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Population structure and history of a phenotypically variable teiid lizard (*Ameiva chrysolaema*) from Hispaniola: the influence of a geologically complex island

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Abstract

Ameiva chrysolaema is distributed across the island of Hispaniola in the West Indies. The species is restricted to dry lowlands between major mountain ranges and along the southern and eastern coasts. Phylogenetic and phylogeographic analyses of mtDNA sequence variation from 14 sampling localities identify at least three independent evolutionary lineages, separated from one another by major mountain ranges. Nested clade phylogeographic analysis (NCPA) suggests a complex history of population fragmentation, consistent with geological evidence of seawater incursions into the Azua and Enriquillo basins during the Pliocene/Pleistocene (~1.6 mya). Significantly negative Fu's F_S values and parameters of mismatch distributions suggest that formerly fragmented populations have recently expanded their ranges. Significantly large average population clade distances (APCD) for two sampling localities in the Azua basin suggest secondary contact at these localities of previously separated populations. The distribution of haplotypes among polymorphic populations of *A. chrysolaema* suggests that variation in dorsal pattern represents a polymorphism within evolutionary lineages. *Ameiva leberi* is ecologically indistinguishable from and syntopic with *A. chrysolaema*. Genetic data suggest that *A. leberi* is a junior synonym of *A. chrysolaema*.

Keywords: *Ameiva chrysolaema*; *Ameiva leberi*; Phylogeography; Biogeography; Species complex; Pattern polymorphism

1. Introduction

Phylogenetic methods may be used to test hypotheses regarding intraspecific variation and relationships as well as patterns and processes of evolution (e.g., Avise, 2000; Avise et al., 1987; Emerson, 2002; Schneider et al., 1998). Phylogeography examines the historical and spatial components of populational lineages and is used to explain evolutionary dynamics of closely related populations. Phylogeography is important to studies of speciation, because the structure of the haplotype tree may identify barriers to gene flow in the biogeographic and demographic histories of species and populations. Further advancements, in terms of explicit statistical methodology (Templeton, 2004; Templeton et al., 1995) and the incorporation of population-genetic analyses, have made this field a powerful area of investigation.

Many wide-ranging species vary geographically, and some of these geographic variants have been classified as subspecies. Phylogeographic studies frequently show that subspecies identified by morphological variation do not represent actual evolutionary units (e.g., Burbrink et al., 2000; Glor et al., 2003; Leaché and Reeder, 2002; Rawlings and Donnellan, 2003), but rather superficially similar populations with disparate evolutionary origins (Schneider et al., 1998; Smith et al., 2001). We apply phylogeographic methodology to clarify the evolutionary history and diversification of *Ameiva chrysolaema* on Hispaniola.

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Ameiva chrysolaema comprises populations of relatively large teiid lizards ubiquitous in dry lowlands on the island of Hispaniola (Schwartz and Henderson, 1991). This species is the most widespread teiid on the island and includes 16 phenotypically variable subspecies (Schwartz and Klinikowski, 1966). Powell (1993) suggests that some subspecies may warrant recognition as species because they represent allopatric lineages that are diagnosably distinct morphologically. Using a combination of phylogenetic methods and nested clade phylogeographic analysis (NCPA) we examine geographic variation within *A. chrysolaema* to determine whether its populations form a single phenotypically variable species or a complex of separately evolving lineages.

The tectonic history of Hispaniola is complex (Lewis and Draper, 1990), and provides numerous opportunities for vicariant fragmentation of *Ameiva* populations. The island was formed by the juncture of the North and South paleoislands probably during the middle Miocene (Graham, 2003). The juncture of the paleoislands is currently marked by the Valle de Neiba-Cul de Sac Plaine in south-central Hispaniola (i.e., the Enriquillo basin, Fig. 1). Areas corresponding to the two paleoislands are called the North and South islands in herpetological literature. McLaughlin et al. (1991) and Mann et al. (1999) document extensive marine incursion in the Azua and Enriquillo basins during the Miocene to lower Pliocene. Quaternary alluvial deposits in the Azua, San Juan, and Enriquillo basins suggest that these basins were under water at least intermittently at this time (McLaughlin et al., 1991). Taylor et al. (1985) examine subaerially exposed coral reef deposits on the fringes of the Enriquillo basin and determine that marine conditions existed there periodically during the Holocene. Incursion of marine water undoubtedly had a major impact on the historical distributions of lowland organisms on Hispaniola during the Pliocene and Quaternary time periods.

Glor et al. (2003) studied *Anolis cybotes* on Hispaniola and revealed that vicariant phenomena greatly contributed to the multiplication of species within this montane taxon. We use our genetic analyses to examine whether similar levels of geographic fragmentation may exist for a lowland species. We predict that *A. chrysolaema* will exhibit allopatric divergence among groups of

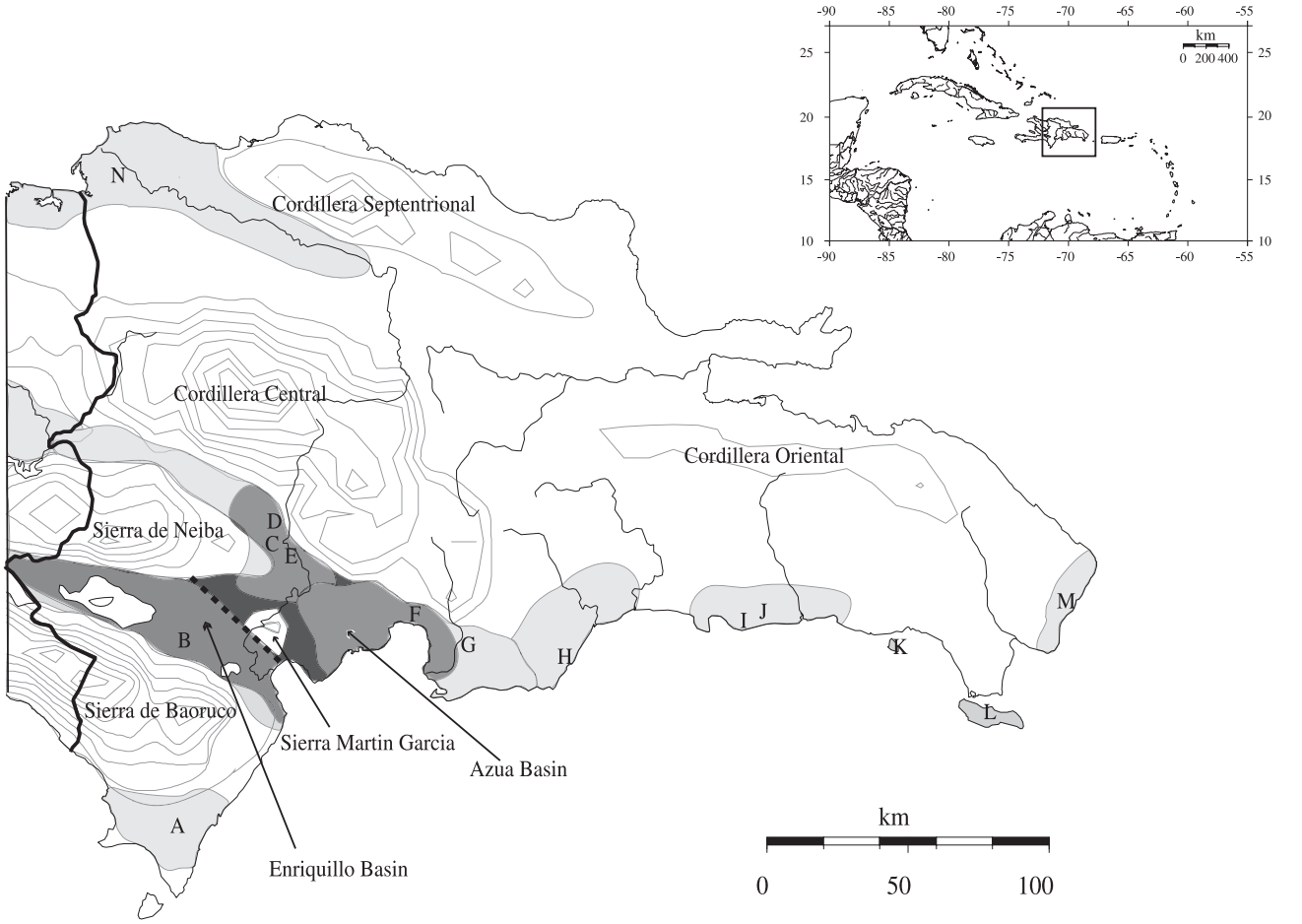

Fig. 1. Species distribution (light shading), location of major relief features, and sampling localities for the individuals used in this study. Dark shading represents lowland basins periodically inundated with seawater (see text). The heavy line in the western Dominican Republic represents the political border with Haiti. Letters represent sampling localities as in Table 1.

populations, but that patterns of vicariant fragmentation will differ from those of *A. cybotes*.

