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# Biogeographic anomaly or human introduction: a cryptogenic population of tree skink (Reptilia: Squamata) from the Cook Islands, Oceania

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Archaeological and molecular data have revealed that the present day faunas of many island groups in Melanesia, Polynesia, and Micronesia are not representative of the biodiversity generated within this region on an evolutionary timescale. Erroneous inferences regarding the mechanisms of speciation and the significance of long distance dispersal in shaping the present diversity of these island systems have resulted from this incomplete diversity and distributional data. The lizard fauna east of Samoa has been suggested to derive entirely from human-mediated introductions, a distribution congruent with biogeographic patterns for other Pacific species. Distinguishing between introduced populations and those that result from natural colonization events is difficult, although molecular data provide a useful means for elucidating population history and identifying the likely sources of introductions. We use molecular data (1726 bp of mitochondrial DNA and 286 bp of nuclear DNA) to evaluate a population of arboreal lizards from the Cook Islands and to determine whether this arboreal skink population is the sole endemic component of the lizard fauna east of Samoa or the result of human-mediated introduction. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, 100, 318–328.

**ADDITIONAL KEYWORDS:** colonization – *Emoia samoensis* species group – Fiji – human-mediated introduction – phylogeography – Samoa – Scincidae – Solomon Islands – Tonga – Vanuatu Archipelago – waif dispersal.

## INTRODUCTION

Research over the last several decades has highlighted the fact that the present day faunas of many insular systems, particularly those of Melanesia, Polynesia, and Micronesia, do not represent the complete biodiversity generated via evolutionary processes in these biodiversity hotspots (Myers *et al.*, 2000; Mittermeier *et al.*, 2005). Within the last 3500 years, humans have colonized the islands of the Pacific Ocean and brought plants and animals with

them, both intentionally (Lum *et al.*, 2006; Anderson, 2009) and as stowaways (Matisoo-Smith *et al.*, 1998; Austin, 1999; Matisoo-Smith & Robins, 2004; Reiff *et al.*, 2006; Wilson & Lum, 2006). Massive extinctions and population extirpation resulted from predation by humans and non-native mammals such as rats, dogs, and pigs (Steadman & Kirch, 1990; Steadman, 1995; Steadman, Pregill & Burley, 2002), as well as from agricultural land conversion and the introduction of agricultural diseases and pests (Prebble & Wilmshurst, 2009). These anthropogenic impacts affected all Pacific bird families and extinction rates may be as high as 50% of the pre-human bird fauna (Steadman, 1993, 2006; Steadman, White & Allen, 1999; Steadman, Plourde & Burley, 2002). Pacific

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island avian extinctions have received much attention (Mead *et al.*, 2002; Huynen *et al.*, 2003; Gemmell, Schwartz & Robertson, 2004; Baker *et al.*, 2005; Boyer, 2008) in part because these extinctions, if unrecognized, mask the true diversity of these biodiversity hotspots. Although the reptilian fauna has received less research attention, similar patterns of extinction have occurred (Pregill & Dye, 1989; Pregill, 1998; Pregill & Steadman, 2000; Mead *et al.*, 2002; Molnar, Worthy & Willis, 2002; Pregill & Worthy, 2003), although perhaps on a smaller scale.

Incomplete distributional and diversity data lead to erroneous inferences regarding the mechanisms of speciation and dispersal in these island systems (Keppel, Lowe & Possingham, 2009). Deciphering biogeographic patterns in the Pacific is further confounded by intra-Pacific translocations of native Pacific fauna and flora by early human colonists (Cowie, 2001; Pregill & Steadman, 2004; Zerega, Ragone & Motley, 2004; Hinkle, 2007; Lee *et al.*, 2007; Keogh *et al.*, 2008). Distinguishing between populations whose distributions result from relatively recent human movements and those that have sporadically dispersed by waif over-water dispersal or other natural means over longer timescales is difficult, but necessary, especially in light of the history of Pacific translocations and ongoing present day introductions (Cowie, 2001; Anderson, 2009).

Several criteria have been suggested for identification of introduced populations: (1) documentation of an introduction or recent arrival; (2) close association with humans or their habitats; (3) a locally limited distribution despite a broader, more widespread distribution elsewhere; or (4) absence of subfossil remains from early archaeological sites (pre-human colonization) followed by increasing frequency in later, post-human colonization sites (Zug, 1991; Weisler, Bollt & Findlater, 2006). Unfortunately, Pacific island fossil and subfossil squamate data are limited (Pregill, 1993) because squamate remains are difficult to locate and identify to the species level (Pregill & Worthy, 2003). Additionally, the reptilian fauna of most Pacific island groups (except New Caledonia) has received little research attention, resulting in a poor historical record of taxonomic diversity and species occurrence data for comparison with modern collections and distributional data (Pregill, 1993; Hamilton, Hartman & Austin, 2009). In the absence of these data, evaluating the origin of a population is difficult (Crombie & Steadman, 1986).

Molecular data can be useful with respect to elucidating population history and identifying the likely source of introductions (Austin, 1999; Austin & Zug, 1999; Vences *et al.*, 2004; Jesus, Brehm & Harris, 2005; Rocha, Carretero & Harris, 2005; Munoz-Fuentes *et al.*, 2006; Kolbe *et al.*, 2007). Populations

of the moth skink, *Lipinia noctua*, sampled from Vanuatu, Fiji, and Polynesia, are extremely genetically similar (0.008% mean divergence across the region for cyt *b*), suggesting human-mediated dispersal, whereas populations from Palau, New Guinea, the Solomon Islands, and Micronesia are genetically differentiated from other archipelagos (9.7% mean divergence for cyt *b*) and show greater haplotype diversity, indicating natural, pre-human dispersal (Austin, 1999). *Gehyra oceanica*, a gecko with a broad Pacific distribution, is genetically variable throughout the Pacific basin, whereas populations of a sympatric congener, *G. mutilata*, are genetically uniform throughout the Pacific (Fisher, 1997). These data suggest a human-mediated colonization history for *Gehyra mutilata*, in contrast to natural dispersal for *G. oceanica* (Fisher, 1997; Rocha, Ineich & Harris, 2009). The interpretation of data for three other gecko species with broad Pacific distributions (*Hemidactylus garnotii*, *Hemidactylus frenatus*, and *Lepidodactylus lugubris*) is less clear (Moritz *et al.*, 1993) and highlights the difficulty in assessing population history. Low allelic diversity and low genetic divergence among and within islands suggest a recent, rapid human-mediated introduction of *L. lugubris* and *H. garnotii* in the Pacific basin, although a source population for these introductions could not be identified (Moritz *et al.*, 1993). By contrast, natural, pre-human dispersal was suggested by high allelic diversity and high genetic divergence within and among populations recovered for *H. frenatus*; documentation of the recent introduction of this species to the region is incongruent with this pattern, however, and suggests the geographic structure recovered was an artefact of sampling (Moritz *et al.*, 1993) or perhaps the result of multiple introductions from more than a single source population.

