

# 11 Relationships and Divergence Times of West Indian Amphibians and Reptiles: Insights from Albumin Immunology

*Carla Ann Hass, Linda R. Maxson, and S. Blair Hedges*

*Abstract* — Seven families of West Indian reptiles and two families of West Indian amphibians were investigated using the immunological technique of micro-complement fixation. These data allowed the examination of relationships among members of each of these families and provided estimates of divergence times, both within the West Indies as well as between mainland and island taxa. Some of these groups are the result of a relatively recent colonization and subsequent radiation (e.g., xenodontine snakes). Other groups show deeper divergences among the West Indian species and were much earlier arrivals to these islands (e.g., amphisbaenids). When examined in conjunction with the geological history of the Caribbean, the divergence times derived from the immunological data suggest overwater dispersal as the primary mechanism for colonization of the West Indies by these terrestrial vertebrates.

## INTRODUCTION

The islands of the West Indies harbor a diverse array of reptiles and amphibians, ranging from the minute gecko *Sphaerodactylus parthenopion* to the imposing *Crocodylus rhombifer*, from the blind, burrowing snake *Typhlops* to the arboreal hylid frogs. Endemic species representing five of the six extant major reptilian lineages (turtles, crocodylians, snakes, lizards, and amphisbaenians) are found on these islands, as are members of four families of frogs (Bufonidae, Dendrobatidae, Hylidae, and Leptodactylidae). Many species are endemic to individual islands, and often are restricted to very small areas within those islands (Schwartz and Henderson, 1991). In addition to morphological studies, data obtained by looking at the variation of molecules among species, both through indirect comparisons of proteins as well as direct comparisons of nucleotide sequences, can offer insights into both the relationships among taxa as well as the timing of divergence events within groups. While there have been molecular studies of some West Indian groups (see Hedges, 1996a, for references) most groups have not been investigated. In this study, we present immunological information for seven groups of reptiles and two families of frogs. The technique of micro-complement fixation (MC'F), which allows the estimation of the number of amino acid differences between proteins, has been used to investigate relationships and divergence times in many vertebrate groups, including West Indian taxa (Hedges et al., 1992; Hass et al., 1993; Hedges, 1996a). The new data presented here extend those studies to additional groups and species of West Indian amphibians and reptiles.

## MATERIALS AND METHODS

Antisera were prepared against 11 species of West Indian reptiles from seven squamate families, and 9 species of amphibians, representing two anuran families (Table 1). The collection localities

**TABLE 1**  
**Titers and Slopes for Antisera against Serum Albumin**  
**from Selected West Indian Reptiles and Amphibians**

Family	Species	No. of Rabbits	Titer	Slope
Bufonidae	<i>Bufo guentheri</i> (BG)	1	1/2800	350
	<i>B. marinus</i> (BM)	2	1/4200	400
	<i>B. peltoccephalus</i> (BP)	2	1/1400	370
Hylidae	<i>Calyptrahyla crucialis</i> (CC)	2	1/2000	350
	<i>Hyla vasta</i> (HV)	2	1/1600	460
	<i>Osteopilus brunneus</i> (OB)	2	1/1800	400
	<i>O. dominicensis</i> (OD)	2	1/3000	400
	<i>O. septentrionalis</i> (OS)	3	1/4700	400
	<i>Osteocephalus taurinus</i> (OT)	2	1/1500	330
Amphisbaenidae	<i>Amphisbaena schmidti</i> (AM)	1	1/3200	400
Anguillidae	<i>Diploglossus delasagra</i> (DD)	1	1/3000	320
	<i>D. pleei</i> (DP)	1	1/4000	300
	<i>D. warreni</i> (DW)	2	1/1600	350
	<i>Wetmorena haetiana</i> (WE)	1	1/1500	400
Iguanidae	<i>Leiocephalus schreibersi</i> (LE)	1	1/4200	450
Teiidae	<i>Ameiva chrysolaeama</i> (AC)	1	1/1800	330
	<i>A. exsul</i> (AE)	1	1/4600	360
Colubridae	<i>Arrhyton landoi</i> (AR)	1	1/2400	450
Tropidophidae	<i>Tropidophis haetianus</i> (TR)	1	1/4400	450
Typhlopidae	<i>Typhlops platycephalus</i> (TY)	1	1/2700	350

for these species, and the species used as antigens are listed in the Appendix. The animals were sacrificed using cryotherapy (Kennedy and Brockman, 1965). In some cases, plasma samples to be used for antibody preparation were pools of multiple individuals from the same population (Appendix). Albumin was isolated from pure plasma or plasma preserved with PPS using polyacrylamide electrophoresis modified from the method of Davis (1964). Antibodies to this extracted albumin were prepared in female New Zealand white rabbits following the method of Maxson et al. (1979) as modified by Hass and Hedges (1991). When antisera were prepared in more than one rabbit, the individual rabbit antisera were pooled in inverse proportion to their titers. Hutchinson and Maxson (1986) showed that antibodies prepared using one rabbit give approximately the same estimates of immunological distance (ID) as do antibody pools.

Micro-complement fixation experiments were performed using standard protocols (Maxson and Maxson, 1990). The data are reported as ID units. These data sets provide primarily one-way estimates of ID values. While reciprocal comparisons give a more accurate approximation of ID values between taxa, one-way distances are useful indicators of the degree of amino acid difference between the albumins of two species. Data sets with reciprocal ID measurements were tested for nonrandom deviations from perfect reciprocity and, when appropriate, the data were corrected by the method of Cronin and Sarich (1975); these corrected data are used in discussion of the data sets.

An independent calibration of the albumin immunological clock for each group investigated in this study is not possible because of the lack of fossil information or independent geological events to use as calibration points. A "standard" calibration (1 ID unit = 0.6 million years of divergence) has been derived for a number of vertebrate groups based upon both fossil and geological information (Wilson et al., 1977; Maxson, 1992), and its consistency over diverse vertebrate lineages justifies its use in this type of study (see the more detailed discussion in Hedges, 1996a). Some of

the new data reported here, and their taxonomic implications, already have been discussed elsewhere (Hedges et al., 1992; Hedges, 1996a).

## RESULTS

### BUFONIDAE

We were able to examine 5 of the 11 species of *Bufo* endemic to the West Indies using MC'F (Table 2). The immunological data suggest that the Cuban species *B. peltocephalus* and *B. taladai* are the most closely related species examined, at an ID of 8. The other Cuban species examined, *B. longinasus*, was as distinct from *B. peltocephalus* as was the Hispaniolan species *B. guentheri*. *Bufo guentheri* and *B. lemur* were separated by an ID value of 18. All of the Cuban species gave ID values within the same range (31 to 38) from *B. guentheri*. Two mainland taxa were examined; *B. granulosis* appeared to be closer to the West Indian species than was *B. marinus*. An antiserum to *B. marinus* gave similar reciprocal values to the West Indian species (0 = 87 ID; approximate values were excluded from means).