Population-genetic hypotheses for *A. chrysolaema* are derived largely from variation in color patterns. Little is known about the dispersal capabilities of *A. chrysolaema*, and ecological studies are available only for populations in the southern Dominican Republic (Powell et al., 1996; Schell et al., 1993; Sproston et al., 1999). Pattern polymorphisms, which are not uncommon in teiid lizards (Axtell, 1961), are observed in three subspecies of *A. chrysolaema*. *Ameiva c. boekeri*, *A. c. richardthomasi*, and *A. c. jacta* all include patterned and unpatterned forms. A second morphologically similar species, *Ameiva leberi*, occurs on the Barahona Peninsula in sympatry with *A. c. ficta*. However, this species is distinguished from *A. chrysolaema* solely on color pattern and the apparent lack of intergradation (Schwartz and Thomas, 1975). Furthermore, these two species are ecologically indistinguishable where sympatric, suggesting that they may represent pattern phases of a single taxon (Sproston et al., 1999). Hower and Hedges (2001) include one specimen of *A. leberi* in their analysis of the relationships among West Indian *Ameiva* and suggest that this species be placed in the synonymy of *A. c. ficta*. We predict, based on the current disjunct distribution of *A. chrysolaema* and the geological history of Hispaniola that substantial geographic structure should exist among populations of *A. chrysolaema*.

2. Materials and methods

2.1. Taxonomic sampling and DNA extraction

We sampled 14 localities, representing the range of *Ameiva chrysolaema* in the Dominican Republic (Fig. 1 and Table 1), including representatives of all mainland subspecies within the Dominican Republic and satellite island populations from Islas Catalina and Saona. Haitian populations were not accessible for this study. Whole genomic DNA was isolated from minced liver or muscle tissue for 55 *A. chrysolaema*, nine *A. leberi*, and four *A. lineolata* using the Qiagen Dneasy Tissue kit (Qiagen, Valencia, CA). Extracted genomic DNA was stored in AE buffer at −20 °C until PCR amplification. *Ameiva lineolata* represented the outgroup for phylogenetic analyses based on results of Hower and Hedges (2001).

2.2. Amplification of ND2, $tRNA^{Trp}$, mtDNA, 12S and 16S rDNA, sequencing, and alignment

An 1200 bp fragment of mtDNA representing the entire sequence of the nitrogen dehydrogenase subunit 2 (ND2) protein-coding gene and tryptophan transfer RNA ($tRNA^{Trp}$) was amplified. This mtDNA fragment was amplified with the L4437 (5′-AAGCTTTCGGG CCCATACC-3′) and H5617b (5′-AAAGTGTCTGAG TTGCATTCAG-3′) primers. PCR amplification used the PCR Core System II PCR kit (Promega, Madison, WI 53711). Standard 50 μl PCRs included 4–6 μl genomic DNA and a cocktail of 49.5% H_2O, 10% 10× buffer, 25 mM $MgCl_2$, dNTPs, 2 pmol primer mix, and 0.5% taq DNA polymerase; the ND2 amplification reactions utilized an annealing temperature of 52 °C.

ND2 products were cleaned with the Viogene Gel-M Gel Extraction System (Viogene, Sunnyvale, CA, USA). Sequencing reactions were run with Big Dye Terminator Ready-Reaction Kits (Perkin–Elmer, Wellesley, MA, USA) on an MJ Research BaseStation automated sequencer (MJ Research, South San Francisco, CA, USA). L4437, H5617b, and L4882 (5′-ACATGACAA AAACTTGCNCC-3′; internal primer) were used to sequence the entire 1100 bp ND2 fragment. Alignment of ND2 sequences was done manually using secondary structural models for the tRNA gene (Kumazawa and Nishida, 1993; Macey et al., 1998).

Approximately 390 bp of the mtDNA 12S ribosomal RNA (rRNA) gene and approximately 1030 bp of the 16S rRNA gene were amplified for 40 *A. chrysolaema*, five *A. leberi*, and two *A. lineolata* using the following primers: 12L5 (5′-GATTAGATACCCCACTATGC-3′) and 12H4 (5′-AGGGTGACGGGCGGTGTGTRC-3′) for the 12S fragment; and 16L20 (5′-TGAAAASCCW AMCGARCYTGRTGATAGCTG-3′), 16H10 (5′-TG ATTACGCTACCTTTGCACGGT-3′), 16L9 (5′-CG CCTGTTTATCAAAAACAT-3′), and 16H13 (5′-CC GGTCTGAACTCAGATCACGTA-3′) for the 16S fragment. Mixed bases are denoted as follows: M (A or C), R (A or G), S (C or G), W (A or T). Sampling for the 12S and 16S sequence data represented a subset of the taxa sampled for the ND2 gene and included members from all sampling localities in an attempt to uncover basal relationships among lineages diagnosed by variation in the ND2 gene. PCR amplification of this region was performed as described above except using an annealing temperature of 55 °C.

12S and 16S products were sent to The DNA Sequencing Center at Brigham Young University (DNASC) for purification via GenClean (Genetix Reagents, NY, USA) and cycle sequencing. Amplification primers were also used in sequencing reactions. Sequence alignment for the 12S and 16S fragments was accomplished using the multiple alignment setting in ClustalX (Thompson et al., 1997). Various gap-opening and gap-extension parameters were used to assess the effects on sequence alignment. The resulting alignments were reviewed by eye and adjusted with reference to secondary structure, using the models of Cannone et al. (2002), in MacClade 4.06 (Maddison and Maddison, 2003). The default values (gap

Table 1
Taxa sampled, sampling localities (Dominican Republic), locality abbreviation, voucher number(s) for specimens collected, geographical position, and GenBank accession numbers

Taxon	Locality	Voucher Number(s)	Position	16S	12S	ND2
A. c. alacris	(D) 19.5 km SE San Juan	BWMC 06846,[a] 06847,[a] 06848, 06849	18°42.784 N, 71°5.332 W	AY292346–AY292347	AY292309–AY292310	AY561640–AY561643
	(E) 3.5 km S Rio Yaque	BWMC 06853,[a] 06851	18°39.019 N, 71°2.038 W	AY292348	AY292311	AY561644–AY561645
	(C) 2.1 km NW Rio Yaque	BWMC 06854[a]	18°41.36 N, 71°3.692 W	AY292349	AY292312	AY561646
A. c. boekeri	(F) Biyeya	ALS 94, 97, 98, 99, 101,[a] 105, 111[a]	18°25.00 N, 70°37.10 W	AY292362 and AY292364	AY292325 and AY292327	AY561664–AY561670
	(G) Honduras	ALS 167,[a] 169,[a,b] 173,[a] 174, 176	18°22.00 N, 70°25.10 W	AY292365–AY292366	AY292328–AY292329	AY561695–AY561699
A. c. ficta	(A) 4 km SSE Los Tres Charcos	ALS, 29,[a] 31,[a] 33,[a] 35,[a] 37, 38	17°49.106 N, 71°25.650 W	AY292335–AY292338	AY292298–AY292301	AY561655–AY561660
A. c. jacta	(M) Juanillo	BWMC 06841, 06842, 06843,[a] 06844,[a,b] 06845,[a,b] 06859[a,b]	18°28.251 N, 68°23.997 W	AY292357	AY292320	AY561689–AY561694
A. c. parvoris	(J) Los Conucos	ALS 8[a]	18°26.10 N, 69°25.10 W	AY292359	AY292322	AY561679
	(I) Los Bancos	ALS 188,[a,b] 193, 197,[a] 199, 200[a]	18°23.10 N, 69°30.00 W	AY292361	AY292324	AY561677–AY561678, AY561680–AY561682
	(K) Isla Catalina	ALS 21, 22, 23,[a] 24, 25	18°21.00 N, 69°00 W	AY292360	AY292323	AY561650–AY561654
A. c. procax	(H) Playa Najayo	ALS 219,[a] 221, 222, 227, 229, 230[a]	18°18.00 N, 70°5.10 W	AY292367	AY292330	AY561683–AY561688
A. c. regularis	(N) Nueva Judea	BWMC 06860,[a,b] 06861,[a,b] 06862[a]	19°43.56 N, 71°40.29 W	AY292334	AY292297	AY561647–AY561649
A. c. richardthomasi	(L) Isla Saona, Mano Juan	ALS 14, 16, 18, 203[a]	18°8.10 N, 68°40.00 W	AY292358	AY292321	AY561700–AY561703
A. c. umbratilis	(B) Los Pasos de Mella	ALS 142,[a] 143,[a] 146,[a] 148,[a] 152,[a] 156[a]	18°21.00 N, 71°25.00 W	AY292350–AY292354 and AY292356	AY292313–AY292317 and AY292319	AY561671–AY561676
A. leberi	(A) 4 km SSE Los Tres Charcos	ALS 41,[a] 57,[a] 83[a]	17°49.106 N, 71°25.650 W	AY292339–AY292342	AY292302–AY292305	AY561661–AY561663
A. lineolata	(D) 19.5 km SE San Juan	BWMC 06850[a]	18°42.784 N, 71°5.332 W	AY292332	AY292295	AY561638
	(C) 2.1 km NW Rio Yaque	BWMC 06852[a]	18°41.36 N, 71°3.692 W	AY292333	AY292296	AY561636
	(E) 3.5 km S Rio Yaque	BWMC 06855, 06856	18°39.019 N, 71°2.038 W			AY561637 and AY561639