#### PACIFIC ISLAND LIZARD FAUNA

In the islands of Oceania, scincid lizards of the genus *Emoia* are a major component of the terrestrial vertebrate fauna, with multiple species occurring on most islands in the region. *Emoia* is species rich: the most recent review of the genus included 72 species (Brown, 1991). The diversity of this genus is undoubtedly greater because morphological and molecular evolution are uncoupled in Pacific skinks (Austin, 1995; Bruna, Fisher & Case, 1995, 1996) and new species of *Emoia* continue to be identified through ongoing surveys (Zug & Ineich, 1995) and molecular analyses (Bruna *et al.*, 1995, 1996; Zug & Gill, 1997). Unraveling the population history of Pacific Island lizards is further hindered by their morphological conservatism (Austin, 1995; Bruna *et al.*, 1996), which creates difficulties in resolving species boundaries, especially for Pacific *Emoia* (Zug & Gill, 1997; Austin & Zug, 1999).

One evolutionary lineage within *Emoia*, the *Emoia samoensis* species group, contains 19 large-bodied, primarily arboreal species distributed throughout the islands of south-central Oceania (Brown, 1991). Species richness within this clade is greatest in the Vanuatu and Fijian archipelagos (Brown, 1991; Hamilton, 2008; Hamilton *et al.*, 2009). Members of this group occur in the Solomon Islands, Vanuatu, the Loyalty Islands, Fiji, Samoa, and Tonga (Brown, 1991). Additionally, a population identified as '*E. trossula*' has been collected from the island of Rarotonga in the Cooks Islands. On the basis of a morphological comparison of museum specimens, Brown (1991) described the distribution of *E. trossula* as Fiji, Tonga, Rotuma, and Rarotonga. The distribution suggested by Brown (1991) is anomalous, however, because the lizard fauna east of Samoa (e.g., the Cook Islands) is thought to result entirely from human-mediated dispersal (Crombie & Steadman, 1986; Case & Bolger, 1991), a pattern congruent with an important Pacific basin biogeographic barrier generated by the Tonga Trench (Stoddart, 1992; Hamilton, Klein, Austin, 2010). As suggested by broader biogeographic patterns, the *samoensis* group population on Rarotonga may have been introduced to Rarotonga from elsewhere in the Pacific, either during the initial human colonization of the Pacific or during subsequent trading voyages among islands (Case & Bolger, 1991; McCormack, 2002). Alternatively, this population may be the sole member of the Cook Islands lizard fauna to have dispersed via natural means and speciated *in situ* (Crombie & Steadman, 1986; Zug, 1991).

#### ARCHAEOLOGICAL EVIDENCE AND LINGUISTIC RELATIONSHIPS

The initial colonization of the Pacific by Austronesian speaking Lapita peoples (Fig. 1) occurred via the Solomon Islands, through Vanuatu and New Caledonia, and eastward to Fiji, Tonga, and Samoa (Kirch & Green, 1987; Kirch, 1988, 2000; Burley & Dickinson, 2001). This colonization history is concordant with the relationship among regional languages (Fig. 1; Gray, Drummond & Greenhill, 2009). Because the Cook Islands were not colonized during the initial wave of human invasion into the Pacific (Kirch *et al.*, 1995), if Lapita peoples transported this lizard during the first stage of human colonization, we would expect to recover evidence of this species on one or more of the islands (potential source populations) involved in this initial migration into Oceania. Expansion into the eastern Pacific, including the Cook Islands, occurred from Tonga between 500 BC and 300 AD (Burley, 1998; Burley & Dickinson, 2001). If humans transferred *samoensis* group lizards among Pacific islands during the initial colonization of the region,

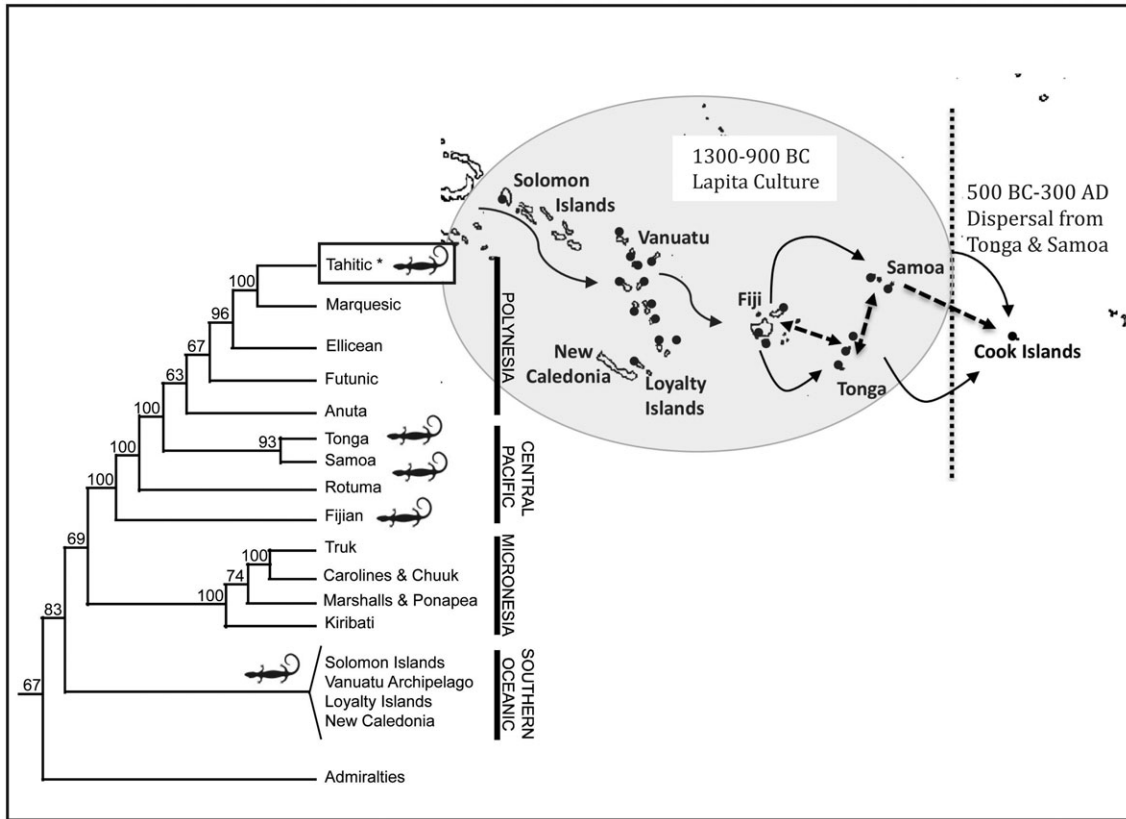
subsequent colonization of the eastern Pacific, or along trade routes, we would recover the genetic signature of these movements in the recovered phylogeny and population demographic structure (Brawley *et al.*, 2009).

