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Molecular Phylogeny and Biogeography of West Indian Teiid Lizards of the Genus *Ameiva*

LINDSEY M. HOWER AND S. BLAIR HEDGES*

**Department of Biology and Institute of Molecular Evolutionary Genetics, 208 Mueller Laboratory, The Pennsylvania State University, University Park, Pennsylvania 16802-5301. sbh1@psu.edu*
Corresponding author: sbh1@psu.edu

ABSTRACT.—Lizards of the genus *Ameiva* (Teiidae) are found throughout the West Indies and in Central and South America. We investigated their phylogenetic relationships and biogeography with new sequences from portions of the 12S and 16S mitochondrial rRNA genes of sixteen West Indian species and three Central and South American species. The West Indian species form a monophyletic group that diverged from the mainland species approximately 25-30 million years ago. The most likely origin of this clade was from South America by dispersal on flotsam. Within the West Indies, species groupings correspond more closely to geography than morphology, revealing several cases of convergence. Four species groups are proposed for the West Indian species: the *auberi* Group (*auberi* and *dorsalis*) occurs on Cuba, Jamaica, and the Bahamas; the *exsul* Group (*exsul*, *polops*, and *wetmorei*) in the Puerto Rico region; the *lineolata* Group (*chrysolaema*, *lineolata*, *maynardi*, and *A. taeniura*) on Hispaniola, Navassa, and the Bahamas; and the *plei* Group (*cineracea, corax, corvina, erythrocephala, fuscata, griswoldi, major, plei*, and *pluvianotata*) is in the Lesser Antilles. Sequence analyses indicate that *A. leberi* of Hispaniola is a junior synonym of *A. chrysolaema*.

INTRODUCTION

The lizard family Teiidae occurs throughout the New World and includes nine genera. They are quick, diurnal species, ranging in size from 7-50 cm snout-vent length (SVL). The genus *Ameiva* includes 32 currently recognized species of lizards found primarily in the West Indies (18 species), but also in Central and South America. They occupy diverse habitats including open savannahs, tropical forests, and sandy beaches. Most species are ground-dwellers, although some ascend trees in search of food (Powell and Censky 2002). *Ameiva* are active foragers and prey primarily on insects, but occasionally on small lizards (*Anolis*) and birds' eggs (Schwartz and Henderson 1991). They exhibit variation in size, coloration and pattern, in the number of femoral pores, and in the number of ventral scales in transverse and longitudinal rows.

The relationships of West Indian species in the genus *Ameiva* have never been comprehensively examined. Past systematic work on this group has involved a taxonomic revision (Barbour and Noble 1915) and morphological analyses of single species or those inhabiting restricted geographic regions (e.g., Baskin and Williams 1966; Schwartz 1966; Schwartz and Klinikowski 1966; Schwartz 1967; Schwartz 1970; Censky and Paulson 1992). None has addressed the entire genus or the entire West Indies. Molecular data bearing on the relationships of West Indian *Ameiva* have been from albumin immunological analyses (Hedges et al. 1992; Hass et al. 2001), but these data have been insufficient to elucidate the phylogenetic history of the species.

Because the West Indies has had a dynamic geologic history, with past connections between some islands and between the proto-Antilles and the mainland, its biota may have arisen by vicariance or dispersal. Many previous molecular studies have addressed this question and have found widespread evidence of dispersal over water (on flotsam) during the Cenozoic for most groups and little support for an ancient fauna that would implicate proto-Antillean vicariance, although some groups have yet to be examined (Rosen

1975; Hedges et al. 1992; Hedges 1996a, 1996b; Hedges 2001).

