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BIOGEOGRAPHY OF EASTERN POLYNESIAN MONARCHS (*POMAREA*): AN ENDEMIC GENUS CLOSE TO EXTINCTION

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Abstract. The passerine genus *Pomarea* (monarchs, Monarchidae) is endemic to eastern Polynesia, where it is distributed on high volcanic islands of the Cook, Society, and Marquesas archipelagos. Recent extinctions of these birds have been documented on several islands, and most of the remaining forms are threatened by introducted rats (*Rattus rattus*) and habitat loss. We used mitochondrial DNA markers to develop a phylogeny of the entire genus *Pomarea*, including extinct taxa. This phylogeny was compared to geological data of the eastern Polynesian islands, with emphasis on the Marquesas archipelago where *Pomarea* has undergone its most extensive diversification. The phylogeny of *Pomarea* monarchs is consistent with the sequential appearance of the Marquesas islands. We approximated the ages of the lineages using molecular-clock and Bayesian methods that incorporate geological data. Both analyses showed differences of 1 to 2 million years between the ages of most islands and the ages of the nodes. We suggest that these differences are due to a latent period during which the islands were emergent but not successully colonized by *Pomarea* taxa. Phylogenetic hypotheses suggest that several species are polyphyletic. We outline the taxonomic consequences of our tree as well as implications for the evolution of sexual dimorphism in monarchs.

Key words: cytochrome b, extinction, Marquesas islands, molecular phylogeny, monarchs, Pomarea.

Biogeografía de *Pomarea*: Un Género Endémico del Este de Polinesia Cercano a la Extinción

Resumen. El género de aves paserinas *Pomarea* (Monarchidae) es endémico del este de Polinesia, donde se distribuye en las islas volcánicas de gran elevación de los archipiélagos Cook, Society y Marquesas. En varias islas se han documentado extinciones recientes de estas aves y la mayoría de las formas remanentes están amenazadas por ratas introducidas (*Rattus rattus*) y por la pérdida de hábitat. Empleamos marcadores de ADN mitocondrial para determinar la filogenia de todo el género *Pomarea*, incluyendo los taxones extintos. Esta filogenia fue comparada con datos geológicos de las islas polinésicas del este, poniendo énfasis en el archipiélago Marquesas donde *Pomarea* ha experimentado la diversificación más amplia. La filogenia de *Pomarea* es consistente con la aparición secuencial de las islas Marquesas. Estimamos las edades de los linajes usando los métodos de reloj molecular y Bayesiano que incorporan datos geológicos. Ambos análisis mostraron diferencias de 1 a 2 millones de años entre las edades de la mayoría de las islas y las edades de los nodos. Sugerimos que estas diferencias se deben a un período de latencia durante el cual las islas estuvieron emergidas pero no fueron colonizadas exitosamente por taxones de *Pomarea*. Las hipótesis filogenéticas sugieren que varias especies son polifiléticas. Destacamos las consecuencias taxonómicas de nuestro árbol así como las implicancias para la evolución del dimorfismo sexual en *Pomarea*.

INTRODUCTION

Islands and their inhabitants have commanded the attention of biologists, as they offer unique opportunities for study of evolutionary biology, biogeography, and applied ecology (Williamson 1981, Whittaker 1998). The fauna and flora of most oceanic islands are highly speciose and endemic, but the time of arrival of most organisms remains poorly documented, except in a few cases (Degnan et al. 1999, Thornton et al. 2002). In fact the process of colonization may be protracted, and can rarely be observed. Archipela-

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gos of volcanic origin are often characterized by the sequential appearance of islands. Successful colonizations and reduced gene flow among such islands are followed, with time, by processes of phenotypic differentiation, often considered adaptive (e.g., Lack 1976, Mayr and Diamond 2001), among populations of different islands. The possibility of dating the emergence of the different islands of an archipelago allows for the evaluation of the time of colonization by plants and animals, and has made them preferred subjects for the study of adaptive radiation (Nunn 1994).

Compared to other groups of organisms, birds in general have good dispersal abilities, and most oceanic islands have been colonized by one or more groups of landbirds (Newton 2003). Among forest birds, monarchs (Monarchidae), a group of passerines widespread in Africa and Australasia (Sibley and Monroe 1990), have been very successful in colonizing isolated islands, especially in the Pacific archipelagos from Melanesia to southeastern Polynesia. We focus here on one monarch genus, *Pomarea*, which is endemic to southeastern Polynesia (Murphy and Mathews 1928, Holyoak and Thibault 1984), with several taxa distributed on the high volcanic islands of the Cook (one taxon), Society (two taxa), and Marquesas archipelagos (seven taxa). This current patchy distribution strongly suggests that unrecorded taxa have disappeared from several other islands, for instance in the Society Islands (Holyoak and Thibault 1984). The Marquesas is the only archipelago where *Pomarea* taxa inhabited most islands, at least until the beginning of the twentieth century (Thibault and Meyer 2001).

The study of patterns of adaptive radiation requires phylogenetic hypotheses, which were often originally based on morphometric characters (Mayr 1940), and can now be supplemented (Grant 2001) or reconsidered (Zink 2002) by study of molecular-genetic characters. Moreover, the latter allow comparisons of the time of colonization given by the molecular clock and the age of islands (Fleischer and McIntosh 2001). In this paper, we use molecular markers to develop a phylogeny of the entire genus *Pomarea*, including recently extinct forms. We focus on Marquesan species because of robust geological data that can be combined with phylogenetic hypotheses, making the Marquesas a unique area for the study of island colonization among passerines. These results have important consequences for classification of the genus, and we outline the implications of this study for the evolution of sexual dimorphism in monarchs.

METHODS

DISTRIBUTION, STATUS, AND MORPHOLOGY OF THE GENUS *POMAREA*

Pomarea monarchs are restricted to the Cook, Society and Marquesas archipelagos (Table 1). Their taxonomy follows Murphy and Mathews (1928), who recognized six species: the Rarotonga Monarch (*Pomarea dimidiata*, monotypic), the Maupiti Monarch (*Pomarea pomarea*, monotypic), the Tahiti Monarch (*Pomarea nigra*, monotypic), the Marquesas Monarch (*Pomarea mendozae*, four subspecies), the Iphis Monarch (*Pomarea iphis*, two subspecies), and the Fatuhiva Monarch (*Pomarea whitneyi*, monotypic). *Pomarea* monarchs inhabit (or inhabited) all forested islands of the Marquesas, but are absent from smaller islands where woody vegetation has disappeared (Motu Iti) or is restricted to scattered *Pisonia grandis* trees (Hatuta‘a and Fatu Huku; Mueller-Dombois and Fosberg 1998).

Plumage evolution in *Pomarea* is complex. Two taxa, *P. nigra* and *P. whitneyi*, have black males and females. Adult males of all four subspecies of *P. mendozae* are also completely black. Adult females of *P. m. mira* and *P. m. nukuhivae* are black and white. Adult females of *P. m. mendozae* and *P. m. motanensis* are black and white, tinged with brown on the belly. Females of *P. m. mendozae* also have a brown tip to the tail. Adult males of *P. iphis* are black and white, and adult females are brown. The Cook archipelago’s only monarch (*P. dimidiata*) is dark slate gray above and white below for the males, and rufous brown for females. The extinct *P. pomarea* is only known from a painting of an ‘‘old male’’ (Lesson and Garnot 1826–1830), which exhibits a black and white pattern. Juveniles of all *Pomarea* taxa are brown.

All *Pomarea* monarchs (*P. pomarea* excepted) are represented by specimens in collections, the most complete being lodged at the American Museum of Natural History, and consisting of birds collected during the Whitney South Sea Expedition. This expedition took place in the early 1920s and included visits to every island of the Marquesas archipelago (January, September–October 1921, September–December 1922;

TABLE 1. Conservation status of the monarchs of eastern Polynesia (BirdLife International 2000).

