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Evolutionary Relationships of the *Anolis bimaculatus* Group from the Northern Lesser Antilles

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ABSTRACT.—**Lizards in the *Anolis bimaculatus* group from the northern Lesser Antilles have played an important role in theoretical and empirical developments in ecology, behavior, and evolution over the last four decades. Despite intense interest, the lack of a formal phylogenetic analysis for the *bimaculatus* group has limited comparative and historical evolutionary analyses. Here we present a phylogenetic analysis of species relationships within the *bimaculatus* group based on separate and combined analyses of mitochondrial DNA and previously published allozyme data. These analyses indicate that (1) the *wattsi* group of small anoles is a basal, well-supported monophyletic group; (2) the large anoles *A. bimaculatus* and *A. leachi* are not sister species—rather, there is a well-supported sister relationship between *A. bimaculatus* and *A. gingivinus*; (3) the *A. marmoratus* complex from the Guadeloupean archipelago is deeply differentiated and paraphyletic, with *A. sabanus*, *A. lividus*, and possibly *A. oculatus* nested within it; (4) the phylogenetic position of *A. leachi* is not well resolved, but a combined analysis of mtDNA and allozyme data favor placing *A. leachi* as the sister taxon to the (*A. marmoratus*, *A. lividus*, *A. sabanus*, *A. oculatus*) group; and (5) the phylogenetic position of *A. nubilus* remains uncertain pending additional data. The proposed phylogeny elucidates the evolutionary history and biogeography of the *bimaculatus* group and allows a reassessment of the character displacement and taxon cycle/loop hypotheses.**

The Caribbean radiation of *Anolis* lizards is one of the best known cases of adaptive radiation (reviewed in Williams, 1983; Losos, 1994; Jackman et al., 1997; Jackman et al., 1999). More than 100 of the approximate 140 species of Caribbean anoles occur on the islands of the Greater Antilles, where most research has been conducted. Nonetheless, the 20 species from the Lesser Antilles have received significant attention, including studies of locomotor behavior (Moermond, 1986), habitat use (Roughgarden et al., 1981, 1983; Losos and de Queiroz, 1997; Staats et al., 1997), size evolution (Roughgarden and Pacala, 1989; Losos, 1990), interspecific interactions (Pacala and Roughgarden, 1982; Roughgarden et al., 1984, 1987; Rummel and Roughgarden, 1985; Schall, 1992), social behavior (e.g., Stamps, 1991; Stamps and Krishnan, 1994a, b, 1995, 1997, 1998); phenotypic and genetic differentiation (Malhotra and Thorpe, 1991a, b, 1993, 1994, 1997a, b; Schneider, 1996), and natural selection (Malhotra and Thorpe, 1991a, 1994).

Traditionally, anoles of the Lesser Antilles have been classified in two distantly related groups, the *roquet* group in the southern Lesser Antilles (north to Martinique), allied to certain South American taxa, and the *bimaculatus* group in the northern Lesser Antilles (from Dominica northward, see Fig. 1), related to other West Indian anoles (Underwood, 1959; Etheridge, 1960). A number of phylogenetic hypotheses, often conflicting with each other, have been proposed for the two groups (e.g., Lazell, 1972; Yang et al., 1974; Gorman and Kim, 1976; Roughgarden et al., 1987). Given the advent of DNA sequencing and advances in analytical techniques, the time seems ripe for a new look at the phylogeny of these groups, particularly given the great breadth of information that could be interpreted in an evolutionary context once a robust hypothesis of relationships is obtained. Recently, such a hypothesis has been derived for the *roquet* group in the southern Lesser Antilles (D. A. Creer, K. de Queiroz, T. R. Jackman, J. B. Losos, and A. Larson, unpubl. data). Here, we present a phylogeny for the *bimaculatus* group of the northern Lesser Antilles based on analysis of mtDNA sequence data in combination with previously published allozyme data (Gorman and Kim, 1976).

MATERIALS AND METHODS

We sequenced a portion of the mitochondrial cytochrome *b* (cyt *b*) gene from at least two individuals from each of 20 populations representing all species from the *bimaculatus* group (sensu Etheridge, 1960; Gorman and Kim, 1976), plus one individual from a Puerto Rican outgroup *A. cristatellus*. The only taxon missing

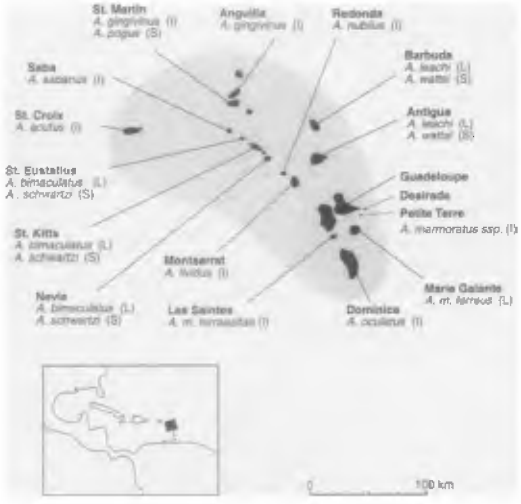

FIG. 1. Distribution of species on islands of the northern Lesser Antilles and their relative body size (after Schoener, 1970): I = intermediate; S = small; and L = large.

from our analysis was *Anolis nubilus* for which tissues were unavailable. Locality and voucher specimen information are contained in Table 1.