With little known of the relationships of West Indian *Ameiva*, it is no surprise that the historical biogeography of the group is poorly known, although some previous authors have offered speculation. Barbour and Noble (1915) suggested that West Indian species had a single origin but they assumed that such an inference argued against dispersal over water on flotsam. However, dispersal can occur at any time, and the probability of success should decline with time as ecological niches are filled on islands (Williams 1969). Later, Baskin and Williams (1966) and Schwartz (1970) speculated that the West Indian lineage (or lineages) arose by one or more dispersals from South America. Their reasoning for a southerly origin was based on the diversity of *Ameiva* (and other teiids) in South America and the direction of ocean currents, which flow from the northeast coast of South America west and north through the West Indies and up into the Gulf Stream. Such a sustained current flow, which likely has operated during the Cenozoic long before the closure of the Isthmus of Panama (Hedges 2001), would have made dispersal over water from North America to the West Indies unlikely. Later, immunological distance data for West Indian *Ameiva* compared with a mainland species indicated that the divergence occurred during the Cenozoic and therefore supported dispersal (Hedges et al. 1992; Hass et al. 2001). In this study, we examine the relationships of West Indian *Ameiva* with DNA sequence data to address their relationships and biogeographic history.

Materials and Methods

This study included nineteen species of *Ameiva*, sixteen of which are indigenous to the West Indies. The remaining three were the Central and South American *A. ameiva, A. festiva*, and *A. undulata*. The outgroup used to root the tree was *Tupinambis teguixin*, a teiid lizard found on the South American mainland. All DNA samples (Table 1) came from frozen tissue collected by SBH and colleagues, except for the mainland species and *A. corax* (see Acknowledgments). Collecting and export permits were obtained in all cases and the work was approved (89R1418) by the Insti-

TABLE 1. Taxa and localities sampled.

Taxon	Tissue catalog number[a]	Geographic distribution
Ameiva ameiva	SBH 267103	Peru: Cuzco Amazónico.
A. auberi	SBH 161973	Cuba: Guantánamo Bay Naval Station.
A. chrysolaema abbotti	SBH 194699	Dominican Republic: Pedernales Prov.; Isla Beata.
A. chrysolaema defensor	SBH 194588	Haiti: Dept. du Nord'Ouest; Bombardopolis.
A. corax	SBH 266428	Anguilla: Little Scrub Island.
A. dorsalis	SBH 194921	Jamaica: Kingston.
A. erythrocephala	SBH 172748	St. Kitts: Godwin Gut.
A. exsul	SBH 190726	Puerto Rico: Guánica.
A. festiva	SBH 266426	Nicaragua: Matagalpa Prov.; El Carmen.
A. fuscata	SBH 194215	Dominica; Soufrière Estate.
A. griswoldi	SBH 192785	Antigua: Great Bird Island.
A. leberi	SBH 194764	Dominican Republic: Pedernales Prov.; Cabo Beata.
A. lineolata	SBH 194700	Dominican Republic: Pedernales Prov; Isla Beata.
A. maynardi	SBH 192970	Bahamas: Inagua; Mathew Town.
A. plei	SBH 266002	St. Maarten.
A. pluvianotata	SBH 192779	Montserrat: St. Peter; Spring Ghut.
A. taeniura	SBH 104391	Haiti: Dept. du Sud-Est; 9.5 km E. Jacmel.
A. undulata	SBH 266425	Guatemala: Izabal Prov.; Los Amates, Rancho Alegre.
A. wetmorei	SBH 190731	Puerto Rico: Isla Caja de Muertos.
Tupinambis teguixin	SBH 267102	Peru: Cuzco Amazónico.

[a]Tissue collection of S. Blair Hedges, Pennsylvania State University.

tutional Animal Care and Use Committee of The Pennsylvania State University.

Methods for DNA extraction and PCR amplification have been presented elsewhere (Hedges et al. 1991). For all twenty species, the 12S gene fragment was amplified using the 12L5/12H4 primer pair (except as noted, primer sequences are described elsewhere; Hedges 1994; Feller and Hedges 1999). The 16S gene fragments of *A. festiva*, *A. corax*, and *A. undulata* were amplified in three segments using the primer pairs 16L20 (TGA AAA SCC WAM CGA RCY TGR TGA TAG CTG)/16H10, 16L9/16H3, and 16L1/16H1. The 16S gene fragments of the remaining seventeen species were amplified in two segments, using the primer pairs 16L20/16H10 and 16L9/16H13. Sequencing was done at The Pennsylvania State University Nucleic Acid Facility. For each region sequenced, the heavy strand and the light strand were aligned to obtain a consensus sequence, and sequences of different species were aligned with CLUSTALX (Thompson et. al. 1997). All sequences have been deposited in Genbank (accession numbers AY359473-512).

