 Australian Journal of Zoology, 1999, **47**, 425–437

Molecular and morphological evolution in the south-central Pacific skink *Emoia tongana* (Reptilia : Squamata): uniformity and human-mediated dispersal

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Abstract

Human-mediated and waif dispersal are both responsible for the distribution of lizards on tropical Pacific islands. The component of each of these dispersal modes to the Pacific herpetofauna, however, is unclear. Morphological conservatism of Pacific lizards, the poor paleontological record on tropical Pacific islands, and minimal research effort in the Pacific (compared with other island systems) has hampered our understanding of waif versus human-mediated patterns. We examine morphological and genetic variation of *Emoia concolor* and *E. tongana* (formerly *E. murphyi*), two scincid lizards, from the south-central Pacific, to assess modes of dispersal and population structure. *Emoia tongana* from Tonga and Samoa is genetically uniform, suggesting that these are synanthropic populations recently introduced, presumably from Fiji. Relatively large genetic divergence is evident for populations of *E. concolor* within the Fijian archipelago, suggesting prehuman intra-archipelago dispersal and isolation.

Introduction

Lizards are successful colonisers of the islands of the tropical Pacific, occurring on most, if not all, islands of several hectares or larger. How did they reach these islands, many of which are a hundred kilometres or more from their nearest neighbour? One hypothesis suggests that the lizard faunas of the islands east of Samoa (168°W) are entirely human dispersed (e.g. Burt and Burt 1932; Gibbons 1985; Crombie and Steadman 1988; Case and Bolger 1991). The lack of endemicity and the morphological uniformity of species composition supports this interpretation of recent human-mediated dispersal rather than an old (tens of thousands to millions of years ago) natural dispersal. Other evidence, however, suggests that some species are capable of long-distance, cross-water dispersal without human assistance. *Brachylophus* in Fiji, an endemic iguanid lizard all of whose relatives are in the Americas, has often been cited as an example of such an event (Cogger 1974; Gibbons 1981 1985; Colgan and Da Costa 1997) and other research supports the cross-water dispersal for large lizards (Censky *et al.* 1998) as well as smaller skinks (Austin 1999). Several recent molecular studies, however, have documented morphological conservatism in Pacific skinks (Donnellan and Aplin 1989; Bruna *et al.* 1995; Austin 1995, 1999). It is therefore possible that these morphologically undifferentiated populations actually represent cryptic endemic species and that the current calculation of Pacific herpetofaunal diversity is an underestimate.

The question of how we recognise natural dispersal events from those that are human-mediated is not readily resolved. Endemism is a widely assumed indicator of natural dispersal (e.g. Adler *et al.* 1995), but this criterion is inadequate for cryptic species. Natural dispersal can be identified in two additional ways. Identification of pre-human fossils would support a natural dispersal hypothesis (Pregill 1998), but very little work has been done on fossil and sub-fossil squamate remains in the central Pacific. Research on the fossil Pacific bird fauna suggests that the extant faunas of Pacific islands are not indicative of original pre-human diversity (Steadman

10.1071/ZO99019 0004-959X/99/050425

1995). Identification of cryptic lizard species via genetic analysis is another method to identify populations that dispersed to isolated archipelagoes before human arrival (Bruna *et al.* 1995; Austin 1999). Aspects of the distribution of *Emoia tongana* in the central Pacific make this species of particular interest to questions concerning natural versus human-mediated dispersal.

Emoia tongana is a moderate-sized (adults 53–75 mm snout–vent length), arboreal scincid lizard found in Futuna, Samoa and Tonga (Zug and Gill 1997). It was originally recognised (Burt 1930) as a distinct member of the *Emoia samoensis* species-group from a single specimen collected in Sava'i, Western Samoa. Subsequently it was discovered on the outlying Tongan island of Niuafo'ou and then from other northern island groups of Tonga. Most recently it was found on Futuna (Gill 1995). This distribution is not matched by any other terrestrial animal (Fig. 1). It does, however, encompass a set of islands ruled by the Tongan monarchy in the 12th and 16–17th centuries (Spennemann 1988). This latter consistency suggests the possibility that *E. tongana* was unintentionally transported by the Tongans from its native island to other islands within the Tongan sphere of influence.

The first effort (Zug and Gill 1995) to examine the mode of dispersal and level of differentiation among the distant insular populations of *E. tongana* revealed a high level of morphological uniformity among all populations. Variation between populations was less than or equal to that within the largest population sample. Because morphological variation, at present, is unable to resolve any aspect of the origin and distribution of *E. tongana*, a more direct examination of genetic variation seems appropriate. We offer here an assessment of genetic variation based on DNA sequence data from 305 aligned nucleotides of the mitochondrial *cytochrome b* gene as a potential means of identifying the source population, and the ages and routes of dispersal. We use quantitative estimates of molecular divergence and phylogenetic relationships to distinguish between natural and human-mediated dispersal in *E. tongana*.