To differentiate between two alternative hypotheses regarding the dispersal and colonization of the Cook Islands by *samoensis* group lizards, in the present study, we examine genetic data from this population and from other *samoensis* group populations collected from throughout the region to evaluate predictions congruent with the introduction of this population by pre-historic Polynesians or Lapita peoples. Introduced populations frequently show a loss of genetic diversity relative to native source populations caused by demographic events such as founder effects and population bottlenecks (Darling *et al.*, 2008; Dlugosch & Parker, 2008; Olivieri, 2009), and the geographic distribution of haplotypes can be used to infer population origin (Darling *et al.*, 2008). Human-aided transport (and a relatively recent colonization event) would be supported by any of the following data: (1) a lack of genetic divergence between the Cook Islands population and one or more populations of *samoensis* group lizards from elsewhere in the region; (2) low allelic diversity in the Cook Islands population; or (3) a close relationship between the Cook Islands population and Tongan or Samoan *samoensis* group populations as predicted by archaeological and linguistic data. Should the Cook Islands population be genetically identical to another *samoensis* group population, it would suggest a likely source for the invasion. Conversely, the natural (waif) dispersal hypothesis would be supported by recovery of any of these patterns: (1) genetic divergence between the Cook Islands population and *samoensis* group populations elsewhere in the region; (2) moderate to high levels of allelic diversity in the Cook Islands population; or (3) an isolation-by-distance model of gene flow among *samoensis* group populations in which more geographically distant populations are also more genetically divergent.

## MATERIAL AND METHODS

### SEQUENCE DATA COLLECTION

Samples from 65 specimens representing 11 species of *Emoia* were included in this study (see Supporting information, Table S1). We used a well-resolved multi-locus phylogeny of this lineage of *Emoia* (Hamilton, 2008) to identify appropriate taxa for this analysis; all members of a strongly supported clade containing the Cook Islands population were included. Although *E. samoensis* group species occur in the Solomon Islands (*Emoia flavigularis*, *Emoia*



**Figure 1.** Map of the Pacific basin showing the regions of Melanesia and eastern Polynesia with the extent of the Lapita culture, the earliest settlers in this region, indicated in grey. Direction of human colonization of the Pacific is indicated by solid black arrows: the Lapita people settled the remote Melanesian Islands of Samoa and Tonga no later than 900 BC (Burley, 1998; Kirch, 2000). A second migration of Lapita people into the more remote Polynesian Islands (the region east of the dotted line) began by 500 BC, with the Cook Islands and the Society Islands colonized first, likely prior to 300 AD (Rolett, 1998). Documented trade routes are indicated by dashed arrows. Pottery shards indicate that Tonga served as a centre of trade between Samoa and Fiji (Weisler & Woodhead, 1995; Burley & Dickinson, 2001), and basalt adzes provide evidence for trade between Samoa and the southern Cook Islands (Weisler & Kirch, 1996). Sample localities for lizards included in this analysis are indicated by black circles. A reconstructed relationship of regional languages based on a recently published comprehensive analysis by Gray *et al.* (2009) is included to provide an explicit null hypothesis of human-mediated dispersal for *Emoia samoensis* group populations in the region. The cladogram presented is modified from a Bayesian majority rule consensus phylogeny of Oceanic and Pacific language groups (Gray *et al.*, 2009). Specifically, branches of the language phylogeny representing geographic regions not sampled in the present study were collapsed without preserving branch length information. The language of the Cook Islands falls within the Tahitian language group (highlighted with the box). Potential source populations for the Cook Islands *Emoia samoensis* group population are indicated with lizard icons on the phylogeny.

*nigra*) and the Loyalty Islands (*Emoia loyaltiensis*), populations from these localities were not included because they are members of different well-supported monophyletic lineages than the population from the Cook Islands (Hamilton, 2008). DNA was isolated from muscle or liver tissues using either a Qiagen DNA Extraction kit in accordance with the manufacturer's instructions or with proteinase K digestion in lysis buffer followed by salt extraction (Aljanabi & Martinez, 1997). We used three mitochondrial loci and one nuclear locus to ensure a mix of relatively

rapidly and slowly evolving gene regions to estimate phylogenetic relationships in this group. We used the double-stranded polymerase chain reaction (PCR) to amplify 1726 bp of mitochondrial (mt)DNA (cyt *b*, Nd4, and CO1) and 289 bp of nuclear DNA (*C-mos*) using previously published primers (see Supporting information, Table S2) in accordance with previously published protocols (Austin *et al.*, 2010). Double-stranded cycle-sequencing was carried out for each amplicon using a BigDye Terminator cycle-sequencing kit, version 3.1 (Applied Biosystems) and sequences

visualized with a 3100 Genetic Analyzer (Applied Biosystems). DNA sequences were edited with SEQUENCHER, version 4.7, visually checked for accuracy, and aligned with CLUSTAL X (Thompson, Higgins & Gibson, 1994).

We were unable to obtain good sequences for one or more gene segments for eight of the 65 individuals (four of 11 species). In most cases only a single gene segment (*C-mos* or Nd4) was not amplified; we were able to amplify *cyt b* and CO1 for all individuals included in the present study. We included individuals with some missing data because phylogenetic information has utility in resolving relationships despite missing data; inclusion of additional individuals is more important for obtaining phylogenetic accuracy than the potential negative effects of missing data (Wiens, 2006; de Queiroz & Gatesy, 2007). We rejected heterogeneity of signal ( $P = 0.40$ ) with a partition homogeneity test conducted in PAUP\* (4.10b), and combined mitochondrial and nuclear data for analysis.

#### PHYLOGENETIC ANALYSIS

Phylogenetic trees were estimated using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). PAUP\* (4.10b) was used to reconstruct MP trees. Characters were equally weighted in heuristic searches using tree-bisection-reconnection branch swapping (to eliminate order biases), no upper bound for MaxTrees, the steepest descent option not in effect, and the MulTrees option selected. Clade support was evaluated by bootstrapping using 1000 pseudoreplicates with the same heuristic search conditions.