[a] Samples for which 12S and 16S sequence data were obtained.
[b] Sequences that are identical to the sequences indicated by the 12S and 16S GenBank accession numbers.

opening = 15, gap extension = 6.66) performed best in limiting the number of alignment-ambiguous sites. The multiple sequence alignment resulted in few gaps of length 2 or 3 with nearly all sites aligning well in all individuals.

2.3. Phylogenetic analyses

Maximum parsimony analyses were performed using PAUP* 4.0b10 (Swofford, 1999). Due to the large number of operational taxonomic units (OTUs), parsimony analyses for each data partition (12S, 16S, and ND2 separately) and the combined data set (including only taxa shared among the independent data sets) employed the heuristic search option with tree-bisection–reconnection (TBR) branch swapping, MULPARS, and 100 random-taxon sequence-addition replicates. Node support in the tree generated from the combined data set was assessed using nonparametric bootstrapping in PAUP* (1000 pseudoreplicates, 100 random taxon-addition replicates; Felsenstein, 1985) and decay indices (i.e., branch support, Bremer, 1994) using TreeRot. v2 (Sorenson, 1999).

ModelTest 3.06 (Posada and Crandall, 1998) was implemented to determine an appropriate model of evolutionary change using the likelihood-ratio test statistic (LRT; Huelsenbeck and Crandall, 1997), which determines whether more parameter-rich models provide a significantly better fit (significantly higher ln-likelihood value) to the data than a less complex model. Goldman (1993) proposed that a χ^2 distribution could be used as an approximation of the underlying distribution of the LRT (Whelan and Goldman, 1999). ModelTest 3.06 determined that the general time reversible model with rate heterogeneity modeled by a discrete gamma distribution (i.e., GTR + Γ; Yang, 1994) appropriately described the data. All "corrected" genetic-distance calculations were performed in MEGA 2.1 (Kumar et al., 2001) using the Tamura–Nei distance correction with rate heterogeneity modeled by a discrete gamma distribution (this is the most complex model available in MEGA 2.1).

Bayesian phylogenetic analyses implementing the GTR + Γ model were conducted using the combined data in the software program MrBayes v3.0 (Huelsenbeck and Ronquist, 2001). All Bayesian analyses were launched using random starting trees and flat priors for starting parameters. Three analyses were run for 1,000,000 generations, implementing four separate Markov chains, sampling every 100th tree resulting in a total of 10,000 sample points (trees from the posterior distribution).

To ensure that the Markov chains had reached stationarity, we plotted the ln-likelihood scores for all sampled trees against the number of generations the Markov chain was run. Stationarity was determined as the point at which the ln-likelihood values reached a stable equilibrium (Huelsenbeck and Ronquist, 2001). Only samples that had reached approximate stationarity were used in evaluating tree topology. All other samples were discarded as "burn in."

Determining that the analyses are not trapped in local optima is important, so three methods were used as evidence of accurate runs (Larget and Simon, 1999; see Leaché and Reeder, 2002). First, analyses were run twice, each beginning with different starting trees. The stationarity levels for each analysis were compared for congruence (Huelsenbeck and Bollback, 2001). Analyses were determined to have converged if the ln-likelihood scores had similar mean values. Second, the Metropolis-coupled Markov Chain Monte Carlo (MCMC) algorithm was used to enhance the exploration of parameter space (Geyer and Thompson, 1995). The default heating value (0.2) was used incrementally to heat four Markov Chains. Finally, the posterior probabilities of the clades contained in the tree estimates were compared for congruence (Huelsenbeck and Imennov, 2002). Clade posterior probabilities greater than or equal to 95% were considered significantly supported (Wilcox et al., 2002).

In one data set, Leaché and Reeder (2002) showed that node support measured with posterior probability values differed substantially from MP bootstrap scores but was more closely correlated with maximum-likelihood bootstrap support values. Additionally, using sequence simulations, Wilcox et al. (2002) suggested that Bayesian posterior probabilities were conservative but more accurate measures support than the nonparametric bootstrap.

2.4. Nested clade phylogeographic analysis, Fu's F_S, and mismatch distributions

We used a nested clade phylogeographic analysis (NCPA, Templeton, 1998, 2004; Templeton et al., 1995) to examine the history of *Ameiva chrysolaema* populations in the central and eastern portions of its distribution (localities B–M in Fig. 1). NCPA provides an objective statistical framework for discriminating among historical (e.g., range expansion and fragmentation) and recurrent (e.g., gene flow and drift) processes that may explain the observed distribution of genetic variation. The haplotype network for the *ND2* data was constructed using the computer program TCS vers. 1.06 (Clement et al., 2000). TCS creates a haplotype network using Statistical Parsimony (Templeton et al., 1992), which outputs the 95% plausible set of most parsimonious linkages among haplotypes. Ambiguous linkages are depicted by "loops" in the haplotype network. The nesting of haplotypes was done by hand following the rules outlined in Templeton and Sing (1993) and Templeton (1998).

Various distance measures used in the NCPA were calculated using GeoDis 2.0 (Posada et al., 2000). The average clade distance (D_C) measures the average distance haplotypes are from the estimated geographical center for all individuals or haplotypes within that particular nesting group; nested clade distance (D_N) measures the average distance individuals or haplotypes are from the estimated geographical center for all haplotypes or groups within the next highest nesting level; interior–tip distances ($I-T_C$, $I-T_N$) measure the relative geographical spread of younger groups (tips) to older groups (interiors), compared to other groups within the same nesting group; and the average population group (clade) distance (APCD) indicates the average pairwise geographic distance between a collecting site (population) and the geographic center of all haplotypes or clades found at that site or population. Significance of the distance measures was calculated by permuting nested groups versus sampling sites 10,000 times. Biological inferences were made for groups that were statistically significantly associated with geography using the updated inference key provided in Templeton (2004).

In addition to NCPA the patterns of genetic variation were examined for each higher-level nesting group (i.e., IV- and V-step groups) using Fu's F_S (Fu, 1997) and mismatch distributions. Fu's F_S test of neutrality uses estimates of the parameter θ to determine whether there is an excess of young or old mutations. Excess of young mutations, assuming neutrality and an infinite-sites model, can provide evidence of population expansion and produces large negative values of F_S (Fu, 1997). Mismatch distributions were calculated for each V-step group to examine changes in population size consistent with inferences from other analyses. Under the infinite-sites model, mismatch distributions are relatively smooth and unimodal under population expansion and ragged and generally multimodal for stationary populations (Harpending et al., 1998). Fu's F_S and parameters for the mismatch distributions were calculated using Arlequin vers. 2.000 (Schneider et al., 2000).

2.5. Divergence times among major groups

Estimates of divergence time between haplotype groups identified in NCPA analyses were calculated based upon an expected evolutionary rate of 0.65% sequence divergence per lineage per million years (Macey et al., 1998) using pairwise Tamura–Nei corrected sequence divergence measures incorporating rate heterogeneity modeled by a discrete gamma distribution. Specifically, we ask whether the divergences marked by significant fragmentation events are roughly concordant with the inferred geological history of Hispaniola (Mann et al., 1991, 1999; McLaughlin et al., 1991).

3. Results

3.1. Sequencing results and alignment

ND2 gene sequences generated during this study are deposited in GenBank (Table 1). We report 1112 bp of sequence for the ND2 and $tRNA^{Trp}$ genes. Five base pairs in the AA stem of the $tRNA^{Trp}$ gene are excluded due to ambiguous alignment. The resulting data matrix includes 1107 nucleotide positions in the final alignment. Of these, 254 sites are variable with 231 informative under parsimony.

