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Morphological and genetic evolution appear decoupled in Pacific skinks (Squamata: Scincidae: *Emoia*)

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SUMMARY

It has been suggested recently that morphological and genetic evolution may be decoupled in skinks, resulting in morphological similarity between species despite extensive genetic divergence. *Emoia cyanura* and *Emoia impar*, recognized recently as cryptic species of skinks sympatric throughout much of the Pacific, are here each shown to be composed of several genetically distinct (on the basis of mitochondrial DNA sequences) but morphologically similar lineages. Furthermore, similarly coloured polymorphic individuals are found in both species, and these individuals have the same mtDNA haplotypes as their sympatric conspecifics. Although the morphological similarity of cryptic species is usually attributed to recent speciation, this is ruled out in the case of *E. cyanura* and *E. impar*, as both species are more closely related genetically to other currently recognized species than they are to each other. We suggest a genetic review of current Pacific skink systematics, given the possibility that morphologically indistinguishable populations may in fact represent cryptic species.

1. INTRODUCTION

Pairs of morphologically similar congeneric species are often used in studies investigating the mechanisms of speciation because their similarity in morphology is usually attributed to recent common ancestry (see, for example, Diamond 1986; Grant 1986). This assumption is rarely tested, however, despite evidence that some morphologically indistinguishable (i.e. cryptic) species are as distinct from each other genetically as morphologically dissimilar species are (for examples, see Dobzhansky & Epling 1944; Patterson & Stone 1952; Boileau 1991; Hedges & Thomas 1991). When morphologically similar taxa are discovered, they provide an opportunity to investigate the ecological and evolutionary mechanisms that may have lead to their similar morphologies (reviewed in Larson 1989).

One group which may be prone to morphological stasis is the scincid lizards of the Pacific. Several studies have indicated that genetic divergence in skinks may proceed much more rapidly than morphological evolution (Donnellan & Aplin 1989; Donnellan & Hutchinson 1990; Hutchinson *et al.* 1990; Hickson *et al.* 1992; Austin 1995). As a result, widespread species as currently recognized from several genera may actually be collections of genetically distinct cryptic species (Donnellan & Aplin 1989; Donnellan & Hutchinson 1990; Hutchinson *et al.* 1990; Ineich & Zug 1991; Austin 1995). Some of these cryptic species have been identified on the basis of non-traditional

morphological characters (Greer & Mys 1987; Ineich & Zug 1991); however, most have been revealed by molecular methods.

The scincid genus *Emoia* is an exceptional system with which to test hypotheses of morphological and evolutionary divergence. Brown (1991) recognized 72 species of *Emoia*, all of which occur in Southeast Asia, the Indo-Australian archipelago and the islands of the Pacific. These 72 species were divided into eight groups or 'evolutionary lineages' based on morphological characters.

Within one of these groups, the *cyanura* group, are two species whose nearly identical morphology and coloration have led to nearly a century of taxonomic confusion: *Emoia cyanura* and *E. impar*. *Emoia cyanura* was believed to be the most widespread skink in the Pacific (Brown 1991; Ineich & Zug 1991) until it was shown to be a pair of cryptic, sympatric species based on five subtle morphological characters (Ineich & Zug 1991). Later, allozyme (Guillaume *et al.* 1994) and mitochondrial DNA sequence data (Bruna *et al.* 1995) supported the two species breakdown.

Studies comparing the morphological characters traditionally used to differentiate between *Emoia* species (see Brown 1991) have demonstrated almost complete morphological overlap between *E. cyanura* and *E. impar* (Ineich & Zug 1991; Zug 1991; Bruna *et al.* 1996), with the exception of those characters determined to be diagnostic. This overlap in morphology is found in several Pacific island groups, including Fiji, the Cook Islands and French Polynesia.

Further complicating classification is the presence of a similar colour polymorphism in both *Emoia cyanura* and *E. impar*. Whereas most *E. cyanura* and *E. impar*

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individuals are dark with three white dorsal stripes, individuals described as 'melanistic' (Oliver & Shaw 1953) or 'bronze' (Crombie & Steadman 1986) have themselves been recognized taxonomically (*Lygosoma arundeli*, Garman 1899; *Lygosoma cyanurum schauinslandi*, Werner 1901). Bronze individuals range in colour from uniformly dark brown (in *E. impar*; Garman 1899; Oliver & Shaw 1953; Crombie & Steadman 1986) to lacking stripes behind the head (*E. cyanura* only; Guillaume *et al.* 1994; Bruna *et al.* 1996). Whereas the uniform, distinct, bronze coloration of *E. impar* individuals may be due to higher levels of melanin, bronze coloration in *E. cyanura* could be the result of increased melanin or the loss of stripe expression. Melanistic and striped *E. impar* were shown to be genetically monotypic on the basis of allozymes (Guillaume *et al.* 1994); however, they were unable to determine if bronze and striped *E. cyanura* are genetically distinct (Guillaume *et al.* 1994).