Taxon	Authority	Archipelago	Island	Conservation status[a]
Rarotonga Monarch				
(*Pomarea dimidiata*)	Hartlaub and Finsch, 1871	Cook Islands	Rarotonga	Endangered
Tahiti Monarch				
(*P. nigra*)	Sparrman, 1786	Society Islands	Tahiti	Critical
Maupiti Monarch				
(*P. pomarea*)	Garnot, 1828	Society Islands	Maupiti	Extinct (1830s)
Iphis Monarch				
(*P. iphis fluxa*)	Murphy and Mathews, 1928	Marquesas	Eiao	Extinct (1977)
(*P. i. iphis*)	Murphy and Mathews, 1928	Marquesas	Ua Huka	Vulnerable
Marquesas Monarch				
(*P. m. mendozae*)	Hartlaub, 1854	Marquesas	Tahuata, Hiva Oa	Extinct (1922, 1975)
(*P. mendozae mira*)	Murphy and Mathews, 1928	Marquesas	Ua Pou	Extinct (1985)
(*P. mendozae nukuhivae*)	Murphy and Mathews, 1928	Marquesas	Nuka Hiva	Extinct (1930s)
(*P. mendozae motanensis*)	Murphy and Mathews, 1928	Marquesas	Mohotani	Endangered
Fatuhiva Monarch				
(*P. whitneyi*)	Murphy and Mathews, 1928	Marquesas	Fatu Iva	Critical

[a] For extinct taxa, the date of the last record appears in parentheses.

FIGURE 1. Map of the eastern Polynesian archipelagos, with the distribution of known *Pomarea* monarchs. The classification follows Murphy and Mathews (1928). Crosses indicate extinct taxa.

E. H. Bryan Jr., American Museum of Natural History, unpubl. data,). Murphy and Mathews (1928) based their revision of the genus *Pomarea* on these specimens and others stored at the British Museum of Natural History. During the course of their study, they described several new species and subspecies (Table 1).

GEOLOGY AND ECOLOGY OF POLYNESIAN ISLANDS

All islands of Polynesia are of volcanic origin. Each archipelago constitutes a ''hotspot'' where magma extrudes from the earth's mantle through the crust to build huge shield volcanoes. The weight of the new island, associated with motion from the hotspot, causes a relatively rapid decrease in island elevation and area, and ultimately the islands become atolls. The Cook and Austral Islands are distributed along a northwest–southeast axis extending 2300 km (Dupon 1993). The 14 volcanic islands of the Society archipelago spread 800 km, and the eight volcanic islands of the Marquesas spread 470 km along similar axes (Fig. 1). Whole-rock ^{40}K-^{40}Ar isotope ages are available for volcanism on all islands with monarch populations (Turner and

Jarrard 1982, Brousse et al. 1990, Desonie et al. 1993, Dupon 1993; Table 2). The age of an island is the maximum age for a population inhabiting it under the assumption that the birds colonized the island shortly after its emergence.

The islands vary in area, elevation, present type of vegetation, and annual rainfall (Table 2), ranging from large, high, humid islands such as Tahiti in the Society Islands, to small, low, and dry islands such as Eiao in the Marquesas. All biota have been extensively modified by human activities, first by Polynesian peoples, then by Europeans, with introductions of plants and animals and disruptions like hunting and fires (Steadman 1995, Kirch and Hunt 1997). The introduction of plants and animals continues to threaten these fragile island ecosystems (Meyer 2004).

PHYLOGENETIC ANALYSIS

Eighteen individuals representing all known species and subspecies of *Pomarea* monarchs were examined (see Appendix for sample origin and GenBank data). Outgroup taxa were selected on the basis of a previous study on monarchs (Pasquet et al. 2002), which showed that *Pomarea* belongs to a group of Australasian monarchs, but suggested no close sister group for this genus. Tissue samples for extant *Pomarea* taxa (*P. m. motanensis*, *P. i. iphis*, *P. whitneyi*, *P. dimidiata*, and *P. nigra*) were collected by JCT during several field trips in eastern Polynesia. A few tail feathers were plucked with clean tweezers from mist-netted birds before their release. Sequencing of the cytochrome *b* gene for extant *Pomarea* taxa was conducted at the Museum National d'Histoire Naturelle (MNHN) using primers L14990 and H15916 (Table 3), with protocols described in Pasquet et al. (2002). Sequences for all extinct and a few extant taxa were conducted from museum skins stored at the American Museum of Natural History. Museum samples were washed with sterile water before extraction, and total genomic DNA was extracted from small pieces (0.5–1 cm^2) of skin using a commercial kit (QiAMP Tissue Kit, Qiagen, Valencia, California). Standard extraction protocols were followed except that the time of proteinase digestion was increased from 2 to 12 hr, with an additional volume (20 μL) of proteinase K. All tubes and reagents were UV-treated for

TABLE 2. Age, location, area, elevation, present type of vegetation, and annual rainfall of islands with extant or extinct monarch populations. Data compiled from Turner and Jarrard (1982), Brousse et al. (1990), Dupon (1993), Robertson et al. (1994), Meyer (1996), Florence and Lorence (1997), Mueller-Dombois and Fosberg (1998), Thibault et al. (2002). See Figure 1 for locations of islands.

Island	Age (Ma)[a]	Area (km^2)	Elevation (m)	Present vegetation type	Annual rainfall (mm)
Rarotonga	ca. 2	67	653	native valley forest	2021–3250
Maupiti	4.4–4.5	12	372	native and secondary moist forests	no data
Tahiti	0.3–1.3	1045	2241	secondary valley forest and native cloud forest	2500–7000
Eiao	5.8–5.7, 5.3–5.0	40	577	dry native and secondary forests	500
Ua Huka	unknown, 2.9–1.4	83	884	native wet and cloud forests	1000
Nuku Hiva	4.8–3.1	339	1224	native wet and cloud forests	1495–3000
Ua Pou	4.5–2.7	105	1203	native moist and wet forests	no data
Hiva Oa	2.7–1.6	315	1276	native wet forest	1789–1816
Tahuata	2.9–1.7	61	1050	native valley, wet, and cloud forests	no data
Mohotani	unknown, 2.2–2.1	13	520	dry secondary forest, native dry and moist forests	500
Fatu Iva	2.4–1.8, 1.7–1.3	85	1125	native wet and cloud forests	1681

[a] Ma = millions of years. Several islands have undergone more than one phase of volcanic activity. Where this is the case, the dates of the phases are listed oldest first, and separated by a comma.

TABLE 3. Primers used for the amplification of a 925-bp portion of cytochrome *b* for *Pomarea* monarchs. The letters L and H refer, respectively, to the light and heavy strands, and the numbers refer to the base position at the 3′ end of the primer in the complete chicken mtDNA sequence (Desjardin and Morais 1990). All primers were specifically designed for this study except L14990 (Kocher et al. 1989; slightly modified from the original sequence), L15383 (Cibois et al. 1999), and H15916 (Edwards et al. 1991).

Primers
L14990-5′-CATCCAACATCTCTGCTTGATGAAA-3′
L15054-5′-ACAGGCCTACTACTAGCCATG-3′
L15134-5′-ACAATTCGGATGACTAATTCG-3′
H15173-5′-TCGGCCGATATGTAGGTAGATGC-3′
L15247-5′-CCTGAAACATTGGAGTCA-3′
H15337-5′-GGGATTGCTGAGAATAGGTT-3′
L15383-5′-GGACAAACACTAGTAGAATG-3′
H15397-5′-AGGATTGTCTACTGAGAA-3′
L15478-5′-CGTAATCGCAGGATTAACACTAG-3′
H15448-5′-ATGGTGTAGTATGGATGGAAGGGAA-3′
L15630-5′-ATTCATCCTACTAGCCACCCTC-3′
H15645-5′-GGTGTGAAGTTTTCTGGGTCTCCT-3′
L15745-5′-CATACGCCATCCTACGATCCA-3′
H15786-5′-GGAGTTAGGAATAGTACTAGGACT-3′
H15916-5′-ATGAAGGGATGTTCTACTGGTTG-3′