Nomenclatural comments

A Tongan population of slender beige *Emoia* was described by Werner (1899) as *Lygosoma cyanogaster* Less. var. *tongana*. Werner indicated that this population, based on two specimens collected by Friedlaender, might represent a distinct species by his addition of '(an n. sp.?)' to the new variety name. The name *tongana* was seemingly forgotten until 1986 when it reappeared in a synonomy of *Emoia concolor* (Brown and Gibbons 1986). The assignment to *E. concolor* seemed appropriate because Werner (1899) had used *Lygosoma cyanogaster* var. *tongana* for a morphologically similar lizard from Fiji, and his description matched the characteristics of *E. concolor*. Brown (1991) and Zug (1991) repeated this synonomic usage.

Burt (1930) recognised *Emoia murphyi* from one slender beige *Emoia* from Samoa. This name was also little used and only in association with Samoan specimens until 1990 when Gill and Rinke (1990) reported it from Tonga (Niuafo'ou, Niuatoputapu, and Va'vau). Zug and Gill (1997) provided the first detailed analysis of morphological variation but failed to recognise the nomenclatural significance of *L. c. tongana* Werner as potential senior synonym of *Emoia murphyi* Burt.

Werner's *tongana* specimens were deposited in the Zoologisches Museum, Berlin. In their preparation of a series of type lists of the amphibians and reptiles held by this museum, Drs R. Günther and A. Bauer relocated the two *tongana* syntypes (ZBM 15702, 57642). Werner's description of *tongana* specimens as light brown lizards (68 and 60 mm SVL) with 28 scale rows at midbody matches, respectively, the two syntypes. Comparison of other characters also show the syntypes to match the *tongana* paradigm, e.g. Fig. 2; thus *tongana* and *murphyi* are conspecific. Because of the minimal use (less than a dozen times since the original description) of *E. murphyi*, there is no justification for setting aside the law of priority. *Emoia tongana* becomes the valid name for this taxon. To avoid future confusion, two other nomenclatural actions are required. First, we designate ZMB 15702 as the lectotype of *Lygosoma cyanogaster* Less. var. *tongana* Werner, 1899. We restrict the type locality to Neiafu [Port of Refuge],