Mitochondrial DNA sequences for the ribosomal 12S and 16S genes generated during this study are deposited in GenBank (Table 1). We report 390 base pairs (bp) of sequence for the 12S rRNA gene and 1030 bp for the 16S rRNA gene, resulting in a total of 1420 bp of sequence. Ambiguous base calls are common in the 5′ and 3′ regions of both fragments. These regions (190 bp) were excised before analysis resulting in 1230 bp of alignable sequence.

Sequence alignments using ClustalX (Thompson et al., 1997) produce few gaps of length two or more. Secondary structural information (Cannone et al., 2002) is used to confirm alignments. A total of 38 bp of sequence is excluded due to dubious alignment. The resulting data matrix contains 1193 bp used in final analyses. Of the 1193 nucleotide positions in the final alignment, 154 sites are variable, and 113 of these are informative under the parsimony criterion.

3.2. Intraspecific phylogeny

Maximum parsimony and Bayesian topologies for the independent 12S, 16S, and ND2 analyses are largely congruent. Because all genes used in this study are linked within the mitochondrial genome and therefore share a common history, and because topological conflict is absent, all data sets are combined for analysis using only individuals shared among the data sets.

The combined data set includes 2299 aligned sites from 37 ingroup haplotypes. Of the aligned nucleotide sites, 365 are variable with 327 of these variable sites informative under parsimony. Parsimony analysis results in 16 equally most parsimonious trees of 490 steps. ModelTest v.3.06 (Posada and Crandall, 1998) selects the GTR + Γ for Bayesian analysis. The Bayesian analysis produces a highly resolved strict-consensus tree with a mean ln-likelihood ($-\ln L$) score of –5756.86 after a burn-in period of 200,000 generations (Fig. 2).

Combined analyses recover a monophyletic *Ameiva chrysolaema* complex with corresponding high support values (bootstrap proportion, 100; decay index, 155; posterior probability, 100). Three other geographic haplotype clades are consistently recovered in both analyses, although the relationships among them are

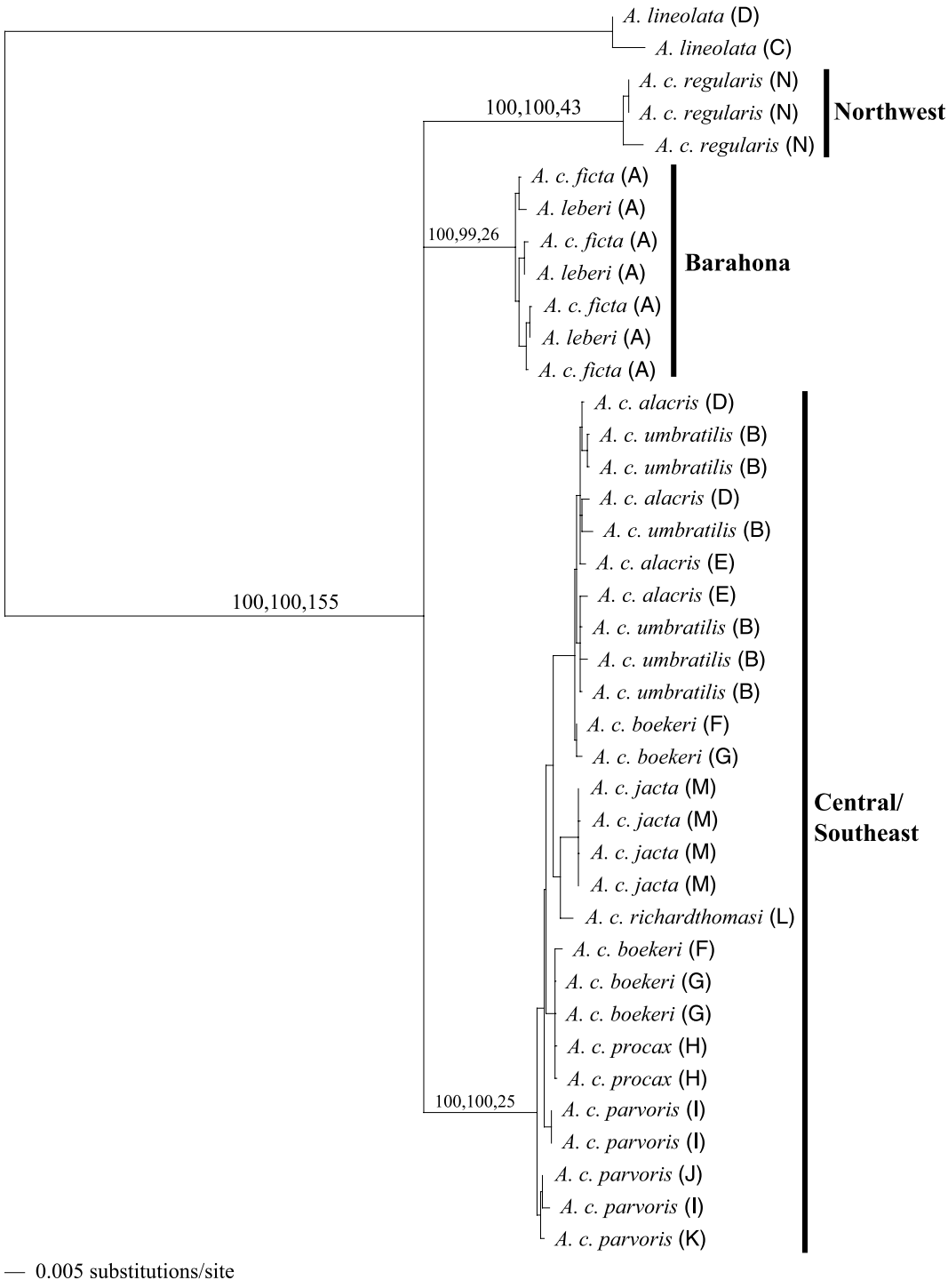

Fig. 2. The 50% majority rule consensus phylogram from the Bayesian analysis. The model of sequence evolution used was the GTR + Γ. Numbers above branches represent posterior probabilities (first), bootstrap proportions (second), and decay indices (third). Branch lengths represent means from 8000 trees sampled (one tree sampled every 100 generations) following the burn-in period of 200,000 generations. Three evolutionary lineages diagnosed by high support and geographically circumscribed haplotype clades are denoted Northwest, Barahona, and Central/Southeast.

ambiguous (Fig. 2): (Northwest) a clade containing haplotypes of *A. c. regularis* from the extreme northwestern Dominican Republic (100, 43, 100), (Barahona) a clade containing haplotypes of the southernmost populations of *A. c. ficta* and *A. leberi* from the Barahona Peninsula (100, 26, 100), and (Central/Southeast) a clade containing the remaining haplotypes from throughout the central portion of the Dominican Republic, along the southern coast, and the easternmost portion of the country (100, 25, 100). Relationships

among haplotypes within the Central/Southeast clade are unclear and reside in a region of the tree dominated by very short branches.

3.3. Phylogeography of the Central/Southeast clade

Due to the low resolution of lineages within the Central/Southeast clade, a phylogeographic approach is implemented to examine the structure and history of populations represented by this clade. The Central/Southeast clade contains haplotypes from throughout the central and eastern sections of the Dominican Republic (localities B–M, Fig. 1). Within this region 11 sampled sites yield 41 haplotypes from 52 individuals assayed (Table 2). The number of haplotypes per sampling site ranges from one to six. The number of pairwise differences among haplotypes ranges from one to 25 (0.09–2.3%) with an average of 13.7 nucleotide differences.

Statistical Parsimony connects haplotypes separated by up to 14 mutational steps within the 95% confidence limit. Two haplotype networks are produced, the connection between which is outside the 95% confidence limit. Networks 1 and 2 are connected with reference to the distribution of pairwise differences among haplotypes. Network 2 is not fully resolved; three loops are encountered. We resolve these loops by breaking connections between haplotypes 22 and 40 (14 steps) and between haplotypes 22 and 33 (9 steps) in Fig. 3. Alternative resolutions are examined, and although lower-level nesting groups differed, higher-level groups and inferences of population history are unchanged. Furthermore, the initial null hypothesis of no geographical association of haplotypes with geography cannot be rejected at low nesting levels (i.e., I- and II-step groups). Nested groups IV-2 and IV-3 are connected by 17–20 mutational steps (Fig. 3) outside the range of statistical parsimony.