DNA was prepared from liver tissue, which had been frozen or fixed in absolute ethanol, using standard phenol-chloroform or NaCl extractions (Maniatis et al., 1982; Miller et al., 1988). We amplified nearly the entire cyt *b* gene via the Polymerase Chain Reaction with primers MVZ49-M13RSP (CGAAGCTTGATATGAAAAACCATCGTTGATAA[A/G]AACAATGACAAT[C/T]ATACGAA), a light-strand primer with the 3′ end at position 16267 of the *Xenopus* mitochondrial genome (Roe et al., 1985), and MVZ14-M13SP (CGCCAGGGTTTTCCCAGTCACGACGGTCTTCATCT[C/T][C/T/A]GG[T/C]TTACAAGAC), a heavy strand primer whose 3′ end is in the Threonine tRNA at position 17422 of the *Xenopus* genome. We then generated single-stranded DNA via asymmetric amplification (Gyllensten and Erlich, 1988) using these same primers at 1:50 concentration. Asymmetric amplifications with these primers provided single-stranded template of a 1110-base-pair (bp) fragment of the cyt *b* gene for direct sequencing. Primers MVZ14-M13SP, MVZ49, and cyt *b*2 (Kocher et al., 1989) were used for sequencing with the Sequenase® ^{35}S sequencing protocol. To assess the utility of the cyt *b* gene for this study, we initially sequenced both light and heavy strands of the 363-bp fragment corresponding to codons 11–131 of the

TABLE 1. Specimens examined.

A. m. setosus	Plage de Clugny, north end Basse Terre, Guadeloupe (N = 2)
A. m. marmoratus	St. Sauveur, southeastern Basse Terre, Guadeloupe (N = 2)
A. m. speciosus	Pointe-a-Pitre, Grande Terre, Guadeloupe (N = 2)
A. m. alliaceus N	Col des Mamelles, 600 m elevation, Basse Terre, Guadeloupe (N = 2)
A. m. alliaceus N	Trace Victor Hugues, 500 m, Basse Terre, Guadeloupe (N = 2)
A. m. girafus	Baillif, southwestern Basse Terre, Guadeloupe (N = 2)
A. m. girafus	Bouillante, western Basse Terre, Guadeloupe (N = 2)
A. m. desiradei	1 km N of Beausejour, Ile de la Desirade, Guadeloupe (N = 2)
A. m. chrysops	Terre de Bas, Iles de la Petite Terre, Guadeloupe (N = 2)
A. m. inornatus	Le Moule, Grande Terre, Guadeloupe (N = 2)
A. m. alliaceus S	Bains Jaunes, 1000 m, southern slope of Soufriere, Basse Terre, Guadeloupe (N = 2)
A. (m.) ferreus	1 km N St. Louis, Marie Galante, Guadeloupe (N = 2)
A. m. terraealtae	Plage de Pompierre, east end of Terre de Haut, Les Iles des Saintes, Guadeloupe
A. m. terraealtae	Plage de Figuierre, west end of Terre de Haut, Les Iles des Saintes, Guadeloupe
A. o. oculatus	Vicinity of Canefield, Dominica
A. o. winstoni	Vicinity of Marigot, Dominica
A. bimaculatus	St. Eustatius
A. bimaculatus	Vicinity Boyd's, Trinity Parish, St. Kitts (N = 2)
A. wattsi	St. Mary's Parish, Antigua
A. wattsi	St. George's Parish, Antigua
A. schwartzi	Trinity Parish, St. Kitts (N = 2)
A. lividus	St. Anthony Parish, Montserrat (N = 2)
A. leachi	St. Mary's Parish, Antigua
A. leachi	St. George's Parish, Antigua
A. gingivinus	Baie aux Prunes, St. Martin
A. gingivinus	Baie Rouge, St. Martin
A. pogus	Pic Paradis, St. Martin (N = 2)
A. sabanus	Windwardsidea, Saba (N = 2)
A. acutus	St. Croix, U.S. Virgin Islands (N = 2)
A. c. cristatellus	Hwy 304 just south of Hwy 116 to Parguera, Puerto Rico

Xenopus genome (Roe et al., 1985) using primers MVZ49 and cyt *b*2. We then sequenced the heavy strand of a 333-bp fragment, corresponding to codons 271–380 in the *Xenopus* genome, from at least one individual from each locality using primer MVZ14-M13SP. This latter region encompasses the variable portion of the gene near the control region of the mitochondrial genome and, in combination with the initial 363-bp fragment, encompasses a large proportion of the most variable sites in the cyt *b* gene (Martin and Palumbi, 1993; Meyer, 1994; Irwin et al., 1991). Sequences were aligned by eye using the amino acid sequences of translated DNA sequences.

For phylogenetic analyses of mitochondrial DNA (mtDNA) data, we used both parsimony and maximum likelihood methods as implemented in PAUP* 4.0d64 (Swofford, 1998). We treated each nucleotide position as a multistate character with up to four states and, for parsimony analyses, employed various weighting schemes for transitions and transversions, and synonymous and nonsynonymous base substitutions (detailed below). For maximum-likelihood (ML) analyses we used a general time reversible model with gamma-distributed rate variation. Both the alpha shape parameter of the gamma distribution and number of invariant sites were estimated using maximum likelihood. Nucleotide frequencies were set to the observed frequency of each nucleotide in the entire dataset. Trees were rooted with *Anolis cristatellus*, a member of the closely related *cristatellus* species group (Etheridge, 1960; Williams, 1976), as the sole outgroup in each analysis.

To examine phylogenetic signal in different types of character state change at different hierarchical levels of relationship, we used the skewness of the tree length distribution (Hillis, 1991; Hillis and Huelsenbeck, 1992) generated from 10,000 random trees or from all trees when the number of taxa included was ≤ 10. To estimate the degree of support for phylogenetic groupings, we calculated decay indices for each clade (Bremer, 1988; Donoghue et al., 1992) and performed phylogenetic analyses on 1000 bootstrap replicates of the dataset (Felsenstein, 1985).