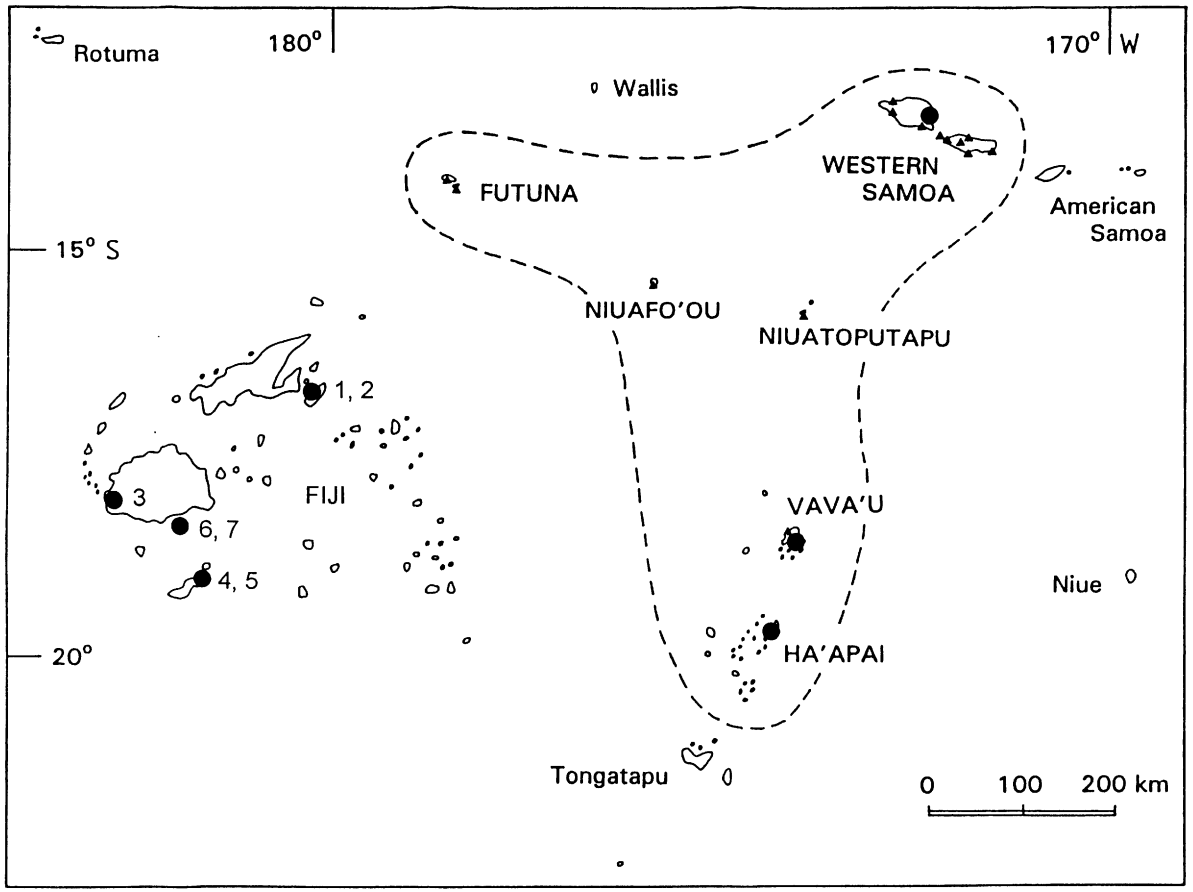

Fig. 1. Distribution of *Emoia tongana*. The triangles denote specimen-vouchered localities; solid circles are localities from which the tissue samples derive, and the numbered Fijian localities correspond to those of the *E. concolor* localities in Table 1 and Fig. 3. (After Zug and Gill 1997).

Vava'u, Vava'u Group, Tonga. Although we have been unable to confirm Friedlaender's itinerary in the Tongan islands, *E. tongana* is not known from Tongatapu, and Neiafu was a common port of call for 19th century shipping.

Thus, we use *Emoia tongana* (Werner) throughout this report.

Materials and Methods

Morphological analysis of *Emoia tongana* was repeated with the addition of specimens of *Emoia concolor* from Rotuma (BMNH 97.7.29.8) and Fiji (MCZ 16932-33, -37, -43, -44; CM 8142; all from Kadavu) to the original sample (Zug and Gill 1997). All institutional acronyms follow Leviton *et al.* (1985). We used the statistical program SYSTAT 6.

Tissue samples

Five *E. tongana* from three localities (Samoa, Va'vau, Ha'apai), seven *E. concolor* from four localities (Taveuni, Viti Levu, Beqa, Kadavu), and a single individual each from the outgroup taxa *Sphenomorphus jobiense*, *E. adspersa*, and *E. cyanogaster* were used for this study (Table 1).

DNA isolation, amplification and sequencing

DNA was isolated from either muscle or liver tissues following the protocols of Hillis *et al.* (1990). Small tissue samples (~50 mg) were digested with 20 µl of 10 mg mL^{-1} proteinase K for 3 h at 60°C in a water bath.

The protocols of Palumbi *et al.* (1991) were followed to amplify double-stranded products. Two oligonucleotide primers were used with the polymerase chain reaction (PCR) to amplify and sequence both complementary strands of a 305 base-pair region of the mitochondrial *cytochrome b* gene. The primers used were L14841 and H15149 (Kocher *et al.* 1989). *Cytochrome b* was chosen because of its general utility for resolving divergences among vertebrates (Graybeal 1994) as well as its usefulness in resolving cryptic Pacific skinks (Bruna *et al.* 1995; Austin 1998, 1999). The specific thermal cycle used is as follows: (*i*) one cycle at 94°C × 3 min, 47°C × 1 min, and 72°C × 1 min; (*ii*) 34 cycles at 94°C × 45 s, 47°C × 45 s, and 72°C × 1 min; (*iii*) one cycle at 72°C × 6 min. PCR reactions were overlayed with three drops of mineral oil. PCR products were sequenced using ABI Prism dRhodamine terminator cycle sequencing kit. Sequences were determined on an ABI 377 DNA automated sequencer.

Phylogenetic analysis

Fifteen sequences were unambiguously aligned using Clustal V (Higgins *et al.* 1991) (see Appendix). *Emoia* belongs to the *Eugongylus* group of lygosomine skinks and trees were rooted using other *Emoia* as well as *Sphenomorphus jobiense*, a member of the lygosomine *Spenomorphus* group (Greer 1974;

Table 1. Species, museum identification numbers, and localities for specimens used in this study
Numbers in parentheses after species correspond to DNA sequences in the Appendix. All acronyms follow Leviton *et al.* (1985). See Fig. 1 for localities named

Genus	Species	Sample size	Museum accession numbers	Locality data
Sphenomorphus	*jobiense*	*n* = 1	TNHC 51276	Papua New Guinea
Emoia	*adspersa*	*n* = 1	USNM 323723	Samoa, Upolu
Emoia	*cyanogaster*	*n* = 1	USNM 333976	Vanuatu, Efate
Emoia	*concolor* (1,2)	*n* = 2	USNM 323523, -24	Fiji, Taveuni
Emoia	*concolor* (3)	*n* = 1	USNM 333224	Fiji, Viti Levu
Emoia	*concolor* (4, 5)	*n* = 2	USNM 333459, -61	Fiji, Kadavu
Emoia	*concolor* (6, 7)	*n* = 2	USNM 333338, -40	Fiji, Beqa
Emoia	*tongana* (1)	*n* = 1	USNM 322748	Samoa, Savai'i
Emoia	*tongana* (2, 3)	*n* = 2	USNM 333672, -73	Tonga, Vava'u
Emoia	*tongana* (4, 5)	*n* = 2	USNM 333761, -62	Tonga, Ha'apai

Hutchinson 1993). Maximum parsimony, maximum likelihood and minimum evolution were the three optimality criteria used to assess phylogenetic relationships (Edwards 1972; Felsenstein 1981).

