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MOLECULAR SYSTEMATICS AND BIOGEOGRAPHY OF ANTILLEAN THRASHERS, TREMBLERS, AND MOCKINGBIRDS (AVES: MIMIDAE)

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ABSTRACT.—We constructed phylogenetic hypotheses for Greater and Lesser Antillean Mimidae, including five endemic species of tremblers and thrashers that represent the best plausible example of an avian radiation within the Lesser Antilles. Phylogenetic relationships were inferred from analysis of 3,491 base pairs (bp) of mitochondrial DNA (mtDNA) and roughly 780 bp of the nuclear-encoded myoglobin gene. We used a subset of mtDNA gene sequences and pcrRFLP analysis to evaluate the phylogeographic relationships among individuals representing island populations of the Brown and Gray tremblers (*Cinclocerthia ruficauda* and *C. gutturalis*), Pearly-eyed Thrasher (*Margarops fuscatus*), Scaly-breasted Thrasher (*Margarops fuscus*), and Antillean and continental populations of the Tropical (*Mimus gilvus*) and Northern mockingbirds (*Mimus polyglottos*). Phylogeographic analysis distinguished three strongly differentiated mtDNA clades among tremblers, as well as distinct southern (St. Lucia and Martinique) and northern (Dominica to Montserrat) mtDNA lineages of the Scaly-breasted Thrasher. Minor geographic subdivision was also observed between continental and Antillean populations of the Tropical Mockingbird. Phylogenetic analyses of species-level Mimidae relationships that are based on mtDNA and nuclear sequences provide strong support for the monophyly and Antillean origin of a clade that consists of the tremblers, Pearly-eyed Thrasher, and Scaly-breasted Thrasher, but reject the monophyly of the genus *Margarops*. Phylogenetic analysis cannot confirm the monophyly of all endemic Antillean mimids because of the apparently contemporaneous diversification of the Antillean White-breasted Thrasher (*Ramphocinclus brachyurus*) with the continental Gray Catbird (*Dumetella carolinensis*) and Black Catbird (*Melanoptila glabrirostris*). However, an insertion and a deletion in the myoglobin intron 2 sequence support grouping the West Indian thrashers and tremblers, from which we infer that the endemic Lesser Antillean mimids are an indigenous radiation. Assuming a constant mtDNA clock for the Mimidae, the splitting of the Northern and Tropical mockingbird lineages is roughly contemporaneous with the separation of the three trembler clades, as well as the two Scaly-breasted Thrasher clades. Application of a mitochondrial DNA clock ticking at 2% sequence divergence per million years (Ma), suggests that the history of the endemic thrasher and trembler lineage in the West Indies extends back about 4 Ma, and the three distinct clades of tremblers split about 2 Ma ago. *Received 12 August 1999, accepted 8 August 2000.*

AMONG BIRDS of the West Indies, few endemic radiations have resulted in sympatric daughter species, and certainly none are comparable to the radiations of Hawaiian honeycreepers (Drepanidinae) and Galapagos finches (Geospizinae). In the Lesser Antillean avifauna, the three endemic Mimidae genera *Margarops*, *Ramphocinclus*, and *Cinclocerthia* constitute the best plausible example of an autochthonous radiation. The five currently recognized species in those genera have partially overlapping distributions in the Lesser Antilles, and four are sympatric on the islands of St. Lucia and Martinique (Fig. 1). In the absence of a mimid phylogeny, however, it is not possible to determine whether the Lesser Antillean mimid endemics are monophyletic and thus represent an indigenous radiation within that island archipelago.

The principal objective of this study was to provide a phylogenetic hypothesis for the genera of mimids found within the Caribbean Basin and assess whether the endemic Lesser Antillean taxa were produced within the islands or represent multiple colonizations from the American continents. In addition to the endem-

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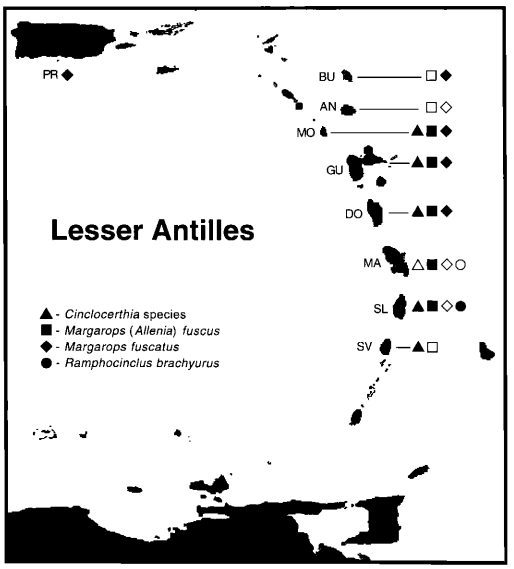

FIG. 1. The geographic distribution of the four species of thrashers and tremblers (Mimidae) found in the Lesser Antilles. Specimens included in this study were collected from islands represented by the filled symbols. Geographic abbreviations are as follows: Puerto Rico (PR), Barbuda (BU), Antigua (AN), Montserrat (MO), Guadeloupe (GU), Dominica (DO), Martinique (MA), St. Lucia (SL), and St. Vincent (SV).

ic thrashers and tremblers, our phylogenetic analysis includes the migratory Gray Catbird (*Dumetella carolinensis*) of North America, the Black Catbird (*Melanoptila glabrirostris*) of northern Central America, the Blue Mockingbird (*Melanotis caerulescens*) of Mexico, and three Caribbean-basin species of mockingbird (*Mimus*; Fig. 2). Our taxonomic sampling of the Mimidae included *Toxostoma* (*T. rufum* and *T. cinereum*) and *Oreoscoptes montanus*, but our initial molecular-systematic results indicated that *Dumetella* and *Melanoptila* are closer relatives of the Antillean-endemic thrashers and tremblers. Accordingly, we deleted *Toxostoma* and *Oreoscoptes* from the present analysis.

The second objective of this study was to provide a phylogeographic description of each West Indian mimid species for which we have moderate samples and broad geographic representation. These species are the Scaly-breasted Thrasher (*Margarops fuscus*), Pearly-eyed Thrasher (*M. fuscatus*), Brown Trembler (*Cinclocerthia ruficauda*), Gray Trembler (*C. gutturalis*), and Tropical and Northern mockingbirds. Finally, our analyses provide a molecular-systematic perspective on the taxonomic status of *Cinclocerthia* and *Margarops* and on the evolutionary status of subspecies in both these genera.

We sequenced the full mitochondrial ATP synthase 6 and 8 genes for two or more individuals representing all species and multiple geographic populations of Lesser Antillean mimids. Phylogenetic analysis of the ATPase sequences formed the basis of our biogeographic appraisal of the two *Margarops* species, *Cinclocerthia*, and the two widespread *Mimus* species. Mitochondrial genotypes were also determined for additional *Margarops fuscus* and *M. fuscatus* individuals using RFLP analysis of PCR-amplified ATPase fragments. Following our initial phylogenetic analyses of Caribbean mimids, we selected 11 species (including outgroups) and a second genetically differentiated population of *C. ruficauda* for a more detailed molecular-systematic analysis. Our phylogenetic hypothesis for Caribbean mimid relationships is based on direct sequence analysis of 3,491 base pairs (bp) of mitochondrial DNA (mtDNA) and approximately 780 bp that represent the nuclear-encoded myoglobin intron 2 and short regions of flanking exons 2 and 3.

STUDY AREA AND TAXA

The Lesser Antilles (Fig. 1) comprise a core chain of six medium-sized, volcanic, oceanic islands with high elevation and considerable environmental heterogeneity (Grenada, St. Vincent, St. Lucia, Martinique, Dominica, and Guadeloupe). Several smaller islands are distributed among the core chain including a group of smaller, more northerly volcanic islands that have high elevations (Montserrat through Saba), and an outer chain of low-lying, dry islands, that consist of uplifted marine sediments, also to the north (the eastern half of Guadeloupe through Anguilla). The Lesser Antilles, excluding Barbados, achieved their present geographic configuration by the middle of the Miocene, at least 15 Ma ago (Donnelly 1985, 1989, Iturralde-Vinent and MacPhee 1999).

We consider the Lesser Antillean archipelago to be considerably older than its contemporary avifauna (Ricklefs and Bermingham 1999). Nonetheless, the West Indian thrashers and tremblers are so distinctive that early workers grouped them variously with the ant thrushes, ovenbirds, wrens, and thrushes (see Gulledge 1975). By the beginning of the twentieth century, ornithologists had reached general agreement on grouping the Antillean forms together