We analyzed the allozyme data of Gorman and Kim (1976) both separately and in combination with the mtDNA data. We constructed Fitch-Margoliash (FM) and neighbor-joining (NJ) trees from the distance matrix presented by Gorman and Kim (1976), using PHYLIP 3.5 (Felsenstein, 1995), and we also analyzed the data in a parsimony framework using the MANOB optimization criterion (Swofford and Berlocher, 1987; Berlocher and Swofford, 1997). For the MANOB analysis, we used step matrices representing the locus-specific Manhattan distances among taxa (see Berlocher and Swofford, 1997). Under the MANOB criterion, internal node assignments are limited to those states observed in the terminal taxa.

In addition, we combined the allozyme and mtDNA data in a parsimony analysis. Because C $\leftrightarrow$ T changes in first positions of mtDNA codons were nearly always synonymous substitutions in Leucine codons (see Results), we applied a step matrix, which counted first-position C $\leftrightarrow$ T changes as one step and all other changes as two steps. Second positions were unordered and given a weight of two so that all changes were counted as two steps. We applied a step matrix to third positions, which counted transversions as two steps and transitions as one. Finally, we applied the Manhattan distance step matrices to the allozyme characters and assigned a weight of two to each of those characters. This resulted in allozyme changes (the origin of a new allele) being counted as two steps, equivalent to nonsynonymous substitutions and third position transversions in the mtDNA. In the combined analysis, all taxa were retained even though allozyme data were lacking for several of the taxa within the *Anolis marmoratus* complex, and mtDNA data were lacking for *A. nubilus*.

Results

We obtained 696-bp of cyt *b* sequence from 48 individuals of *Anolis* from the Northern Lesser Antilles (sequences available in Genbank, Accession numbers AF212110–AF212129). Sequence differences within localities were generally low, with zero to three silent transitions between sequences in *A. ferreus* ($N = 2$), *A. m. desiradei* ($N = 2$), *A. m. inornatus* ($N = 2$), *A. pogus* ($N = 2$), *A. sabanus* ($N = 2$), *A. bimaculatus* ($N = 3$), *A. leachi* ($N = 2$), *A. gingivinus* ($N = 2$), *A. lividus* ($N = 2$), *A. m. chrysops* ($N = 2$), *A. m. terrealtae* ($N = 2$), and *A. acutus* ($N = 2$). Sequences within *A. oculatus* ($N = 2$) differed by nine silent transitions, whereas sequences within *A. wattsi* ($N = 2$) and *A. schwartzi* ($N = 2$) differed at 21 and 17 sites respectively. Sequences from populations of *A. marmoratus* on the main islands of the Guadeloupean archipelago display strong geographic structure (Schneider, 1993, 1996) and differed at up to 65 sites (9.3% observed sequence divergence; Table 2).

To reduce the size of the dataset for phylogenetic analyses, we combined similar sequences from the same locality (differing at 2% of sites or less) into single OTUs, scoring variable sites as polymorphic in the combined dataset. With unordered characters and 100 replicates of random taxon addition, a heuristic search using parsimony criteria resulted in a single tree of 1052 steps (Fig. 2A). The tree is rooted with *An-*

TABLE 2. Observed (above diagonal) and Kimura two-parameter (Kimura 1980; below diagonal) distances among OTUs.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	*A. m. marmoratus*		0.094	0.057	0.058	0.062	0.078	0.071	0.088	0.106	0.146	0.134	0.171	0.165	0.157	0.175	0.186	0.174	0.068	0.207	0.231
2	*A. lividus*	0.103		0.088	0.085	0.089	0.092	0.107	0.094	0.114	0.142	0.149	0.179	0.170	0.163	0.170	0.189	0.196	0.094	0.207	0.240
3	*A. m. inornatus*	0.060	0.095		0.007	0.071	0.078	0.072	0.083	0.109	0.151	0.126	0.171	0.165	0.163	0.180	0.187	0.180	0.079	0.203	0.236
4	*A. m. chrysops*	0.062	0.092	0.007		0.073	0.075	0.068	0.081	0.108	0.153	0.128	0.175	0.161	0.157	0.179	0.186	0.181	0.081	0.199	0.236
5	*A. m. girafus*	0.065	0.096	0.076	0.078		0.029	0.067	0.082	0.106	0.148	0.140	0.159	0.156	0.153	0.181	0.176	0.182	0.013	0.203	0.224
6	*A. m. alliaceus N*	0.084	0.100	0.083	0.080	0.030		0.072	0.079	0.118	0.145	0.152	0.166	0.165	0.156	0.186	0.183	0.197	0.043	0.207	0.236
7	*A. m. desiradei*	0.076	0.118	0.077	0.072	0.072	0.077		0.091	0.118	0.159	0.154	0.174	0.161	0.165	0.183	0.189	0.186	0.081	0.207	0.239
8	*A. m. alliaceus S*	0.096	0.102	0.090	0.087	0.088	0.085	0.099		0.111	0.137	0.135	0.160	0.151	0.152	0.180	0.186	0.190	0.095	0.197	0.223
9	*A. m. ferreus*	0.117	0.126	0.121	0.120	0.117	0.132	0.132	0.123		0.150	0.164	0.184	0.158	0.159	0.176	0.185	0.181	0.116	0.204	0.245
10	*A. m. terraealtae*	0.167	0.161	0.174	0.176	0.170	0.166	0.184	0.155	0.172		0.156	0.189	0.163	0.175	0.171	0.180	0.196	0.145	0.219	0.244
11	*A. oculatus*	0.151	0.169	0.141	0.143	0.159	0.175	0.176	0.152	0.191	0.180		0.184	0.183	0.167	0.187	0.188	0.207	0.142	0.212	0.251
12	*A. gingivinus*	0.199	0.211	0.201	0.206	0.183	0.192	0.204	0.185	0.218	0.223	0.217		0.156	0.130	0.171	0.171	0.205	0.164	0.205	0.222
13	*A. leachi*	0.190	0.196	0.191	0.186	0.178	0.191	0.186	0.173	0.182	0.187	0.216	0.178		0.160	0.169	0.161	0.191	0.165	0.184	0.222
14	*A. bimaculatus*	0.180	0.188	0.188	0.180	0.174	0.178	0.190	0.174	0.181	0.204	0.194	0.146	0.184		0.179	0.170	0.195	0.162	0.175	0.228
15	*A. schwartzi*	0.203	0.195	0.210	0.208	0.211	0.218	0.213	0.210	0.204	0.198	0.218	0.197	0.195	0.208		0.082	0.142	0.186	0.156	0.224
16	*A. wattsi*	0.219	0.222	0.221	0.219	0.205	0.215	0.223	0.218	0.217	0.212	0.220	0.197	0.184	0.196	0.089		0.135	0.185	0.174	0.210
17	*A. pogus*	0.202	0.231	0.209	0.212	0.213	0.234	0.217	0.224	0.211	0.233	0.247	0.244	0.226	0.229	0.160	0.152		0.193	0.183	0.243
18	*A. sabanus*	0.072	0.102	0.085	0.087	0.013	0.045	0.087	0.104	0.129	0.166	0.161	0.190	0.191	0.186	0.217	0.217	0.226		0.208	0.227
19	*A. acutus*	0.248	0.248	0.243	0.236	0.242	0.249	0.248	0.233	0.243	0.267	0.253	0.244	0.214	0.202	0.176	0.201	0.212	0.250		0.194
20	*A. cristatellus*	0.283	0.296	0.291	0.292	0.271	0.290	0.295	0.270	0.305	0.303	0.314	0.268	0.268	0.280	0.272	0.250	0.301	0.277	0.230	