Phylogenetic trees were generated using Neighbor-joining (NJ) in MEGA (version 2.1, Kumar et. al. 2001) and Maximum Likelihood (ML) in MOLPHY (version 2.3, Adachi and Hasegawa 1996). Alignment gaps were not included in analyses. NJ analyses used Kimura 2-parameter and Tamura-Nei models, with transitions included or excluded. ML analyses used the HKY model. Bootstrap values were used to examine nodal support, using the 95% cut-off level for significance.

Published immunological data for the protein serum albumin provided one-way distances from *Ameiva chrysolaema* and *A. exsul* antisera to antigens of twelve species of *Ameiva* in our study (Hass, Maxson, and Hedges 2001). These data were used to calibrate divergence times in our sequence analyses by establishing a relationship between immunological distance (ID), for which a time relationship already exists (Maxson 1992), and Tamura-Nei transversion distance. Calibration with immunological distance was made because of the lack of fossil calibrations for this group in the West Indies. To do this, Tamura-Nei transversion distances were plotted against the corrected ID values from which a linear relationship was obtained (regression line fixed through origin). The transversion distance was used to avoid transition saturation error. The sequence calibration was established using the immunological calibration of one ID unit = 0.6 million years (Maxson 1992). A linearized tree (Takezaki et al. 1995) was constructed and calibrated.

RESULTS

Our combined alignment of 12S and 16S mitochondrial rRNA gene sequences totaled 1,259 nucleotide sites. The plot of transition/transversion ratios versus sequence divergence (not shown) was typical of interspecific comparisons of mitochondrial sequences in exhibiting transition saturation at distances higher than approximately 0.1 (e.g., Hedges et al. 1991; Pramuk et al. 2001). Therefore, our phylogenetic and molecular clock analyses are based primarily on Tamura-Nei transversion distances (Table 2).

Phylogenetic trees (Fig. 1) support the monophyly of the West Indian species at high (>98%) bootstrap confidence. The NJ and ML trees were identical except for the single node with <50% bootstrap confidence concerning the relationships of the three mainland species. Four groups are defined in the trees showing concordance with geography: a Lesser Antillean clade, a group containing *A. auberi* (Cuba, Bahamas) and *A. dorsalis* (Jamaica), a group containing the two Puerto Rican species *A. exsul* and *A. wetmorei*, and a fourth group containing the Hispaniolan species and *A. maynardi* (Bahamas). Support for each of the groups ranges from 68-100%. A neighbor-joining tree constructed using transitions and transversions by the Kimura 2-parameter distance method shows higher support for those same four groups (91-100%).

Relationships among the six Lesser Antillean species are well supported (>90%) and resolve the following relationships: ((((*A. griswoldi*, *A. pluvianotata*) *A. erythro-*