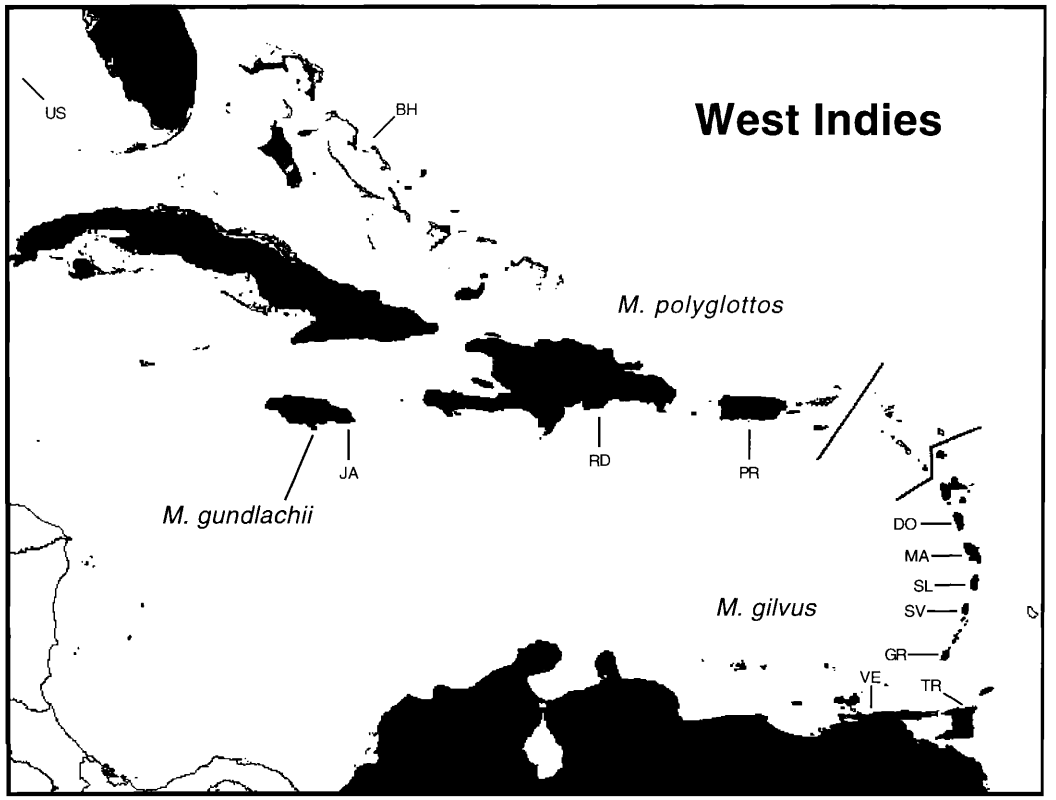

FIG. 2. The geographic distribution of the three species of mockingbirds (*Mimus*) found in the West Indies. Lines indicate the southern extent of *Mimus polyglottos* and the northern extent of *M. gilvus* in the Antilles. *Mimus gundlachii* is found on the Bahama Islands and keys off the northern coast of Cuba in addition to the Jamaican distribution pictured. Geographic abbreviations are as follows: United States (US), Bahamas (BH), Jamaica (JA) Dominican Republic (RD), Puerto Rico (PR), Dominica (DO), Martinique (MA), St. Lucia (SL), St. Vincent (SV), Grenada (GR), Trinidad (TR), and Venezuela (VE).

with other mimids as a separate family, the Mimidae. Nevertheless, the position of the Antillean thrashers and tremblers within that family, their relationships to each other, and diversification of each of the species among islands are still poorly understood.

Margarops and *Allenia* have always been grouped together and, indeed, are usually treated as congeneric (Bond 1950, 1963; AOU 1983). Similarly, *Ramphocinclus* and *Cinclocerthia* are often grouped together. Both Bond (1963) and Zusi (1969) noted similarities between skulls and plumage of those two species and those of the Blue Mockingbird (*Melanotis caerulescens*), which prompted inclusion of *Melanotis* in our analysis of the monophyly of Lesser Antillean tremblers and thrashers. The catbirds have been included in this study as possible close relatives of the Lesser Antillean mimids because of our preliminary phylogenetic analyses and their Caribbean Basin distribution. The migratory Gray Catbird breeds throughout most of North America and on the island of Bermuda and winters to the south in Central America and the Greater Antilles (AOU 1983). The Black Catbird has a Caribbean-slope distribution from northern Honduras to Yucatan, Mexico (AOU 1983). Our molecular-systematic analysis was rounded out with the mockingbirds of the genus *Mimus*, which are not considered closely related to the Antillean trembler, thrashers, or the catbirds and thus provided an unambiguous outgroup for evaluating relationships among those species. In addition, inclusion of Antillean *Mimus* species completed our phylogeographic appraisal of geographically widespread Antillean mimids.

MATERIAL AND METHODS

Field methods and tissue collection.—Samples were collected by mist-netting and imported under the appropriate permits during field work on the following islands: Bahamas, 1993; Barbuda, 1993; Domin-

ica, 1991; Grenada, 1992; Guadeloupe, 1993; Jamaica, 1995; Martinique, 1991; Montserrat, 1993; Puerto Rico, 1993 and 1994; Republic of Dominica, 1994; St. Lucia, 1991; St. Vincent, 1993; Trinidad and Chacachacare, 1995; and Venezuela, 1992. We drew blood and excised tissue samples nondestructively in accordance with our collecting permits following the procedure described by Baker (1981), except that we surgically removed a thin, triangular piece of the pectoral muscle. In the field, blood samples were stored at ambient temperature in Queen's lysis buffer and tissue samples were stored at ambient temperature in salt-dimethyl sulfoxide (DMSO) solution (Seutin et al. 1991). Our analyses include eight additional mimid samples representing other collections and four catalogued specimens (see Appendix).

Initially, we sequenced the mitochondrial ATP synthase 6 (ATPase 6, 684 bp) and 8 (ATPase 8, 168 bp) genes for two individuals that were randomly chosen from each species and each location where samples were available (Table 1). One representative of each species and mtDNA clade was selected for further sequencing of the following additional genes or gene regions: the complete sequence for mitochondrial protein-coding NADH dehydrogenase 2 gene (ND2, 1041 bp), partial sequences for the mitochondrial protein-coding cytochrome oxidase I gene (COI, 627 bp), and ribosomal genes (12S, 399 bp, and 16S, 572 bp plus or minus insertions and deletions), and approximately 780 bp representing the nuclear-encoded myoglobin gene.

DNA extraction, amplification, and sequencing.—DNA was extracted by digesting 0.1 to 0.5 g of ground pectoral muscle or 20 to 40 μL of blood in 500 μL of 2× CTAB buffer solution and 10 μL of a 10 mg/mL Proteinase K solution at 54°C for 6 to 14 h (Murry and Thompson 1980). A typical DNA extraction yielded a volume of 400 μL, of which 1 μL was used to seed our Polymerase Chain Reaction (PCR) amplifications.

Amplification of all mtDNA genes and gene regions was carried out in 50 μL reactions under the following conditions: 1 μL DNA (about 15–20 ng); 1× PCR Buffer II (Perkin-Elmer); 2.0 mM $MgCl_2$, 2 μM each of dATP, dCTP, dGTP, and dTTP; 2 pM of each primer; and 0.25 μL of Amplitaq polymerase (Perkin-Elmer). Reactions were denatured for 3 min at 94°C, followed by 25 thermal cycles of 94°C denaturing for 45 s, 54°C annealing for 45 s, and 72°C extension for 1 min, and terminated with a 5 min extension at 72°C. We used the following primer pairs to amplify the mtDNA gene or gene region specified: ATPase 6,8 gene region, COIIGQL, and COIIIHMH (see acknowledgements); cytochrome oxidase subunit I, COIa, and COIf (Palumbi 1996); NADH dehydrogenase subunit II, METb, and TRPc (see acknowledgements); 12S ribosomal RNA, 12SA, and 12SB originally described in Kocher et al. (1989) but modified as described by Palumbi (1996); and 16S ribosomal RNA, 16Sar, and 16Sbr (Palumbi 1996). The myoglobin gene region was amplified under the same conditions as the mitochondrial reactions, except that an annealing temperature of 60°C was used with the amplification primer pairs MYO2 and MYO3 (Slade et al. 1993) and MYO2 and MYO4 (TCTGGAGAGACAGTGAGGTCTAG).

Typically we observed a single amplification product, which was cut from the gel and extracted using the "Gene Clean II" kit (Bio 101, Inc., Vista, California) and resuspended in 25 μL of ddH_2O or the GELase™ Agarose Gel-Digesting Preparation and the "Fast Protocol" method (Epicentre Technologies, Madison, Wisconsin). Purified amplification products were cycle-sequenced using the Taq-DyeDeoxy Terminator Cycle Sequencing kit (Applied Biosystems, Inc., Forest City, California) and the following sequencing primers: ATPase 6,8, COIIGQL, A8PWL, A6TPL (see acknowledgements), and COIIIHMH; COI, COIa, and COIf (Palumbi et al. 1992); ND2, METb, ND2SCL, ND2LSH, and TRPc (see acknowledgements); 12s, 12SA, and 12SB (Palumbi 1996); 16s, 16Sar, and 16Sbr (Palumbi 1996); and myoglobin, MYO2, MYO3 (Slade et al. 1993), and MYO4. Sequencing conditions were 25 cycles of 96°C for 30 s, 50°C for 15 s and 60°C for 4 min. The cycle sequencing product was purified over Centri-Sep columns (Princeton Separations, Inc., Adelphia, NJ) and prepared for analysis using either an ABI 373A or 377 automated DNA sequencer.

Following gel electrophoresis, chromatograms were imported into SeqEd™ (1.0.3s, Applied Biosystems) and aligned by eye. Nucleotide sequences were checked for reading-frame errors, termination codons, and improbable replacement substitutions. Protein-coding sequences were translated in MacClade (Version 3.07, Maddison and Maddison 1992) and compared to the amino acid sequence for homologous mitochondrial genes published for the chicken (Desjardins and Morais 1990). A Nexus file was created with each gene or gene region established as a separate partition. In the case of the ATPase 6 and 8 genes, which have a 10-bp overlap, this strategy leads to a duplication of sequence. Nucleotide position 9246 (relative to the chicken [*Gallus gallus*]) in the 10-bp overlap was phylogenetically informative but the duplicated information has no significant influence on the ensuing analyses. Site 9249 in this region was also polymorphic but represented an autapomorphic change in *M. gundlachii*.

We verified the identity of myoglobin intron 2 by comparing the flanking sequences (exon 2 and 3) to the *Manorina melanocephala* (Meliphagidae) exon 2 sequence reported by Heslewood et al. (1998) (GenBank accession number: U40497) and *Sericornis magnirostris* (Acanthizidae) exon 3 reported by Slade et al. (1993) (GenBank accession number: L17493).

RFLP analysis.—Owing to the relatively large number of *Margarops* individuals collected, we deter-

TABLE 1. Species and geographic distributions of the Mimidae included in this study.