30 min before use, and extraction tubes containing no sample were used as a control for contamination. DNA extracted from museum skins was degraded, so fragment sizes for amplification were small (approximately 200 bp). Specific primers were designed for the *Pomarea* monarchs (Table 3), and a section of the cytochrome *b* gene was amplified using seven overlapping fragments. PCR amplifications were done in 25-μL reactions with 2 μL of template and 0.4 μM final concentration for primers. The thermocycling procedure was a hot-start PCR (HotStarTaq, Qiagen) with an initial denaturation of 15 min at 95°C, followed by 40 cycles of 30 sec at 95°C, 40 sec at annealing temperature (50°C), and 40 sec at 72°C for elongation. PCR products were purified using GeneClean (Bio101, Q-biogene, Carlsbad, California) kits. These products were resuspended in 12 μL of water, and then sequenced in an ABI 9600 thermocycler (Applied Biosystems, Foster City, California) in both directions in 7-μL total volume reactions containing 2.5 μL of PCR products, 3 μL of Terminator Mix (dRhodamine, Applied Biosystems) and 1.5 μL of primer (10 μM). Sequenced reactions were cleaned of excess nucleotides by ethanol precipitation, using 74 μL of a solution containing 10 mL of ethanol (70%) and 10 μL of magnesium chloride (0.5 M), dried and resuspended in 1.8-μL formamide loading dye. Reactions were then electrophoresed on an Applied Biosystems 377 automated sequencer. Contig alignments were created using Sequencher (Genecodes, Ann Arbor, Michigan). Accuracy of the DNA sequencing was verified by sequencing both heavy and light strands of PCR fragments.

Phylogenetic analyses were first performed under the maximum-parsimony (MP) criterion, conducted with PAUP* 4.0b10 (Swofford 2002). Tree topologies were evaluated with heuristic searches including 100 replicates of the random-taxon sequence-addition option with tree-bisection-and-reconnection (TBR) branch swapping. The robustness of the clades was assessed by bootstrap analysis with 1000 iterative resamplings using heuristic searches (Felsenstein 1985). Second, the data were analyzed under the maximum-likelihood (ML) criterion. The fit of several nested models was evaluated using the program Modeltest 3.06 (Posada and Crandall 1998), first given a neighbor-joining tree fitted to Jukes-Cantor distances (Jukes and Cantor 1969; this is the default option in ModelTest), second given the MP topology. Both searches gave the same model of evolution, selected by comparison of nested models with increasing complexity using the likelihood-ratio statistic ($-2\ln[\Delta L]$, where ΔL is the difference in log-likelihood between the two models tested). A ML search was conducted using the selected model and parameters, TBR branch swapping, with 100 replicates of the random-taxon sequence-addition option. The robustness of the clades was again assessed by bootstrap analysis with 100 iterative resamplings using the same parameters used for the ML search. Third, the data were subjected to Bayesian phylogenetic analyses, using both versions of MrBayes 2.01/3.0 (Huelsenbeck and Ronquist 2001). All runs were performed with the best ML model with all parameters estimated during the analysis, 250 000 generations, four chains running simultaneously from random tree (''heated'' chains), sampled every 10 generations, and with the ''burn-in'' period estimated graphically (Huelsenbeck et al. 2002).

Different topologies as well as different *a priori* hypotheses regarding the position of particular taxa were compared using both the Shimodaira-Hasegawa (SH) test statistic (Shimo-

daira and Hasegawa 1999), and the SOWH test (Goldman et al. 2000). We used PAUP* to conduct SH tests, with resampling estimated log-likelihood (RELL) optimization and 100 000 bootstrap replicates. The protocol suggested in Goldman et al. (2000) was followed to perform the SOWH test, using the program Seq-Gen 1.2.5. (Rambaut and Grassly 1997) to generate 100 simulated data sets via parametric bootstrapping (general time reversible model, option REV).

We conducted two analyses to estimate divergence times among monarchs. First a calibration was used under the hypothesis of a molecular clock. This hypothesis was first tested by comparing the likelihood of the ML tree with and without a molecular clock imposed, using a likelihood-ratio test (Swofford et al. 1996) that assumes that the test statistic follows a chi-square distribution with $n - 2$ degrees of freedom, where n is the number of taxa (Felsenstein 1988). We used the evolutionary rate proposed by Fleischer et al. (1998) of 1.6% divergence per million years (Ma) as the best estimate for passerine cytochrome *b* divergence. Second, we used Bayesian methods to estimate divergences times for the *Pomarea* monarchs (Thorne et al. 1998, Kishino et al. 2001). These methods do not assume a molecular clock and allow for multiple geological or fossil calibrations to be included simultaneously in the analysis in the form of constraints on divergence times. In this case, only geological information on Marquesan islands were used as constraints, as fossils for *Pomarea* are unknown (Steadman 1989). Because of computational limitations, the data set was restricted to 13 taxa (see Appendix), with only one individual per taxon and fewer outgroups. The topologies used were either the ML tree (Fig. 2) or the more conservative topology shown in Figure 3. The branch length variance-covariance structure was estimated using the program *estbranches* (Thorne et al. 1998, Kishino et al. 2001), with model parameters calculated using PAUP* under the F84 model (Kishino and Hasegawa 1989). The output from *estbranches* was then used as the input file for the program *multidivtime* (Thorne et al. 1998, Kishino et al. 2001). The upper estimates for the age of islands were used as constraints in the analysis (see Table 2 for references and Fig. 2 for node numbering): Eiao (5.8 Ma, node 3), Nuku Hiva (4.8 Ma, node 4), Ua Pou (4.5 Ma, node 6), and Tahuata (2.9 Ma, node 7). Chains were run using all or a combination of these constraints. The oldest island age estimate (Eiao) was included in all analyses as the oldest estimate for the archipelago. Markov chain Monte Carlo analyses were run for one million generations, with chains sampled every 100 generations, after discarding the ''burn-in'' of 100 000 generations. The convergence of posterior probabilities among runs was monitored.

RESULTS

SEQUENCES AND DIVERGENCE

New sequences obtained from the cytochrome *b* locus were deposited in GenBank under accession numbers AY262702–AY262718 (Appendix). The alignment was straightforward with no indels, as expected for a protein-coding gene. We translated the nucleotide sequences to proteins using MacClade (Maddison and Maddison 1992) and found no stop codons. We detected no contamination in the negative controls. Given the alignment of 925 bp, 27% of sites were variable, and 19% were parsimony-informative (Table 4). The distribution of the variation was codon-position dependent, with 16% of the variable characters in first position (15% for parsimony-informative characters), 0.06% in second (0.05% for parsimony-informative characters), and 77% in third position (79% for parsimony-informative characters). A few individuals shared the same haplotype: *P. i. iphis*_1 and *P. i. iphis*_2; *P. m. motanensis*_5, *P. m. motanensis*_6, and *P. m. mendozae*_2. Pairwise uncorrected sequence divergences varied from 0.2% between *P. m. motanensis*_3 and the haplotype of *P. m. motanensis*_5, to 11.6% between the outgroups Blue-mantled Paradise-Flycatcher (*Trochocercus cyanomelas*) and the Satin Flycatcher (*Myiagra cyanoleuca*). Among *Pomarea* taxa, the average was $3.8 \pm 1.8\%$, and among taxa endemic to the Marquesas Islands the average was $3.1 \pm 1.5\%$. We assessed saturation in our sequences by plotting the uncorrected sequence divergence versus the divergence based on transitions and transversions for each codon position: no saturation was detected among *Pomarea* sequences, except the third position showed multiple substitutions in the outgroups, indicated by a slight plateau in the curve (results not shown). Therefore no weighting schemes were applied to the data.

TABLE 4. Pairwise sequence divergence found in 925 bp of cytochrome *b* for *Pomarea* taxa (%, uncorrected value).