The presence of a bias in the type of base substitutions has been well documented (Brown *et al.* 1982; Vigilant *et al.* 1989; Knight and Mindell 1993; Thorpe *et al.* 1994). Transitions generally occur at a much higher frequency than transversions (Vigilant *et al.* 1989). Estimation of the transition/transversion bias from the data themselves may underestimate the ratio due to multiple substitutions (Purvis and Bromham 1997). Maximum likelihood was therefore used to estimate the transition/transversion (TI/TV) ratio.

All phylogenetic estimation was done using PAUP* test version 4.0d64, written by D. L. Swofford. For likelihood analyses, the two-parameter HKY85 model was implemented (Hasegawa *et al.* 1985) and rates were assumed to follow a gamma distribution with the shape parameter estimated via maximum likelihood. Starting branch lengths were obtained using the Rogers–Swofford approximation method. Molecular clock constraints were not enforced. Starting trees were obtained via stepwise addition. The branch-swapping algorithm used was tree bisection-reconnection (TBR). Steepest descent option was not in effect, and the MULPARS option was used. The branch and bound search option was used for parsimony, but all likelihood and minimum evolution searches were done using the heuristic search option in PAUP* with 100 random addition sequences.

Phylogenetic confidence

Confidence in the phylogenetic signal for the molecular data set was assessed in four ways. First, maximum parsimony, maximum likelihood, and minimum evolution were used to estimate a phylogenetic hypothesis. Second, all three analyses were bootstrapped to assess phylogenetic confidence for each node (Felsenstein 1985; Swofford and Olsen 1990; Hillis and Bull 1993). The degree of congruence between all analyses was used as an assessment of topological confidence. Third, for the parsimony analyses, signal to noise ratio was examined using the permutation-tailed-probability (PTP) test implemented in PAUP*. Finally, presence of a significant phylogenetic signal was assessed using the $g1$ statistic estimated from 100 000 random trees (Hillis and Huelsenbeck 1992).

Results

Morphology

Six meristic scalation (superciliaries, eyelid, dorsals, midbody, fore- and hindfoot fourth digital lamellae) proved to have the best discriminatory power although their use in a principal component analysis (PCA) showed no geographic segregation (Zug and Murphy 1997). Adding the only known Rotuman *'E. concolor*' specimen and six Fijian *E.concolor* to the original *E. tongana* sample yielded similar results with no clustering of any geographic subsample (Fig. 2). The Rotuman and Fijian specimens lay within the *E. tongana* cluster. The outlier is a Niuafo'ou *E. tongana* which has an anomalous number of hindfoot lamellae. The first three principal components account for 92.2% of the total variance (66.4, 14.7, 11.1%, respectively); fore- and hindfoot lamellae are the major loading characters on the first component, forefoot lamellae on the second, and dorsals on the third.

DNA sequences

In total, 305 unambiguously aligned sites for 15 taxa were used in the phylogenetic analysis (GenBank accession numbers AF151648–AF151662: Appendix). Of these, 106 sites were variable and 71 were parsimony informative. There were no insertions or deletions. For the entire data matrix a TI/TV ratio of 3.15 was estimated using maximum likelihood. Empirical base composition was: A = 0.257, C = 0.270, G = 0.168, and T = 0.305. The estimated value of the gamma shape parameter estimated via maximum likelihood was 0.233.

Maximum parsimony (MP), maximum likelihood (ML), and minimum evolution (ME) reconstructed a single tree with the same topology (Fig. 3). The single MP tree found was 325.6 steps in length and the –ln likelihood was 1225.917 for the ML tree. Fractional tree lengths result from non-integer estimates of the TI/TV ratio. All nodes of the resulting tree, except one, are well supported by bootstrap values (1000, 100 and 1000 pseudoreplicates for MP, ML and ME, respectively: Hillis and Bull 1993). The $g1$ (estimated from 100 000 randomly generated trees) was –0.87, indicating a significant phylogenetic signal ($P < 0.01$) (Hillis and Huelsenbeck