Genus	Species[a]	Geographic location[b]																		
		VE	TR	GR	SV	SL	MA	DO	GU	MO	BU	PR	RD	BH	JA	US	MX	Total[c]	A68[d]	RFLP	Other[e]
Cinclocerthia	*gutturalis*					2	0											2	2		1
Cinclocerthia	*ruficauda*				1			7	4	9								21	21		2
Dumetella	*carolinensis*													2				2	2		1
Margarops	*fuscatus*					0	0	2	8	25	2	20	0	0				57	22	46	1
Margarops	*fuscus*			EX[f]	0	6	1	4	5	16	EX							32	10	23	1
Melanoptila	*glabrirostris*																2	2	2		1
Melanotis	*caerulescens*																2	2	2		1
Mimus	*gilvus*	2	4	2	2	2	2	1	0									15	15		1
Mimus	*gundlachii*													0	1			1	1		1
Mimus	*polyglottos*											2	2	2	2	1		9	9		1
Ramphocinclus	*brachyurus*					2	0											2	2		1

Numbers provide counts of the individuals genotyped for each population and the different molecular markers; genotype counts include 0 values to identify any locations where the species occurs but were not collected for this study (see also Figs. 1 and 2).

[a] Species names follow conventions of the American Ornithologists' Union (1998).

[b] Geographic abbreviations are as follows: Venezuela (VE), Trinidad (TR), Grenada (GR), St. Vincent (SV), St. Lucia (SL), Martinique (MA), Dominica (DO), Guadeloupe (GU), Montserrat (MO), Barbuda (BU), Puerto Rico (PR), Dominican Republic (RD), Bahamas (BH), Jamaica (JA), United States (US), and Mexico (MX).

[c] Total = total number of individuals of each species genotyped using DNA sequence, RFLP data, or both.

[d] mtDNA ATPase synthase 6 and 8 genes.

[e] Other = mtDNA gene regions NADH dehydrogenase subunit II gene, partial cytochrome oxidase subunit I gene, partial 12S ribosomal RNA gene, partial 16S ribosomal RNA gene, and nuclear-encoded myoglobin intron 2.

[f] EX = A historical record of extirpation.

mined mtDNA genotypes of *M. fuscatus* and *M. fuscus* by analyzing endonuclease restriction sites. *Margarops* ATPase 6,8 sequences were examined for endonuclease restriction sites that distinguished the mtDNA clades identified by phylogenetic analysis of these genes (Bermingham et al. 1996, Lovette et al. 1999b). The ATPase 6,8 gene region was amplified for all *Margarops* and 5 μL of PCR product was digested with 5 units of enzyme for 4 h using the buffers and temperatures recommended by New England BioLabs. Digestion products were loaded onto a 2% agarose gel run in 1× Tris-borate buffer (pH 8.0) (Sambrook et al. 1989) containing ethidium bromide (1 mg/mL). The gels were photographed and fragment sizes were compared to those anticipated by our sequence analysis.

Molecular characterization and analysis.—We used the filter option in MacClade (Version 3.07, Maddison and Maddison 1992) to combine identical sequences and thus reduce the time required for numerical analysis. Variable and phylogenetically informative sites were identified. All unique sequences were imported into Sequencer Version 4.0.8a (B. Kessing pers. comm.) to determine base composition and nucleotide bias with respect to codon position. Bias in nucleotide usage was calculated using the C index (Irwin et al. 1991). To quantify inter-sequence variation in nucleotide usage, we calculated the coefficient of variation (CV) of the proportion of each base in the different sequences for each of the three codon positions. The CVs of the four nucleotides at each codon position were then averaged to quantify overall inter-sequence variability by position. PAUP*, version 4.0b1 (Swofford 1998), and PUZZLE 4.0 (Strimmer and von Haeseler 1996, 1997) were used to calculate the Ts/Tv ratio and gamma distribution rate parameters (alpha) for each of the different genes.

Phylogeographic analysis.—Phylogeographic analysis of all ATPase 6,8 sequences for each of the five species represented by multiple Caribbean populations was based on neighbor-joining (NJ) and maximum parsimony (MP) analyses using PAUP*, version 4.0b1 (Swofford 1998), and maximum likelihood (ML) using PUZZLE. Genetic distances were based on the HKY85 model of nucleotide substitution (Hasegawa et al. 1985). The average divergence within and between mtDNA clades representing each species was determined with Sequencer Version 4.0.8a. MtDNA clade designations were based on the ATPase phylogenetic analysis and the clades were defined by reciprocal monophyly, although we recognized that additional sampling might reveal a different picture of the relationship.

Phylogenetic analysis.—Our molecular-systematic analysis of Caribbean mimids focused on 12 taxa. We used the partition homogeneity test of Farris et al. (1995) implemented in PAUP* (version 4.0d63) with 100 replicates to determine whether the different mitochondrial and nuclear gene regions could be combined for phylogenetic analysis. The likelihood-ratio test implemented in MODELTEST (Posada and Crandall, 1998) was utilized to select the model of molecular evolution used for our ML analyses of the combined data. PAUP* was used to produce MP, NJ, and ML trees for comparison across different analytical methods and gene combinations. Our MP analyses utilized the Goloboff fit criterion with $k = 2$ (Goloboff 1993). Our NJ analyses were based on genetic distances calculated with the LogDet model (Steel 1994) as a contrast to the class of site-to-site rate variation models evaluated by MODELTEST. We used 1,000 bootstrap replications to assess confidence for all pictured phylogenetic hypotheses. Maximum likelihood and parametric bootstrapping (Huelsenbeck et al. 1996) were utilized to test the monophyly of the Antillean tremblers and thrashers and the monophyly of the genus *Margarops* on the basis of the full 4,271 nucleotide data set. For each of the tests of monophyly, we used the program Seq-Gen (Rambaut and Grassly 1997) to generate 100 simulated data sets from which we developed our null distribution of log-likelihood scores for trees constrained by the hypothesis of monophyly.

Rate heterogeneity was tested using PAUP* to determine whether the phylogenetic branch lengths for Caribbean mimids were consistent with a molecular clock. Maximum likelihood scores, for trees with and without a molecular clock enforced, were statistically compared using the KH test (Kishino and Hasegawa, 1989). In turn, we used the two-cluster and branch-length tests of Takezaki et al. (1995) to further examine molecular rate constancy among Caribbean mimid lineages.

RESULTS

Our molecular-systematic study of Antillean mimids utilized the 842-bp sequence of the mitochondrial ATPase 6,8 genes for the phylogeographic analysis of the island and mainland populations of five widespread Antillean mimid taxa (Fig. 3). In the second stage of our study, we increased our taxon and nucleotide sampling to assess the likelihood that Lesser Antillean tremblers and thrashers represented a monophyletic lineage. To this end, we sequenced 3,491 nucleotides representing the single mitochondrial locus and approximately 780 nucleotides of the nuclear-encoded myoglobin intron 2 for one representative of each of 12 terminal mtDNA clades identified in our preliminary phylogenetic analyses. All DNA sequences utilized in this study can be retrieved from GenBank using the following accession num-

TABLE 2. Molecular characterization of the mitochondrial genes and myoglobin intron 2 used in the molecular systematic analysis of Caribbean mimids. Values are percentages except for the Ts/Tv ratio and alpha values; numbers in parentheses represent the absolute number of sites. The twelve individuals sequenced for all gene regions were included in this analysis.

	A8	A6	COI	ND2	Ribosomal	Myoglobin
			Nucleotide Composition			
G	8.1	12.2	17.3	12.7	23.0	22.9
A	30.2	29.4	28.6	30.3	29.3	29.0
T	22.5	22.6	24.2	21.1	20.8	26.5
C	35.9	35.8	29.9	35.8	26.9	21.6
			Nucleotide Bias			
1st Position	24.9	24.0	6.9	18.5		
2nd Position	32.4	33.9	21.5	30.8		
3rd Position	44.2	46.0	50.2	43.7		
4-fold sites	44.1	45.0	52.3	42.7		
Total	21.5	20.3	11.3	21.6	8.3	7.3
			Percent Variable Sites			
1st Position	10.7 (18)	6.0 (41)	0.8 (5)	7.9 (82)		
2nd Position	3.0 (5)	1.3 (9)	0.0 (0)	2.7 (28)		
3rd Position	20.2 (34)	23.4 (160)	19.8 (124)	22.2 (231)		
4-fold sites	8.9 (15)	13.9 (95)	12.1 (76)	11.4 (119)		
Total	33.9 (57)	30.7 (210)	20.6 (129)	32.8 (341)	7.7 (75)[a]	4.7 (33)[a]
			Percent Informative Sites			
1st Position	7.7 (13)	3.4 (23)	0.3 (2)	4.9 (51)		
2nd Position	1.2 (2)	0.6 (4)	0.0 (0)	1.6 (17)		
3rd Position	10.7 (18)	16.7 (114)	10.5 (66)	15.1 (157)		
4-fold sites	5.4 (9)	10.5 (72)	5.9 (37)	7.7 (80)		
Total	19.6 (33)	20.6 (141)	10.8 (68)	21.6 (225)	4.1 (40)[a]	3.0 (21)[a]
			Ts/Tv Ratio			
	4.92 ± 1.29	10.96 ± 1.2	6.46 ± 0.94	12.21 ± 0.63	3.45 ± 0.15	4.29 ± 0.23
			Alpha Value			
	0.27	0.13	0.10	0.16	0.02	0.02

[a] Indels not included

bers for the mitochondrial genes: AF140899–AF140986 (ATPase 6,8); AF140999–AF141010 (COI); AF140887–AF140898 (ND2); AF140987–AF140998 (12S); AF140863–AF140874 (16S). The myoglobin accession numbers are: AF140875–AF140886.