TABLE 2. Kimura transversion distances for West Indian lizards of the genus *Ameiva* and the outgroup (*Tupinambis teguixin*).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1. *A. ameiva*																			
2. *A. auberi*	0.073																		
3. *A. c. abbotti*	0.065	0.041																	
4. *A. c. defensor*	0.067	0.039	0.005																
5. *A. corax*	0.064	0.033	0.029	0.029															
6. *A. dorsalis*	0.073	0.015	0.040	0.040	0.030														
7. *A. erythrocephala*	0.063	0.037	0.036	0.033	0.017	0.033													
8. *A. exsul*	0.065	0.039	0.024	0.023	0.025	0.038	0.031												
9. *A. festiva*	0.069	0.069	0.059	0.055	0.054	0.070	0.055	0.057											
10. *A. fuscata*	0.066	0.035	0.030	0.029	0.013	0.032	0.014	0.027	0.056										
11. *A. griswoldi*	0.069	0.032	0.036	0.035	0.015	0.033	0.010	0.029	0.057	0.012									
12. *A. leberi*	0.065	0.039	0.002	0.003	0.027	0.038	0.035	0.023	0.057	0.029	0.035								
13. *A. lineolata*	0.072	0.038	0.029	0.027	0.035	0.039	0.042	0.030	0.06	0.036	0.039	0.027							
14. *A. maynardi*	0.071	0.041	0.028	0.028	0.035	0.038	0.043	0.029	0.064	0.037	0.040	0.028	0.009						
15. *A. plei*	0.069	0.039	0.035	0.035	0.007	0.035	0.023	0.031	0.061	0.019	0.021	0.033	0.041	0.041					
16. *A. pluvianotata*	0.069	0.034	0.035	0.033	0.015	0.033	0.010	0.029	0.055	0.012	0.005	0.033	0.039	0.041	0.021				
17. *A. taeniura*	0.067	0.037	0.024	0.024	0.030	0.035	0.041	0.028	0.061	0.034	0.038	0.023	0.014	0.015	0.035	0.036			
18. *A. undulata*	0.071	0.071	0.072	0.068	0.060	0.073	0.061	0.063	0.059	0.063	0.063	0.070	0.065	0.066	0.064	0.061	0.063		
19. *A. wetmorei*	0.062	0.039	0.028	0.028	0.027	0.033	0.033	0.019	0.055	0.027	0.033	0.026	0.030	0.031	0.031	0.031	0.029	0.064	
20. *Tupinambis*	0.12	0.124	0.111	0.111	0.102	0.119	0.113	0.113	0.123	0.112	0.111	0.109	0.118	0.123	0.109	0.113	0.123	0.131	0.111

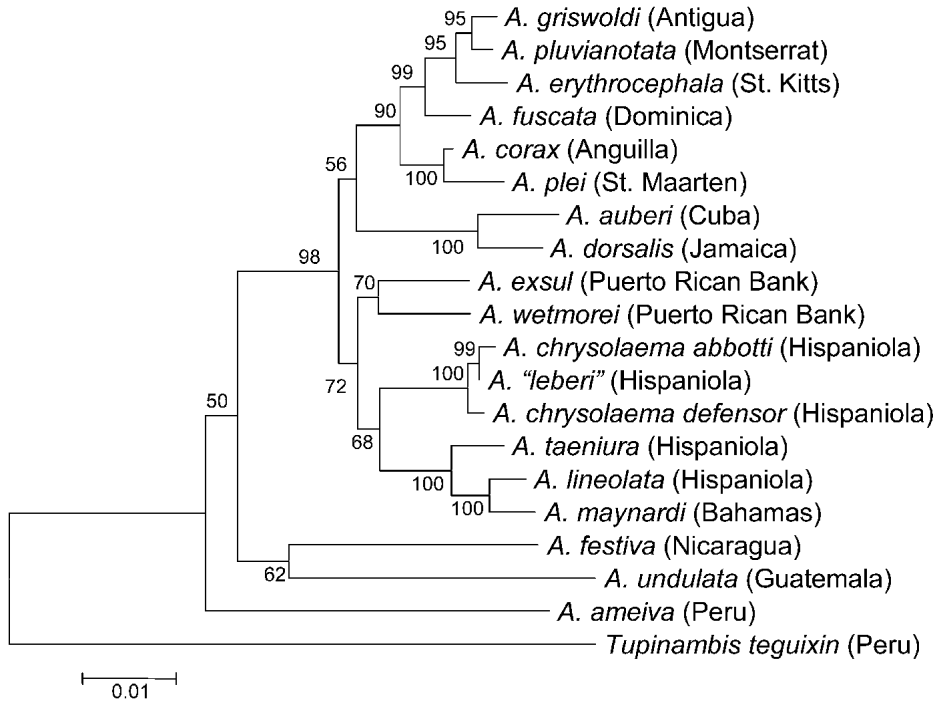

FIG. 1. Molecular phylogeny of lizards of the genus *Ameiva* from analysis of 12S and 16S mitochondrial rRNA sequences. Bootstrap proportions are indicated on nodes. The tree was constructed with neighbor-joining using the Tamura-Nei model (transversions only) and rooted with *Tupinambis teguixin*.