### HYLIDAE

There were noticeable deviations in reciprocity in this data set, particularly for the *Calyptahyla crucialis* and *Hyla vasta* antisera (Table 3). Therefore, the data matrix was corrected using the method of Cronin and Sarich (1975). The most closely related species are *C. crucialis* and an undescribed *Osteopilus* species from Jamaica, with an ID value of 11. *Calyptahyla crucialis* and *O. brunneus* also showed a low mean ID value (16). These two species gave low ID values to the Jamaican species *H. marianae*, with higher values to *H. wilderi*. The Hispaniolan species *O. dominicensis* had an ID of 20 to both *H. pulchrilineata*, another Hispaniolan species, and to the Jamaican species *H. marianae*; the Jamaican species *C. crucialis* and *Osteopilus* sp. nov. were slightly more divergent. The Cuban species *O. septentrionalis* gave marginally higher average ID

**TABLE 2**  
**One-Way Immunological Distances from *Bufo guentheri* (BG), *B. peltocephalus* (BP), and *B. marinus* (BM) Antisera to Other West Indian Bufonids and Representative Mainland Species**

Island	Species	BG	BP	BM
		Correction Factor		
		1.23	0.84	—
Hispaniola	<i>Bufo guentheri</i> (BG)	0	<b>44 (37)</b>	~96
Cuba	<i>B. peltocephalus</i> (BP)	<b>30 (37)</b>	0	79
	<i>B. longinasus</i>	25 (31)	46 (39)	—
	<i>B. taladai</i>	31 (38)	10 (8)	—
Puerto Rico	<i>B. lemur</i>	15 (18)	~53 (~44)	—
Mainland	<i>B. granulosis</i>	—	62 (52)	61 <sup>a</sup>
	<i>B. marinus</i> (BM)	96	>100 (>84)	0

*Note:* Reciprocal ID values are in bold. Values in parentheses are corrected ID values based upon reciprocal comparisons. A dash indicates that experiment was not performed. Approximate estimates are indicated by ~.

<sup>a</sup> ID value from Maxson, 1984.

**TABLE 3**  
**Immunological Distances from Five Antisera to Other West Indian Hylids**  
**and a Representative Mainland Hylid**

Island	Species	CC	OB	HV	OD	OS	OT
		Correction Factor					
		0.588	1.36	1.88	0.877	0.819	—
Jamaica	<i>Calyptrahyla crucialis</i> (CC)	0	11 (17)	21 (40)	25 (26)	46 (46)	87
	<i>Hyla marianae</i>	25 (18)	13 (20)	22 (41)	19 (20)	39 (39)	—
	<i>H. wilderi</i>	36 (26)	26 (41)	42 (79)	44 (46)	49 (49)	—
	<i>Osteopilus brunneus</i> (OB)	20 (15)	0	23 (43)	34 (35)	48 (48)	100
	<i>Osteopilus</i> sp. nov.	15 (11)	24 (38)	29 (54)	21 (22)	48 (48)	—
Hispaniola	<i>H. heilprini</i>	—	—	97 (182)	—	—	—
	<i>H. pulchrrilineata</i>	26 (19)	20 (32)	24 (45)	19 (20)	40 (40)	—
	<i>H. vasta</i> (HV)	73 (53)	27 (43)	0	42 (44)	46 (46)	— <sup>a</sup>
	<i>O. dominicensis</i> (OD)	39 (28)	19 (30)	26 (49)	0	37 (37)	73
Cuba	<i>O. septentrionalis</i> (OS)	43 (31)	35 (55)	30 (56)	37 (38)	0	83
Mainland	<i>Osteocephalus taurinus</i> (OT)	~118 (~86)	98 (156)	— <sup>a</sup>	~110 (~114)	78 (78)	0

Note: Reciprocal ID values are in bold. Values in parentheses are corrected ID values following the method of Cronin and Sarich; one-way ID values also were corrected. A dash indicates that experiment was not performed. Approximate estimates are indicated by ~.

<sup>a</sup> Experiment was done but no cross reaction was seen.

**TABLE 4**  
**One-Way Immunological Distances from**  
***Amphisbaena schmidti* Antiserum to Other**  
**West Indian and Mainland Amphisbaenids**

Island	Species	AM
Puerto Rico	<i>Amphisbaena bakeri</i>	31
	<i>A. caeca</i>	39
	<i>A. fenestrata</i>	28
	<i>A. schmidti</i> (AM)	0
	<i>A. xera</i>	35
Hispaniola	<i>A. caudalis</i>	60
	<i>A. gonavensis</i>	144
	<i>A. innocens</i>	83
Cuba	<i>A. manni</i>	16
	<i>A. cubana</i>	29
Mainland	<i>Cadea blanooides</i>	69
	<i>A. alba</i>	91
	<i>Rhineura floridana</i>	156

values to the other West Indian taxa, ranging from 37 to 49 ID. *Hyla vasta*, from Hispaniola, was more divergent, with IDs to the other taxa ranging from 40 to 79. Among all of the species endemic to the West Indies, *H. heilprini* was the most divergent. Only the *H. vasta* antiserum, which strongly underestimates ID values, would cross-react with *H. heilprini* and the adjusted ID value was 182. The West Indian taxa gave lower ID values, ranging from 73 to 156, to *Osteocephalus taurinus*, a mainland species ( $\bar{x}$  = 96 ID).

**TABLE 5**  
**Immunological Distances among West Indian Members of the Family Anguidae**

Island	Species	DW	WE	DD	DP
		0.72	1.3	1.06	—
		<b>Correction Factor</b>			
Hispaniola	<i>Celestus curtissi</i> #1	14 (10)	8 (10)	102 (108)	—
	<i>C. curtissi</i> #2	13 (9)	5 (6)	105 (111)	— <sup>a</sup>
	<i>C. darlingtoni</i>	2 (1)	4 (5)	102 (108)	—
	<i>C. stenurus</i>	14 (10)	4 (5)	102 (108)	— <sup>a</sup>
	<i>C. macrotus</i>	16 (12)	13 (17)	97 (103)	—
	<i>C. sp. nov.</i>	10 (7)	5 (6)	99 (105)	—
	<i>Diploglossus carraui</i>	0	4 (5)	94 (100)	—
	<i>D. warreni</i> (DW)	0	<b>4 (5)</b>	<b>99 (105)</b>	— <sup>a</sup>
	<i>Sauresia agasepsoides</i>	9 (6)	5 (6)	97 (103)	—
	<i>S. sepsoides</i>	12 (7)	5 (6)	98 (104)	—
	<i>Wetmorena haetiana</i> (WE)	<b>14 (10)</b>	0	<b>103 (109)</b>	— <sup>a</sup>
Jamaica	<i>Celestus barbouri</i>	13 (9)	10 (13)	98 (104)	—
	<i>C. cruscus cruscus</i>	15 (11)	9 (12)	114 (121)	—
	<i>C. c. cundalli</i>	15 (11)	13 (17)	101 (107)	—
Cuba	<i>D. delasagra</i> (DD)	<b>129 (94)</b>	<b>86 (112)</b>	0	<b>46</b>
Puerto Rico	<i>D. pleii</i> (DP)	~140 (~101)	86 (112)	<b>26 (28)</b>	0
Mainland	<i>Ophiodes striatus</i>	—	54	—	—

Note: Reciprocal ID values are in bold. Values in parentheses are corrected ID values based upon reciprocal comparisons. A dash indicates that experiment was not performed. Approximate estimates are indicated by ~.

<sup>a</sup> Experiment was done but no cross reaction was seen.

#### AMPHISBAENIDAE

These data suggest that the closest relative to the Puerto Rican species *Amphisbaena schmidti* is a Hispaniolan species, *A. manni* (Table 4). The other Puerto Rican species ranged from 28 to 39 ID units from *A. schmidti*. The Cuban species *A. cubana* also was within this range. The Hispaniolan species *A. caudalis* and the Cuban species *Cadea blanoides* showed similar levels of divergence from *A. schmidti*. The Hispaniolan species *A. innocens* and the mainland species *A. alba* showed a higher level of divergence. Finally, the Hispaniolan species *A. gonavensis* showed a degree of divergence similar to that of a mainland species placed in another family, *Rhineura floridana* (Rhineuridae).