Significant associations of haplotype groups and geography occur at four different nesting levels including the total cladogram (Table 3). The oldest inferred event is allopatric fragmentation between groups V-1 (populations in the Enriquillo and Azua basins) and V-2 (all remaining populations including those in the eastern Azua basin, populations F and G) (Fig. 4). Within group V-2 a fragmentation event is inferred between groups IV-1 and IV-2. Within group IV-2, no distinction can be made between restricted gene flow with isolation by distance versus past fragmentation. Finally, within group III-1 restricted gene flow with isolation by distance is inferred between populations F, G, and H. A graphical description of the distributions of major nested groups and the inferences made by NCPA is provided in Fig. 4.

The most interesting and unexpected inference is a fragmentation event between nested groups V-1 and

Table 2
Distribution of *A. chrysolaema* haplotypes (columns) from each sampled location (rows; Table 1) included in the Central/Southeast clade (Fig. 2)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
B	1	1	1	1	1	1																																			
C									1																																
D							2	1					1																												
E							1			1																															
F											1			1	1	1			1						1	1														
G												1								1	1	1		1																
H																	1	1				1	1				1	1												
I																																								
J																																				1				
K																													3	1	1	1	1	1	1	1				
L																																								
M																																						2	1	2	1
Σ	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	2	1	2	1

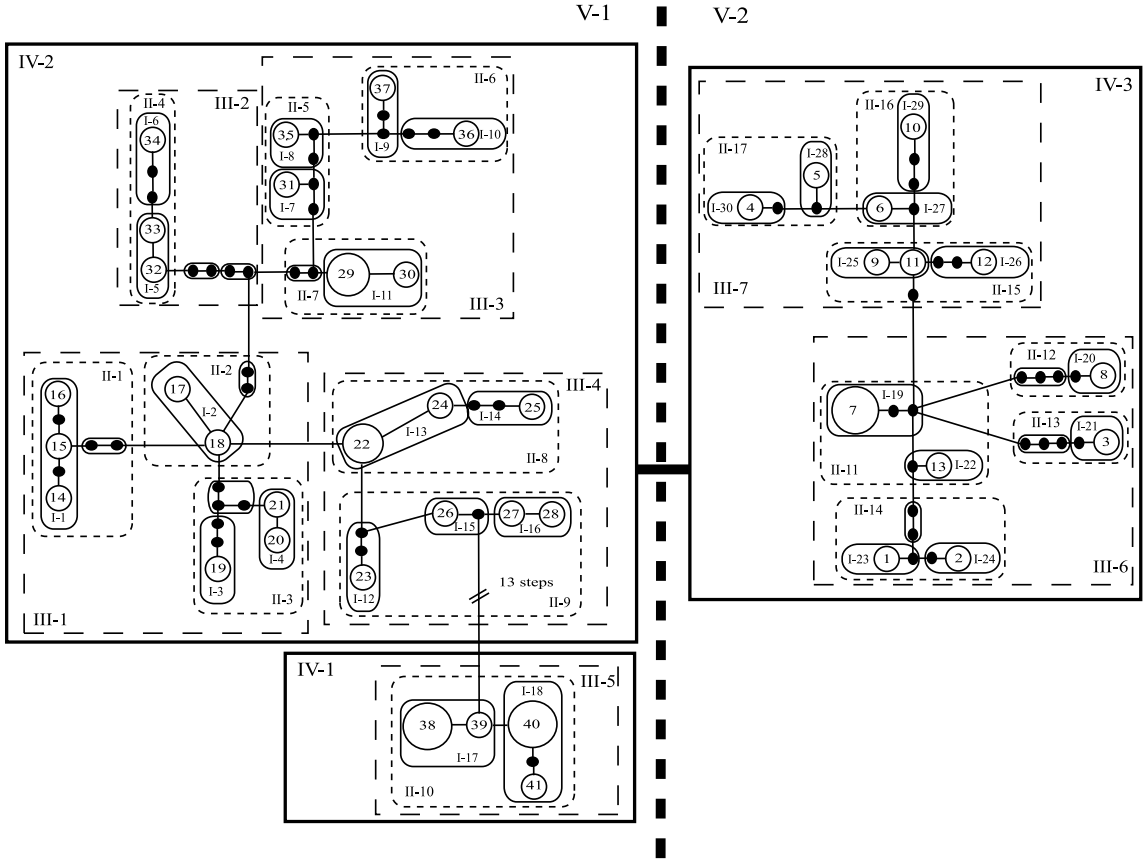

Fig. 3. Statistical Parsimony haplotype network with completed nesting design. Circled numbers denote haplotypes (columns of Table 2), with circle size proportional to haplotype frequency. Filled black circles indicate unobserved intermediate haplotypes. Each line represents a single mutational step between two haplotypes. Haplotypes belonging to the same group-level are enclosed in boxes. At the IV-step level, phylogroups IV-1 and IV-2 are connected by 17–20 mutational steps. Group-level descriptions are given within each box containing the observed haplotypes.

Table 3
χ^2 test of geographical association of nested groups and biological inferences drawn from the inference key (Templeton, 2004)

Groups Nested with	Permutational χ^2 statistic	*P*	Chain of inference	Inference
Clade III-1	12.00	0.026	1-2-3-4-NO	IbD
Clade IV-2	41.40	0.000	1-2-3-4-9-10-NO	IbD or past fragmentation
Clade V-1	33.00	0.000	1-19-NO	Past fragmentation
Entire cladogram	40.29	0.000	1-2-3-4-9-NO	Past Fragmentation

P is the probability of obtaining a χ^2 statistic greater than or equal to the observed by 9999 random permutations of the contingency table. IbD is the abbreviation for isolation by distance.

V-2. Because haplotypes from localities F and G are shared among these groups, analyses of the average population clade (group) distances (APCD) are used to examine the possibility of secondary contact at these locations (Fig. 5). There are no significant APCD values at the I-, II-, or III-step levels. At the IV-step level locality G shows a significantly large APCD value; however, because no fragmentation event is inferred at this level, secondary contact is not suggested. At the V-step level significantly large APCD values are identified at localities F and G (Fig. 5). Because a previous fragmentation event is inferred at this level in the NCPA, secondary contact is suggested at localities F and G (Fig. 4). This secondary contact zone lies within the Azua basin, an area subjected to recurring inundation during the Pliocene and Quaternary.

Populations, or groups of populations, that have recently made secondary contact are expected to have undergone population growth or expansion. Haplotype diversity and nucleotide diversity values are calculated for each V-step phylogroup. Nucleotide and haplotype diversities for each phylogroup are consistent with the hypothesis of population expansion (V-1, nucleotide diversity = 0.0049, haplotype diversity = 0.971; V-2, nucleotide diversity = 0.0095, haplotype diversity = 0.989).

