millipore, Billerica, MA), following the manufacturer's protocol. The sequencing reactions were prepared with BigDye Terminator v3.1 Cycle sequencing kit (Applied Biosystems), following the manufacturer's protocol. The samples were sequenced in both directions. Electrophoresis was carried out on an ABI PRISM 3730 Analyser (Applied Biosystems). The sequences were edited using the ContigExpress function in Vector NTI v10 (Invitrogen, Carlsbad, CA). For the nuclear genes, we used parsimony to manually resolve alleles in heterozygous individuals. In individuals where phase could not be resolved, PCR products were cloned and several clones sequenced for each product. We used a StrataClone PCR Cloning Kit (Agilent Technologies, Santa Clara, CA), following the manufacturer's recommendations. The clones were sequenced as described above.

Data analysis

The sequences were aligned in Geneious v4.5.5 (Drummond et al. 2008). The coding sequences were translated to protein sequences in ContigExpress to verify that the reading frame was not disrupted by premature stop codons or deletions, as a further check of sequence quality and locus identity. We used DNAsp v5 (Librado and Rozas 2009) to characterize within-population genetic diversity, estimate haplotype diversity, and characterize statistical properties of the sequences. Haplotype networks were generated in TCS v1.21 (Clement

Table 1. Sequences, PCR conditions, and references for the six loci used.

Locus	Reference	Ta (°C)	Forward (5′–3′)	Reverse (5′–3′)
NADH dehydrogenase subunit 2 (*ND2*)	Macey et al. (1997)	55	GCACTMATYATTRCAACWTGACA	TTGGGTGTTTAGCTGTTA
NADH dehydrogenase subunit 4 (*ND4*)	Primers developed by author	54	TCAATAAAACTATGCTACCC	AATTAGCAGTTCTTTGTGTG
Rhodopsin intron 4	In house resource at the South Australian Museum	54	GCTCAGCCATCTACAATCC	CATGATCATACAGTTACGG
Unknown intron	In house resource at the South Australian Museum	62	TGGACAACATCAAGCCCAC	GGTGAACTCCTTGCCAAAG
AKAP9	Townsend et al. (2008)	58	AGCARATWGTRCAAATGAARCARGA	TCHAGYTTYTCCATRAGTTCTGTTG
PTPN12	Townsend et al. (2008)	58	AGTTGCCTTGTWGAAGGRGATGC	CTRGCAATKGACATYGGYAATAC

et al. 2000). We used the corrected AIC score (Akaike 1979) in Mr.ModelTest v2.3 (Nylander 2004) to select the appropriate models of nucleotide substitution for each locus and data partition. We investigated the degree of substitution saturation between the outgroup taxa and the ingroup using DAMBE (Xia 2001).

Bayesian analysis was carried out in MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001), using samples with sequence for both *ND2* and *ND4*. Due to the low number of variable sites and hence limited information, we chose to make the lowest possible number of partitions; thus concatenating the two datasets and combining the first and second codon positions. The following partitions and models were used: first and second (GTR+I+G), third (GTR+G), and tRNA (HKY+I). The analysis was run four times with 10,000,000 MCMC iterations, and sampled every 1000 generation, thus generating 10,000 trees per run. The analyses were checked for convergence in Tracer v1.5 (Rambaut and Drummond 2007) and AWTY (Nylander et al. 2008). The runs were combined and the first 4000 of the 40,000 trees were discarded as burn-in. We used TreeAnnotator v1.5.4 (Rambaut and Drummond 2008) to generate a maximum clade credibility consensus tree. Fig Tree v1.2.2 (Rambaut 2008) was used to edit the consensus tree.

We quantified the divergence between different islands for the concatenated mitochondrial dataset using the Tamura and Nei distance method with 10,000 permutations in ARLEQUIN v3.1 (Excoffier et al. 2005). Due to small sample sizes, the populations from Ngela and Malaita were omitted from this analysis. The larger sample sizes and multiple collecting locations for Choiseul and Isabel allowed for an additional pairwise comparison between the eastern and western sampling areas on each of these islands.

A Mantel test for IBD using the mitochondrial data was carried out using the IBDWeb Service v3.16 (Jensen et al. 2005). We performed two separate analyses wherein the geographic distances were defined as: (1) the distance (km) separating the actual sample locations on the respective islands, and (2) the minimum span of open water between the islands, without taking the specific locations on the respective islands into consideration.

We attempted to date the splits between different *Corucia* clades using BEAST v1.5.4 (Drummond and Rambaut 2007). The partitions and models of evolution were identical to the above-described MrBayes analysis. We selected a UPGMA (Unweighted-Pair Group Method with Arithmetic means) generated starting tree with a coalescent constant size tree prior and a relaxed clock with uncorrelated log-normal site model. The priors were specified with the following calibrations: Emergence of the Western Province provides an upper limit for colonization of this part of the archipelago and was set to maximum 3 MYA with a uniform distribution. The split between the ingroup and outgroups has been estimated to be 26 MYA (±5.1) (Skinner et al. 2011). The MCMC chain was run four times for 10,000,000 generations, sampling every 1000 trees. After examining the posterior probabilities in Tracer, we discarded the first 10% of trees as burn-in. A maximum clade credibility consensus tree was generated from the remaining trees using TreeAnnotator. The consensus tree was edited in Fig Tree.

Results

There were large differences among loci in the number of variable sites (Table 2). As expected, the mitochondrial sequences were the most informative, followed by nuclear noncoding and nuclear coding loci. Different numbers of haplotypes were identified using TCS and DNAsp, this is due to how the two programs treat missing data. Analysis in DAMBE suggests the mitochondrial data have not been subject to substitution saturation.