Molecular characterization and phylogenetic information content of the mtDNA and nuclear genes used to analyze Caribbean mimid relationships.— Compared to the homologous amino acid sequences for the chicken, mimids exhibit a single amino acid codon insertion in the ATPase 8 sequence between positions 44 and 45, but ATPase 6, COI, and ND2 have neither insertions nor deletions. Among the 12 mimids analyzed extensively in this study, those in the genus *Mimus* exhibited two phylogenetically informative insertions within the 12S ribosomal DNA sequence. One insertion was also shared by *Melanotis caerulescens.* The 16S ribosomal sequence exhibited only a single insertion, an autapomorphy in *M. caerulescens.*

Table 2 presents nucleotide frequencies, nucleotide bias, percentage variability, percentage informative nucleotide positions, Ts/Tv ratios, and the gamma-distribution parameters for the different genes and gene regions employed in this study. The ATPase (31.3% variable) and ND2 (32.8% variable) regions appear to be evolving at a similar rate to one another, and more rapidly than either COI (20.6% variable) or the ribosomal regions (7.7% variable). The majority of the variable sites within the coding regions are at third positions with the highest percentage in COI at 96.1%.

The mimid myoglobin intron 2, lying between myoglobin exons 2 and 3, ranges in length from 679 bp to 699 bp (average = 690) owing to indel variation. The myoglobin intron 2 was highly conserved and the majority of informative sites distinguished *Mimus* from the remaining mimid genera. Intron 2 was flanked by 16 base pairs of exon 2, and was identical to the published Meliphagidae sequence (Hesle-

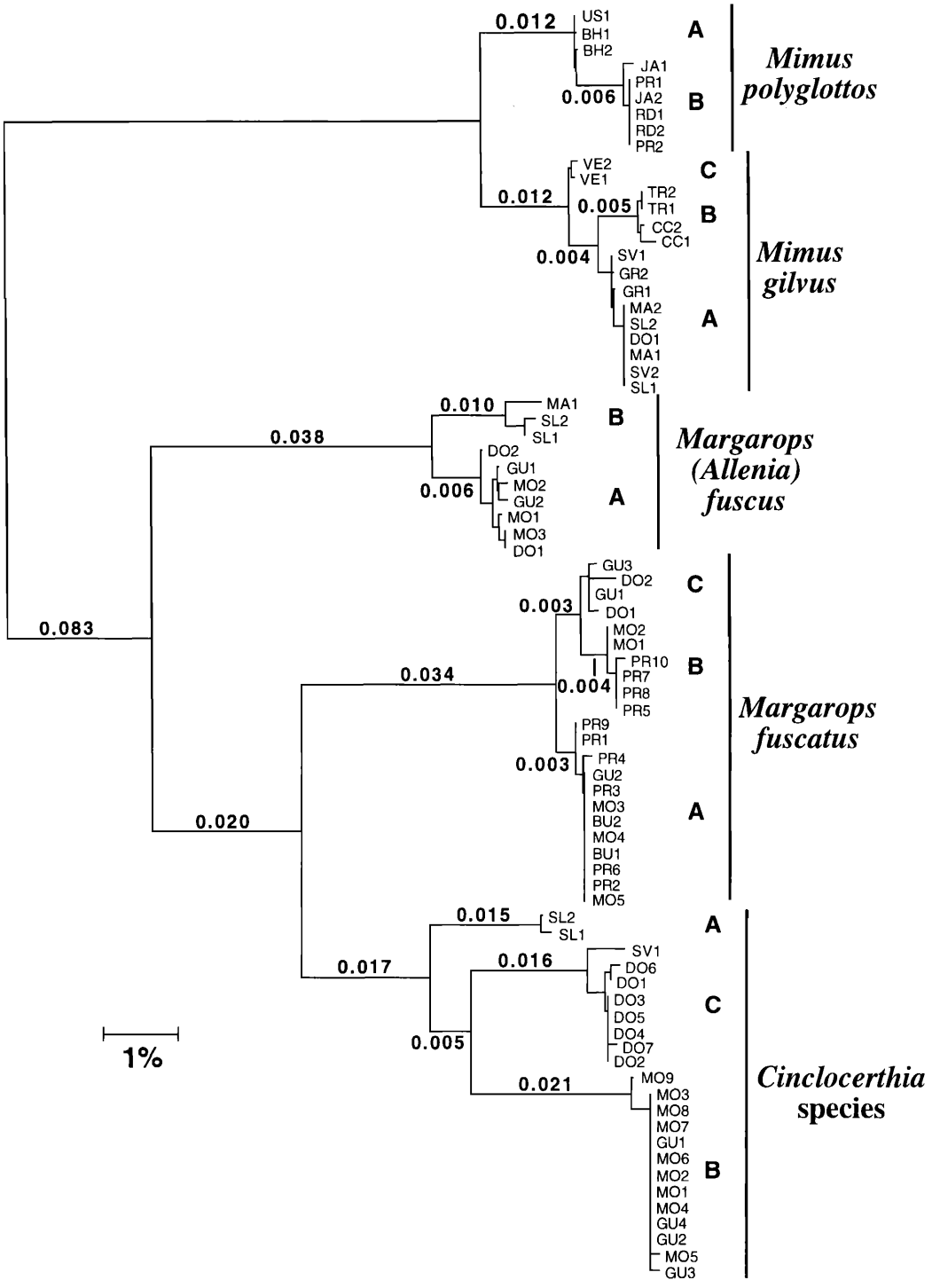

FIG. 3. The phylogeographic structure of mitochondrial ATPase 6,8 lineages for five species or species groups (*Cinclocerthia*) of Caribbean Mimidae. The neighbor-joining tree is based on HKY85 genetic distances and permits a visual comparison of the patterns of conspecific mtDNA lineage relationships among species or species groups. The figure is not presented as a hypothesis for the phylogenetic relationships among Caribbean mimid species (see Figs. 4–6). The letters A, B, and C indicate genetically distinct mtDNA clades

TABLE 3. HKY85 genetic distances, standard errors, and ranges (given in parentheses) among conspecific mtDNA clades for the five Caribbean Mimidae species analyzed for phylogeographic structure (see Fig. 3). The letters A, B, and C identify genetically distinct mtDNA clades within each species or species group (*Cinclocerthia*) pictured in Figure 3 and carry no meaning between species.

Clade designations	Clade designations		
	A	B	C
		***Cinclocerthia* species**	
A	0.12 ± 0.0 (0.12–0.12)		
B	4.0 ± 0.08 (3.92–4.17)	0.07 ± 0.10 (0.0–0.35)	
C	4.28 ± 0.16 (4.04–4.68)	4.01 ± 0.16 (3.79–4.56)	0.30 ± 0.32 (0.0–0.95)
		Margarops fuscatus	
A	0.06 ± 0.07 (0.0–0.24)		
B	1.16 ± 0.10 (0.95–1.43)	0.10 ± 0.08 (0.0–0.24)	
C	0.96 ± 0.15 (0.71–1.31)	0.72 ± 0.16 (0.47–1.07)	0.29 ± 0.16 (0.12–0.47)
		Margarops (Allenia) fuscus	
A	0.22 ± 0.10 (0.0–0.35)		
B	2.14 ± 0.11 (1.92–2.29)	0.55 ± 0.38 (0.12–0.83)	
		Mimus gilvus	
A	0.06 ± 0.06 (0.0–.12)		
B	0.91 ± 0.06 (0.83–0.95)	0.20 ± 0.10 (0.0–0.24)	
C	0.73 ± 0.08 (0.59–0.83)	1.13 ± 0.14 (0.95–1.31)	0.12 ± 0.0 (0.12–0.12)
		Mimus polyglottos	
A	0.0 ± 0.0 (0.0–0.0)		
B	0.63 ± 0.09 (0.59–0.83)	0.08 ± 0.11 (0.0–0.24)	

wood et al. 1998) except for a single C-T transition in *Melanotis caerulescens*. On the other flank, we sequenced between 39 and 77 bp (av. = 72) of exon 3 of which six sites (8% of the region) in the Mimidae differed from the Acanthizidae exon 3 sequence published by Slade et al. (1993). In total we analyzed an average of 778 bp of myoglobin sequence per individual.

Among the 12 mimid taxa included in this analysis, and considering the genus *Mimus* as "ancestral," the myoglobin intron 2 region revealed seven indel events, five of which were phylogenetically informative (Figs. 4, 5, and 6). Three of the phylogenetically informative indels were confined to *Mimus* and consisted of three, 4-bp deletions. The other two informative indels were observed only in *Cinclocerthia, Margarops,* and *Ramphocinclus* and consisted of an insertion of 1 bp and a deletion of 7 bp. The autapomorphic indels were a 2-bp insertion in *Melanotis caerulescens* and a 4-bp deletion in *Mimus gundlachii.*

mtDNA phylogeography of Antillean Mimidae.— Mitochondrial ATPase 6,8 sequence data were utilized to analyze 79 individuals representing 3 mimid genera and 6 species (Table 1): *Cinclocerthia ruficauda, C. gutturalis, Margarops fuscatus, M. fuscus, Mimus gilvus,* and *M. polyglottos.* We observed 40 distinct haplotypes distributed across species as follows: *Cinclocerthia ruficauda,* 9; *C. gutturalis,* 2; *Margarops fuscatus,* 10; *M. fuscus,* 9; *Mimus gilvus,* 7; and *M. polyglottos,* 3. Of those taxa, *Cinclocerthia* spp. exhibited the largest number of informative sites with 49, followed by *Margarops fuscus* with 18, *M. fuscatus* with 12, *Mimus gilvus* with 11, and *M. polyglottos* with 5.

We observed a one-to-one correspondence between named species and mtDNA haplotype clades; in all cases, mtDNA synapomorphies and reciprocal monophyly supported recognized species. Additional phylogenetically informative variation was observed within *Cinclocerthia* and *Margarops fuscus.* The ATPase-

←

within each species or species group (*Cinclocerthia*) referenced in Table 3 and have no meaning between species. Taxon labels reference the geographic source of the mtDNA lineages as follows: United States (US), Bahamas (BH), Jamaica (JA) Dominican Republic (RD), Puerto Rico (PR), Barbuda (BU), Antigua (AN), Montserrat (MO), Guadeloupe (GU), Dominica (DO), Martinique (MA), St. Lucia (SL), St. Vincent (SV), Grenada (GR), Chacachacare (CC), Trinidad (TR), and Venezuela (VE).