#### ANGUIDAE

The albumin ID values show a clear dichotomy within the West Indian anguid lizards (Table 5). Two species of *Diploglossus*, *D. delasagra* (Cuba) and *D. pleii* (Puerto Rico), had ID values of approximately 107 units (mean of corrected values) to the other West Indian anguids examined. These two species had a mean corrected reciprocal value of 37 from each other. In contrast, the antisera against the two Hispaniolan species, *Wetmorena haetiana* and *D. warreni*, consistently gave low ID values (ranging from 0 to 17) to the species of *Celestus*, *Sauresia*, and Hispaniolan *Diploglossus* examined. These data do not provide sufficient resolution to examine the phylogenetic relationships among the members of this group. The mainland species *Ophiodes striatus* was tested against the antiserum to *W. haetiana* and gave an ID value of 54.

**TABLE 6**  
**One-Way Immunological Distances from the**  
*Leiocephalus schreibersi* Antiserum to Other West Indian  
*Leiocephalus* and Representative Mainland Iguanids

Island	Species	LE
Hispaniola	<i>Leiocephalus schreibersi</i> (LE)	0
	<i>L. barahonensis</i> #1	0
	<i>L. barahonensis</i> #2	3
	<i>L. lunatus</i>	1
	<i>L. melanochlorus</i>	1
	<i>L. personatus</i>	1
	<i>L. semilineatus</i>	4
Cuba	<i>L. carinatus</i>	3
	<i>L. cubensis</i>	14
	<i>L. macropus</i>	7
	<i>L. raviceps</i>	10
	<i>L. stictigaster</i>	4
Bahamas — East Plana Cay	<i>L. greenwayi</i>	6
Bahamas — Great Inagua	<i>L. inaguae</i>	0
Bahamas — San Salvador	<i>L. loxogrammus</i>	10
Bahamas — Acklin's Island	<i>L. punctatus</i>	7
Mainland	<i>Crotaphytus collaris</i>	40 (46)
	<i>Sceloporus spinosus</i>	63 (58)
	<i>Tropidurus peruvianus</i>	83 (80)
	<i>T. hispidus</i>	87

Note: ID values in parentheses are reciprocal values from antisera of other iguanid species to *L. schreibersi*.

## IGUANIDAE

The one-way immunological distances from the antiserum against *Leiocephalus schreibersi*, a Hispaniolan species, give some insights into the relationships among the members of this endemic West Indian genus (Table 6). It is clear that all of the species examined are closely related to one another. The largest immunological distance was 14 ID. There are many species that gave ID values within the error range of the technique ( $\pm 2$  ID units), indicating that their albumin molecules have very similar amino acid sequences. The ID values to Hispaniolan species ranged from 0 to 4 ID, while the ID values to the Cuban species ranged from 3 to 14 ID. One Bahamian species, *L. inaguae*, had an ID of 0 to *L. schreibersi*. The other Bahamian species, *L. greenwayi*, *L. loxogrammus*, and *L. punctatus*, had ID values within the range of those seen to Cuban species. The *Leiocephalus* antiserum also was used to determine ID values for some mainland species within the family Iguanidae. The lowest ID value (with a mean value of 43 for reciprocal comparisons) seen was to *Crotaphytus collaris*, a species that occurs in North America. *Sceloporus spinosus*, another North American species, gave a mean ID value of 60. The two South American *Tropidurus* examined, *T. peruvianus* and *T. hispidus*, gave ID values over 80.

## TEIIDAE

The two antisera prepared do not show any clearly defined patterns of albumin variation among the West Indian *Ameiva* (Table 7). *Ameiva chrysoleama* and *A. chrysoleama* #3, both from Hispaniola, are very closely related, with an ID value of 1. However, the remaining species of West Indian

**TABLE 7**  
**One-Way Immunological Distances from *Ameiva chrysoleama* (AC)**  
**and *A. exsul* (AE) Antisera to Other West Indian *Ameiva* and**  
**Representative Mainland Teiids**

Island	Species	Correction Factor	
		1.23	0.86
Hispaniola	<i>Ameiva chrysoleama</i> (AC)	0	<b>63 (54)</b>
	<i>A. chrysoleama</i> #3	1 (1)	61 (52)
	<i>A. lineolata</i>	38 (47)	47 (40)
	<i>A. taeniura</i>	—	46 (40)
Puerto Rico	<i>A. exsul</i> (AE)	<b>44 (54)</b>	0
	<i>A. wetmorei</i>	30 (37)	39 (34)
Cuba	<i>A. auberi</i>	50 (62)	64 (55)
Bahamas	<i>A. maynardi</i>	40 (49)	44 (38)
Lesser Antilles — St. Kitts	<i>A. erythrocephala</i>	37 (46)	70 (60)
Lesser Antilles — Antigua	<i>A. griswoldi</i>	34 (42)	50 (43)
Lesser Antilles — Montserrat	<i>A. pluvianotata</i>	42 (52)	58 (50)
Mainland	<i>A. ameiva</i>	50 (62)	69 (59)
	<i>Cnemidophorus uniparens</i>	53 (65)	73 (63)
	<i>Tupinambis</i>	>144	168 (144)

Note: Reciprocal ID values are in bold. Values in parentheses are corrected ID values based upon reciprocal comparisons. A dash indicates that experiment was not performed.

*Ameiva* ranged from 34 to 62 ID units (corrected values). The mainland species *A. ameiva* was at the upper end of the range of IDs found within the West Indies. The ID value from *A. exsul* to *A. ameiva* previously has been reported to be 79 (Hedges et al., 1992); additional experiments gave a lower value (69). Two other teiid lizards were compared. *Cnemidophorus uniparens* gave ID values slightly higher than those seen to the mainland *Ameiva*, while the ID values to *Tupinambis* were very large, essentially at the measurement limit of the technique (Maxson and Maxson, 1986).

## COLUBRIDAE

All of the West Indian xenodontine snakes tested gave low ID values (20 or less) to the *Arrhyton landoi* antiserum (Table 8). Within the genus *Arrhyton*, all of the Cuban species examined gave ID values within the error limit of MC'F ( $\pm 2$  ID), indicating that their albumins have almost identical amino acid sequences. The Jamaican and Puerto Rican species gave slightly higher ID values, ranging from 6 to 11. However, this level of differentiation also was seen to members of three other West Indian genera, *Antillophis*, *Hypsirhynchus*, and *Ialtris*. The remaining three West Indian genera, *Alsophis*, *Darlingtonia*, and *Uromacer*, gave higher ID values (ranging from 12 to 20 ID). An ID value of 11 was reported for *Darlingtonia* by Hedges et al. (1992), but that value has been revised by further experiments. The South American xenodontines showed divergences ranging from 21 to 42 ID, and the Central American xenodontines were the most divergent taxa examined, with an average ID of 58.