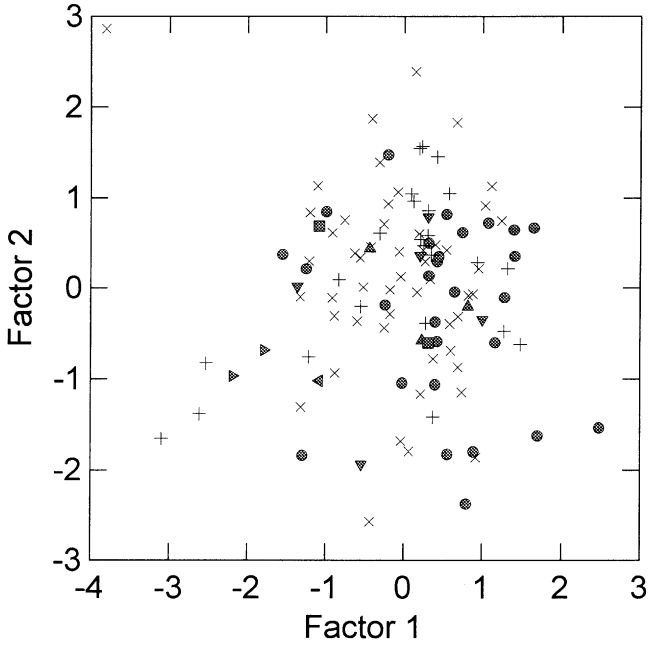

Fig. 2. Distribution of the individuals of the *Emoia tongana* sample in standardised Principal Components space (factor scores, from covariance matrix and no axis rotation). Each locality depicted by a different symbol: ●, Samoa; ×, Niuafo'ou; +, Vava'u; ▲, Ha'apai; ▼, Futuna; ◀, Rotuma; ▶, Fijian *E. concolor*; ■, syntypes of *Lygosoma cyanogaster tongana* Werner, 1899.

1992). The PTP test resulted in a significant (P = 0.01) difference between the most parsimonious tree and trees generated from random permutations of the data matrix, suggesting that significant phylogenetic signal was present.

The matrix for uncorrected and corrected pair-wise genetic distances for all nucleotide sites, is presented in Table 2. *Cytochrome b* is a protein-encoding gene and, as expected, most of the variation was at third-position sites (85/106) with fewer (21/106) changes at first and second positions.

Mean interspecific uncorrected pair-wise distances between *E. tongana* and *E. concolor* were 0.088 (s.d. = 0.004, range = 0.082–0.092). Within *E. concolor*, the mean uncorrected pair-wise distance between Viti Levu and Beqa was 0.018 (s.d. = 0.002, range = 0.016–0.02), between Viti Levu/Beqa and Kadavu it was 0.065 (s.d. = 0.002, range = 0.062–0.069), between Taveuni and Kadavu it was 0.074 (s.d. = 0.009, range = 0.066–0.082), and between Tavenui and Viti Levu/Beqa it was 0.083 (s.d. = 0.004, range = 0.079–0.088) (Table 2).

The five individuals of *E. tongana* are genetically identical, suggesting a very recent introduction across two archipelagoes and three populations (Savai'i, Samoa; Vava'u, Tonga; Ha'apai, Tonga) (Table 2, Fig. 3). In contrast, the seven individuals of *E. concolor* from Fiji show a strong population structure and relatively large levels of genetic divergence. For *E. concolor*, the intrapopulational variation ranges from <1% (0.0032) for Kadavu to approximately 4% (0.0393) for Taveuni and interpopulational variation ranges from 0.01795 between Beqa and Viti Levu to 0.0737 between Tavenui and Kadavu (Table 2). The Beqa and Viti Levu populations are genetically similar, which is not surprising given their geographic proximity: Beqa Island is a satellite of Viti Levu less than 10 km distant from the main island.

Table 2. Distance matrix of HKY'85 corrected genetic distances (above diagonal) (Hasegawa *et al.* 1985) and uncorrected *p* distances (below diagonal)

		1	2	3	4	5	6	7	8	9	10	11
1	*S. jobiense*	–	0.2338	0.2028	0.2259	0.2350	0.2173	0.2547	0.2546	0.2172	0.2176	0.2414
2	*E. adspera*	0.2000	–	0.2136	0.2241	0.2152	0.2515	0.2415	0.2414	0.2426	0.2471	0.2285
3	*E. cyanogaster*	0.1770	0.1803	–	0.2351	0.2168	0.1995	0.2257	0.2256	0.2085	0.2128	0.2182
4	*E. concolor* (1)	0.1934	0.1901	0.2000	–	0.0409	0.0915	0.0880	0.0880	0.0919	0.0956	0.1000
5	*E. concolor* (2)	0.2000	0.1836	0.1868	0.0393	–	0.0840	0.0693	0.0693	0.0845	0.0881	0.0925
6	*E. concolor* (3)	0.1868	0.2098	0.1737	0.0852	0.0786	–	0.0692	0.0655	0.0165	0.0200	0.1001
7	*E. concolor* (4)	0.2131	0.2032	0.1934	0.0819	0.0655	0.0655	–	0.0032	0.0695	0.0693	0.1000
8	*E. concolor* (5)	0.2131	0.2032	0.1934	0.0819	0.0655	0.0623	0.0032	–	0.0658	0.0731	0.1000
9	*E. concolor* (6)	0.1868	0.2032	0.1803	0.0852	0.0786	0.0163	0.0655	0.0623	–	0.0099	0.0928
10	*E. concolor* (7)	0.1868	0.2065	0.1836	0.0885	0.0819	0.0196	0.0655	0.0688	0.0098	–	0.0886
11	*E. tongana* (1–5)	0.2032	0.1934	0.1868	0.0918	0.0852	0.0918	0.0918	0.0918	0.0852	0.0819	–