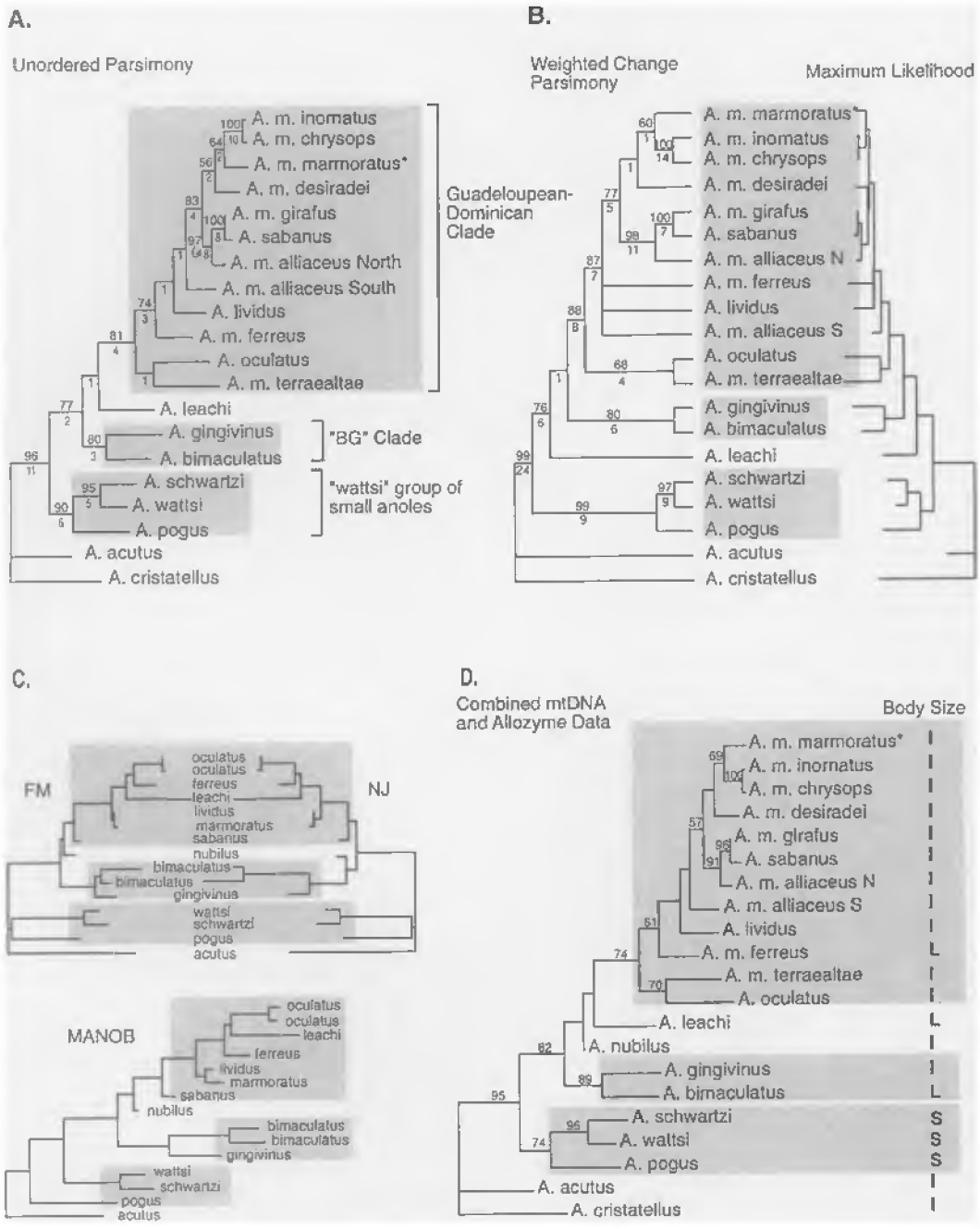

FIG. 2. (A) Minimum length tree with all characters unordered (1052 steps; CI = 0.506). Bootstrap values from 1000 bootstrap replicates are shown above the nodes (values of less than 50% are not shown). Values below nodes are decay indices. Shaded boxes identify important clades discussed in the text. (B) Weighted-change parsimony and maximum-likelihood trees generated from mtDNA data. (C) Fitch-22 Margoliash (FM), neighbor-joining (NJ), and MANOB trees constructed from allozyme data presented by Gorman and Kim (1976). (D) Single most-parsimonious tree resulting from analysis of the combined mtDNA and allozyme data. Values above the branches are bootstrap values from 1000 bootstrap replicates. Values less than 50% are not shown. Body size for each species is shown in the right hand column: I = intermediate; L = Large; and S = small. * The OTU *Anolis marmoratus marmoratus* here represents the phylogenetic position of sequences from three described subspecies (*A. m. marmoratus, A. m. speciosus,* and *A. m. setosus*), which together form an exclusive group within which sequences differ by less than 2%.

TABLE 3. Phylogenetic signal in different partitions of the dataset as shown by g_1-statistics of tree length distribution for 10,000 random trees (or all possible trees if less than 10 taxa were included). Analyses are presented such that the first subset of taxa represents the deepest divergences in the tree, with subsequent analyses adding taxa that represent successively shallower levels of divergence. Synonymous transitions (C↔T changes in first positions of leucine codons and all third-position transitions) represent the fastest evolving character state changes and show significant phylogenetic signal only for the most recent divergences while slowly evolving classes of changes show significant phylogenetic signal for even the deepest relationships. ** = $P \leq 0.01$; * = $0.01 < P \leq 0.05$; ns = $P > 0.05$.

Taxa included	Synonymous transitions	Transversions and nonsynonymous transitions	All characters (unordered)	Informative characters
A. m. marmoratus, A. oculatus, A. leachi, A. bimaculatus, A. pogus	−0.049 ns	−0.962*	−0.299 ns	92
Above + *A. gingivinus*	−0.217 ns	−1.166**	−0.545*	129
Above + *A. m. terrealtae*	−0.384 ns	−0.782**	−0.541**	150
Above + *A. schwartzi*	−0.208 ns	−1.046**	−0.794**	169
Above + *A. wattsi*	−0.446**	−0.899**	−0.700**	178
Above + *A. (m.) ferreus*	−0.348**	−1.069**	−0.730**	186
Above + any other of the Guadeloupean clade	**	**	**	≤205