	1	2	3	4	5	6	7	8	9
1 *P. nigra*	—								
2 *P. dimidiata*	4.86	—							
3 *P. iphis iphis*	5.70	5.63	—						
4 *P. iphis fluxa*	6.80	5.26	5.36	—					
5 *P. whitneyi*	6.12	5.35	3.63	4.14	—				
6 *P. mendozae motanensis*	7.33	6.19	4.59	4.33	2.40	—			
7 *P. mendozae mira*	6.83	5.75	4.11	4.17	2.68	2.76	—		
8 *P. mendozae nukuhivae*	6.17	5.41	4.27	2.92	3.80	3.78	3.90	—	
9 *P. mendozae mendozae*	7.11	6.02	4.54	4.22	2.29	0.43	2.71	3.62	—

PHYLOGENETIC RECONSTRUCTION

Topologies differed slightly depending on the method used for phylogenetic reconstruction, with differences restricted to short branches. Trees from the different methods were, however, not significantly different from one another according to SH tests ($P = 0.33$ for MP-ML, 0.45 for MP-Bayesian, and 0.23 for ML-Bayesian tree comparisons). These uncertainties deal with (1) the relative position of *P. nigra* and *P. dimidiata* at the base of the *Pomarea* tree, and (2) the relative positions of *P. i. iphis*, *P. i. fluxa*, and *P. m. nukuhivae* among Marquesas monarchs. Parsimony analysis yielded three equally parsimonious trees (501 steps). Under the maximum-likelihood criterion, the model fitting the data best was the TVM + G model, which assumes equal substitution rates for transitions but different rates for transversions, and no invariant sites. The parameters estimated were the following: the probabilities for the six substitution types R_{mat} = (6.9498, 60.2190, 6.9198, 1.4828, 60.2190, 1), and shape parameter $\alpha = 0.1634$. Finally, there was no significant variation in the posterior probabilities among the different runs of the Bayesian searches. All methods of analysis supported the monophyly of the *Pomarea* taxa (Fig. 2). *Pomarea nigra* and *P. dimidiata* were basal and the Marquesas endemics formed a clade. *Pomarea iphis fluxa*, *P. mendozae nukuhivae*, and *P. i. iphis* formed a paraphyletic group with short branches. The remaining taxa were monophyletic, but their relationships were not fully resolved, apart for *P. m. mendozae* and *P. m. motanensis*. Among these, the individual from Hiva Oa (*P. mendozae mendozae*_9) was separated from the other *P. m. mendozae* and *P. m. motanensis* individuals (from Tahuata and Mohotani, respectively). We also investigated the significance of alternative topologies by testing first the monophyly of *Pomarea iphis* (i.e., *P. i. iphis* and *P. i. fluxa*), and second the monophyly of *Pomarea mendozae* (*P. m. mendozae*, *P. m. nukuhivae*, *P. m. mira*, and *P. m. motanensis*): both SH and SOWH tests indicated the rejection of the null hypothesis of monophyly ($P < 0.001$).

DATING

For estimating the age of *Pomarea* lineages we focused on the three best-supported nodes (labeled on Fig. 2): node 3, the separation between the basal Marquesan monarchs (*P. i. fluxa*, *P. m. nukuhivae*, and *P. i. iphis*) and an ancestral *Pomarea* stock; node 6, the divergence between the basal Marquesan taxa and the clade uniting *P. m. mira*, *P. m. mendozae*, *P. m. motanensis* and *P. whitneyi*; and node 7, the divergence between *P. m. mendozae–P. m. motanensis* and *P. m. mira–P. whitneyi*. The likelihood of the tree with a molecular clock imposed was not significantly different from the tree without a molecular clock ($P = 0.33$), suggesting no detectable rate variation among taxa. Thus, under the assumption that sequences of cytochrome *b* evolved in a clocklike fashion among monarchs, we estimated node 3 to be 3.6 ± 0.3 Ma, node 6, 2.5 ± 0.2 Ma, and node 7, 1.6 ± 0.1 Ma (using 1.6% sequence divergence per Ma). All Bayesian clock analyses converged to the following estimates for the nodes of interest: node 3 was estimated at 3.0 to 3.3 Ma, node 6 between 1.6 and 1.8 Ma, and node 7 between 0.41 and 0.45 Ma (intervals indicate values for the different runs, with different prior parameters for the Bayesian analyses and different combinations of geological constraints; values and SDs for the run using all four constraints were 3.2 ± 1.3 Ma,

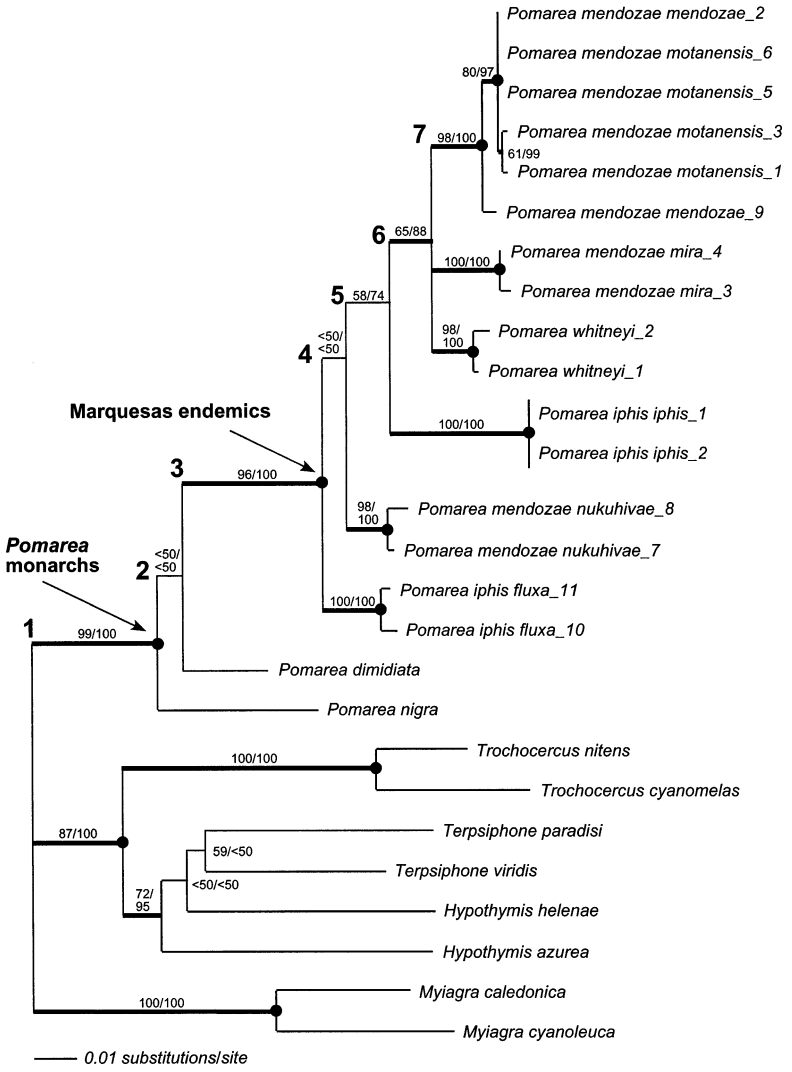

FIGURE 2. Phylogenetic tree for the *Pomarea* monarchs based on cytochrome *b* sequences. The maximum-likelihood (ML) topology is shown, and branch lengths are proportional to the number of substitutions per site. Numbers on branches indicate ML bootstraps and Bayesian posterior probabilities. Thick branches with a dot indicate clades that were recovered in all analyses with a posterior probability greater than 95% for the Bayesian analysis and with bootstrap support greater than 80% in the MP and ML searches. Thick branches without dots indicate clades that were recovered in all analyses but with lower support. Nodes among *Pomarea* monarchs are numbered from 1 to 7.

1.6 ± 0.7 Ma, and 0.4 ± 0.3 Ma for nodes 3, 6, and 7, respectively).