The GTR+I+G model was selected as the best fitting model of DNA substitution for the combined 2015-bp dataset using the Bayesian information criterion implemented in MODELTEST, version 3.7 (Posada & Crandall, 1998; Posada & Buckley, 2004). Under this model, ML heuristic searches were conducted using the hill-climbing algorithm in GARLI, version 0.96 (Zwickl, 2006) with a random starting tree and default settings for the genetic algorithm. Identical topologies and nearly identical likelihood scores were obtained for five separate GARLI runs and 1000 bootstrap pseudoreplicates were used to assess support for the resulting ML topology.

For BI, we used the Akaike Information Criterion in MrModelTest version 2.2 (Nylander *et al.*, 2004) to select the best fitting model of DNA substitution. Markov chain Monte Carlo (MCMC) analyses were run on two different datasets with MrBayes, version 3.1 (Ronquist & Huelsenbeck, 2003). The first dataset included 939 bp of mitochondrial data (*cyt b* and CO1) for all 65 individuals, whereas the second dataset

included 1726 bp of mitochondrial data (*cyt b*, CO1, and Nd4) for 46 individuals. Two simultaneous independent runs of one cold and three heated MCMC chains, each with a different starting random tree, were conducted for  $5 \times 10^6$  generations and trees were sampled every 1000 generations. To evaluate the consistency of the results obtained from MrBayes, all analyses were repeated. We examined potential scale reduction factors (PSRFs) and the standard deviation of split frequencies to determine that runs converged on stationarity; PSRF values of 1.0 and an average SD of split frequencies for both runs less than 0.01 indicated that both runs had converged on a stationary distribution. We also used Tracer version 1.4 (Rambaut & Drummond, 2007) to examine traces and determine if effective sample sizes were adequate ( $\geq 200$ ) for estimates of the posterior distribution of tree likelihood and model parameters; the results obtained indicated that convergence had been reached and that the models had mixed well. For each independent run, the first 2000 trees were discarded as burn-in and a 50% majority-rule consensus tree was constructed from the remaining trees.

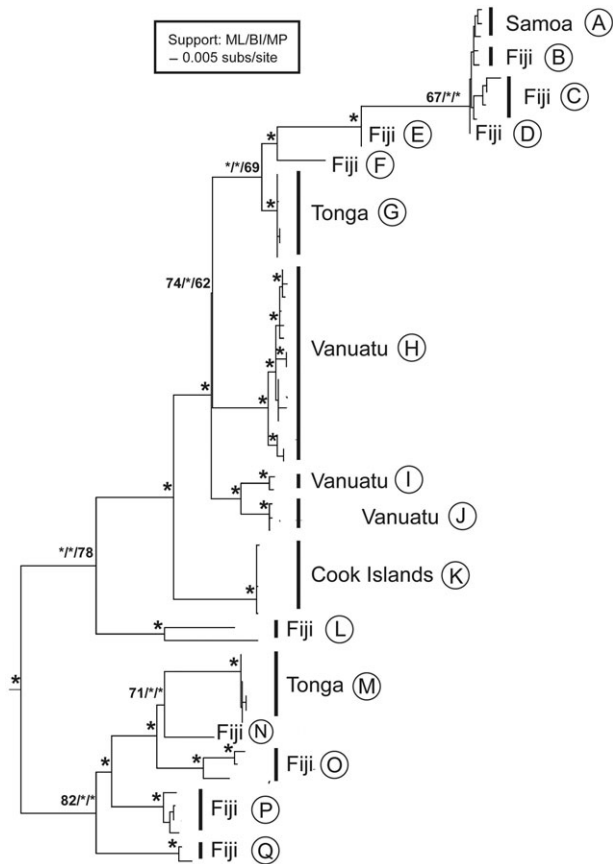
#### COMPARISON OF MOLECULAR PHYLOGENY AND LINGUISTIC DATA

The phylogenetic hypothesis we inferred for *E. samoensis* group populations was compared with the topology of the linguistic phylogeny constructed by Gray *et al.* (2009) to evaluate the level of congruence in branching patterns. We estimated an overall topological score (Nye, Lio & Gilks, 2006), comprising a measure of topological similarity between trees ([http://www.mas.ncl.ac.uk/~ntmwn/phylo\\_comparison/pairwise.html](http://www.mas.ncl.ac.uk/~ntmwn/phylo_comparison/pairwise.html)). We chose this algorithm because it is specifically designed to allow comparison between topologies constructed using different genes for the same set of taxa. Because the models of evolution are likely quite different for the molecular dataset used to reconstruct the *E. samoensis* group tree and the gains and loss of various linguistic characters used to reconstruct the relationship among languages, a method relying on the assumption of identical models of evolution for both trees would not be appropriate. Additionally, because the rates of change may differ for these two types of data, we did not include branch length information in the comparison. The topology score is computed by matching branches in the two trees that share a similar partition of leaf nodes and forming an alignment between the trees. To obtain the overall topology score, the algorithm uses a two-step process: first, each pair of edges is assigned a score based on the topological similarity of the branches and, second, the branches are paired up to optimize the global score (Nye *et al.*, 2006). In

addition to providing an overall topology score, this method also highlights regions of congruence and conflict between trees.

RESULTS

Reconstructed phylogenies inferred by MP, ML, and BI methods all had the same general topology; thus, only the ML tree is presented (Fig. 2) with support values generated under MP, ML, and BI shown for each node. The six individuals from the Cook Islands were recovered as a single, monophyletic clade (Clade



**Figure 2.** Maximum likelihood (ML) phylogeny reconstructed using the GTR+I+G model of DNA substitution for a 2015-bp dataset consisting of mitochondrial (*cyt b*, ND4, and CO1) and nuclear (*C-mos*) DNA. Bootstrap values (based on 1000 pseudoreplicates) and Bayesian posterior probabilities [Bayesian inference (BI)] are shown for each node: ML/BI/maximum parsimony (MP). Individual support values  $\geq 85\%$  (ML and MP) or 0.9 (BI) are indicated by an asterisk (\*); nodes for which all three support measures are  $\geq 85\%$  (ML or MP) or 0.9 (BI) are indicated by a single asterisk (\*). Branch lengths are proportional to the number of substitutions per site (scale bar). Members of each clade are listed in the Supporting information (Table S1).