Table 2. Sequence information and variability of genetic markers. N indicates the number of samples sequenced, alignment length in bp, the number of variable sites, number of parsimony informative (PI) sites, the number of variable sites per bp for each locus, indels listed by length in bp, number of haplotypes observed, and the haplotype diversity. For haplotypes observed, the numbers outside brackets refer to the number of haplotypes identified by DNAsp while the numbers in brackets refer to the number of haplotypes identified by TCS.

	ND2/ND4	*AKAP9*	Unknown intron	*Rhodopsin*	*PTPN12*
N	57	27	33	61	41
Length (bp)	1698	742	594	871	672
Variable sites	144	3	7	12	7
PI sites	124	2	5	8	5
Variable sites (%)	0.085	0.003	0.012	0.014	0.009
Indels	0	0	9	0	0
No. of haplotypes	33	3 (4)	8 (13)	11	6 (7)
Haplotype diversity	0.972	0.211	0.758	0.516	0.460

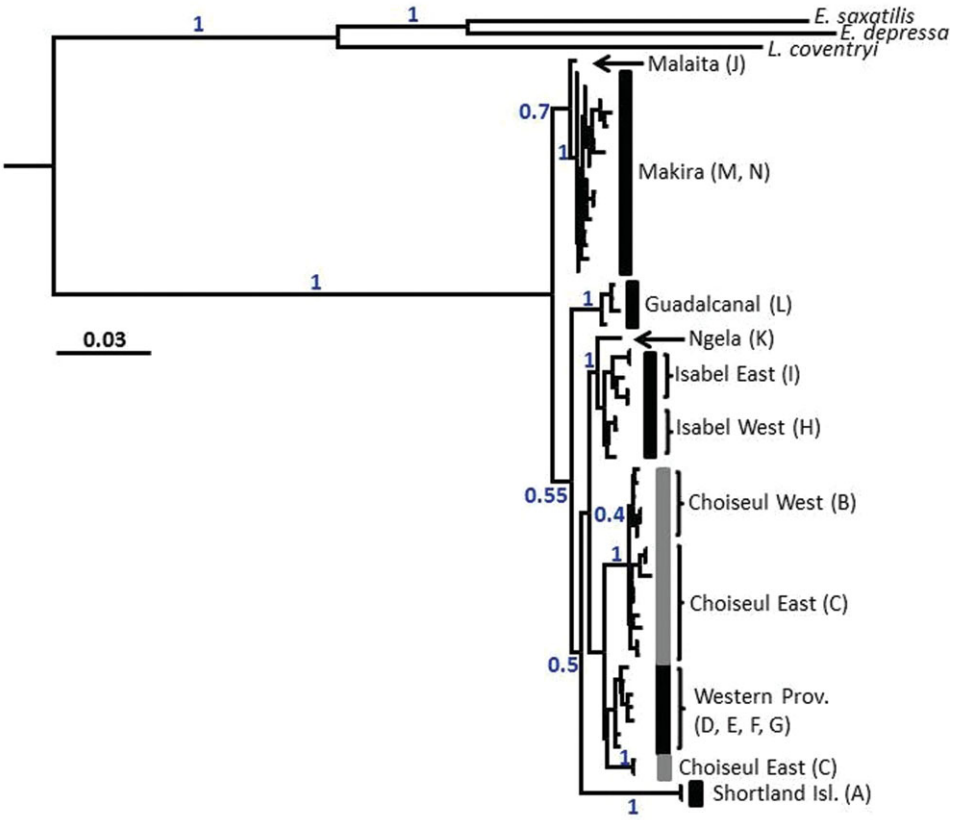

Figure 3. Maximum clade credibility consensus tree from 36,000 trees after four combined MrBayes runs of 10,000,000 MCMC iterations each. Letters in brackets refer to the sampling locations on Figure 1. Numbers represent the posterior probabilities.

Phylogenetic relationships between island populations

A maximum clade credibility tree from the 36,000 trees using the four combined runs of Bayesian inference is presented in Figure 3. There was weak support in the deeper nodes in the tree, while the support toward the tips was very strong for some clades. The deepest split within the ingroup was between populations from Makira/Malaita and those from the remainder of the sampled islands. Apart from populations from Choiseul and the Western Province, all islands were monophyletic with strong support. The Western Province samples were nested within the Choiseul clade with strong support. Additionally, there was monophyly for the eastern (location I) and western (location H) sampling locations on Isabel, with a support of 0.7 (support not shown on tree). As for the two sampling locations on Choiseul, the western (B) sampling location was monophyletic but was nested among the east Choiseul (C) haplotypes, and was therefore paraphyletic with both west Choiseul and the Western Province. The sample from Ngela was placed as a sister group to the samples from Isabel, while Makira and Malaita were sister clades. The samples from Shortland Islands were somewhat divergent from the remainder but nested close to the samples from Isabel. The trace files for the runs indicated that these analyses had converged (data not shown). However, due to the divergence between *Corucia* and the outgroup (26 MYA), the placement of the root in the ingroup is probably imprecise (Piller and Bart 2009).

Interisland genetic divergence

We calculated genetic divergence based on mitochondrial data between the different island populations in ARLEQUIN (Fig. 4). Pairwise F_{st} values between the samples from the Shortland Islands and those from the other islands in the archipelago were typically higher than values derived from comparisons among the other islands. The samples from Western Province had lower pair wise F_{st} values with samples from Choiseul and Isabel than with samples from the remainder of the islands. The pairwise F_{st} value for Makira and all other islands was the second highest after the Shortland Islands. None of the pairwise values were below the 0.05 α-level of significance. For the respective sampling locations within the islands of Choiseul and Isabel (not included in Fig. 4), the pairwise F_{st} values were 0.42 ($P \lll 0.001$)