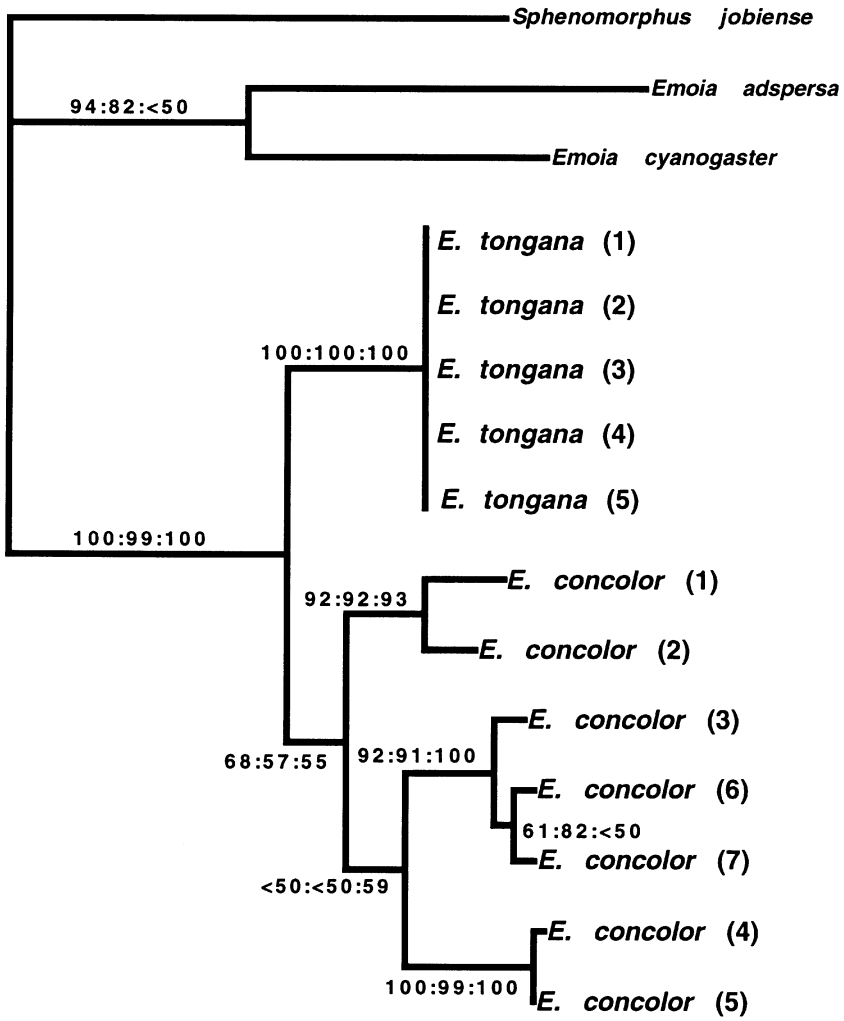

Fig. 3. Phylogram of the maximum likelihood tree obtained from PAUP* searches using *Sphenomorphus jobiense* as the outgroup. The maximum parsimony and minimum evolution trees are identical in topology to this tree. Numbers at nodes represent bootstrap proportions for 1000, 100, and 1000 pseudoreplicates for parsimony, likelihood, and minimum evolution analyses, respectively. Numbers after each taxon refer to sequence data in the Appendix and locality data in Table 1.

Discussion

Emoia tongana is similar in ecology, behaviour, body size, and coloration to *E. concolor* of the Fijian Islands (Zug and Gill 1997). Similarly, all aspects of scalation are shared by these two taxa, with their ranges of values strongly overlapping or identical. This similarity is evident in the position of the Rotuman and Fijian *E. concolor* within the *E. tongana* PCA morphological space (Fig. 2). Because of the similarity of these two species, geography and not morphology has been used to differentiate them. The identification of the Rotuman specimen as an *E. concolor* is questionable, because only *E. concolor* was recognised when the Rotuman specimen was collected in 1895 and that specimen, the only one from Rotuma, was properly assigned to *E. concolor*. The down-current proximity of Rotuma to Futuna and Samoa and the

Polynesian populace of Rotuma hints that the Rotuman population, if it still persists, is actually *E. tongana*.