DISCUSSION

ORIGIN OF THE *POMAREA* MONARCHS

The taxa *P. nigra* and *P. dimidiata* are basal in the *Pomarea* phylogenetic tree, suggesting a southwest origin for the Marquesas endemics. The past occurrence of monarchs on other Society islands, like *P. pomarea* on Maupiti (the oldest island of the Society archipelago) indicates that *Pomarea* monarchs were probably more widespread in eastern Polynesia before the introduction of black rats (*Rattus rattus*; Thibault et al. 2002). *Pomarea dimidiata* inhabits Rarotonga, on the Cook-Austral chain, a moderately old island surrounded by several older ones, whereas *P. nigra* lives on a young island

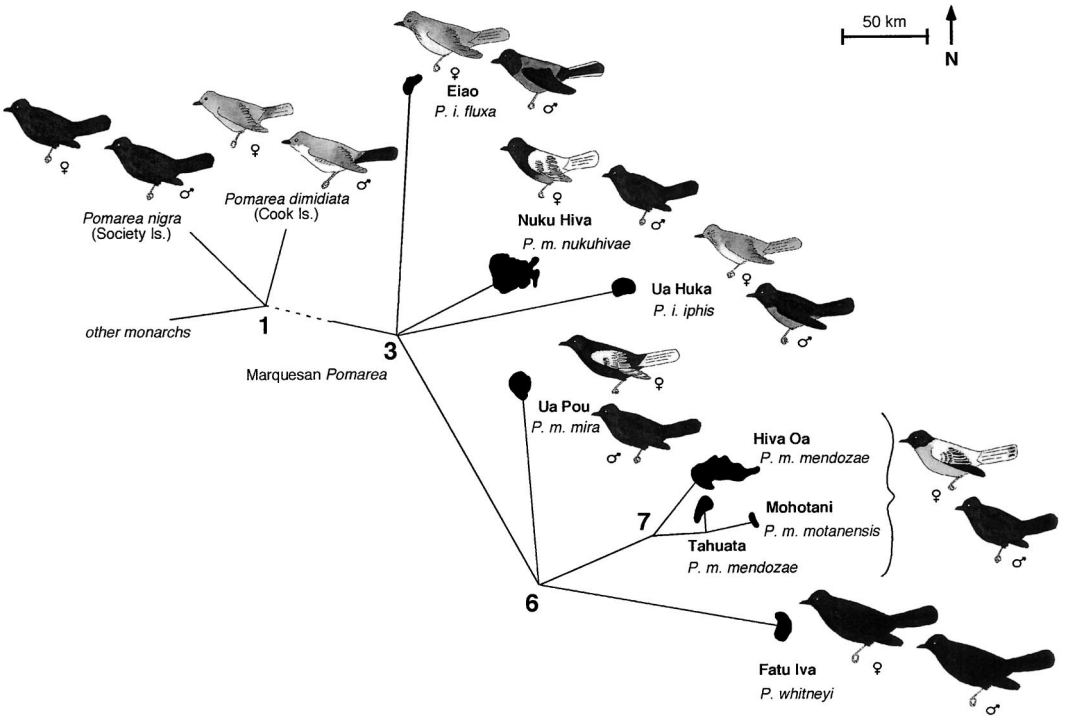

FIGURE 3. Phylogenetic tree for the *Pomarea* monarchs mapped on the Marquesas Islands (figures redrawn by P. Couprie from Holyoak and Thibault 1977). Branch lengths are not proportional to sequence evolution. *Pomarea* taxa endemic to other Polynesian archipelagos are connected to the Marquesan topology with a dashed line.

(Tahiti) whose emergence was contemporary with the youngest Marquesas islands (Table 2). It is possible that *P. nigra* was closely related to other monarchs from the Society Islands, now extinct.

The volcanic history (i.e., the date of change from volcano to atoll) of the Society and Marquesas Islands, respectively 5 and 6 Ma (Dupon 1993), was shorter than for the Hawaii Islands (16 Ma; Clague 2001), where the islands are larger. In the Marquesas, the oldest volcano (Eiao) is still above sea level. The diversification of the Marquesas monarchs follows a north–south pattern that corresponds to the sequence of appearance of the islands in the archipelago. Figure 3 maps the phylogenetic relationships of *Pomarea* monarchs onto the islands. Three taxa, *P. i. fluxa*, *P. m. nukuhivae*, and *P. i. iphis*, are basal in the tree with uncertainty with regard to their relative positions. The remaining taxa, *P. m. mira*, *P. m. mendozae*, *P. m. motanensis*, and *P. whitneyi*, form a clade in which a close relationship is suggested between *P. m. mendozae* and *P. m. motanensis*, especially between taxa from Tahuata (*P. m. mendozae*) and Mohotani (*P. m. motanensis*). This result is consistent with the proximity of the islands and the possibility either of gene flow between the islands or incomplete lineage-sorting among taxa.

DATING OF THE MARQUESAN COLONIZATION

The dating of node 3 (the separation of the basal Marquesan monarchs, *P. i. fluxa*, *P. m. nukuhivae*, and *P. i. iphis*, from an ancestral *Pomarea* stock) is the same with the two methods of calibration. It suggests that the colonization of the oldest Marquesan islands by a *Pomarea* ancestor took place 1 or 2 Ma after the emergence of the oldest islands (Eiao, 5.8 Ma, and Nuku Hiva, 4.8 Ma). Ua Huka is supposedly much more recent (2.9 Ma), but the age of this island is probably underestimated because the dating was made on the more recent internal volcano and the oldest external volcano has not been studied yet (Brousse et al. 1990). The two methods differ on the calibration of nodes 6 and 7, with a 1-

Ma difference between estimates based on molecular clock and on geological data. Explaining this discrepancy is difficult: one possibility is an acceleration of the rate of sequence evolution among these taxa, undetected by the likelihood-ratio test, but important enough to be noticeable in an analysis that does not impose a molecular clock. The birds of clade 6 inhabit the youngest islands of the archipelago, Hiva Oa, Mohotani, Tahuata, and Fatu Iva (Table 2).

Despite discrepancies for the most recent nodes, both methods of analysis agree that the divergences observed in the sequences from the extant taxa (including some that became extinct in historical times) are more recent than the estimated ages of the islands of the archipelago. Two explanations, at least, are possible. First, the sequence divergences and the phylogeny observed at present do not reflect the true evolution of the taxa but only the most recent events of speciation, which were preceded by a more ancient history of speciation and extinction of lineages. The scenario is, however, not testable in the absence of fossil data for *Pomarea* monarchs in Polynesia (Steadman 1989). Moreover, the cluster of extant and recently extinct taxa, coherent with the sequential appearance of the islands, suggests that the mtDNA gene tree accurately portrays the history of these taxa (Moore 1995). Thus we favor a second explanation, in which the differences between the ages of the islands and the ages of the nodes are due to a latent period ranging from 1 to 2 Ma for most islands (more in the case of Ua Pou) during which the islands were emerging but not yet suitable for successful colonization by *Pomarea* taxa.

TAXONOMIC IMPLICATIONS AND CONSERVATION

Species definitions for the Marquesas monarchs have been traditionally based on morphology (Murphy and Mathews 1928, Holyoak and Thibault 1984). Plumage coloration and size were the two factors used for the distinction of the three species of the archipelago: (1) *Pomarea iphis* (Iphis Monarch), with two subspecies, *P. i. iphis* and *P. i. fluxa*, which share similar plumage patterns but inhabit two islands 160 km apart, (2) *Pomarea mendozae* (Marquesas Monarch), with four subspecies, *P. m. mendozae*, *P. m. motanensis*, *P. m. mira*, and *P. m. nukuhivae*, distributed on five islands, each subspecies differing from the other by the plumage coloration of the females, and (3) *Pomarea whitneyi* (Fatuhiva Monarch), found on only one island. This species' larger size and lack of sexual dichromatism are diagnostic. Ranking allopatric populations is a long-recognized challenge for the biological species concept (Cracraft 1983). As for many other allopatric populations of birds (Banks 1964), delimitations of species boundaries in insular monarchs were based more on an estimation of similarity than on a unique combination of characters. Results of our phylogenetic analysis suggest that taxa inhabiting each island of the Marquesas archipelago are reciprocally monophyletic, with the exception of taxa from Hiva Oa, Tahuata (both *P. m. mendozae*), and Mohotani (*P. m. motanensis*). Uncorrected genetic distances also show a relatively high degree of genetic differentiation between taxa: the average for all monarchs of the archipelago is 3.1 ± 1.5%, with a maximum value between *Pomarea iphis* subspecies (5.4% between the two allopatric groups). The mean divergence for the *P. mendozae* group is 2.2 ± 1.5%, with a maximum divergence of 3.8% between *P. m. nukuhivae* and the other *P. mendozae* subspecies. These genetic distances range above the level of divergence of cytochrome *b* sequences for most passerine species: 1.4% for *Phylloscopus collybita* (Helbig et al. 1996); 1.2% for *Petrochelidon fulva* (Kirchman et al. 2000); 1.3% for oropendolas (cytochrome *b* and ND2 sequences; Price and Lanyon 2002). Thus, the monophyly of the taxa found on each island, the islands' isolation, with large stretches of water between suitable habitats, and the morphological differentiation that is diagnostic for most populations, even if mostly based on female plumage, argue in favor of the recognition of more taxa at the species level under a phylogenetic species concept (Zink and McKitrick 1995). The only exception deals with the three closely related populations of Hiva Oa, Tahuata (both *P. m. mendozae*) and Mohotani (*P. m. motanensis*), which are unresolved in the phylogenetic tree, share little genetic divergence (0.4%) and very little morphological variation (only variation on the tip of the tail in females). Today, Hiva Oa is separated from Tahuata by a narrow channel (ca. 4 km), and present bathymetry (ca. 50 m depth) suggests that both islands were joined only a few thousand years ago and that their populations of monarchs were isolated rel-

TABLE 5. Proposed new classification for the *Pomarea* monarchs. See Table 1 for describers and conservation status.