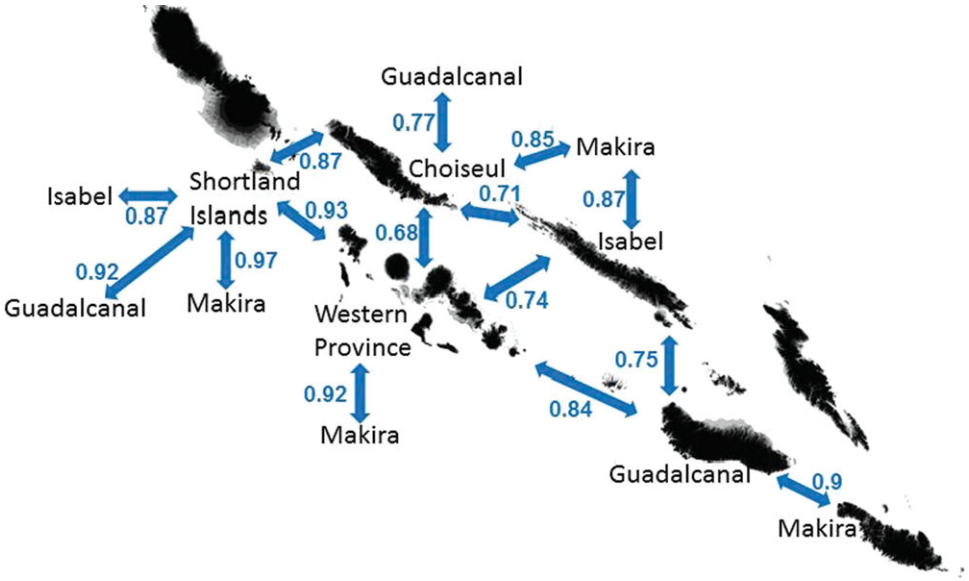

Figure 4. Map of the Solomon Archipelago with pairwise F_{st} values between islands populations of *Corucia zebrata* in the Solomon Archipelago using the combined *ND2* and *ND4* sequences. None of the pairwise values were below the 0.05 α-level of significance.

between the eastern and western sampling site of Choiseul and 0.62 ($P \lll 0.001$) between the eastern and western sampling site of Isabel.

Isolation by distance

A Mantel test did not detect a significant IBD from the combined data ($r^2 = 0.04$; $P = 0.12$) when analyzed with the geographic distance between sample locations. However, when geographic distance was set as the minimum span of open water between sampled islands, there was significant IBDM ($r^2 = 0.19$; $P = 0.045$; Fig. 5).

Haplotype networks

For the mitochondrial loci (Fig. 6), the separate islands constituted separate networks with the exception of Malaita that was included in a network with Makira, and the Western Province that was included in a network with Choiseul. The mitochondrial networks suggested that the haplotypes in the Western Province originated from Choiseul and that the samples from Malaita were genetically close to those from Makira. For the nuclear loci (Fig. 7) on the other hand, there was no concordance between haplotype and island origin as the most frequent allele in *rhodopsin* and *PTPN12* was present on all islands. There were few haplotypes present in *AKAP9*. Here, one haplotype was restricted to the Shortland Islands and another haplotype was restricted to Isabel, but there was no further sorting. The multiple linkages in the unknown intron indicate recombination, and involve alleles from all the sampled islands except the Shortland Islands.

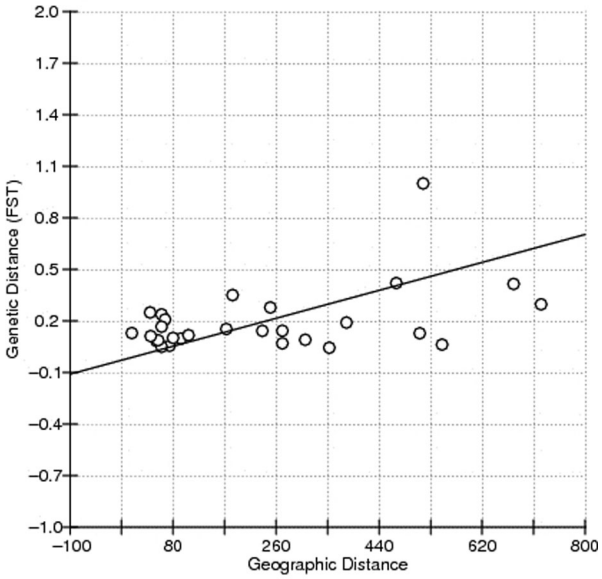

Figure 5. A Mantel test carried out on mitochondrial data with genetic distances set as the minimum span of open water between islands. Geographic distance (km) is on the *x*-axis and genetic distance (F_{st}) is on the *y*-axis.

Dating of colonization events within the Solomon Islands

Our attempt to derive a date for the colonization events of *C. zebrata* using priors with specified divergence times produced a tree topology (Fig. 8) that was different from the tree presented in Figure 3. The samples were placed in the