On the basis of work by Thorpe *et al.* (1994), and González *et al.* (1996) on *Gallotia* from the Canary Islands, a very rough rule of thumb is that for *cytochrome b* approximately 24% sequence divergence relates to generic-level separation, 10–12% sequence divergence corresponds to specific-level separation, and 5% or less relates to subspecies-level separation. The mean sequence divergence between *E. tongana* and *E. concolor* is 8.8%, which borders on specific-level divergence. Sequence divergence within *E. concolor*, however, is also large (up to about 8%). Our results show that *E. tongana* is the sister lineage to the Fijian *E. concolor* although the bootstrap support for this is only moderate (68 : 57 : 55: Fig. 3). It is possible that inclusion of more samples of *E. concolor* in the future will show *E. concolor* to be non-monophyletic. On the basis of the relatively large levels of sequence divergence within *E. concolor*, this species may in fact represent several cryptic species: the degree of sequence divergence among geographically widespread populations suggests that considerable *in situ* evolution has occurred within the Fiji Archipelago.

Although the populations of *E. tongana* sampled are genetically identical, they are 8.8% divergent from the populations of *E. concolor* that we sampled. Further, the *E. tongana* clade is the sister lineage to the *E. concolor* clade (not nested within), and thus the geographic affinity and source population of *E. tongana* is unclear. The source population will be identifiable by sharing a similar genetic composition with the Tonga and Samoa populations although displaying more genetic (haplotype) diversity. Further sampling, presumably within the Fijian archipelago, is necessary to resolve this question. It appears that the Tongan colonisation in the 12th and 16–17th centuries is the likely dispersal agent of *E. tongana* into Tonga and Samoa from the Fiji Archipelago. It is possible that *E. concolor* simply represents a single species with a large degree of genetic population structure and that *E. tongana* represents one of those populations. Given the morphological, genetic, and phylogenetic information, however, it seems appropriate to continue to view *E. tongana* as a valid species.

These *E. tongana* data and the uniformity of central Oceania skinks confirms the influence of Polynesian voyagers on the inter-island-group transport of lizards and on the present distributional patterns of these lizards. Our data do not identify the source of the Samoan and Tongan *E. tongana*; we hypothesise that a population from Rotuma, Niuafo'ou, or an island of the Fijian Lau group served as the source. Our data also emphasise the necessity of broad and cautious analyses of the genetic composition of each Pacific taxon before drawing extensive biogeographic conclusions, and, further, the necessity of linking these genetic heritage data derived from molecular and morphological studies with species-occurrence data from pre-human fossil faunas. Only such combination will result in conclusions reflecting biological reality.

Acknowledgments

We thank the National Research Institute of Papua New Guinea, whose help made CCA's research in Papua New Guinea possible (Papua New Guinea export permits 900201, 910230, and 910275 to CCA). Guy Kula and Lester Seri from the Papua New Guinean Department of Environment and Conservation provided valuable assistance. Don Colgan provided encouragement and support with the laboratory component of this research. Don Colgan and Allen Greer provided valuable comments on an earlier version of this paper. David Swofford kindly provided access to early versions of PAUP*. CCA was supported by a National Science Foundation Postdoctoral Fellowship (INT 9505429) and a Myer Postoctoral Fellowship from the Evolutionary Biology Unit of the Australian Museum.

GRZ's research in Fiji, Samoa, and Tonga were approved and assisted by the Ministry of Primary Industries and Cooperatives, Department of Agriculture, Forests and Fisheries, and Ministry of Lands, Survey & Natural Resources, respectively. We thank these agencies and their staffs for this valuable support. GRZ's field and laboratory studies on the Pacific herpetofauna were possible through the support of colleagues and resources of the National Museum's

Department of Vertebrate Zoology, travel support from Transworld Airlines, and funding by the Smithsonian Scholarly Studies and the Research Opportunities Programs.

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Appendix. 305 base-pair sequence for 15 taxa for the *cytochrome b* gene aligned with the outgroup *Sphenomorphus jobiense*