K) with a sister relationship to a large clade containing populations from Samoa and Fiji (Clades A–F), a taxon endemic to Tonga (Clade G), and three species endemic to the Vanuatu Archipelago (Clades H–J; Fig. 2). The Cook Islands *samoensis* population is genetically distinct from all other populations included in the phylogeny, and divergent from its closest relatives, three species endemic to the Vanuatu Archipelago: the Cook Islands population is 8.5% divergent (1726 bp mtDNA; 9.8% for *cyt b*) from Clade J, 10.2% divergent (1726 bp mtDNA; 12.7% for *cyt b*) from Clade I, and 11.3% divergent (1726 bp mtDNA; 9.7% for *cyt b*) from Clade H (Fig. 2). The Cook Islands *samoensis* population is also divergent from geographically proximate populations: 17.5% divergent (1726 bp mtDNA; 13.1% for *cyt b*) from Samoa (Clade A) and 12.5% (1726 bp mtDNA; 14.8% for *cyt b*; Clade G) and 28.8% (1726 bp mtDNA; 30.6% for *cyt b*; Clade M) divergent from the two Tongan populations (Fig. 2). Despite this genetic distinctiveness, within-clade allelic diversity is low ( $< 1\%$  for combined dataset and 1726 bp mtDNA), and only a single *cyt b* haplotype was recovered in the Cook Islands population.

The score of overall topological similarity was 33%, indicating that molecular and language-based phylogenies are incongruent. Linguistically, the Cook Islands are most closely related to the islands of Samoa and Tonga (Fig. 1), with Samoan and Tongan languages having a sister taxa relationship. The *E. samoensis* populations from Samoa and Tonga do not form a monophyletic group in our phylogeny or cluster with the population from the Cook Islands (Fig. 2), and genetic divergence between the Cook Islands population and populations in Samoa and Tonga is high.

DISCUSSION

Whether the phylogenetic relationships among these *E. samoensis* group species support the human-mediated dispersal hypothesis or the dispersal of the Rarotonga population by natural means (and thus represents the sole endemic species of Cook Islands reptile) remains unclear. The data are concordant with some of the predictions generated for each hypothesis. Rarotonga is monophyletic and well-differentiated (divergence from all other clades  $> 6\%$  for combined mtDNA and nuclear data;  $> 8\%$  for 1726 bp mtDNA;  $> 9\%$  for *cyt b*) from other species in the recovered topology (Fig. 2). Natural dispersal and speciation on Rarotonga is supported by recovery of a monophyletic lineage that is genetically distinct from other species; however, natural dispersal and subsequent genetic differentiation would, when given enough time, produce allelic diversity within Raro-

tonga. By contrast, the topology of the recovered phylogeny shows very low intra-population genetic diversity (measured as the maximum intra-population pairwise difference) (0.3% for complete dataset; 0.14% for 1726 bp mtDNA; no variation for *cyt b*) within the Cook Islands population (Fig. 2), supporting human-mediated dispersal.

Low intra-island genetic diversity has been reported from reptile populations within their natural range (Brown & Pestano, 1998; Carranza *et al.*, 2000; Brehm *et al.*, 2003), highlighting the potential for low intra-island genetic diversity to result from other factors. Conversely, introduced populations do not always have low genetic diversity, as genetic diversity may actually increase as a result of invasion (Kolbe *et al.*, 2004, 2007). Inferences about population history from measures of allelic diversity must be relative and based on comparisons that account for phylogeny and geography. Closely-related congeners in this analysis have higher levels of intra-island allelic diversity than the Cook Islands population. *Emoia trossula* from a single island in Fiji (Clade C) have an intra-population genetic diversity of 0.7% (for 1726 bp mtDNA; 0.9% for *cyt b*), and intra-island genetic diversity for the Vanuatu endemics *Emoia aneityumensis* (Clade H) and *Emoia nigromarginata* (Clade I) are 4.3% (for 1726 bp mtDNA; 0.7% for *cyt b*) and 0.5% (for 1726 bp mtDNA; 0.3% for *cyt b*), respectively.

The distinctiveness of the Rarotonga population coupled with such low intra-population allelic variation does not strongly support a single scenario. There are two possible explanations for this contradictory result. (1) The Cook Islands population may represent a previously unrecognized species endemic to Rarotonga, whose ancestors colonized Rarotonga via natural dispersal, not human transport. The low allelic diversity recovered from this population could result from a subsequent population bottleneck, perhaps as the result of a typhoon, or be a stochastic effect of sampling. However, individuals were sampled from two sites on opposite sides of the island. This natural dispersal scenario is supported by the high level of genetic divergence between the Rarotonga population and other species in the phylogeny (Fig. 2). (2) An alternative explanation is that the Rarotonga population derives from a human-mediated introduction, as suggested by reduced allelic diversity within the population. The source population – an unsampled *Emoia* species – is not included in this phylogeny, resulting in the observed pattern of monophyly and high divergence from other species (Fig. 2). The large geographic expanse of the Pacific Ocean and extreme isolation of remote islands result in uneven sampling across the region, especially within Fiji, and, for some areas, comprehensive biotic surveys have not yet been

conducted. Unquestionably, the Rarotonga population represents an undescribed species under either scenario, although the native range (and thus the origin of the potential introduction) remains unresolved.

Relationships among Melanesian and Polynesian languages and the colonization route of the Pacific by Lapita peoples predict a dispersal pathway from the Solomon Islands eastwards into the Vanuatu Archipelago, the Loyalty Islands, and New Caledonia, and then further eastwards to Fiji, Samoa and Tonga (Fig. 1). The predicted phylogenetic topology for this introduction scenario is identical to the topology predicted by natural dispersal from New Guinea or the Solomon Islands and eastward into the Pacific via a stepping stone dispersal pathway, as has been suggested for most *Emoia* species groups (Gibbons, 1985; Brown & Gibbons, 1986; Brown, 1991). Our topology does not provide evidence for a unidirectional colonization of the Pacific Islands from the Solomon Islands eastwards (Fig. 2). Although the Rarotonga population has a sister taxa relationship with a large clade containing species from Vanuatu, Fiji, Samoa, and Tonga, populations from other island groups fall out across multiple clades in the reconstructed phylogeny, suggesting a more complex pattern of dispersal and speciation in the Pacific within this lineage of *Emoia*.

Archaeological evidence suggests that Tonga served as a centre for trade during early Polynesian history, with trade routes established between Tonga and Samoa, Tonga and Fiji, and Tonga and the Cook Islands, and there is even evidence for trade with Vanuatu (Kirch & Green, 1987; Kirch *et al.*, 1995; Burley, 1998; Burley & Dickinson, 2001). Direct trade between Samoa and the southern Cook Islands is inferred from recovery of basalt adzes from pre-historic sites in the Cook Islands (Weisler & Woodhead, 1995; Weisler & Kirch, 1996). We suggest that the introduction of a *samoensis* group species to Rarotonga lies within this complex history of migrations and trade. The complexities of human movements in Oceania prevent us from determining the origin and timing of this introduction. The complexity of inter- and intra-archipelago voyaging of people throughout Samoa, Fiji, and Tonga suggest these island groups as the potential native range and source of the introduction of the population on Rarotonga. If this is the case, the source population remains undiscovered.