cephala) *A. fuscata*) (*A. corax*, *A. plei*)). Relationships among the Hispaniolan species define the following relationships: ((*A. leberi, A. chrysolaema abbotti*) *A. chrysolaema defensor*) (*A. taeniura* (*A. lineolata, A. maynardi*)). Therefore, the Bahaman species *A. maynardi* appears to be derived from Hispaniola (*A. lineolata*). The relationships of the four West Indian groups are not well supported.

The regression of serum albumin ID (Hass et al. 2001) with sequence divergence (D) from this study (Tamura-Nei transversions) resulted in a calibration of 1 D = 1402 ID = 841 million years of pairwise divergence (Fig. 2). Branch lengths did not differ greatly among taxa (average of 9% deviation from mean root-to-tip length) and therefore a linearized tree was constructed and calibrated (Fig. 3). However, the branch length test (Takezaki et al. 1995) identified two species as evolving significantly slower (*A. corax*) and faster (*A. undulata*) than the average root-to-tip rate. After removal of those two species, no species were rejected for significant rate variation. The timetree (Fig. 3) shows divergence times calculated after removal of those species, but includes the two species (dashed lines) for comparison. This timetree suggests that the West Indian Clade split from the mainland species approximately 25-30 million years ago (Ma) whereas the radiation of the four groups within the West In-

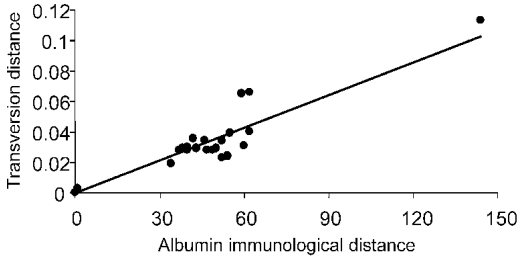

FIG. 2. Plot of sequence divergence (Tamura-Nei transversion distance) versus serum albumin immunological distance with regression line fixed through the origin ($r^2 = 0.8293$; $y = 7.134 \times 10^{-4}$ x).