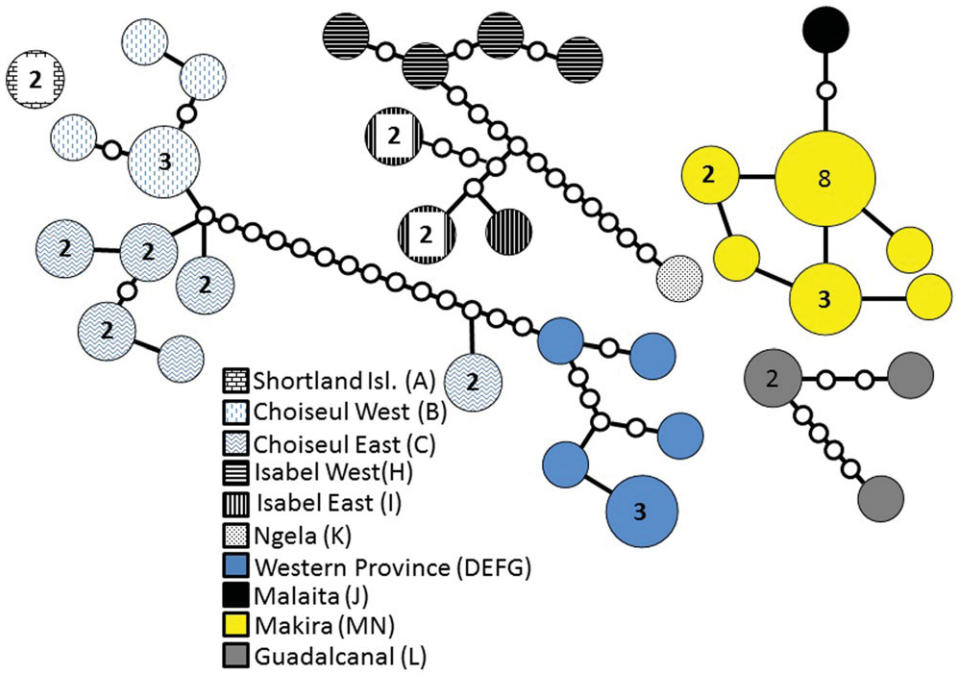

Figure 6. Haplotype networks for *ND2* and *ND4*. Numbers inside circles indicate the number of individuals with that haplotype. Circles without numbers are haplotypes represented by only one individual. Letters in brackets refer to the sample locations on Figure 1. A branch represents a single substitution and empty circles represent hypothetical haplotypes. Isabel constituted a separate network, as did Guadalcanal and the Shortland Islands. Malaita was joined in a separate network with Makira. Choiseul and the Western Province were joined in a separate network.

same clades in both trees, but the placement of the different clades in relation to each other was not concordant in the two trees. This was reflected in the support for the respective nodes, which in both trees was low in the deeper nodes and high toward the tips. The analysis suggested that *C. zebrata* colonized the Solomon Archipelago within the last 1–4 million years, and that some islands may have been colonized within the last 100,000–500,000 years, although no firm inferences about the site and timing of initial colonization and subsequent spread could be made. The large range for the 95% highest posterior densities for the outgroup and the root to the ingroup indicated the large degree of uncertainty in relation to the dating of the nodes.

Discussion

Genetic distance and monophyly in relation to Pleistocene land bridges

Analyses of F_{st} values did not support the Pleistocene land bridge hypothesis that predicted reduced genetic distance between islands connected during the LGM and higher genetic divergence between islands that remained isolated during the LGM. This hypothesis predicted that populations on Makira and Malaita should have the highest pairwise F_{st} values, both to each other and to populations on other islands, while the F_{st} value between populations on Choiseul and Isabel should be low. Our results only partly supported those predictions in that the samples from the isolated island of Makira were highly divergent. Although samples from the previously connected islands of Choiseul and Isabel showed somewhat lower genetic divergence (Figs. 3 and 4), they were at the same time highly divergent from each other, with a high F_{st} value and contained different strongly supported clades (see Figs. 3, 4, and 6). Most islands, including those that were previously connected during the LGM, were monophyletic, which indicated that episodes of gene flow between the islands have been rare and that the genetic lineages on separate islands are probably the result of single colonization events (or single sources of colonization) on the respective islands. Bougainville, Choiseul, Isabel, and Ngela were joined by land bridges during the LGM (see Fig. 1). The Shortland Islands are situated within less than 8 km of Bougainville and were likely to have been included in the Great Bukida landmass. Indeed, the lowest pairwise F_{st} values for samples from the Shortland Islands were between the islands of Choiseul and Isabel, thus suggesting that the animals on the Shortland Islands are genetically closer to Choiseul and Isabel than to animals from the rest of the archipelago. This is congruent with expectations based on geological data. According to McCoy (2006), *Corucia* on the Shortland Islands belong to *C. z. alfredschmidti*; however, our results were somewhat ambiguous in this respect: the samples from the Shortland