The extensive distribution of some monotypic species of Pacific lizards (including *E. cyanura* and *E. impar*) is thought to be the result of recent, human-mediated dispersal (Kluge 1969; Dye & Steadman 1990; Brown 1991; Case *et al.* 1994). The nearly identical morphology and extensive ranges of *E. cyanura* and *E. impar* could be the result of recent speciation, followed by rapid and simultaneous dispersal across the Pacific. Extensive geographic range, however, has also been described as one feature which may indicate the presence of cryptic species (Baverstock *et al.* 1984). If morphological conservatism is a general feature of scincid evolution, then the extensive geographic ranges of *E. cyanura* and *E. impar* might actually represent the composite ranges of several cryptic species, rather than those of two species widely dispersed by humans.

2. MATERIALS AND METHODS

Mitochondrial DNA (mtDNA) sequences have been used extensively to infer phylogenetic relationships and test phylogeographic hypotheses (see recent studies by Joseph & Moritz 1993; Avise 1994; Lento *et al.* 1994; Malhotra & Thorpe 1994; Sturmbauer & Meyer 1994). We estimated the amount of genetic divergence within and between *E. cyanura* species by comparing 935 base pairs (b.p.) (with a few exceptions, see figure 1 legend) of the mtDNA gene cytochrome b (cyt b) from ten *E. cyanura* and ten *E. impar* collected in several regions of the Pacific as well as four *E. pseudocyanura*, one *E. isolata*, and one *E. caeruleocauda*. Three *E. cyanura* and *E. impar* sequences and the *E. caeruleocauda* sequence were from Bruna *et al.* (1995). Localities of collection of all individuals are listed in the Appendix.

DNA was isolated from all individuals using the sodium chloride extraction (Miller *et al.* 1988). The target locus was amplified by using the polymerase chain reaction (PCR) with published primers (Kocher *et al.* 1989; Palumbi *et al.* 1991; Richman & Price 1992; Radtkey *et al.* 1995). Sequencing template for seven individuals was generated using asymmetric PCR (Gyllenstein & Erlich 1988). For an additional nine individuals, template was generated using a TA cloning kit[®] (Invitrogen) following manufacturer's protocols. All templates were sequenced using Sanger *et al.*'s (1977) chain termination method.

We estimated the Jukes-Cantor (1969) genetic divergence between individuals by using the computer program PHYLIP

(Felsenstein 1989). A phylogeny of all haplotypes was created using the maximum parsimony algorithm of the computer program PAUP (Phylogenetic Analysis Using Parsimony, version 3.0s (Swofford 1990)). *E. caeruleocauda* was used as an outgroup. It is classified in a different subgroup of the *cyanura* evolutionary lineage as the other species considered in this study (Brown 1991). All substitutions were weighted equally. If several individuals had identical haplotypes, only one individual of that haplotype was used in the phylogenetic reconstruction. The confidence of each node was assessed by bootstrap analysis (400 replications).

Because there was a moderately high sequence divergence rate between some pairs of species, we were concerned about homoplasy from multiple substitutions confusing the phylogenetic signal. Consequently, we constructed a phylogeny based on weighting transitions less than transversions (which are less frequent). To determine the appropriate weighting factor, we did a linear regression on the number of transitions versus the number of transversions for all pairwise taxa comparisons with up to 12% sequence divergence (Sturmbauer & Meyer 1992). A phylogeny based on these weightings was then compared to the one reconstructed by weighing all substitutions equally.

All sequences are available in Genbank, under accession numbers U20451-U20457 and U49333-U49348.