Taxa	Location
Pomarea dimidiata	Rarotonga (Cook Islands)
Pomarea nigra	Tahiti (Society Islands)
Pomarea pomarea	Maupiti (Society Islands)
Pomarea iphis	Ua Huka (Marquesas)
Pomarea fluxa	Eiao (Marquesas)
Pomarea nukuhivae	Nuku Hiva (Marquesas)
Pomarea mira	Ua Pou (Marquesas)
Pomarea whitneyi	Fatu Iva (Marquesas)
P. m. mendozae	Hiva Oa, Tahuata (Marquesas)
P. mendozae motanensis	Mohotani (Marquesas)

atively recently. Mohotani is separated from Hiva Oa by a larger channel (17 km), but exchanges between populations could have occurred. The present situation, however, with only one population remaining on Mohotani, makes further studies of this hypothesis testable only with the use of additional museum skins. Thus, we propose a new classification for the *Pomarea* monarchs (Table 5).

Five of these taxa are now extinct (see Table 1 for details) and the others are threatened at different levels (Robertson et al. 1994, BirdLife 2000, Thibault and Meyer 2001). The introduction of the black rat since the late eighteenth century constitutes a major threat to the survival of these species (Robertson et al. 1998, Thibault et al. 2002). It has also been demonstrated that two introduced birds, the Indian Myna (*Acridotheres tristis*) and the Red-vented Bulbul (*Pycnonotus cafer*), are aggravating the decline of the Tahiti Monarch by their aggressive behavior (Thibault et al. 2002, Blanvillain et al. 2003). Populations on small islands are also endangered by the reduction of forest cover (e.g., on Mohotani only 15–20% of the native forest is left). Our primary recommendations for conservation of the remaining populations of Polynesian monarchs include (1) the prevention of black rat colonization in the islands they have yet to reach (e.g., Ua Huka); (2) rat control on islands already infested, to help stabilize or restore monarch populations (Thibault et al. 2002); and (3) translocation to predator-free islets, although such attempts will require restoration of native ecosystems (e.g., Mehetia in the Society Islands).

CONTRAST BETWEEN MORPHOLOGICAL TRAITS AND MOLECULAR PHYLOGENY

Phylogenetic reconstructions are crucial for understanding the function and evolution of sexual dichromatism (Badyaev and Hill 2003). Mapping basic plumage characters of *Pomarea* monarchs onto the molecular phylogeny based on the cytochrome *b* gene suggests several cases of convergence. First, if sexual dimorphism is simply treated as a single character, then our results show that the two *Pomarea* monarchs which do not exhibit sexual dimorphism in plumage coloration are located at opposite ends of the phylogenetic tree (basal for *P. nigra* and terminal for *P. whitneyi*). The sister taxon of *Pomarea* is still unknown, as the only other phylogeny of monarchs focused mainly on African taxa and did not include comprehensive taxon sampling for the whole family (Pasquet et al. 2002). However, it is more parsimonious in this case to infer that *Pomarea*'s most recent ancestor also exhibited plumage difference between males and females, a trait that is widespread among South Pacific monarchs (*Metabolus rugensis*, *Clytorhynchus* spp., *Myiagra* spp., some *Monarcha* spp., but no *Mayrornis* spp.). Similarly, other recent studies have suggested that sexual dichromatism is often an ancestral rather than a derived state (Burns 1998 for tanagers; Kimball et al. 2001 for *Polyplectron* pheasants).

Second, two main trends of plumage evolution are shown among sexually dimorphic Marquesan monarchs: (1) black males and bicolored females that are different from the immature plumage, and (2) bicolored males and brown females that are similar to the immatures. The traditional classification unites these morphotypes into two species, *P. mendozae* and *P. iphis*. However, the phylogenetic analysis showed the polyphyly of these groupings (Fig. 2). This suggests that similar plumage patterns arose independently during *Pomarea* evolution. Many molecular-phylogenetic studies have shown that bird species defined by plumage coloration were paraphyletic, suggesting convergent evolution (spinetails, Garcia-Moreno et al. 1999; Australian scrubwrens, Joseph and Moritz 1993; Blue Tit [*Parus caeruleus*] and Willow Tit [*Parus montanus*], Salzburger, Martens, and Sturmbauer 2002, Salzburger, Martens, Nazarenko et al. 2002; Galapagos finches, Zink 2002; Yellow Wagtail [*Motacilla flava*] and Citrine Wagtail [*Motacilla citreola*], Pavlova et al. 2003). The

causes of incongruence between morphological traits and phylogenies based on molecular characters are complex (reviewed in Funk and Omland 2003). When looking at the differences in morphology and coloration among the different taxa of *Acrocephalus* warblers and monarchs of the Marquesas archipelago, Murphy (1938:137) thought that they were ''undoubtedly mutational,'' with no ''conceivable causative relation to the environment.'' Holyoak and Thibault (1977) hypothesized a relationship between coloration pattern of monarchs and presence of sclerophyllous vs. humid forests: paler forms inhabit moderately elevated and dry islands, whereas darker ones are found on elevated and wet islands, which are also the youngest islands of the archipelago. For instance, monarchs of both sexes are black in Tahiti and Fatu Iva, two young islands covered originally by humid forests. This observation is in general conformity with Gloger's rule, defined as the expectation that plumages of birds are darker in more humid environments (Campbell and Lack 1985). Support for this rule has been provided for North American birds (Zink and Remsen 1986). Moreover, some immature plumages have been retained independently in females in the driest islands (*P. iphis* on Ua Huka, *P. fluxa* on Eiao, *P. dimidiata* on Rarotonga), whereas females distinct from immatures are found in wetter and higher islands. Nevertheless, this argument does not explain why males of the *mendozae* group are all black, virtually impossible to tell apart by plumage coloration, whereas females can be distinguished. The discovery of bone remains of an undescribed species of *Myiagra* on Ua Huka (Steadman 1989) suggests that several monarch species may have coexisted on one island. Therefore, further investigation, particularly paleontological, will be necessary to understand this phenomenon, which may involve sexual selection.

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LITERATURE CITED

BADYAEV, A. V., AND G. E HILL. 2003. Avian sexual dichromatism in relation to phylogeny and ecology. Annual Review of Ecology and Systematics 34:27–49.

BANKS, R. C. 1964. Geographic variation in the White-crowned Sparrow *Zonotrichia leucophrys*. University of California Publications in Zoology 70: 1–122.

BIRDLIFE INTERNATIONAL. 2000. Threatened birds of the world. Lynx Edicions, Barcelona, and BirdLife International, Cambridge, UK.

BLANVILLAIN, C., J. M. SALDUCCI, G. TUTURURAI, AND M. MAEURA. 2003. Impact of introduced birds on the recovery of the Tahiti Flycatcher (*Pomarea nigra*), a critically endangered forest bird of Tahiti. Biological Conservation 109:197–205.