olis cristatellus as the sole outgroup and is presented with a basal trichotomy because the relationship of *A. acutus* to the *bimaculatus* and *cristatellus* species groups is uncertain (see Gorman and Atkins, 1969; Lazell, 1972; Williams, 1976; Roughgarden et al., 1987).

The minimum length tree contains a well-supported monophyletic group of sequences from the *wattsi* group of small-bodied anoles (*A. schwartzi, A. wattsi,* and *A. pogus*), but sequences from the large-bodied anoles that occur on two-species islands (*A. bimaculatus* and *A. leachi*) are not sister taxa. In the minimum length tree, *A. gingivinus* (an intermediate-sized anole) and *A. bimaculatus* are sister species (henceforth the BG clade), and *A. leachi* is the sister group to the Guadeloupean-Dominican clade (which contains sequences from *A. marmoratus* ssp., *A. lividus, A. sabanus,* and *A. oculatus*). However, the position of *A. leachi* relative to the BG clade is unresolved in the 50% majority rule consensus of the bootstrapped data (see Fig. 2A). Sequences from the Guadeloupean Archipelago are not monophyletic and the clade stemming from their most recent common ancestor also contains sequences from *A. lividus* (from Montserrat) and *A. sabanus* (from the island of Saba, approximately 200 km northwest of Guadeloupe), and also possibly *A. oculatus* from Dominica, although this latter relationship is not strongly supported (Fig. 2A).

Use of unordered character states is perhaps the simplest assumption, but for nucleotide sequence data, it may not always be most appropriate. Methods of phylogenetic reconstruction using parsimony perform best when the rate of character state change is low (Felsenstein, 1978, 1981; Huelsenbeck and Hillis, 1993), but characters (sites) at different positions within codons of mitochondrial protein-coding genes change at radically different rates; synonymous substitutions occur at a much higher rate than nonsynonymous substitutions, and there is a strong transition bias (Irwin et al., 1991; Martin and Palumbi, 1993). As a heuristic, we used the skewness of tree-length distribution (Hillis, 1991; Hillis and Huelsenbeck, 1992) to examine phylogenetic signal in synonymous and nonsynonymous substitutions at various nodes in the tree representing different levels of divergence (Table 3). Synonymous transitions (including both third-position transitions and first-position C ↔ T changes in leucine codons) represent the most frequent type of character state change in the dataset, and the phylogenetic signal in those characters is mainly among terminal taxa at the tips of the tree. In contrast, nonsynonymous transitions and all transversions contain phylogenetic signal for even the deepest relationships.