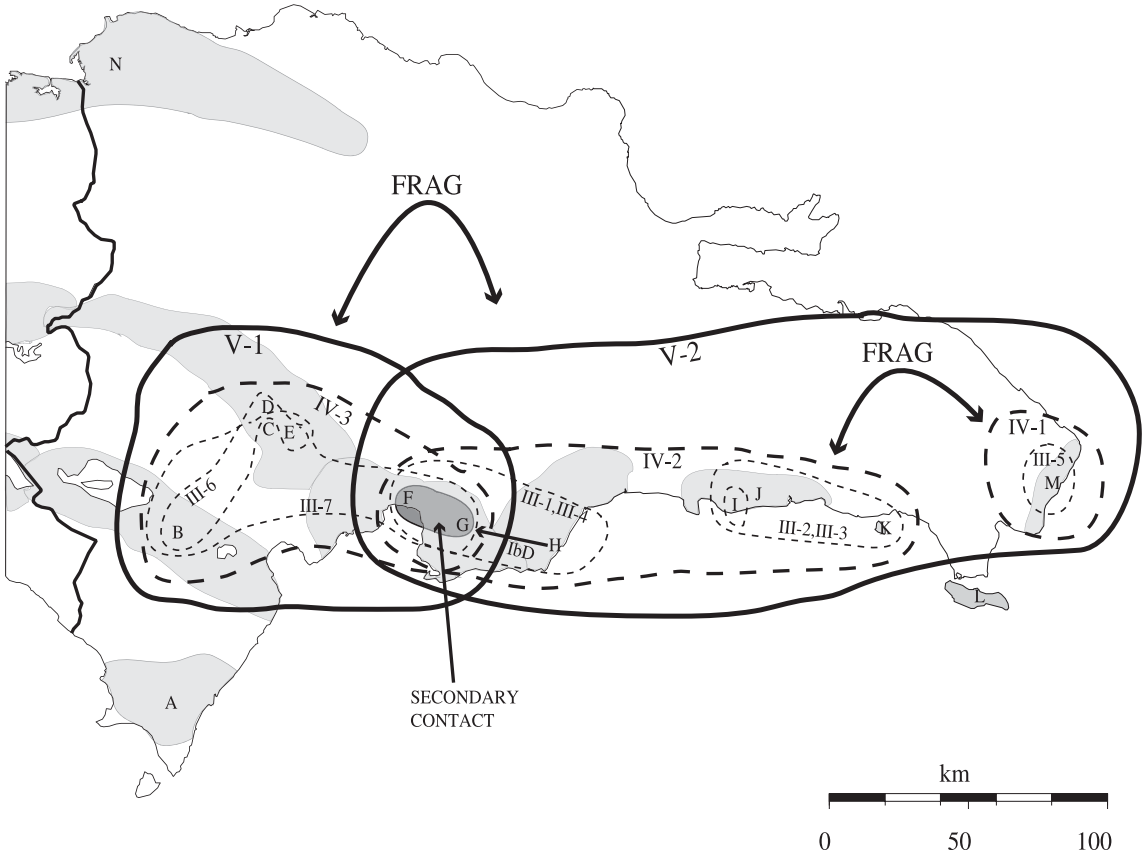

Fig. 4. Geographical distribution of III-, IV-, and V-step nested groups with inferred events or processes. Geographic patterns are consistent with isolation by distance among populations except where noted as fragmentation (frag) or secondary contact. The areas of inferred secondary contact between V-step phylogroups are designated by darker shading around localities F and G.

Population expansion within each phylogroup is suggested also by significantly large values of F_S (Fu, 1997), and parameters of the mismatch distributions do not differ significantly from a sudden-expansion model (Table 4).

3.4. Pattern polymorphism

Haplotypes from Isla Catalina are most closely related to haplotypes from the adjacent mainland and differ by an average of 4.3 substitutions (0.4%). Haplotypes from Isla Saona are divergent from all other haplotypes and are separated by an average of 17.3 substitutions (1.56%).

Four populations of *Ameiva chrysolaema* are polymorphic for the presence or absence of a dorsal pattern. Haplotypes from these populations (F, G, L, and M; Fig. 1) are scattered throughout the network and indicate no relationship between dorsal pattern and evolutionary relatedness of haplotypes. *Ameiva leberi* has been considered a distinct species based on the lack of dorsal patterning relative to sympatric *A. c. ficta*. Haplotypes of *A. leberi* are interspersed throughout the Barahona clade and are shared with *A. c. ficta*.

3.5. Divergence times among phylogroups

Phylogroups V-1 and V-2 have a corrected pairwise sequence divergence of 2.1%. Implementing a clock calibration of 0.65% per lineage per my (million years) (Macey et al., 1998) results in a divergence time of approximately 1.6 mya (million years ago). The corrected divergence among phylogroups IV-1 and IV-2 is 1.7%, suggesting a fragmentation event approximately 1.3 mya.

4. Discussion

4.1. Geographical patterns and genetic structure

Many phylogeographic studies have uncovered a high level of genetic differentiation among geographic populations in various types of organisms (e.g., Austin et al., 2002; Matthee and Flemming, 2002; Milot et al., 2000; Wilke and Pfenninger, 2002; Zamudio et al., 1997). These results suggest that named species often represent groups of divergent evolutionary lineages and that historically we have underestimated evolutionary diversity.

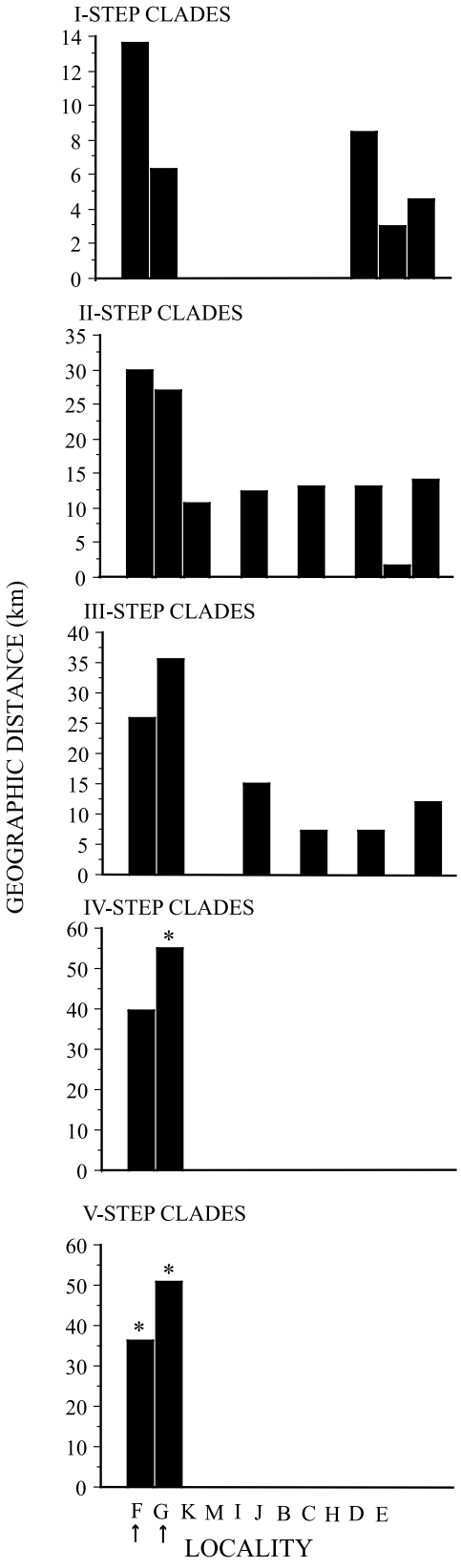

Fig. 5. Average geographic distances for population groups (clades) used to identify an area where two previously fragmented groups of populations made secondary contact. Asterisks mark clade distances significantly large at the 5% level ($P < 0.05$). Secondary contact is inferred for populations F and G (marked with arrows).

However, determining which lineages deserve specific recognition is problematic. The number of species definitions is nearly as numerous as the researchers implementing them (de Queiroz, 1998, 1999). In this paper, we take a conservative approach to species diagnosis, requiring additional data to test the hypotheses generated by molecular data. We invoke the cohesion species concept (Templeton, 1989), which permits grouping of distinct evolutionary lineages as one species if they are judged genetically and ecologically exchangeable (sensu Templeton, 1989).

The distribution of genetic variation across three regions separated by the mountain ranges of Hispaniola highlights the integral role that geography has played in the history of *Ameiva chrysolaema*. Population N in the northwest (Northwest clade, Fig. 2) is highly divergent from all other populations (14.1%) indicating that this region has been isolated for approximately 10 my. Population A (Barahona clade, Fig. 2) in the extreme southern region is also highly divergent (11.8%) indicating divergence approximately 9 mya (late Miocene). Genetic variation among the remaining populations is discussed below. The high level of genetic differentiation among populations on either side of the Cordillera Central and Sierra de Baoruco indicates that these mountain ranges have served to isolate populations of *A. chrysolaema*. The three haplotype clades (Northwest, Barahona, and Central/Southeast, Fig. 2) diagnose independent population lineages.

Further subdivision of the Central/Southeast clade is indicated by NCPA. Two fragmentation events are identified within the Central/Southeast clade, one isolating population M from the remaining populations and the second between phylogroups V-1 and V-2. These fragmentation events suggest that as many as three additional population lineages may exist within the Central/Southeast clade. The existence of multiple independent population lineages rejects the first null hypothesis (i.e., that organisms sampled are from a single evolutionary lineage) in testing for cohesion species (Templeton, 2001). Therefore, *A. chrysolaema* likely represents a complex of multiple geographically circumscribed species. The second hypothesis of ecological/genetic exchangeability could not be tested due to the overall lack of relevant ecological data.