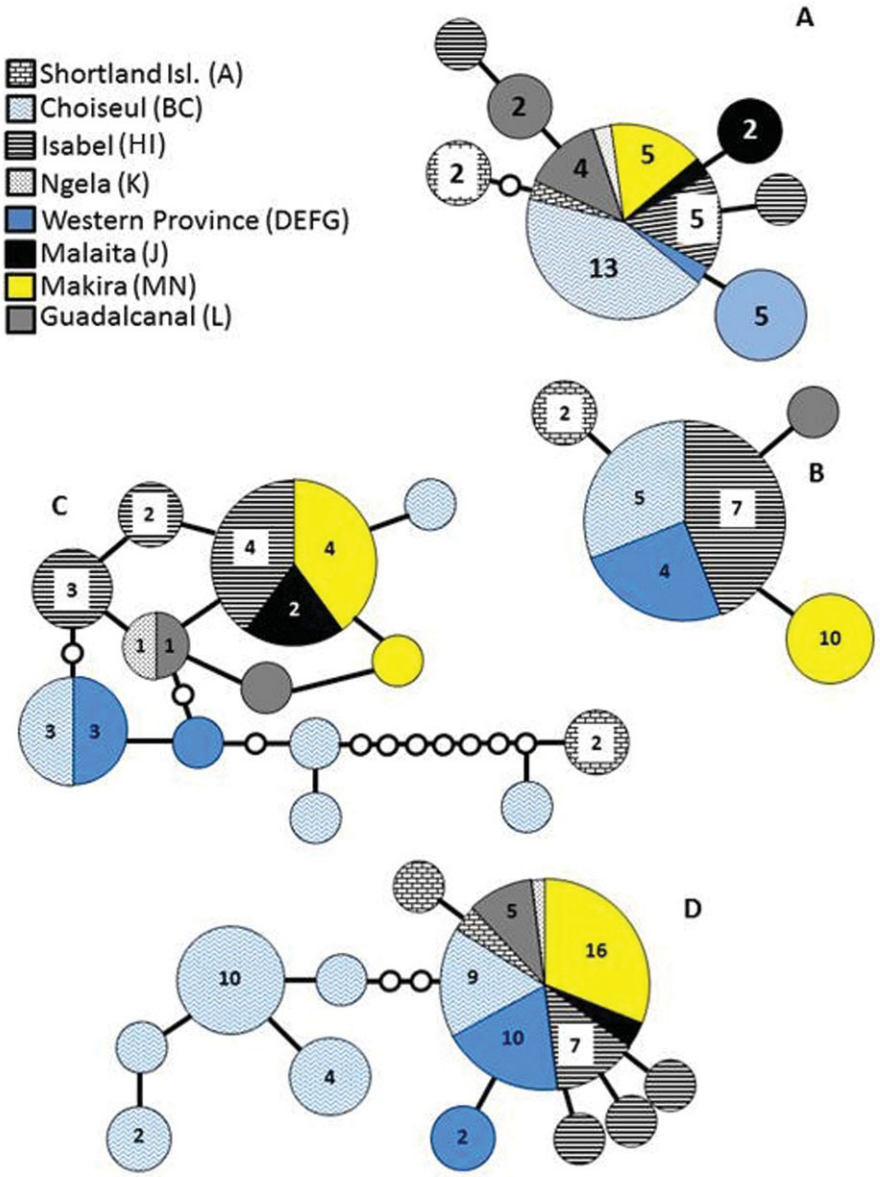

Figure 7. Haplotype networks for (A) *PTPN12*, (B) *AKAP9*, (C) the unknown intron and (D) *rhodopsin*. Numbers inside circles indicate the number of individuals with that haplotype. Circles without numbers are haplotypes represented by only one individual. Letters in brackets refer to the sample locations on Figure 1. A branch represents a single substitution and empty circles represent hypothetical haplotypes. For *PTPN12*, the Shortland Islands, Ngela, and the Western Province are represented by one individual each in the pie chart. For *rhodopsin*, Ngela is represented by one individual and the Shortland Islands and Malaita are represented by two.

Islands were divergent, but still nested within the remainder of the samples (Fig. 3) and with only slightly higher F_{st} values than those for Makira (Fig. 4). Hybridization between *C. z. alfredschmidti* and *C. c. zebrata* on the Shortland Islands is a possibility. Ultimately, inclusion of samples from Bougainville is required to provide a robust molecular genetic test of the systematic status of *C. z. alfredschmidti* and *C. z. zebrata*.

Nuclear markers and incomplete lineage sorting

Nuclear haplotypes shared between different islands (Fig. 7) indicated incomplete lineage sorting, which may produce gene trees that are either not congruent with species trees (Moran and Kornfield 1993), or incongruent with the true phylogeographic pattern of *C. zebrata*, in the case of the

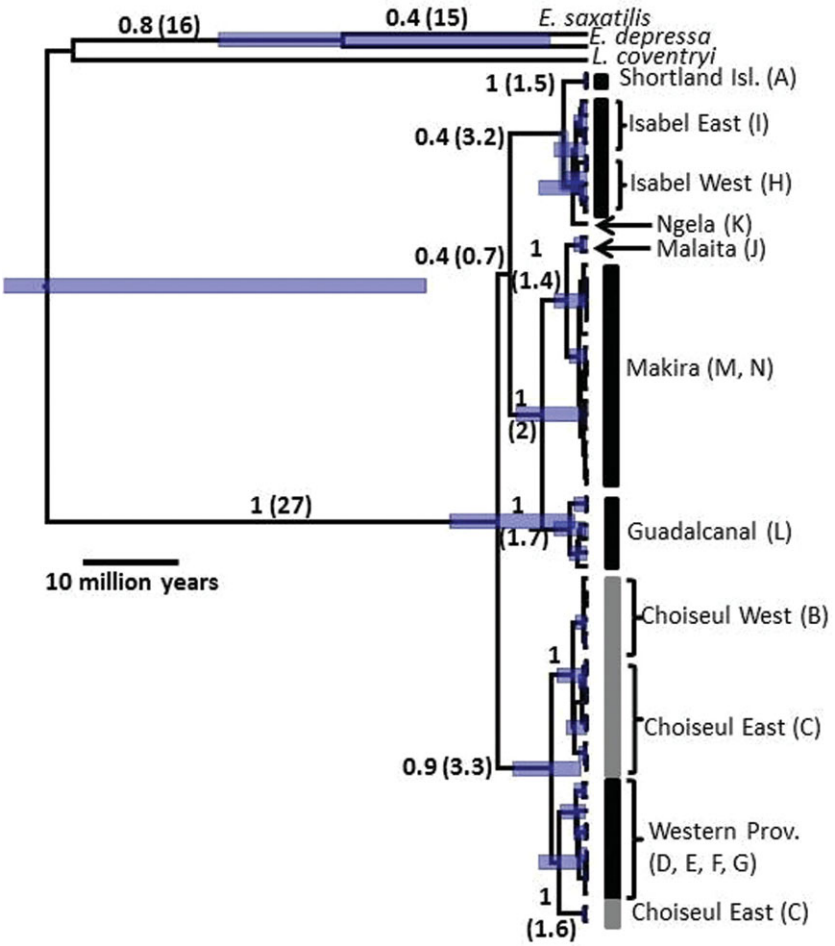

Figure 8. Maximum clade credibility consensus trees from BEAST. Numbers outside of brackets represent the posterior probabilities and numbers inside brackets are MYA since divergence. Horizontal blue bars are the 95% highest posterior densities for the most important nodes.