To see whether accounting for these differences in phylogenetic signal at different depths in the tree would help resolve the deep relationships within the *bimaculatus* group, we searched for the most-parsimonious tree using step-matrices that reduced by a factor of two the cost (in number of steps) of transitions at third positions and C ↔ T transitions in first positions (nearly all of which were synonymous changes in leucine codons). Second position changes of all kinds, third-position transversions, and non-C ↔ T changes at first positions carried twice the cost of third-position transitions and first-position C ↔ T changes. A heuristic search with random taxon addition (100 replicates) resulted in two equally parsimonious trees of 1398 steps, the strict consensus of which is shown in Figure

TABLE 4. Results (*P*-values) from Templeton (1983) one-tailed signed-ranks tests of alternative topologies. *P*-values indicate the probability that alternative trees are not significantly worse explanations of the data than the most-parsimonious tree. Three separate tests were conducted for each comparison: (1) using the mtDNA dataset with character-state changes unordered and of equal weight and comparing alternative trees against the tree shown in Fig. 2A; (2) using the mtDNA dataset with character states partially ordered and weighted ("weighted-change" as described in the text) and comparing alternative trees against the weighted-change parsimony tree shown in Fig. 2B; and (3) using the allozyme dataset and the MANOB assumptions and comparing the alternative trees against the MANOB tree in Fig. 2C. The tests using the allozyme dataset included only those taxa for which allozyme data were complete (see Fig. 2C). Alternative topologies were produced by constraining the relationships of interest and searching for the most-parsimonious tree containing those relationships (heuristic search with 100 replicates of random taxon addition when employing the mtDNA dataset with all taxa, or branch and bound searches using the allozyme dataset with 15 taxa).

Test trees	Dataset and assumptions		
	mtDNA unordered	mtDNA weighted change	Allozymes MANOB
mtDNA unordered	—	>0.80	>0.60
mtDNA weighted-change or ML	>0.50	>0.80	>0.50
Allozyme MANOB and distance trees (Fig. 2C)	<0.01	<0.01	>0.80
Most-parsimonious tree with *A. leachi* nested within the Guadeloupean-Dominican clade (not as the sister group to the GD clade)	0.01	<0.05	—
Most-parsimonious tree with *A. leachi* as the sister group to the Guadeloupean-Dominican clade	—	>0.40	>0.50
Most-parsimonious tree with *A. leachi* and *A. bimaculatus* as sister taxa	<0.01	<0.01	<0.01
Most-parsimonious tree with (leachi,(bimaculatus,gingivinus))	>0.20	>0.10	>0.30

2B. As in the most-parsimonious tree with unordered characters, the large anoles (*A. bimaculatus* and *A. leachi*) are not sister taxa, and the small *wattsi* group anoles (*A. schwartzi, A. wattsi,* and *A. pogus*) form a well-supported clade that is the sister group to all other taxa. These trees differ from the most-parsimonious trees in the placement of *A. leachi* but otherwise are similar. Further reducing the cost of fast evolving character state changes does not significantly alter the relationships shown in Figure 2B.

Maximum-likelihood (ML) analysis of the sequence data under a general time-reversible model with gamma-distributed rate variation among sites resulted in a tree that is similar in most respects to the weighted-change parsimony consensus tree (Fig. 2B). We tested the three alternative topologies (Fig. 2A, B) in a parsimony framework using Templeton's (1983) two-tailed signed-ranks test with character changes unordered and of equal weight, or partially ordered and weighted as in the weighted-change parsimony analysis. None of the trees differs significantly from any other ($P \geq 0.50$ in all cases; Table 4).

Distance and parsimony analyses of Gorman and Kim's allozyme data (Gorman and Kim, 1976) resulted in trees (Fig. 2C) that were similar to each other and to the mtDNA trees (Fig. 2A, B). Neighbor-joining (NJ) and Fitch-Margoliash (FM) trees (Fig. 2C) produced from Gorman and Kim's genetic distance matrix are similar to the mtDNA phylogeny in that they contain a group of small, terrestrial anoles (the *wattsi* group), show *A. gingivinus* as the sister taxon to *A. bimaculatus,* and show a close relationship between Guadeloupean anoles (*A. marmoratus*) and *A. lividus.* The MANOB tree is similar in most respects except that it shows the *wattsi* group as paraphyletic. The allozyme trees all contain the following nested groups: (((*ferreus, oculatus, leachi*), (*lividus, marmoratus*)), *sabanus*). Although the monophyly of the largest of these groups is consistent with the trees produced from the mtDNA data, the mitochondrial and allozyme trees disagree substantially on relationships within this putative clade. The precise topology suggested by the allozyme trees is incongruent with the mtDNA sequence data (signed-ranks test; $P < 0.01$; Table 4). However, trees with *A. leachi* as the sister to the Guadeloupean-Dominican taxa do not differ significantly from the most-parsimonious mtDNA trees ($P > 0.10$; Table 4). The allozyme data are consistent with the trees suggested by the mtDNA data in that none of the mtDNA trees is significantly worse than the MANOB tree in signed-ranks tests using the allozyme data (Table 4). Interestingly, the inconsistency between the allozyme and mtDNA trees may be the result of different rooting of the (Guadeloupean-Dominican, *A. leachi*) group. If, in the allozyme

trees, the (Guadeloupean-Dominican, *A. leachi*) group was rooted on the branch leading to *A. leachi*, the allozyme trees would be nearly identical to the unordered mtDNA topology (Fig. 2A).