3. RESULTS

(a) Phylogenetic analysis

There were three equally parsimonious trees with a minimum number of 534 changes and a consistency

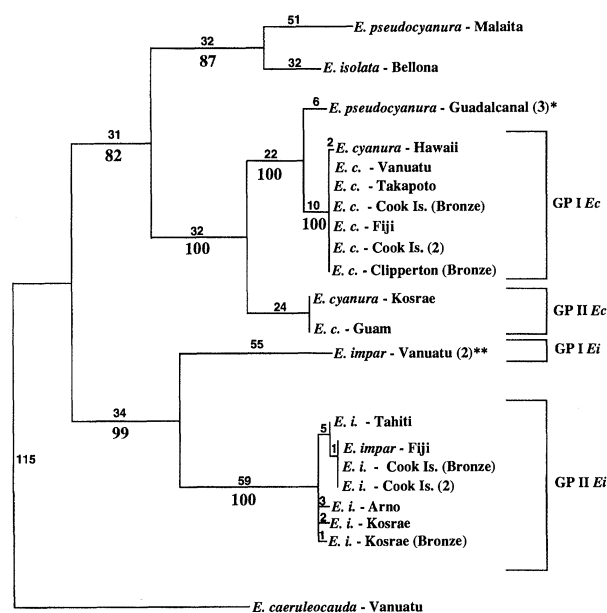


Figure 1. Phylogenetic tree depicting the relationships between five species of *E. cyanura* from different Pacific island groups inferred from 935 b.p. of the cyt b gene. Numbers above branches indicate the number of inferred nucleotide substitutions along that branch; those below branches are bootstrap frequencies (400 replications). The number in parentheses following the location indicates the number of individuals from that island sequenced if more than one. Bronze individuals are also indicated in parentheses. *E. cyanura* is abbreviated as Ec, *E. impar* is abbreviated as Ei. Group I and II Ec and Ei are denoted with brackets. *An 875 b.p. fragment was sequenced for individual number 2 and a 300 b.p. fragment for individual number 3; **a 470 b.p. fragment was sequenced for individual number 2

Table 1. Pairwise comparison of five *Emoia* species from several Pacific island groups.

(Numbers above the diagonal represent total changes between individuals, numbers below the diagonal represent the Jukes-Cantor genetic distances (number of nucleotide substitutions per site $\times 100$). For those localities with identical haplotypes, only one individual is listed. [*Emoia cyanura* from Rarotonga, Takapoto, Vanuatu, and Clipperton had the same haplotype. *Emoia cyanura* from Kosrae had the same haplotype as *E. cyanura* from Guam. *Emoia impar* from Rarotonga had the same haplotype as those from Fiji. Both *Emoia pseudocyanura* from Guadalcanal had the same haplotype, as did both *E. impar* from Vanuatu.] Brz = bronze individual.)

		1	2	3	4	5	6	7	8	9	10	11	12	13	
<i>E. pseudocyanura</i>	Malaita	1		129	83	160	129	125	134	149	140	129	139	139	140
<i>E. pseudocyanura</i>	Guadalcanal	2	15.71		111	172	18	16	50	148	140	129	136	141	144
<i>E. isolata</i>	Bellona	3	9.76	13.26		155	116	114	110	150	134	126	135	136	137
<i>E. caeruleocauda</i>	Vanuatu	4	20.45	22.09	19.67		174	174	158	164	172	166	170	173	175
<i>E. cyanura</i>	Hawaii	5	15.85	2.01	14.06	22.59		2	55	146	143	134	141	146	147
<i>E. impar</i>	Fiji	6	15.42	1.8	13.89	22.68	0.22		55	143	143	132	139	143	146
	Guam	7	16.31	5.65	13.09	19.92	6.29	6.32		148	143	133	140	143	147
	Vanuatu	8	18.43	18.15	18.5	20.85	18.05	17.77	18.08		117	110	112	114	115
	Fiji	9	17.46	17.46	16.66	22.55	18.04	18.17	17.79	14.26		1	7	6	5
	Tahiti	10	16.42	16.27	15.89	22.11	17.17	17	16.77	13.59	0.12		6	4	5
	Kosrae (brz)	11	17.38	16.96	16.88	22.34	17.8	17.65	17.43	13.64	0.79	0.7		3	3
	Kosrae	12	17.19	17.34	16.73	22.41	18.23	17.9	17.57	13.67	0.67	0.45	0.34		1
	Arno	13	17.07	17.53	16.64	22.36	18.1	18.1	17.86	13.63	0.55	0.57	0.33	0.11	

index of 0.76. The differences between these three trees are solely in the placement of three very similar *Emoia impar* taxa (Arno and the two Kosrae individuals) all within the same Group 2 clade, with the remainder of the tree unchanged. The consensus of the three trees is shown in figure 1. The ratio of transitions to transversions was 2.5:1 ($y = 2.5x + 4.9$, $r^2 = 0.955$). The consensus tree constructed by weighting base substitutions according to this ratio did not differ from the tree presented in figure 1 (which is based on transversions and transitions weighted equally).