BROUSSE, R., H. G. BARSCZUS, H. BELLON, J.-M. CANTAGREL, C. DIRAISON, H. GUILLOU, AND C. LEOTOT. 1990. Les Marquises (Polynésie française): volcanologie, géochronologie, discussion d'un modèle de point chaud. Bulletin de la Société géologique de France 6:933–949.

BURNS, K. J. 1998. A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): the role of female versus male plumage. Evolution 52:1219–1224.

CAMPBELL, B., AND E. LACK. 1985. A dictionary of birds. T and AD Poyser for the British Ornithologists' Union, Calton, UK.

CIBOIS, A., E. PASQUET, AND T. S. SCHULENBERG. 1999. Molecular systematics of the Malagasy babblers (Passeriformes: Timaliidae) and warblers (Passeriformes: Sylviidae), based on cytochrome *b* and 16S rRNA sequences. Molecular Phylogenetics and Evolution 13:581–595.

CLAGUE, D. A. 2001. The growth and subsidence of the Hawaiian-Emperor volcanic chain, p. 35–66. *In* A. Keast and S. E. Miller [EDS.], The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes. SBP Academic Publishing, Amsterdam.

CRACRAFT, J. 1983. Species concepts and speciation analysis. Current Ornithology 1:159–187.

DEGNAN, S. M., I. P. F. OWENS, S. M. CLEGG, C. C. MORITZ, AND J. KIKKAWA. 1999. MtDNA microsatellites and coalescence: tracing the colonization of Silvereyes through the southwest Pacific. Proceedings of the International Ornithological Congress 22:1881–1898.

DESJARDIN, P., AND R. MORAIS. 1990. Sequence and gene organization of the chicken mitochondrial genome: a novel gene order in higher vertebrates. Journal of Molecular Biology 212:599–634.

DESONIE, D. L., R. A. DUNCAN, AND J. H. NATLAND. 1993. Temporal and geochemical variability products of the Marquesas hotspot. Journal of Geophysical Research 98(N0.B10):17649–17665.

DUPON, J.-F. [ED.], 1993. Atlas de la Polynésie française. Editions de l'ORSTOM (Institut français de recherche scientifique pour le développement en coopération), Paris.

EDWARDS, S. V., P. ARCTANDER, AND A. C. WILSON. 1991. Mitochondrial resolution of a deep branch in the genealogical tree for perching birds. Proceedings of the Royal Society of London B 243: 99–107.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using bootstrap. Evolution 39: 783–791.

FELSENSTEIN, J. 1988. Phylogenies from molecular sequences: inference and reliability. Annual Review of Genetics 22:521–565.

FLEISCHER, R. C., AND C. E. MCINTOSH. 2001. Molecular systematics and biogeography of the Hawaiian avifauna. Studies in Avian Biology 22:51–60.

FLEISCHER, R. C., C. E. MCINTOSH, AND C. L. TARR. 1998. Evolution on a volcanic conveyor belt: using phylogeographic reconstruction and K-Ar based ages of the Hawaiian Islands to estimate molecular evolutionary rates. Molecular Ecology 7:533–545.

FLORENCE, J., AND D. H. LORENCE. 1997. Introduction to the flora and the vegetation of the Marquesas Islands. Allertonia 7:226–237.

FUNK, D. J., AND K. E. OMLAND. 2003. Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. Annual Review of Ecology and Systematics 34:397–423.

GARCIA-MORENO, J., P. ARCTANDER, AND J. FJELDSÅ. 1999. A case of rapid diversification in the Neotropics: phylogenetic relationships among *Cranioleuca* spinetails (Aves, Furnariidae). Molecular Phylogenetics and Evolution 12:273–281.

GOLDMAN, N., J. P. ANDERSON, AND A. G. RODRIGO. 2000. Likelihood-based tests of topologies in phylogenetics. Systematic Biology 49:652–676.

GRANT, P. R. 2001. Reconstructing the evolution of birds on islands: 100 years of research. Oikos 92: 385–403.

HELBIG, A. J., J. MARTENS, I. SEIBOLD, F. HENNING, B. SCHOTTLER, AND M. WINK. 1996. Phylogeny and species limits in the Palaearctic chiffchaff *Phylloscopus collybita* complex: mitochondrial genetic differentiation and bioacoustic evidence. Ibis 138: 650–666.

HOLYOAK, D. T., AND J.-C. THIBAULT. 1977. Habitats, morphologie et inter-actions écologiques des oiseaux insectivores de Polynésie orientale. L'Oiseau & Revue française d'Ornithologie 47:115–147.

HOLYOAK, D. T., AND J.-C. THIBAULT. 1984. Contribution à l'étude des oiseaux de Polynésie orientale. Mémoires du Muséum National d'Histoire Naturelle, Paris 127:1–209.

HUELSENBECK, J. P., AND F. RONQUIST. 2001. MrBayes: Bayesian inference of phylogenetic trees. Bioinformatics 17:754–755.

HUELSENBECK, J. P., B. LARGET, R. E. MILLER, AND F. RONQUIST. 2002. Potential applications and pitfalls of Bayesian inference of phylogeny. Systematic Biology 51:673–688.

JOSEPH, L., AND C. MORITZ. 1993. Phylogeny and historical aspects of the ecology of eastern scrubwrens *Sericornis* spp. Molecular Ecology 2:161–170.

JUKES, T. H., AND C. R. CANTOR. 1969. Evolution of the protein molecules, p. 21–132. *In* H. N. Munro [ED.], Mammalian protein metabolism. Academic Press, New York.

KIMBALL, R. T., E. L. BRAUN, J. D. LIGON, V. LUCCHINI, AND E. RANDI. 2001. A molecular phylogeny of the peacock-pheasants (Galliformes: *Polyplectron* spp.) indicates loss and reduction of ornamental traits and display behaviours. Biological Journal of the Linnean Society 73:187–198.

KIRCH, P. V., AND T. L. HUNT [EDS.]. 1997. Historical ecology in the Pacific Islands. Yale University Press, New Haven, CT.

KIRCHMAN, J. J., L. A. WHITTINGHAM, AND F. H. SHELDON. 2000. Relationships among Cave Swallow populations (*Petrochelidon fulva*) determined by comparisons of microsatellite and cytochrome *b* data. Molecular Phylogenetics and Evolution 14: 107–121.

KISHINO, H., AND M. HASEGAWA. 1989. Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order in Hominoidea. Journal of Molecular Evolution 29:170–179.

KISHINO, H., J. L. THORNE, AND W. J. BRUNO. 2001. Performance of a divergence time estimation method under a probabilistic model of rate evolution. Molecular Biology and Evolution 18:352–361.

KOCHER, T. D., W. K. THOMAS, A. MEYER, S. V. EDWARDS, S. PAABO, AND F. X. VILLABLANCA. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences 86:6196–6200.

LACK, D. 1976. Island biology illustrated by the land birds of Jamaica. Blackwell, Oxford, UK.

LESSON, R. P., AND P. GARNOT. 1826–1830. Zoologie. 2 Vol. + 1 atlas. *In* L. I. Duperrey [ED.], Voyage autour du monde, exécuté par ordre du roi, sur la corvette de Sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825. A. Bertrand, Paris.

MAYR, E. 1940. Speciation phenomena in birds. American Naturalist 74:249–278.

MAYR, E., AND J. DIAMOND. 2001. The birds of northern Melanesia. Oxford University Press, Oxford, UK.

MADDISON, W. P., AND D. R. MADDISON. 1992. MacClade: analysis of phylogeny and character evolution. 4.0. Sinauer, Sunderland, MA.

MEYER, J.-Y. 1996. Espèces et espaces menacés de la Société et des Marquises. Contribution à la biodiversité de la Polynésie française No. 1–5. Délégation à l'Environnement/Délégation à la Recherche, Papeete, French Polynesia.

MEYER, J.-Y. 2004. French Polynesia, p. 22–34. *In* C. Shine, J. K. Reaser, and A. T. Gutierrez [EDS.], Invasive alien species in the austral Pacific region. National reports and directory of resources. Global Invasive Species Programme, Cape Town, South Africa.

MOORE, W. S. 1995. Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus nuclear-gene trees. Evolution 49:718–726.