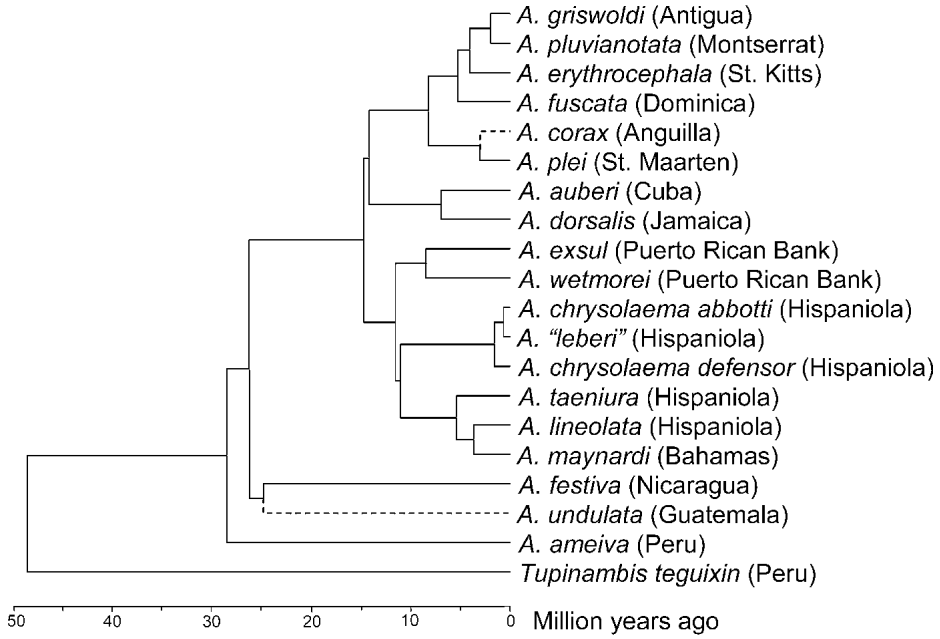

FIG. 3. Timetree of lizards of the genus the *Ameiva* from analysis of 12S and 16S mitochondrial rRNA sequences. The tree was constructed with the Tamura-Nei model (transversions only) and calibrated with the immunological distance relationship (Figure 2) (see text). Dashed lines are lineages rejected in rate tests.

dies occurred 10-15 Ma and radiation of species within each of the groups occurred since about 10 Mya.

DISCUSSION

Four endemic West Indian species of *Ameiva* were not included in our study. Two of those, *A. cineracea* (Guadeloupe) and *A. major* (Martinique), are presumed to be extinct (Schwartz and Henderson 1991). Baskin and Williams (1966) considered them to be closest relatives. Because of their geographic location, we tentatively associate them with the Lesser Antillean clade while recognizing that they are morphologically distinct and might represent a separate lineage. *Ameiva corvina* occurs only on Sombrero Island and was not obtainable for this study, but it is essentially indistinguishable from *A. corax* (Censky and Paulson 1992), a member of the Lesser Antillean clade. *Ameiva polops* is an endangered species found on Saint Croix; U.S. government regulations prevented us from sampling this taxon, even in a non-invasive manner. However, it is morphologically similar to nearby *A. wetmorei* of the Puerto Rican clade and presumably closely related to that species. *Ameiva ameiva* is a wide-ranging Neotropical species that occurs in the West Indies (southern Lesser Antilles, Swan Island, Isla de Providencia); our sample of this species was from Peru.

The four geographic groups identified in the phylogenetic analysis, within the West Indian Clade, can be recognized as species groups. The *auberi* Group (Cuba, Jamaica, Bahamas) contains two species: *A. auberi* and *A. dorsalis*. The *exsul* Group (Puerto Rico region) contains three species: *A. exsul*, *A. polops*, and *A. wetmorei*. The *lineolata* Group (Hispaniola, Navassa, Bahamas) contains four species: *A. chrysolaema*, *A. lineolata*, *A. maynardi*, and *A. taeniura*. The *plei* Group (Lesser Antilles) contains nine species: *A. cineracea, A. corax, A. corvina, A. erythrocephala, A. fuscata, A. griswoldi, A. major, A. plei*, and *A. pluvianotata*. Because we found *A. leberi* to be essentially identical to a nearby population of *A. chrysolaema* and because it was never very well differen-

tiated ecologically (Sproston et al. 1999) or morphologically except in pattern (Schwartz and Klinikowski 1966), we consider *A. leberi* to be a junior synonym of *A. chrysolaema*. Apparently it is a color morph of the latter species. Additional genetic sampling among populations of *A. chrysolaema* (M. Gifford and R. Powell unpublished data) will further address this question.

The finding of a single West Indian Clade of *Ameiva* agrees with early speculation of a "common stock of many of the Antillean forms" (Barbour and Noble 1915). If this clade were an ancient product of proto-Antillean vicariance, the divergence time estimate between it and mainland species should be greater (e.g., 70-80 Mya) than we observe (25-30 Mya). Therefore, the West Indian Clade most likely arose by a single fortuitous dispersal event over water on floating debris (flotsam). It is not surprising that our time estimate is similar to that (~36 Mya) presented earlier (Hedges et al. 1992; Hass et al. 2001) because our sequence divergence calibration is derived from those immunological data. Although the conclusion is the same, the two estimates differ slightly because the earlier estimate was based on a single pairwise comparison of the two species used to produce antisera whereas our estimate here derives from a regression of additional one-way immunological comparisons with other species. It is not known which of the two is more accurate. However, in the absence of a Tertiary fossil record for West Indian *Ameiva*, such molecular clock estimates provide useful information for investigating the evolutionary history of this group of lizards.