Combining the allozyme and mtDNA data (as described in the Materials and Methods section) resulted in a single tree (Fig. 2D), which is similar in most respects to the mtDNA trees. The 50% majority rule bootstrap consensus tree of the combined data is nearly identical to the mtDNA bootstrap consensus tree (compare Fig. 2A, D). The allozyme data do not significantly improve the resolution of relationships above that of the mtDNA data alone except that there is additional bootstrap support for the sister relationship of *A. bimaculatus* and *A. gingivinus*. The combined data favor placing *A. leachi* as the sister group to the Guadeloupean-Dominican clade (which is also consistent with the presence of a clade containing *A. leachi*, *A. oculatus*, *A. marmoratus*, *A. lividus*, and *A. sabanus* in the separate allozyme and unordered mtDNA trees), but the precise placement of *A. leachi* is not strongly supported in any analysis. We regard the tree shown in Figure 2D as the best estimate of phylogeny from the available data.

Discussion

Our phylogenetic analysis reveals two surprises. First, *A. sabanus*, from the island of Saba, is nested within *A. marmoratus* from Guadeloupe. In terms of gross morphology, *A. sabanus* is very similar to *A. marmoratus* (Losos and de Queiroz, 1997; but see Lazell, 1972, who sees affinities between *A. sabanus* and the *wattsi* group), although its spotted pattern does not closely resemble that of any of the diverse populations of *A. marmoratus*. These results suggest a recent colonization event followed by rapid evolutionary change in body coloration, or alternatively, long-distance dispersal from Guadeloupe to Saba and hybridization with a preexisting population resulting in mtDNA introgression. By contrast, the close relationship of *A. lividus* and *A. marmoratus* has long been suspected (e.g., Lazell, 1972) and was corroborated by Gorman and Kim (1976). In addition, our results suggest that populations on the islands of Les Saintes, situated between Dominica and Guadeloupe (Fig. 1), may be more closely related to *A. oculatus* from Dominica than they are to *A. marmoratus*, even though previous studies (Lazell, 1964, 1972) have treated the Les Saintes populations as a subspecies of *A. marmoratus*. *Anolis oculatus* from Dominica is characterized by a unique karyotype (Gorman and Atkins, 1969), and examination of the karyotype from Les Saintes, in addition to further mtDNA sampling within *A. oculatus*, may help resolve the relationships among the Guadeloupean and Dominican anoles.

Previous Phylogenetic Hypotheses

Phylogenetic relationships among taxa within the *bimaculatus* group have been considered previously in three studies. Based on external anatomy, Lazell (1972:100) presented a hypothetical diagrammatic scheme of the evolution of this group. Gorman and Kim (1976) presented a UPGMA phenogram of Nei's (1972) genetic distance estimated from protein electrophoretic variation. Finally, Roughgarden et al. (1987) suggested a phylogeny based on a variety of disparate data, drawn primarily from the previous two studies.

Lazell (1972) did not present his scenario in the form of a phylogenetic tree but provided sufficient detail that phylogenetic relationships can be determined. Importantly, Lazell identified a closely related group of small anoles, the *wattsi* group, which he considered a single species with four subspecies, and he recognized the close relationship among *A. marmoratus*, *A. lividus*, and *A. oculatus*. We also note that he considered *A. leachi* and *A. bimaculatus* to be conspecific and *A. nubilus* to be closely related to *A. bimaculatus*.

The phylogenetic hypothesis proposed by Roughgarden et al. (1987) was not based on any formal analysis; hence, we will not consider it explicitly, but, because it was based in large part on Gorman and Kim's (1976) study, most of our comments below pertain to it as well. We do note, however, that Roughgarden considered the *wattsi* group of small anoles as monophyletic, considered *A. marmoratus*, *A. lividus*, and *A. oculatus* as a monophyletic group, and left the relationships of *A. bimaculatus*, *A. leachi*, *A. gingivinus* unresolved. Neither Roughgarden (1987) nor Lazell (1972) suggested a close relationship between *A. sabanus* and *A. marmoratus*.

Gorman and Kim (1976) presented a UPGMA tree based on Nei's genetic distance (Nei, 1972). Their UPGMA tree differs substantially from our FM and NJ trees which were constructed using the same distance matrix. The discrepancy likely results from the restrictive assumption of equal rates of evolution among taxa imposed by UPGMA (reviewed by de Queiroz and Good, 1997). Interestingly, trees constructed from the allozyme data (NJ, FM, and MANOB trees) are inconsistent with the mtDNA data (Table 4), but the converse is not true—trees constructed from the mtDNA dataset are not inconsistent with the allozyme data (Table 4). This result may stem from the allozyme dataset lacking the power to reject alternative topologies (i.e., the pattern of informative character covariation in the allozyme dataset may be so weak

as to allow many alternative topologies), whereas the strong patterns of character covariation in the mtDNA dataset allow the rejection of many alternative topologies. Additional data from nuclear markers are needed to examine the concordance between evolutionary histories of nuclear and mitochondrial genomes.

In summary, the available mtDNA and allozyme data suggest that the Guadeloupean-Dominican clade of taxa (including *A. lividus* and *A. sabanus*) form a monophyletic group exclusive of the other *bimaculatus* group taxa. The position of *A. nubilus*, for which DNA sequences are not available, differs in the allozyme trees (Fig. 2C) and remains uncertain pending additional data. The position of *A. leachi* is unresolved but its placement as the sister group to the Guadeloupean-Dominican group (as in Fig. 2D) is consistent with both mtDNA and allozyme data. More important, the large anoles *A. bimaculatus* and *A. leachi* are not sister taxa, whereas the small anoles *A. wattsi*, *A. schwartzi*, and *A. pogus* form a well-supported monophyletic group.