TABLE 4. RFLP genotypes observed for the two *Margarops* species across the Antillean islands of Puerto Rico (PR), Barbuda (BU), Montserrat (MO), Guadeloupe (GU), Dominica (DO), Martinique (MA), and St. Lucia (SL). Numbers include genotypes determined by RFLP, sequence assays, or both.

Sequence-based clade name[a]	Genotype	Geographic location							Total
		PR	BU	MO	GU	DO	MA	SL	
				Margarops fuscatus					
Clade A	AAA	10	2	3	1				16
Clade A	CAA	6							6
Clade B	BBA	4		22					26
Clade C	ABB				6	2			8
Clade C	CBB				1				1
Total									57
				Margarops (Allenia) fuscus					
Clade A	DD			15	5	4			24
Clade A	DE			1					1
Clade B	EE						1	6	7
Total									32

[a] Clade names are based on the groups identified on the ATPase tree presented in Figure 3.

based tree depicted in Figure 3 is based on a NJ analysis of HKY85 genetic distances and is used simply to provide a visual comparison of patterns of conspecific mtDNA lineage relationships among species or species groups (*Cinclocerthia*). Although principal features of the NJ tree pictured in Figure 3 were also present in the ML and MP trees, we defer presentation of more detailed phylogenetic results to the next section where we provide the phylogenetic hypotheses for Caribbean mimids and outgroups.

The most striking phylogeographic result is the genetic divergence among *Cinclocerthia* populations and species. Island populations on Guadeloupe and Montserrat form a mtDNA clade that is sister to a clade representing the disjunct *Cinclocerthia* populations of St. Vincent and Dominica. The average distance between members of the Guadeloupe/Montserrat and Dominica/St. Vincent clades is 4.0%. The geographically intermediate *Cinclocerthia* population from St. Lucia represents a distinct mtDNA clade, with average distances to the other two clades of 4.0 and 4.3% respectively.

Margarops fuscus populations were grouped in two clades, one (clade A) representing the more northern Lesser Antillean islands of Montserrat, Guadeloupe, and Dominica, and the other (clade B), representing the more southern Lesser Antillean islands of Martinique and St. Lucia. An average distance of 2.1% separated haplotypes in the two clades. *Mimus gilvus* also exhibited phylogeographic structure in the eastern Caribbean, with the Lesser Antillean populations being distinctive from those in Trinidad and, especially, in Venezuela. The divergence among mtDNA clades of *Mimus gilvus* was less than that between clades of *M. fuscus*, ranging from 0.7 to 1.1%. *Margarops fuscatus* displayed a moderate level of haplotype variation that lacked any apparent geographic pattern. Divergence between the three, lettered mtDNA haplotype *Margarops fuscatus* clades ranged from 0.5 to 1.4% (Table 3). Excluding Barbuda, from which two individuals of *Margarops fuscatus* had identical haplotypes, intra-island haplotype divergences ranged between 0.5 and 0.7%. Within populations of the other four species, the combined average haplotype divergence was 0.10% with a range of 0.0 to 0.35%. In general, genetic variability within mtDNA clades was low (Table 3).

Subsequently, we used RFLP analysis to determine the genotypes of 57 additional individuals representing the two *Margarops* species, bringing the total number of *Margarops* sampled to 89. *Dde*I, *Hha*I, and *Hinf*I endonucleases were diagnostic for *M. fuscatus* mtDNA clades A, B, and C (Fig. 3), and identified the following RFLP genotypes (fragment sizes were deduced from the ATPase sequence data and are given in parentheses): *Dde*I-A (455, 319, 193, 54), *Dde*I-B (648, 319, 54), *Dde*I-C (774, 193, 54), *Hha*I-A (780, 241), *Hha*I-B (1021), *Hinf*I-A (991, 30), and *Hinf*I-B (596, 395, 30). *Msp*I and *Taq*I were diagnostic for the two *M. fuscus* clades (A and B, Fig. 3) and identified the following genotypes: *Msp*I-D (590, 431), *Msp*I-E (1021), *Taq*I-D (718, 275, 28), and *Taq*I-E (718, 159, 116,

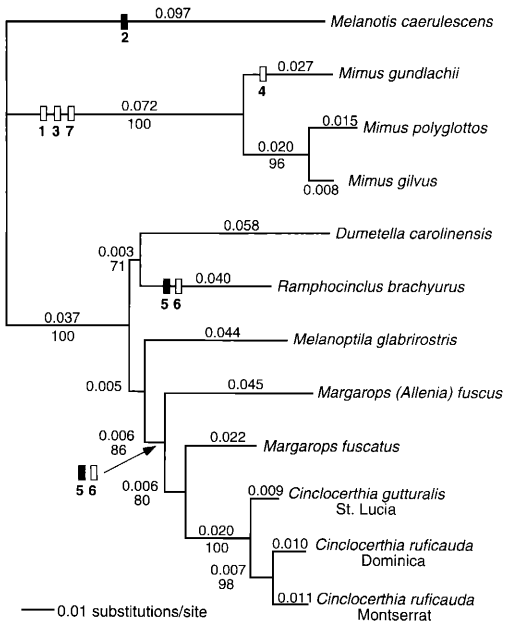

FIG. 4. Maximum-likelihood-based phylogenetic hypothesis for the Antillean tremblers, thrashers, and outgroups (Mimidae). The tree is based on analysis of approximately 4,270 bp of combined mitochondrial and nuclear-encoded myoglobin DNA sequence. Genetic distances are shown above the branches and were calculated using a general time-reversible nucleotide substitution model (see text for details). Confidence in the branching order was assessed with 1,000 bootstrap estimates with the proportion of times that a clade was supported shown beneath the branch leading to the clade. Myoglobin intron 2 insertions (filled rectangles) and deletions (open rectangles) are presented in one of several minimum mutation step pathways. The tree was rooted using *Mimus* and *Melanotis* as outgroups.

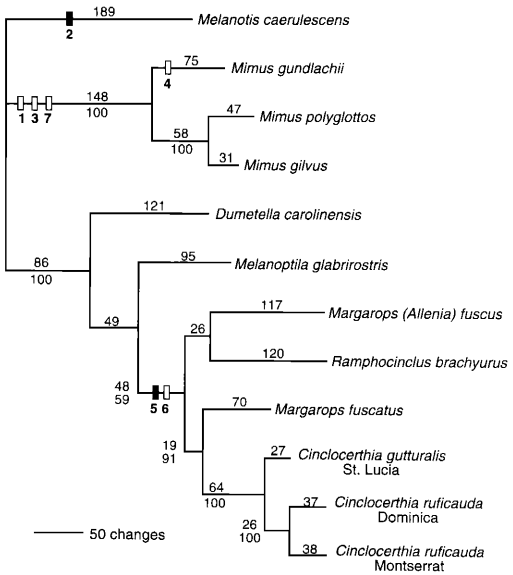

FIG. 5. Maximum-parsimony-based phylogenetic hypothesis for the Antillean tremblers, thrashers, and outgroups (Mimidae). The parsimony analysis was a branch-and-bound analysis of the combined mitochondrial and myoglobin sequence data using a Goloboff fit of $k = 2$. The resulting consistency index was 0.67. The number of nucleotide changes along a branch are shown above the branch. Bootstrap values based on 1,000 replicates are presented beneath the branches. Myoglobin intron 2 insertions (dark rectangles) and deletions (open rectangles) are mapped in the single most parsimonious reconstruction of their evolution. The tree was rooted using *Mimus* and *Melanotis* as outgroups.

28). Table 4 lists clade designations and associated genotype patterns produced by the restriction enzymes. Only a single individual from the *M. fuscus* population on Montserrat displayed a novel RFLP genotype (DE) not observed in the initial sequence-based analyses. Subsequent ATPase sequencing and phylogenetic analysis of that individual placed it within clade A. The RFLP data provided additional support for the phylogeographic separation of the two *M. fuscus* clades documented by our sequence-based analysis of smaller numbers of individuals. Increasing the sample size of *M. fuscatus* indicated that mtDNA clades, while co-occurring on three of five islands, present an uneven geographic distribution perhaps reflecting different colonization and demographic histories of the island populations (Table 4).

Molecular systematics of Caribbean Mimidae.—For further appraisal of the phylogenetic relationships of the Caribbean mimids, we selected one representative of each *Maragarops* species and the three distinct mtDNA clades of the genus *Cinclocerthia*. We included a representative from each of the two Antillean endemic species (*Ramphocinclus brachyurus* and *Mimus gundlachii*) for which we had samples from only a single population. *Dumetella carolinensis* and *Melanotis caerulescens* represented putative outgroups, whereas *Melanoptila glabrirostris* and the *Mimus* species served as certain outgroups for the Antillean endemic thrashers and tremblers. Phylogenetic analysis was based on the roughly 4,270 nucleotides of combined data, given that a partition homogeneity test (Farris

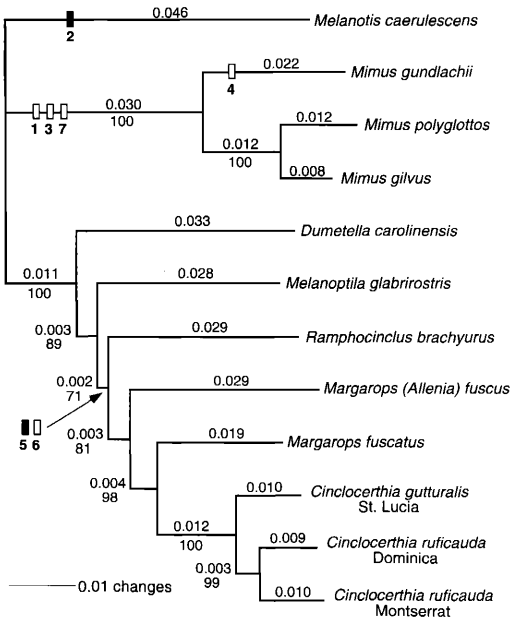

FIG. 6. Neighbor joining-based phylogenetic hypothesis for the Antillean tremblers, thrashers, and outgroups (Mimidae). Genetic distances are shown above the branches and were calculated using a LogDet–paralinear nucleotide substitution model and the combined mitochondrial and myoglobin data. Bootstrap values based on 1000 replicates are presented beneath the branches. Myoglobin intron 2 insertions (dark rectangles) and deletions (open rectangles) are mapped in the single most parsimonious reconstruction of their evolution. The tree was rooted using *Mimus* and *Melanotis* as outgroups.

et al. 1995) on the combined data set for all the mtDNA regions (6 partitions; 3,491 bp) and the nuclear region (1 partition, 699 bp) indicated that the gene regions did not differ significantly, whether tested as 7 gene partitions (P = 0.88) or two partitions (mtDNA and myoglobin; P = 0.98).