Dots indicate a match with the first taxon, *S. jobiense*. The first base corresponds to the first position of a codon

```
S. jobiense           TTCGGATCTCTACTTGGAATTTGCCTAATCGCACAAGTATTCACAGGCCT
E. adspersa           ..T..T..A..TT.A..C..G.....T..TATT.....CA....C..A..
E. cyanogaster        ..T..C..C..C..A..TG.C.....T....TT.....GA....C..A..
E. concolor (1)       ..T..C..AT..T.A..GG.G.....T..AAT....A.CC.T........
E. concolor (2)       ..T..C..AT..T.A...G.G..T..T..AAT....A.TC.T........
E. concolor (3)       ..T..C..CT....A...G.G.........AT....A.TC..........
E. concolor (4)       ..T..C..CT..T.A...G.G.....TG.GAT....A.TC.T........
E. concolor (5)       ..T..C..CT..T.A...G.G.....TG.GAT....A.TC.T........
E. concolor (6)       ..T..C..CT....A...G.G.....C...AT....A.TC..........
E. concolor (7)       ..T..C..CT....A...G.G.........AT....A.TC..........
E. tongana (1-5)      ..T..C..CT..T.A...G.C.....T..TAT....A.TC.T........

S. jobiense           ATTTTTAGCAATACACTACACAGCAGATATCTCATCCGCTTTTTCATCAG
E. adspersa           .........C.....T...........C.....C..A..C........C.
E. cyanogaster        ...C.....C........T..............C..A..A........C.
E. concolor (1)       C..CC.......................C..T.....A..A........C.
E. concolor (2)       C..CC.......................C..T.....A..A........C.
E. concolor (3)       C..CC.......................C........A..A........C.
E. concolor (4)       C..CC.......................C........A..A........C.
E. concolor (5)       C..CC.......................C........A..A........C.
E. concolor (6)       C..CC.......................C........A..A........C.
E. concolor (7)       C..CC.......................C........A..A........C.
E. tongana (1-5)      T..CC.G.............................A..A........C.

S. jobiense           TTGCACACATCTGTCGCGACGTCCAATATGGGTGACTAATCCGAAACCTC
E. adspersa           .A..............A..T........C..C..G..T..T.....T...
E. cyanogaster        .C..C.....T.....A..............C..................
E. concolor (1)       .A...........C..............C..T.....T...........T
E. concolor (2)       .A...........C..............C..C.....T...........T
E. concolor (3)       .A...........C..............C..C.....T...........T
E. concolor (4)       .A...........C..............C..C..G..T...........T
E. concolor (5)       .A...........C..............C..C..G..T...........T
E. concolor (6)       .A...........C..............C..C.....T...........T
E. concolor (7)       .A...........C..............C..C.....T...........T
E. tongana (1-5)      .A.....................T.....C..C.....T..T.........

S. jobiense           CACGCAAACGGTGCCTCTCTATTCTTCATTTGTCTATACTTACATATTGG
E. adspersa           ..T..T.....G.....AA....T..T..C...A.T...C.C.....C..
E. cyanogaster        ..T..C.....A......A.G..T..T.....CA.C........C.....
E. concolor (1)       ..T..C.....A.....AA....T..T..C...A.T..TC.T...G....
E. concolor (2)       ..T..C.....A.....AA....T..T..C...A.T...C.T...G....
E. concolor (3)       ..T..C.....A..T...A....T..T......A.C...C.....G....
E. concolor (4)       ..T..C.....A.....AA....T..T.....CA.C...C.G...G....
E. concolor (5)       ..T..C.....A.....AA....T..T.....CA.C...C.G...G....
E. concolor (6)       ..T..C..T..G......A....T..T......A.C...C.....G....
E. concolor (7)       ..T..C..T..G......A....T..T......A.C...C.....G....
E. tongana (1-5)      ..T..C.....G.....AA....T..T.....CA.T...C....CG....
```

Appendix. *continued*

```
S. jobiense          CCGAGGCCTCTACTATGGCTCTTACATGTACAAAGAAACTTGAAACATTG
E. adspersa          .........A.............T....TT.............T....
E. cyanogaster       ...G.....A.....C.....G.................C........C.
E. concolor (1)      ..............C.....A.............G..C..........
E. concolor (2)      .........A.....C.....G..T.............C.....T..C.
E. concolor (3)      ......G..A.....C.....A.....A...........C.....T....
E. concolor (4)      ......A..A.....C.....A.....A...........C.....T..C.
E. concolor (5)      ......G..A.....C.....A.....A...........C.....T..C.
E. concolor (6)      ......G..A.....C.....A.....A...........C.....T....
E. concolor (7)      ......AT.A.....C.....A.....A...........C.....T....
E. tongana (1-5)     ......TT.A.....C.....A..T...........G..C.....T....

S. jobiense          GAGTAATTCTACTACTACTTGTAATAGCAACTGCCTTCGTAGGCTACGTA
E. adspersa          .T........T...T....A..T........C...........T..T..C
E. cyanogaster       .C........T.....C..C..T...........A.....G.....T..T
E. concolor (1)      .C..T..C...........GAC......T..A........C........C
E. concolor (2)      .C..T..C...........GAC......T..A........C........T
E. concolor (3)      .C..CG.C.........T.AAC......T..A..A.....C........C
E. concolor (4)      .C..T..C.....T...T.AAC......T..A........T........G
E. concolor (5)      .C..T..C.....T...T.AAC......T..A........T........G
E. concolor (6)      .C..CG.C.........T.AAC......T..A........C........C
E. concolor (7)      .C..CG.C.........T.AAC......T..A........C........C
E. tongana (1-5)     .C..CG.C...........GAC......T..A........T........C

S. jobiense          CTACC
E. adspersa          ..T..
E. cyanogaster       T....
E. concolor (1)      .....
E. concolor (2)      .....
E. concolor (3)      T....
E. concolor (4)      ..G..
E. concolor (5)      ..G..
E. concolor (6)      T....
E. concolor (7)      T....
E. tongana (1-5)     .....
```

Manuscript received 15 March 1999; accepted 7 June 1999