(b) *Sequence divergence within Emoia cyanura, E. impar, and E. pseudocyanura*

Divergence between *Emoia impar* individuals from the Cook Islands, Tahiti, Fiji, Arno and Kosrae (henceforth referred to as Group II *E. impar*) was less than 1.0%. *Emoia cyanura* individuals from Hawaii, Fiji, Clipperton, Takapoto, Vanuatu, and the Cooks (Group I *E. cyanura*) differed from each other by less than 0.25%. *Emoia cyanura* from Guam and Kosrae (referred to as Group II *E. cyanura*) differed from Group I *E. cyanura* populations by 6.3%, and *E. impar* from Vanuatu (Group I *E. impar*) differed from Group II *E. impar* by 13%. Surprisingly, the *E. pseudocyanura* from Malaita differed from the Guadalcanal population by 16% and falls into a different clade, with *E. isolata* as its closest relative.

Percent sequence divergence and absolute genetic distance between and within taxa are listed in table 1. All bronze individuals had the same mtDNA haplotype as their conspecifics from the same population with the exception of Kosrae's bronze and striped *E. impar*, which differed by three base pairs.

(c) *mtDNA divergence between species*

Group I *E. cyanura* differed from Group II *E. impar* by 17–18% and from *E. isolata*, Guadalcanal *E.*

pseudocyanura, Malaita *E. pseudocyanura* and *E. caeruleocauda* by 15%, 2%, 15% and 23% respectively. Group II *E. cyanura* differed from Group II *E. impar* by 18% and from *E. isolata*, Guadalcanal *E. pseudocyanura*, Malaita *E. pseudocyanura* and *E. caeruleocauda* by 14%, 6%, 15% and 22% respectively. Group II *E. impar* were 19–22% divergent from *E. caeruleocauda*, *E. isolata*, Guadalcanal *E. pseudocyanura* and Malaita *E. pseudocyanura*. Group I *E. impar* were 18–21% divergent from *E. caeruleocauda*, *E. isolata*, Guadalcanal *E. pseudocyanura*, and Malaita *E. pseudocyanura* (table 1).

4. DISCUSSION

(a) *The ubiquity of cryptic species*

Perhaps the most surprising result is the potential presence of cryptic species within both the *Emoia cyanura* and the *E. impar* clades. *Emoia cyanura* from Guam and Kosrae, which have classically been identified as conspecific with to the other populations sampled (Brown & Falanruw 1972; Rodda *et al.* 1991; figure 1), are 6% divergent. This is almost three times the amount of mtDNA divergence by which *E. pseudocyanura* from Guadalcanal, considered a distinct species, differs from Group I *E. cyanura* populations. *Emoia impar* from Vanuatu is even more distantly related to its 'conspecifics', differing from Group II *E. impar* by 13% (figure 1). The monophyly of these genetic lineages is supported by bootstrap frequencies of 100%. Even more extreme is the level of divergence between *Emoia pseudocyanura* individuals from Malaita and Guadalcanal, which are not even monophyletic. Malaita's *E. pseudocyanura* is 16% divergent from its 'conspecifics' on Guadalcanal (which are part of the *cyanura* clade while Malaita's are not), and its monophyly with *E. isolata* is supported by a bootstrap frequency of 87%. When Brown (1991) described the species *E. pseudocyanura*, he noted that specimens from

Malaita differed slightly in colour pattern from those on Guadalcanal, and he decided not to include those Malaita specimens as paratypes for the species. It will be interesting to see where the Bougainville population, which differs in midbody scale rows (Brown 1991), falls with respect to the Guadalcanal and Malaita 'species'.

These levels of *cyt b* divergence are comparable to those found between the other species in this study, as well as between other congeneric species of reptiles (Hedges *et al.* 1991; Hickson *et al.* 1992; Thorpe *et al.* 1994; Radtkey *et al.* 1995; Radtkey 1996). A more complete morphological study of these species is clearly called for based on these molecular results. Careful reanalysis might discover subtle morphological differences which could be used to distinguish between allopatric, genetically distinct populations in both the *E. cyanura* and *E. impar* clades.