MODELTEST (Posada and Crandall 1998) indicated that a general time-reversible (GTR) "6 ST" substitution model (Rodríguez et al. 1990) incorporating an estimated proportion of 0.44 invariable sites and a gamma distribution shape parameter of 0.28 best fit the combined data. The mimid tree based on this model is presented in Figure 4. However, the log-likelihood estimated for ML tree (–ln L: 13132.27) was not significantly better than the log-likelihoods calculated for two alternative topologies identified by MP (–ln L: 13149.08) and NJ LogDet (–ln L: 13139.53) analyses (Figs. 5 and 6, respectively).

All analyses identified three deeply joined mimid lineages (Figs. 4, 5, and 6). One of these lineages includes the three species of *Mimus*, the second is formed by *Melanotis caerulescens*, and the third comprises the catbirds and Antillean thrashers and tremblers. All trees also group the three *Cinclocerthia* mtDNA lineages with *Margarops fuscatus*. That result was strongly supported in the MP (91% bootstrap) and NJ (98% bootstrap) analyses, but less so in the ML analysis (80% bootstrap). There was also concordance across all analyses regarding the relationships among the three *Mimus* species with *M. polyglottos* and *M. gilvus* sharing more recent ancestry with each other than with *M. gundlachii*.

Differences in the three trees lie in the highly unstable position of *Ramphocinclus brachyurus*. In the ML tree (Fig. 4), *Ramphocinclus* grouped with *Dumetella* outside *Melanoptila* and the *Cinclocerthia*/*Margarops* clade, whereas in the MP (Fig. 5) and NJ (Fig. 6) trees *Ramphocinclus* joins the other Antillean thrashers and tremblers as the sister group to *Melanoptila*. Although both the MP and NJ analyses support the monophyly of the Antillean thrashers and tremblers, the bootstrap-based confidence of monophyly is not strong. Furthermore, the position of *Ramphocinclus* changes between the MP tree, where it is the sister of *Margarops fuscus*, and the NJ tree, where it is the sister taxa of the remaining Antillean endemic tremblers and thrashers. The monophyly of the Antillean thrashers and tremblers is further supported by the myoglobin indel data (Figs. 4, 5, and 6), although those data do not resolve the position of *Ramphocinclus* within the Antillean clade.

The phylogenetic resolution afforded by mtDNA, whether protein coding or ribosomal sequences, was clearly greater than that of the nuclear myoglobin intron. However, LogDet distances connecting sister taxa or a terminal taxon and the basal node of its sister clade (n = 11) were not strongly correlated for protein-coding and ribosomal mtDNA sequences (r = 0.41, P = 0.21). Distances calculated for the myoglobin intron 2 were 0 for 5 of the branches, corresponding to mtDNA protein distances less than 6–9% and ribosomal distances less than 1.45%. Myoglobin distances (including zeros) were positively correlated with ribosomal

($r = 0.80$, $P = 0.003$, $n = 11$) but not significantly with mtDNA protein ($r = 0.39$, $P = 0.24$, $n = 11$) distances. When regressions were forced through the origin, percentage of nucleotide substitution was observed to increase 0.19 (±0.03) times as rapidly in rDNA sequences and 0.11 (±0.03) times as rapidly in the myoglobin intron 2 as in protein-coding mtDNA sequences.

The robust grouping of *Cinclocerthia* with *Margarops fuscatus* prompted us to test the monophyly of the genus *Margarops*. The null hypothesis of *Margarops* monophyly was rejected with 95% confidence based on a maximum-likelihood ratio test and parametric bootstrapping (Huelsenbeck et al. 1996). The same analytical approach failed to reject the null hypothesis of monophyly for the entire group of Antillean thrashers and tremblers, but the test also failed to reject the alternate hypotheses in which either *Melanoptila* or *Dumetella* were placed inside *Ramphocinclus*.

The Kishino-Hasegawa (1989) test demonstrated a significant log-likelihood difference between the best tree and one for which nucleotide substitutions were assumed to be clock-like. The non-clock-like molecular evolution of the mimids was explored in greater detail with the Takezaki et al. (1995) two-cluster and branch-length tests. The two-cluster test did not uncover significant rate variation between a cluster composed of catbirds and Antillean thrashers and tremblers, and a second cluster including *Melanotis* and *Mimus* species. We next centered our focus on catbirds and Antillean endemic thrashers and tremblers and used MODELTEST (Posada and Crandall 1998) to find the best model and parameters for that group alone. Although the analytical outcome was the same as previously described for the full taxonomic sample of 12 mimid taxa (a GTR model of evolution and a tree with the same internal topology for the group as presented in Fig. 4), the parameters, particularly gamma (13.00), differed considerably. We used that tree to compare the root-to-tip branch length of each taxon with the average root-to-tip distance (branch-length test), and determined that *Dumetella*, and the two *Margarops* species had significantly different branch lengths than the average.

Discussion

We touch upon four issues in this discussion: (1) the relative phylogenetic information content of the gene regions sequenced in this study; (2) the phylogeography of several species of West Indian mimids for which we have sampled multiple island populations; (3) the molecular phylogenetics of West Indian mimid species; and (4) the taxonomic implications of our molecular phylogenetic analysis. The West Indian mimids are particularly interesting because of their high level of endemism (three or four endemic genera) and the possible monophyly of some or all of the West Indian endemic genera. In so far as those genera do constitute a single clade, they would represent the only radiation of birds within the West Indies that has led to substantial sympatry on individual islands (four taxa on St. Lucia and Martinique in the Lesser Antilles). In addition, although two of the endemic taxa (*Margarops fuscus* and *M. fuscatus*) are widely distributed throughout the Lesser Antilles, *Cinclocerthia* has fewer, more highly differentiated island populations, and *Ramphocinclus* is restricted to two islands. Thus, it would be instructive to determine whether distribution and taxonomic differentiation are related to phylogenetic history.

Phylogenetic information content.—Nucleotide bias, transition/transversion bias, and heterogeneity among sites in the rate of nucleotide substitution are important considerations in making inferences about phylogenetic trees (Li 1997). Among the gene regions sequenced in this analysis, the 12S and 16S ribosomal regions and the myoglobin intron 2 showed the least nucleotide bias and the most uniform nucleotide composition overall. The mtDNA ND2 and ATPase 6 and 8 regions showed the greatest nucleotide bias, with a deficiency of G and excess of C and, to a lesser extent, A. Nucleotide bias was greatest at the third position. Mirroring differences in nucleotide bias, the ND2 and ATPase 6 and 8 regions exhibited the highest percentages of variable sites (33 and 31%), and ribosomal regions (7.7%) and myoglobin intron 2 (9.4%) exhibited the lowest percentages. The COI region was intermediate in variability, primarily because of extreme conservatism in the first and second positions relative to those in ND2 and ATPase 6 and 8. The proportion of phylogenetically informative sites

and the transition/transversion ratio paralleled the percentage of variable sites (Table 2). Although the myoglobin intron 2 was relatively invariant, even the absence of divergence in that sequence is informative. In this study, comparisons between taxa with 0.0% divergence were associated with mtDNA sequence distances of 2.8–8.8%, whereas comparisons with myoglobin intron 2 divergences exceeding 0.0% were associated with mtDNA distances of 6.2–14.7%.

Phylogeography.—All endemic West Indian mimid species are characterized by moderately long basal branches and various depths of terminal diversification as measured by mtDNA divergence (Fig. 3). The relatively long basal branches compared to short genetic distances within taxa suggest a fairly high turnover of lineages and relatively short coalescence time within the West Indies, a finding that applies generally to the Lesser Antillean taxa that we have studied (Seutin et al. 1993, 1994; Bermingham et al. 1996, Lovette et al. 1998, 1999a).

The deeper splitting of lineages in *Margarops fuscus* and *Cinclocerthia* is generally congruent with geographical distribution. The two clades of *M. fuscus* correspond to populations on the northern Lesser Antillean islands from Montserrat through Dominica (clade A) and the southern islands of Martinique and St. Lucia (clade B). Although Dominica and Martinique are separated by only 33.8 km, we found a distinct genetic break between *M. fuscus* from those islands. *M. fuscus* is thought to be extinct on Barbuda and Grenada at the northern and southern extremes of the distribution, and we did not sample the species on St. Vincent.

The phylogeography of the *Cinclocerthia* populations indicates a dynamic history within the Lesser Antilles (Figs. 1 and 3). On one hand, deep splits between some islands suggest long evolutionary independence and lack of migration among islands. On the other hand, the presence of closely related genotypes on other islands suggests continued inter-island movement or recent colonization. It is remarkable that movement might have occurred between the Guadeloupe and Montserrat *C. ruficauda* populations to the north as evidenced by their membership in clade B, but not between Guadeloupe and Dominica trembler populations to the south. *Cinclocerthia ruficauda* from Nevis to Saba are indistinguishable from individuals on Montserrat (Hellmayr 1934) and Guadeloupe (Storer 1989). In the absence of samples for genetic analysis from the more northern islands, the simplest explanation for that pattern of uniformity is that *C. ruficauda* has recently colonized those islands from Guadeloupe.