## TROPIDOPHIDAE

A dichotomy in ID values among West Indian *Tropidophis* is obvious (Table 9). The antiserum against a *T. haetianus* from Jamaica gave much lower ID values (range 1 to 9) to eight species of Cuban and Bahamian *Tropidophis* than it did to *T. haetianus* from Hispaniola. This dichotomy was

**TABLE 8**  
**One-Way Immunological Distances from *Arrhyton landoi* (AR)**  
**Antiserum to Other West Indian and Mainland Xenodontine Snakes**

Island	Genus	Species	AR	
Cuba	<i>Arrhyton</i>	<i>dolichura</i>	0	
		<i>landoi</i> #1 (AR)	0	
		<i>landoi</i> #2	0	
		<i>procerum</i>	0	
		<i>supernum</i> #1	0	
		<i>supernum</i> #2	0	
		<i>taeniatum</i>	0	
		<i>tanyplectum</i>	0	
		<i>vittatum</i>	2	
Jamaica		<i>callilaemum</i>	6	
		<i>funereum</i>	9	
		<i>polylepis</i>	11	
Puerto Rico		<i>exiguum</i>	6	
Cuba	<i>Antillophis</i>	<i>andreae</i>	11	
Hispaniola		<i>parvifrons</i>	6	
Hispaniola	<i>Hypsirhynchus</i>	<i>ferox</i>	6	
		<i>scalaris</i>	8	
	<i>Ialtris</i>	<i>dorsalis</i> #1	10	
		<i>dorsalis</i> #2	10	
		<i>Darlingtonia</i>	<i>haetiana</i>	15
	Cuba	<i>Alsophis</i>	<i>cantherigerus</i>	19
Puerto Rico	<i>portoricensis</i>		15	
Bahamas — Nassau		<i>vudii</i>	12	
Lesser Antilles — Antigua		<i>antiguae</i>	14	
Lesser Antilles — Montserrat		<i>antillensis</i>	16	
Hispaniola	<i>Uromacer</i>	<i>catesbyi</i> #1	20	
		<i>catesbyi</i> #2	15	
		<i>frenatus</i>	18	
		<i>oxyrhynchus</i>	17	
			<i>cabella</i>	31
Mainland — South American Clade	<i>Liophis</i>	<i>melanostigma</i>	23	
			<i>leucomelas</i>	42
	<i>Oxyrhopus</i>		21	
	<i>Thamnodynastes</i>		29 (42)	
Mainland — Central American Clade	<i>Xenodon</i>	<i>severus</i>	58	
		<i>Dipsas</i>	<i>catesbyi</i>	57
		<i>Leptodeira</i>		

Note: The value in parentheses is a reciprocal ID value from an antiserum to *Xenodon severus*.

so striking, and unexpected, that multiple individuals from Hispaniola were examined to ensure that this difference was real. The ID values to those Hispaniolan snakes ranged from 23 to 29. The mainland species, *T. paucisquamis*, gave an ID value of 70, much larger than any values seen within the West Indies. *Tropidophis* does not seem to be clearly allied to any other lineage of snakes. Although the ID to *Boa constrictor* was lower than to the other lineages examined, that value (141) is approaching the upper limit of this technique (Maxson and Maxson, 1986).

#### TYPHLOPIDAE

The antiserum against the Puerto Rican species *Typhlops platycephalus* gave low ID values (ranging from 1 to 5) to three Puerto Rican species and the two species from the Lesser Antilles (Table 10).



**TABLE 9**  
**One-Way Immunological Distances from**  
***Tropidophis haetianus* (TR) Antiserum to Other**  
**West Indian and Mainland Tropidophiids, and**  
**Selected Representatives of Other Snake Families**

Island	Taxon	TR
Jamaica	<i>Tropidophis haetianus stejnegeri</i> #1 (TR)	0
	<i>T. haetianus stejnegeri</i> #2	0
	<i>T. haetianus stullae</i>	0
Cuba	<i>T. feicki</i>	9
	<i>T. fuscus</i>	4
	<i>T. maculatus</i>	4
	<i>T. melanurus</i>	2
	<i>T. pardalis</i>	5
	<i>T. pilsbryi</i>	4
	<i>T. wrighti</i>	4
Bahamas	<i>T. canus</i>	1
Hispaniola	<i>T. haetianus haetianus</i> #1	25
	<i>T. haetianus haetianus</i> #2	23
	<i>T. haetianus haetianus</i> #3	29
	<i>T. haetianus haetianus</i> #4	28
	<i>T. haetianus haetianus</i> #5	25
	<i>T. haetianus humerus</i>	24
Mainland	<i>T. paucisquamis</i>	70
	Boidae: <i>Boa constrictor</i>	141
	Elapidae: <i>Naja naja</i>	171
	Pythonidae: <i>Python molarus</i>	~185
	Colubridae: <i>Coluber constrictor</i>	~185
	Colubridae: <i>Arrhyton landoi</i>	~180

Note: Approximate estimated are indicated by ~.

The exception is the Puerto Rican *T. rostellatus*, which gave an ID value of 31. The Cuban species *T. biminensis* and *T. lumbricalis* both gave an ID value of 14. The widest range of ID values is seen among the Hispaniolan species, which ranged from 17 to 44. The Jamaican species *T. jamaicensis* gave an ID value within this range. *Typhlops luzonensis*, a species from the Philippines, was quite divergent, at 96 ID. Species from two other scolecophidian families were included, *Liotyphlops* (Anomalepidae) and *Leptotyphlops* (Leptotyphlopidae), and both of these gave very high ID values to *T. platycephalus*.

## DISCUSSION

### BUFONIDAE

Two Cuban species, *Bufo peltoccephalus* and *B. taladai*, shared a common ancestor approximately 5 million years ago (mya). *Bufo peltoccephalus* diverged from the other species examined (from Cuba, Hispaniola, and Puerto Rico) about 22 to 23 mya. The Hispaniolan species *B. guentheri* and the Puerto Rican *B. lemur* diverged approximately 11 mya. The ID values from the *B. guentheri* antiserum give a divergence time of 19 to 23 mya from the three Cuban species examined. While the mainland affinities of this group are not yet known, the ID value to *B. granulosis* indicates that they had diverged from mainland taxa by about 31 mya.

**TABLE 10**  
**One-Way Immunological Distances from *Typhlops platycephalus* (TY) Antiserum to Other West Indian and Mainland Typhlopids, and Selected Representatives of Other Scolecophidian Families**

Island	Taxon	TY
Puerto Rico	<i>Typhlops granti</i>	5
	<i>T. hypomethes</i>	1
	<i>T. platycephalus</i> (TY)	0
	<i>T. richardi</i>	2
	<i>T. rostellatus</i>	31
Lesser Antilles	<i>T. guadaloupensis</i>	4
	<i>T. monastus</i>	4
Cuba	<i>T. biminensis</i>	14
	<i>T. lumbricalis</i>	14
Hispaniola	<i>T. capitulatus</i>	18
	<i>T. hectus</i>	17
	<i>T. pusillus</i>	18
	<i>T. schwartzi</i>	22
	<i>T. sulcatus</i>	26
	<i>T. syntherus</i>	44
	<i>T. titanops</i>	29
Jamaica	<i>T. jamaicensis</i>	20
Mainland	<i>T. luzonensis</i>	96
	Anomalepididae: <i>Liotyphlops</i>	157
	Leptotyphlopidae: <i>Leptotyphlops</i>	150

Maxson (1984) examined albumin ID variation in the genus *Bufo* and found that the Old World species (Eurasian and African) diverged from the New World species about 65 to 75 mya (~110 to 120 ID units). No West Indian toads were included in that study, but the data obtained here indicate that West Indian *Bufo* are much closer to New World species of *Bufo* than to Old World species. This does not support the recognition of a separate genus (*Peltophryne*) for the West Indian species. Although Graybeal (1997), in a study of cytochrome *b* DNA sequences in bufonids, did not significantly resolve the position of the *B. peltoccephalus* group, she also found it to be nested among New World species of *Bufo* in her best supported trees.