According to the dispersal model of Caribbean biogeography, the nearly unidirectional flow of water currents in the West Indies would have brought debris from the northeastern coast of South America to the islands throughout the Cenozoic, favoring an origin from that continent rather than North or Central America (Hedges 2001). In the case of *Ameiva*, an origin from North America is unlikely because no living or fossil species is native to southeastern United States. The greater species diversity of *Ameiva* in the central and eastern portion of the West Indies, especially the Lesser Antilles, compared with Cuba, agrees with current directions and favors a South American (versus Central American) origin for West Indian *Ameiva*. Also, the fact that two additional Lesser Antillean species are not included in this analysis, yet are considered to be the "most highly differentiated" morphologically (Baskin and Williams 1966) further supports a South America origin.

If dispersal followed current patterns in the West Indies, it should be reflected in the phylogenetic relationships of the species. In some cases this is true, but in other cases it is not clearly evident. For example, the southernmost species of the Lesser Antillean clade in our study is *A. fuscata* of Dominica, and it is phylogenetically basal among species in that group. However, a clade of two species from the northern Lesser Antilles, *A. corax* and *A. plei*, also is basal in that clade. Therefore, if dispersal followed water currents it would suggest at least two dispersals to the northern islands occurred from the central or southern islands. That, and other more complicated (e.g., "leap-frog" or "bypass") dispersal models have been proposed for Lesser Antillean *Ameiva* (Baskin and Williams 1966). Without knowing the phylogenetic position of the two extinct species, and the relationships of the four major groups in the West Indies, it is not yet possible to make any additional comparisons between phylogeny and direction of dispersal.

Nonetheless, the relationship of *A. maynardi* from Inagua Island in the Bahamas, nested within a clade of species from Hispaniola, agrees with current flow directions and supports an origin of that species by dispersal from Hispaniola sometime in the Pliocene (2-5 Mya). This disagrees with an earlier suggestion that *A. maynardi* is a close relative of *A. wetmorei* and dispersed from Puerto Rico (Barbour and Noble 1915). The other Bahaman species, *A. auberi*, also occurs on Cuba where it is widespread and differentiated into 40 subspecies (Schwartz and McCoy 1970; Schwartz and Henderson 1991). Because of this distribution, and the fact that much of the Bahamas Bank was submerged in the Pliocene and Pleistocene

during sea level highs, an origin of Bahaman *A. auberi* from Cuba has been assumed (Schwartz and McCoy 1970).

A close relationship between Cuban and Jamaican species of *Ameiva* based on morphology (Schwartz 1970) was confirmed by our sequence data. The time estimate for their divergence (~6 Mya) implicates dispersal because these two islands have not been in contact since the late Mesozoic (>70 Mya; Pindell 1994). However, the direction of dispersal is not known. Although Jamaica is east and south of much of Cuba, suggesting a Jamaica-to-Cuba dispersal direction as being most likely, currents flow to the south between Cuba and Haiti (Windward Passage) thus making a Cuba-to-Jamaica dispersal also possible. In addition, Jamaica was further to the west in the past, because of motion on the Caribbean Plate (Pindell 1994).

The phylogeny of West Indian *Ameiva* (Fig. 1) reveals several cases of morphological convergence. For example, *A. lineolata* (Hispaniola) and *A. wetmorei* (Puerto Rico) are small species with well-developed stripes and bright blue tails. *Ameiva chrysolaema* (Hispaniola) and *A. exsul* (Puerto Rico) are large species with a duller color pattern and similarities in head markings. These morphological similarities led previous workers to suggest a close relationship between the small, striped species and the larger and less brightly colored species (Cochran 1941), thus inferring two biogeographic connections between Hispaniola and Puerto Rico. However, the sequence phylogeny does not support those connections and instead indicates that they are the result of morphological convergence: the Hispaniolan species are part of a Hispaniolan radiation and the Puerto Rican species are part of a radiation on the Puerto Rican Bank.

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