The disjunction between the closely related members of clade C on Dominica and St. Vincent is more problematic because it requires either long-distance colonization from one of those islands to the other, or stepping-stone colonization between the two islands with the subsequent disappearance of *C. ruficauda* genotypes from the intervening *C. gutturalis* (clade A) island populations. The nuclear myoglobin intron 2 exhibited no differentiation among clades of tremblers and thus cannot help to resolve that problem. Supposing that *C. ruficauda* coexisted recently with *C. gutturalis* on Martinique and St. Lucia, it is surprising that the latter two populations have retained their distinctive appearance and especially that St. Vincent birds do not resemble St. Lucia birds more closely than they resemble Dominica birds.

Numbers of individuals sampled from Dominica (7), St. Lucia (2), and St. Vincent (1) were small enough that the observed distribution of lineages might have resulted from nonrandom sampling from a homogeneous distribution of haplotypes occurring from Dominica south to at least St. Vincent. However, a uniform distribution of genotypes over the islands between St. Vincent and Dominica is highly unlikely. If haplotypes were present in proportions of 50% A and 50% C, the probability of drawing the observed distribution would be only $0.5^{10} = 0.001$, and the probability of any disjunct pattern would be only 0.002. Even if proportions were 80% A and 20% C, the probability of drawing the observed distribution would be $0.8^8 \times 0.2^2$, or only 0.0067. The probability of that result is maximized when the proportion of the St. Vincent genotype is 1/8, in which case the probability is 0.049.

It is also highly unlikely for two reasons that birds from Dominica were introduced recently to St. Vincent. First, nucleotide divergence in the ATPase 6,8 region between the C group of mtDNA haplotypes on St. Vincent and Dominica averages 0.83%, which exceeds the range of divergence found within most island populations of Lesser Antillean birds (e.g. Seutin et

al. 1993, 1994; Lovette et al. 1998). The highest within-island divergence observed among *Cinclocerthia* haplotypes was 0.35%. Second, the chance of drawing one genotype from a population (the St. Vincent sample) for which seven independent draws (the Dominica sample) came up with alternative (albeit closely related) genotypes is slim.

Thus, the parsimonious alternative to a sampling explanation for the observed disjunction is fairly recent long-distance colonization of St. Vincent from Dominica. Because the St. Vincent haplotype is considerably more distant from the Dominican haplotypes (0.71–0.95%) than any of the Dominican haplotypes are from each other (0.00–0.35%), sufficient divergence appears to have occurred between the islands to rule out the possibility of pre-Columbian human transport. In our analyses of other taxa in the Lesser Antilles, long-distance colonization events appear to be uncommon. Further resolution of the Dominica–St.-Vincent disjunction in *Cinclocerthia* will require additional sampling from these islands plus from St. Lucia and Martinique, as well as alternative genetic assays.

Margarops fuscatus exhibits considerable genetic diversity within the Lesser Antilles and Puerto Rico (Fig. 3), and intrapopulation distances on the well-sampled islands of Puerto Rico, Montserrat, and Guadeloupe averaged 0.63, 0.64, and 0.68%; however, the species shows relatively less geographical structuring than *M. fuscus* or *Cinclocerthia*. Clade A is found throughout most of the species distribution (Fig. 1); it is most common on Puerto Rico and appears to be absent from Dominica in the south. Clade B predominates on Montserrat, where 22 out of 26 individuals had that haplotype, but this clade was also found on Puerto Rico. Clade C is restricted in our sample to Guadeloupe and Dominica.

The two widespread species of *Mimus* show little differentiation within the West Indies (Figs. 2 and 3). However, populations of *M. polyglottos* in the Greater Antilles (clade B: Jamaica, Puerto Rico, and the Dominican Republic) are distinguishable from those in the Bahamas and also from our single North American specimen (clade A) by average genetic distances of 0.6–0.7%. Lesser Antillean *M. gilvus* (clade A) are distinguishable from birds in Trinidad and Venezuela (clades B and C) by distances of 0.71–0.95%. The lack of differentiation among populations of *M. gilvus* in the Lesser Antilles (inter-island distances 0.00–0.12%) suggests that gene flow connects the island populations. Alternatively, tropical mockingbirds may have recently spread throughout the islands from a center within the Lesser Antilles, having originally colonized the islands from the mainland sometime in the past.

Assuming clock-like behavior of nucleotide substitution in the mtDNA ATPase 6,8 gene region, and a rate of divergence of 0.02 per million years (Fleischer et al. 1998), it is possible to assign approximate relative ages to the diversification of contemporary clades. These estimates vary from 2.0–2.1 Ma for *Cinclocerthia*, to 1.1 Ma for *M. fuscus*, 0.5–0.6 My for *M. fuscatus*, and perhaps 0.4–0.6 Ma for *M. gilvus*, and 0.3 Ma for *M. polyglottos*, although the mimid phylogenetic tree exhibits significant rate heterogeneity. Thus, diversification of contemporary lineages shows no particular temporal congruence, which might have occurred if diversification had responded to a single strong external signal in the environment (Pregill and Olson 1981). In addition, diversification of individual island populations dates from as long ago as 2.1 Ma, well before the onset of the Pleistocene glacial cycles. However, the phylogeography of Caribbean mimids and the lack of sequence divergence among many island populations, also provides a record of gene flow or colonization events among islands that have continued to the present in some cases.

When we consider all mimid taxa, it is apparent that genetic breaks within species in the Lesser Antilles appear at different places: South-America–Grenada (*Mimus gilvus*), St.-Vincent–St.-Lucia (*Cinclocerthia*), St. Lucia/Martinique–Dominica (*Cinclocerthia*), Martinique–Dominica (*Margarops fuscus*), Dominica–Guadeloupe (*Cinclocerthia*), and Guadeloupe–Montserrat (*Margarops fuscatus*). That lack of geographic congruence and the different relative ages of the genetic breaks suggest that the phylogeography of each of the mimid species has developed independently within the Lesser Antilles.

Genetic and taxonomic differentiation.—The intraspecific diversification of island populations of West Indian mimids has long been acknowledged by the many subspecific names assigned to those taxa. In several cases, our sampling of

multiple island taxa permits us to comment on how well subspecific designations match molecular phylogeographic results.

The trembler *Cinclocerthia* has been subdivided into as many as six named units (Davis and Miller 1960). The absence of mtDNA differentiation among the northern islands occupied by this taxon suggests that the separation of *C. r. pavida* (Montserrat) and *C. r. tremula* (Guadeloupe) is not warranted, a conclusion also reached using morphometric criteria by Storer (1989), who grouped those island populations together in *C. r. tremula*. Similarly, *C. r. ruficauda* of Dominica and *C. r. tenebrosa* of St. Vincent are sister taxa, although they exhibit moderate genetic differentiation (d = 0.83%). Storer (1989) recognized the similarity between those two forms, as opposed to differences between other island populations. He also emphasized the distinctiveness of *C. r. gutturalis* of Martinique and *C. r. macrorhyncha* of St. Lucia by elevating those two island populations to specific rank, *C. gutturalis*. Unfortunately, we did not sample *Cinclocerthia* on Martinique and so we cannot comment on the genetic similarity of the Martinique and St. Lucia populations. Storer's careful study of morphological characters of *Cinclocerthia* generally parallels the genetic distinctions obtained in this study, although he recognized only two principal *Cinclocerthia* lineages, whereas the molecular data identify three distinct lineages.

Although Bond (1950) recognized no subspecific differentiation in *Margarops fuscus*, Buden (1993) grouped populations from Guadeloupe and islands to the north (*M. f. hypenemus*), as distinct from populations on Dominica, Martinique, and St. Vincent (*M. f. fuscus*), and on St. Lucia (*M. f. schwartzi*). Our molecular data are incongruent with that arrangement because they place birds from Dominica with those from Guadeloupe and Montserrat, and birds from Martinique with those from St. Lucia. We did not sample birds from St. Vincent and so we cannot comment on the supposed disjunction in *M. f. fuscus*. However, Kratter and Garrido (1996) later separated St. Vincent birds (*M. f. vincenti*) on the basis of the extent of the white tips on the outer tail feathers. Buden's subspecific distinctions are based on measurements, which permitted the quantitative clustering of some populations. However, morphological characters appear evolutionarily labile compared to mtDNA divergence, and they do not identify monophyletic groupings of populations in this species.

Within the area considered in this study, Bond (1950) recognized two subspecies of *Margarops fuscatus*, namely *M. f. fuscatus*, occurring from the Greater Antilles to Antigua and Barbuda in the northern Lesser Antilles, and *M. f. densirostris*, occurring from Montserrat and Guadeloupe south. For the most part, *M. fuscatus* shows no consistent geographical pattern in genetic variation. However, the relative numbers of individuals from Montserrat, Guadeloupe, and Dominica that are assigned to clades B and C, in comparison to clade A *M. fuscatus* that predominate on islands to the north, suggest that the differences noted by Bond may indicate a period of separation between *M. fuscatus* populations in the southern and northern parts of its range.

Ramphocinclus populations on St. Lucia and Martinique have been variously distinguished as separate species (Ridgway 1907) or well-marked subspecies (Hellmayr 1934, and more recent treatments). We did not sample the endangered *Ramphocinclus* population on Martinique and therefore cannot comment on the genetic divergence among those populations. The absence of subspecies distinctions in West Indian populations of *Mimus gilvus* and *M. polyglottos* is consistent with the absence of significant mtDNA genetic differentiation between island populations. The Antillean populations of *M. gilvus* are recognized as a distinct subspecies (*M. g. antillarum*, Bond 1950), which is consistent with their moderate genetic distance from populations in Trinidad and Venezuela.