current study. The more structured data from mitochondrial loci are likely a result of the smaller effective population size and thus shorter coalescence time for the mitochondrial genome. Monophyly is expected to require considerably more time to develop for nuclear loci due to the larger effective population size for the nuclear genome (Nei 1987), sometimes up to several million years (Hudson and Turelli 2003). The smaller effective population size for the mitochondrial genome will lead to stronger effects of demographic stochasticity. These effects can be enhanced during founding events by small population sizes and by multiple impregnations of founding females. The latter will be an important factor among agestructured species with overlapping generations such as *C. zebrata*. In light of the relatively recent divergence of *C. zebrata* (Fig. 8), incomplete lineage sorting on nuclear loci was not surprising, and suggested that gene flow between islands has happened too recently to allow for complete sorting of nuclear loci, yet rarely enough to allow for reciprocal sorting of mitochondrial haplotypes (with the exception of Choiseul and the Western Province). Theoretically, this pattern could also be explained by male-biased dispersal, however given that inter-island gene flow in *C. zebrata* is likely to be the result of stochastic events (see below), this explanation is improbable. Nuclear loci were included in the analysis as evolutionary relationships inferred from one gene tree may be insufficient for estimations of the true species tree (Moore 1995). However, in this case the divergences between the different populations were too shallow for nuclear loci to yield useful phylogenetic information.

Intraspecific variation in *C. zebrata* versus general patterns in pacific taxa

Based on the data presented in this paper, we rejected the hypothesis that Pleistocene land bridges can explain much of the intraspecific variation found in *C. zebrata*. This differed from the pattern reported for the Solomon Archipelago *Melonycteris* fruit bats by Pulvers and Colgan (2007), where the current biogeographic regions were best explained by geographic conditions during the LGM, and where no genetic

differences were detected between populations inhabiting islands previously connected by land bridges. A similar pattern has been found for a number of bird species (Smith and Filardi 2007; Uy et al. 2009), again suggesting that Pleistocene land bridges have affected the current patterns of genetic diversity in avian taxa on the Solomon Archipelago. It is plausible that the different pattern for *C. zebrata* is a consequence of the much greater dispersal ability of avian taxa. It is not known if the Pleistocene habitat between the islands of Bougainville, Choiseul, Isabel, and Ngela was suitable for *C. zebrata* or whether the land bridge habitats supported a vegetation matrix that would encourage dispersal to more appropriate habitat during the last LGM. Habitat unsuitable for *C. zebrata* may have allowed easier dispersal for volant animals than for large lizards. The fact that the extreme ends of Choiseul and Isabel represent distinct populations of *C. zebrata* (Figs. 3 and 6) suggests that the species infrequently disperses over distances such as the length of Choiseul or Isabel. Siler et al. (2010), found that genetic diversity within geckos on the Philippine Archipelago were often greater within islands than between islands, a result that is comparable to the large genetic divergence found for *C. zebrata* within the islands of Choiseul and Isabel. Moreover, according to Esselstyn and Brown (2009), the distribution of genetic lineages of shrews on the Philippine Archipelago can also be explained by current islands and to a certain degree by IBD. Again, this is concordant with results on *C. zebrata*, where genetic lineages are largely structured into clades that represent the modern islands (Figs. 3 and 6) and where the size of the dispersal barrier (IBD) appeared to explain approximately 20% of the intraspecific variation (Fig. 5). It is possible that the pattern described in Heaney (2005) where the current allozyme distribution in rodents is largely explained by Pleistocene shore lines is an oversimplification, and that ecological factors such as habitat preference and IBD (Roberts 2006) are equally important.

Conservation managers should be aware that biogeographic regions cannot be directly extrapolated between taxa with differing dispersal abilities.

Colonization history and dating of colonization events within the Solomon Islands

The Western Province has been isolated since it was formed but is situated in geographical proximity to Choiseul, and separated from it by approximately 60 km of open water. The low F_{st} value between the Western Province and Choiseul was in concordance both with the tree topologies in Figure 4, where the Western Province was nested within Choiseul and with the haplotype network in Figure 6. This suggested that the Western Province was colonized by animals from the geologically much older Choiseul. Given the young age of the Western Province, a direction of colonization events from the nearby Choiseul to the Western Province is concordant with expectations based on geological data. With the exception of this Western Province example, it was difficult to infer a dispersal pattern among any other of the islands from our phylogenetic reconstruction (Figs. 4 and 8). Pulvers and Colgan (2007) argued that fruit bats (*Melonycteris*) most likely colonized the Solomon Archipelago from east to west, starting at Makira, as bats on Makira appear most basal in the *Melonycteris* phylogeny. Pulvers and Colgan (2007) did not acquire samples from Bougainville. When a mitochondrial phylogeny of *C. zebrata* is reconstructed without samples from the Shortland Islands (data not shown), the tree topology resembles that of *Melonycteris* in Pulvers and Colgan (2007). A more complete sampling regime may thus alter the topology of the tree and it is plausible that a similar effect may occur if Bougainville samples were included in the *Melonycteris* phylogeny. A rapid and recent radiation across the archipelago with subsequent isolation could explain the results of the current study. This hypothesis is supported by results from dating using BEAST, which suggested that *C. zebrata* colonized the archipelago during the last 1–4 million years (Fig. 8). This is surprising given that *C. zebrata* diverged from the other genera of the *Egernia* group approximately 26 MYA, and one would therefore expect a deeper divergence for some clades. It is possible that Bougainville is the site of initial colonization and that the species was restricted to this island for several million years prior to dispersal to other islands. Another scincid taxon *Tribolonotus* radiated primarily from Bougainville and it is plausible that Bougainville (which is close to the larger land mass of New Guinea) is the source of a number taxa that have spread to the eastern islands of the Solomon Archipelago (Austin et al. 2010). Bougainville must be included among the *C. zebrata* sample locations in order to test this hypothesis. *Corucia zebrata* has probably colonized across the Solomon Archipelago by over-water dispersal on flotsam, which is a kind of colonization mechanism that has been observed for *Iguana iguana* in the Caribbean archipelago (Censky et al. 1998) and that is assumed to the mechanism behind the Caribbean *Anolis* radiation (Schoener and Schoener 1984; Glor et al. 2005), as well as radiation of reptiles of the Mexican Revillagige Islands (Brattstrom 1990). *Corucia zebrata* is a canopy dwelling species, and one tree may be inhabited by several lizards (Hagen and Bull 2011). Rafts comprising large trees may therefore contain a number of *C. zebrata,* thus facilitating successful establishment upon arrival. The herbivorous diet of the species would prolong survival of individuals on rafts that contained tree foliage. Phylogenetic comparisons with other species, such as the native frog *Litoria lutea*, with a lower tolerance for exposure to sea water, fewer on-raft feeding opportunities

and thus lower dispersal ability than *C. zebrata,* would give a more complete understanding of the historical biogeography of the Solomon Archipelago.