While morphological stasis in skinks has only recently been suggested, genetic divergence and morphological similarity have been well documented in plethodontid salamanders (reviewed in Larson 1989; Wake 1993). Speciation events in salamanders, as identified by fixed allelic differences (Larson 1984) and chromosomal variation (Sessions & Kezer 1987) are only occasionally accompanied by morphological changes (Larson 1989). In the Plethodontidae, morphological novelties are thought to occur at a much slower rate than genetic discontinuity, resulting in morphologically indistinguishable cryptic species. An alternate mechanism has been proposed for morphological similarity in Lake Tanganyika's *Tropheus* cichlid fish (Sturmbauer & Meyer 1994). In this case, common morphology is not due to a slower rate of evolution, because in a fraction of the time in which Lake Tanganyika's cichlids remained unchanged, a species flock of over 200 species flourished in Lake Victoria (Meyer *et al.* 1990). The common morphology in these cichlids is thought to be maintained by stabilizing selection due to ecological niche packing (Sturmbauer & Meyer 1992). Finally, species might remain morphologically similar despite extensive genetic divergence due to stabilizing selection on morphology, convergence or parallel evolution following speciation due to similar evolutionary pressures in different locations (Cody 1969; Pianka 1973; Charlesworth *et al.* 1982; Charlesworth & Lande 1982; Wake *et al.* 1983; Turner 1986; Williamson 1987; Larson 1989; Sturmbauer & Meyer 1992). Extensive sampling and genetic analysis of geographically widespread skinks will likely reveal the presence of additional cryptic species, given the probable lack of gene flow between geographically isolated Pacific island groups.

(b) Are *Emoia cyanura* and *Emoia impar* closest relatives?

The *Emoia cyanura* and *E. impar* clades are not each other's closest relatives, therefore the high level of morphological similarity between them does not appear to be the result of recent speciation. Group I *Emoia cyanura* are closely related to Guadalcanal's *E. pseudocyanura*, however, differing by only 2%. This lower level of divergence, along with similarities in

coloration and scale counts (Brown 1991), suggests that *E. pseudocyanura* in Guadalcanal is a relatively recent speciation event from *cyanura* stock.

Five of the species included in this study have similarly striped back patterns (*Emoia cyanura*, *E. impar*, *E. isolata*, *E. pseudocyanura*, and *E. caeruleocauda*) as do several other species in the genus. Without a more thorough historical and ecological study, however, we cannot determine if morphological similarity in these species is the result of convergence on, or stabilizing selection for the striped pattern.

(c) Evolution of melanism

Bronze *cyanura* and *impar* individuals from Rarotonga have the same mtDNA haplotype as striped conspecifics from the same population, and the bronze *E. impar* individual from Kosrae differed from striped conspecifics on Kosrae by only three base pairs, indicating that bronze individuals are not a distinct species. The bronze *Emoia cyanura* from Clipperton has the same mtDNA haplotype as striped *E. cyanura* from Fiji.

Whereas colour polymorphisms are commonly found in invertebrates (see, for example, Sheppard & Cook 1962; Owen 1963; Hughes & Mather 1986), amphibians (see Volpe 1956; Matthews & Pettus 1966) and snakes (see Patch 1919; Klauber 1936; Wüster & Thorpe 1994), fewer examples are found in lizards (Schoener & Schoener 1976; Milton 1990; Brown *et al.* 1991; Ota *et al.* 1995; Radtkey *et al.* 1995; Forsman & Shine 1995). A potential advantage to melanism is increased efficiency in thermoregulation, especially in forested habitats where light may be patchy and lower in intensity. For example, differences in the rate at which solar radiation is converted into body heat have been documented in the adder *Vipera berus* (Andrén & Nilsen 1981), and differences in body temperature of melanistic and nonmelanistic garter snakes (*Thamnophis sirtalis*) have also been recorded (Gibson & Falls 1979). Melanism is potentially disadvantageous, however, if it increases predation risk. Melanistic individuals are potentially more visible to sight oriented predators and may be subject to predation in certain habitats (for examples, see Kettlewell 1955; Andrén & Nilsen 1981; Luiselli *et al.* 1994). Alternatively, melanistic individuals are hidden against other habitat backgrounds (Brown *et al.* 1991; Censky & Paulson 1992).