Molecular systematics.—Our extended analysis of DNA sequences for each clade of Antillean endemics and other species of Caribbean-basin mimids allows us to address three issues concerning relationships among West Indian endemic mimids: (1) the species-level differentiation of the tremblers (*Cinclocerthia*), (2) the relationships among *Margarops* and *Cinclocerthia*, and (3) the monophyly of the Antillean endemic thrashers.

Storer (1989) placed the tremblers of Martinique and St. Lucia in a separate species (*C. gutturalis*, the Gray Trembler) on the basis of differences in plumage coloration and reduced sexual dimorphism in culmen length in the St. Lucia population. That resulted in the Brown

Trembler (*C. ruficauda*) having a geographic disjunction between populations on Dominica and St. Vincent. The molecular data support the species-level distinctiveness of *C. gutturalis*, but are also evidence for a split almost as deep between *C. ruficauda* populations on Dominica and St. Vincent, on one hand, and Guadeloupe and Montserrat, on the other (Figs. 3–6). *Cinclocerthia gutturalis* appears to be the basal member of the group, and bootstrap support for the sister status of the two *C. ruficauda* lineages was high in all analyses (Figs. 4–6). Application of a molecular clock suggested that differentiation of the three *Cinclocerthia* lineages probably occurred in the late Pliocene.

The second systematic issue addressed by our analysis involves the monophyly of the genus *Margarops* and its relationship to *Cinclocerthia*. *Margarops fuscus*, the Scaly-breasted Thrasher, was originally allied with the Forest Thrush (*Cichlherminia lherminieri*: Turdidae) (Sclater 1871). However, Cory (1891) placed the Scaly-breasted Thrasher in the genus *Allenia* in the Mimidae following arguments for the removal of this thrasher from the Turdidae (Stejneger 1883). Following Bond (1956), *Allenia* is usually merged with the Pearly-eyed Thrasher in the genus *Margarops*. Zusi's (1969) comparison of skeletons representing all 13 genera of Mimidae suggested that *Cinclocerthia* is closest to *Margarops*. However, analyses based on skull anatomy led Zusi to suggest that both *Margarops* species share a more recent common ancestor than either shares with *Cinclocerthia*. The mtDNA results support Zusi's conclusion regarding the generally close relationship between *Cinclocerthia* and *Margarops*, but the skull characters that set *Cinclocerthia* apart from the other two species are not paralleled by the pattern of molecular differentiation. Forcing the pairing of the *Margarops* species with *Cinclocerthia* as their sister taxon in any of the trees presented in Figure 4 significantly reduced the likelihood of the trees. Forcing the pairing of *M. fuscus* with *Cinclocerthia* also produced an unlikely arrangement. As it stands at present, the genus *Margarops* is probably paraphyletic with *M. fuscus* (*Allenia*) basal to *M. fuscatus* and *Cinclocerthia*.

Our third issue concerns the monophyly of the endemic Antillean thrashers and the possible adaptive radiation of the group within the West Indies, most likely the Lesser Antilles. We are reasonably confident of the monophyly of *Margarops* and *Cinclocerthia*. Considering the present Lesser Antillean distributions of those genera and the fact that the Puerto Rican population of *Margarops fuscatus* shares genotypes with birds on Montserrat, Barbuda, and Guadeloupe, it is plausible that that clade radiated within the Lesser Antilles. Less certain, however, are the phylogenetic positions of the Lesser Antillean White-breasted Thrasher *Ramphocinclus* and the continental *Dumetella* and *Melanoptila*.

Bond (1963) regarded *Cinclocerthia* and *Ramphocinclus* as a group related to *Melanotis*; *Margarops* represented a second group not closely related to any mainland genus. Clearly that interpretation is incorrect on the basis of our data. *Melanotis* is basal within the mimids, and *Melanoptila* groups more closely with the Antillean forms as well as with *Dumetella*. Bond further noted that all the Antillean thrasher and trembler species have immaculate, greenish blue eggs, like those of *Melanotis*, *Melanoptila*, and *Dumetella*, but unlike those of any species of *Mimus*. Depending on the phylogenetic position of *Melanotis*, that character either links *Melanotis* to the West Indian thrashers, albeit deeply within the mimid phylogeny, or it represents the primitive egg coloration of the Mimidae (shared by some members of the sister taxon Sturnidae), which was subsequently lost in the genus *Mimus*.

Melanoptila, *Dumetella*, and *Ramphocinclus*, together with the *Margarops–Cinclocerthia* clade, clearly constitute a monophyletic group, with *Melanotis* and *Mimus* as outgroups. If *Ramphocinclus* were basal within the Antillean endemics, then one could plausibly postulate a Lesser Antillean radiation for all the endemic taxa from a single Antillean ancestor. However, if *Ramphocinclus* grouped with either *Dumetella* or *Melanoptila*, or formed a polytomy with both of them, then one could postulate that *Ramphocinclus* and the *Margarops–Cinclocerthia* clade were independently derived from an ancestor with a broad former distribution that included continental Central and North America. In the unlikely circumstance that *Ramphocinclus* is basal to the entire clade, including *Dumetella* and *Melanoptila*, then either the clade had an Antillean origin and later colonized the continent or *Ramphocinclus* is an island relic of an extinct

lineage with a broad, continent-based distribution.

Phylogenetic analyses based on sequence divergence are ambivalent about the placement of *Ramphocinclus, Dumetella,* and *Melanoptila.* The neighbor-joining tree places the continental species as basal to the Antillean endemics, although bootstrap support for this arrangement is not strong, and forcing *Melanoptila* interior to *Ramphocinclus* does not lengthen the tree significantly. The maximum parsimony tree also supports the monophyly of the Antillean endemics, but links *M. fuscus* and *Ramphocinclus* (Fig. 5). The maximum-likelihood tree places *Dumetella* and *Ramphocinclus* together and places *Melanoptila* with the other Antillean endemics, but the basal internode branches are short and poorly supported (Fig. 4). Thus, our sequence-based analysis does not resolve the relative positions of the basal taxa in the clade containing the endemic Antillean mimids. However, additional support for uniting the Antillean endemic genera comes from two indels in the myoglobin intron 2, which are shared by *Ramphocinclus, Margarops,* and *Cinclocerthia.* Because the likelihood of obtaining those same indels independently is small, those characters appear to provide good synapomorphies for the Antillean endemics.

Whether the polytomy of *Melanoptila, Dumetella,* and the Antillean thrashers is hard or soft would be difficult to determine without additional sequencing of nuclear genes. The basal node of this clade in the neighbor-joining tree subtends a genetic distance of 10.7% for protein-coding mtDNA sequences. Considering the nucleotide substitution bias in those regions, the saturation level for nucleotide substitutions is probably close to 15% for transitions in third-position sites (Seutin and Bermingham unpubl. data), and so additional sequencing of the mitochondrial genome might increase resolution somewhat. Slower-evolving nuclear protein coding regions might show less homoplasy, but long nucleotide sequences would be needed to provide sufficient informative characters. Noncoding regions hold out the possibilities of phylogenetically informative indels, such as those observed in the mimid myoglobin intron 2.

Regardless of whether the apparent polytomy at the base of the catbird–thrasher clade is hard or soft, it is clear that at an ATPase 6,8 nucleotide divergence of between 9 and 11%, the ancestor(s) of the clade were distributed on both the continent and within the West Indies. *Ramphocinclus* and the *Margarops–Cinclocerthia* clade likely are independent relics of those ancestral taxa and possibly are derived from the same colonization of the West Indies by a continental mimid. If the observed unique indels held those genera together, then they could represent a radiation derived from a unique Antillean ancestor, comparable to the radiations of Darwin's finches and Hawaiian honeycreepers.

The phylogeography of extant mimids suggests that colonization of the Lesser Antilles by the ancestor(s) of the endemic genera must have occurred by way of the Greater Antilles, but at present there is no extant endemic trembler or thrasher in the Greater Antilles. *Margarops fuscatus* on Puerto Rico is clearly derived from the Lesser Antilles. Thus, the West Indian mimids apparently persisted on several islands in the Lesser Antilles, occasionally undergoing periods of spread within the islands, followed by species formation and extinction of island populations. If we assumed that speciation requires allopatric separation of gene pools on different islands, then we would have to postulate that the generation of the *Margarops–Cinclocerthia* clade within the Lesser Antilles involved as many as 16 phases of island colonization. That figure represents one colonization phase at each node in the clade, including the contemporary distributions of undifferentiated populations on more than one island. Frequent extinctions of island populations are also implied by the absence of highly divergent haplotypes of the same species on a single island. Overall, the picture painted by phylogeographic and molecular systematic analysis of Antillean mimids is one of a high level of evolutionary dynamism when viewed on the scale of a few million years.

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APPENDIX. Mimidae taxa included in this study that represent other collections and museum catalog specimens.

Species	Voucher location[a]	Catalog number	Tissue location[a]	Tissue number	Location
Cinclocerthia ruficauda	USNM	612562[b]	USNMLMS	B-2134	St. Vincent
Margarops fuscatus	LSUMNS	150140	LSUMNS	B-11316	Puerto Rico
Margarops fuscatus	LSUMNS	112318	LSUMNS	B-18097	Puerto Rico
Melanoptila glabrirostris	No Voucher		LSUMNS	B-0081	Mexico
Melanoptila glabrirostris	No Voucher		LSUMNS	B-0082	Mexico
Melanotis caerulescens	No Voucher		LSUMNS	B-0022	Mexico
Melanotis caerulescens	No Voucher		LSUMNS	B-0048	Mexico
Mimus polyglottos	SBCM	53786	LSUMNS	B-21369	California, United States

[a] Museum codes: United States National Museum of Natural History (USNM), United States National Museum Laboratory of Molecular Systematics (USNMLMS), Louisiana State University Museum of Natural Science (LSUMNS), and San Bernardino County Museum (SBCM).

[b] Specimen prepped as a skeleton.