Body Size Evolution

The distribution of body sizes among species in the Lesser Antilles is decidedly nonrandom (Schoener, 1970; Losos, 1990): species occurring alone on an island tend to be intermediate in size, whereas on two-species islands, a large and a small species are usually found (Fig. 1). The two exceptions to this are the solitary large anole (*A. marmoratus ferreus*) from Marie Galante, and the coexistence of a small (*A. pogus*) and an intermediate-sized anole (*A. gingivinus*) on St. Martin (Fig. 1). Schoener (1970) and Williams (1972; see also Lazell, 1972:99) suggested that the pattern of body-size distribution could result from character displacement, in which two similar and presumably intermediate-sized species came into sympatry and then diverged in body size to minimize competition. Losos (1990) tested this hypothesis in a phylogenetic context and concluded that large and small size had each evolved once in the *bimaculatus-leachi* and *wattsi* clades, respectively, and that this pattern was consistent with a character displacement explanation (for further discussion of the statistical analysis underlying these conclusions, *see* Miles and Dunham, 1996; Butler and Losos, 1997). However, this analysis was conducted using the phylogeny of Roughgarden et al. (1987) with the trichotomy involving *A. bimaculatus*, *A. leachi*, and *A. gingivinus* resolved in favor of an *A. bimaculatus–A. leachi* sister taxon relationship following Lazell's taxonomy (1972). However, the existing molecular data do not support a sister relationship of *A. bimaculatus* and *A. leachi*: both the allozyme and mtDNA data unambiguously reject any tree with a sister relationship between *A. bimaculatus* and *A. leachi* ($P < 0.01$ for both datasets; Table 4).

Because *A. bimaculatus* and *A. leachi* are not sister taxa, evolutionary changes in size must have occurred more frequently than Losos (1990) concluded. Depending on how the relationship of *A. leachi* is finally resolved, large body size may have evolved separately (twice) in *A. leachi* and *A. bimaculatus* or once in their common ancestor. We note that large body size may have evolved as many as three times in the *bimaculatus* group as a whole, if we consider the solitary large anole *A. m. ferreus* (see Lazell, 1972; Roughgarden and Fuentes, 1977), and that the more frequently body size is inferred to have changed, the less reliable are our reconstructions of ancestral states likely to be (e.g., Schluter et al., 1997; Cunningham et al., 1998). If *A. leachi* is the sister group to the BG clade, then large body size may have evolved only once in the common ancestor of *A. bimaculatus* and *A. leachi*, with a reversion to intermediate size in *A. gingivinus*. The most-parsimonious tree with *A. leachi*, *A. bimaculatus*, and *A. gingivinus* as a monophyletic group is not incompatible with the available data (Table 4). If, in fact, large size only evolved once in the common ancestor of *A. bimaculatus* and *A. leachi*, then a hypothesis of character displacement, with the *wattsi* complex evolving small size concurrently, would still be tenable, although the reversion of *A. gingivinus* to intermediate size while in sympatry with *wattsi* complex species would require explanation. However, if large size evolved independently in *A. bimaculatus* and *A. leachi*, then a character displacement hypothesis becomes less tenable. The reason is that a character displacement hypothesis implies simultaneous change in size in two species—one getting larger and the other getting smaller—and thus implies that the number of increases in size should be the same as the number of decreases. Of course, ad hoc scenarios could always be devised to account for this discrepancy.

As an alternative evolutionary explanation for size distributions in the northern Lesser Antilles, Roughgarden and Pacala (1989) suggested a taxon cycle hypothesis, which was later modified to a taxon loop hypothesis (Roughgarden, 1992, 1995). This hypothesis assumes that intermediate size is optimal for anoles on the Lesser Antilles and that larger species are behaviorally dominant over smaller ones. Hence, if an island with an intermediate-sized species is invaded by a larger species, the larger species will begin to evolve toward intermediate size while the initially intermediate-sized species evolves to smaller size to lessen competitive effects (for a discussion of the data relevant to this and the character displacement hypothesis, see Rough-

garden and Pacala, 1989; Roughgarden, 1992, 1995; Losos, 1992). The taxon cycle/loop hypothesis seems to require some additional assumptions. For one, it requires dispersal of large-sized lizards from a source where intermediate size is not optimal. For another, it equates behavioral dominance with competitive dominance but then assumes that evolution of small size by the smaller species is advantageous because it lessens competition despite the fact that it increases the disadvantage of the species in terms of behavioral dominance. Evidently the assumption is that the disadvantage in behavioral dominance is less important in terms of natural selection than the advantage in terms of reduced competition.

In the particular scenario proposed by Roughgarden and Pacala (1989), Guadeloupe or Dominica is the source for large-bodied colonists that would initiate a taxon cycle/loop. If that were true, *A. bimaculatus* and *A. leachi* sequences would be embedded within the Guadeloupean-Dominican clade of sequences, and this is not the case. However, if large body size in *A. leachi* and *A. bimaculatus* only evolved once, then the common ancestor of the BG clade would have been large and reversion to intermediate size in *A. gingivinus* could be consistent with a modified taxon loop/cycle hypothesis, although the lack of an allopatric large ancestral population would still be problematic.

Conclusions

Resolving the relationships of *A. leachi* is necessary to further understand patterns of body-size evolution in the anoles of the *bimaculatus* species group. In addition, our unexpected findings on the position of *A. sabanus* and the relationships between Guadeloupean and Dominican populations deserves further study. The phylogeny presented above resolves some important issues in the evolution and biogeography of the *bimaculatus* group of anoles and provides the framework for future phylogenetic analyses of nuclear and mitochondrial genes targeting poorly supported nodes in this tree.

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