The physiological and molecular basis of melanism and stripe loss remains to be determined. Is it due to an increase in melanocytes or perhaps the suppression or loss of genes normally responsible for stripe production, and is the same mechanism operating in the both *E. impar* and *E. cyanura*? Without such information, it is impossible, at this stage, to know if the joint occurrence of so called 'bronze' individuals in both species is due to the inheritance of a polymorphism from a common ancestor or due to convergence at the level of the phenotype. The presence or absence of stripe/bronze polymorphisms in the several other species in figure 2 could shed some light on the question by the application of a parsimonious character reconstruction (Brooks & McLennan 1991). However, even this basic

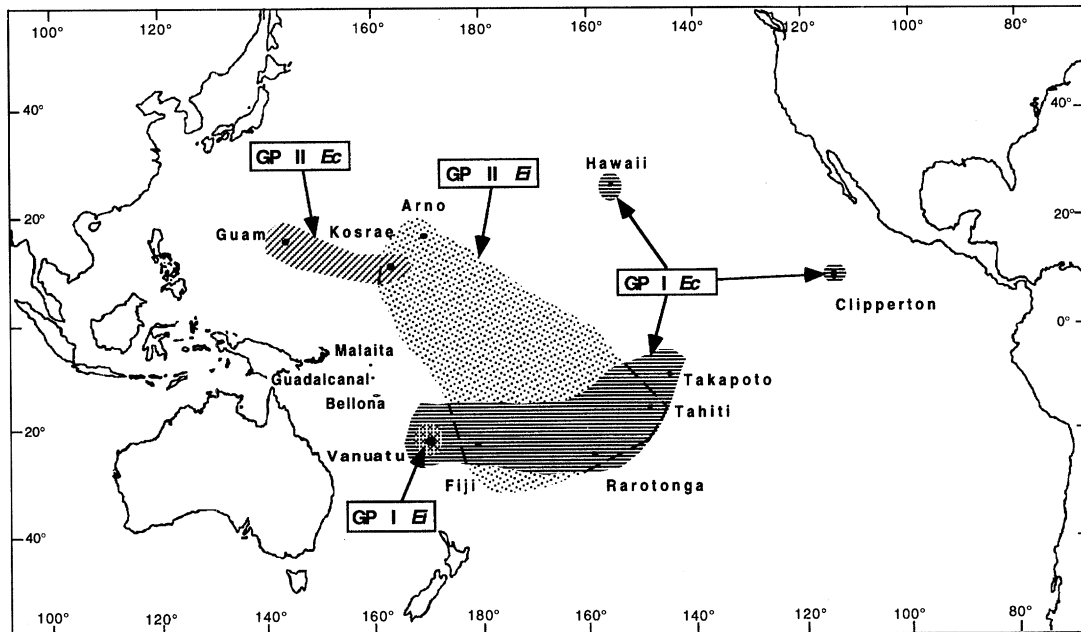


Figure 2. Distribution of Group I and II *Emoia cyanura* and Group I and II *E. impar* haplotypes (GP I *E. c.*, GP II *E. c.*, GP I *E. i.*, GP II *E. i.*, respectively) from populations included in this study. The complete range of the *E. cyanura* and *E. impar* morphotypes is given in Ineich and Zug (1991). *Emoia cyanura* and *E. impar* are found on several islands not included in this study, including the Solomon Islands and the Marquesas. *Emoia impar* is also present in Hawaii.

information is incomplete for these understudied species (Vanuatu 'impar' and Micronesia 'cyanura'). Moreover, similar looking phenotypes could result from fundamentally different molecular and physiological mechanisms confounding the application of parsimony based solely on phenotype.

Regardless of the historical evolutionary path of the colour polymorphism in the two species, the phenotypic similarity may be maintained by similar selection pressures. For example, bronze coloration in *Emoia* might be the result of selection based on predator defense and thermoregulation. On Rarotonga (Cook Islands), most bronze *E. impar* appear to be found in the forested interior of the island (G. McCormack, personal communication), although they have been captured along roadways and in open, disturbed habitats (Crombie & Steadman 1986; Bruna *et al.* 1996). Furthermore, a survey of bronze *E. impar* from museum collections indicates that they are found almost entirely on the high volcanic and forested islands of the Pacific (R.N. Fisher, unpublished results.), which may indicate that there can be a selective advantage to bronze coloration in darker, forested locations. A different mechanism may be operating on the *E. cyanura* population found on Clipperton Island's Black Rock. Although darker coloration may be detrimental to individuals in contrasting backgrounds, they may have higher survival in habitats in which the melanism acts as camouflage (Keister 1975; Rounsevell *et al.* 1985; Censky & Paulson 1992). Clipperton Rock is a large, black, volcanic outcropping (Skaggs 1989) in which it would clearly be advantageous to have dark coloration. Individuals which were striped rather than entirely bronze could easily be seen by birds and other predators. Selection might arguably favour the spread