Differentiating between human-mediated dispersal and waif over-water dispersal is difficult, especially in light of accidental and intentional translocations by Lapita people and early Polynesians. Although different population histories have unique predicted phylogenetic and population demographic signals, choosing between alternative predicted patterns and



the associated population history is not always possible. Our lack of knowledge of species' ranges, poorly resolved taxonomy and species boundaries, and inadequate sampling can lead to an inability to differentiate among potential scenarios. Inferences regarding population history must be viewed in light of the limits of the data to avoid erroneous conclusions. By utilizing multiple approaches to data analysis and evaluating patterns of genetic variation, introduction hypotheses can be appropriately evaluated.

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#### REFERENCES

**Aljanabi SM, Martinez I. 1997.** Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic Acids Research* **25**: 4692–4693.

- Anderson A. 2009.** The rat and the octopus: initial human colonization and the prehistoric introduction of domestic animals to Remote Oceania. *Biological Invasions* **11**: 1503–1519.
- Austin CC. 1995.** Molecular and morphological evolution in South Pacific scincid lizards: morphological conservatism and phylogenetic relationships of Papuan *Lipinia* (Scincidae). *Herpetologica* **51**: 291–300.
- Austin CC. 1999.** Lizards took express train to Polynesia. *Nature* **397**: 113–114.
- Austin CC, Spataro M, Peterson S, Jordan J, McVay JD. 2010.** Conservation genetics of Boelen's python (*Morelia boeleni*) from New Guinea: reduced genetic diversity and divergence of captive and wild animals. *Conservation Genetics*. DOI 10.1007/s10592-009-9931-z.
- Austin CC, Zug GR. 1999.** Molecular and morphological evolution in the south-central Pacific skink *Emoia tongana* (Reptilia: Squamata): uniformity and human-mediated dispersal. *Australian Journal of Zoology* **47**: 425–437.
- Baker AJ, Huynen LJ, Haddrath O, Millar CD, Lambert DM. 2005.** Reconstructing the tempo and mode of evolution in an extinct clade of birds with ancient DNA: the giant moas of New Zealand. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 8257–8262.
- Boyer AG. 2008.** Extinction patterns in the avifauna of the Hawaiian Islands. *Diversity and Distributions* **14**: 509–517.
- Brawley SH, Coyer JA, Blakeslee AMH, Hoarau G, Johnson LE, Byers JE, Stam WT, Olsen JL. 2009.** Historical invasions of the intertidal zone of Atlantic North America associated with distinctive patterns of trade and emigration. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 8239–8244.
- Brehm A, Jesus J, Spinola H, Alves C, Vicente L, Harris DJ. 2003.** Phylogeography of the Madeiran endemic lizard *Lacerta dugesii* inferred from mtDNA sequences. *Molecular Phylogenetics and Evolution* **26**: 222–230.
- Brown WC. 1991.** Lizards of the genus *Emoia* (Scincidae) with observations on their evolution and biogeography. *Memoirs of the California Academy of Sciences* **15**: 1–94.
- Brown WC, Gibbons J. 1986.** Species of the *Emoia samoensis* group of lizards (Scincidae) in the Fiji Islands, with descriptions of two new species. *Proceedings of the California Academy of Sciences* **44**: 41–53.
- Brown RP, Pestano J. 1998.** Phylogeography of skinks (Chalcides) in the Canary Islands inferred from mitochondrial DNA sequences. *Molecular Ecology* **7**: 1183–1191.
- Bruna EM, Fisher RN, Case TJ. 1995.** Cryptic species of Pacific skinks (*Emoia*): further support from mitochondrial DNA sequences. *Copeia* **1995**: 981–983.
- Bruna EM, Fisher RN, Case TJ. 1996.** Morphological and genetic evolution appear decoupled in Pacific skinks (Squamata: Scincidae: *Emoia*). *Proceedings of the Royal Society of London Series B, Biological Sciences* **263**: 681–688.
- Burley DV. 1998.** Tongan archaeology and the Tongan past, 2850–150 bp. *Journal of World Prehistory* **12**: 337–392.
- Burley DV, Dickinson WR. 2001.** Origin and significance of a founding settlement in Polynesia. *Proceedings of the*