The population history within the Central/Southeastern clade appears relatively complex and indicates a strong influence of processes occurring in the geological past. The oldest historical event identified is fragmentation between groups of populations east and west of the Azua basin (Fig. 4). This fragmentation is marked by a relatively high number of substitutions (17–20, 2.1% corrected sequence divergence) and is consistent with geological evidence suggesting seawater incursion during the late Pliocene/early Pleistocene (~1.8 mya, McLaughlin et al., 1991). The estimated molecular

Table 4
Evidence for population growth of phylogroups V-1 and V-2 based upon Fu's F_S-statistic (Fu, 1997) and parameters of the mismatch distribution

Phylogroup	F_S	P_F	τ	θ_0	θ_1	P	Raggedness
V-1	−6.329	0.001	5.372	0.001	129.053	0.829	0.019
V-2	−14.851	>0.0001	5.391	7.781	25.703	0.400	0.016

P_F is the probability that the simulated F_S (1000 bootstrap replicates) is less than or equal to the observed F_S. P is the probability that random mismatch distributions (1000 bootstrap replicates) have a larger sum of squared deviations than the model distributions. Raggedness is Harpending's (1998) raggedness index, which measures the "smoothness" of the mismatch distribution. All parameters and test statistics are consistent with a model of population growth (expansion).

divergence (~1.6 mya) is compatible with the geological record for this region of Hispaniola (~1.8 mya). Populations F and G mark an inferred secondary contact zone between these fragmented population lineages, which presumably occurred upon recession of sea water during the Pleistocene or Holocene (McLaughlin et al., 1991; Taylor et al., 1985). During this time the Azua and Enriquillo basins were inundated intermittently (McLaughlin et al., 1991) but these inundations left no detectable signature on mtDNA variation. Mismatch distributions and Fu's F_S (Fu, 1997) calculations are consistent with the hypothesis of population expansions from either side of the Azua basin.

A second fragmentation event was inferred between population M and the remaining populations (Fig. 4) dating to approximately 1.3 mya. The geological history of this region of the Dominican Republic is less well characterized than the Azua and Enriquillo basins, so causative explanations for this fragmentation event are tentative. The hiatus between population M and remaining populations appears real, however. Schwartz and Klinikowski (1966) suggest that populations on the eastern end of the country may have recently undergone range contractions; however, this hypothesis cannot be examined here. It seems possible, considering that the extreme southeast region of the Dominican Republic is relatively low in elevation, that this area was periodically inundated with seawater similar to the Azua and Enriquillo basins.

4.2. Status of *A. leberi* and pattern polymorphism

Schwartz and Thomas (1975) elevated *Ameiva leberi* to specific status based on the absence of a dorsal pattern and lateral fields and apparent lack of intergradation with sympatric *A. c. ficta*. Sproston et al. (1999) found no evidence of resource partitioning between these two taxa and suggested that they may represent one polymorphic taxon. Data reported in this study support the hypothesis of Sproston et al. (1999). Haplotypes of *A. c. ficta* and *A. leberi* are shared, are nested within the same clade in the phylogenetic estimates, and are less than 0.04% divergent from one another. Data from this study in conjunction with those reported by Sproston et al. (1999) indicate that *A. leberi* is not distinct and should be considered a junior synonym of *A. chrysolaema* (a conclusion consistent with Hower and Hedges, 2001). All other polymorphic populations of *A. chrysolaema* show no relationship between phenotype and evolutionary relatedness, suggesting that the variation represents polymorphism within evolutionary lineages.

5. Conclusions

The phylogenetic and phylogeographic analyses of *Ameiva chrysolaema* and *A. leberi* suggest a strong influence of geological and physiographic processes. The topographically complex nature of the island has isolated populations into at least three independent evolutionary lineages. Subsequently within the Central/Southeast clade, inundation of the Azua basin during the late Pliocene/early Pleistocene (~1.6 mya) fragmented populations on the east and west of the basin. Upon recession of the seawater the two fragmented populations made secondary contact. *Ameiva chrysolaema* is likely a species complex with some lineages polymorphic with respect to dorsal pattern.

Only one other phylogeographic study of another Hispaniolan taxon is available for comparison (Glor et al., 2003). Little geographic concordance exists between patterns of genetic fragmentation in this data set and that of Glor et al. (2003). The ecological attributes of the two taxa differ, causing them to perceive geographic barriers differently. The relative depths of the deepest divergences among populations of *A. chrysolaema* are within the range of divergences among populations of *A. cybotes*; however, the barriers recognized by *A. chrysolaema* are generally not recognized by *A. cybotes*. *Anolis cybotes* is generally a montane species with various divergent parapatric populations and closely related species occupying lowland xeric situations, whereas *A. chrysolaema* is restricted to xeric low-elevation environments. The contrasting phylogeographic patterns of *A. chrysolaema* versus the *A. cybotes* group provide, respectively, expected vicariant patterns for lowland ground-dwelling versus montane arboreal lizards on Hispaniola. We predict that other *Ameiva* species on Hispaniola and similarly ground-dwelling *Leiocephalus* should exhibit phylogeographic patterns comparable to those reported here for *A. chrysolaema*.

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References

Austin, J.D., Lougheed, S.C., Neidrauer, L., Chek, A.A., Boag, P.T., 2002. Cryptic lineages in a small frog: the post-glacial history of the spring peeper, *Pseudacris crucifer* (Anura: Hylidae). Mol. Phylogenet. Evol. 25, 316–329.

Avise, J.C., 2000. Phylogeography: The History and Formation of Species. Harvard University Press, Cambridge, MA.

Avise, J.C., Arnold, J., Ball Jr., R.M., Bermingham, E., Lamb, T., Neigel, J.E., Reeb, C.A., Saunders, N.C., 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. Annu. Rev. Ecol. Syst. 18, 489–522.

Axtell, R.W., 1961. *Cnemidophorus inornatus*, the valid name for the little striped whiptail lizard, with the description of an annectant subspecies. Copeia 1961, 148–158.

Bremer, K., 1994. Branch support and tree stability. Cladistics 10, 295–304.

Burbrink, F.T., Lawson, R., Slowinski, J.B., 2000. Mitochondrial DNA phylogeography of the polytypic North American Rat Snake (*Elaphe obsoleta*): a critique of the subspecies concept. Evolution 54, 2107–2118.

Cannone, J.J., Subramanian, S., Schnare, M.N., Collett, J.R., D'Souza, L.M., Du, Y., Feng, B., Lin, N., Madabusi, L.V., Muller, K.M., Pande, N., Shang, Z., Yu, N., Gutell, R.R., 2002. The comparative RNA web (CRW) site: an online database of comparative sequence and structure information for ribosomal, intron, and other RNAs. Bioinformatics 3, 2, Correction: Bioinformatics, 3, 15.

Clement, M.D., Posada, D., Crandall, K.A., 2000. TCS: a computer program to estimate gene genealogies. Mol. Ecol. 9, 1657–1660.

de Queiroz, K., 1998. The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. In: Howard, D.J., Berlocher, S.H. (Eds.), Endless Forms: Species and Speciation. Oxford University Press, Oxford, England, pp. 57–75.

de Queiroz, K., 1999. The general lineage concept of species and the defining properties of the species category. In: Wilson, R.A. (Ed.), Species: New Interdisciplinary Essays. MIT Press, Cambridge, MA, pp. 49–89.

Emerson, B.C., 2002. Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. Mol. Ecol. 11, 951–966.

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

Fu, Y.X., 1997. Statistical tests of neutrality of mutations against population growth, hitchhiking, and background selection. Genetics 147, 915–925.

Geyer, C.J., Thompson, E.A., 1995. Annealing Markov-chain Monte-Carlo with applications to ancestral inference. J. Am. Stat. Assoc. 90, 909–920.

Glor, R.E., Kolbe, J.J., Powell, R., Larson, A., Losos, J.B., 2003. A comparative analysis of morphological diversification in Hispaniolan trunk-ground anoles (*Anolis cybotes* group). Evolution 57, 2383–2397.

Goldman, N., 1993. Statistical tests of models of DNA substitution. J. Mol. Evol. 37, 50–61.

Graham, A., 2003. Geohistory models and Cenozoic paleoenvironments of the Caribbean region. Syst. Bot. 28, 378–386.

Harpending, H.C., Batzer, M.A., Gurven, M., Jorde, L., Rogers, A.R., Sherry, S.T., 1998. Genetic traces of ancient demography. Proc. Natl. Acad. Sci. USA 95, 1961–1967.

Hower, L.M., Hedges, S.B., 2001. Molecular phylogeny and biogeography of West Indian teiid lizards of the genus *Ameiva*. Caribb. J. Sci. 39, 298–306.

Huelsenbeck, J.P., Bollback, J.P., 2001. Empirical and hierarchical Bayesian estimation of ancestral states. Syst. Biol. 50, 351–366.

Huelsenbeck, J.P., Crandall, K.A., 1997. Phylogeny estimation and hypothesis testing using maximum likelihood. Annu. Rev. Ecol. Syst. 28, 437–466.

Huelsenbeck, J.P., Imennov, N.S., 2002. Geographic origin of human mitochondrial DNA: accommodating phylogenetic uncertainty and model comparison. Syst. Biol. 50, 155–165.