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Appendix 1

Table A1. ABTC numbers, date of collection, Island, sample location, latitude, and longitude for *Corucia zebrata* sampled across the Solomon Archipelago. Sample locations refer to letters in Figure 1. The following samples were used as outgroup samples (ABCT and Genbank accession numbers for ND2 and ND4 in brackets): *Egernia depressa* (ABTC 101643 – JQ305710 and JF813064), *E. saxatilis* (ABTC 6964 – JQ305711 and JQ305712), and *Lissolepis coventryi* (ABTC 58241 – JQ305713 and JQ305714). Some samples were not collected by the author. Collection dates and some GPS locations for these were not available (N/A).

ABTC #	Date collected	Island / Prov.	Location	Latitude	Longitude	Genbank accession number ND2	Genbank accession number ND4	Genbank accession number AKAP9	Genbank accession number PTPN12	Genbank accession number Rhodopsin	Genbank accession number Unknown intron
112751	4/17/2008	Shortland Isl.	A	−7.1105	155.8481	JQ904677	JQ898430	JQ361807	JQ954419	JQ963955	JQ954454
112752	4/18/2008	Shortland Isl.	A	−7.1105	155.8481	JQ904676	JQ898429	JQ361806	JQ954418	JQ963954	JQ954453
50312	N/A	Choiseul	B	N/A	N/A	JQ904658	JQ898411	JQ361799	JQ954409	JQ963935	JQ954445
50368	N/A	Choiseul	B	N/A	N/A	JQ904657	JQ898410	N/A	JQ954408	JQ963934	JQ954444
50412	N/A	Choiseul	B	N/A	N/A	JQ904655	JQ898408	JQ361797	JQ954428	JQ963932	N/A
50417	N/A	Choiseul	B	N/A	N/A	JQ904654	JQ898407	JQ361796	N/A	JQ963931	N/A
50418	N/A	Choiseul	B	N/A	N/A	JQ904653	JQ898406	JQ361795	JQ954429	JQ963926	N/A
50408	N/A	Choiseul	B	N/A	N/A	JQ904656	JQ898409	JQ361798	JQ954407	JQ963933	JQ954443
112753	4/25/2008	Choiseul	C	−7.0644	157.083	JQ904675	JQ898428	N/A	JQ954417	JQ963953	JQ954452
112754	4/26/2008	Choiseul	C	−7.0588	157.09036	JQ904674	JQ898427	N/A	JQ954416	JQ963952	JQ954451
112755	4/26/2008	Choiseul	C	−7.0567	157.09364	JQ904673	JQ898426	N/A	JQ954415	JQ963951	JQ954450
112756	4/26/2008	Choiseul	C	−7.0531	157.10176	JQ904672	JQ898425	N/A	JQ954414	JQ963950	N/A
112757	4/26/2008	Choiseul	C	−7.0567	157.09364	JQ904671	JQ898424	N/A	N/A	JQ963949	N/A
112758	4/26/2008	Choiseul	C	−7.0567	157.09364	JQ904670	JQ898423	N/A	N/A	JQ963948	N/A
112759	4/26/2008	Choiseul	C	−7.0588	157.09036	JQ904669	JQ898422	N/A	JQ954433	JQ963947	N/A
112760	4/27/2008	Choiseul	C	−7.0644	157.083	JQ904668	JQ898421	N/A	JQ954432	JQ963946	N/A
112761	4/27/2008	Choiseul	C	−7.0543	157.1097	JQ904666	JQ898419	N/A	JQ954430	JQ963943	N/A
112762	4/27/2008	Choiseul	C	−7.0542	157.10758	JQ904665	JQ898418	N/A	JQ954431	JQ963942	N/A
112763	4/27/2008	Choiseul	C	−7.0543	157.10971	JQ904664	JQ898417	JQ361804	JQ954427	JQ963941	N/A
92642	N/A	Western Prov.	F	−8.31	157.52	JQ904648	JQ898402	JQ361794	JQ954405	JQ963925	JQ954440
92643	N/A	Western Prov.	G	−8.19	157.49	JQ904647	JQ898401	JQ361793	N/A	JQ963924	N/A
98185	7/10/2007	Western Prov.	E	−8.6224	157.33044	JQ904688	N/A	N/A	N/A	JQ963975	N/A
98186	7/10/2007	Western Prov.	E	−8.6224	157.33044	JQ904678	N/A	N/A	N/A	JQ963956	JQ954459
98187	7/10/2007	Western Prov.	E	−8.6224	157.33044	JQ904667	JQ898431	N/A	JQ954420	JQ963945	JQ954455
98188	7/12/2007	Western Prov.	E	−8.6084	157.32992	JQ904659	JQ898420	JQ361805	JQ954413	JQ963944	N/A
98189	7/12/2007	Western Prov.	E	−8.6152	157.33188	JQ904652	JQ898412	JQ361800	JQ954410	JQ963936	N/A
98190	7/14/2007	Western Prov.	E	−8.6178	157.33061	JQ904651	JQ898405	N/A	N/A	JQ963930	N/A
98191	7/30/2007	Western Prov.	D	−8.3129	157.27008	JQ904650	JQ898404	N/A	N/A	JQ963929	JQ954442
92645	N/A	Isabel	I	N/A	N/A	JQ904646	JQ898400	JQ361792	N/A	JQ963923	JQ954439
92646	N/A	Isabel	I	N/A	N/A	JQ904645	JQ898399	N/A	N/A	JQ963922	JQ954438
92647	N/A	Isabel	I	N/A	N/A	JQ904644	JQ898398	JQ361791	JQ954404	JQ963921	N/A
92648	N/A	Isabel	I	−8.17	159.33	JQ904643	JQ898397	JQ361790	JQ954403	JQ963920	N/A

Table A1. Continued.