## HYLIDAE

While these immunological data cannot give a detailed picture of relationships among these species of West Indian hylid frogs, general patterns are apparent. The Jamaican species, and two Hispaniolan species, *Hyla pulchrrilineata* and *Osteopilus dominicensis*, appear to form a group. The Cuban species *O. septentrionalis* is slightly more divergent, while the Hispaniolan species *H. vasta* appears to be the basal taxon for this group of West Indian hylids. Within this West Indian group, the casque-headed frogs, members of the genera *Osteopilus* and *Calyptahyla*, do not form a distinct group, as suggested by Trueb and Tyler (1974), but are interspersed among the West Indian species of *Hyla*. The ID values to *Osteocephalus taurinus* range from 73 into the 100s, with a mean ID of 96, which gives a divergence time of 58 mya, if this is the sister group to the West Indian hylid radiation. *Hyla heilprini* is clearly outside of the radiation of West Indian hylid frogs and most likely represents a second colonization of the West Indies by this family.

## AMPHISBAENIDAE

The results obtained for the West Indian amphisbaenids indicate that *Amphisbaena schmidti* last shared a common ancestor with other Puerto Rican species about 17 mya. It is more closely related to the Hispaniolan species, *A. manni*, and this suggests that there was a dispersal event approximately 10 mya. Details of the relationships among the species of West Indian amphisbaenids currently are being studied using sequence data from mitochondrial genes. Most of the West Indian taxa apparently diverged from mainland species by about 55 mya, based upon the immunological comparison to *A. alba*, a species from South America. These data led Hedges (1996a) to suggest that *Cadea* be synonymized within *Amphisbaena*, because it gave a lower ID value than did some congeners examined.

Among the West Indian species, *A. gonavensis* is the most divergent. The level of divergence seen is close to that for a species that is placed in another family, the Rhineuridae. Until additional information is available, we cannot determine if *A. gonavensis* represents an earlier colonization event (about 86 mya), or is a recent colonist from a divergent mainland lineage. Although they gave different ID values from the *A. schmidti* antiserum, *A. innocens* and *A. gonavensis* are unusual among West Indian *Amphisbaena* in having a large number ( $2N = 50$ ) of chromosomes; other West Indian species examined have  $2N = 36$  chromosomes (Cole and Gans, 1987; Hass and Hedges, unpublished). In this respect, they resemble some South American species with high numbers of chromosomes.

## ANGUIDAE

The recognition of the genus *Celestus* and the allocation of species of West Indian anguids to genera have been the subject of much debate (Boulenger, 1885; Burt and Burt, 1932; Underwood, 1959; Strahm and Schwartz, 1977; Savage and Lips, 1993). Although earlier workers considered the condition of the claw sheath to be an important character, Strahm and Schwartz (1977) primarily used the degree of development of canals in the osteoderms to allocate the diploglossine taxa to different genera. Wilson et al. (1986) determined that these osteoderm patterns are a reflection of ontogeny, with the radix more developed in older animals, and their work suggested that these patterns may be of limited use as phylogenetic characters. Savage and Lips (1993) resurrected the earlier classification based on presence (*Diploglossus*) or absence (*Celestus*) of a claw sheath. They considered the genera *Sauresia* and *Wetmorena* to be more closely related to *Diploglossus* because they have a claw sheath (Savage and Lips, 1993).

The immunological data support the placement of the three large Hispaniolan species (*anelpistus*, *carrui*, *warreni*) in the genus *Celestus* (Savage and Lips, 1993). However, these data also indicate that the species currently recognized as *Celestus*, *Sauresia*, and *Wetmorena* comprise a closely related group, *contra* Savage and Lips (1993). Because only two antisera from species within this group were available, the immunological data cannot be used to determine relationships among the species. However, the data suggest that these species last shared a common ancestor relatively recently, within the last 10 million years. Therefore, the use of the condition of the claw sheath to determine relatedness seems to be inappropriate. Instead, a character deemed important by Underwood (1959), direct contact of the nasal and rostral scales, is in better agreement with the molecular results. Based upon the immunological data, we recommend that *Sauresia* and *Wetmorena* be synonymized within *Celestus* (following Hedges, 1996a). The Cuban and Puerto Rican species of *Diploglossus* examined appear to have diverged from each other about 22 mya; they are distantly related (64 mya) to the other West Indian species examined. The mainland species, *Ophiodes striatus*, appears to have diverged from the West Indian *Celestus* about 32 mya.

Based upon the immunological data, it would appear that the West Indies were colonized at least twice by anguid lizards, assuming one colonization event for *Diploglossus* and another for *Celestus*. However, a clearer understanding of the historical biogeography of this group must await

additional data from the mainland taxa. The fact that the West Indian *Celestus* are most closely related to the mainland *Ophiodes* than to *Diploglossus*, and the peculiar distribution of the mainland taxa (Savage and Lips, 1993), complicates biogeographical inferences.

#### IGUANIDAE

Species in the genus *Leiocephalus* represent a relatively recent radiation. The immunological data indicate that the oldest divergences within this genus occurred less than 10 mya. Relationships among the species within this group have been investigated using data from sequences of mitochondrial genes. Those data (Hass et al., unpublished) are concordant with the patterns seen here. One Bahamian species, *L. inaguae*, is within the cluster of Hispaniolan species, while *L. greenwayi*, *L. loxogrammus*, and *L. punctatus*, also from the Bahamas, show ID values similar to those for Cuban taxa.

The immunological data suggest that the closest mainland relatives of *Leiocephalus* are the crotophytine lizards. This divergence dates to about 26 mya, and this group may have arisen from a colonization of the West Indies from North America, rather than South or Central America (Hedges, 1996b). These data are inconsistent with the placement of *Leiocephalus* within the Tropidurinae. Because of this inconsistency, and similar results obtained in other molecular studies (Macey et al., 1997), we do not follow the taxonomic recommendations of Frost and Etheridge (1989) for iguanian lizards.

#### TEIIDAE

The ID values obtained indicate that divergences among some West Indian *Ameiva* are not recent. *Ameiva chrysolema* and *A. chrysolema* #3 diverged from each other very recently. However, the next most recent divergence for both *A. exsul* and *A. chrysolema* is at a corrected ID value of 34 to 37, approximately 20 to 22 mya. These data do not provide a clear pattern of relationships among the West Indian members of this genus. The mainland species *A. ameiva* gives higher ID values to both antisera, indicating a divergence time of approximately 36 mya. However, these ID values are only slightly lower than those to the *Cnemidophorus uniparens*, another mainland species of teiid. The South American teiid, *Tupinambis*, is distantly related to the West Indian *Ameiva*.

#### COLUBRIDAE

The low ID values seen indicate that divergences among the many species of West Indian xenodontines have occurred within the last 12 million years. The other Cuban species of *Arrhyton* could not be distinguished immunologically from *A. landoi*, despite morphological distinctions and sympatry among some species (Hedges and Garrido, 1992). One reciprocal ID value was available, measured from an antiserum against *Xenodon severus* to *A. landoi*. The difference in reciprocity (26 vs. 42) does suggest that the *A. landoi* may underestimate ID values. While these data cannot be used to determine phylogenetic relationships, they do suggest that *Alsophis*, *Darlingtonia*, and *Uromacer* are the most divergent genera of West Indian xenodontines. The immunological data also show that the degree of divergence to the mainland taxa is at the upper end of the divergences seen within the West Indies, supporting the hypothesis of a large monophyletic clade of West Indian xenodontines. Evidence from mitochondrial DNA sequences (Vidal et al., 2000) also supports this same monophyletic group. Both the ID data and the sequence data support a South American origin for the endemic West Indian xenodontines, perhaps as recently as 13 mya.