- National Academy of Sciences of the United States of America* **98**: 11829–11831.
- Carranza S, Arnold EN, Mateo JA, Lopez-Jurado LF. 2000.** Long-distance colonization and radiation in gekkonid lizards, *Tarentola* (Reptilia: Gekkonidae), revealed by mitochondrial DNA sequences. *Proceedings of the Royal Society of London Series B, Biological Sciences* **267**: 637–649.
- Case TJ, Bolger DT. 1991.** The role of introduced species in shaping the distribution and abundance of island reptiles. *Evolutionary Ecology* **5**: 272–290.
- Cowie RH. 2001.** Invertebrate invasions on Pacific Islands and the replacement of unique faunas: a synthesis of land and freshwater snails. *Biological Invasions* **3**: 1023–1037.
- Crombie RI, Steadman DW. 1986.** The lizards of Rarotonga and Mangaia, Cook Island Group, Oceania. *Pacific Science* **44**: 4–57.
- Darling JA, Bagley MJ, Roman J, Tepolt CK, Geller JB. 2008.** Genetic patterns across multiple introductions of the globally invasive crab genus *Carcinus*. *Molecular Ecology* **17**: 4992–5007.
- Dlugosch KM, Parker IM. 2008.** Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology* **17**: 431–449.
- Fisher RN. 1997.** Dispersal and evolution of the Pacific Basin gekkonid lizards *Gehyra oceanica* and *Gehyra mutilata*. *Evolution* **51**: 906–921.
- Gemmell NJ, Schwartz MK, Robertson BC. 2004.** Moa were many. *Proceedings of the Royal Society of London Series B, Biological Sciences* **271**: S430–S432.
- Gibbons JRH. 1985.** The biogeography and evolution of Pacific island reptiles and amphibians. In: Grigg G, Shine R, Ehmann H, eds. *Biology of Australasian frogs and reptiles*. Chipping Norton, NSW: Surrey Beatty & Sons Pty Ltd, 125–142.
- Gray RD, Drummond AJ, Greenhill SJ. 2009.** Language phylogenies reveal expansion pulses and pauses in Pacific settlement. *Science* **232**: 479–483.
- Hamilton AM. 2008.** Species boundaries, biogeography, and intra-archipelago genetic variation within the *Emoia samoensis* species group in the Vanuatu Archipelago and Oceania. PhD Thesis, Louisiana State University.
- Hamilton AM, Hartman JH, Austin CC. 2009.** Island area and species diversity in the southwest Pacific Ocean: is the fauna of Vanuatu depauperate? *Ecography* **32**: 247–258.
- Hamilton AM, Klein ER, Austin CC. 2010.** Biogeographic breaks in Vanuatu, a nascent oceanic archipelago. *Pacific Science* **64**: 149–159.
- Hinkle AE. 2007.** Population structure of Pacific *Cordyline fruticosa* (Laxmanniaceae) with implications for human settlement of Polynesia. *American Journal of Botany* **94**: 828–839.
- Huynen L, Millar CD, Scofield RP, Lambert DM. 2003.** Nuclear DNA sequences detect species limits in ancient moa. *Nature* **425**: 175–178.
- Jesus J, Brehm A, Harris DJ. 2005.** Phylogenetic relationships of *Hemidactylus* geckos from the Gulf of Guinea islands: patterns of natural colonizations and anthropogenic introductions estimated from mitochondrial and nuclear DNA sequences. *Molecular Phylogenetics and Evolution* **34**: 480–485.
- Keogh JS, Edwards DL, Fisher RN, Harlow PS. 2008.** Molecular and morphological analysis of the critically endangered Fijian iguanas reveals cryptic diversity and a complex biogeographic history. *Philosophical Transactions of the Royal Society B, Biological Sciences* **363**: 3413–3426.
- Keppel G, Lowe AJ, Possingham HP. 2009.** Changing perspectives of the biogeography of the tropical South Pacific: influences of dispersal, vicariance, and extinction. *Journal of Biogeography* **36**: 1035–1054.
- Kirch PV. 1988.** The spatial and temporal boundaries of Lapita. In: Kirch PV, Hunt TL, eds. *Archaeology of the Lapita cultural complex: a critical review*. Seattle, WA: Thomas Burke Memorial Washington State Museum Research Report 5. 9–31.
- Kirch PV. 2000.** *On the road of the winds: an archaeological history of the Pacific Islands before European contact*. Berkeley, CA: University of California Press.
- Kirch PV, Green RC. 1987.** History, phylogeny, and evolution in Polynesia. *Current Anthropology* **28**: 161–185.
- Kirch PV, Steadman DW, Butler VL, Hather J, Weisler MI. 1995.** Prehistory and human ecology in Eastern Polynesia: excavations at Tangatatau rockshelter, Mangaia, Cook Islands. *Archaeology in Oceania* **30**: 47–65.
- Kolbe JJ, Glor RE, Schettino LRG, Lara AC, Larson A, Losos JB. 2004.** Genetic variation increases during biological invasion by a Cuban lizard. *Nature* **431**: 177–181.
- Kolbe JJ, Glor RE, Schettino LR, Lara AC, Larson A, Losos JB. 2007.** Multiple sources, admixture, and genetic variation in introduced *Anolis* lizard populations. *Conservation Biology* **21**: 1612–1625.
- Lee T, Burch JB, Coote T, Fontaine B, Gargominy O, Pearce-Kelly P, Foighil DO. 2007.** Prehistoric inter-archipelago trading of Polynesian tree snails leaves a conservation legacy. *Proceedings of the Royal Society of London Series B, Biological Sciences* **274**: 2907–2914.
- Lum JK, McIntyre JK, Greger DL, Huffman KW, Vilar MG. 2006.** Recent Southeast Asian domestication and Lapita dispersal of sacred male pseudohermaphroditic ‘tuskers’ and hairless pigs of Vanuatu. *Proceedings of the National Academy of Sciences of the United States of America* **103**: 17190–17195.
- McCormack G. 2002.** Cook Islands biodiversity strategy and action plan. Report of biodiversity workshops prepared by the National Steering Committee, Government of the Cook Islands, 81 pp.
- Matisoo-Smith E, Roberts RM, Irwin GJ, Allen JS, Penny D, Lambert DM. 1998.** Patterns of prehistoric human mobility in Polynesia indicated by mtDNA from the Pacific rat. *Proceedings of the National Academy of Sciences of the United States of America* **95**: 15145–15150.
- Matisoo-Smith E, Robins JH. 2004.** Origins and dispersals of Pacific peoples: evidence from mtDNA phylogenies of the Pacific rat. *Proceedings of the National Academy of Sciences of the United States of America* **101**: 9167–9172.