Huelsenbeck, J.P., Ronquist, F., 2001. Mr. Bayes v2: Bayesian inference of phylogeny. Bioinformatics 17, 754–755.

Kumar, S., Tamura, K., Jakobsen, I.B., Nei, M., 2001. MEGA 2: Molecular Evolutionary Genetics Analysis Software. Arizona State University, Tempe, AZ, USA.

Kumazawa, Y., Nishida, M., 1993. Sequence evolution of mitochondrial tRNA genes and deep-branch animal phylogenetics. J. Mol. Evol. 37, 380–398.

Larget, B., Simon, D.L., 1999. Markov Chain Monte Carlo algorithms for the Bayesian analysis of phylogenetic trees. Mol. Biol. Evol. 16, 750–759.

Leaché, A.D., Reeder, T.W., 2002. Molecular systematics of the Eastern fence lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood and Bayesian approaches. Syst. Biol. 51, 44–68.

Lewis, J.F., Draper, G., 1990. Geology and tectonic evolution of the northern Caribbean margin. In: Dengo, D., Case, J.E. (Eds.), The Geology of North America Vol. H The Caribbean Region. Geol. Soc. Am., Boulder, CO, pp. 77–140.

Macey, J.R., Schulte, J.A., Ananjeva, N.B., Larson, A., Rastegar-Pouyani, N., Shammakov, S.M., Papenfuss, T.J., 1998. Phylogenetic relationships among agamid lizards of the *Laudakia caucasia* species group: testing hypotheses of biogeographic fragmentation and an area cladogram for the Iranian Plateau. Mol. Phylogenet. Evol. 10, 118–131.

Maddison, D.R., Maddison, W.P., 2003. MacClade 4, vers. 4.06. Sinauer Associates, Sunderland, MA.

Mann, P., Draper, G., Lewis, J.F., 1991. An overview of the geologic and tectonic development of Hispaniola. In: Mann, P., Draper, G., Lewis, J.F. (Eds.), Geologic and Tectonic Development of the North America-Caribbean Plate Boundary in Hispaniola. Geol. Soc. Am. Spec. Pap., vol. 262, pp. 1–28.

Mann, P., McLaughlin, P.P., van den Bold, W.A., Lawrence, S.R., Lamar, M.E., 1999. Tectonic and eustatic controls on Neogene evaporitic deposition in the Enriquillo basin, Dominican Republic. In: Mann, P., Hsü, K.J. (Eds.), Sedimentary Basins of the World: Caribbean Basins. Elsevier, Amsterdam, The Netherlands, pp. 287–341.

Matthee, C.A., Flemming, A.F., 2002. Population fragmentation in the southern rock agama, *Agama atra*: more evidence for vicariance in Southern Africa. Mol. Ecol. 11, 465–471.

McLaughlin, P.P., van den Bold, W.A., Mann, P., 1991. Geology of the Azua and Enriquillo basins, Dominican Republic; 1, Neogene lithofacies, biostratigraphy, biofacies, and paleogeography. In: Mann, P., Draper, G., Lewis, J.F. (Eds.), Geologic and Tectonic Development of the North America-Caribbean Plate Boundary in Hispaniola. Geol. Soc. Am. Spec. Pap., vol. 262, pp. 337–366.

Milot, E., Gibbs, H.L., Hobson, K.A., 2000. Phylogeography and genetic structure of northern populations of the yellow warbler (*Dendroica petechia*). Mol. Ecol. 9, 667–681.

Posada, D., Crandall, K.A., 1998. ModelTest: testing the model of DNA substitution. Bioinformatics 14, 817–818.

Posada, D., Crandall, K.A., Templeton, A.R., 2000. GeoDis: a program for the cladistic nested analysis of the geographical distribution of genetic haplotypes. Mol. Ecol. 9, 487–488.

Powell, R., 1993. Comments on the taxonomic arrangement of some Hispaniolan amphibians and reptiles. Herpetol. Rev. 24, 135–137.

Powell, R., Parmerlee Jr., J.S., Smith, D.D., 1996. Evidence of spatial niche partitioning by a Hispaniolan lizard community in a xeric habitat. In: Powell, R., Henderson, R.W. (Eds.), Contributions to West Indian Herpetology: A Tribute to Albert Schwartz. Society for the Study of Amphibians and Reptiles, pp. 317–326.

Rawlings, L.H., Donnellan, S.C., 2003. Phylogeographic analysis of the green python, *Morelia viridis* reveals cryptic diversity. Mol. Phylogenet. Evol. 27, 36–44.

Schell, P.T., Powell, R., Parmerlee Jr., J.S., Smith, D.D., Lathrop, A., 1993. Natural history of *Ameiva chrysolaema* (Sauria, Teiidae) from Barahona. Dominican Republic. Copeia, 859–862.

Schneider, C.J., Cunningham, M., Moritz, C., 1998. Comparative phylogeography and the history of endemic vertebrates in the wet tropical rainforests of Australia. Mol. Ecol. 7, 487–498.

Schneider, S., Roessli, D., Excoffier, L., 2000. Arlequin, A Software for Population Genetic Data Analysis, Version 2.0. University of Geneva, Geneva.

Schwartz, A., Henderson, R.W., 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. University Press, Florida, Gainesville.

Schwartz, A., Klinikowski, R.F., 1966. The *Ameiva* (Lacertilia: Teiidae) of Hispaniola. II. Geographic variation in *Ameiva chrysolaema* Cope. Bull. Mus. Comp. Zool. 133, 425–487.

Schwartz, A., Thomas, R., 1975. A check-list of West Indian amphibians and reptiles. Carnegie Mus. Nat. Hist. Spec. Pub. 1, 1–216.

Smith, T.B., Schneider, C.J., Holder, K., 2001. Refugial isolation versus ecological gradients. Genetica 112, 383–398.

Sorenson, M.D., 1999. TreeRot, version 2. Boston University, Boston, MA.

Sproston, A.L., Glor, R.E., Hartley, L.M., Censky, E.J., Powell, R., Parmerlee Jr., J.S., 1999. Niche differences among three sympatric species of *Ameiva* (Reptilia: Teiidae) on Hispaniola. J. Herpetol. 33, 131–136.

Swofford, D.L., 1999. PAUP*: Phylogenetic Analysis Using Parsimony (* and other methods). Version 4.0. Sinauer Associates, Sunderland, MA.

Taylor, F.W., Mann, P., Valastro Jr., S., Burke, K., 1985. Stratigraphy and radiocarbon chronology of a subaerially exposed Holocene coral reef, Dominican Republic. J. Geol. 93, 311–332.

Templeton, A.R., 1989. The meaning of species and speciation: a genetic perspective. In: Otte, D., Endler, J.A. (Eds.), Speciation and its Consequences. Sinauer, Sunderland, MA, pp. 3–27.

Templeton, A.R., 1998. Nested clade analysis of phylogeographic data: testing hypotheses about gene flow and populations history. Mol. Ecol. 7, 381–397.

Templeton, A.R., 2001. Using phylogeographic analyses of gene trees to test species status and processes. Mol. Ecol. 10, 779–791.

Templeton, A.R., 2004. Statistical phylogeography: methods of evaluating and minimizing inference errors. Mol. Ecol. 13, 789–809.

Templeton, A.R., Sing, C.F., 1993. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping. IV. Nested analysis with cladogram uncertainty and recombination. Genetics 134, 659–669.

Templeton, A.R., Crandall, K.A., Sing, C.F., 1992. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. Genetics 132, 619–633.

Templeton, A.R., Routman, E., Phillips, C.A., 1995. Separating population structure from population history: a cladistic analysis of the geographical distribution of mitochondrial DNA haplotypes in the tiger salamander, *Ambystoma tigrinum*. Genetics 140, 767–782.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F., Higgins, D.G., 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res. 24, 4876–4882.

Whelan, S., Goldman, N., 1999. Distributions of statistics used for the comparison of models of sequence evolution in phylogenetics. Mol. Biol. Evol. 16, 1292–1299.

Wilcox, T.P., Zwickl, D.J., Heath, T.A., Hillis, D.M., 2002. Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. Mol. Phylogenet. Evol. 25, 361–371.

Wilke, T., Pfenninger, M., 2002. Separating historic events from recurrent processes in cryptic species: phylogeography of mud snails (*Hydrobia* spp.). Mol. Ecol. 11, 1439–1451.

Yang, Z., 1994. Estimating the pattern of nucleotide substitution. J. Mol. Evol. 39, 105–111.

Zamudio, K.R., Jones, K.B., Ward, R.H., 1997. Molecular systematics of short-horned lizards: biogeography and taxonomy of a widespread species complex. Syst. Biol. 46, 248–305.