#### TROPIDOPHIDAE

The immunological data suggest that the Jamaican and Cuban species of *Tropidophis* have diverged fairly recently, probably sharing a common ancestor within the last 6 million years. This is in sharp

contrast to the Hispaniolan *Tropidophis*, which diverged from other West Indian *Tropidophis* approximately 16 mya. The populations on Jamaica and Hispaniola clearly represent two different species. Because the type locality for *T. haetianus* is in Hispaniola, the Jamaican species should be recognized as *T. jamaicensis*, the oldest available name for the Jamaican populations (Schwartz and Henderson, 1991). The West Indian species last shared a common ancestor with mainland *Tropidophis* about 42 mya. All ID values to snakes from other families are at the upper limit of this technique and do not provide reliable information on the affinities of the Tropidophidae to other snake families.

## TYPHLOPIDAE

These data suggest that the majority of the Puerto Rican species and the species found in the Lesser Antilles diverged relatively recently, about 3 mya. The species on Cuba, Jamaica, and Hispaniola are more divergent, last sharing a common ancestor with the Puerto Rican species between 8 and 17 mya. *Typhlops rostellata* is the exception among the Puerto Rican species, and appears to have diverged from the others species on that island over 18 mya. This may represent an old Puerto Rican lineage, or that species may have colonized the island more recently, perhaps from Hispaniola. These data cannot distinguish between those alternatives. *Typhlops syntherus* is the most distant of the West Indian species from *T. platycephalus*, with a divergence time of about 26 mya.

The degree of divergence between West Indian *Typhlops* and another member of this genus from the Philippines indicates that they have been separated for about 58 million years. The divergences between the family Typhlopidae and the other two families within the Scolecophidia are old, probably dating to the Cretaceous.

## CONCLUSIONS

The albumin immunological data for the different groups of West Indian amphibians and reptiles show very diverse patterns (Table 11). The data indicate that the fauna of these islands is composed of some recent radiations, such as the lizards of the genus *Leiocephalus*, which have diversified within the last 10 million years. This same pattern is seen within the xenodontine snakes, which diverged from mainland taxa only about 13 mya.

There are some taxa where dichotomous patterns of relationships are seen. Within the anguid lizards, the West Indian members of the genus *Celestus* have speciated within the last 10 million years. In contrast, the two species of *Diploglossus* are more distantly related, having diverged about 22 mya, and they last shared a common ancestor with the West Indian *Celestus* approximately 64 mya. These West Indian *Celestus* appear to be more closely related to some mainland taxa, with an estimated divergence time of 32 million years from *Ophiodes*. Within the West Indian snakes of the genus *Tropidophis*, the Bahamian, Cuban, and Jamaican species are closely related, having speciated within the last 6 million years. In contrast, the Hispaniolan members of this group diverged approximately 16 mya.

Finally, there are groups where the majority of immunological values indicate that the divergences among the species are not recent. Within the amphisbaenians, divergences range from 17 to 41 million years. One species, *Amphisbaena gonavensis*, with a divergence of over 80 million years from *A. schmidtii*, probably represents a separate colonization of the West Indies from the mainland. The lizards of the genus *Ameiva* also show a wide range of divergence times, from 0 to 38 mya. The oldest dates are approximately the same as the estimate divergence time from the mainland *Ameiva*.

As first presented by Hedges et al. (1992), and discussed extensively by Hedges (1996a), these albumin immunological data support overwater dispersal during the Cenozoic as the mechanism for colonization of the West Indies by all of the groups discussed here. DNA sequence studies are now under way to elucidate the relationships within each of these groups to further enhance our understanding of West Indian biogeography.

**TABLE 11**  
**Summary Table of Times of Origin for the West Indian Groups Examined**  
**in This Study, and of the Earliest Divergence within Each Group**

Group	Time of (mya)	
	Origin	Earliest Divergence within the West Indies
Bufonidae	31 ± 4.3	23 ± 4.5
Hylidae	58 ± 5.8 <sup>a</sup>	34 ± 4.4 <sup>b</sup>
Amphisbaenidae	55 ± 5.6	41 ± 4.6 <sup>c</sup>
Anguidae — <i>Celestus</i>	32 ± 4.3	10 ± 5.4
Anguidae — <i>Diploglossus</i>	Comparison not available	22 ± 4.5
Iguanidae	26 ± 4.4	8 ± 5.5
Teiidae	36 ± 4.4	38 ± 4.4
Colubridae (Xenodontinae)	13 ± 5.1	12 ± 5.2
Tropidophidae	42 ± 4.6	16 ± 4.9
Typhlopidae	58 ± 5.8	26 ± 4.4

*Note:* The estimates of time of origin were based upon the ID value to the most closely related non-West Indian taxon (lowest ID value). If multiple estimates to a single taxon were available, the mean value was used (excluding any approximate estimates, as indicated by ~ in the previous tables). The earliest divergence time among the West Indian species was based on the highest ID value seen from an antiserum against a West Indian species to another West Indian species. Calibration error estimates were obtained following the methods described in Hedges et al. (1994).

<sup>a</sup> *Hyla heilprini* is considered to represent a separate lineage (see Discussion).

<sup>b</sup> The ID values to *H. wilderi* were significantly different from those to other taxa and therefore they were not used in this estimate (see Table 3).

<sup>c</sup> *Amphibaena gonavensis* and *A. innocens* appear to represent a lineage that is distinct from the other West Indian amphisbaenians, so they were not used in this estimate (see Discussion).

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## APPENDIX: COLLECTING LOCALITIES AND VOUCHER SPECIMENS

Numbers refer to tissue samples in the following collections: (LM = Linda Maxson; RH = Richard Highton; SBH = S. Blair Hedges). An asterisk (\*) indicates species for which an antiserum was made.

**Bufonidae.** *Bufo*: Hispaniola: \**guentheri*, Dominican Republic, Independencia, 12.2 km W Cabral (SBH 101227). Cuba: \**peltocephalus*, Guantánamo Bay U.S. Naval Station, Golf Course/Nursery (SBH 161934); *longinasus*, Sancti Spiritus, north slope of Pico Potrerillo (LM 2782); *taladai*, Santiago de Cuba, La Esmajagua (SBH 190537). Puerto Rico: *lemur* (SBH 190648-50). Mainland: *granulosus*, Brazil (LM 329); *marinus*, Costa Rica (LM 206).

**Hylidae.** Jamaica: \**Calyptrahyla crucialis*, St. Elizabeth, Mandeville, Marshall's Pen (LM 2570); *Hyla marianae*, Trelawny, Quick Step (RH 56382); *Hyla wilderi*, Trelawny, Quick Step (RH 56379); \**Osteopilus brunneus*, Trelawny, Quick Step (LM 1190); *Osteopilus* sp. nov., Trelawny, 5 mi WNW Quick Step (RH 60045). Hispaniola: *Hyla heilprini*, Dominican Republic, La Vega, 10.5 km W Hayaco (SBH 101105-06); *Hyla pulchrrilineata*, Dominican Republic, El Seibo, 4.1 km S Sabana de le Mar (SBH 101086); \**Hyla vasta*, Haiti, Dept. de l'Ouest, Furcy (SBH 160414, 160417); \**Osteopilus dominicensis*, Dominican Republic, Barahona, 15.8 km S Cabral (SBH 101244). Cuba: \**Osteopilus septentrionalis*, United States: Florida (LM 1768). Mainland: \**Osteocephalus taurinus*, Peru, Cuzco Amazónico (LM 1866).