MUELLER-DOMBOIS, D., AND F. R. FOSBERG. 1998. Vegetation of the tropical Pacific islands. Springer-Verlag, New York.

MURPHY, R. C. 1938. The need of insular exploration as illustrated by birds. Science 88:533–539.

MURPHY, R. C., AND G. M. MATHEWS. 1928. Birds collected during the Whitney South Sea Expedition. V. American Museum Novitates 337:1–18.

NEWTON, I. 2003. The speciation and biogeography of birds. Academic Press, London.

NUNN, P. D. 1994. Oceanic islands. Blackwell, Oxford, UK.

PASQUET, E., A. CIBOIS, F. BAILLON, AND C. ERARD. 2002. What are African monarchs (Aves, Passeriformes)? A phylogenetic analysis of mitochondrial genes. Comptes-Rendus de l'Académie des Sciences. Paris, Sciences de la Vie 325:107–118.

PAVLOVA, A., R. M. ZINK, S. V. DROVETSKI, Y. RED'-KIN, AND S. ROHWER. 2003. Phylogeographic patterns in *Motacilla flava* and *Motacilla citreola*: species limits and population history. Auk 120: 744–758.

POSADA, D., AND K. A. CRANDALL. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818.

PRICE, J. J., AND S. C. LANYON. 2002. A robust phylogeny of the oropendolas: polyphyly revealed by mitochondrial sequence data. Auk 119:335–348.

RAMBAUT, A., AND N. C. GRASSLY. 1997. Seq-Gen: an application for the Monte Carlo simulation of DNA sequence evolution along phylogenetic trees. Version 1.2.5. Computer Applications in the Biosciences 13:235–238.

ROBERTSON, H. A., J. R. HAY, E. K. SAUL, AND G. V. MCCORMACK. 1994. Recovery of the Kakerori: an endangered forest bird of the Cook Islands. Conservation Biology 8:1078–1086.

ROBERTSON, H. A., E. SAUL, AND A. TIRAA. 1998. Rat control in Rarotonga—some lessons for mainland islands in New Zealand. Ecological Management 6:1–12.

SALZBURGER, W., J. MARTENS, AND C. STURMBAUER. 2002. Paraphyly of the Blue Tit (*Parus caeruleus*) suggested from cytochrome *b* sequences. Molecular Phylogenetics and Evolution 24:19–25.

SALZBURGER, W., J. MARTENS, A. A. NAZARENKO, Y.-H. SUN, R. DALLINGER, AND C. STURMBAUER. 2002. Phylogeography of the Eurasian Willow Tit (*Parus montanus*) based on DNA sequences of the mitochondrial cytochrome *b* gene. Molecular Phylogenetics and Evolution 24:26–34.

SHIMODAIRA, H., AND M. HASEGAWA. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Molecular Biology and Evolution 13:964–969.

SIBLEY, C. G., AND B. L. MONROE JR. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, CT.

STEADMAN, D. W. 1989. Extinction of birds in eastern Polynesia. A review of the record, and comparison with other Pacific island groups. Journal of Archaeological Sciences 16:177–205.

STEADMAN, D. W. 1995. Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. Science 267:1123–1131.

SWOFFORD, D. L. 2002. PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland, MA.

SWOFFORD, D. L., J. L. THORNE, J. FELSENSTEIN, AND B. M. WIEGMANN. 1996. The topology-dependent permutation test for monophyly does not test for monophyly. Systematic Biology 45:575–579.

THIBAULT, J.-C., J.-L. MARTIN, A. PENLOUP, AND J.-Y. MEYER. 2002. Understanding the decline and extinction of Monarchs (Aves) in Polynesian islands. Biological Conservation 108:161–174.

THIBAULT, J.-C., AND J.-Y. MEYER. 2001. Contemporary extinction and population decline of the monarchs (*Pomarea* spp.) in French Polynesia, South Pacific Ocean. Oryx 35:73–80.

THORNE, J. L., H. KISHINO, AND I. S. PAINTER. 1998. Estimating the rate of evolution of the rate of molecular evolution. Molecular Biology and Evolution 15:1647–1657.

THORNTON, I. W. B., S. COOK, J. S. EDWARDS, R. D. HARRISON, C. SCHIPPER, M. SHANAHAN, R. SINGADAN, AND R. YAMUNA. 2002. Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. VII. Overview and discussion. Journal of Biogeography 28:1389–1408.

TURNER, D. L., AND R. D. JARRARD. 1982. K-Ar dating of the Cook-Austral chain: a test for the hot-spot hypothesis. Journal of Volcanology and Geothermic Research 12:187–220.

WHITTAKER, J. 1998. Island biogeography. Ecology, evolution, and conservation. Oxford University Press, Oxford, UK.

WILLIAMSON, M. 1981. Island populations. Oxford University Press, Oxford, UK.

ZINK, R. M. 2002. A new perspective on the evolutionary history of Darwin's finches. Auk 119: 864–871.

ZINK, R. M., AND M. C. MCKITRICK. 1995. The debate over species concepts and its implications for ornithology. Auk 112:701–719.

ZINK, R. M., AND J. V. REMSEN JR. 1986. Evolutionary processes and patterns of geographic variation in birds. Current Ornithology 4:1–69.

APPENDIX. Sample data for individuals of *Pomarea* used in this study. AMNH = American Museum of Natural History, New York; MNHN = Muséum National d'Histoire Naturelle, Paris; MZC = Museum of Zoology, Copenhagen.

Taxon	Sample number	Collection locality	GenBank accession number
*Pomarea mendozae mendozae*_9[ab]	AMNH 196018	Hiva Oa, Marquesas	AY262707
*Pomarea mendozae mendozae*_2[ab]	AMNH 196154	Tahuata, Marquesas	AY262706
*Pomarea mendozae mira*_3[ab]	AMNH 195866	Ua Pou, Marquesas	AY262708
*Pomarea mendozae mira*_4[a]	AMNH 195867	Ua Pou, Marquesas	AY262709
*Pomarea mendozae motanensis*_5[a]	AMNH 199013	Mohotani, Marquesas	AY262712
*Pomarea mendozae motanensis*_6[a]	AMNH 196086	Mohotani, Marquesas	AY262713
*Pomarea mendozae motanensis*_1[b]	MNHN D54	Mohotani, Marquesas	AY262710
*Pomarea mendozae motanensis*_3	MNHN D61	Mohotani, Marquesas	AY262711
*Pomarea mendozae nukuhiva*_7[ab]	AMNH 195970	Nuku Hiva, Marquesas	AY262714
*Pomarea mendozae nukuhiva*_8[a]	AMNH 195969	Nuku Hiva, Marquesas	AY262715
*Pomarea iphis fluxa*_10[ab]	AMNH 195922	Eiao, Marquesas	AY262703
*Pomarea iphis fluxa*_11[a]	AMNH 195920	Eiao, Marquesas	AY262704
*Pomarea iphis iphis*_1[b]	MNHN D41	Ua Huka, Marquesas	AF135053
*Pomarea iphis iphis*_2	MNHN D42	Ua Huka, Marquesas	AY262705
*Pomarea whitneyi*_1[b]	MNHN D60	Fatu Iva, Marquesas	AY262717
*Pomarea whitneyi*_2	MNHN D55	Fatu Iva, Marquesas	AY262718
Pomarea dimidiata[b]	MNHN D44	Rarotonga, Cook Is.	AY262702
Pomarea nigra[b]	MNHN D43	Tahiti, Society Is.	AY262716
Trochocercus nitens[b]	MNHN 3–28	Cameroon	AF096470
Trochocercus cyanomelas	MZC 03874	Tanzania	AF096469
Terpsiphone paradisi[b]	MNHN 5–53	Laos	AF096466
Terpsiphone viridis	MNHN 2–23	Cameroon	AF094616
Hypothymis azurea	MNHN 4–10B	Thailand	AF096467
Hypothymis helenae	MZC 03728	Philippines	AF096468
Myiagra caledonica[b]	MNHN CG 1979–922	Loyalty Is.	AF096463
Myiagra cyanoleuca	AMNH FB1048	Australia	AF096464

[a] Sampled from museum skin.
[b] Individuals included in the reduced data set used to estimate divergence times.