ABTC #	Date collected	Island / Prov.	Location	Latitude	Longitude	Genbank accession number ND2	Genbank accession number ND4	Genbank accession number AKAP9	Genbank accession number PTPN12	Genbank accession number Rhodopsin	Genbank accession number Unknown intron
92649	N/A	Isabel	I	−8.17	159.33	JQ904642	JQ898396	JQ361789	JQ954402	JQ963919	JQ954437
112764	4/4/2008	Isabel	H	−7.5908	158.6666	JQ904663	JQ898416	N/A	N/A	JQ963940	JQ954449
112765	4/5/2008	Isabel	H	−7.5908	158.6666	JQ904662	JQ898415	JQ361803	N/A	JQ963939	JQ954448
112766	4/5/2008	Isabel	H	−7.5908	158.6666	JQ904661	JQ898414	JQ361802	JQ954412	JQ963938	JQ954447
112767	4/5/2008	Isabel	H	−7.5908	158.6666	JQ904660	JQ898413	JQ361801	JQ954411	JQ963937	JQ954446
101358	11/27/2007	Ngela	K	−9.066	160.29907	JQ904679	JQ898432	N/A	JQ954421	JQ963957	JQ954456
92650	N/A	Malaita	J	−9.07	160.57	N/A	JQ898395	N/A	N/A	JQ963918	JQ954436
92651	N/A	Malaita	J	−9.07	160.57	JQ904641	JQ898394	N/A	JQ954401	JQ963917	JQ954435
98192	8/7/2007	Guadalcanal	L	−9.4918	159.98455	JQ904649	N/A	N/A	JQ954406	JQ963928	N/A
98193	8/9/2007	Guadalcanal	L	−9.4881	159.98464	JQ904638	JQ898403	N/A	JQ954398	JQ963927	JQ954441
98194	8/9/2007	Guadalcanal	L	−9.4881	159.98464	JQ904698	JQ898450	N/A	JQ954426	JQ963974	N/A
98195	8/9/2007	Guadalcanal	L	−9.4881	159.98464	JQ904697	JQ898449	N/A	N/A	JQ963973	JQ954462
101356	11/14/2007	Guadalcanal	L	−9.4863	159.98668	JQ904680	JQ898434	JQ361808	JQ954422	JQ963958	N/A
101357	11/15/2007	Guadalcanal	L	−9.4898	159.98959	N/A	JQ898433	N/A	N/A	N/A	N/A
101341	11/17/2007	Ugi (Makira Prov.)	M	−10.245	161.75409	JQ904696	JQ898448	N/A	N/A	JQ963972	JQ954461
101342	11/18/2007	Ugi (Makira Prov.)	M	−10.243	161.7531	JQ904695	JQ898447	N/A	N/A	JQ963971	JQ954460
101343	11/18/2007	Ugi (Makira Prov.)	M	−10.243	161.7526	JQ904694	JQ898446	N/A	N/A	JQ963970	N/A
101344	11/18/2007	Ugi (Makira Prov.)	M	−10.222	161.73497	JQ904693	JQ898445	N/A	N/A	JQ963969	N/A
101345	11/18/2007	Ugi (Makira Prov.)	M	−10.222	161.73497	JQ904692	N/A	N/A	N/A	N/A	N/A
101346	11/19/2007	Ugi (Makira Prov.)	M	−10.233	161.74234	JQ904691	JQ898444	N/A	N/A	JQ963968	N/A
101347	11/19/2007	Ugi (Makira Prov.)	M	−10.233	161.74234	JQ904690	JQ898443	JQ361814	N/A	JQ963967	N/A
101348	11/19/2007	Ugi (Makira Prov.)	M	−10.233	161.74234	JQ904689	JQ898442	JQ361813	N/A	JQ963966	N/A
101349	11/19/2007	Ugi (Makira Prov.)	M	−10.25	161.75721	JQ904687	JQ898441	JQ361812	JQ954425	JQ963965	N/A
101350	11/19/2007	Ugi (Makira Prov.)	M	−10.25	161.75721	JQ904686	JQ898440	JQ361811	JQ954424	JQ963964	N/A
101351	11/24/2007	Makira	N	−10.458	161.94318	JQ904685	JQ898439	N/A	JQ954423	JQ963963	N/A
101352	11/24/2007	Makira	N	−10.457	161.94197	JQ904684	JQ898438	JQ361810	N/A	JQ963962	JQ954458
101353	11/27/2007	Makira	N	−10.457	161.94197	JQ904683	JQ898437	JQ361809	N/A	JQ963961	JQ954457
101354	11/27/2007	Makira	N	−10.457	161.94197	JQ904682	JQ898436	N/A	N/A	JQ963960	N/A
101355	11/27/2007	Makira	N	−10.457	161.94197	JQ904681	JQ898435	N/A	N/A	JQ963959	N/A
92652	N/A	Makira	N	−10.31	161.55	JQ904640	JQ898393	JQ361788	JQ954400	JQ963916	N/A
92653	N/A	Makira	N	−10.31	161.55	JQ904639	JQ898392	N/A	JQ954399	JQ963915	JQ954434