**Amphisbaenidae.** *Amphisbaena*: Puerto Rico: *bakeri*, 5.8 km S Mora (SBH 172208); *caeca*, 6.8 km S Mamey (SBH 172233); *fenestrata*, USVI, St. Thomas, Dorothea Estate (SBH 161375); \**schmidti*, 12 km SSE Arecibo (SBH 172169, SBH 172171, SBH 172173); *xera*, Playa de Tamarindo (SBH 101727). Hispaniola: *caudalis*, Haiti, Grande'Anse, 11.8 km S Pestel (SBH 191845); *gonavensis*, Dominican Republic, Pedernales, Hoyo de Pelempito (SBH 192635); *innocens*, Haiti, Sud, 11 km N Camp Perrin (SBH 103823-24); *manni*, Dominican Republic, Hato Mayor, 9.5 km W Sabana de la Mar (SBH 102373). Cuba:  *cubana*, Guantánamo Bay U.S. Naval Station, Nursery (SBH 161959); *Cadea blanoides*, Pinar del Rio, Viñales, Cueva de San Jose Miguel. Mainland: *alba*, Peru, Cuzco Amazónica (LM 1988); *Rhineura floridana*, Florida, Hillsborough, Plant City (SBH 172913).

**Teiidae.** *Ameiva*: Hispaniola: \**chrysolaeama* #1, Dominican Republic, Independencia, Tierra Nueva (SBH 102872, SBH 102874, SBH 102878); *chrysolaeama* #2, Dominican Republic, Pedernales, 2 km S Oviedo (SBH 102628); *chrysolaeama* #3, Dominican Republic; Barahona, vicinity of Barahona (SBH 101429); *lineolata*, Haiti, l'Artibonite, 1.1 S Colminy (SBH 191673); *taeniura*, Haiti, Sud'Est, 9.5 km E Jacmel (SBH 104391). Puerto Rico: \**exsul*, 12 km radius of Arecibo (SBH 172203-204); *wetmorei*, Isla Caja de Muertos (SBH 190731). Cuba: *auberi*, Guantánamo U.S. Naval Station, South Toro Cay (SBH 161973). Bahamas: *maynardi*, Great Inagua (SBH 192970). Lesser Antilles: *erythrocephala*, St. Kitts, Godwin Gut (SBH 172748); *griswoldi*, Antigua, Great Bird Island (SBH 192785); *pluvianotata*, Montserrat, St. Peter, Spring Ghut (SBH 192779). Mainland: *ameiva*, Peru, Cuzco Amazónico (LM 1993); *Cnemidophorus uniparens* (LM 2997); *Tupinambis teguixin*, Peru, Cuzco Amazónico (LM 2421).

**Anguidae.** Hispaniola: *Celestus curtissi* #1, Dominican Republic, Pedernales, Juancho (SBH 102707); *Celestus curtissi* #2, Dominican Republic, Pedernales, 6.4 km SW and 0.7 km SE Juancho (SBH 102610); *Celestus darlingtoni*, Dominican Republic, La Vega, ca. 37 km SE Constanza (SBH 161687); *Celestus macrotus*, Haiti, Sud'Est, ca. 15 km W Gros Cheval (SBH 104405); *Celestus stenurus*, Dominican Republic, Independencia, 1 km E Tierra Nueva (SBH 102917); *Celestus* sp.



nov., Dominican Republic, Independencia, 23.9 km SE Puerto Escondido (SBH 192480); *Diploglossus carraui*, Dominican Republic (SBH 191573); \**Diploglossus warreni*, pet trade (SBH 172914); *Sauresia agasepsoides*, Dominican Republic, Barahona, 13.7 km (airline) E Canoa (SBH 160188-90); *Sauresia sepsoides*, Dominican Republic, Hato Mayor, 9.5 km W Sabana de la Mar (SBH 102369); \**Wetmorena haetiana*, Dominican Republic, Barahona, 15.3 km S and 6.7 km E of Cabral (SBH 102565-566). Jamaica: *Celestus barbouri*, Trelawny, vicinity of Quick Step (SBH 161120); *Celestus cruscus cruscus*, Hanover, 3.2 km SE Content (SBH 101572); *Celestus cruscus cundalli*, Portland, 1.3 km WSW Section (SBH 172465). Cuba: \**Diploglossus delasagra*, Guantánamo, 1 km SW San Luis de Potosí (SBH 191015). Puerto Rico: \**Diploglossus pleii*, 5.5 km N Rio (SBH 161370), about 5 km SE Maricao and 6 km NW Sabana Grande (SBH 172199-200). Mainland: *Ophiodes striatus* (MVZ 191047)

**Iguanidae. *Leiocephalus*:** Hispaniola: \**schreibersi*, Dominican Republic, Independencia, Tierra Nueva (SBH 102721, SBH 102879-880, SBH 102889); *barahonensis* #1, Dominican Republic, Pedernales, about 2 km S Ovedö (SBH 102645); *barahonensis* #2, Dominican Republic, Independencia, 5.1 km SE Puerto Escondido (SBH 192536); *lunatus*, Dominican Republic, Altigracia, 1 km W Boca de Yuma (SBH 160123); *melanochlorus*, Haiti, Grande'Anse, about 3 km N Bois Sec (SBH 103721); *personatus*, Dominican Republic, Maria Trinidad Sanchez, 4 km SE Nagua (SBH 103024); *semilineatus*, Haiti, l'Ouest, 11.7 km E Thomazeau (SBH 191661-63). Cuba: *carinatus*, Guantánamo, Guantánamo Bay U.S. Naval Station, pump station and water tower on leeward side of bay (SBH 161965); *cubensis*, Matanzas, Soplillar (SBH 172490); *macropus*, Guantánamo, Guantánamo Bay U.S. Naval Station, pistol range on leeward side of bay (SBH 161984); *raviceps*, Guantánamo, Guantánamo Bay U.S. Naval Station, pistol range on leeward side of bay (SBH 161980); *stictigaster*, Guantánamo, Tortuguilla (SBH 190161). Bahamas: *greenwayi*, East Plana Cay (SBH 192972); *inaguae*, Great Inagua (SBH 192973); *loxogrammus*, San Salvador (SBH 192971), *punctatus*, Acklin's Island (SBH 192975). *Crotaphytus collaris* (LM 2534). *Sceloporus spinosus* (LM 2264). *Tropidurus peruvianus* (LM 1556B). *Tropidurus hispidus* (LM 2795).