of such a polymorphism, which would serve as a defence against predation.

(d) Implications for *Emoia* biogeography

The equator has previously been suggested to be a potential barrier to gene flow between conspecific populations north and south of the equator (R. N. Fisher, submitted). Populations of the gecko *Gehyra oceanica* from the north Pacific are genetically distinct from those in the south possibly due to ocean currents which flow east to west above and below the equator but never north to south, inhibiting gene flow (R. N. Fisher, submitted). In contrast, *Gehyra mutilata* is genetically monotypic across the entire Pacific, which points strongly to human mediated dispersal (R. N. Fisher, submitted). Although the observed distribution of *Emoia* haplotypes could be the result of localized adaptation, our results suggest a similar biogeographic pattern, with evidence of both genetic divergence north and south of the equator and dispersal by humans.

Based on their geographic distribution of *Emoia* haplotypes (figure 2), it appears that the immediate ancestor of the *E. cyanura/isolata/pseudocyanura* clade probably originated in the Solomon Islands in the southwestern Pacific (Brown 1991). One dispersal event across the equator resulted in the separation and subsequent allopatric speciation of Group II *E. cyanura*. The southern populations on Bellona and Malaita also became isolated and eventually distinct (*E. isolata* and both '*E. pseudocyanura*'). Finally, human dispersal (as indicated by highly similar mtDNA haplotypes) probably resulted in *E. cyanura*'s spread across the remainder of the South Pacific and into the geographically isolated islands of Clipperton and Hawaii.

The ancestor of the *Emoia impar* clade could have arisen in or near Vanuatu, and a single dispersal event, either to the eastern Pacific (perhaps Fiji) or to the north (the Micronesian region) may have resulted in the speciation of the Group II *E. impar*. There is only a hint of an equatorial division within the Group II *E. impar* (northern and southern populations differ by only about 1%) so the similarity in mtDNA sequences here supports the hypothesis that Group II *E. impar* have subsequently been dispersed more recently, perhaps by humans.

Future ecological studies of Pacific skink fauna should consider the possibility that morphologically similar populations can represent genetically and historically distinct cryptic species. Despite nearly identical morphologies, the high level of mtDNA sequence divergence between *Emoia cyanura* and *E. impar* clades suggests more ancient evolutionary divergence. This morphological similarity leaves open the question of ecological differences between these species when found in sympatry. Ongoing studies are investigating the selective pressures responsible for the high degree of morphological similarity and genetic differentiation.

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APPENDIX

The following *Emoia* individuals were used for phylogenetic reconstruction in this study. *Emoia cyanura* – Hawaii: Case Lab HBS 10755; Vanuatu: United States National Museum (USNM) 333977; Fiji: California Academy of Sciences (CAS) 196381; Clipperton, CAS 195918; Cook Islands: CAS 183331, CAS 196383, Case Lab RNF 0707 (bronze); Takapoto: Case Lab RNF 0784; Kosrae: CAS 183942; Guam: CAS 184020. *Emoia impar* – Fiji: CAS 196380; Cook Islands: CAS 183334, CAS 196382, Case Lab RNF 0661 (bronze), Case Lab RNF 0631 used in photo); Arno Case Lab TC 2157; Kosrae: CAS 183937, CAS 183951 (bronze); Vanuatu: USNM 333995, USNM 333997. *E. caeruleocauda* – Vanuatu: USNM 333959. *E. pseudocyanura* – Guadalcanal, Solomon Islands: tissue collected in the field by M. McCoy and shipped to our laboratory in ethanol; Malaita, Solomon Islands: tissue collected in the field by D. Maerufa and shipped to our laboratory in ethanol. *E. isolata* – Bellona, Solomon Islands: tissue collected in the field by M. McCoy and shipped to our laboratory in ethanol.

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