- Mead JI, Steadman DW, Bedford SH, Bell CJ, Spriggs M. 2002.** New extinct Mekosuchine crocodile from Vanuatu, South Pacific. *Copeia* **2002**: 632–641.
- Mittermeier RA, Gil PR, Hoffman M, Pligrim J, Brooks T, Mittermeier CG, Lamoreux J, da Fonseca GAB. 2005.** *Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions*. Arlington, VA: Conservation International.
- Molnar RE, Worthy TH, Willis PMA. 2002.** An extinct Pleistocene endemic Mekosuchine crocodylian from Fiji. *Journal of Vertebrate Paleontology* **22**: 612–628.
- Moritz C, Case TJ, Bolger DT, Donnellan S. 1993.** Genetic diversity and the history of Pacific Island house geckos (*Hemidactylus* and *Lepidodactylus*). *Biological Journal of the Linnean Society* **48**: 113–133.
- Munoz-Fuentes V, Green AJ, Sorenson MD, Negro JJ, Vila C. 2006.** The ruddy duck *Oxyura jamaicensis* in Europe: natural colonization or human introduction? *Molecular Ecology* **15**: 1441–1453.
- Myers NA, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000.** Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–859.
- Nye TMW, Lio P, Gilks WR. 2006.** A novel algorithm and web-based tool for comparing two alternative phylogenetic trees. *Bioinformatics* **22**: 117–119.
- Nylander JAA, Ronquist F, Huelsenbeck JP, Nieves-Aldrey JL. 2004.** Bayesian phylogenetic analysis of combined data. *Systematic Biology* **53**: 47–67.
- Olivieri I. 2009.** Alternative mechanisms of range expansion are associated with different changes of evolutionary potential. *Trends in Ecology and Evolution* **24**: 289–292.
- Posada D, Buckley TR. 2004.** Model selection and model averaging in phylogenetics: advantages of the AIC and Bayesian approaches over likelihood ratio tests. *Systematic Biology* **53**: 793–808.
- Posada D, Crandall KA. 1998.** MODELTEST: testing the model of DNA substitutions. *Bioinformatics* **14**: 817–818.
- Prebble M, Wilmshurst JM. 2009.** Detecting the initial impact of humans and introduced species on island environments in Remote Oceania using palaeoecology. *Biological Invasions* **11**: 1529–1556.
- Pregill G. 1993.** Fossil lizards from the late Quaternary of 'Eua, Tonga'. *Pacific Science* **47**: 101–114.
- Pregill G. 1998.** Squamate reptiles from prehistoric sites in the Mariana Islands. *Copeia* **1998**: 64–75.
- Pregill G, Dye T. 1989.** Prehistoric extinction of giant iguanas in Tonga. *Copeia* **1989**: 505–508.
- Pregill GK, Steadman DW. 2000.** Fossil vertebrates from Palau, Micronesia: a resource assessment. *Micronesica* **33**: 137–152.
- Pregill GK, Steadman DW. 2004.** South Pacific iguanas: human impacts and a new species. *Journal of Herpetology* **38**: 15–21.
- Pregill GK, Worthy TH. 2003.** A new iguanid lizard (Squamata, Iguanidae) from the late quaternary of Fiji, southwest Pacific. *Herpetologica* **59**: 57–67.
- de Queiroz A, Gatesy J. 2007.** The supermatrix approach to systematics. *Trends in Ecology and Evolution* **22**: 34–41.
- Rambaut A, Drummond AJ. 2007.** *Tracer*, Version 1.4. Available at: <http://beast.bio.ed.ac.uk/Tracer>
- Reiff D, Kaneko A, Amos M, Lum JK. 2006.** The genetic diversity of *Anopheles punctulatus* of Vanuatu: stowing away to remote Oceania? *American Journal of Human Biology* **18**: 269–269.
- Rocha S, Carretero MA, Harris DJ. 2005.** Diversity and phylogenetic relationships of *Hemidactylus* geckos from the Comoro islands. *Molecular Phylogenetics and Evolution* **35**: 292–299.
- Rocha S, Ineich I, Harris DJ. 2009.** Cryptic variation and recent bipolar range expansion within the Stump-toed Gecko *Gehyra mutilata* across Indian and Pacific Ocean islands. *Contributions to Zoology* **78**: 1–8.
- Rolett BV. 1998.** *Hananiai: prehistoric colonization and cultural change in the Marquesas Islands (East Polynesia)*. New Haven, CT: Yale University Publications in Anthropology.
- Ronquist F, Huelsenbeck JP. 2003.** MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.
- Steadman DW. 1993.** Biogeography of Tongan birds before and after human impact. *Proceedings of the National Academy of Sciences of the United States of America* **90**: 818–822.
- Steadman DW. 1995.** Prehistoric extinction of Pacific island birds: biodiversity meets zooarchaeology. *Science* **267**: 625.
- Steadman DW. 2006.** A new species of extinct parrot (Psittacidae: *Ecectus*) from Tonga and Vanuatu, South Pacific. *Pacific Science* **60**: 137–145.
- Steadman DW, Kirch PV. 1990.** Prehistoric extinction of birds on Mangaia, Cook Islands, Polynesia. *Proceedings of the National Academy of Sciences of the United States of America* **87**: 9605–9609.
- Steadman DW, Plourde A, Burley DV. 2002.** Prehistoric butchery and consumption of birds in the Kingdom of Tonga, South Pacific. *Journal of Archaeological Science* **29**: 571–584.
- Steadman DW, Pregill GK, Burley DV. 2002.** Rapid prehistoric extinction of iguanas and birds in Polynesia. *Proceedings of the National Academy of Sciences of the United States of America* **99**: 3673–3677.
- Steadman DW, White JP, Allen J. 1999.** Prehistoric birds from New Ireland, Papua New Guinea: extinctions on a large Melanesian island. *Proceedings of the National Academy of Sciences of the United States of America* **96**: 2563–2568.
- Stoddart DR. 1992.** Biogeography of the tropical Pacific. *Pacific Science* **46**: 276–293.
- Thompson JD, Higgins DG, Gibson TJ. 1994.** CLUSTALW: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* **22**: 4673–4680.
- Vences M, Wanke S, Vietes DR, Branch WR, Glaw F, Meyer A. 2004.** Natural colonization or introduction? Phylogeographical relationships and morphological differentia-

- tion of house geckos (*Hemidactylus*) from Madagascar. *Biological Journal of the Linnean Society* **83**: 115–130.
- Weisler MI, Bolt R, Findlater A. 2006.** A new eastern limit of the Pacific flying fox, *Pteropus tonganus* (Chiroptera: Pteropodidae), in prehistoric Polynesia: a case of possible human transport and extirpation. *Pacific Science* **60**: 303–411.
- Weisler MI, Kirch PV. 1996.** Interisland and interarchipelago transfer of stone tools in prehistoric Polynesia. *Proceedings of the National Academy of Sciences of the United States of America* **93**: 1381–1385.
- Weisler MI, Woodhead JD. 1995.** Basalt Pb isotope analysis and the prehistoric settlement of Polynesia. *Proceedings of the National Academy of Sciences of the United States of America* **92**: 1881–1885.
- Wiens JJ. 2006.** Missing data and the design of phylogenetic analyses. *Journal of Biomedical Informatics* **39**: 34–42.
- Wilson ML, Lum JK. 2006.** Lineage sharing and gene flow in Vanuatu and the Pacific: a mtDNA analysis of *Rattus exulans* as a proxy for human settlement and interactions. *American Journal of Human Biology* **18**: 282–282.
- Zerega NJC, Ragone D, Motley TJ. 2004.** Complex origins of breadfruit (*Artocarpus altilis*, Moraceae): implications for human migrations in Oceania. *American Journal of Botany* **91**: 760–766.
- Zug GR. 1991.** *Lizards of Fiji: natural history and systematics*. Honolulu: Bishop Museum Press.
- Zug GR, Gill BJ. 1997.** Morphological variation of *Emoia murphyi* (Lacertilia: Scincidae) on islands of the southwest Pacific. *Journal of the Royal Society of New Zealand* **27**: 235–242.
- Zug GR, Ineich I. 1995.** A new skink (*Emoia*, Lacertilia, Reptilia) from the forest of Fiji. *Proceedings of the Biological Society of Washington* **108**: 395–400.
- Zwickl DJ. 2006.** Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. PhD Thesis, University of Texas at Austin.

## SUPPORTING INFORMATION

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

**Table S1.** Samples included in the present study. CAS, California Academy of Sciences; LSUMZ, Louisiana State University Museum of Natural Science; MNHN, Museum National d'Histoire Naturelle, USNM, United States National Museum. Phylogenetic placement (Fig. 2) indicated by 'clade.'

**Table S2.** Primers used in the present study.

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