**Trophidophidae. *Tropidophis*:** Jamaica: \**haetianus stejnegeri* #1, Trelawny, vicinity of Quick Step (SBH 103592); *haetianus stejnegeri* #2, Trelawny, 0.3 km W Duncans (SBH 101580); *haetianus stullae*, Clarendon, Portland Ridge (SBH 103593). Cuba: *feicki*, Pinar del Río, Soroa (SBH 172745); *fuscus*, Guantánamo, Minas Amores (SBH 190300); *maculatus*, Pinar del Río, Soroa (SBH 191543); *melanurus*, Pinar del Río, Soroa (SBH 172610); *pardalis*, La Habana, Narigon (SBH 191545); *pilsbryi*, Santiago de Cuba, Simpatía (SBH 191368); *wrighti*, Guantánamo, 2 km N La Municipión (SBH 191066). Bahamas: *canus*, Andros (RH 54403). Hispaniola: *haetianus haetianus* #1, Haiti: Sud (RH 54404); *haetianus haetianus* #2, Dominican Republic, El Seibo, 4.1 km S Sabana de la Mar (SBH 101398); *haetianus haetianus* #3, Dominican Republic, Samana, 6 km SSW Las Galeras (SBH 103121); *haetianus haetianus* #4, Haiti, Sud, 8.6 km SW Carrefour Joute on the Prequille de Port Salut (SBH 192361); *haetianus haetianus* #5, Dominican Republic, El Seibo, Nisibon (SBH 192455), *haetianus hemurus*, Dominican Republic, La Altigracia; 28 km NW Higüey (SBH 192454). Mainland: *paucisquamis*, Brasil, São Paulo, Boracéia (LM 908). Other taxa: *Boa constrictor*, pet trade (RH 54430). *Naja naja*, pet trade (RH 58101). *Python molarus*, pet trade (RH 56048). *Coluber constrictor* (#4). *Arrhyton landoi*, Guantánamo, Guantánamo Bay U.S. Naval Station, vicinity of John Paul Jones Hill (SBH 161893-895).

**Typhlopidae.** Puerto Rico: *Typhlops granti*, Bosque Estatel de Guanica (SBH 172210); *Typhlops hypomethes*, University of Puerto Rico campus at Rio Piedras (SBH 161807); *Typhlops hypomethes*, University of Puerto Rico campus at Rio Piedras (SBH 172150); \**Typhlops platycephalus*, 12.3 km SSE Arecibo (SBH 172180); *Typhlops richardi*, British Virgin Islands; Guana Island (SBH 172759); *Typhlops rostellatus*, 12.3 km SSE Arecibo (SBH 172174). Lesser Antilles: *Typhlops guadeloupensis*, Guadeloupe, Pointe de la Grande'Anse (SBH 102276), *Typhlops monastus*, Nevis, 0.3 km N Cotton Ground (SBH 172760). Cuba: *Typhlops biminensis*, Guantánamo, Playites de Cajobabo (SBH 190234); *Typhlops lumbricalis*, Havana, National Botanical Garden (SBH 172600). Hispaniola: *Typhlops capitulatus*, Haiti, l'Ouest, Soliette (SBH 103826); *Typhlops hectus*, Dominican Republic,

Barahona, 13.5 km SW Barahona (SBH 102665); *Typhlops pusillus*, Dominican Republic, Azua, 18 km NNW Azua (SBH 160284); *Typhlops schwartzi*, Dominican Republic, El Seibo, Nisibón (SBH 192458); *Typhlops sulcatus*, Dominican Republic, Pedernales, SW of Enriquillo (SBH 102438); *Typhlops syntherus*, Dominican Republic, Pedernales, SW of Enriquillo (SBH 102437); *Typhlops titanops*, Dominican Republic, Pedernales, 20 km N Pedernales (SBH 160293). Jamaica: *Typhlops jamaicensis*, St. Mary, 6.2 km W Oracabessa (SBH 172445). Philippines: *Typhlops luzonensis*, Negros Island, Negros Oriental Province, Valenica Municipality, Bong Bong Barrio, Camp Lookout (SBH 194117). Mainland: *Leptotyphlops*, Trinidad (SBH 175446); *Liotyphlops albirostris*, Venezuela, Caracas (SBH 172151).

**Colubridae (Xenodontinae).** Bahamas: *Alsophis vudii*, New Providence, Sandy Port (SBH 192985). Cuba: *Arrhyton dolichura*, Havana, National Botanical Garden (SBH 172601); \**Arrhyton landoi* #1, Guantánamo Bay U.S. Naval Station (SBH 161893-95, SBH 161985); *Arrhyton landoi* #2, Guantánamo, 3.5 km E Tortuguilla (SBH 191258); *Arrhyton procerum*, Matanzas, Playa Giron (SBH 191526); *Arrhyton supernum* #1, Guantánamo, SW slope of El Yunque de Baracoa (190230); *Arrhyton supernum* #2, Guantánamo, Monte Libano, ca. 20 km SSE La Tagua (SBH 191153); *Arrhyton taeniatum*, Guantánamo Bay U.S. Naval Station, ca. 0.2 km E Windmill Beach (SBH 171002); *Arrhyton tanyplectum*, Pinar del Río, 4 km NW San Vicente (SBH 191492); *Arrhyton vittatum*, Pinar del Río, Cueva de San Miguel (SBH 191491), *Antillophis andreaei*, Pinar del Río, Soroa (SBH 172603); *Alsophis cantherigerus*, Pinar del Río, 2.0 km W Vinales (SBH 172602). Hispaniola: *Antillophis parvifrons protenus*, Dominican Republic, Barahona, 19.5 km SW Barahona (SBH 103086); *Darlingtonia haetiana*, Haiti, Grande'Anse, ca. 2-3 km S Castillon (SBH 103806-10); *Hypsirhynchus ferox*, Dominican Republic, Barahona, vicinity of Barahona (SBH 101393); *Hypsirhynchus scalaris*, Haiti, Grande'Anse, 7.2 km S Roseaux (SBH 191992); *Ialtris dorsalis* #1, Haiti, Grande'Anse, ca. 3 km N Bois Sec (SBH 103702); *Ialtris dorsalis* #2, Haiti, Grande'Anse, 7.5 km N Beaumont (SBH 192360); *Uromacer catesbyi* #1, Dominican Republic, Monte Plata, 2.8 km N Yamasa (SBH 101397); *Uromacer catesbyi* #2, Dominican Republic, La Altagracia, 4.4 km W Canada Honda (SBH 192456); *Uromacer frenatus frenatus*, Haiti, Grande'Anse, ca. 6 km E Jeremie (SBH 104668); *Uromacer oxyrhynchus*, Dominican Republic, La Altagracia, 4.4 km W Canada Honda (SBH 192457). Jamaica: *Arrhyton callilaemum*, St. Mary, 2.9 km N Port Maria (SBH 172463); *Arrhyton funereum*, St. Mary, Port Maria, 2.9 km N Port Maria (SBH 172462); *Arrhyton polylepis*, Portland, 0.3 km S Alligator Church (SBH 101581). Lesser Antilles: *Alsophis antiquae*, Antigua, Great Bird Island (SBH 192790); *Alsophis antillensis*, Montserrat (SBH 192791). Puerto Rico: *Arrhyton exiguum*, 1.9 km NE Vista Alegre (SBH 160050); *Alsophis portoricensis*, 1.5 km W Playa de Tamarindo (SBH 160062). Mainland: *Dipsas catesbyi*, Peru, Pasco, 1.5 km NW Cacazu (SBH 171139); *Leptodeira* sp., Panama (LM1145); *Liophis cabella*, Peru, Pasco, Oxapampa (SBH 171143); *Liophis melanostigma*, Brazil, São Paulo, Boraceia (LM 904); *Oxyrhopus leucomeles*, Peru, Pasco, Oxapampa (SBH 171142); *Thamnodynastes* sp., Peru, Madre de Dios, Tambopata Reserve (LM 1104); *Xenodon severus* (RH 68185).